

ABSTRACT

SEARCY, STEVEN PHILIP: Is Growth a Reliable Indicator of Essential Fish Habitat? (Under the direction of David B. Eggleston).

Estuarine habitats serve as important nurseries for many species of juvenile fishes and invertebrates. Due to concerns about declining fishery stocks and habitat degradation, it is critical that the value of different habitats be evaluated, so that areas that are most important can be prioritized for habitat conservation and restoration. This dissertation used Atlantic croaker (*Micropogonias undulatus*) as a model species to quantitatively examine patterns of early juvenile nursery habitat use, factors influencing growth and mortality, and to test the widely held assumption that 'growth is a valid indicator of habitat quality'. A unique aspect of this study was consideration of how growth and survival of juvenile Atlantic croaker were influenced by the joint effects of individual (larval and juvenile growth) and cohort (density-dependent) characteristics, as well as biotic and abiotic characteristics of the nursery. Late-larval and early juvenile Atlantic croaker were collected weekly, using a 1-m beam trawl in river, upper-estuary, and creek habitats of two estuaries (White Oak River estuary and Newport River estuary, North Carolina, USA), sampled during two seasons (fall and spring) of two recruitment years (2001-2002 and 2002-2003). Subsequent analysis of otolith microstructure was used to provide estimates of growth rates, population age structure, and mortality. Juvenile Atlantic croaker were most abundant in oligohaline river nursery areas (primary nursery area), with the upper-estuary serving as an important 'refuge' habitat following periods of high freshwater outflow that forced fish down-estuary. In addition to management implications (i.e., time and area closures of shrimp trawling), such flood events have important implications for growth-based assessment of habitat quality: A positive

covariance between larval and juvenile growth was found only after periods in which croaker were displaced from river nursery areas, when food was apparently in short supply. Atlantic croaker cohorts from both estuaries also exhibited evidence for selective mortality favoring survival of individuals that were faster growing as larvae and early juveniles, as well as evidence for density-dependent growth (i.e., slower average cohort growth rates at higher conspecific density). The results of this study indicate that growth is not a robust indicator of habitat quality. Unless factors such as previous environmental history, density-dependence, and selective mortality are accounted for, growth-based assessment of habitat quality may reach incorrect conclusions regarding the value of different habitats.

Is Growth a Reliable Indicator of Essential Fish Habitat?

by

Steven Philip Searcy

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for Degree of
Doctor of Philosophy

MARINE, EARTH AND ATMOSPHERIC SCIENCES

Raleigh

2005

APPROVED BY:

Dr. David B. Eggleston
Chair of Advisory Committee

Dr. Jonathon A. Hare

Dr. James A. Rice

Dr. John M. Miller

DEDICATION

This dissertation is dedicated to the memory of family members whose lives have ended during my academic career and those whose lives have just begun.

BIOGRAPHY

Steven Searcy was born on December 21, 1972 in Northampton, Massachusetts. Steven received a Bachelor of Science degree from the University of New Hampshire (UNH) in 1994, with a major in Biology (Marine option) and a minor in Anthropology. At UNH, he volunteered for three years in the lab of Dr. Larry Harris, which culminated in his senior thesis project examining ‘community level impacts of foraging by herbivorous fishes’ at the Hawaii Institute of Marine Biology. After graduation from UNH, he worked for one year as an intern at Scripps Institution of Oceanography under the direction of Drs. Paul Dayton, Mia Tegner, and Larry Basch investigating settlement dynamics of sea urchins in the Point Loma kelp bed, San Diego, CA. In 1996, Steven returned to the east coast and entered the graduate program at the Marine Sciences Research Center (University at Stony Brook). With Dr. Su Sponaugle as an advisor, he received a Master’s degree investigating selection on early life history traits of two common coral reef fishes in Barbados, WI. Not yet weary of the academic life, in 1999 he enrolled in the Ph.D. program at North Carolina State University under the direction of Dr. David Eggleston. During the course of completing his dissertation in coastal North Carolina he learned: (1) estuaries are muddy, (2) all boats breakdown, and (3) that y’all can be used as a singular or plural pronoun.

I hope y’all enjoy reading this dissertation.

ACKNOWLEDGEMENTS

Financial support for the research described here was provided by National Sea Grant funding (F/H-02 to D. Eggleston, J. Hare, and S. Searcy), the National Science Foundation (OCE 0221099 to D. Eggleston, R. Forward, and T. Hopkins), as well as Sigma-Xi Grant-in-aid of Research, PADI-AWARE foundation, Budweiser Conservation Scholarship (to S. Searcy). The completion of labor-intensive field and laboratory work would not have been possible without the assistance or advice of the following individuals: L. Avens, J. Breeden, J. Buckel, K. Craig, B. Deegan, C. Huggett, S. Kemp, B. Laban, M. Lewis, P. McDougall, H. Sandstrom, C. Taylor, H. Walsh, M. Wuenschel.

In particular, I would like to thank my advisor, Dave Eggleston, for his continued guidance and support in this research project, as well as for providing travel and research opportunities to the Bahamas and Florida Keys. I also thank Jon Hare and the NOAA Beaufort lab for initially providing laboratory space, supplies, and advice to begin this (and a variety of other) research projects. I would also like to thank family members who have provided emotional and financial support throughout my entire academic career. Finally, special thanks to my wife, Nathalie Reyns, who has helped with all aspects of this dissertation.

TABLE OF CONTENTS

LIST OF TABLES.....	Page viii
LIST OF FIGURES.....	x
INRODUCTION	1
Literature Cited.....	6
 CHAPTER 1: Patterns of estuarine nursery habitat use for juvenile Atlantic croaker, <i>Micropogonias undulatus</i>	 10
Abstract.....	11
Introduction.....	12
Materials and Methods.....	14
Results and Discussion.....	17
Conclusions.....	20
Literature Cited.....	23
Figure Legends.....	33
 CHAPTER 2: Estuarine environment influences the relationship between larval and juvenile growth for Atlantic croaker, <i>Micropogonias undulatus</i>	 46
Abstract.....	47
Introduction.....	48
Materials and Methods.....	49
Results.....	56
Discussion.....	58
Literature Cited.....	62
Figure Legends.....	67
 CHAPTER 3: Is growth an accurate indicator of juvenile habitat quality?.....	 72
Abstract.....	73
Introduction.....	74
Materials and Methods.....	77
Results.....	84
Discussion.....	86
Conclusions.....	91
Literature Cited.....	94
Figure Legends.....	110

TABLE OF CONTENTS (continued)

	Page
CHAPTER 4: Estuarine-specific early juvenile survival and the importance of post-settlement density-dependent mortality.....	116
Abstract.....	117
Introduction.....	118
Materials and Methods.....	121
Results.....	129
Discussion.....	132
Conclusions.....	137
Literature Cited.....	139
Figure Legends.....	154
 CONCLUSION.....	 162
Literature Cited.....	169
 APPENDICES.....	 172
1. Atlantic croaker, <i>Micropogonias undulatus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the Newport River estuary, NC.....	173
2. Spot, <i>Leiostomus xanthurus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the Newport River estuary, NC.....	175
3. Pinfish, <i>Lagodon rhomboides</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the Newport River estuary, NC.....	177
4. Southern flounder, <i>Paralichthys lethostigma</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the Newport River estuary, NC.....	179
5. Summer flounder, <i>Paralichthys dentatus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the Newport River estuary, NC.....	181
6. Atlantic croaker, <i>Micropogonias undulatus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the White Oak River estuary, NC.....	183
7. Spot, <i>Leiostomus xanthurus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the White Oak River estuary, NC....	185

8. Pinfish, <i>Lagodon rhomboides</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the White Oak River estuary, NC.....	187
9. Southern flounder, <i>Paralichthys lethostigma</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the White Oak River estuary, NC.....	189
10. Summer flounder, <i>Paralichthys dentatus</i> . Density and standard length measures with associated standard error from 1-m beam trawl collections in the White Oak River estuary, NC.....	191

LIST OF TABLES

CHAPTER 1	Page
1. Results of two-way ANOVA for early-juvenile Atlantic croaker abundance in the Newport River and White Oak River estuaries, North Carolina, USA.....	31
2. Results of two-way ANOVA for juvenile Atlantic croaker abundance in the Newport River and White Oak River estuaries, North Carolina, USA.....	32
CHAPTER 2	
1. Relationship between cohort specific larval and subsequent juvenile growth using Pearson correlation coefficients for fish collected in the White Oak and Newport River estuaries, North Carolina, USA.....	66
CHAPTER 3	
1. Selective mortality of larval otolith growth for Atlantic croaker cohorts within the White Oak River and Newport River estuaries, North Carolina, USA.....	103
2. Selective mortality of juvenile otolith growth for Atlantic croaker cohorts within the White Oak River and Newport River estuaries, North Carolina, USA.....	104
3. Somatic growth estimate for early juvenile Atlantic croaker collected in the White Oak and Newport River estuaries, North Carolina, USA.....	105
4. Repeated measures MANOVA results for between-estuary comparisons of 'initial' and 'survivor' group larval otolith growth.....	106
5. Repeated measures MANOVA results for between-estuary comparisons of 'initial' and 'survivor group' juvenile otolith growth.....	107
6. Factors selected as significant ($P < 0.10$) for multiple regression analysis of juvenile croaker otolith growth with data from the White Oak and Newport River estuaries pooled.....	108
7. Regression parameters and squared partial correlation coefficients for multiple regression analysis of residual juvenile croaker otolith growth within the White Oak and Newport River estuaries, North Carolina, USA.....	109

LIST OF TABLES (continued)

CHAPTER 4	Page
1. Estimates of instantaneous mortality and Per capita mortality for weekly hatch-date cohorts of Atlantic croaker collected in the Newport and White Oak River estuaries, North Carolina, USA.....	150
2. Results of one-way ANOVA for the White Oak River estuary examining differences in instantaneous mortality, peak and final Atlantic croaker abundance between year and season.....	151
3. Regression parameters and squared partial correlation coefficients for instantaneous mortality of weekly hatch-date Atlantic croaker cohorts as the dependent variable, and log (x+1) transformed flounder and croaker abundance, and log transformed salinity as independent variables.....	152
4. Regression parameters and squared partial correlation coefficients for final abundance of weekly hatch-date Atlantic croaker cohorts as the dependent variable, and log (x+1) transformed flounder and peak croaker abundance, and log transformed salinity as independent variables.....	153

LIST OF FIGURES

CHAPTER 1	Page
1. Location of the White Oak and Newport River estuaries, North Carolina, USA.....	36
2. Total abundance of early-juvenile Atlantic croaker in river and creek stations of the White Oak and Newport River estuaries, North Carolina, USA. during Spring 2002, Fall 2002, and Spring 2003 collection seasons.....	37
3. Total abundance of juvenile Atlantic croaker (>13 mm standard length) in river and creek stations of the White Oak and Newport River, North Carolina, USA. estuaries during Spring 2002, Fall 2002, and Spring 2003 collection seasons.....	38
4. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker during Spring 2002 in the White Oak River estuary, North Carolina, USA.....	39
5. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker during Fall 2002 in the White Oak River estuary, North Carolina, USA.....	40
6. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker Spring 2003 in the White Oak River estuary, North Carolina, USA.....	41
7. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker during Spring 2002 in the Newport River estuary, North Carolina, USA.....	42
8. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker during Fall 2002 in the Newport River estuary, North Carolina, USA.....	43
9. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker during Fall 2002 in the Newport River estuary, North Carolina, USA.....	44
10. Relationship between salinity and abundance of juvenile Atlantic croaker in the White Oak and Newport River estuaries, North Carolina, USA. for all collection dates.....	45

LIST OF FIGURES (continued)

CHAPTER 2	Page
1. Location of the White Oak River and Newport River estuaries, North Carolina, USA.....	68
2. Relationship between larval otolith growth and (A). juvenile somatic growth (B). juvenile otolith growth.....	69
3. Relationship between salinity and significant correlations between larval and juvenile growth for weekly cohorts of fish collected in the White Oak and Newport River estuaries, North Carolina, USA.....	70
4. Regression between larval growth inertia correlation coefficient and (A). proportion of empty stomachs (B). residual of condition (C). change in salinity.....	71
CHAPTER 3	
1. Location of White Oak and Newport River estuaries, North Carolina, USA.....	112
2. Relationship between (A). nearshore water temperature and average natural log transformed larval Atlantic croaker otolith growth (B) estuarine water temperature and average natural log transformed juvenile Atlantic croaker juvenile otolith growth.....	113
3. Comparison of (A) larval Atlantic croaker otolith growth between initial groups and survivor groups within the White Oak and Newport River estuaries, North Carolina, USA (B) between estuary comparisons of initial and survivor groups.....	114
4. Relationship between dependent and independent variables used in multiple regression analyses.....	115

LIST OF FIGURES (continued)

CHAPTER 4	Page
1. Location of White Oak River and Newport River estuaries, North Carolina, USA.....	156
2. Comparison of instantaneous mortality for early juvenile Atlantic croaker in the Newport and White Oak River estuaries.....	157
3. Seasonal average peak Atlantic croaker abundance and final Atlantic croaker abundance.....	158
4. Relationship between instantaneous mortality and three independent variables used in multiple regression analyses.....	159
5. Relationship between per capita mortality rate and total juvenile Atlantic croaker abundance in the White Oak and Newport River estuaries.....	160
6. Relationship between final and peak Atlantic croaker abundance in the White Oak River and Newport River estuaries.....	161

INTRODUCTION

Worldwide, coastal development and degradation threaten nearshore and estuarine environments that are vital to the early growth and survival of many coastal fishery species (NRC 1992, Hinrichsen 1998). As a result, it is widely recognized that we need to accurately evaluate the quality of different juvenile nursery habitats so that we can document the extent to which anthropogenic factors affect habitat quality, and if necessary, specific areas can be prioritized for protection (Able 1999, Beck et al. 2001, Necaise et al. 2005). Habitat quality, however, is difficult to classify because linkages between fish and their habitats are often complex and dynamic (Able 1999). In an effort to help prioritize high quality ‘Essential Fish Habitats’ (EFH) for protection the U.S. National Marine Fisheries Service (NMFS) established four criteria which can be used to identify EFH (NMFS 1997): 1) presence-absence of the target species or assemblage, 2) distribution and abundance, 3) habitat-specific growth, reproduction and survival, and 4) per capita production of juveniles. Although these EFH criteria provide an important first objective step in prioritizing important habitats for conservation, ambiguity in the relationship of the four EFH criteria hinders the effectiveness of EFH designation as a tool for conservation and management. This dissertation addresses ambiguity in EFH levels 2 and 3 by testing the widely held assumption that ‘growth is a valid indicator of habitat quality’, and by testing specific hypotheses concerning patterns of early juvenile Atlantic croaker (*Micropogonias undulatus*) nursery habitat use, and habitat specific demographic rates (growth and mortality). A unique contribution of this dissertation is consideration of how growth and mortality are influenced by the joint effects of fish cohorts (density dependence) and individual characteristics (selective mortality).

Chapter 1 (EFH level 2)

The objective of this chapter was to improve our understanding of Atlantic croaker, *Micropogonias undulatus*, nursery habitat use by examining patterns of distribution and abundance over a range of different environmental conditions within and between two North Carolina estuaries. Level two of the NMFS-EFH criteria focuses on distribution and abundance patterns. Previous studies have documented that Atlantic croaker utilize deep, upper-estuary oligohaline channels as nursery habitats (Weinstein 1979, Ross 2003); however, the role of shallow upper-estuary tidal creeks has not been simultaneously investigated. This chapter addresses the hypothesis that deep oligohaline river channels will have consistently higher densities of early juvenile (< 13 mm standard length) and juveniles (>13 mm standard length) croaker than upper-estuary tidal creek nurseries, irrespective of time. Furthermore, qualitative analysis of weekly field collections of Atlantic croaker were used to describe how croaker nursery habitat changed in response to fluctuating environmental conditions. Ultimately, knowledge of how a species' nursery habitat use changes with environmental conditions is a prerequisite to employing effective habitat-based management strategies (i.e., time and area closures, Rooker et al. 2004) that may be critical to ensuring successful growth and survival (Able et al. 1999).

