A Synthesis of Red Drum Feeding Ecology and Diets from North Carolina and South Carolina

A Thesis submitted for completion of M.S. degree

Tyler Peacock 7/1/2014

Advisor: Dr. Anthony Overton Department of Biology

Absract:

The trophic interactions of the red drum Sciaenops ocellatus have been previously researched. However diet data on the largest adults (>750mm TL) are very limited. As fisheries management moves towards a goal of multi-species and ecosystem-based strategies, information on trophic inter-relationships of the system must be characterized for effective understanding and application to future modelling efforts and management decisions. Predatory effects on forage species are an important component of this, and examining the diet of the predator is the most efficient way to identify prey species interactions and potential removal rates through predation mortality. Red drum abundance has increased since the implementation of more conservative management strategies and major decreases in commercial fishing effort on the species. Because of these changes in abundance and the lack of diet data for larger adult red drum, this study was conducted to identify the trophic relationships and potential forage

species effects of these predators. This study will 1) Identify, classify, and compare diets of large adult red drum in North Carolina and South Carolina and 2) synthesize a pooled standardized diet composition from all previously published red drum diet studies across its range (excluding larvae). First, the trophic relationships of large adult red drum (>750mm TL), Sciaenops ocellatus, in the coastal waters of South Carolina (N=146) and North Carolina (N=51), from 2007-2011 were examined. Stomach samples were collected by North Carolina Division of Marine Fisheries and South Carolina Department of Natural Resources during their annual fall longline surveys. Red drum in North Carolina fed predominantly on blue crab (Callinectes sapidus) which made up 51% of the diet by number and occurred in 48% of the stomachs. The diet of red drum in South Carolina was more diverse that in North Carolina, where red drum consumed mostly Atlantic menhaden (Brevoortia tyrannus) and a diverse group of marine decapods and brachyurans. Prey species contribution varied between years, with increases in blue crab in North Carolina red drum and Atlantic menhaden for South Carolina red drum. The differences in diet between the states are likely because of prey assemblage differences between the predominantly estuarine habitat in North Carolina and the coastal marine habitat in South Carolina. Although the diet composition of red drum was different between SC and SC they fed at similar trophic levels. Secondly, ten previously published diet studies on red drum (excluding larval diets) were collected via a thorough literature search and diet data were pooled by prey group and size-class of the predator. Standardized diet compositions were examined and analyzed by cluster analysis to determine groupings of similarity. Juvenile and sub-adult red drum had very similar diets on each coast, feeding on mysids, shrimp, and crabs, which was attributed to their inhabiting similar nursery areas. Adult red drum diets were similar, feeding mostly on fish and crabs. This was attributed to adults residing in coastal waters instead of the inshore nursery areas. This study has made the adult diet of red drum and a large-scale diet characterization of the species available for application to future management.

A Synthesis of Red Drum Feeding Ecology and Diets from North Carolina and South Carolina

by

Tyler A. Peacock

APPROVED BY:

DIRECTOR OF
DISSERTATION/THESIS: _____

(Anthony S. Overton, PhD)

COMMITTEE MEMBER: _____

(Joseph J. Luczkovich, PhD)

COMMITTEE MEMBER:

(Stephen A. Arnott, PhD)

COMMITTEE MEMBER: _____

(Frederick S. Scharf, PhD)

CHAIR OF THE DEPARTMENT
OF (Biology):

(Jeff McKinnon, PhD)

DEAN OF THE GRADUATE SCHOOL: _____

Paul J. Gemperline, PhD

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Table of Contents

List of Figures	iii
List of Tables	iii
Ch. 1 Introduction	1
I. Background	1
Red Drum Biology	1
Management	2
II. Diet Studies	3
III. Relevance and Applications	5
IV. Projects and Goals	6
Literature Cited	9
Figures	13
Figure 1 Timeline of Previous Diet Studies	13
Tables	14
Table 1 Previously Published Red Drum Diet Studies	14
Chapter II: Responses in Feeding Ecology of Adult Red Drum to Prey Assembla	age Differences in NC and
	0
SC	•
SC	
SC	
SC	
SC Introduction II. Methods Field Collections	
SC Introduction II. Methods Field Collections North Carolina	15
SC Introduction II. Methods Field Collections North Carolina South Carolina	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis Data Analysis	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis Data Analysis Diet Structure	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis Data Analysis Diet Structure Results	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis Data Analysis Diet Structure Results IV. Discussion	15
SC Introduction II. Methods Field Collections North Carolina South Carolina Stomach Contents Analysis Data Analysis Diet Structure Results IV. Discussion Implications	15

Tables	43
VII. Figure and Tables	45
Figures:	45
Figure 1: NC DMF Sampling Locations	45
Figure 2: SC DNR Sampling Locations	46
Figure 3: Size Histogram of Sampled Red Drum	47
Figure 4: Prey Species Accumulation Curves	48
Figure 5: %N and %FO by State and Year	49
Figure 6: %N and %FO by State	50
Figure 7: MDS Plot of %N Diet Data	51
Figure 8 Logistic Regression of Penaeid Shrimp Appearing as Prey	52
Figure 9: PCA Plot of %N Diet Data	53
Figure 10: Histogram of ETLs Encountered	54
Table 1: Previous Red Drum Diet Studies and Results	55
Table 2: Sample Sizes by State and Year	56
Table 3: List of All Prey Species Encountered	57
Table 4: Simper Results	58
Table 5: Logistic Regression Results	59
CH. 3: Synthesized Feeding Ecology of the Red Drum Sciaenops ocellatus: Population Scale Trophic	
Interactions of the Atlantic and Gulf Coasts	
Introduction	
Methods	
Results	
Discussion	
Literature Cited	
List of Figures and Tables	73
Figures	73
Tables	74
Figures and Tables	74
Figures	74
Figure 1 Standardized Diet Composition of Juvenile Red Drum	74
Figure 2 Standardized Diet Composition of Sub-Adult Red Drum	75
Figure 3 Standardized Diet Composition of Adult Red Drum	75

Figure 4 Pooled Diet Composition by Size-class	76
Figure 5 Pooled Diet Composition of Red Drum by Coast and Size –class	77
Figure 6 Cluster Analysis and % Diet Composition of Red Drum	78
Figure 7 Timeline of Previous Diet Studies	79
Tables	
Table 1: Previously Published Red Drum Diet Studies	
Ch. 4 Discussion	81
I. Applications for Research	81
II. Validation, Limitations, and Future Research	82
Literature Cited	
Figures	
Figure 1 Timeline of Previous Diet Studies	

List of Figures

1.1 Timeline of Previously Published Red Drum Diet Studies	12
2.1 NC DMF Sampling Locations	44
2.2 SC DNR Sampling Locations	45
2.3 Size Histogram of Sampled Red Drum	46
2.4 Prey Species Accumulation Curves	47
2.5 %N and %FO by State and Year	48
2.6 %N and %FO by State	49
2.7 MDS Plot of %N Diet Data	50
2.8 Logistic Regression of Penaeid Shrimp Appearing as Prey	51
2.9 PCA Plot of %N Diet Data	52
2.10 Histogram of ETLs Ecountered	53
3.1 Standardized Diet Composition of Juvenile Red Drum	73
3.2 Standardized Diet Composition of Sub-adult Red Drum	73
3.3 Standardized Diet Composition of Adult Red Drum	74
3.4 Pooled Diet Composition by Size-class	74
3.5 Pooled Diet Composition by Coast and Size-class	75
3.6 Cluster Analysis and % Diet Composition of Red Drum	76
3.7 Timeline of Previous Diet Studies	77
4.1 Timeline of Previous Diet Studies	85
List of Tables 1.1 Previously Published Red Drum Diet Studies	13
2.1 Previous Red Drum Diet Studies and Results	54
2.2 Sample Sizes by State and Year	55
2.3 List of All Prey Species Encountered	
2.4 SIMPER Results	57
2.5 Logistic Regression Results	58
3.1 Previously Published Red Drum Diet Studies	78

Ch. 1 Introduction

I. Background

Red Drum Biology

The red drum *Sciaenops ocellatus* is a predatory, coastal dependent spawning teleost that is a popular recreational gamefish on both the Atlantic and Gulf Coasts. These fish are identifiable by their large size, reddish dorsal coloration, and ocellae (spots) on the dorsum and/or caudal peduncle (Pearson 1928). Because of the large size attained by adults, they have limited natural mortality from predation and have exhibited longevity of over 50 years (Pearson 1928).

DISTRIBUTION AND HABITAT

Red drum generally inhabit coastal waters of the southern Atlantic and Gulf states of the U.S., but have been observed as far north as Maine (Lux & Mahoney 1969) and as far south as Veracruz Mexico (Castro-Aguirre 1980). Red drum are coastally dependent spawners, utilizing estuarine and riverine systems as nursery habitat as juveniles and sub-adults (Pearson 1928, U.S. FWS 1985, Wenner et al. 1990, Arnott et al. 2010). Protected areas such as seagrass beds, saltmarsh, and tidal creeks are all ideal habitat for young of year red drum as they are productive shelters from predation (Peters & McMichael 1987, Rooker et al. 1997, Adams & Tremain 2000, Scharf 2000, Stunz et al. 2002, Powers 2012). Red drum remain in these nursery habitats until they exit the estuaries and creeks to join the spawning population offshore as adults (Wenner et al. 1990, Bacheler et al. 2009, Paramore 2011). Life history information is limited for these offshore red drum.

REPRODUCTION AND MATURITY

The larval stage of red drum (<10mm) is long-lived (7 months) for a fish (Peters & McMichael 1987, Wenner et al. 1990), and once the juvenile stage is reached natural mortality levels decline significantly, especially those due to environmental factors (Wenner et al. 1990). Juveniles grow exponentially as they consume larger prey (Scharf 2000), and at 10 months the transition to the sub-

adult stage begins as they move to larger creeks and rivers (Wenner et al. 1990). Late maturity accompanies the long lifespans of red drum, and males mature at earlier ages and smaller sizes than females. Males usually mature when around 2 years old and 500mm , while females mature at 3 or 4 years and 800mm (U.S. FWS 1985, Ross et al. 1995). Some individuals remain in nursery areas until 4 years of age (Scharf 2000), with maturity cueing the migration to the spawning population farther offshore. Spawning adults are dependent on estuaries and nearshore coastal waters for reproduction, returning to their natal area each year during late summer and early fall as part of the spawning aggregation (Patterson et al. 2004). After these spawning events, larvae enter the estuaries and rivers on surface currents to reach nursery habitat farther inshore (Peters & McMichael 1987, Wenner et al. 1990).

Management

Regulations

On the Atlantic Coast, red drum are managed under the Atlantic States Marine Fisheries Commission (ASMFC) fisheries management plan (FMP). They are no longer commercially fished in most Atlantic states, with North Carolina as the only commercial fishery over 22500 kg in landings per year (ASMFC 2013). Red drum are now considered a "gamefish" in South Carolina, and a ban was placed on the sale of native fish in Florida (ASMFC 2013). The ASMFC enacted the use of slot size limits for the harvest of red drum, with varying size requirements by state. Most slot sizes range between 350 and 680mm, and there are bag limits on the number of fish per angler-day (NCDMF 2008, ASMFC 2013).

Gulf Coast regulations are set under the Gulf States Marine Fisheries Commission (GSMFC), but the most recent amendment to the FMP was in 1986 (NMFS 1986). Gulf Coast red drum are also managed with a slot size limit, usually between 400 and 760mm, with bag limits for recreational anglers. Mississippi is currently the only Gulf of Mexico state with an active commercial fishery (~16000 kg per year) for red drum (Powers & Burns 2010).

Stock Status

In the 1980s and 1990s, there were concerns of overfishing and that further reduction in the spawning stock of red drum could affect maintenance of the population (Vaughan & Carmichael 2000). The cessation of most commercial fishing on the Atlantic Coast and more restrictive regulations that have decreased fishing mortality have seen major improvements in the status of red drum (increased spawning potential ratio and escapement rates), and they are no longer considered overfished on the Atlantic Coast (NCDMF 2008, ASMFC 2013). While there is harvesting of red drum recreationally, the use of slot size limits has created a mortality bottleneck that protects the spawning stock biomass and aids recruitment success (ASMFC 2012, 2013). These methods have been very beneficial, but efforts must continue to monitor juvenile and sub-adult escapement rates to the spawning population (ASMFC 2002, NCDMF 2008), as available information is limited about mortality rates and population structure of the spawning stock (NCDMF 2008, ASMFC 2012). On the Gulf Coast, estimates predict the red drum stocks have rebounded after closure of the federal fishery in the late 1980s, but an updated stock assessment is needed. However, limited data on escapement rates, recruitment, and mortality have been reported in the past decade. Projections show declining escapement rates below the 30% threshold target as well as declining recruitment (Powers & Burns 2010). Future research in the Gulf of Mexico on red drum is needed to determine stock status and identify any management implications.

II. Diet Studies

Stomach Contents Analysis

Diet analysis through the examination of stomach contents has been a standard practice in fisheries management for many years (Hyslop 1980). It is useful when examining inter-species and intraspecies interactions, and the seasonal and spatial variation in them, among other variables (Pasquaud et al. 2007). With limited ability to observe food web processes in real time, this method allows the researcher to determine the trophic relationships of a system based on predator-prey interactions. To ensure complete data, these studies must account for the frequency of prey items as well as volumetric

or importance measurements (Hyslop 1980). The use of multivariate analyses on diet data can describe the dynamic feeding structure of the system much more effectively than abundance measures alone (Pasquaud et al. 2007). Use of such methods allows for examining effects of other variables in conjunction with diet composition such as sub-locations, time, season, body size, as well as testing for any ontogenetic shifts in the diet.

There are also issues with diet analysis over a large geographical range through different habitats, as environmental and community differences are likely. Previous research has been limited to taxonomic comparisons of trophic status between groups, which may present inherent bias towards finding groups significantly different from an ecological perspective. Diet analysis and comparison through trophic levels instead of species allows for a novel approach to examining diet differences between groups by limiting the assumption of the same prey assemblages existing between locations. Trophic level determination and modelling has been a valuable descriptor of systems, but inclusion of these in diet analysis for comparisons is a newer approach (Cortes 1999, Ebert & Bizzarro 2007). Once these trophic levels are calculated, they can be directly compared to determine the overall position/niche of the predator in the food web regardless of community structure or variability of the environment (Livingston 1982, Cortes 1999, Ebert & Bizzarro 2007).

Diet Synthesis

As the red drum has a large geographical distribution and long lifespan, identifying and understanding any differences in diet structure by location and age/size-class is very important for encompassing management efforts. Large scale pooled diet compositions allow for general information to be applied to management strategies at a species level, even over large areas (Walter et al. 2003). This method was well suited with the limited spatial and temporal scope of any one study and the prevalence of previously published data on red drum. A synthesis of diet information through standardized diet compositions provides a viable alternative to accessing or collecting raw data over

such a large extent (Cortes 1999, Walter et al. 2003). The compilation of such a dataset allows for easily applicable general trends in trophic relationships across the distribution of a target species.