Chapters 2 and 3 (EFH Level 3)

Level three of the NMFS-EFH criteria is based on indices of growth, reproduction, or survival that are often used to assess habitat quality. A common assumption throughout the fisheries, habitat, and stock enhancement literature is that growth is a valid indicator of habitat quality. It is assumed that larger, faster growing fish are healthier and have experienced more

favorable abiotic and biotic conditions than smaller, slower growing fish (Guindon and Miller 1995, Baltz et al. 1998, Able et al. 1999, Meng et al. 2000, Phelan et al. 2000, Stunz et al. 2002, Necaise et al. 2005). However, prior to use of growth as an index of habitat quality, it is important to recognize that growth rates may be affected by alternative mechanisms not typically associated with habitat quality, such as selective mortality of slower (or faster) growing individuals, previous growth history, and negative density dependence (i.e., lower growth at higher conspecific densities). Unless alternative mechanisms that can influence growth are addressed, growth based assessment of habitat quality may prioritize habitats as EFH for the wrong reasons.

Chapter 4 (EFH Level 3)

Investigating early juvenile mortality may be particularly important in identifying factors that contribute to the nursery value of different habitats (i.e., how many individuals will contribute to the adult stock; Beck et al. 2001). Early juvenile mortality may result from abiotic (i.e., temperature, salinity, and dissolved oxygen: Breitburg 1992, Rutherford and Houde 1995, Gillanders and Kingsford 2002, Miller et al. 2003), and biotic conditions (i.e., food availability and predator abundance: Phillips et al. 1995, Tupper and Boutilier 1995, Rilling and Houde 1999, Rooker et al. 1999), the importance of which can be mediated by cohort (i.e., density-dependent mortality, Hixon and Carr 1997, Anderson 2001, Webster 2003), and individual characteristics of fish (selective mortality acting on phenotypic traits, Campana 1996, Ottersen and Loeng 2000). Although abiotic, biotic, cohort, and individual characteristics can all influence early recruitment success, the relative importance of these factors has not been jointly considered. Such information is critical to making informed decisions regarding habitat

conservation, identifying feasible sites for introduction of hatchery-reared organisms for stock enhancement purposes, and understanding factors influencing variable recruitment success (Grimes 1998, Beck et al. 2001).

Significance

Increased understanding of factors that influence growth, survival, and abundance of estuarine-dependent juvenile fishes is important to support habitat restoration, conservation (EFH), and fisheries management efforts. This dissertation assesses nursery habitat use of early juvenile Atlantic croaker, *Micropogonias undulatus*, examines factors influencing early recruitment dynamics of estuarine-dependent fishes, and tests the underlying assumptions of the use of growth as an index of habitat quality. It is critical to test the assumption that high growth is a reflection of high habitat quality so that criteria for EFH and site selection for stock enhancement can be refined, if necessary, or so we can proceed with confidence in assuming that high growth reflects “good” habitat. Examination of the relationship between early juvenile mortality with larval supply, larval characteristics, and abiotic and biotic characteristics of the estuarine environment will help us to better understand processes that occur during this critical period. Conclusions regarding the evaluation of habitat quality and early juvenile mortality are likely applicable to other estuarine-dependent fishes. Ultimately, better information on How, When, and Why estuarine-dependent fishes utilize nursery environments is a central component of fishery and habitat management plans, and will allow better expenditures of limited money, time, and effort.

LITERATURE CITED

- Able, K. W. 1999. Measures of juvenile fish habitat quality: Examples from a National Estuarine Research Reserve. Pages 134-147 in L. R. Benaka, editor. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Bethesda, Maryland.
- Able, K. W., J. P. Manderson, and A. L. Studholme. 1999. Habitat quality for shallow water fishes in an urban estuary: the effects of man-made structures on growth. Marine Ecology Progress Series **187**:227-235.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology **82**:245-257.
- Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. Environmental biology of fishes **53**:89-103.
- Beck, M. W., K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, M. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience **51**:633-641.
- Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. Ecological monographs **62**:525-546.
- Campana, S. E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Marine Ecology Progress Series **135**:21-26.
- Gillanders, B. M., and M. J. Kingsford. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. Oceanography and Marine Biology **40**:233-309.

- Grimes, C. B. 1998. Marine stock enhancement: sound management or techno-arrogance? *Fisheries* **23**:18-23.
- Guindon, K. Y., and J. M. Miller. 1995. Growth potential of juvenile southern flounder, *Paralichthys lethostigma*, in low salinity nursery areas of Pamlico sound, North Carolina. *Netherlands Journal of Sea Research* **34**:89-100.
- Hinrichsen, D. 1998. Coastal waters of the world: Trends, threats, and strategies. Island Press, Washington D.C.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946-949.
- Meng, L., C. Gray, B. Taplin, and E. Kupcha. 2000. Using winter flounder growth rates to assess habitat quality in Rhode Island's coastal lagoons. *Marine Ecology Progress Series* **201**:287-299.
- Miller, M. J., D. M. Nemerson, and K. W. Able. 2003. Seasonal distribution, abundance, and growth of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay and adjacent marshes. *Fishery Bulletin* **101**:100-115.
- Necaise, A. M. D., S. W. Ross, and J. M. Miller. 2005. Estuarine habitat evaluation measured by growth of juvenile summer flounder *Paralichthys dentatus* in a North Carolina estuary. *Marine Ecology Progress Series* **285**:157-168.
- NMFS. 1997. Magnuson-Stevens Act provisions: essential fish habitat: interim final rule and request for comments. *Federal Register* [Docket 96103033-7238-04; I.D. 120996A]: 66-66559.
- NRC. 1992. Restoration of aquatic ecosystems: Science, technology, and public policy. National Academy Press, Washington, D.C.

- Ottersen, G., and H. Loeng. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. *ICES Journal of Marine Science* **57**:339-348.
- Phelan, B. A., R. Goldberg, A. Bejda, J. Pereira, S. Hagan, P. Clark, A. L. Studholme, A. Calabrese, and K. W. Able. 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. *Journal of Experimental Marine Biology and Ecology* **147**:1-28.
- Phillips, J. M., J. R. Jackson, and R. L. Noble. 1995. Hatching date influence on age-specific diet and growth of age-0 largemouth bass. *Transactions of the American Fisheries Society* **124**:370-379.
- Rilling, G. C., and E. D. Houde. 1999. Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. *Fishery Bulletin* **97**:555-569.
- Rooker, J. R., S. A. Holt, G. J. Holt, and L. A. Fuiman. 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. *Fishery Bulletin* **97**.
- Rooker, J. R., A. M. Landry, B. W. Geary, and J. A. Harper. 2004. Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper. *Estuarine, Coastal and Shelf Science* **59**:653-661.
- Ross, S. W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin* **101**:384-404.

- Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fishery Bulletin **93**:315-332.
- Stunz, G. W., T. J. Minello, and P. S. Levin. 2002. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. Marine Ecology Progress Series **238**:227-236.
- Tupper, M., and R. G. Boutilier. 1995. Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. Journal of Experimental Marine Biology and Ecology **191**:209-222.
- Webster, M. S. 2003. Temporal density dependence and population regulation in a marine fish. Ecology **84**:623-628.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fishery Bulletin **77**:339-357.

CHAPTER 1

Patterns of estuarine nursery habitat use for juvenile Atlantic croaker, *Micropogonias undulatus*

ABSTRACT

The objective of this study was to improve our understanding of juvenile Atlantic croaker, *Micropogonias undulatus*, nursery habitat use by (1) testing the hypothesis that deep river-channels would have consistently higher densities of early-juvenile and juvenile Atlantic croaker than upper-estuary tidal creeks, irrespective of time, and (2) examining how Atlantic croaker nursery habitat use changes with regard to fluctuating environmental conditions. Juvenile Atlantic croaker were collected weekly using a 1-m beam trawl during three collection periods (Spring 2002, Fall 2002, Spring 2003), along a gradient of estuarine habitats (river, upper-estuary, and creek) in two estuaries (the White Oak River and Newport River estuaries, North Carolina, USA). Juvenile Atlantic croaker abundances were consistently higher in river than creek habitats. However, nursery use patterns were dynamic, with Atlantic croaker moving up- and down-estuary in relation to salinity. In particular, following periods of high freshwater runoff, croaker were displaced down-river from 'primary' river nursery areas, to areas in the upper-estuary. Thus, deep river channels are important nursery habitat for early-juvenile croaker, but croaker nursery habitat also encompasses the upper-estuary during flood events. Recognition of the dynamic nature of juvenile Atlantic croaker nursery habitat use is critical to making effective fishery management decisions (e.g., conservation of river habitats, and temporary time closures for upper-estuary shrimp trawling).

INTRODUCTION

The importance of estuaries as juvenile nurseries for many economically and ecologically important fish species has been recognized for nearly a century (reviewed in Beck et al. 2001). Delineating entire estuaries as nurseries, however, does little to identify important functional relationships or interactions between a fish species and habitat characteristics (Minello 1999). Rather, identification of a species' nursery habitat requires measuring distribution and abundance patterns over a range of different habitats and environmental conditions, and in multiple study systems (Goldberg et al. 2002). Due to concerns about habitat destruction and alteration, it is critical to identify patterns of nursery habitat use so that areas essential for growth and survival can be prioritized for conservation (Minello 1999).

Descriptions of nursery habitat use by fish species are typically based on habitat characteristics known to be ecologically meaningful such as vegetation type (i.e., marsh, seagrass, Gray et al. 1998), bottom-structure (i.e., reefs, shellbanks, Rooker et al. 2004), substrate-type (i.e., sand or mud, Burke 1995, Walsh et al. 1999), geomorphology (i.e., creek, river, Rozas and Odum 1987), and hydrology (i.e., depth, temperature, salinity, Miltner et al. 1995, Martino and Able 2003). Such habitat designations, however, fail to incorporate the dynamic nature of many estuarine environments (Peterson 2003). The use of intensive field surveys has shown that distributions of even highly site-attached species may change with temporal variations in abiotic conditions such as anoxia (e.g., Breitburg 1994) and freshwater runoff (e.g., Gillanders and Kingsford 2002).

An alternative approach to the use of intensive field surveys to examine temporal changes in nursery habitat use is to use 'natural tags' (i.e., elemental composition of

otoliths, stable isotope analysis) that integrate chemical environmental signals, thereby making it possible to identify past habitats and environmental conditions that a fish has experienced (reviewed in, Gillanders et al. 2003). For example, otolith trace-element chemistry has been used to show that the ‘nursery role’ (i.e., contribution to adult stock, Beck et al. 2001) of different habitats may vary from year-to-year (Kraus and Secor 2005), and stable isotope analysis has been used to show that patterns of nursery habitat use for some fish species may change through ontogenetic development (Litvin and Weinstein 2004). Identification of such temporal changes in nursery habitat use are a prerequisite to employing effective habitat-based management strategies that may be critical to ensuring successful growth and survival (Able et al. 1999).

The objective of this study was to improve our understanding of Atlantic croaker, *Micropogonias undulatus*, nursery habitat use by examining patterns of distribution and abundance within and between two North Carolina estuaries. Previous studies have documented that Atlantic croaker utilize deep, oligohaline river channels as nursery habitats (Weinstein 1979, Ross 2003); however, the role of shallow upper-estuary tidal creeks and adjacent deep oligohaline river channels has not been investigated simultaneously. Although creeks may be dismissed as important nursery areas due to their small size, the importance of a nursery habitat should be based on its per-unit area contribution to adult stock (*sensu* Minello 1999) rather than its areal coverage (Beck et al. 2001). This study addressed the hypothesis that deep river channels will have consistently higher densities of early-juvenile croaker (< 13 mm standard length) and juvenile croaker (>13 mm standard length) than shallow upper-estuary creeks, irrespective of time. Furthermore, qualitative analysis of weekly field collections was

used to examine how Atlantic croaker nursery habitat change in distribution along a river-to-upper-estuary gradient with regard to change in salinity.

MATERIALS AND METHODS

Atlantic croaker is an economically and ecologically important fish in southeastern United States and Gulf of Mexico estuaries. Along the east coast of the United States, adults spawn on the continental shelf, and following offshore pelagic development, late-stage larvae ingress into estuaries and settle in low salinity nursery areas (Weinstein 1979, Ross 2003). Atlantic croaker is an ideal study species with which to investigate processes that influence early-juvenile distribution and abundance patterns, because juveniles typically remain in nursery areas for the first year of development (Miller and Able 2002), and south of Cape Hatteras, NC, adults have a protracted spawning season which extends from August to May (Hettler and Chester 1990), allowing for tracking of multiple cohorts over a range of different environmental conditions.

Fish sampling and habitat characterization

Juvenile Atlantic croaker distribution and abundance patterns was investigated in two tidal and well-mixed estuaries in southeast North Carolina, USA: the White Oak River and Newport River estuaries (Figure 1, Wilkens and Lewis 1971, Kirby-Smith and Costlow 1989). As croaker larvae typically ingress to NC estuaries at lengths below 13 mm (Warlen 1980, Warlen and Burke 1990), in this study, early-juvenile croaker are defined as individuals that are < 13 mm. and croaker > 13 mm are referred to as juveniles. In both estuaries, Atlantic croaker were collected at stations along the salinity

gradient (upstream to downstream) selected to bracket expected juvenile Atlantic croaker nursery habitat. Stations sampled within each estuary included river (stations # 1-4), upper-estuary (station # 5), and creek (station #6-7) areas (Figure 1). As potential Atlantic croaker nurseries, river and creek habitats differed in many key physical and chemical attributes: river nurseries were larger in area, deeper (~3 m deep compared to creek areas which were ~1 m deep at high tide), and lower in salinity (average spring 2003 salinity at the mouth of river and creek habitats of the White Oak / Newport River estuaries respectively: River = 0.5 / 2.5 ppt; Creek = 4 / 12 ppt).

In the Newport River estuary, collections were made for seven weeks during fall (November-December) and spring (February-April) of two recruitment seasons (2001-2002 and 2002-2003). In the White Oak River estuary, collections were made during spring 2002 and fall-spring 2002-2003. Each station was sampled weekly for abiotic conditions (temperature and salinity, YSI-85), and juvenile demersal fishes using three replicate tows (typically for one minute each) of a 1-m beam trawl (1-mm mesh upper- and side-panels and a 3-mm mesh bottom-panel) deployed from a small boat (~6 m) and covering ~ 60 m. Due to the shallow nature of both estuaries, beam trawl tows were restricted to the last two hours of daytime flood tide and. Trawls were always pulled against prevailing currents and tow speed standardized by gauging speed against emergent features in the water (i.e., crab pot buoys and stakes) or the shoreline. Trawl samples were sorted in the field and all fishes were preserved in 95% ethanol.

Beam trawl capture efficiency is known to vary with both size and species of fish targeted (Kuipers 1975, Kuipers et al. 1992, Rozas and Minello 1997). For example, beam trawl efficiency for juvenile flatfish (40-120 mm) collected in muddy and sand

habitats can range from 52% for juvenile plaice, *Pleuronectes platessa*, 20% for sole (*Solea solea*), and 23 % for dab (*Limanda limanda*) (Rogers and Lockwood 1989). Beam trawl capture success may also vary according to length, with beam trawl efficiencies for juvenile plaice, *Pleuronectes platessa*, reported as 33% for newly-metamorphosed 10 mm juveniles, 57% for juveniles between 50-60 mm, and 46% for 70 mm juveniles (reviewed in Rogers and Lockwood 1989).

Gear efficiency may also vary among habitat types (Kuipers et al. 1992). Although a recent study by Kellison et al. (2003), found no difference in 2-m beam trawl efficiency for summer flounder (30-90 mm TL, *Paralichthys dentatus*) collected between beach and salt marsh habitats near the Newport River, NC; within habitat variation in gear efficiency was sometimes high due to low efficiency in sites harboring subtidal oyster (*Crassostrea virginica*) populations. In the current study, gear efficiency was not corrected for due to the narrow size range of croaker collected (10 – 20 mm), and unstructured, relatively homogeneous mud-bottom in all sampling stations. Thus, gear efficiency was likely constant for all samples collected. The ‘uncorrected’ density estimates ($\pm$ SE) of fish commonly collected are recorded in Appendices 1-10.

Data analysis

Prior to data analyses, all croaker abundance estimates were $\log(x+1)$ transformed to meet assumptions of normality and homogeneity of variance (Sokal and Rohlf 1995). Preliminary analysis suggested that the dynamics of each estuary should be considered independently (i.e., there were significant estuary-factor interactions), therefore, separate two-way analysis of variance (ANOVA) models were calculated for each estuary to compare Atlantic croaker abundance among three collection periods

(spring 2002, fall 2002, spring 2003), two nursery habitats (creek or river), and a 'collection period x nursery habitat' interaction. Since the number of sampling dates varied by collection period (6 in spring 2002, and 7 in fall 2002 and spring 2003), type III sums of squares were used to interpret ANOVA results (Sokal and Rohlf 1995).