III. Relevance and Applications

Red Drum

Red drum stocks are almost fully recovered through most of their distribution (Powers & Burns 2010, ASMFC 2013). This represents a community-level change in population structure and size that has the potential to affect prey species stocks through predation. This pattern of recovering stocks in conjunction with current management (mortality bottleneck within slot size restriction) has the potential to increase the total number of adults, as both natural and fishing mortality are limited once red drum reach a large enough size. This could in turn increase predation mortality on forage species of the adult populations. In previous red drum diet studies, data on adult diets is limited, especially on the Atlantic Coast (Table 1). By filling the gap in diet information with a diet study of adults from North and South Carolina we can complete the full diet profile for red drum for use in future management strategies and improve efforts to manage both red drum and their prey.

Future stock assessments and research in the Gulf of Mexico have been requested (Powers & Burns 2010) because the last published data is dated. The same applies to diet data for red drum on the Gulf Coast. Several studies date to the 1970s and 1980s, with only one published since 2000 (Figure 1). Dated previous studies should be validated for application to future management to account for the possible fluctuations in prey species composition being reflected in the diet.

Multi-species Management

Traditional management has focused on maximizing catch from a fishery resource, but fails to account for other factors that may lead to over-harvesting (Bax 1998, Froese et al. 2008). Considering management from an ecological standpoint can provide insight into other aspects of fish populations and community level effects (Bax 1998, Fowler 1999, Fowler et al. 2013). Multi-species management

has been a growing area of interest in fisheries management for some time (Christensen & Victoria 1996, Fowler 1999, Latour et al. 2011, Fowler et al. 2013). As management efforts strive for increased understanding and effectiveness, characterization of trophic relationships and predator-prey effects is needed (Pasquaud et al. 2007). This information can be included in population and ecosystem level models to improve the understanding of dynamic inter-relationships and direct effects of predators (Whipple et al. 2000). While accumulation of ecosystem-level data is not an immediate prospect, current information can be applied as it becomes available (Marasco et al. 2007, Froese et al. 2008, Fogarty 2014). Modelling efforts for management plans must include predation mortality of managed prey species in conjunction with fishing mortality to increase effectiveness (Whipple et al. 2000). Sampling of diet can even allow insight into community assemblages as surrogate sampling units for the target habitat, especially the benthos (Link 2004).

IV. Projects and Goals

CH. 2: North Carolina and South Carolina Adult Red Drum Feeding Ecology SUMMARY

Diet data for adult red drum on the Atlantic Coast does not include information on large adults (>750mm) (Table 1), so this research was concerned with characterizing the diet structure of these larger adults from both North and South Carolina. Adult red drum were collected by the South Carolina Department of Natural Resources and the North Carolina Division of Marine Fisheries for age and growth through longline sampling. The diet of adults from both states was then characterized via stomach contents analysis of the sacrificed fish from 2007-2010 and 2011-2012 in North Carolina and 2008 and 2010-2012 for South Carolina. Diet composition and diversity were then compared between states through percent by number, percent frequency of occurrence, and Shannon-Weiner diversity indices. Multivariate analyses were performed to determine any impacts of other variables, such as length of the predator or year of sampling, on diet composition. Effective trophic levels of adults were also determined by the use of ETL data from an ECOPATH model of Core Sound, North Carolina (Deehr

et al. 2014) that was assigned to prey species. The presence of any differences in diet diversity between states was tested by an ANOVA.

OBJECTIVES

- 1. Identify prey species consumed by adult red drum in North Carolina and South Carolina waters.
- 2. Compare and contrast diet composition between North Carolina and South Carolina in terms of contributing prey species, diet diversity, and trophic level of the predator.
- 3. Determine any temporal patterns in feeding ecology between years of sampling.

HYPOTHESES

I hypothesized several general trends in the adult diet. First, the general diet of large predators like adult red drum should reflect available forage species and community structure. Preliminary studies in North Carolina found the diet to be dominated by blue crab and finfish (Paramore 2011), while for a previous study on smaller adults in South Carolina there were more Atlantic menhaden, penaeid shrimp, and diverse benthic decapods (Wenner et al. 1990). These patterns were expected to continue, and also for the estuary-inhabiting red drum from Pamlico Sound to exhibit lower overall diet diversity than their coastal ocean counterparts in South Carolina, as estuaries are generally highly productive areas with lower overall diversity as a result of the variability of habitat conditions (Day et al. 1989, Able & Fahay 2010). While slight variation in prey contribution between years was expected (Overstreet & Heard 1978, Scharf & Schlicht 2000), it was not possible to test seasonality as samples were all collected during the fall.

CH. 3: Pooled Diet and Synthesized Feeding Ecology for Atlantic and Gulf Coast Red Drum SUMMARY

Pooled diet composition of red drum was calculated from 10 previously published diet studies for large scale ecosystem-level applications to management and modelling. Diet metrics were compiled into standardized diet compositions between studies for direct comparison. Pooling of metrics does not affect the overall findings, as these are usually redundant measures (MacDonald & Green 1983). Pooling prey species and families together does decrease resolution, however, especially when the original study identified prey to the species level. The pooled diet of red drum was then examined and size-based and locational shifts in feeding ecology were identified. Atlantic and Gulf Coast diets were compared overall and within size-classes, and important prey species interactions were described.

OBJECTIVES

- 1. Conduct a thorough literature search for available previously published diet studies on red drum across their distribution.
- 2. Pool red drum diet data into comparable prey and size-class groupings for identification of large scale patterns.
- 3. Describe general trends in feeding ecology by size-class and by coast (Atlantic vs. Gulf)
- 4. Identify potential predatory impacts on prey species by red drum for application to management.

HYPOTHESES

The diet structure of red drum was expected to undergo ontogenetic shifts at certain important transitional periods in their life history, especially with regard to habitat usage. Shifts in diet composition can clearly identify these changes in feeding habits (Facendola & Scharf 2012, Baker et al. 2014). While larval diets were not examined in this study, red drum should experience an ontogenetic shift between larval and juvenile diet from differences in habitat usage and gape limitation (Galarowicz et al. 2006). Extrapolating this pattern to later life stages indicates that red drum diets should reflect the transition between sub-adults and adults when these fish leave nursery areas and join the spawning population in the coastal ocean (Wenner et al. 1990, Bacheler et al. 2009, ASMFC 2013). It was also hypothesized that prey assemblage changes between Atlantic and Gulf Coast habitats would be reflected in the diet composition of red drum of all size-classes, and that diets from each coast would be more similar within each group.

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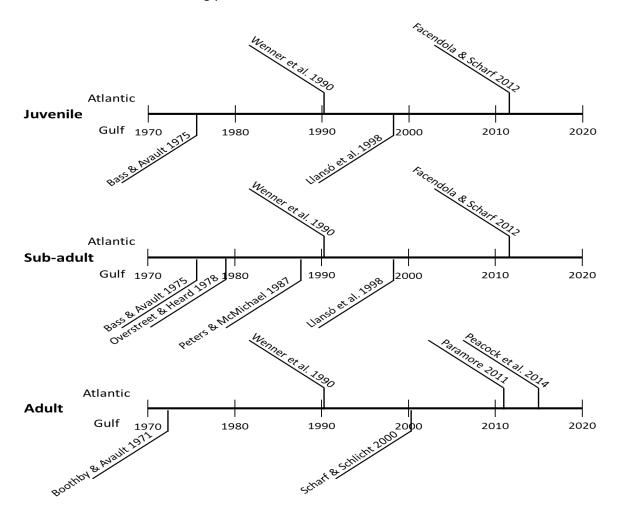
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Figures

Figure 1 Timeline of Previous Diet Studies

Timeline of previous red drum diet studies separated by coast and size-classes. Several sources reported diet information on multiple sizeclasses and were listed accordingly.



Tables

Table 1 Previously Published Red Drum Diet Studies

Red drum diet studies including locations, methods, summarized results, and size ranges for each project. For percentage metric methods, %V is volume, %FO is frequency of occurrence, %N is number, %W is weight, %DW is dry weight, and IRI is an index of relative importance. Season indicates when the red drum where collected, N/A represents a study where season was not indicated or used for analysis. Primary prey are the major prey found in the diet by each study.

				Size				%	
Source	Year	Location	Method	Range	Ν		Season	Empty	Primary Prey
							Year-round,		Decapods, fish, benthic
Bass and Avault	1975	LA	%F <i>,</i> %V	8-183mm		568	N/A	5.1	invertebrates
Boothby and				250-					
Avault	1971	Southeast LA	%F	932mm		349	Year-round	28	Crabs, shrimp, fish
			IRI, %F, %N,	19-			Year-round,		
Llansó et al	1998	Tampa Bay, FL	DW	590mm		263	N/A	2	Decapods, crustaceans, fish
Overstreet and		Mississippi Sound,		190-	107 (22	2			
Heard	1978	MS	%FO	1020mm	adults)		Year-round		Penaeid shrimp, crabs, fish
Peters and				1.6-					Copepods, mysids, crabs, finfish,
McMichael	1987	Tampa Bay, FL	%N, %V	300mm		863	N/A	2.8	decapods
Scharf and			%FO, %N,	350-					
Schlicht	2000	Galveston Bay, TX	%W	750mm		598	Fall, Spring	30.2	Decapods, teleosts
				10-					
Wenner	1990	SC	%W, %N	>530mm		540	N/A	34	Fish, crustaceans
		Pamlico Sound,							
Paramore	2011	NC	%N	Adults		41	Fall	46	Blue crab, copepods
Facendola and				113-					
Scharf	2012	New River, NC	%FO, %W	731mm		880	May-January		Penaeid shrimp, crabs, fish
		Pamlico Sound,							
Peacock et al	2014	NC; SC	%N, %FO	>750mm		197	Fall		Blue crab, decapods, fish
		•	•						, , ,

Chapter II: Responses in Feeding Ecology of Adult Red Drum to Prey Assemblage Differences in NC and SC

ABSTRACT

We examined the trophic relationships of large adult red drum (>750mm TL), Sciaenops ocellatus, in the coastal waters of South Carolina (N=146) and North Carolina (N=51), from 2007-2011. Stocks of red drum have increased since the implementation of more conservative management strategies and major decreases in commercial fishing effort on the species. Because of this and the lack of diet data for larger adult red drum, this study was conducted to identify the trophic relationships and potential forage species effects of these predators. Stomach samples were collected by North Carolina Division of Marine Fisheries and South Carolina Department of Natural Resources during their annual fall longline surveys. Red drum in North Carolina fed predominantly on blue crab (Callinectes sapidus) which made up 51% of the diet by number and occurred in 48% of the stomachs. The diet of red drum in South Carolina was more diverse than in North Carolina, where red drum consumed mostly Atlantic menhaden (Brevoortia tyrannus) and a diverse group of marine decapods and brachyurans. Prey species contribution did vary between years, with increases in blue crab consumption for North Carolina red drum and Atlantic menhaden by South Carolina red drum through time, although the major prey contributors were consistent. The differences in diet between the states are likely because of prey assemblage differences between the predominantly estuarine habitat in North Carolina and the coastal marine habitat in South Carolina. Although the diet composition of red drum was different between SC and SC they fed at similar trophic levels.

KEY WORDS: Feeding ecology; diet; red drum; stomach contents analysis

Introduction

The red drum *Sciaenops ocellatus* is a benthic feeding predatory Sciaenid, identifiable by its large size, reddish color, sub terminal mouth, and oscillated spot on the caudal peduncle of the tail. This species inhabits estuarine and coastal waters from the Gulf of Mexico to Delaware, with limited commercial fishing effort on stocks (Pearson 1928, Lux & Mahoney 1969). In most Atlantic states the red drum has been designated a "gamefish" or commercial and recreational harvests have been limited, providing added protection for nursery areas and the spawning stock of the populations (ASMFC 2013). Red drum on the Atlantic coast are currently managed under the Atlantic States Marine Fisheries Commission (ASMFC) management plan, but spawning populations of adults experience limiting mixing and are considered separate localized sub-populations that enter different spawning grounds and rely on different areas as nursery habitat (ASMFC 2002, Paramore 2011). There is a preference for increased salinity with age in red drum, so the large adults of the population predominantly reside in a marine environment during most of the year (ASMFC 2002, Neill et al. 2004). They return to nearshore marine or estuarine nursery areas to spawn from August to October in both North and South Carolina (Beck et al. 2001, Bacheler, Paramore, Burdick, et al. 2009).

Trophic interactions allow insight into many aspects of the biology of a system, and stomach contents analysis is the most accepted, efficient, and accurate practice to determine these interrelationships in the food web (Hyslop 1980). It is useful when examining inter-species and intra-species interactions, and the seasonal and spatial variation in them, among other variables (Pasquaud et al. 2007). With limited ability to observe food web processes in real time, this method allows the researcher to determine the trophic relationships of a system based on predation. These studies must account for the frequency of prey items as well as volumetric or importance measurements to ensure complete data (Hyslop 1980). Multi-species fisheries management methods are becoming more accepted, and pressure to incorporate predator-prey interactions and predation mortality into stock assessments continues to increase (Christensen & Victoria 1996, Bax 1998, Woodward & Bishop 1999, Whipple et al. 2000, Pasquaud et al. 2007, Morishita 2008). These types of strategies are viable even on limited scales with the current information available about a system, relying on gradual change instead of large scale immediate changes in management paradigms (Cochrane 1999, Marasco et al. 2007, Froese et al. 2008, Link & Idoine 2009). Specifically, there has been interest in managing forage fish species, that are not necessarily commercially harvested themselves, to support recreational and commercial effort on their predators (Stephenson 1997). Underestimation of total mortality of the prey or the importance of a prey species to the predator can have bottom up consequences, resulting in systems lacking the necessary forage base to support a population (Knapp 1950).

As juveniles, red drum feed primarily on copepods and mysid shrimp throughout their distribution (Boothby & Avault 1971, Bass & Avault 1975, Peters & McMichael 1987, Paramore 2011). In North Carolina, the ontogenetic shift in feeding occurring at the sub-adult stage is characterized by blue crab and assorted finfish species appearing in the diet (Bacheler, Paramore, Buckel, et al. 2009, Paramore 2011). In a preliminary study conducted by Paramore (2011) in North Carolina, adult red drum diets also consisted of mostly blue crab ($64\%_{FO}$) with some finfish species ($64\%_{FO}$). Blue crab contributed the most by weight for both studies above. For juvenile and sub-adult South Carolina red drum (<530mm), fiddler crabs *Uca pugnax* constituted 52% of the diet by number and 33% by volume, with some finfish and other decapods present. Finfish contributed the most by number and volume for red drum greater than 530mm ($46\%_N$, $79\%_V$), with brachyuran and other crabs present (Wenner et al. 1990).

Previous diet studies mostly exclude larger red drum (>750mm TL), and in several studies where red drum of this size were included, the sample sizes were small (Table 1). Once red drum reach this length, they are well outside the slot limit in every Atlantic state and are part of the spawning stock of

the population (ASMFC 2002). These larger adults reside offshore, returning to natal nearshore or estuarine areas to spawn seasonally (ASMFC 2002, NCDMF 2008). Influxes of these large predators can impact forage species, many of which are commercially valuable (Stephenson 1997). Previous research on the Atlantic coast has been limited to fish less than 600mm total length (Peters & McMichael 1987, Wenner et al. 1990, Llansó et al. 1998, Paramore 2011). Diet data from the Gulf Coast has included larger adult fish more than 750mm total length in the past, though these adults represent a minority (>20%) of the samples (Knapp 1950, Boothby & Avault 1971, Bass & Avault 1975, Overstreet & Heard 1978, Soto et al. 1998, Guillory & Prejean 1999, Holt & Holt 2000, Scharf & Schlicht 2000a). The average size at catch of red drum from commercial fishing data (NC only) has been increasing over time with new management strategies (ASMFC 2002, NCDMF 2008).

We examined the spatiotemporal feeding ecology of these larger adult red drum (>750mm TL) in both Pamlico Sound, North Carolina, and offshore of the South Carolina coast for multiple years of collected data. Diets of North Carolina and South Carolina individuals were compared with traditional diet metrics and multivariate analyses. We expected the diets of the red drum to reflect the conditions they were collected in, with estuarine conditions of Pamlico Sound driving lower diversity compared to South Carolina marine areas: North Carolina red drum exhibiting a less diverse diet with a few dominant prey items while South Carolina red drum prey were more diverse and dominant prey items were not as clearly defined (Costanza et al. 1993, Hagan & Able 2003, Able & Fahay 2010). We characterize the diet and prey composition for adult red drum (>750 mm TL) in North Carolina and South Carolina to determine important prey species during the fall seasons.

II. Methods

Field Collections

North Carolina

The NC Division of Marine Fisheries (NC DMF) has been conducting a bottom longline survey for red drum in the Pamlico Sound and near coastal waters of Hatteras and Ocracoke inlets since 2007 (August-October) (Figure 1). A stratified random sampling approach was conducted at night, when catch per unit effort was highest. Quadrants of southeastern Pamlico Sound The longline was 1500m of 227kg test monofilament line, anchored and buoyed at each end. The gangions (individual lines) consist of a 0.7m 91kg leader with a 15/0 circle hook, attached to the main line at ~15m intervals with a stainless steel longline clip. Soaking time was limited to ~30 minutes for each set. Bait was primarily chopped mullet *Mugil cephalus*, and when unavailable, Atlantic menhaden *Brevoortia tyrannus* and squid *Loligo pealeii were* used as alternatives. The location of capture, size, sex, and weight of fish, as well as environmental conditions were recorded during each longline set. Randomly selected fish were sacrificed and the otoliths and the stomachs were removed and immediately frozen for analysis. Stomachs that did not contain any prey were excluded from the analysis. Stomach samples were collected from 2007-2012 (no stomach samples were collected in 2010).

South Carolina

The South Carolina Department of Natural Resources (SC DNR) has maintained a red drum longline surveying program in their waters since 1994 during September-November. While the longline survey has been conducted since 1994, the current methods have only been in place since the 2007. Longline sets were conducted during the day from Winyah Bay in the north to Port Royal Sound near the Georgia border in the south (Figure 2). The main line is 617 m of 273 kg test monofilament line with

stop sleeves at 30 m intervals. Clip on gangions consisting of a 2.5mm diameter stainless steel longline clip and 4/0 swivel attached to 0.5m of 91kg test monofilament and a 15/0 circle hook are placed at ~15.2m intervals. There are 40 hooks per set and 10-12 sets are made during each sampling day. Bait used consisted of Atlantic mackerel *Scomber scombrus*, mullet *Mugil cephalus*, or other available baitfish. Stratified random sampling was used every year of the survey through pre-determined sampling areas. Random samples of fish (30-50 individuals per identified stratum) are sacrificed for otolith studies and histological maturity testing from gonadal tissue, with stomachs also removed for diet analysis. The stomach samples were not selected randomly and were selected based on the presence of food. Stomachs from 2008 and 2010-2012 were used for this project. South Carolina samples collected before 2011 were preserved in a 10% formalin buffered seawater solution. All samples collected after 2011 South Carolina were frozen in individual Ziploc bags.

Stomach Contents Analysis

Stomach contents were identified to the lowest taxonomic level depending on the level of degradation and digestion. Many stomachs contained severely masticated prey, especially pre-2011 South Carolina stomachs stored for up to 4 years in buffered seawater, so some prey items could only be identified to the family level. Prey items that could not be identified to family we classified as "Unidentified Fish" or "Invertebrates". This was especially true for teleost prey species, as masticated and partially digested prey deteriorated further and any coloration faded after contact with the formalin. Invertebrate prey items were sometimes crushed and mangled, and unique coloration patterns, shell shape, or cheliped structures were used as identifiers. In the case of decapod prey, chelipeds and carapace fragments were counted to provide the best estimate of the number consumed. Prey items were separated and total length (cm) and wet mass (g) was measured. Those that were severely masticated or incomplete had a backbone length measurement taken in the place of total length to ensure a representation of the size of the prey item. Bait was easily distinguishable based on

shape and type. Representative samples of individual prey species were retained for reference in 95% ethanol. References used for prey species identification included "Shrimps, Lobsters, and Crabs of the Atlantic Coast" by Austin Williams, "Shallow-Water Marine Benthic Macro-Invertebrates of South Carolina" by Richard S. Fox and Edward E. Ruppert, and Peterson Field Guides for fish and invertebrates of the Atlantic Coast.

Data Analysis

Diet Structure

Large adult red drum (>750 mm TL) were the target group from each state, and for analysis purposes were separated by year to examine temporal diet variability within each state. Two standard indices were calculated to describe the presence of prey in the individuals sampled: relative abundance ($\%_N$) of prey to the total number of prey items, and frequency of prey occurrence ($\%_{FO}$) (Hyslop 1980). Percent by number ($\%_N$) allows for a simple percentage contribution of the number of a prey type consumed from the total number of prey consumed. It provides an accurate measure of predator effects on mortality of prey, but can over represent the importance of smaller prey that are often consumed in larger numbers; but are only contributing a small amount of biomass to the total intake by the predator (Hyslop 1980). The percent by number metric is calculated as:

$$\%N = \frac{P_i}{P} * 100$$

where the total amount a given prey type comprises (*Pi*) of all prey items found in all samples of the analysis unit (*P*): state, year, and size (Hyslop 1980). Frequency of occurrence is an effective alternative to %N in that is does not have the same tendency to over-represent more numerous prey that do not appear frequently in the diet, but appear in large numbers. It is also preferable to percent by weight or bulk measures with smaller sample sizes, limiting the effects of rare prey, error in separation of

"clumped" prey in the stomach, or unsuccessful identification from severe mastication (Baker et al. 2014). Percent frequency of occurrence of prey items is calculated as:

$$\%FO = \left(\left(\frac{N_i}{N} * 100 \right) / \sum_{i=1}^{N_i} \left(\frac{N_i}{N} * 100 \right) \right) * 100$$

where instances of each prey occurring in individual diets are N_i , which are then weighted by the total number of stomachs/fish in the group N to report how often an individual had consumed that prey type. Individuals often consume more than one prey type, so the total percentage for this metric can be over 100, so frequency of occurrence was normalized by 100% to give percent frequency occurrence ($\%_{FO}$) (Hyslop 1980, Rudershausen et al. 2010, Baker et al. 2014).

The adequacy of sample sizes of red drum was determined with a cumulative prey curve (species accumulation curve). The curve was plotted as the number of new species found in each stomach against the total number of stomachs analyzed (Ferry & Cailliet 1996). The curve from the diet data was plotted and represented as *Sobs*. When the curve becomes asymptotic, no new prey species are being found and sampling effort is sufficient. Prey curves were calculated for each state separately.

Diet diversity was also calculated for each state with the Shannon-Weiner (S-W) diversity index, conducted only on stomachs containing prey. Percent by number diet was used, and the contribution of each prey type was summed for each state. It was calculated as:

$$H' = \sum_{i=1}^{s} p_i * \ln p_i$$

where H' is S-W diversity index, S represents the number of prey species encountered and P_i represents the proportion by number of prey species i. The Shannon–Wiener index (H`) was used to evaluate the diet diversity between states based on prey taxa abundance. Statistical differences in diversities between states were tested by analysis of variance (ANOVA) (Somerton 1991). Effective trophic levels were used as an alternative to prey species composition, allowing for a direct comparison between North and South Carolina regardless of any prey assemblage changes. When samples collected in estuarine habitat in Pamlico Sound and samples from coastal South Carolina are directly compared, the potential changes in native prey species may drive a diet difference even if the red drum in both states inhabit the same niche/trophic level. By replacing the diet composition by species with an average trophic measurement for each fish, a direct comparison is possible. Each prey species was assigned an effective trophic level (ETL) value obtained from an ECOPATH model. Published data on ETLs for prey species were obtained from an ECOPATH model of the Pamlico Sound food web (Deehr 2012). Those species that did not occur in Pamlico Sound were estimated by averaging the ETLs of other members of the same family or similar (Table 3). The trophic level of each individual red drum was calculated by summing the percent contribution of each prey type by weight multiplied by the ETL, then adding 1 to the total and compared between states. An ANOVA was used to determine any differences in ETL between states.

Data Analysis

To analyze how the diets of the red drum were related to state of origin, total length, and year of collection we used the statistical package PRIMER-E v. 6.0 (Clarke & Gorley 2006). Percent number diet data were standardized by the total and square root transformed to normalize the distribution. A Similarity Percentage test (SIMPER) was performed to identify species that contributed to the dissimilarity of diet between the states and determine if there was a difference in diet composition between states. The results from SIMPER determine whether an one-way analysis of similarity (ANOSIM) testing the data against a null distribution is suitable (Clarke & Gorley 2006). A Bray-Curtis similarity matrix was created with each individual fish diet datum (stomach containing food) as a replicate. Similarity matrices between samples were constructed using the Bray-Curtis index and data were standardized (as a percentage) to minimize the discrepancy between samples (Legendre &

Legendre 2012). We performed an ANOSIM to evaluate which of the factors significantly influenced which food items were consumed. The ANOSIM test computes a global R-statistic value plotted on the probability distribution of the data as well as a p-value. R-statistics should be < 0.15 for a normal/null distribution within groups, and a p-value > 0.05 represents a similar distribution between groups (Clarke & Gorley 2006). A Similarity Percentage analysis was used to determine the average similarity in diet between individuals and the dissimilarity between populations. For another quantification of prey community structure, red drum diet (%N) data were ordinated using non-metric multidimensional scaling (MDS), which plots samples spatially as they relate to each other instead of on axes, and these were visually inspected for patterns in state similarity or dissimilarity (Clarke & Gorley 2006).

Principal component analysis (PCA) is a method for characterizing diet variability between groups, relying on the calculation of a correlation matrix of the original data. Through the analysis, eigenvalues and eigenvectors are calculated, which allow for numerical comparison of areas of variance (prey contributions) between groups. Principal component axes 1 through 3 were plotted to show the clustering of similar data points (individual red drum) on a biplot frame as well as the graphical representation of the eigenvalues and eigenvectors that indicate the areas/prey species accounting for most of the variability in the diet between groups (Crow 1978). Fish feeding on more dominant prey items will be plotted farther from the origin of the plot, while those feeding on rarer prey will cluster around the origin, allowing for a visual representation of fish with similar diets appearing near each other (Billy et al. 2000, Rudershausen et al. 2010). The PCA was conducted with %N data in this analysis, with each fish plotted as a single data point. Points are plotted around the origin based on diet composition, with each prey species as a different vector out from the origin. The more a given prey type contributes to a difference in diet, the larger the eigenvalue will be, resulting in a greater distance from the origin. Prey most responsible for differences will have the largest eigenvectors, while others

clustered near the origin have low eigenvector values. Individual observations were assigned a symbol representing the state of collection.

Logistic regression were used to determine whether the likelihood of consuming a prey species was affected by red drum size (TL) or region. This analysis models probabilities from binary presence/absence data for prey along a gradient of a quantitative continuous variable. Regressions were performed to estimate the probability of each given prey type appearing in the diet with respect to predator total length (covariate) or region (categorical factor). A binary dataset created from %N data (only stomachs containing prey) was used for the logistic regression analysis. State was entered as a factor in the model, and a regression line was then plotted along a gradient of total length of the predator. Only the most common prey (blue crab, penaeid shrimp, and Atlantic menhaden) in each state were modeled. Regressions were also calculated for teleost and decapod prey groups as a whole to examine any trends in piscivory or molluscivory between states.

Results

North Carolina Diet

Red drum collected in Pamlico Sound ranged from 800 to 1300mm TL, with a mean TL of 1079mm (±112 SD) (Figure 3a). The species accumulation curve for North Carolina sampling became asymptotic at 30 stomach samples (excluding empty stomachs), indicating sufficient data collection, with 51 actually examined (Figure 4). The diet of North Carolina drum consisted of 14 prey species, (6 invertebrate and 8 teleost fish species). While decapod prey constituted 56 %_N and 70 %_{FO}, there were only four decapod species consumed. Blue crab *Callinectes sapidus* was the most frequently occurring prey item, frequently over 50% by number and frequency of occurrence for all years (Table 3, Figure 5). Longfin squid *Loligo pealeii* (3.0 %_N, 3.1 %_{FO}) did appear in the diet of two fish as well, being the only

cephalopod prey found in the diet (Table 3). Clupeids and unidentified fish were also common prey items, both 12 $%_{FO}$ and $%_{N}$ (Table 3). Other teleost species found less frequently were Atlantic croaker *Micropogonias undulatus* (4.5 $%_{N}$, 4.6 $%_{FO}$), pinfish *Lagodon rhomboides* (3.0 $%_{N}$, 3.1 $%_{FO}$), and tonguefish *Symphurus plaguisa* (3.0 $%_{N}$, 3.1 $%_{FO}$) (Table 3).

South Carolina

South Carolina red drum collected for this study ranged from 750 to 1100mm TL, with a mean TL of 982mm (±75 SD) (Figure 3b). South Carolina required more samples to account for all prey species, which can be attributed to the larger number of species in that habitat, reaching an asymptote near 150 samples (Figure 4). The diet of South Carolina red drum consisted of 29 prey species (15 invertebrate and 13 teleost fish species). Of the 15 invertebrate species encountered, nine were decapod crustaceans, while fish prey consisted of eight different families but were dominated by Atlantic menhaden (Table 3). The group of decapod prey included Atlantic mud crabs *Panopeus herbstii* (5.9 $%_{N}$, 6.0 $%_{FO}$), mottled shore crabs *Pachygraspus transversus* (<1.0 $%_{N}$, 1.6 $%_{FO}$), stone crabs *Menippe mercenaria* (1.5 $%_{N}$, 2.4 $%_{FO}$), coarsehanded lady crabs *Ovalipes epheliticus* (2.0 $%_{N}$, 2.4 $%_{FO}$), and calico box crabs *Hepatus epheliticus* (<1.0 $%_{N}$, 1.6 $%_{FO}$), as well as blue crab (5.9 $%_{N}$, 8.8 $%_{FO}$) and penaeid shrimp species (4.9 $%_{N}$, 6.0 $%_{FO}$) (Table 2). Data for %N and %FO for each year shows a pattern of increasing amounts of Atlantic menhaden present in the diet: 11 $%_{N}$ in 2008 to 54 $%_{N}$ in 2012. Decapods remained important prey through time, with blue crab between 5.0 and 10 $%_{N}$, with shrimp and other crabs near 3.0 and 15 $%_{N}$ respectively (Figure 5).