Patterns of juvenile Atlantic croaker nursery habitat use within the White Oak River and Newport River estuaries also were described by examining the relationship between salinity and weekly distribution and abundance patterns among river and estuary stations (stations # 1-5). For clarity and ease of interpretation, creek stations were not included in weekly descriptions of distribution and abundance: Juvenile croaker were rarely present in creek habitats (see results below), and preliminary analysis indicated that croaker presence/absence in creeks was independent from croaker distribution shifts in the river and estuary stations.

RESULTS and DISCUSSION

Early-juvenile (< 13 mm) and juvenile (> 13 mm) Atlantic croaker were significantly more abundant in river habitats than creek habitats (Tables 1 and 2, Figures 2 and 3). Occurrence of early-juveniles in river nursery areas is likely a combination of both active and passive concentration mechanisms (e.g., Lawler et al. 1988). For example, late-stage Atlantic croaker larvae exhibit flood-tide transport (Churchill et al. 1999), which involves vertical migration in the water column during incoming flood tides (typically at night), and returning to near-bottom during subsequent ebb-tides, where water velocities are reduced by bottom friction (Forward and Tankersley 2001). After moving up-estuary, higher abundance of early-juvenile croaker in river than creek areas

may be the result of flux (i.e., larger rivers have greater water exchange than smaller creeks), or behavioral selection of rivers, which have relatively lower salinity and greater depth than tidal creeks. The periodic observation of high abundances of early-juvenile croaker in creek habitats (i.e., White Oak River: 26 December 2002; Newport River: 20 December 2002; Figure 2), suggests that ‘typical’ transport patterns that deliver early-juvenile croaker to river habitats may occasionally be redirected by other mechanisms such as wind-driven transport (e.g., Eggleston et al. 1998). The relatively low juvenile croaker abundances in creek habitats following peaks in early-juvenile abundance (Figure 2 and 3), suggests that mortality in creek areas is high, or that early-juveniles found in creeks are transients (i.e., they did not settle and stay, Bell and Westoby 1986).

River nursery area use by juvenile Atlantic croaker was dynamic and no single station in either estuary consistently had the highest abundance (Figures 4-9). Croaker abundance was generally highest in the middle portion of the sampling stations (station # 2-4, Figure 1), which suggests that the sampling locations chosen effectively bracketed Atlantic croaker nursery habitat. Croaker abundance patterns shifted up- and down-estuary in relation to salinity (e.g., Figure 4). In both estuaries, juvenile Atlantic croaker abundances were highest in nearly freshwater (0 ppt.), with very few croaker above ~13 ppt. (Figure 10). The utilization of a relatively wide range of salinities by juvenile Atlantic croaker observed in this study is in agreement with previously published results (Weinstein 1979, Ross 2003), and is not surprising given that Atlantic croaker are euryhaline and can tolerate a wide range of conditions (Peterson et al. 1999). Overall, the results of this study suggest that salinity rather than any specific geographic feature (i.e.,

river or creek) may be the most appropriate metric for designating Atlantic croaker nursery habitat.

While salinity in the Newport River and White Oak River estuaries appears to be an important factor influencing croaker distribution, previous work in other estuarine systems suggests that fish distribution patterns may be influenced by other abiotic factors including temperature, turbidity, dissolved oxygen, and depth (Weinstein et al. 1980, Peterson and Ross 1991, Breitburg 1992, Rakocinski et al. 1992, Szedlmayer and Able 1996, Wagner and Austin 1999), biotic factors such as food availability, competition and predation (Ogburn-Matthews and Allen 1993, Lankford and Targett 1994, Kamermans et al. 1995), as well as the interaction between abiotic and biotic factors (Rowe and Dunson 1995).

Although river areas were the primary nursery habitat utilized by juvenile Atlantic croaker in our study system, the upper estuary may serve as an important nursery habitat during periods when river nursery areas are compressed due to freshwater runoff. More frequent occurrences of juvenile Atlantic croaker in the upper portion of the White Oak River estuary (13 of 20 collections, Figures 4 - 6) than in the upper Newport River estuary (6 of 20 collections, Figures 7 - 9) likely reflects differences in geomorphology between estuaries. The Newport River estuary has a distinct sill at the mouth of the river followed by a wide (~ 1 km), shallow mud-flat (< 0.25 m at low tide, Kirby-Smith and Costlow 1989) that may act as a barrier retaining croaker in river areas. Alternatively, in the White Oak River estuary, the depth transition between 'river' and 'estuary' is less distinct (Wilkins and Lewis 1971), which may allow croaker to move in and out of river

areas more easily in the White Oak River than the Newport River estuary (compare Figures 6 and 9).

The upper-estuary is particularly important following high levels of freshwater runoff. On two occasions during spring 2003, juvenile Atlantic croaker in the Newport River estuary were completely absent from river nurseries (11 and 25 March 2003, Figure 9). Since croaker are often found in freshwater (e.g., Figure 4, 05 March 2002), downriver movement of croaker is likely the direct effect (physical forcing of croaker downstream) or indirect effect (movement of prey resource downstream) of high hydrodynamic flow. Differences in hydrodynamic flow between estuaries (the Newport River had substantially faster flow than the White Oak River, personal observation) is the likely the reason that juvenile Atlantic croaker were able to remain in the White Oak River during periods when the entire river was fresh (0 ppt., Figure 6). The importance of high levels of freshwater discharge to nursery habitat redistribution of juvenile estuarine fishes is widely recognized (Rogers et al. 1984, Meng and Matern 2001, Kimmerer 2002, Young and Potter 2002, Garcia et al. 2003). To date, however, the demographic significance of flushing events to growth and mortality of estuarine fish and crustaceans remains unclear (but see chapter 2).

Conclusion

Juvenile Atlantic croaker abundance patterns were consistently higher in river than creek habitats. Within river areas, freshwater runoff is an essential factor determining patterns of Atlantic croaker nursery habitat use. In both estuaries in this study, juvenile Atlantic croaker move up- and down-river in relation to salinity, with

highest croaker abundances found in salinities ranging from 0-13 ppt. Furthermore, following periods of high freshwater runoff, croaker may (for a short period of time) move from river nursery areas into alternative upper-estuary habitat, which suggests that salinity rather than any specific geographic feature of a river or creek may be most appropriate metric for designating Atlantic croaker nursery habitat.

Recognition of the dynamic nature of Atlantic croaker nursery habitat use has important management implications. For example, following periods of high freshwater runoff, Atlantic croaker juveniles may be collected as by-catch in the commercial shrimp-trawl fishery. Temporary closures of commercial fishing in the upper-estuary following freshwater events may increase juvenile croaker survival and ultimately contribute more fish to the adult stock. Finally, it is important to recognize that changes in estuarine hydrology caused by dam construction, dredging, increasing or decreasing runoff can modify an estuary's salinity regime, resulting in changes to patterns of Atlantic croaker nursery habitat use and potentially to their growth and survival.

The well-defined nature of Atlantic croaker nursery habitat (i.e., deep river) in the White Oak River and Newport River estuaries, makes this an ideal system in which to investigate factors influencing the early population dynamics of estuarine dependent fishes. After initial settlement, croaker emigration out of and immigration into river areas is minimal (periods following high freshwater runoff excluded), and therefore growth and mortality estimates can be attributed to abiotic and biotic components of the river nursery environment. Typically, field studies investigating habitat-specific growth and mortality have been restricted to highly site-attached species such as reef fishes (reviewed in, Sale 1991, 2002). Studies on reef fishes have highlighted the importance of factors such as

individual characteristics (larval and juvenile growth rates, Searcy and Sponaugle 2001, Bergenius et al. 2002), as well as density dependence (e.g., Hixon and Carr 1997, Anderson 2001, Webster 2003) to subsequent growth and survival. It is unknown if similar processes apply to estuarine fish species. Investigation of factors that influence growth of estuarine fishes is critical, as growth has been proposed as a criterion for designation of Essential Fish Habitat (EFH, NOAA 1996), and a common assumption throughout marine ecological and fisheries literature is that growth is a valid indicator of habitat quality. Investigating factors that influence growth of Atlantic croaker in our study system presents a unique opportunity to test underlying assumptions of ‘growth as an index of habitat quality’ that should be applicable to other commercially and ecologically important estuarine fishes. Unless alternative mechanisms that can influence growth are accounted for (previous growth history, density dependence, selective mortality; Chapter 2 and 3), growth-based assessment of habitat quality and EFH may prioritize habitats for conservation for the wrong reasons.

LITERATURE CITED

- Able, K. W., J. P. Manderson, and A. L. Studholme. 1999. Habitat quality for shallow water fishes in an urban estuary: the effects of man-made structures on growth. *Marine Ecology Progress Series* **187**:227-235.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* **82**:245-257.
- Beck, M. W., K. L. J. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**:633-641.
- Bell, J. D., and M. Westoby. 1986. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology* **104**:275-295.
- Bergenius, M. A., M. G. Meekan, D. R. Robertson, and M. I. McCormick. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**:521-525.
- Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. *Ecological Monographs* **62**:525-546.
- Breitburg, D. L. 1994. Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Marine Biology* **120**:615-625.

- Burke, J. S. 1995. Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. *Journal of Fish Biology* **47**:355-366.
- Churchill, J. H., R. B. Forward, R. A. Luettich, J. L. Hensch, W. F. Hettler, L. B. Crowder, and J. O. Blanton. 1999. Circulation and larval fish transport within a tidally dominated estuary. *Fisheries Oceanography* **8**:173-189.
- Eggleston, D. B., D. A. Armstrong, W. A. Elis, and W. S. Patton. 1998. Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae. *Marine Ecology Progress Series* **164**:73-82.
- Forward, R. B., Jr., and R. A. Tankersley. 2001. Selective tidal-stream transport of marine animals. *Oceanography and Marine Biology Annual Review* **39**:305-353.
- Garcia, A. M., J. P. Vieira, and K. O. Winemiller. 2003. Effects of 1997-1998 El Nino on the dynamics of the shallow-water fish assemblage of the Patos Lagoon Estuary. *Estuarine, Coastal and Shelf Science* **57**:489-500.
- Gillanders, B. M., K. W. Able, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* **247**:281-295.
- Gillanders, B. M., and M. J. Kingsford. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology* **40**:233-309.
- Goldberg, R., B. Phelan, J. Pereira, S. Hagan, P. Clark, A. Bejda, A. Calabrese, A. Studholme, and K. W. Able. 2002. Variability in habitat use by young-of-the-year

- winter-flounder, *Pseudopleuronectes americanus*, in three northeastern U.S. estuaries. *Estuaries* **25**:215-226.
- Gray, C. A., R. C. Chick, and D. J. McElligott. 1998. Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. *Estuarine, Coastal and Shelf Science* **46**:849-859.
- Hettler, W. F., and A. J. Chester. 1990. Temporal distribution of ichthyoplankton near Beaufort inlet, North Carolina. *Marine Ecology Progress Series* **68**:157-168.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946-949.
- Kamermans, P., K. Y. Guindon, and J. M. Miller. 1995. Importance of food availability for growth of juvenile southern flounder (*Paralichthys lethostigma*) in the Pamlico River estuary, North Carolina, USA. *Netherlands Journal of Sea Research* **34**:101-109.
- Kimmerer, W. J. 2002. Physical, biological, and management responses to variable freshwater flow into the San Francisco estuary. *Estuaries* **25**:1275-1290.
- Kirby-Smith, W. W., and J. D. Costlow. 1989. The Newport River estuarine system. UNC-SG-89-04, UNC Seagrant Publication, Beaufort, NC.
- Kraus, R. T., and D. H. Secor. 2005. Application of the nursery-role hypothesis to an estuarine fish. *Marine Ecology Progress Series* **291**:301-305.
- Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). *Netherlands Journal of Sea Research* **9**:69-85.

- Kuipers, B. R., B. Maccurrin, J. M. Miller, H. W. Van der Veer, and J. I. J. Witte. 1992. Small trawls in juvenile flatfish research: their development and efficiency. Netherlands Journal of Sea Research **29**:109-117.
- Lankford, T. E., and T. E. Targett. 1994. Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): effects of temperature and salinity on feeding, growth, and survival. Marine Biology **119**:611-620.
- Lawler, J. P., M. P. Weinstein, H. Y. Chen, and T. L. Englert. 1988. Modeling of physical and behavioral mechanisms influencing recruitment of spot and Atlantic croaker to the Cape Fear Estuary. American Fisheries Society Symposium **3**:115-131.
- Martino, E. J., and K. W. Able. 2003. Fish assemblages across the marine to low salinity transition zone of a temperate estuary. Estuarine, Coastal and Shelf Science **56**:969-987.
- Meng, L., and S. A. Matern. 2001. Native and introduced larval fishes of Suisun marsh, California: The effects of freshwater flow. Transactions of the American Fisheries Society **130**:750-765.
- Miller, M. J., and K. W. Able. 2002. Movements and growth of tagged young-of-the-year Atlantic croaker (*Micropogonias undulatus* L.) in restored and reference marsh creeks in Delaware Bay, USA. Journal of Experimental Marine Biology and Ecology **267**:15-33.
- Miltner, R. J., S. W. Ross, and M. H. Posey. 1995. Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthurus*) in tidal nurseries. Canadian Journal of Fisheries and Aquatic Sciences **52**:971-982.

- Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of Essential Fish Habitat. *in* L. R. Benaka, editor. Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Bethesda, Maryland.
- NOAA. 1996. Magnuson-Stevens Fishery Conservation and Management Act amended through 11 October 1996. National Marine Fisheries Service, National Oceanic and Atmospheric Administration technical memorandum NMFS-F/SPO-23. U.S. Department of Commerce. Washington, D.C.
- Ogburn-Matthews, V., and D. M. Allen. 1993. Interactions among some dominant estuarine nekton species. *Estuaries* **16**:840-850.
- Peterson, M. S. 2003. A conceptual view of environment-habitat-production linkages in tidal river estuaries. *Reviews in Fisheries Science* **11**:291-313.
- Peterson, M. S., B. H. Comyns, C. F. Rakocinski, and G. L. Fulling. 1999. Does salinity affect somatic growth in early juvenile Atlantic croaker, *Micropogonias undulatus* (L.)? *Journal of Experimental Marine Biology and Ecology* **238**:199-207.
- Peterson, M. S., and S. T. Ross. 1991. Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. *Estuarine, Coastal and Shelf Science* **33**:467-483.
- Rakocinski, C., D. M. Baltz, and J. W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* **80**:135-148.
- Rogers, S. G., T. E. Targett, and S. B. Van Sant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: The influence of springtime freshwater conditions. *Transactions of the American Fisheries Society* **113**:595-606.

- Rogers, S. I., and S. J. Lockwood. 1989. Observations on the capture efficiency of a two-metre beam trawl for juvenile flatfish. *Netherlands Journal of Sea Research* **23**:347-352.
- Rooker, J. R., A. M. Landry, B. W. Geary, and J. A. Harper. 2004. Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper. *Estuarine, Coastal and Shelf Science* **59**:653-661.
- Ross, S. W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin* **101**:384-404.
- Rowe, C. L., and W. A. Dunson. 1995. Individual and interactive effects of salinity and initial fish density on a salt marsh assemblage. *Marine Ecology Progress Series* **128**:271-278.
- Rozas, L. P., and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* **20**:199-213.
- Rozas, L. P., and E. P. Odum. 1987. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. *Estuaries* **10**:36-43.
- Sale, P. F. 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, New York.
- Sale, P. F. 2002. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, New York.
- Searcy, S., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* **82**:2452-2470.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry The Principles and Practice of Statistics in Biological Research*, third edition. W.H. Freeman and Company, New York.