NC Vs SC Diet Comparison

The overall diet differed in %N and %FO between states. Teleost prey was more common in South Carolina fish (51.8 $%_{FO}$, 63.9 $%_{N}$, 13 species), with North Carolina individuals feeding less on fewer

fish prey species (46.8 %_{F0}, 38.8 %_N, 8 species). While North Carolina individuals consumed more decapod crustaceans (70.3 %_{F0}, 56.7 %_N, 4 species), South Carolina diets consisted of a more diverse group of decapod prey than in North Carolina fish, mostly xanthid and brachyuran crabs (52.4 %_{F0}, 30.6 %_N, 10 species) (Figure 6, Table 3). South Carolina red drum also occasionally fed on blue crabs (8.8 %_{F0}) and Atlantic mud crab *Panopeus herbstii* (6.0 %_{F0}) (Table 3). There was a significant difference in Shannon-Wiener diversity (H') between states (ANOVA, F=5.62, p=0.0188). Mean H' (±SE) for North Carolina fish was 2.0 (±0.07) and was 2.6 (± 0.04) for South Carolina red drum.

There was a significant difference in overall diet between states (R= 0.081, *P*=0.02) also indicating high within group variability (Figure 7). SIMPER analysis showed strong average dissimilarity of 88.3% in the diet between states. Diets of individual fish within each state were not very similar, however, with only 14.3% and 32.4% average similarity between individuals for North and South Carolina respectively (Table 4). Blue crab contributed almost all (90%) of the diet similarity for North Carolina red drum, while Atlantic menhaden and teleost prey contributed 35% and 42% of the difference for South Carolina samples (Table 4). Conversely, these groups were major contributors to the dissimilarity between states: blue crab 26%, Atlantic menhaden 15%, and teleost prey 15% (Table 4).

Logistic regressions of diet data showed significant relationships between several prey types and the state of collection. Blue crab (P> χ^2 =<0.0001) and Atlantic menhaden (P> χ^2 =0.012) were both significantly more prevalent in one state, with blue crab 8.275 times as likely in North Carolina samples and Atlantic menhaden 0.318 times as likely in North Carolina as South Carolina (Table 5). Decapod prey (P> χ^2 =0.1403) and penaeid shrimp (P> χ^2 =0.1845) were common in both states, but teleost prey (P> χ^2 =0.0052) were .0353 times as likely to appear in the diet of North Carolina individuals as in South Carolina (Table 5). Penaeid shrimp (TL P> χ^2 =0.021) was the only prey type that was significantly related to the size of the predator (Table 5), with a decreasing likelihood of appearing in the diet as total length increased (Figure 8). Several dominant prey groups were responsible for the differences between states, with fish from each state clustering together in PCA graphical output. The first 2 principal components explained 42% of the variability in the data, and the first 5 components explained 62%. Blue crab, other fish species, and Atlantic menhaden were the species closest to the correlation circle of the plot, which are the farthest from the origin, signify a dominant prey group, and explain most of the separation between states (Figure 9). The eigenvectors (lines associated with prey species) showed that North Carolina drum were strongly correlated to having a large contribution by blue crab in the diet, with the most separation on the PC1 plane (Figure 9). There was also a significant amount of penaeid shrimp and other fish species responsible for separation of North Carolina individuals. For South Carolina red drum, however, most of the diet was correlated with feeding on menhaden, with high PC2 scores, and the diverse group of marine invertebrates prevalent in South Carolina waters. Benthic marine invertebrate species (mostly decapods) were clustered around the origin with small eigenvalues, but because of the diet diversity no individual species was dominant enough to disperse away from the origin (Figure 9).

The mean effective trophic level for North Carolina fish (3.65 ± 0.689 SD) was slightly higher than South Carolina (3.42 ± 0.638 SD) but the difference was not significant (ANOVA p=0.056, F=3.68). The most common ETL values observed for red drum were between 2 and 3, with a value of 3 the most common in both states (54% in NC, 35% in SC) (Figure 10).

IV. Discussion

Pamlico Sound and coastal South Carolina provide very different habitat conditions to red drum, from salinity and assemblage differences to varying commercial fishing effort (Day et al. 1989, Latour et al. 2001, Stewart & Scharf 2008, Able & Fahay 2010, ASMFC 2013). Specifically, when red drum migrate inshore to spawn during the fall months in North Carolina, they experience large changes in habitat

conditions such as turbidity, salinity, and potential prey by entering the estuarine conditions of Pamlico Sound. Conversely, South Carolina red drum were collected in coastal marine habitat or deeper water estuarine locations. The transition from marine to estuarine areas normally encompasses a decline in overall diversity, with fewer species dominating a very productive ecosystem (Day et al. 1989, Costanza et al. 1993, Able & Fahay 2010). We anticipated the diet to reflect these differences, expecting North Carolina red drum to exhibit a lower overall S-W diversity and have a few dominant prey types compared to the diet of South Carolina red drum. We found North Carolina red drum to have a diet diversity of 2.0 (±0.07), while South Carolina diets were more diverse with an H' of 2.6 (± 0.04).

Diet metrics reflected the differences in available prey relative to habitat differences between the estuary of Pamlico Sound and the coastal marine habitat where South Carolina samples were collected. North Carolina red drum fed more on blue crab than South Carolina red drum, even though blue crabs inhabit both Pamlico Sound and the South Carolina coastline (Archambault et al. 1990, NCDMF 2004, Eggleston et al. 2009). South Carolina red drum were more piscivorous, with more clupeid and teleost prey occurring in the diet. This increase in piscivory could be caused by seasonal behavioral changes in red drum entering Pamlico Sound to spawn, possibly switching to a more opportunistic feeding strategy, or because the large numbers of blue crab in the estuary are easier prey (Etherington & Eggleston 2000, Eggleston et al. 2009). There is no targeted commercial fishery for Atlantic menhaden in South Carolina, and populations are stable, so they likely provide a very accessible prey source offshore for South Carolina red drum (ASMFC 2012). Many other predators consume Atlantic and Gulf menhaden, fulfilling their "role" as baitfish. Cobia Rachycentron canadum, striped bass, spiny dogfish Squalus acanthias, bluefish Pomatomus saltatrix, spotted seatrout Cynoscion nebulosus, dolphinfish Coryphaena hippurus, yellowfin tuna Thunnus albacares, and even Bluefin tuna T. thynnus all utilize these menhaden species in the intersection of their ranges (Grant 1962, Arendt et al. 2001, Russell 2002, Uphoff 2003, Walter & Austin 2003, Butler et al. 2010, Rudershausen et al. 2010). In

Chesapeake Bay, Uphoff (2003) found that Atlantic menhaden were not only important as a forage species for striped bass, but supported many other fish species and birds. Samples were collected during the spawning season for red drum in both states, so differences in prey access/availability for blue crab were possible. Larger predators have been observed targeting easier prey to mitigate the costs of pursuit versus energy gained, and profitability of prey is an important factor (Trenkel et al. 2003, Galarowicz et al. 2006). ANOSIM and SIMPER results show that while individuals within each state had diverse diets with high within group variability, they consisted of different prey based on state of collection. The very low (14.8%) within group similarity for South Carolina red drum is likely attributed to the increased diversity in prey species for that state, as each individual has an increased potential of a unique diet composition at the time of collection and "dominant" prey items associated with South Carolina fish are less likely (Table 4).

Comparisons by ETL are very effective when assemblage changes are likely, or overall indicators of the trophic status of the system are needed (Polis & Holt 1992, Pauly et al. 1998). Analysis by ETL provided a novel method for comparing diets between locations and mitigating the effects of different prey assemblages on niche/diet estimation because diet composition is not categorically based on prey species, instead only considering the trophic level of the predator. Inter-species trophic level comparisons are commonly performed in diet studies as a standardization of diet composition (Cortes 1999, Morato et al. 2003). Diversity estimates for prey species also supported our initial hypothesis, with the marine red drum in South Carolina significantly more diverse in terms of prey consumed than the North Carolina fish. Even though the prey diversity is different in an estuarine environment versus the marine, the overall niche of the predator is very similar (ANOVA). The difference in ETLs was only marginally significant, indicating that even with different prey assemblages adult red drum maintained a similar predatory relationship with their environment but slight differences in the structure of the trophic web between locations may appear in the calculated ETL of the predator. Red drum had the

highest ETL of any teleosts in Pamlico Sound (3.74), and the only aquatic organisms higher were bottlenose dolphins *Tursiops truncates* (4.14), Atlantic sharpnose sharks *Rhizoprionodon terraenovae* (3.99), and Smooth dogfish *Mustelus canis* (4.05) (Deehr et al. 2014). With limited numbers of sharks in Pamlico Sound, red drum are higher in the relative trophic web than in South Carolina, where sharks inhabit both the coastal ocean and shallow rivers and estuaries (Bearden 1965, Castro 1993). South Carolina red drum may also experience competition with shark species, especially with regards to pelagic teleost prey (Bangley 2011, Shiffman 2011). Cownose rays *Rhinoptera bonasus* (3.44) are benthic feeding generalists, and exhibit similar seasonal movement patterns to the red drum, moving into Pamlico Sound during late summer and migrate through coastal South Carolina (Goodman et al. 2011, Deehr et al. 2014). These elasmobranchs also consume shellfish species and are piscivorous, likely competing for benthic crustaceans in a similar niche to the adult red drum (Goodman et al. 2011).

Sampling efforts for collecting adult red drum for this project were restricted to only the fall months in both North and South Carolina, when the catch per unit effort was highest for longlining. This leaves the possibility that red drum in both states resided offshore in similar marine habitats during the other months when samples were not collected. Red drum show seasonal differences in diet composition on the Gulf Coast, either related to behavior of the predator or availability of prey species (Boothby & Avault 1971, Overstreet & Heard 1978, Scharf & Schlicht 2000a). A diet study conducted on North Carolina fish when offshore may result in more similar diets between states with a uniformly marine habitat. Sampling was conducted in the fall months in both states because of the higher concentration of larger adult red drum during the spawning season, and catch per unit effort in other seasons is very low (Paramore 2011). Tagging data from North Carolina showed that red drum tags from sampling in Pamlico Sound were returned in the surf and inlets of the Outer Banks in other seasons, and that most of the offshore population enters their natal estuary to spawn (Luczkovich et al. 2008, Bacheler, Paramore, Burdick, et al. 2009, Bacheler et al. 2010, Paramore 2011). South Carolina adult red

drum remain offshore to spawn, while larvae and juveniles use surface tidal flow to enter the estuary post-spawn (Wenner 1992). Some red drum spawning in North Carolina may migrate into Virginia estuaries or remain offshore to spawn as well (Bacheler, Paramore, Burdick, et al. 2009).

These samples also had the benefit of multiple sampling years (4 in SC, 5 in NC), allowing for temporal analysis. The use of longer term datasets is beneficial in diet studies because of the lack of assemblage characterization in real time with diet studies and the large area predatory fish can cover. This mitigates the effects of time periods or individual samples that were outside the observed "norm" for the species in that area (Garrison & Link 2000, Link et al. 2002, Link 2004). When the time period is long enough, fish stomachs can even be used as a surrogate for surveying prey assemblages over time (Link 2004). Temporal analysis showed increasing trends for blue crab and Atlantic menhaden appearing in the diet in North Carolina and South Carolina, respectively. These trends were accompanied by a decrease in piscivory on other finfish species in each state as the amount of blue crab and Atlantic menhaden in the diet increased (Figure 5). Atlantic menhaden are not a targeted commercial species in South Carolina, but are harvested for bait in North Carolina and Virginia, mostly for crab pot baiting (ASMFC 2012). Atlantic menhaden have been listed as experiencing overfishing, but are not yet overfished (ASMFC 2012). Blue crab have been listed as a species of concern because of declining catch rates below the 10 year average, but they are not currently considered overfished (NCDMF 2004, 2012, 2013).

Our sample sizes were small when empty stomachs were excluded, especially when examining differences between years and for North Carolina analysis. However, prey accumulation curves for both North and South Carolina were becoming asymptotic within our sample range, so effort was adequate to identify the constituent prey species for this study. Our findings have been reinforced by previous small-scale red drum diet studies conducted in both North Carolina and South Carolina. Paramore (2011) analyzed the diets of larger red drum while evaluating the efficacy of longline collections in

Pamlico Sound. The sample size was small (n=41), but the preliminary findings were that blue crab $(64\%_{FO})$ and finfish $(64\%_{FO})$ made up the diet of red drum in Pamlico Sound, with blue crab as the dominant prey by weight. The diet of South Carolina red drum identified by Wenner et al (1990) included large adults, and identified brachyuran crabs $(21\%_N, 15\%_V)$, fiddler crabs $(19\%_N, 2\%_V)$, and finfish $(46\%_N, 79\%_V)$ such as spot *Leiostomus xanthurus* and Atlantic menhaden as major prey types. Wenner et al (1990) encountered more crabs in the diet of adults, but there was a negative trend between size and crab appearing as prey. This pattern may have continued with the larger adults (>750mm) presented here from those that were 530mm and up in that study. Adult red drum diets on the Gulf coast were similar as well, including Gulf menhaden *B. patronus*, other teleosts, penaeid shrimp species, and other decapods (Boothby & Avault 1971, Overstreet & Heard 1978).

Our understanding of adult red drum feeding ecology in North and South Carolina is limited to the late summer and early fall during spawning aggregations. Red drum on the Gulf coast have seasonal variation in their diet, mostly switching between either Gulf menhaden, blue crab, or penaeid shrimp species based on the seasonal changes in the abundance of those prey items (Boothby & Avault 1971, Overstreet & Heard 1978, Scharf & Schlicht 2000b). Sampling both populations when they inhabit similar habitat types during the rest of the year would allow for a full characterization of the seasonal effects on their diet. Despite this shortcoming, the effects of the large spawning aggregations on local forage species during that season can be better estimated and applied to future management strategies.

Implications

More recently, management strategies have started to include trophic dynamics and predatorprey interactions when implementing new regulations because of the push for prey species to be managed in relation to the requirements of the predatory (often popular recreational or other commercially important) species (Stephenson 1997). As of the most recent Amendment to the Interstate Fishery Management Plan for Atlantic menhaden, a multi-species model that includes effects

of predation on the population of menhaden as well as their effects on predator abundance as a forage source will be used to guide menhaden harvest towards sustainable levels (ASMFC 2012). Blue crab harvest is the most valuable commercial fishery in North Carolina, and Pamlico Sound constitutes a large portion of the fishing area, but the cumulative guild predatory effects on the populations are unknown in North Carolina (NCDMF 2004). With blue crab as the primary prey for adult red drum in North Carolina and an increasing trend in blue crab in the diet of the adults entering the estuary (Figure 7), there may be future management implications for multi-species or ecosystem based strategies. Other fish species have been recorded feeding on blue crab, such as striped bass Morone saxatalis, and Atlantic croaker (Orth et al. 1999, Spier 1999). Combined predation between these species may have larger impacts on blue crab and other forage species. When striped bass enter shallower nursery habitats with sea grass beds the rate of blue crab consumption increased compared to individuals in open water, which may contribute to the difference in blue crab consumption between North Carolina and South Carolina red drum (Spier 1999). Currently, the blue crab harvest in North Carolina is managed so that commercial harvest does not coincide with the spawning season from May to August (NCDMF 2004). This blue crab spawning season overlaps with red drum entering Pamlico Sound in late July and August, and the increasing trend of blue crab in the diet may be attributed to increased interaction of these spawning individuals. There is also the potential to effect recruitment through predation mortality by red drum of spawning adult blue crabs. Mortality estimates may not fully account for this interaction, as blue crab catches have remained below the 10-year mean (NCDMF 2004). Atlantic menhaden is not commercially fished in South Carolina, nor are the diverse brachyuran and other decapod species consumed by the offshore red drum, but multi-species management of forage species is still an important factor to preserve the recreational value of the red drum (Knapp 1950, Stephenson 1997, ASMFC 2012). The increases in Atlantic menhaden and blue crab appearing the diet of red drum

may be an ecosystem indicator of recovering stocks, as these predators have more access to them as forage species.

Management strategies enacted by the ASMFC currently allow harvest of red drum in a "slot" size, usually between 381 and 711 mm total length with bag limits of 3 to 5 fish along the Atlantic coast. North Carolina is currently the only state in the ASMFC to allow commercial harvest of red drum, but similar limits are in place on slot size and total allowable harvest. These conditions create the possibility of an increase in the number of the large adults of the species both offshore of South Carolina and the spawning population entering Pamlico Sound. Commercial catch data in North Carolina showed a trend towards increasing length of red drum caught through time, with shift of about 150mm from samples taken in 1986-1990 to 1992-1998 (ASMFC 2002). In the future , this could cause top-down changes in the food web with increased predation on forage species by adult red drum as well as potential increases in natural mortality that would require consideration in management (Verity & Smetacek 1996, Bax 1998).

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VI. Index of Figures and Tables

Figures

Figure 1 NC Sampling Locations

Map of longline sampling locations conducted by the North Carolina Division of Marine Fisheries for the red drum survey in Pamlico Sound, NC. Sets were placed along the eastern edge of the sound on the inshore side of the outer banks from north of Cape Hatteras to Portsmouth Island. Gear was also set around the mouth of the Neuse River.

Figure 2 SC Sampling Locations

Map of longline sampling locations conducted by the South Carolina Department of Natural Resources for the red drum survey. Longline sets were conducted in 4 general areas offshore of the South Carolina coast. The sampling areas from north to south were offshore of Winyah Bay, Charleston Harbor, St. Helena Sound, and Port Royal Sound.

Figure 3 Size Histogram of Red drum collected

Size Histogram of Red Drum (TL mm) collected for the study, separated by North Carolina and South

Carolina. Values represent the percentage of samples each length increment contributes to the total of samples.

Figure 4 Prey Species Accumulation Curves

Prey Accumulation Curve for Adult Red drum for the diet of North Carolina (N=51) (4a) and South Carolina (N=146) (4b) red drum sampled. Prey species are summed cumulatively across the number of samples (individual stomachs), effectively plotting the rate at which new species are encountered. Once the curve becomes asymptotic, no new species are likely to appear in further sampling. Sobs represents the actual data, with sampling events (individual stomachs) plotted against the number of new prey species that appear.

Figure 5 Stacked Bar Graph of %N and %FO Diet Data

Percent by number (%N) and percent frequency of occurrence (%FO) diet data for North Carolina and

South Carolina. Samples were not collected in 2007 or 2009 in South Carolina and 2010 in North

Carolina.

Figure 6 Stacked Bar Graph of % N and % FO by State

Stacked bar graph of total percent by number (%N) and percent frequency of occurrence (%FO) for

North (N=51) and South Carolina (N=146) across all years, separated by state. Samples were not

collected in 2007 or 2009 in South Carolina and 2010 in North Carolina.

Figure 7 MDS Plot of %N Diet Data by State

Multidimensional scaling plot of % N diet data for adult red drum for North and South Carolina.

Individual samples are plotted in space by their relationship to one another based on the composition of

the sample (diet of the red drum for this study). There are no axes or units, instead samples separate or

cluster together based on similarity or dissimilarity to one another. North Carolina samples are

represented as orange triangles, while South Carolina samples are represented as green circles.

Figure 8 Logistic Regression Plot of Penaeid Shrimp Appearing as Prey

Logistic regression of penaeid shrimp as prey from a binary (presence/absence) representation of percent by number diet data. Probabilities of a prey type appearing for each state (North Carolina or South Carolina) were plotted along a gradient of total length (mm) of the predator (red drum).

Figure 9 PCA of %N Diet Data by State

Principal component analysis output of % by number diet data for North and South Carolina. Individual samples are scored based on principal component axes based on their composition (diet). The presence of certain prey drives the separation or clustering of similar samples. These largest eigenvectors (represented by prey items) are presented.

Figure 10 Histogram of Effective Trophic Levels

Histogram of the calculated effective trophic levels of red drum for North and South Carolina. These were calculated based on the prey found in the stomach of the drum using previous ECOPATH food web data for Pamlico Sound (Deehr 2012). The average trophic level of prey in the stomach was calculated, then 1 was added to represent the change to the next trophic level. Values are presented separated by state as a percentage of the total number of samples, with North Carolina represented by green bars and South Carolina represented by red bars.

Tables

Table 1 Previously Published Red Drum Diet Studies

List of previously published diet information on red drum across their distribution, including the size of fish examined, the sample size, diet metrics used, general findings, and the location of study.

Table 2 Sample Sizes by State and Year

Sample size of red drum from both North and South Carolina for all years sampled excluding fish that

had empty stomachs.

Table 3 List of Prey Species Encountered

List of all prey species encountered in the diet of red drum. The common name, scientific name, and effective trophic level (ETL) are presented for each species, assigned from ECOPATH software. ETL values with an * were modified or estimated, as they were not directly calculated in the model used. Percent frequency of occurrence (%FO) data is also shown for each species for both North Carolina and South Carolina. Highlighted species had a %FO of 5% or more. Percent by number (%N) is presented for prey for each state. Both %FO and %N are also presented for larger groupings by state. If (---) is listed, then that prey was not encountered in the state in question.

Table 4 SIMPER Results

Similarity Percentage (SIMPER) results on percent by number diet data for North and South Carolina red drum. The average % similarity between individuals in each state is presented, as well as the overall dissimilarity between the states. Prey groups that contributed the most to differences in diet and their % contribution are presented. Blue crab was the only major contributor to North Carolina differences.

Table 5 Logistic Regression Results

Results of logistic regressions performed on presence/absence data for prey species in North Carolina and South Carolina red drum diets. Probabilities were modeled for occurrence in each state as a function of total length (TL) of the predator. State and TL were both tested as response variables in the regression models. Significant χ^2 results (<0.05) are bolded. Regressions were run on species that contributed to differences between the states: blue crab, Atlantic menhaden, and penaeid shrimp. Larger groupings of teleost prey and decapod crustaceans were tested as well. The odds ratio results are presented as well as the probability estimate a given prey type indicates a North Carolina fish.

VII. Figure and Tables

Figures:

Figure 1: NC DMF Sampling Locations

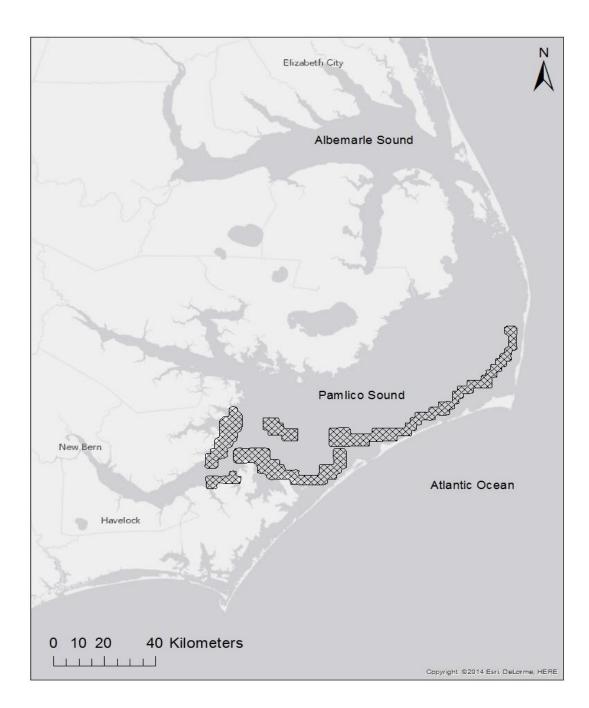


Figure 2: SC DNR Sampling Locations



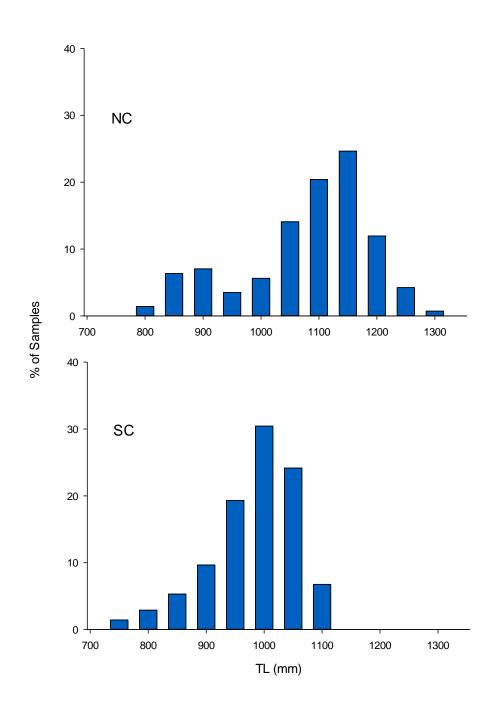


Figure 3: Size Histogram of Sampled Red Drum



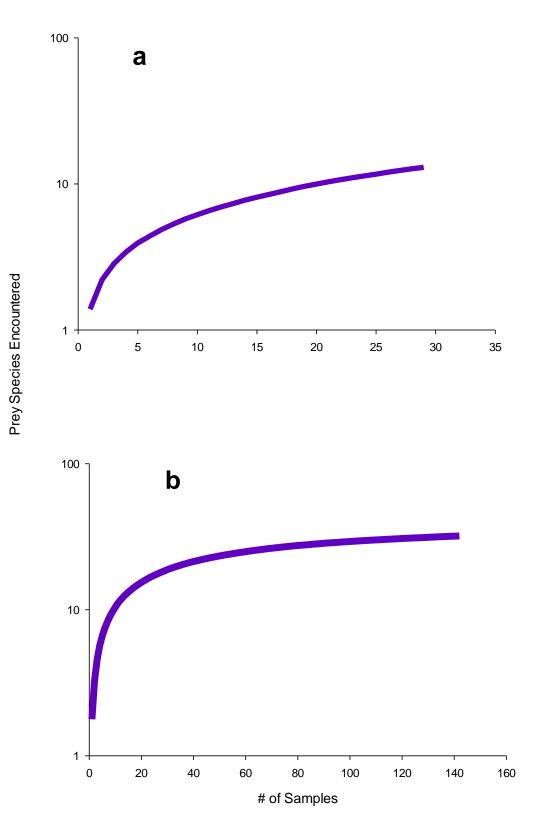
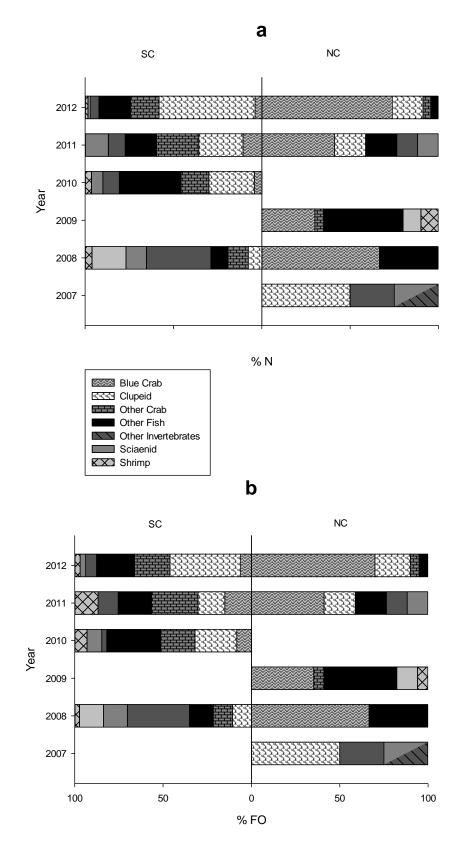


Figure 5: %N and %FO by State and Year





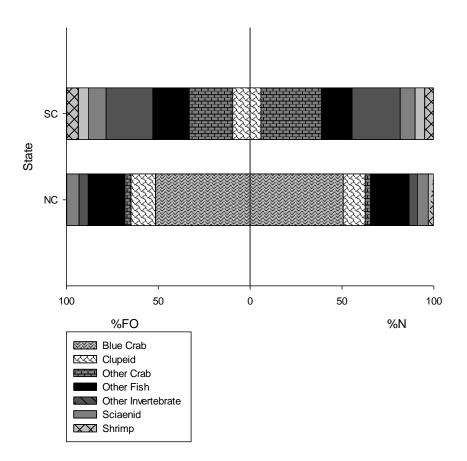
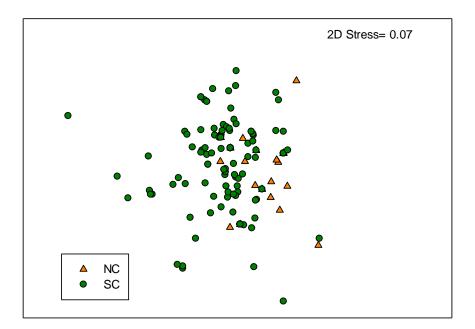