- Szedlmayer, S. T., and K. W. Able. 1996. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. *Estuaries* **19**:697-709.
- Wagner, M. C., and H. M. Austin. 1999. Correspondence between environmental gradients and summer littoral fish assemblages in low salinity reaches of the Chesapeake Bay, USA. *Marine Ecology Progress Series* **177**:197-212.
- Walsh, H. J., D. S. Peters, and D. P. Cyrus. 1999. Habitat utilization by small flatfishes in a North Carolina estuary. *Estuaries* **22**:803-813.
- Warlen, S. M. 1980. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Pages 204-214 in 34 Annual conference of southeastern association of fish and wildlife agencies, Nashville.
- Warlen, S. M., and J. S. Burke. 1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries* **13**:453-461.
- Webster, M. S. 2003. Temporal density dependence and population regulation in a marine fish. *Ecology* **84**:623-628.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin* **77**:339-357.
- Weinstein, M. P., S. L. Weiss, R. G. Hodson, and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fishery Bulletin* **78**:419-436.
- Wilkins, E. P. H., and R. M. Lewis. 1971. Abundance and distribution of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. *Fishery Bulletin* **69**:783-789.

Young, G. C., and I. C. Potter. 2002. Influence of exceptionally high salinities, marked variations in freshwater discharge and opening of estuary mouth on the characteristics of the ichthyofauna of a normally-closed estuary. *Estuarine, Coastal and Shelf Science* 55:223-246.

TABLE 1. *Micropogonias undulatus*. Results of two-way ANOVA for early-juvenile Atlantic croaker abundance (< 13 mm standard length) in the Newport River and White Oak River estuaries, North Carolina, USA. Factors include collection period (Spring 2002, Fall 2002, Spring 2003) and habitat (River, Creek). Within each estuary, river was defined as the primary, deep (~3 m at high-tide) freshwater tributary; creek was defined as a smaller, shallow (~1 m at high-tide) tributary. Prior to analyses, early-juvenile Atlantic croaker abundance was log (x+1) transformed to meet assumptions of ANOVA.

Estuary	Factor	DF	SS	MS	F	P
Newport River (log x+1)	Location	1	19.30	19.30	5.80	<0.05
	Collection	2	26.21	13.11	3.94	<0.05
	Location*Collection	2	10.73	5.37	1.61	NS
	Error	32	106.52	3.33		
White Oak River (log x+1)	Location	1	45.15	45.15	17.12	<0.001
	Collection	2	22.07	11.04	4.18	<0.05
	Location*Collection	2	3.37	1.68	0.64	NS
	Error	32	84.39	2.64		

TABLE 2. *Micropogonias undulatus*. Results of two-way ANOVA for juvenile Atlantic croaker abundance (> 13 mm standard length) in the Newport River and White Oak River estuaries, North Carolina, USA. Factors include collection period (Spring 2002, Fall 2002, Spring 2003) and habitat (River, Creek). Within each estuary, river was defined as the primary, deep (~3 m at high-tide) freshwater tributary; creek was defined as a smaller, shallow (~1 m at high-tide) tributary. Prior to analyses, juvenile Atlantic croaker abundance was log (x+1) transformed to meet assumptions of ANOVA.

Estuary	Factor	DF	SS	MS	F	P
Newport River (log x+1)	Location	1	86.16	86.16	54.78	<0.001
	Collection	2	8.84	4.42	2.81	NS
	Location*Collection	2	20.97	10.48	6.67	<0.01
	Error	32	50.32	1.57		
White Oak River (log x+1)	Location	1	51.93	51.93	28.60	<0.001
	Collection	2	0.44	0.22	0.12	NS
	Location*Collection	2	5.86	2.93	1.61	NS
	Error	32	58.10	1.81		

FIGURE LEGENDS

Figure 1. Location of the White Oak and Newport River estuaries, North Carolina, USA.

Inset shows location of beam-trawl stations within each river (1-4), upper-estuary (5), and creek areas (6-7) of each estuary.

Figure 2. Total abundance of early-juvenile Atlantic croaker (<13 mm standard length) in river and creek stations of the White Oak and Newport River estuaries, North Carolina, USA. during Spring 2002, Fall 2002, and Spring 2003 collection seasons. Within each estuary, river was defined as the primary, deep (~3 m at high-tide) freshwater tributary; creek was defined as a smaller, shallow (~1 m at high-tide) tributary. Abundance was standardized to 15 minute tow duration. The symbol 'x' indicates that no fish were collected on that date.

Figure 3. Total abundance of juvenile Atlantic croaker (>13 mm standard length) in river and creek stations of the White Oak and Newport River estuaries, North Carolina, USA. during Spring 2002, Fall 2002, and Spring 2003 collection seasons. Within each estuary, river was defined as the primary, deep (~3 m at high-tide) freshwater tributary; creek was defined as a smaller, shallow (~1 m at high-tide) tributary. Abundance was standardized to 15 minute tow duration. The symbol 'x' indicates that no fish were collected on that date.

Figure 4. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Spring 2002 in the White Oak River estuary, North Carolina, USA. For station location see Figure 1.

Figure 5. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Fall 2002 in the White Oak River estuary, North Carolina, USA. For station location see Figure 1.

Figure 6. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Spring 2003 in the White Oak River estuary, North Carolina, USA. For station location see Figure 1.

Figure 7. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Spring 2002 in the Newport River estuary, North Carolina, USA. For station location see Figure 1.

Figure 8. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Fall 2002 in the Newport River estuary, North Carolina, USA. For station location see Figure 1.

Figure 9. Relationship between salinity (ppt) and abundance of juvenile Atlantic croaker (>13 mm standard length, 3 min tow duration) during Fall 2002 in the Newport River estuary, North Carolina, USA. For station location see Figure 1.

Figure 10. Relationship between salinity and abundance of juvenile Atlantic croaker (> 13 mm standard length, 3 min tow duration) in the White Oak and Newport River estuaries, North Carolina, USA. for all collection dates.

Figure 1.

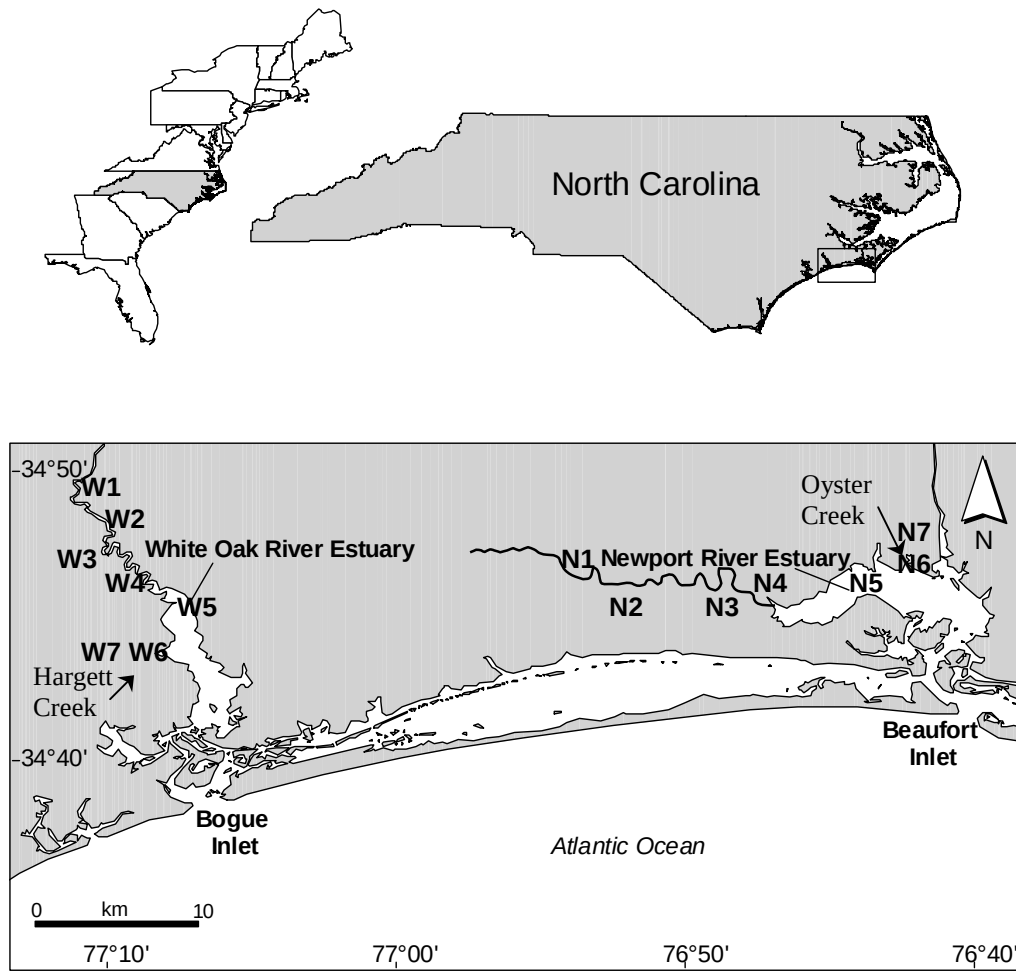


Figure 2.

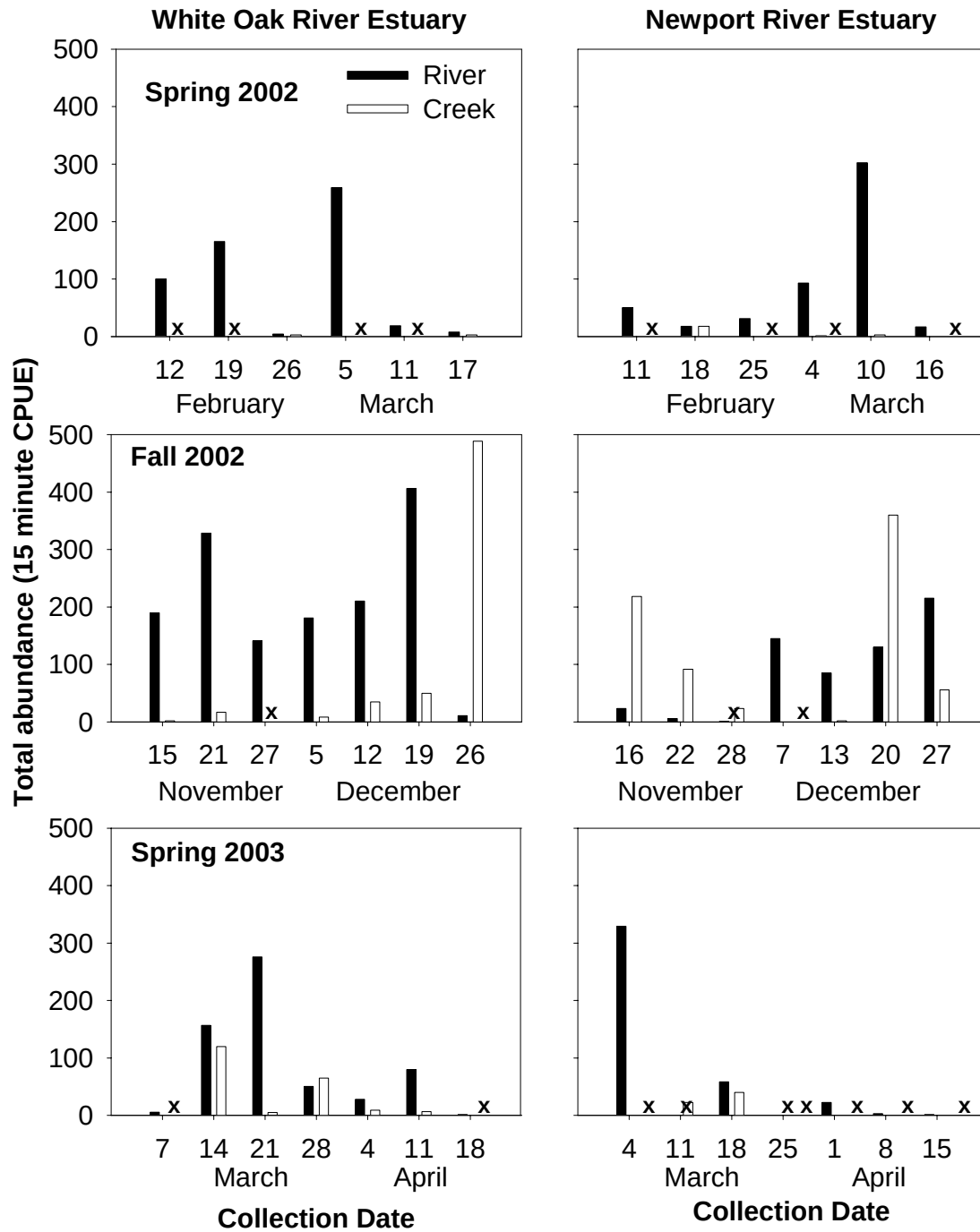


Figure 3.

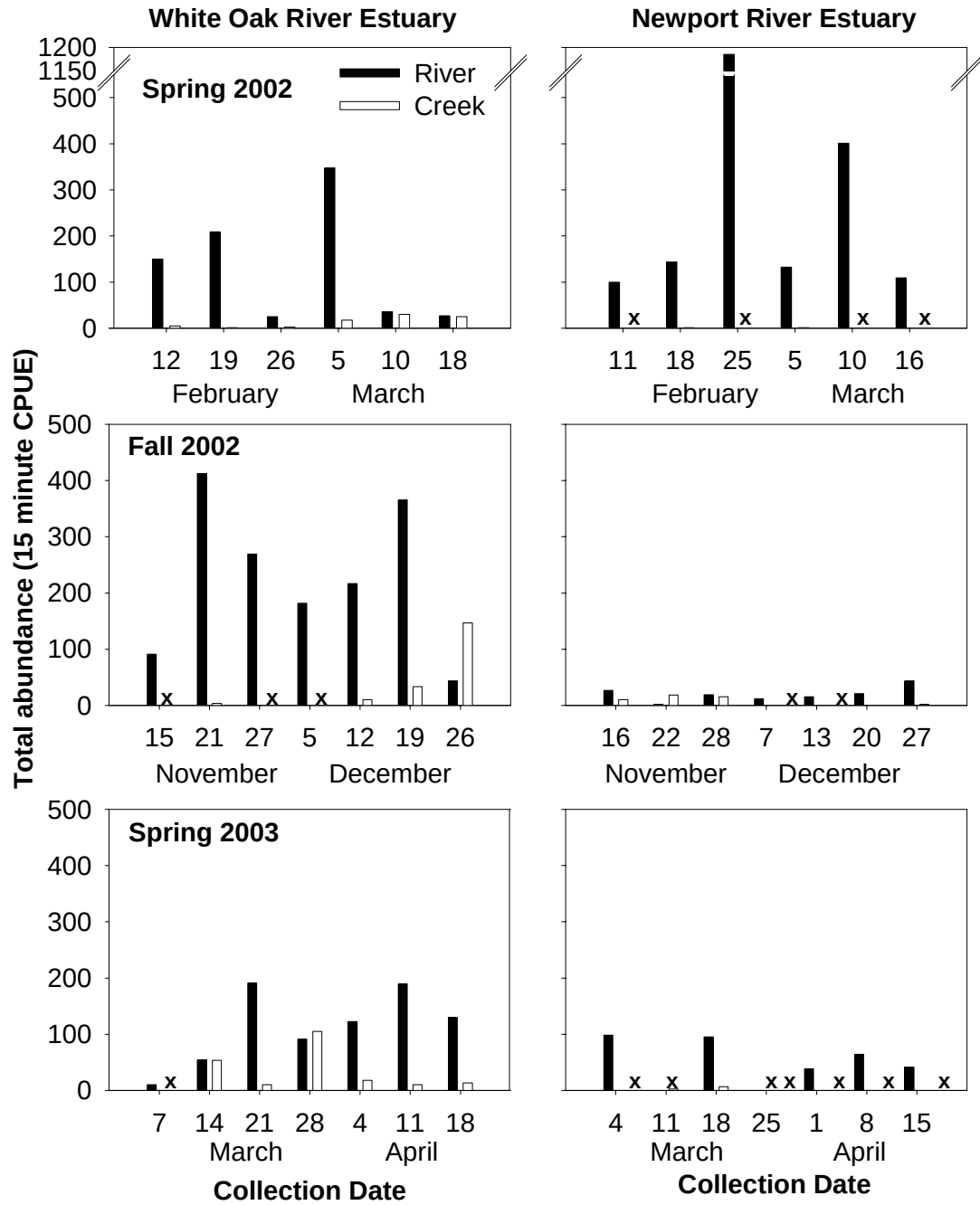


Figure 4.