Figure 7: MDS Plot of %N Diet Data



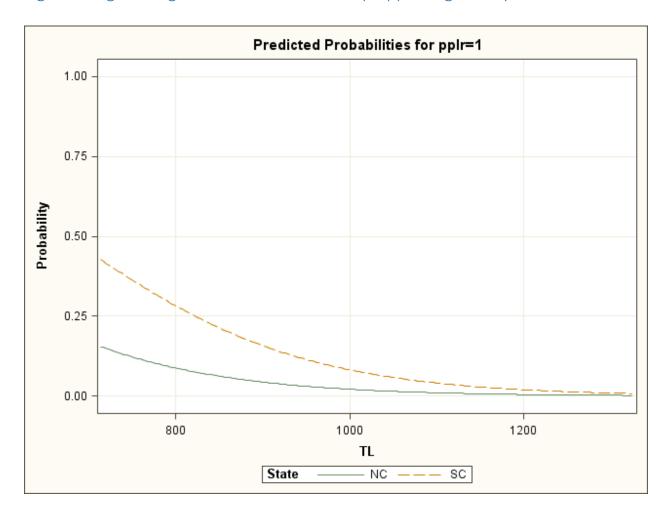


Figure 8 Logistic Regression of Penaeid Shrimp Appearing as Prey



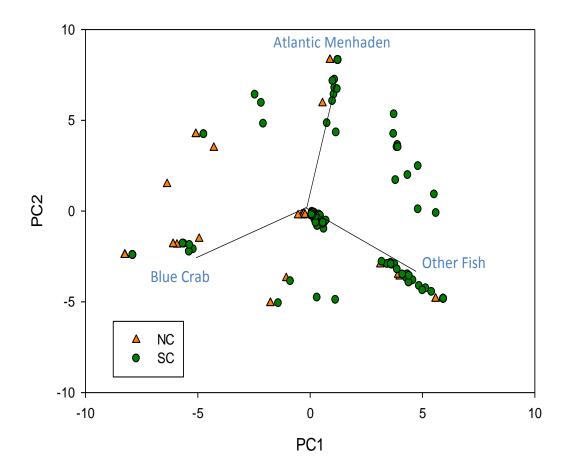


Figure 10: Histogram of ETLs Encountered

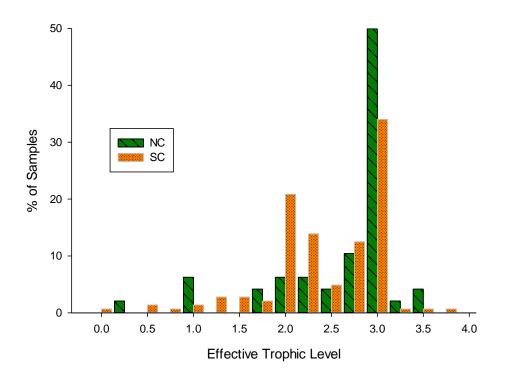


Table 1: Previous Red Drum Diet Studies and Results

weight, and IRI is Index of Relative of Importance. For this study, adults are those fish 750mm and larger.								
Source	Location	Method	Size Range	N	% Empty	Primary prey		
Bass and Avault 1975	LA	% F, V	8- 183mm	568	5.1	Decapods, fish, benthic invertebrates		
Boothby and Avault 1971	Southeast LA	% F	250- 932mm	349	28	Crab, shrimp, fish		
Guillory and Prejean 1999	Gulf of Mexico	Gulf of Mexico						
Knapp 1950	ТХ	% O			34.2	Crabs, shrimp, fish		
Llansó et al 1998	Tampa Bay, FL	IRI, % F, N, DW	19- 590mm	263	2	Decapod and nondecapod crustaceans, fish		
Orth et al 1999	VA							
Overstreet and Heard 1978	Mississippi Sound, MS	% O	190- 1020mm	107 (22 adults)	2.8	Panaeid shrimp, crabs, fish		
Peters and McMichael 1987	FL	% N, V	1.6- 300mm	863	30.2	Copepods, mysids, crab, finfish, decapods		
Scharf and Schlicht 2000	Galveston Bay, TX	% FO, N, W	350- 750mm	598	34	Decapods, teleosts		
*Spier 1999	Chesapeake Bay, MD							
Wenner et al 1990	SC		<275mm	540		Fish, crustaceans		
Paramore 2011	Pamlico Sound, NC		Juvenile	41	46	Blue Crab, Copepods		
Holt and Holt 2000	Aransas Bay, TX	IRI, %F	Larval	156	17	Nauplii, velliger		

Table 1: Red drum diet studies including locations, methods, summarized results, and size ranges for each project. For methods, % V is volume, % F is frequency, % O is occurrence, % N is number, % DW is dry weight, and IRI is Index of Relative of Importance. For this study, adults are those fish 750mm and larger.

Table 2: Sample Sizes by State and Year

Sample size of red drum collected by state and year.

Years with a "---" had no samples.

SC		NC			
Year	Ν	Year	N		
2007		2007	5		
2008	24	2008	4		
2009		2009	12		
2010	43	2010			
2011	31	2011	13		
2012	48	2012	17		
Total:	146		51		

Table 3: List of All Prey Species Encountered

All prey species found in the stomachs of red drum sacrificed for this study, including assigned effective trophic level (ETL) from ECOPATH software and the sources for ETL data. ETL values with an * were modified or estimated, as they were not directly calculated in the model used. Percent frequency of occurrence data is also shown for each species for both North Carolina and South Carolina. Highlighted species had a %FO of 5% or more. Total biomass recovered of each prey type is also listed.

Prey Type	Scientific Name	ETL	NC %FO		NC %N		NC Biomass (g)	SC Biomass (g
Decapod Crustaceans			70.3	52.4	56.7	30.6		
Blue crab	Callinectes sapidus	3.01	47.7	8.8	50.7	5.9	1079.27	516.14
Penaeid shrimp	Penaeus spp.	2.8*	1.5	6.0	3.0	4.9	5.15	260.39
Portunid crab	Portunis spp.	2.9	1.5		1.5		0.19	
Stone crab	Menippe mercenaria	2.9		2.4		1.5		504.39
Calico box crab	Hepatus epheliticus	2.9**		1.6		<1		73.76
Atlantic mud crab	Panopeus herbstii	2.9	1.5	6.0	1.5	5.9	4.35	385.51
Coarsehanded lady crab	Ovalipes epheliticus	2.9**		2.4		2.0		195.34
Mottled shore crab	Pachygrapsus transversus	2.9**		1.6		<1		51.16
Other crab	Brachyuridae spp.	2.9**		5.6		4.0		226.67
Majid Crab	Majidae spp.	2.9*		1.2		1.5		180.86
Teleosts			46.8	51.8	38.8	63.9		
Atlantic Menhaden	Brevoortia tyrannus	2.11	12.3	16.5	11.9	26.4	215.86	5816.95
Unidentified fish	Teleostei	2.93**	12.3	20.5	11.9	21.5	44.18	1629.57
Clupeid	Clupeidae	2.11*		6.0		6.4		728.52
Atlantic croaker	Micropogonias undulatus	2.69	4.6	<1	4.5	<1	37.54	262.19
Tonguefish	Symphurus plaguisa	3.58**	3.1		3.0		30.49	
Pinfish	Lagodon rhomboides	2.3	3.1		3.0		15.18	
Spot	Leiostomus xanthurus	2.58	1.5	1.6	1.5	<1	60.78	542.56
Oyster toadfish	Opsanus tau	2.3**		1.2		<1		352.33
American eel	Anguilla anguilla	3.58**		2.0		1.2		83.64
Lizardfish	Synodus foetens	3.58***	1.5	<1	1.5	<1	39.48	574.51
Harvestfish	Peprilus alepidotus	3.18		<1		<1		77.88
Spotted seatrout	Cynoscion nebulosus	3.72		<1		<1		93.89
Mullet	Mugil cephalus	2		<1		<1		239.01
Hogchoker	Trinectes maculatus	3.58***		<1		<1		24.39
Spadefish	Chaetodipterus faber	3.37	1.5		1.5			
Sciaenid	Sciaenidae	3.2*		3.2		3.2		302.74
Other Invertebrates			10.6	11	4.5	5.2		
Amphipod	Amphipoda	2.2		<1		<1	13.89	0.61
Squid	Loligo pealeii	3.59	3.1		3.0		26.84	
Snail	Littorina littorea	2.54	1.5		1.5		0.46	
Sand dollar	Melitta isometra	2.21		2.0		1.2		30.23
Isopod	Isopoda	2.2		2.0		1.2		5.67
Hermit Crab	Paguridae spp.	2.9**		2.4		3.0		31.37
Clam	Bivalvia	2.02		1.6		1.2		16.01
Mole crab	Emerita talpoida	2.5**		<1		<1		30.17
Horseshoe crab	Limulus polyphemus	2.9**		<1		<1		27.75
Chondricthyans				<1		<1		
Stingray	Dasyatis sabina	3.54		<1		<1		99.59

Table 4: Simper Results

Simper Results. Average similarity (within each state) and dissimilarity (between each state) (%) of diet of red drum between North Carolina and South Carolina. The percent contribution of prey types to the similarity or dissimilarity among groups is presented for the major contributors (>10%).

Comparison Group		% Contribution to diet differences			
	Average %				
		Atlantic			
	Similarity	Other Teleosts		Blue Crab	
			Menhaden		
	22.44			00.00	
NC	32.41			90.90	
SC	14.28	42.32	35.11	7.40	
Average % D	issimilarity				
NC vs. SC	88.29	14.70	14.60	26.30	

Table 5: Logistic Regression Results

Results of logistic regressions perfromed on presence/absence data for prey species in each state. Probalities were modeled for occurrence in each state as a function of total length (TL) of predator. State and total length were both tested as response variables, significant p-values (<.05) are bold. The probability of a given prey item appearing in the diet is also presented.

Prey Species	State Estimate	State p>χ2	TL Estimate	TL p>χ2	Odds Ratio Pt Estimate for State	Probaility of Appearing
Blue Crab	1.0566	<0.0001	0.00157	0.399	8.275	0.27
Atlantic Menhaden	-0.5724	0.012	0.000437	0.8136	0.318	0.32
Penaeid Shrimp	-0.7035	0.1845	-0.00742	0.021	0.245	0.08
Teleosts	-0.52	0.0052	0.00109	0.439	0.353	0.37
Decapods	0.2755	0.1403	0.000706	0.6642	1.735	0.56

CH. 3: Synthesized Feeding Ecology of the Red Drum *Sciaenops ocellatus*: Population Scale Trophic Interactions of the Atlantic and Gulf Coasts

Introduction

Like many coastal predatory fish, the red drum, Sciaenops ocellatus, is a popular recreational and commercial species. These fish are known to feed on commercially important species such as blue crab Callinectes sapidus, clupeids, and penaeid shrimp (Pearson 1928, Knapp 1950) while being a desirable sport fish and popular menu item. There is a long history of recreational and commercial exploitation of the species, with large commercial harvests that were not originally heavily regulated because of the lack of data comparing effort to overall catch. However, size limits have been in place for many years (Pearson 1928). Recreational fishing for sub-adults in shallow waters has gained popularity in many states, and in North Carolina large adults have become a significant catch and release fishery (Paramore 2011, ASMFC 2013). More conservative management strategies have since been introduced, with increasing restrictions on landings and slot size limits for both commercial harvest and recreational catches (ASMFC 2002, 2013, NCDMF 2008). Florida, South Carolina, Pennsylvania, Rhode Island, and Maine either no longer have commercial fishery for red drum or have prohibited it, while red drum are commercially fished on most of the Gulf Coast (ASMFC 2013). Releases now account for 90% of the total recreational catch, and recreational harvests are 60% of total landings for Atlantic states (ASMFC 2013). States under the ASMFC mostly manage red drum under a slot size limit between 350 and 680mm (ASMFC 2013), with similar size restrictions on the Gulf Coast for recreational catches between 400 and 760mm (Florida Fish and Wildlife Commission, Louisiana Department of Wildlife and Fisheries, Mississippi Department of Marine Resources, Texas Parks and Wildlife). This represents the potential for a large scale change in population structure of red drum throughout its distribution and in turn predation effects on forage species, many of which are important commercially fished species.

Predation impacts on forage species populations have been well documented, for example by Hartman & Margraf (1993), Carpenter et al. (1985). Predation impacts within nursery areas are also an area of concern for management because of the potential effects on juvenile recruitment and success (Sheaves 2001).

Diet studies are very effective methods for characterizing trophic interactions in a system, but are usually spatially and temporally limited in scope, especially with migratory species (Cailliet 1976, Hyslop 1980, Cortes 1999). By collecting and synthesizing all previously published research on a species, trends can be examined both spatially and temporally (Walter et al. 2003). Red drum diet studies have been conducted for most age and size ranges and along both the Atlantic and Gulf coasts (Table 1). With the limited scope of any one study and the prevalence of previously published research, a synthesis of all diet information through standardized diet compositions is a viable method for characterizing the diet of a predator without requiring access to the raw data (Cortes 1999). This method allows for different diet metrics to be standardized between studies, regardless of what diet metric was originally presented. Different diet metrics often indicate similar findings when presented together, and this redundancy lessens the effects of pooling the diet data on the results (MacDonald & Green 1983).

Our objectives were to describe the large scale patterns in feeding ecology for red drum throughout its life stages along the Atlantic and Gulf Coast through a standardized diet, and identify any ontogenetic or seasonal shifts in diet habits. These findings can provide information for the development of multi-species management plans that account for predatory effects on forage species as well as conservation and management of red drum both in nursery areas and in coastal waters.

Methods

Previously published diet data on red drum of all ages for both the Atlantic and Gulf coasts were collected via a thorough literature search (Table 1). Studies were conducted in Louisiana, Mississippi,

Florida, Texas, Georgia, South Carolina, and North Carolina. Within this large geographical area the research was conducted throughout many decades, with some studies dating back to the 1970s and a study as recent as 2014. Many different sizes of red drum were examined, with different size-classes and groupings between each study. Larval red drum diets were not considered for this publication. Prey groupings varied as well, with some studies reporting diet at species level, while others used family-level groupings for large groups such as copepods and mysids. Diet metrics were not always consistent between sources for defining prey composition, so standardization of metrics to a common unit was required for direct comparison and pooling of diet data.

Percent by number (%N), percent frequency of occurrence (%FO), percent frequency (%F), percent occurrence (%O), percent volume (%V), percent dry weight (%DW), and index of relative importance (IRI) were all used for at least one study, so these were compiled into a new unit of standardized diet composition outlined by both Cortes (1999)and Walter et al (2003):

$$P_j = \sum_{i=1}^n P_{ij} N_i / \sum_{j=1}^m \left(\sum_{i=1}^n P_{ij} N_i \right)$$

where P_{ij} is the proportion of prey category j in study i, N_i is the number stomachs containing food that were used to calculate P_{ij} in each study, n is the number of previous studies referenced, m is the number of prey categories and $\sum P_{ij} = 1$.

Of the previously studies, 70% used more than one metric to characterize the diet, so when multiple measures were presented they were combined (Table 1). Redundancy in diet metrics allows for pooling of metrics with minimal effects on the overall results (MacDonald & Green 1983), so the method outlined by Cortes allows for a simple adjustment (1999). For example, if %FO and %N were presented:

$$P_{ii} = (\% N + \% FO)/2.$$

Studies that divided samples by size class were re-arranged into larger groupings for our analysis into new size categories and prey groups. Eleven prey groups were used to calculate the standardized diet composition for all ages/size classes of red drum: Crabs, Shrimp, Fish, Mysids, Other Crustaceans, Other Decapods, Amphipods, Polychaetes, Other, and Echinoderms. Prey groupings were pooled based on the resolution of the original research, i.e. majid crabs, blue crabs and other callinectid crabs were combined as "Crabs", any teleost prey were presented as "Fish", while more obscure/rare decapod and crustacean prey were pooled into "Other Decapods" and "Other Crustaceans". Prey types that were very rare or originally presented as unknown or other were pooled into the category "Other". Prey types that represented a large portion of the diet were left un-pooled, such as mysid shrimp listed as "Mysids". Diet data were then summarized into groupings for three size classes of red drum: juveniles (<70mm), sub-adults (70-200mm), and adults (>200mm). Assumptions were made for these groupings, as the size ranges originally presented by studies overlapped with other size classes in some cases. Groupings were assigned based on the majority of the size range of the study in question.

We performed a multivariate cluster analysis to determine groupings of diet similarity by study, age class, and coast of the study (Atlantic or Gulf). A cluster analysis created from a Bray-Curtis similarity resemblance matrix of the standardized, square-root transformed diet data was used to identify these groupings (Clarke & Gorley 2006). PRIMER V6 was used for all multivariate analyses. This provided a normalized distribution of the samples without overweighting "0" values for items that did not occur in the diet.

Results

Diet Composition by Size Class

JUVENILES

Mysid shrimp were a major prey contributor for juvenile red drum in every study compiled for both the Atlantic and Gulf Coasts (Figure 1). Peters & McMichael (1987) found these mysid shrimp (75 % of diet) to dominate the diet of juveniles from Tampa Bay, Florida. South Carolina juvenile red drum also consumed mysids, but grass shrimp *Palaemonetes spp.* and copepods were important prey as well (Wenner 1992). While mysids were important prey in Louisiana, Bass & Avault's (1975) findings showed fish to be equally important contributors to the diet (Figure 1). These juveniles fed mostly on other sciaenids such as croaker *Micropogonias undulatus* and spot *Leiostomus xanthurus*, with Gulf menhaden *Brevoortia patronus* and anchovies *Anchoa spp.* as other common teleost prey.

SUB-ADULTS

The diet of sub-adult red drum was variable between studies. In South Carolina mysid shrimp were the largest contributor, while crabs and other shrimp species constituted the remainder of the diet (Figure 2) (Wenner 1992). Peters & McMichael (1987) found decapod crustaceans as the dominant prey in Tampa Bay, Florida while Llansó et al. (1998) identified polychaetes as the dominant prey type in a different part of Tampa Bay Florida. Bass & Avault's (1975) diet investigation concluded that for Louisiana sub-adults, mysids, decapods, and teleosts were the major prey. Overall, sub-adult red drum were not particularly piscivorous, instead mostly feeding on mysids, decapods, and shrimp on both coasts.

ADULTS

Teleosts, crabs, and shrimp were the most common major prey groups found in the diet of adult red drum (Figure 3). Boothby & Avault (1971) found the diet of adult red drum in Louisiana to be evenly distributed between crabs, shrimp and fish (Figure 3). In Mississippi the diet was more diverse, also including polychaetes and other decapods (Overstreet & Heard 1978). In the same study the diet of Georgia red drum was also characterized, with other crustaceans and echinoderms replacing shrimp (Figure 3). In Texas, Scharf & Schlicht (2000) found a diet consisting mainly of teleosts, shrimp, and crabs (Figure 3). South Carolina adults fed mostly on fish and crabs, but unlike the smaller adults 170-530mm, the individuals over 530mm did not consume shrimp (Wenner et al. 1990). A more recent examination of South Carolina diets showed that large adults (>750mm) did consume shrimp, but were

mostly piscivorous except for a contingent of varied crab species (Peacock et al. 2014). A preliminary study conducted by Paramore (2011) on adult red drum in North Carolina found the diet to be equally divided between finfish and blue crab.

When the diets were pooled by red drum size class, the similarities between juvenile and subadult red drum feeding on mysids, polychaetes, fish, and other decapods in similar proportions were clear. Adult red drum fed on crabs and fish in much larger proportions than younger red drum (Figure 4). This increase in piscivory and feeding on crabs likely represents the only major ontogenetic shift in red drum diets excluding larval feeding.

Gulf vs. Atlantic Coast Diet

Diets did differ by coast for each size-class of red drum. The pooled diet composition for juveniles showed Atlantic Coast red drum were more piscivorous than on the Gulf Coast, as well as more crabs and shrimp appearing in the diet. Gulf Coast juveniles did consume teleosts, but the major diet contributors were mysids and assorted decapods (Figure 5a). The diet differences for sub-adults were similar to those of juveniles, with Atlantic diets containing mostly crabs, fish, and shrimp while polychaetes, other decapods, and mysids dominated the diet on the Gulf coast (Figure 5b). Piscivory was a major component of the diet for adults on both coasts, with Atlantic red drum consuming crabs as the second dominant prey type. On the Gulf Coast, the other large portion of the diet was divided evenly between crabs (20%) and shrimp (20%) (Figure 5c).

Cluster analysis of diet studies determined that the groups with the most similar diets were adult red drum from the Atlantic Coast, clustering together because of the large amounts of crab and fish prey in the diet (Figure 6). Adult red drum from both coasts were all in the same large cluster of 50% similarity. Juvenile and sub-adult diets did cluster by coast, but generally size-classes were not very similar to each other (Figure 6). Juveniles and sub-adults from Bass & Avault's (1975) research were

very similar because of the large amount of mysid shrimp appearing, while the presence of polychaetes clustered juveniles and sub-adults from Llansó et al (1998) together.

Seasonality

Most of the previous research used did not present information on the seasonality of diets, but some patterns in migratory and seasonal effects on the diet were identified. There were two studies conducted on adult red drum (Boothby & Avault 1971, Scharf & Schlicht 2000b, Peacock et al. 2014) and three on juveniles and (Overstreet & Heard 1978, Facendola & Scharf 2012) that included some information on seasonality in their analysis. Scharf & Schlicht (2000) observed an increase in piscivory in the spring that accompanied an increase in abundance of Gulf menhaden offshore of Texas. Conversely, in the fall months the red drum fed on the more abundant shrimp in the Gulf (Figure 3). Boothby & Avault (1971) encountered similar diet patterns in Louisiana, with fish more prevalent in the winter and spring, with shrimp abundant in the summer and fall. During fall and late summer in Pamlico Sound North Carolina, red drum consumed mostly blue crab Callinectes sapidus while in South Carolina Atlantic menhaden *Brevoortia tyrannus* and other decapods were the main previtems (Peacock et al. 2014). Juvenile diets in the New River, North Carolina exhibited seasonal patterns in diet composition, with crustaceans dominating the diet for summer and early fall, with a shift to piscivory in the winter (Facendola & Scharf 2012). In Mississippi Sound, penaeid shrimp dominated the diet of juvenile red drum during the fall, with blue crab appearing more often during the spring and summer (Overstreet & Heard 1978).

Discussion

General Trends

The presence of mysids, amphipods, copepods, or polychaetes in the diet was characteristic of juvenile and sub-adult red drum associated with shallow nursery areas. Mysids remained important prey for red drum up to 80mm, while copepods were mostly limited to those less than 20mm. Shrimp were of decreasing importance with size, while there was a positive relationship between size and

feeding on crabs. In Tampa Bay, the diet differences between Llansó et al (1998) and Peters & McMichael (1987) for juvenile and sub-adult red drum are likely because of different sampling durations (Llansó et al August-May, Peters & McMichael September-November) affecting prey assemblages within the area. Larger red drum in South Carolina did not have large amounts of crab in their diet (Peacock et al. 2014), but Wenner et al (1990) found crabs to be a major component of the diet of red drum from 170mm to fish larger than 530mm. Smaller adults examined by Wenner et al (1990) had more crabs in the diet than individuals greater than 530mm, so there appeared to be a negative relationship with crab appearing in the diet as the fish became larger. As red drum studied by Peacock et al (2014) were even larger (over 750mm), this trend may have continued, explaining the decreased number of crabs in these larger individuals.

ONTOGENETIC SHIFTS

Feeding ecology did not appear to differ significantly between juveniles and sub-adults in most studies. The main prey types were very similar between these younger fish, likely reflecting the available prey assemblage within different habitat types and between coasts. Red drum collected by Peters & McMichael (1987), Bass & Avault (1975), and Llansó et al. (1998) were all juveniles and subadults in nursery habitat areas in Tampa Bay, Florida or Louisiana salt marsh nursery areas. As these fish were collected in similar habitats, the diet should reflect this regardless of size-class because of the similarity of prey assemblages between study areas. Bass & Avault's (1975) identified fish prey as a major diet component for juveniles while other studies on juveniles and sub-adults found mostly invertebrate prey. There was a clearer difference for the adult diet of red drum on both coasts: as red drum move out of nursery areas to join to spawning population and inhabit coastal waters there is an increase in piscivory and feeding on decapod crustaceans. This can likely be attributed to differences in available prey assemblages as young adults leave nursery areas for open water or selectivity towards larger prey.

SEASONALITY & MIGRATIONS

Several studies (Boothby & Avault 1971, Overstreet & Heard 1978, Scharf & Schlicht 2000b, Facendola & Scharf 2012) included seasonality in their sampling design, which identified the trends of larger amounts of shrimp during the fall or fish present in the diet during the spring for red drum. Overstreet & Heard (1978) also found that blue crab became more important prey in the summer. The most unifying pattern between studies is the increase in importance of fish prey during winter months. This pattern was attributed to differences in the relative abundance of major forage species and likely did not reflect selective feeding behavior of the adults by the researchers (Boothby & Avault 1971, Overstreet & Heard 1978, Scharf & Schlicht 2000b). Shrimp are more abundant in Gulf of Mexico during the fall, while teleosts are more abundant there in the spring (Overstreet & Heard 1978, Scharf & Schlicht 2000a). In North Carolina and South Carolina, adult red drum experience similar coastal marine habitat and prey assemblages for most of the year (Wenner et al. 1990, ASMFC 2002, NCDMF 2008, Paramore 2011). However, South Carolina adults remain i to spawn during the sampling season in the fall while North Carolina individuals enter Pamlico Sound to spawn during the same time period (Wenner et al. 1990, Paramore 2011). This difference in prey assemblages in the spawning habitat area (coinciding with the sampling season) is likely the cause of diet differences in the adults between North Carolina and South Carolina (Peacock et al. 2014).

Methodological Considerations

Resolution is an important factor when identifying differences in diet structure between groups. While some error is inherent when examining diets, such as mastication affecting prey species identification and differences in the taxonomic levels reported for prey, pooling using compound and standardized indices decreases resolution even further (Baker et al. 2014). Differences in resolution of the taxonomic level that prey species were identified to dictated larger groupings when data was compiled. The predator size class divisions among studies also may have also affected groupings for the pooled study. Pooling results from percent frequency of occurrence into larger groupings has the

potential to overinflate the importance of that group if those prey are not found exclusively in separate stomachs (MacDonald & Green 1983). Pooling metrics such as percent volume and percent frequency of occurrence can also down-weight very abundant prey that did not represent a large portion of the diet by volume, but less abundant prey items that were larger are down-weighted as well. Percent frequency of occurrence is a popular diet metric (70% of sources for this study), but presents different issues for pooling diet data: first, members of larger taxonomic groupings that occur in the same stomach can be over-represented. Secondly, a frequency of occurrence measure does not usually sum to 100%, which necessitates standardizing values to 100% for direct comparisons/pooling with percent by number and weight. While there are limitations of resolution and with the accuracy of pooled metrics, pooling these indices is an effective method for identifying large scale patterns in the diet of a predator like the red drum. Also, diet studies for Gulf Coast red drum are dated (Table 2), and as such a validation of the reported findings with current conditions would strengthen any applications of the synthesized diet.

Applications

Information on the feeding ecology and subsequent predatory effects of different size-classes of red drum on the Atlantic and Gulf Coasts described by this study will be valuable for use in ecosystem based fisheries management strategies. Predator-prey relationships are an important facet of these new strategies (Whipple et al. 2000), especially when applied to prey species population models. The large scale of the synthesized diets of red drum allows for more holistic management strategies to be implemented quickly and easily based off of general findings. Temporal variation in the diet of red drum requires further study. Preliminary findings indicated that seasonal prey availability was a large factor in determining diet composition. Habitat and prey assemblage requirements for juveniles and sub-adults are very similar, dictated by their residence in nursery areas. Future population models and management strategies should account for the ontogenetic shift in the diet of red drum leaving nursery

areas to join the spawning population offshore, as it reflects exploitation of new prey assemblages. Diet studies on red drum from the Gulf Coast are dated (Figure 7) and an updated stock assessment is in progress. Validation of these older studies could further increase the accuracy and effectiveness of these findings for future management.

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List of Figures and Tables

Figures

Figure 1 % Standardized Diet Composition of Juvenile Red Drum

Stacked bar graph of pooled percent standardized diet composition (SDC) for juvenile red drum. Standardized diet composition was calculated from pooled diet data for prey categories from previously published diet studies. Samples (studies) are separated by coast of origin (Atlantic or Gulf).

Figure 2 % Standardized Diet Composition of Sub-adult Red Drum

Pooled percent standardized diet composition (SDC) for Sub-adult red drum. Standardized diet composition was calculated from pooled diet data for prey categories from previously published diet studies. Samples (studies) are separated by coast of origin (Atlantic or Gulf).

Figure 3 % Standardized Diet Composition of Adult Red Drum

Pooled percent standardized diet composition for adult red drum. Standardized diet composition was calculated from pooled diet data for prey categories from previously published diet studies. Samples (studies) are separated by coast of origin (Atlantic or Gulf).

Figure 4 Pooled Diet Composition by Coast and Size-class

Pooled standardized diet composition of red drum taken from previously published red drum diet studies. Standardized diet composition was calculated from pooled diet data for prey categories from previously published diet studies. Samples (pooled studies) are separated by coast of origin (Atlantic or Gulf) and size-class (Juvenile, Sub-adult, or Adult).

Figure 5 Pooled Diet Composition by Size-class

Pooled standardized diet composition of red drum taken from previously published red drum diet studies. Standardized diet composition was calculated from pooled diet data for prev categories from previously published diet studies. Samples (pooled studies) are separated by size-class (Juvenile, Sub-adult, or Adult).

Figure 6 Cluster Analysis and Standardized Diet Composition of Diet Studies

Cluster analysis performed on all red drum diet studies used. Studies (samples) are labeled by size-class and coast of sampling. Cluster groupings are based on percent similarity between samples. Points on the cluster diagram correspond to the standardized diet composition presented below each point. Some studies presented diet data for multiple size-classes and were divided for analysis and labeled accordingly.

Figure 7 Timeline of Previous Diet Studies

Timeline of previous red drum diet studies separated by coast and size-classes. Several sources reported diet information on multiple size-classes and were listed accordingly.

Tables

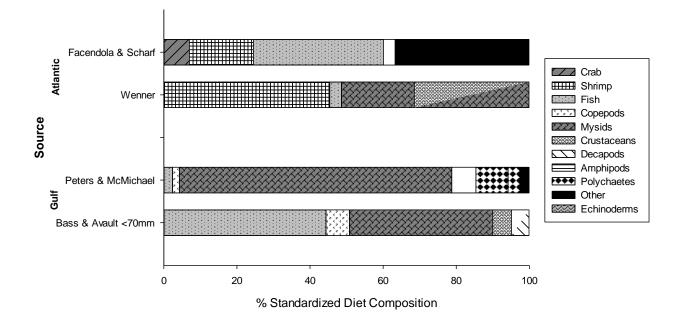
Table 1 Red Drum Diet Studies

Previously published diet information on red drum across their distribution, including the size of fish examined, the sample size, diet metrics used, general findings, and the location of study. Results from these sources were used to calculate the large scale diet profile of red drum in this study.