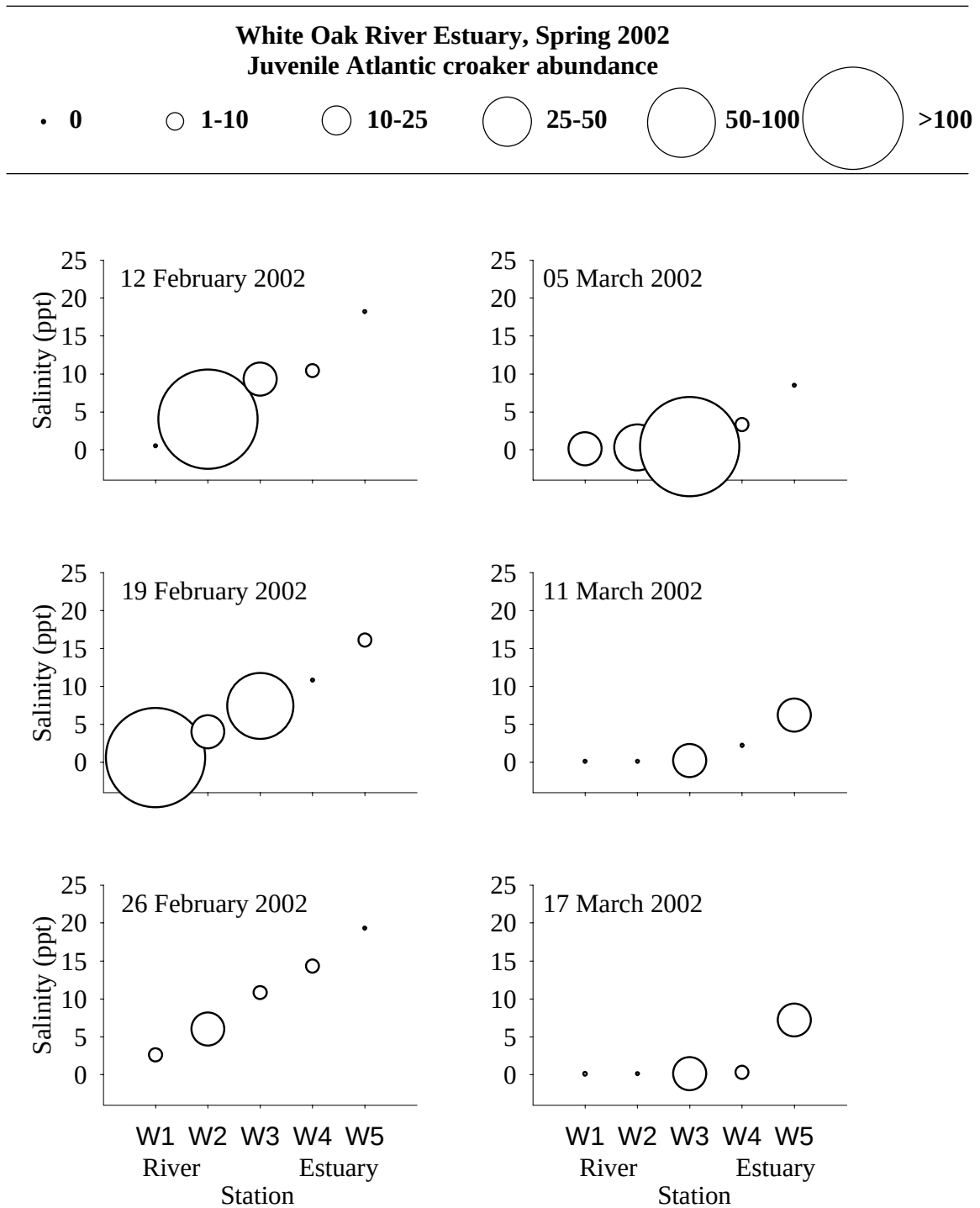


Figure 5.

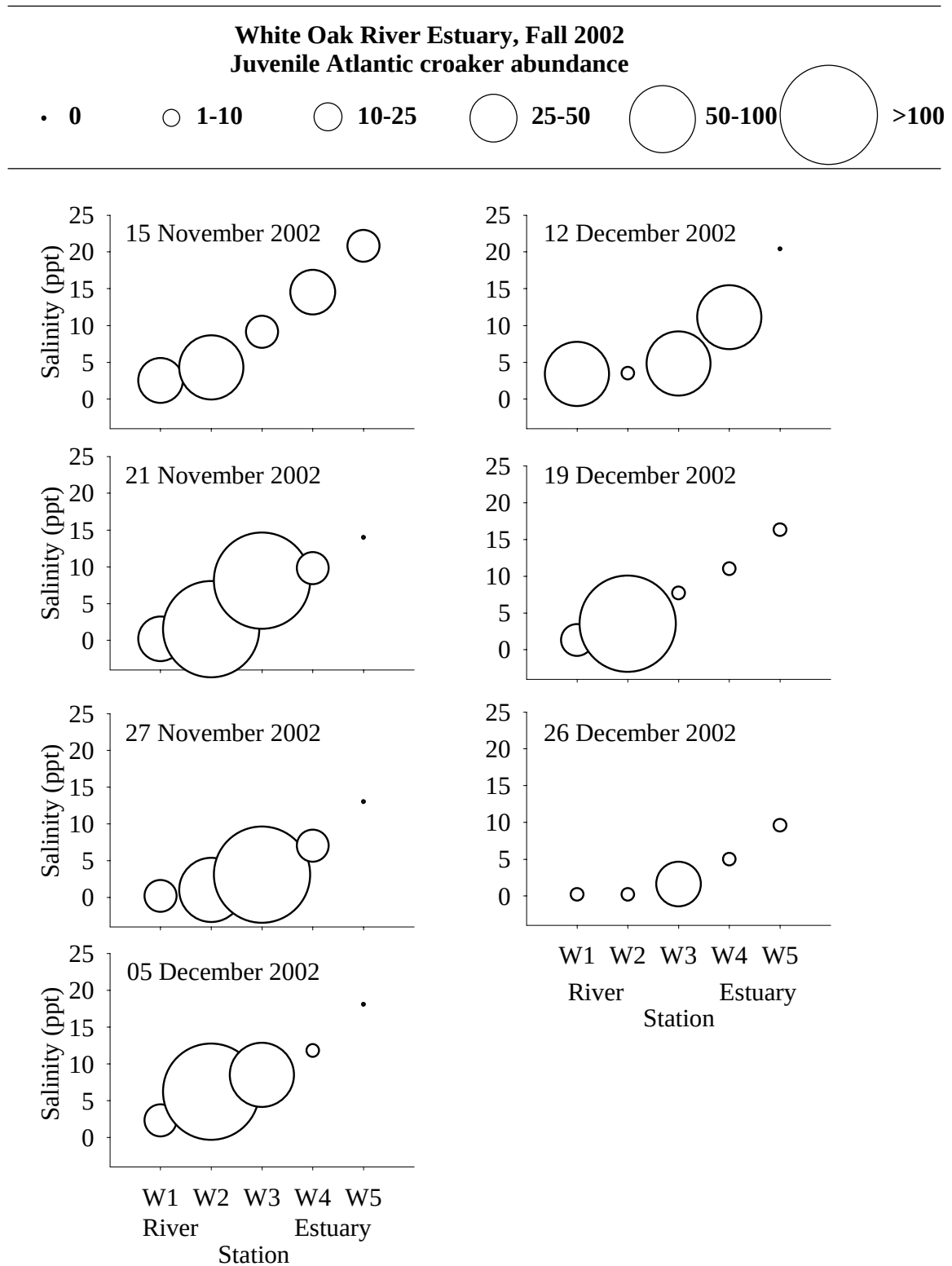


Figure 6.

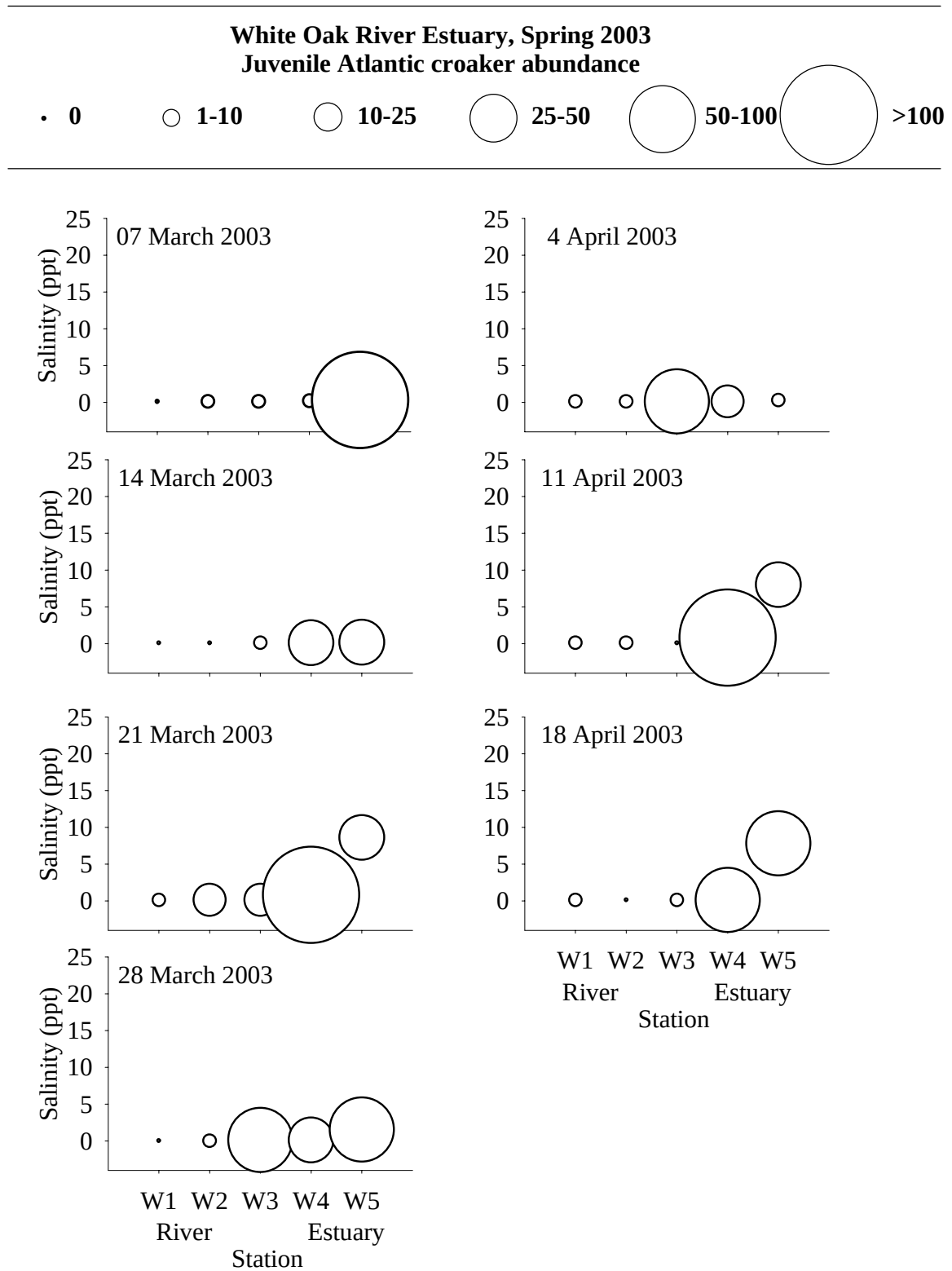


Figure 7.

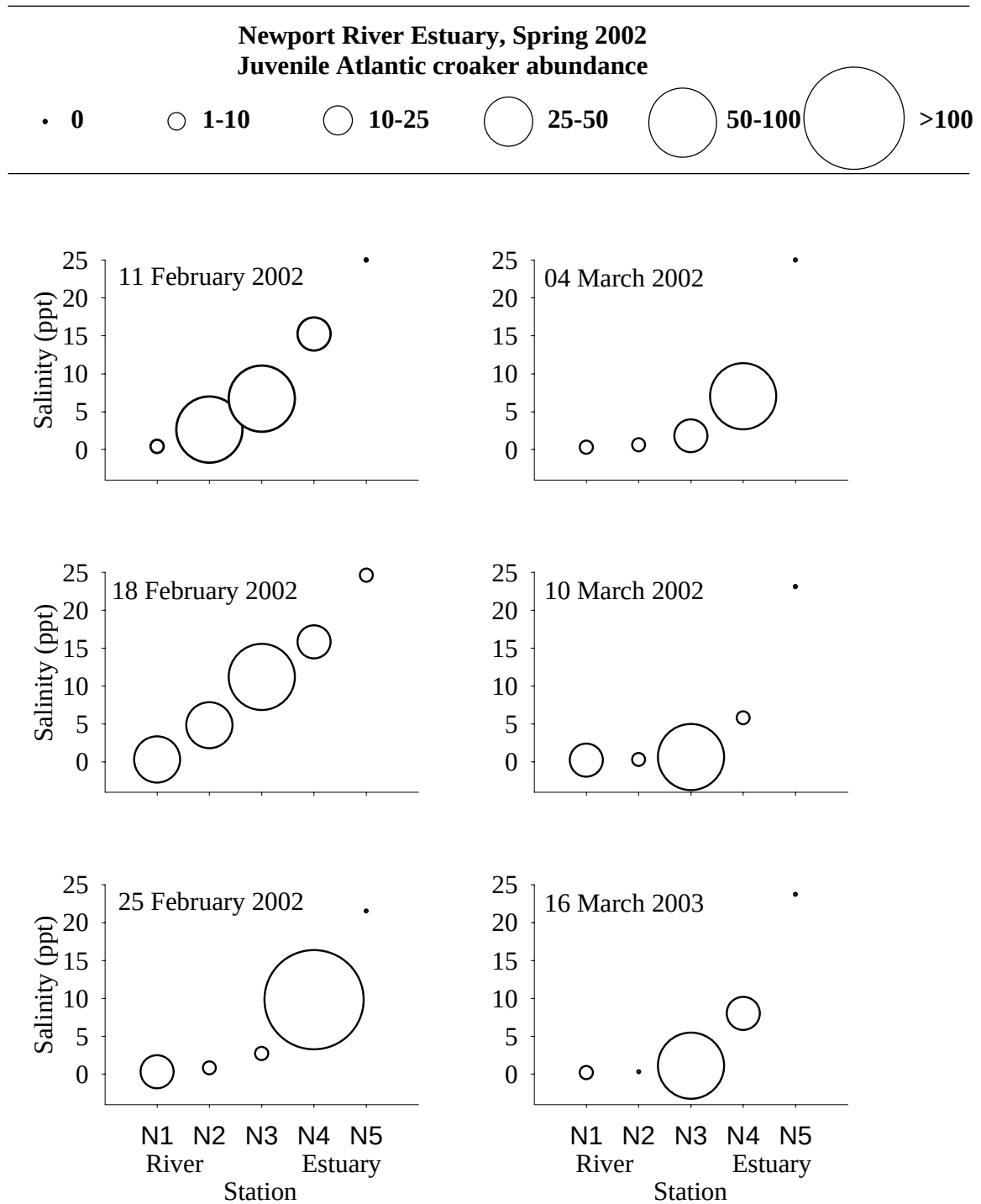


Figure 8.

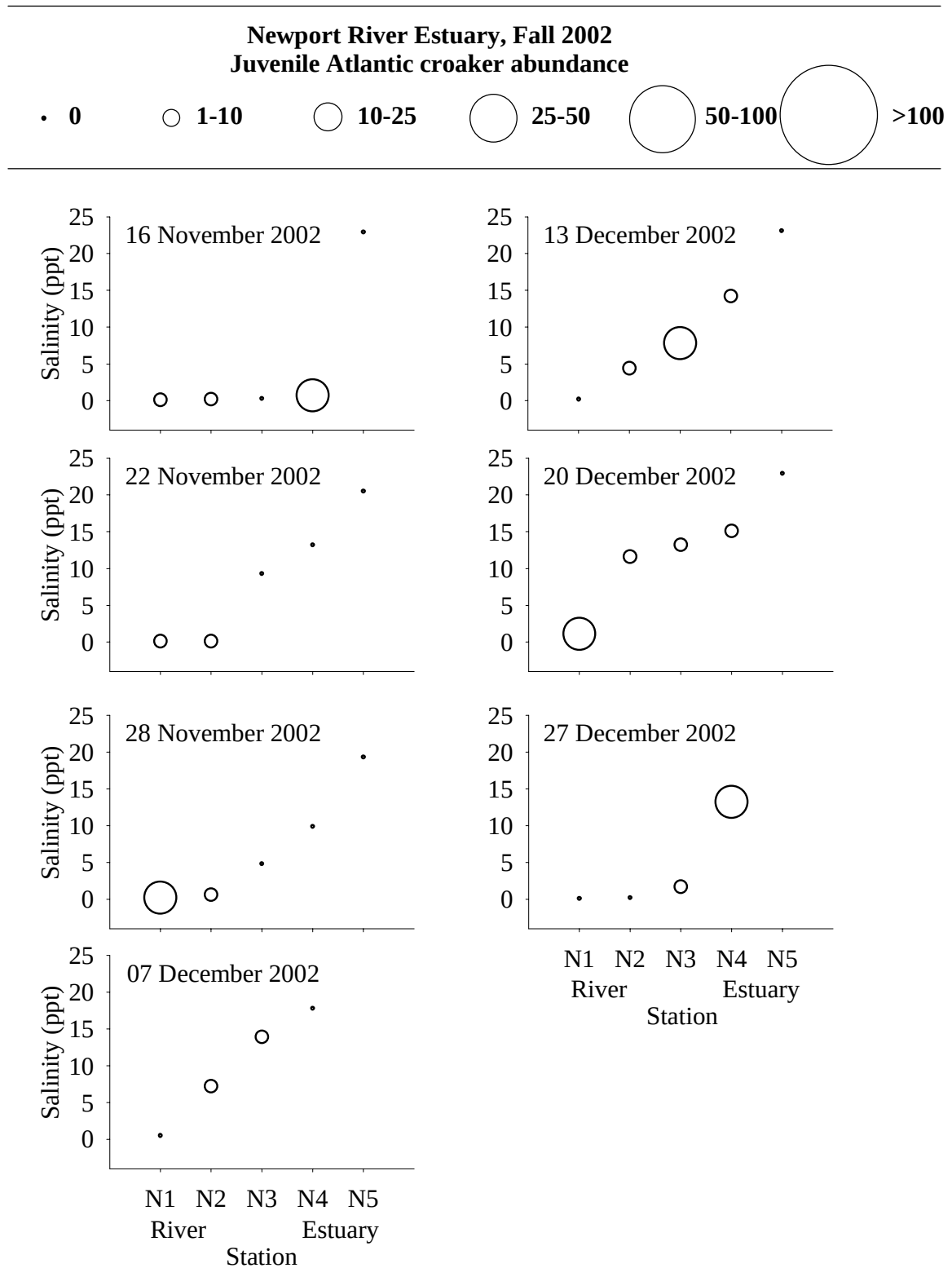


Figure 9.

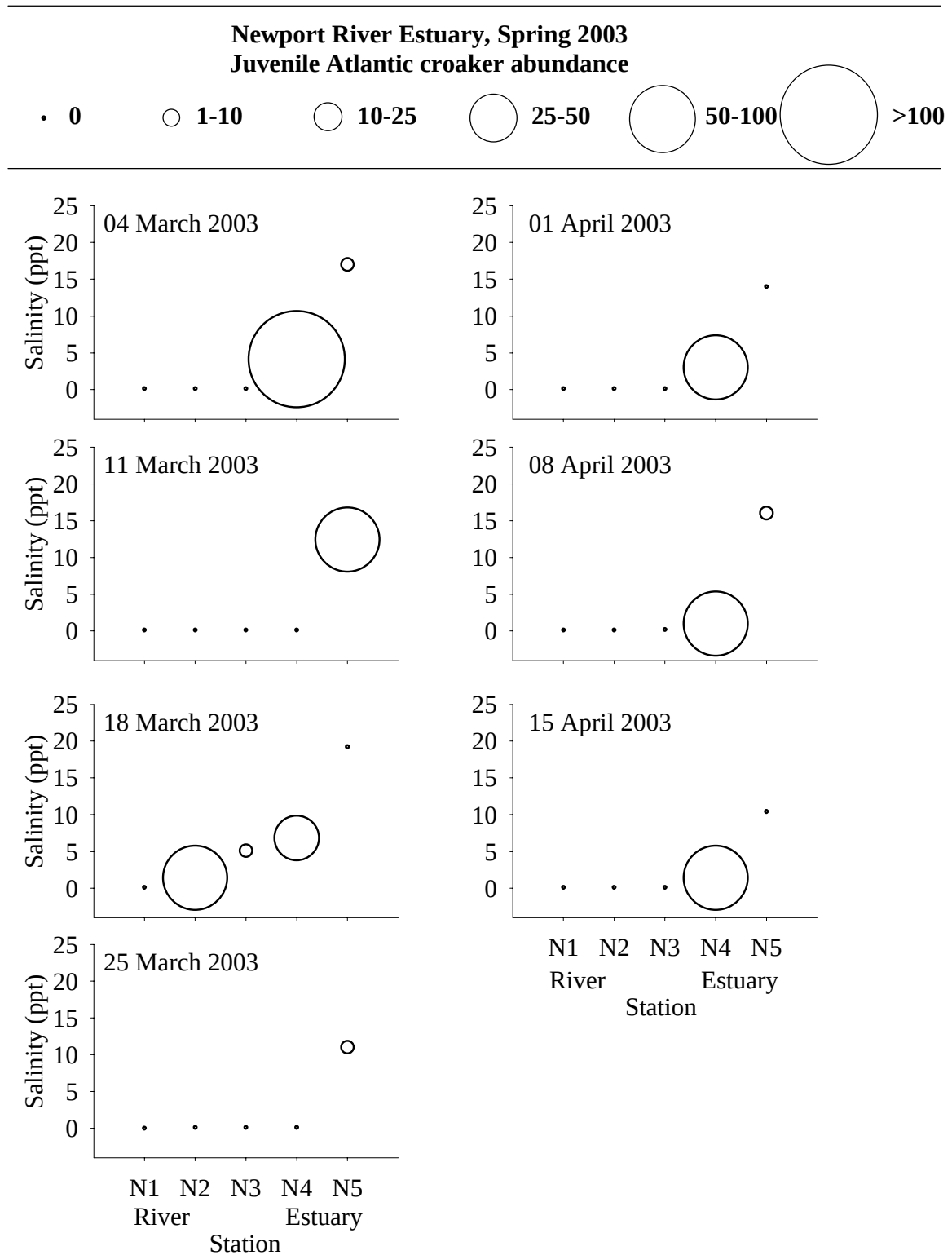
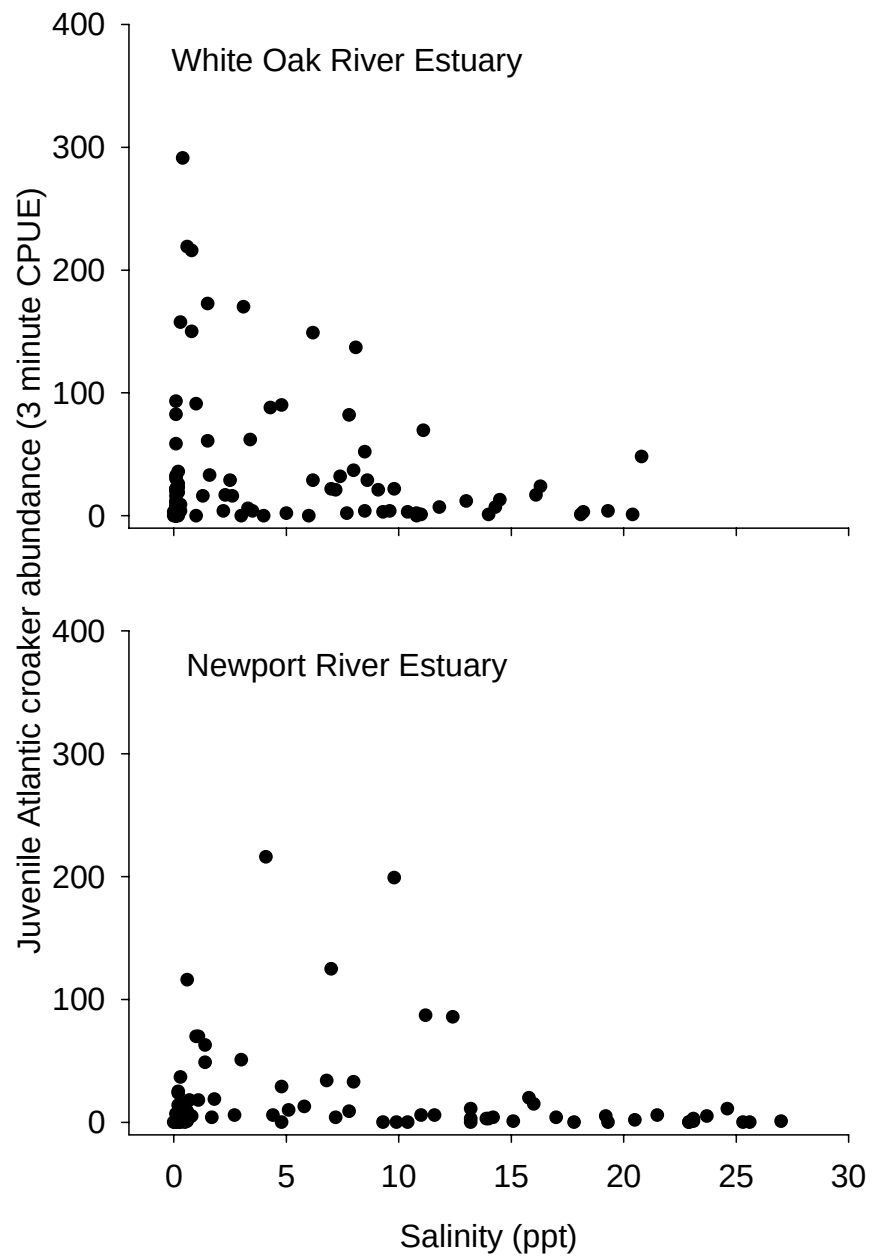


Figure 10.



CHAPTER 2

Estuarine environment influences the relationship between larval and juvenile growth for Atlantic croaker, *Micropogonias undulatus*

ABSTRACT

For organisms with complex life cycles, such as insects, amphibians, marine invertebrates and fishes, there is growing recognition that juvenile traits may be dependent on previous larval history. The dependence of growth rates between ontogenetic stages is critical to recognize as juvenile growth has been linked to selective mortality in a variety of taxa, and in fishes, growth rates are often used to assess habitat quality. In this study, both positive (larval-growth-inertia) and negative (compensatory growth) relationships between larval and juvenile growth rates (larval-growth-inertia) were investigated using the estuarine fish Atlantic croaker, *Micropogonias undulatus*, as a model species. The relationship between larval and juvenile growth was examined using both a controlled laboratory study and replicated field experiments, which spanned a range of environmental conditions. Although there was no relationship between larval and juvenile growth rates in the laboratory experiment, results from the field study suggest that larval-growth-inertia was event-driven, caused by high levels of freshwater runoff leading to reduced feeding success when fish were displaced from their initial up-estuary settlement areas. Future research should recognize the role that variable environments play in our ability to detect the relationship of life-history traits between ontogenetic stages.

INTRODUCTION

In organisms with complex life cycles such as insects, amphibians, marine invertebrates and fishes, there is growing recognition that life history stages cannot be viewed independently (Pechenik et al. 1998, Metcalfe and Monaghan 2001). To date, most theoretical and empirical studies investigating processes that occur across life-history transitions have focused on how larval history influences age and length-at-metamorphosis to the juvenile stage (Reznick 1990, Rowe and Ludwig 1991, Bradshaw and Johnson 1995). More recently, researchers have begun to directly investigate how larval traits may drive later characteristics such as fecundity (Berven 1990, Taylor et al. 1998) and juvenile growth rates (Searcy and Sponaugle 2000, Phillips 2002, Relyea and Hoverman 2003). Recognition of the potential dependence of growth in one life history stage on growth in the previous stage is critical, especially if juvenile size and growth are used to forecast survival potential (e.g., Pechenik et al. 1998, Searcy and Sponaugle 2001, Altwegg and Reyer 2003) and assess the quality of juvenile habitats (Sogard 1992, Nécaise et al. 2005).

In fishes, the use of growth rates as an index of habitat quality is based on the widely held assumption that relatively high fish growth rates are a consequence of high quality habitat in the form of appropriate abiotic conditions, superior food, and refuge from predators (Sogard 1997). High juvenile growth rates, however, could simply reflect a positive (larval-growth-inertia) or negative (compensatory) relationship between larval and juvenile growth rates. For example, previous studies working with a variety of organisms have shown that small size at the larval-juvenile transition may result in both slower (McCormick and Molony 1992, Goater 1994, Pechenik et al. 1998) and faster

juvenile growth (reviewed in: Arendt 1997, Metcalfe and Monaghan 2001). Ultimately, if relatively high growth rates often correspond to characteristics of an individual that arrives at a particular location, rather than specific characteristics of the site or habitat type, then use of growth may be an inappropriate index of habitat quality.

Due to logistical difficulties in obtaining information on individual growth rates of mobile animals in the field, most studies investigating the relationship between larval and juvenile traits have been conducted in the laboratory or in field enclosures. Given the typically high growth plasticity characteristic of many species, it is critical to test whether results from controlled environments are applicable in field settings. In this respect, fishes are ideal candidates for field studies as the otoliths (ear-stones) of many fishes have daily rings which allow one to back-calculate individual records of age, hatch-date, and age-specific growth history (Thorrold and Hare 2002). In this study, we used the estuarine fish, Atlantic croaker, *Micropogonias undulatus*, in both a controlled laboratory experiment and replicated field studies that spanned a wide range of environmental conditions to test the null hypothesis that there is no correlation between larval and juvenile growth.

MATERIALS AND METHODS

Atlantic croaker, *Micropogonias undulatus*, is a commercially important sciaenid fish that is a dominant component of the demersal nekton community along the Atlantic and Gulf coasts of the United States. In our study region (North Carolina, USA; Fig. 1) Atlantic croaker spawn primarily over the continental shelf and have a protracted spawning season that extends from September through April (Hettler and Chester 1990). Following pelagic larval development on the continental shelf, Atlantic croaker ingress

into estuaries, and typically settle in low-salinity, upper-estuary channels, which they use as juvenile nursery areas (Ross 2003). In this study, we consider the period of time prior to estuarine ingress as ‘larval’, the period following ingress as ‘juvenile’, and croaker collected at the mid-estuary site to be ‘ingress-age’.

Otoliths

Both field and laboratory components of this study relied heavily on information obtained from otoliths. Caution is required when translating otolith growth rates into somatic growth as otolith increment deposition is not always daily, and periods of stress may decouple otolith and somatic growth (reviewed in: Thorrold and Hare 2002). Therefore, patterns of otolith growth were examined directly without converting to somatic measures; this approach provides a useful, albeit conservative measure of fish growth (Chambers and Miller 1995).

To prepare otoliths for analysis, left sagittae were removed, mounted in epoxy, sectioned along the frontal plane, and polished to the core. All otoliths were examined using a transmitted light microscope at 400x magnification with a rotating polarized filter placed between the light source and the first stage. Otolith images were captured with a frame grabber and increment count and widths (distance between two sequential increments) were measured using Image Pro Plus 4.5 image analysis software at 800x. Each otolith was read a minimum of two times and selection criteria to determine which (if any) otolith measure would be used followed previously published methods (Searcy and Sponaugle 2001).

Laboratory Experiment

The laboratory component was designed to test whether larval and juvenile growth was positively or negatively correlated in a controlled environment. Ingress-age Atlantic croaker were collected from a mid-estuary station in the Newport River Estuary, North Carolina on November 23, 2003 during night-time flood tide with a passively fished 0.5 m² plankton net with 1-mm mesh. Atlantic croaker were then transported to the lab, where they were immersed for 24 hours in 18 ppt estuarine water from the collection site combined with a 100-mg/l solution of alizarin complexone to mark the otoliths of each fish (Ahrenholz et al. 1995). The alizarin mark allowed the larval (pre-capture) and juvenile (post-capture) periods to be identified in subsequent otolith analyses (see below). Following the 24-hour marking period, each fish was placed in an individual 0.95 liter container (n=100), held in a controlled temperature water bath at 15°C and exposed to ambient photoperiod. Over the next two days, salinity was uniformly decreased by mixing natural seawater with distilled water to reach 10 ppt (typical salinity in Atlantic croaker nursery areas; Fig. 2) fish were then kept in these conditions for the 4-week experiment. Croaker were fed recently hatched *Artemia ad-libitum* so that after 24 hours there were still *Artemia* visible in each container. Prior to the daily feeding, leftover *Artemia* and waste material were removed, and approximately 33% of the water was replaced.