Figures and Tables

Figures

Figure 1 Standardized Diet Composition of Juvenile Red Drum



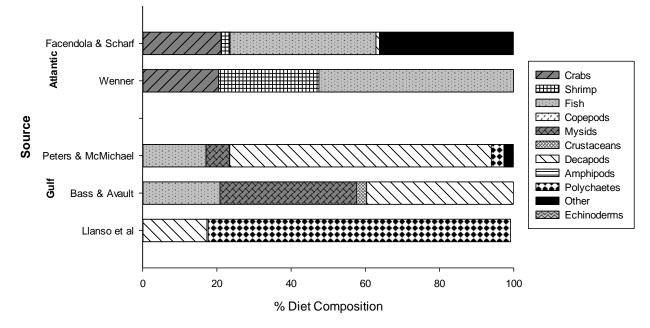
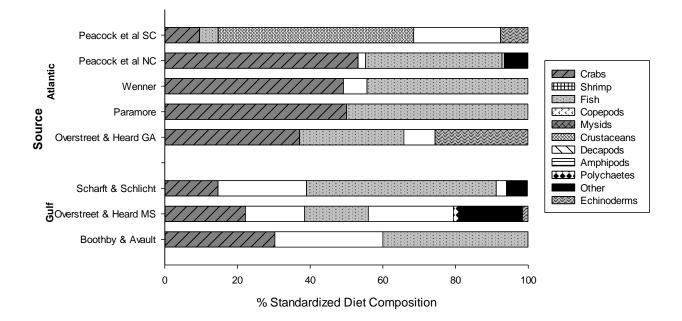
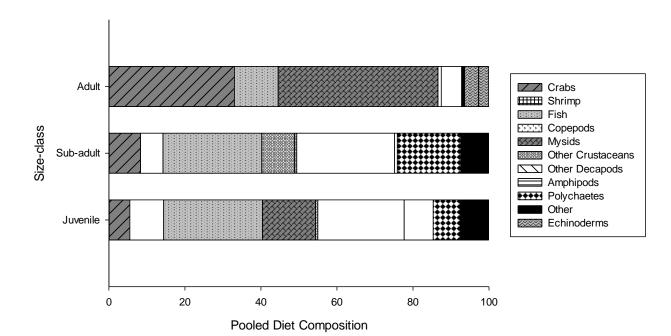


Figure 2 Standardized Diet Composition of Sub-Adult Red Drum









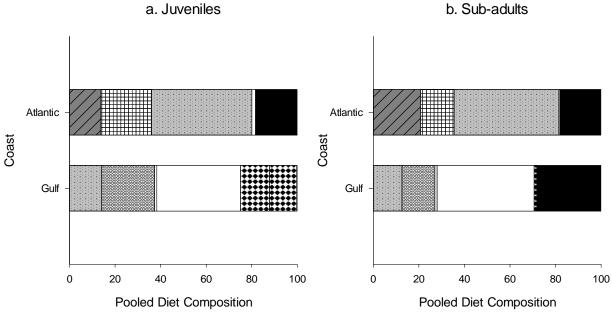
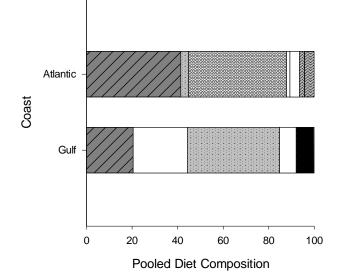
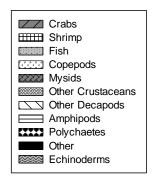
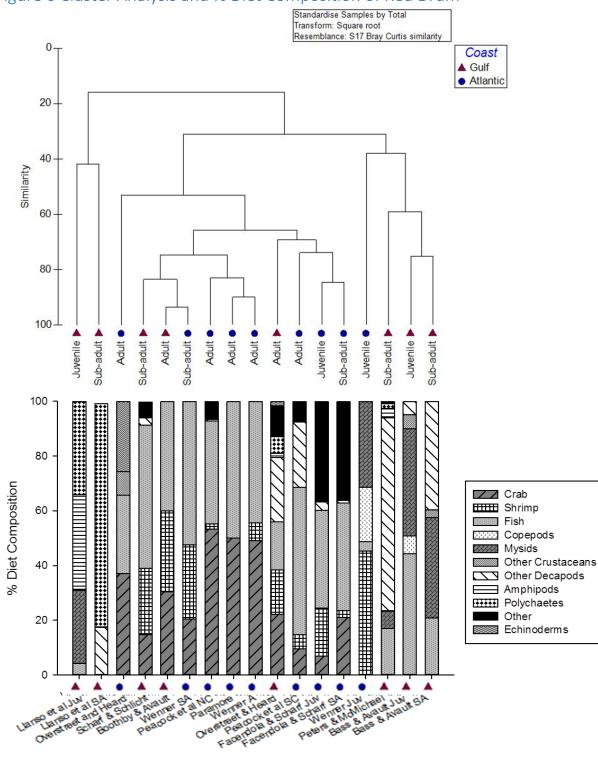


Figure 5 Pooled Diet Composition of Red Drum by Coast and Size –class a. Juveniles b. Sub-adults

c. Adults









Source

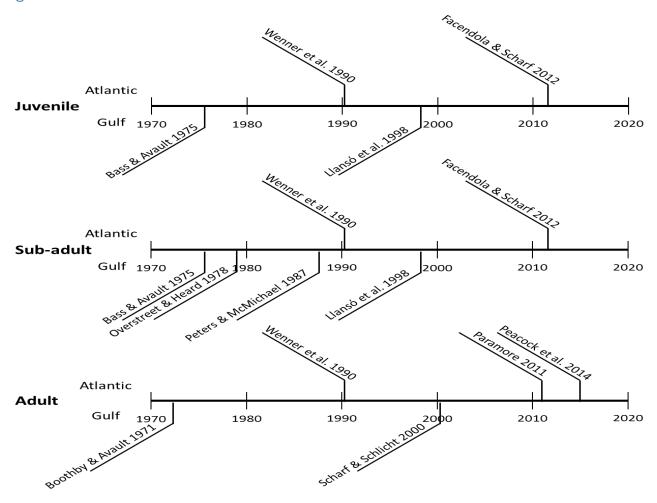


Figure 7 Timeline of Previous Diet Studies

Tables

Table 1: Previously Published Red Drum Diet Studies

Red drum diet studies including locations, methods, summarized results, and size ranges for each project. For percentage metric methods, %V is volume, %FO is frequency of occurrence, %N is number, %W is weight, %DW is dry weight, and IRI is an index of relative importance. Season indicates when the red drum where collected, N/A represents a study where season was not indicated or used for analysis. Primary prey are the major prey found in the diet by each study.

							%	
Source	Year	Location	Method	Size Range	N	Season	Empty	Primary Prey
						Year-round,		
Bass and Avault Boothby and	1975	LA	%F, %V	8-183mm 250-	568	N/A	5.1	Decapods, fish, benthic invertebrates
Avault	1971	Southeast LA	%F IRI, %F, %N,	932mm 19-	349	Year-round Year-round,	28	Crabs, shrimp, fish
Llansó et al Overstreet and	1998	Tampa Bay, FL Mississippi Sound,	DW	590mm 190-	263 107 (22	N/A	2	Decapods, crustaceans, fish
Heard Peters and	1978	MS	%FO	1020mm 1.6-	adults)	Year-round		Penaeid shrimp, crabs, fish Copepods, mysids, crabs, finfish,
McMichael	1987	Tampa Bay, FL	%N, %V %FO, %N,	300mm 350-	863	N/A	2.8	decapods
Scharf and Schlicht	2000	Galveston Bay, TX	%W	750mm 10-	598	Fall, Spring	30.2	Decapods, teleosts
Wenner	1990	SC	%W, %N	>530mm	540	N/A	34	Fish, crustaceans
Paramore Facendola and	2011	Pamlico Sound, NC	%N	Adults 113-	41	Fall	46	Blue crab, copepods
Scharf	2012	New River, NC Pamlico Sound,	%FO, %W	731mm	880	May-January		Penaeid shrimp, crabs, fish
Peacock et al	2014	NC; SC	%N, %FO	>750mm	197	Fall		Blue crab, decapods, fish

Ch. 4 Discussion

I. Applications for Research

Complete Diet Characterization

Reporting the missing information on the diet of adult red drum *Sciaenops ocellatus* for the North and South Carolina coasts enhances the understanding of trophic interactions that accompany the adults migrating inshore during spawning season. We have also identified the differences in diet composition between North Carolina and South Carolina red drum. Contributing to full characterization of diet structure is important component for complete understanding and effective management of fisheries from an ecosystem level (Pasquaud et al. 2007). Future assessments can now better account for the predatory effects of adult red drum on the forage species of each state.

Multi-species Management and Models

By identifying the diet structure of adult red drum, forage species can now be managed with input for predation mortality in conjunction with fishing mortality and natural mortality estimates. As of the most recent amendment to the Atlantic States Marine Fisheries Commission Interstate Fishery Management Plan for Atlantic menhaden *Brevoortia tyrannus*, the inclusion of predator prey interactions to guide management strategies and harvests towards sustainability was a stated goal for the fishery (ASMFC 2012).

The large scale spatiotemporal patterns in the diet of red drum described by synthesizing previously published research into a pooled diet composition are valuable for use in modelling of both predator-prey interactions and population dynamics (Whipple et al. 2000). These general results can also be applied towards ecosystem based and multi-species fisheries management strategies even though many trophic webs are not fully characterized (Brodziak & Link 2002, Link 2002, Fogarty 2014).

Scenarios, Uses, and Specific Needs

Modelling efforts are concerned with potential changes in predator or prey populations in the future, as well as anthropogenic and environmental effects on those populations and the ecosystem as a whole. However, many diet studies do not report data in a format that can be input in ECOPATH or other ecosystem models (%FO, %N). Biomass data is the primary format used in these models. However, in the absence of this, logistic regressions can be used to calculate probabilities a given prey item will be consumed/appear in a predator's stomach and estimates of vulnerability for predation/consumption models.

Large scale scenarios for the application of this data includes the use of red drum as an indicator species, examining the diet composition for changes that may reflect prey species abundance (blue crab and Atlantic menhaden for example). Top down effects of changes in red drum populations and changes in commercial fishing effort and regulations can be applied as well. This is especially important as more and more regulations dictate population structure in attempts to control fishing effects on stocks. By identifying ontogenetic shifts in the age structure of red drum, these life stanzas can be parameterized for increased accuracy modelling. There is also the potential for long term effects of slot-size management to change the overall size and age structure of the red drum population, and in turn cause increased mortality for prey species. In the future red drum populations may even need to be controlled to allow for continued harvest of prey species in commercial fisheries.

II. Validation, Limitations, and Future Research

North and South Carolina Diets

The diet composition of adult red drum examined did reflect the results of previous studies. The importance of blue crab *Callinectes sapidus* and other brachyurans to the adult diet was also seen in Paramore (2011), Wenner et al. (1990), Scharf & Schlight (2000) and Overstreet & Heard (1982). For Wenner et al. (1990), blue crab was a much larger contributor to the diet in South Carolina than in our findings, however there was a negative relationship between size and blue crab appearing in the diet.

As the adults in that study were smaller (>530mm vs >750mm) that trend may have continued with the larger adults examined in our study. Wenner et al. (1990) also identified shrimp as common prey. The large component of fish prey was supported by other adult diet studies as well (Boothby & Avault 1971, Overstreet & Heard 1982, Wenner et al. 1990, Scharf & Schlicht 2000, Bacheler, Paramore, Buckel, et al. 2009) from both the Atlantic and Gulf Coasts. Deehr et al. (2014) calculated an average effective trophic level (ETL) of 3.74 for Core Sound, North Carolina red drum across all seasons, which supports the 3.65 and 3.42 ETLs calculated for North Carolina and South Carolina red drum, respectively.

There were several limitations in the characterization and comparison of diets between North Carolina and South Carolina red drum. Firstly, the study was limited by the seasons that samples were collected in, as collecting adults when they congregate for spawning is much more efficient. This eliminates any examination of seasonal patterns in adult diets in either state. As these adults inhabit coastal waters for most of the year unless migrating for spawning aggregations (Wenner et al. 1990, Bacheler, Paramore, Burdick, et al. 2009), the habitat and diet may be more similar between states during the rest of the year. In conjunction with this, all sampled adults were spawning which may have impacted other behaviors such as active foraging vs. opportunistic feeding and position in the water column. For analysis by ETL, while the calculated values were supported by Deehr et al. (2014), many assumptions and approximations were made to account for prey types that were not included in the same ECOPATH of Core Sound. These "missing" prey types were especially common in South Carolina diets, as Core Sound and Pamlico Sound are more similar. This may have impacted our findings and indicated a difference in trophic levels between states when actual ETL values for those prey may differ significantly. There was also a baseline error in the ECOPATH model used where detritus may have an ETL of greater than 1 because of the microorganisms that reside in/on such material. This may have decreased the calculated ETL of Atlantic menhaden, and subsequently the overall ETL of each state. If this was the case, then the error magnified by the large contribution of Atlantic menhaden in South

Carolina diets may drive the slight difference in ETL between states instead of the actual prey consumed (Deehr et al. 2014).

Synthesis

Synthesized diet composition inherently is not likely to be validated by another study on the same species, but the method has been used to characterize the diets of other predators (Cortes 1999, Walter et al. 2003, Ebert & Bizzarro 2007). While the applications of such large scale pooled diet composition are numerous, there are inherent shortcomings from the assumptions made when compiling previously published diet data. Because the originally presented diet metrics are generally redundant (MacDonald & Green 1983), pooling of diet metrics does not usually over-inflate or downweight prey types (Cortes 1999). Pooling diet data still reflects the findings of the original study, but resolution is lost with larger groupings that are needed for standardizing prey types and percent composition, especially in diet studies where prey were identified to the species level (Cortes 1999). My findings should reflect the overall diet proportionally, even though resolution is decreased. Detecting statistically significant differences in the diet of red drum between states and size classes is more difficult with a study such as this because of the decreased resolution and categorization of prey species. Despite this, general trends in spatial and life-stage diet differences can be identified, as well as major prey contributors.

Effective Trophic Level Analysis

Diet analysis by ETL is not limited by differences in prey assemblages, seasonality, habitat type, etc., and as such is one of the only ways to directly compare trophic relationships numerically (Ebert & Bizzarro 2007). Such comparisons are not even limited by the species of the predator, and can aid in niche/guild determination and food web description (Christian & Luczkovich 1999, Deehr et al. 2014). This method is limited by information on the trophic levels of prey species, however, unless it is possible for researchers to sample and determine ETLs for the prey assemblages of sample areas. Our findings

indicated slight differences in trophic level between states, but trophic levels calculated for both North Carolina and South Carolina red drum were close to the original ETL reported by Deehr et al. (2014). As the ETLs for some prey species had to be estimated (mostly South Carolina prey species), application of an ECOPATH model of coastal South Carolina would improve the accuracy of these findings.

Future Research

Further examination of adult red drum diets should attempt to compare the diet composition directly between North and South Carolina when all of the fish are in a coastal ocean habitat. Any diet differences could then be attributed to either prey selectivity or assemblage differences and validated by observations or faunal sampling of the areas. However, I expect the diet between states while red drum are offshore to be more similar. The accuracy of an ETL analysis could be improved by including all observed prey in an ECOPATH model of the system instead of relying on approximations for assigned ETLs. Previously published studies included little information on prey selectivity by red drum of any life stage, with most studies attributing seasonal and locational differences in diet to differing prey assemblages. More information such as prey selectivity indices would be useful in determining if any prey are preferred forage species of red drum or if feeding is abundance/opportunity driven. Also, completion of validating diet studies for Gulf Coast red drum would improve understanding of the system there, as diet research there is dated (Figure 1).

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Figures

Figure 1 Timeline of Previous Diet Studies

Timeline of previous red drum diet studies separated by coast and size-classes. Several sources reported diet information on multiple sizeclasses and were listed accordingly.