To obtain a measure of somatic growth, digital photos of each fish were taken immediately after the alizarin marking and at weekly intervals until the end of the experiment for a total of 5 weekly measurements. To ensure accurate length measurements, Atlantic croaker were decanted into a narrow glass photography container

that restricted fish from moving horizontally (turning right or left), and positioned in front of a metric ruler. A total of 5-10 images of each fish were then taken using a macro lens attached to a digital camera. Average standard length (0.1 mm SL) for individual fish was calculated from the three best (individually calibrated) digital images using Image Pro Plus 4.5 image analysis software.

Data Analysis

Before applying information obtained from otoliths in this study, it was necessary to validate a positive relationship between otolith and somatic growth as well as daily otolith increment deposition. In total, 100 fish were used to examine the relationship between otolith increment count following the alizarin mark and actual number of days passed. A linear regression was calculated between number of increments after the alizarin mark and the known number of days from marking (Ahrenholz et al. 1995). The slope of the regression was then compared to a slope of 1 to test the null hypothesis that increment formation rate was 1 increment d⁻¹. Next, a regression was calculated between juvenile otolith growth (28 d post alizarin mark) and juvenile somatic growth (same 28 d period) to ensure that otolith growth and somatic growth were positively related (Thorrold and Hare 2002).

The influence of a variety of larval traits on subsequent juvenile growth was then examined using three approaches. First, to allow comparison of laboratory with field results (presented later) the Pearson correlation coefficient was calculated between juvenile and larval otolith growth and juvenile somatic and larval otolith growth. Second, multiple regression models with juvenile somatic growth as the dependent variable and several larval traits (larval otolith growth; age-at-ingress; and standard

length-at-ingress) as the independent variables were examined. Third, the coefficient of partial determination was calculated (squared partial correlation coefficients) using type II sums of squares to examine how much of the variation in juvenile growth could be explained by each independent variable while holding the other independent variables constant (PROC REG, SAS Institute). The three methods outlined above were calculated using a variety of estimates of average larval growth (1-30d, 8-30d, final 7d of larval period) and average juvenile growth (1 week, 1 month). All analyses produced similar results. Therefore, only comparisons of average larval (1-30d) and juvenile (1 mo.) growth are presented.

Field Study

Collection method

The field component of this project was designed to examine the relationship between larval and juvenile growth under natural field conditions. Previous work in North Carolina suggests that Atlantic croaker move rapidly up-estuary to riverine nursery areas (Weinstein 1979). Hatch-date cohorts of Atlantic croaker were tracked from initial estuarine ingress through early juvenile development using seven weekly collections in the fall (November-December) and spring (February-April) of two recruitment seasons (2001-2002 and 2002-2003) in the Newport River Estuary, and spring 2002 and fall-spring 2002-2003 in the White Oak River Estuary (Fig. 1), North Carolina, USA. Early juvenile Atlantic croaker, were collected using a 1-m beam trawl with 1-mm mesh upper- and side-panels and a 3-mm mesh bottom-panel at five stations within each estuary ranging from polyhaline (>20 ppt) mid-estuary to oligohaline (0 ppt) riverine areas (Fig. 1). Due to the shallow nature of both estuaries, beam trawl tows were restricted to the

last two hours of daytime floodtide, and at each station three replicate tows of 1 minute each were completed covering an area of $\sim 60 \text{ m}^2$. Beam trawl catch efficiency is known to vary according to species and size of targeted animal (Kuipers 1975, Kuipers et al. 1992, Rozas and Minello 1997), and was not corrected for in this study (but see Searcy Chapter 1 for a discussion of beam trawl efficiency). For reference, density estimates ($\pm$ SE) of fish commonly collected in this study are provided in Appendices 1-10.

Temperature and salinity were measured at each sampling station using a handheld YSI-85 instrument (YSI, Yellow Springs, Ohio, USA). In the spring of 2003, hourly measures of salinity and temperature were also obtained by deploying YSI-6600 multiparameter dataloggers at the head of each estuary (Figure 1).

In the laboratory, otoliths were dissected from thirty randomly selected ingress-age fish from the mid-estuary stations and thirty randomly selected juvenile fish collected in the riverine stations (see ‘Otoliths’ section for processing information) from each collection date. Dissected fish were then dried at 60°C for 24 hours and weighed. To determine feeding success for each collection date, an additional thirty fish collected in the riverine stations from each sampling date were randomly chosen for stomach content analysis (recorded as the proportion of fish from each collection date that had empty stomachs).

Data Analysis

The primary goal of the field portion of this study was to examine the relationship between juvenile and larval otolith growth. Therefore, it was essential that larval and juvenile periods of growth be distinguished. As a conservative measure of ingress-age, the general range in age-at ingress was established for each estuary in each season from

weekly mid-estuary trawl collections. Outliers were eliminated and the minimum and maximum age at ingress were used to conservatively differentiate larval (pre-ingress) and juvenile (post-ingress) periods: ages younger than the youngest fish collected were considered 'larval' and ages older than the oldest fish collected were considered 'juvenile'. Inspection of age-at-ingress data for Atlantic croaker from our mid-estuary collections revealed that Atlantic croaker generally ingressed between 30-40 d post-hatch in our fall collections and 40-50 d post-hatch in our spring collections. Therefore, assumed larval and juvenile ages for the fall were <30 d (larval) and >40 d (juvenile), and for the spring were <40 d (larval) and >50 d (juvenile). For analyses of beam trawl collections, only weekly hatch-date cohorts from which a minimum of 10 fish were aged were used to calculate Pearson correlation coefficients between larval otolith growth (10 d prior to ingress period) and juvenile otolith growth (5 d after ingress period). In total, 27 weekly hatch-date cohorts were included in this analysis.

To relate cohort-specific larval-growth-inertia correlations to abiotic and biotic conditions experienced by that cohort within juvenile nursery areas, multiple regression analysis was used. The univariate correlation between juvenile and larval otolith growth (larval growth inertia, LGI correlation coefficient) was the dependent variable and abiotic factors (average temperature, average salinity, and maximum change in salinity as an indicator of flooding events) and biotic factors (feeding, condition, catch-per-unit-effort (CPUE), average larval, and average juvenile growth) were independent variables.

Temperature and salinity were obtained where the riverine portion of each river opened up into the estuary (Fig. 1) from twice-weekly measures taken at high tide. During spring 2003, daily average salinity and temperature values in each estuary was calculated from

hourly measurements collected by YSI-6600 dataloggers. Change in salinity was calculated as the largest change in daily salinity (either positive or negative) observed. To assess the trophic consequences of croaker displacement down-estuary during heavy rainfall events (see Results below), an estimate of feeding success was defined as the proportion of fish that had empty stomachs, and an index of individual fish condition (fatness) was calculated using Fulton's condition factor ($\text{Weight} / \text{Length}^3$; Wootton 1990) and standardized to length by taking the residuals of condition on length. As most fish were collected at one station within a sampling date, CPUE was calculated by averaging catch per one-minute tow over three tows from the station where most Atlantic croaker were collected on each sampling date. For multiple regression analysis, all LGI correlation coefficients were used as dependent variables as even non-significant results likely still capture the direction and general effect size of the relationship. Prior to analysis, data were tested for normality, homogeneous variances, and collinearity (PROC UNIVARIATE and REG, SAS institute). In addition to standard regression output, the coefficient of partial determination was calculated for each independent variable to estimate the proportion of variability in the LGI coefficients that could be explained by each independent variable while holding the others constant.

RESULTS

Lab Experiment

Otolith increments were formed daily and otolith growth was positively related to somatic growth, providing a basis for using otolith characteristics as measures of size and growth in juvenile Atlantic croaker. The slope of the linear regression of 'otolith increments from the alizarin mark' on 'known days from the alizarin mark' was not

significantly different than 1 ($b=0.9831 (\pm 0.017 \text{ SE})$, $t\text{-stat}=56.26$, $p<0.001$). Further, the y-intercept of the regression was not significantly different than zero ($a=0.3055 (\pm 0.46 \text{ SE})$, $t\text{-stat}=0.67$, $p>0.05$). There was also a positive and significant relationship for the regression of post-ingress otolith growth with somatic growth over the same time interval ($y = 17.882x + 1.036$; $r^2 = 0.4023$), which suggests that early juvenile Atlantic croaker otolith growth generally follows somatic growth.

There was no evidence of larval growth-inertia in the laboratory experiment. Pearson correlation coefficients between larval otolith growth and subsequent juvenile somatic growth ($r = 0.05$), and between larval otolith growth and juvenile otolith growth ($r=0.20$) were not significantly different than zero (Figure 2). The multiple regression with average somatic juvenile growth as the dependent variable and length- and age-at-ingress, and average larval otolith growth as factors suggested that these factors, reflecting larval history, explained a small portion of subsequent juvenile growth ($r^2 = 0.2178$, $p<0.0001$). The coefficients of partial determination indicated that length-at-ingress was the only statistically significant factor and explained 14% ($t = -3.47$, $p<0.0001$) of the variation in somatic juvenile growth: smaller fish-at-ingress grew faster than larger fish-at-ingress.

Field Study

The occurrence of significant correlations between larval and juvenile growth had a similar temporal pattern between estuaries. Significant correlations for the same weekly fall 2002 cohort was found in both the Newport and White Oak River estuaries and in spring 2003 three significant correlations in the Newport corresponded with one

significant and two moderately non-significant ($p < 0.15$) correlations in the White Oak River (Figure 3, Table 1).

The multiple regression of the larval-growth inertia correlation coefficients with abiotic and biotic factors was highly significant ($r^2 = 0.74$ $p < 0.01$). Variance inflation factors were < 10 for all independent variables suggesting multicollinearity was not a problem (Neter et al. 1996). The coefficients of partial determination revealed that variation in the LGI correlation coefficient was significant and positively accounted for by the proportion of fish that had empty stomachs (56%, $t = 4.34$, $p < 0.001$), individual condition (26%, $t = 2.3$, $p < 0.05$), and change in salinity (27%, $t = -2.35$, $p < 0.05$; Figure 4a,b,c). These results indicate that following periods of freshwater runoff, when feeding conditions were poor, fish with relatively high condition had a positive relationship between larval and juvenile growth.

DISCUSSION

Although there was no evidence for compensatory growth or larval-growth-inertia (LGI) in the controlled lab experiment, field study results suggest that LGI was expressed only when croaker were flushed down-estuary to presumably low-food habitats during high rainfall events (see below). Despite lack of LGI in the laboratory study, there was evidence that larval history could influence juvenile traits, as there was a weak negative relation between length-at-ingress and subsequent juvenile growth. Fish that were smaller at ingress grew faster during the initial post-ingress period allowing them to reduce the size difference with fish that had ingressed at larger sizes. This result is consistent with previously reported results from a variety of taxa which suggest that

length differences at the larval-juvenile transition do not continue to diverge during the juvenile period (Goater 1994, Searcy and Sponaugle 2000).

One criticism of the laboratory portion of this study, as well as other studies conducted in controlled environments, is the degree to which experimental conditions reflect what actually occurs in natural environments. This is particularly important in studies that have management implications, as misleading information only hinders effective policy implementation. In the laboratory study, by using wild-caught fish it was possible to determine how natural growth variability transferred to patterns of juvenile growth without the confounding effects of variable abiotic conditions, feeding environments, intra- and inter-specific competition and predation. Such baseline data from a controlled laboratory environment are critical so that if results in field studies deviate from expectation likely proximate causes can be explored.

In the field component of this project, results don't support the occurrence of compensatory growth or general acceptance of larval growth inertia, except during certain extreme events associated with high levels of freshwater runoff (as evidenced by a rapid decline in salinity to near 0 ppt; Fig. 3), in which larval and juvenile growth may be correlated following periods of poor feeding success (partial correlation results). As juvenile Atlantic croaker typically occupy low-salinity habitats (e.g., Weinstein 1979, Ross 2003), occurrence of LGI is likely related to reduced feeding success caused by high levels of freshwater runoff flushing prey from Atlantic croaker nursery areas rather than salinity-induced physiological constraints. Overall, this study supports the observation that juvenile environment, either through feeding conditions (current study) or predator environment (McCormick and Hoey 2004) can influence the relationship of

growth across life history stages. Occurrence of LGI cautions against the use of early juvenile growth as an index of habitat quality, especially for organisms that inhabit dynamic environments.

The observation that larval-growth-inertia was most prevalent during periods of low feeding success may be explained by two non-exclusive scenarios. First, rapid larval otolith growth may be associated with higher early-juvenile condition such that fast growing larvae had higher condition (Hovenkamp and Witte 1991, McCormick and Molony 1992, Suthers et al. 1992), and consequently were able to continue growing faster within juvenile nursery environments. This is supported by the partial correlation results, which suggest that cohorts that have higher condition (fatter) are more likely to have a larger LGI correlation coefficient. Another possibility that may explain LGI results is that rapid larval growth is positively related to development of juvenile feeding structures, such that individuals that were faster growing as larvae are better able to feed as juveniles during low food conditions (McCormick and Molony 1992, Pechenik et al. 1998). Indeed, juvenile Atlantic croaker do have slow development of sense organs and feeding structures (Chao and Musick 1977), which is consistent with LGI having a developmental basis. Regardless, if the observed larval-growth-inertia during periods of low feeding success is associated with physiological condition or development, estimates of habitat quality based on early juvenile otolith increments can clearly be affected by larval growth.

It is important to note that the larval-growth-inertia relationship would not have been observed had this study simply ended with the laboratory component, or if the field study had not spanned a wide-range of environmental conditions. Results suggest that

the underlying intrinsic growth relationship of no LGI (as found in our laboratory experiment as well as most cohorts in our field study) may be disrupted by extrinsic factors. Indeed, if the larval-juvenile growth relationship is positively associated with low feeding success, LGI may be applicable as an indicator of early juvenile feeding success. Overall, the implications of this study suggest that it is important to consider larval history, especially if juvenile mortality is size- or growth-dependent, as well as if juvenile traits are used to infer quality of the juvenile environment. Future work on other organisms should recognize the role dynamic environments play in the ability to detect dependence of traits between earlier and later ontogenetic stages.

ACKNOWLEDGMENTS: We are grateful to N. Reyns, H. Sandstrom, M. Lewis, P. McDougall, for help during fieldwork and E. Laban, and M. Wuenschel for advice on laboratory components of this project. This manuscript benefited from reviews by JK. Craig, M. Wuenschel. This work was supported by the National Sea Grant Office, the National Science Foundation (OCE 0221099), Sigma-Xi, PADI-AWARE, and Budweiser conservation scholarships to SPS.

LITERATURE CITED

- Ahrenholz, D. W., G. R. Fitzhugh, J. A. Rice, S. W. Nixon, and W. C. Pritchard. 1995. Confidence of otolith ageing through the juvenile stage for Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin **93**:209-216.
- Altwegg, R., and H.-U. Reyer. 2003. Patterns of natural selection on size at metamorphosis in water frogs. Evolution **57**:872-882.
- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Quarterly review of biology **72**:149-177.
- Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology **71**:1599-1608.
- Bradshaw, W. E., and K. Johnson. 1995. Initiation of metamorphosis in the pitcher-plant mosquito: effects of larval growth history. Ecology **76**:2055-2065.
- Chambers, R. C., and T. J. Miller. 1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. Pages 155-175 in D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. University of South Carolina Press.
- Chao, L. N., and J. A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River Estuary, Virginia. Fishery Bulletin **75**:657-702.
- Goater, C. P. 1994. Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. Ecology **75**:2264-2274.
- Hettler, W. F., and A. J. Chester. 1990. Temporal distribution of ichthyoplankton near Beaufort inlet, North Carolina. Marine Ecology Progress Series **68**:157-168.

- Hovenkamp, F., and J. I. J. Witte. 1991. Growth, otolith growth and RNA/DNA ratios of larval plaice *Pleuronectes platessa* in North Sea 1987-1989. Marine Ecology Progress Series **70**:105-116.
- Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). Netherlands Journal of Sea Research **9**:69-85.
- Kuipers, B. R., B. Maccurrin, J. M. Miller, H. W. Van der Veer, and J. I. J. Witte. 1992. Small trawls in juvenile flatfish research: their development and efficiency. Netherlands Journal of Sea Research **29**:109-117.
- McCormick, M. I., and A. S. Hoey. 2004. Larval growth history determined juvenile growth and survival in a tropical marine fish. Oikos **106**:225-242.
- McCormick, M. I., and B. W. Molony. 1992. Effects of feeding history on the growth characteristics of a reef fish at settlement. Marine Biology **114**:165-173.
- Metcalf, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution **16**:254-260.
- Necaise, A. M. D., S. W. Ross, and J. M. Miller. 2005. Estuarine habitat evaluation measured by growth of juvenile summer flounder *Paralichthys dentatus* in a North Carolina estuary. Marine Ecology Progress Series **285**:157-168.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models. Irwin, Chicago, Illinois, USA.
- Pechenik, J. A., D. E. Wendt, and J. N. Jarrett. 1998. Metamorphosis is not a new beginning. BioScience **48**:901-910.
- Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology **83**:2562-2574.

- Relyea, R. A., and J. T. Hoverman. 2003. The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. *Oecologia* **134**:596-604.
- Reznick, D. N. 1990. Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): an experimental evaluation of alternative models of development. *Journal of Evolutionary Biology* **3**:185-203.
- Ross, S. W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin* **101**:384-404.
- Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**:413-427.
- Rozas, L. P., and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* **20**:199-213.
- Searcy, S., and S. Sponaugle. 2000. Variable larval growth in a coral reef fish. *Marine Ecology Progress Series* **206**:213-226.
- Searcy, S., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* **82**:2452-2470.
- Sogard, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* **85**:35-53.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**:1129-1157.
- Suthers, I. M., A. Fraser, and K. T. Frank. 1992. Comparison of lipid, otolith and morphometric condition indices of pelagic juvenile cod *Gadus morhua* from the Canadian Atlantic. *Marine Ecology Progress Series* **84**:31-40.

- Taylor, B. W., C. R. Anderson, and B. L. Peckarsky. 1998. Effects of size at metamorphosis on stonefly fecundity, longevity, and reproductive success. *Oecologia* **114**:494-502.
- Thorrold, S. R., and J. A. Hare. 2002. Otolith applications in reef fish ecology. Pages 243-264 *in* P. F. Sale, editor. Coral Reef Fishes. Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin* **77**:339-357.

Table 1. *Micropogonias undulatus*. Relationship between cohort specific larval and subsequent juvenile growth using Pearson correlation coefficients for fish collected in the White Oak and Newport River Estuaries, NC. Fall (or Spring) cohorts for each estuary compare average larval growth for 20-29 (31-40) days post-hatch with average juvenile growth for 40-44 (50-54) days post-hatch. Significant (Sig.) correlations ($P < 0.05$) are denoted by *, and moderately non-significant correlations ($P < 0.15$) by MNS.

	Hatch-date	White Oak River Estuary				Newport River Estuary			
		n	corr.	p	sig.	n	corr.	p	sig.
Fall 2001	15-21 Oct	-				22	0.01	0.97	
	22-28 Oct	-				12	0.20	0.53	
	29 Oct – 4 Nov	-				17	0.57	0.02	*
Spring 2002	23-30 Dec	9	0.06	0.37		13	0.10	0.75	
	1-7 Jan	14	0.09	0.75		9	0.48	0.19	
	8-14 Jan	12	0.10	0.75		9	0.58	0.19	
Fall 2002	22-28 Sep	11	0.43	0.19		-			
	7-14 Oct	23	0.44	0.03	*	10	0.80	0.003	*
	22-30 Oct	30	0.11	0.57		27	0.19	0.34	
	1-7 Nov	-				19	0.51	0.03	*
Spring 2003	1-7 Jan	9	0.53	0.14	MNS	10	-0.21	0.46	
	8-14 Jan	20	0.28	0.24		11	0.17	0.62	
	15-21 Jan	36	0.39	0.02	*	39	0.45	0.005	*
	22-28 Jan	64	0.18	0.15	MNS	37	0.43	0.008	*
	29 Jan – 4 Feb	41	0.25	0.1	MNS	58	0.37	0.004	*
	5-11 Feb	23	0.24	0.27		34	0.21	0.24	

FIGURE LEGENDS

Figure 1. Location of White Oak River and Newport River estuaries, North Carolina, USA. Inset shows location of upper-estuary beam-trawl (triangles) and deployment site of YSI-6600 multiparameter dataloggers (crosses).

Figure 2. *Micropogonias undulatus*. Relationship between larval otolith growth and juvenile somatic growth (A) and juvenile otolith growth (B) for fish that survived the duration of the laboratory experiment (n=80). Pearson correlation coefficients were non-significant: $r = 0.05$ and 0.20 respectively.

Figure 3. *Micropogonias undulatus*. Relationship between salinity (upper portion of figure) and significant correlations between larval and juvenile growth (lower portion of figure) for weekly cohorts of croaker collected in the White Oak (A, C) and Newport River estuaries (B, D), North Carolina, USA. Both significant ($P < 0.05$) and non-significant juvenile intervals upon which each correlation is based are represented by separate dashes. Juvenile intervals that had a moderately non-significant ($P < 0.15$) relationship between larval and juvenile growth are represented by two dots (C.). In the White Oak River estuary no collections were made in Fall 2001 (A) and no salinity data are available for winter 2002-2003 (C.).

Figure 4. *Micropogonias undulatus*. Regression between larval growth inertia correlation coefficient and (A) proportion of empty stomachs ($y = 0.57x + 0.1$, $R^2 = 0.22$); (B) residual of condition $y = 0.11x - 0.03$, $R^2 = 0.04$; and (C) change in salinity, $y = -6.8x + 2.1$, $R^2 = 0.16$. Dashed lines are 95% confidence intervals.

Figure 1.

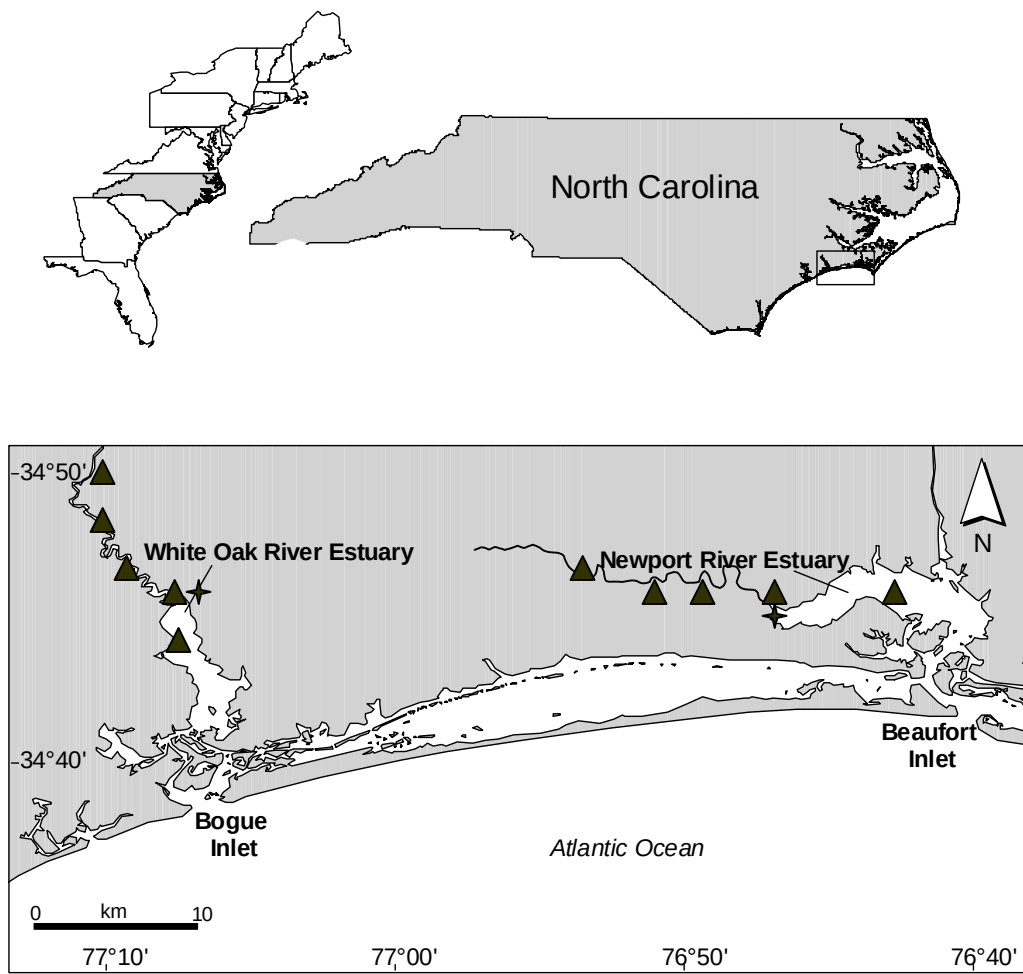


Figure 2.

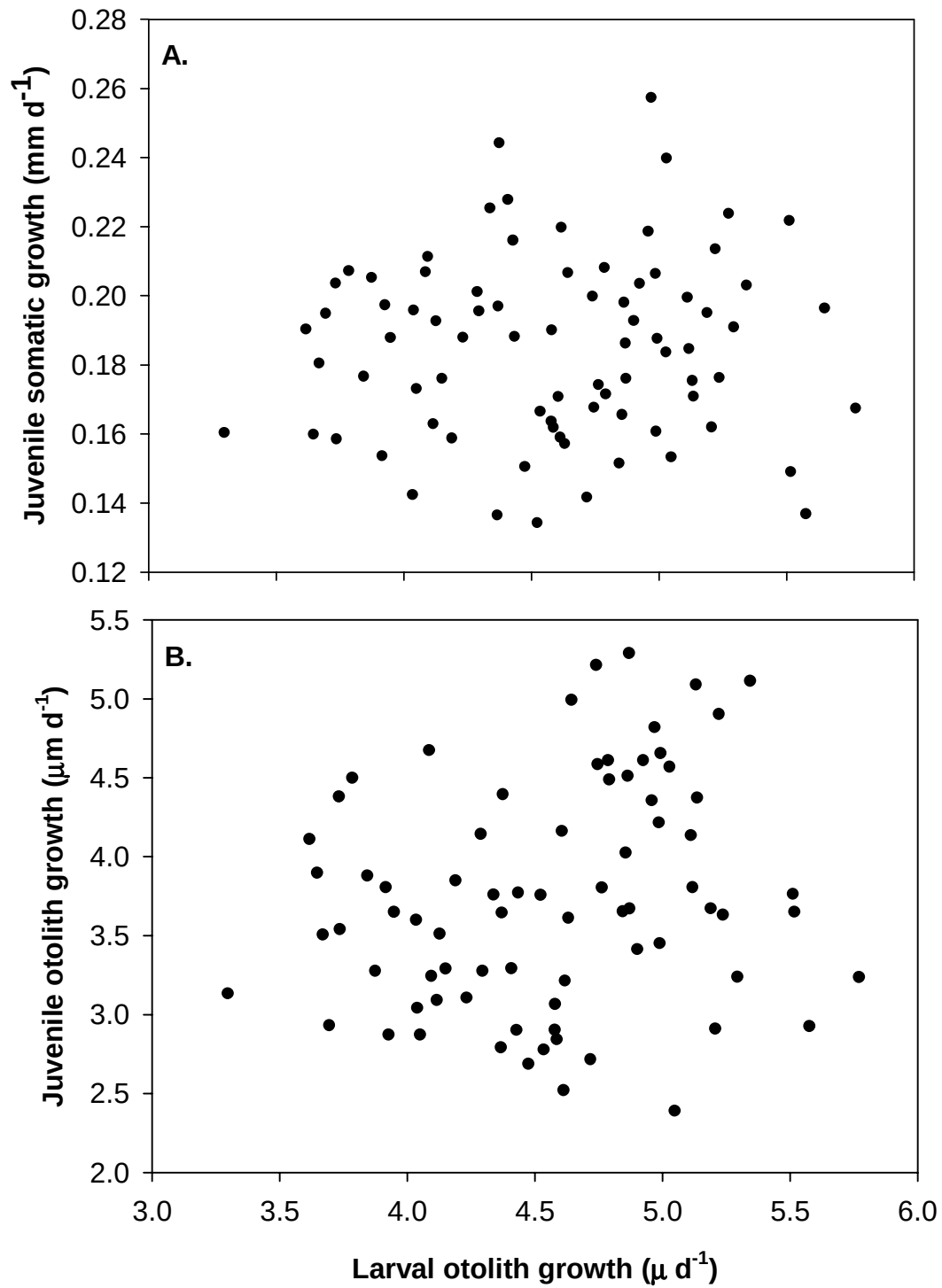


Figure 3.

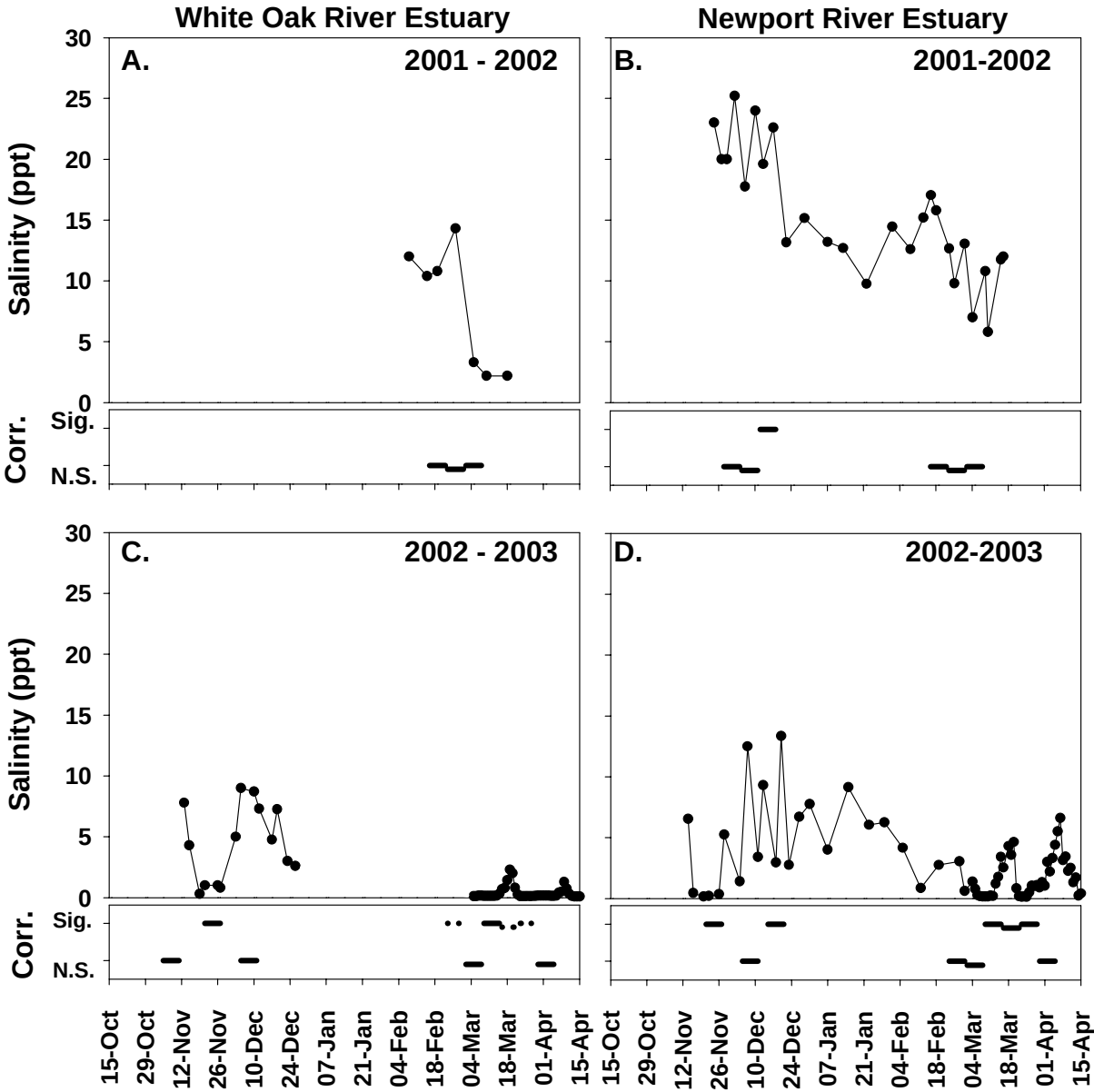
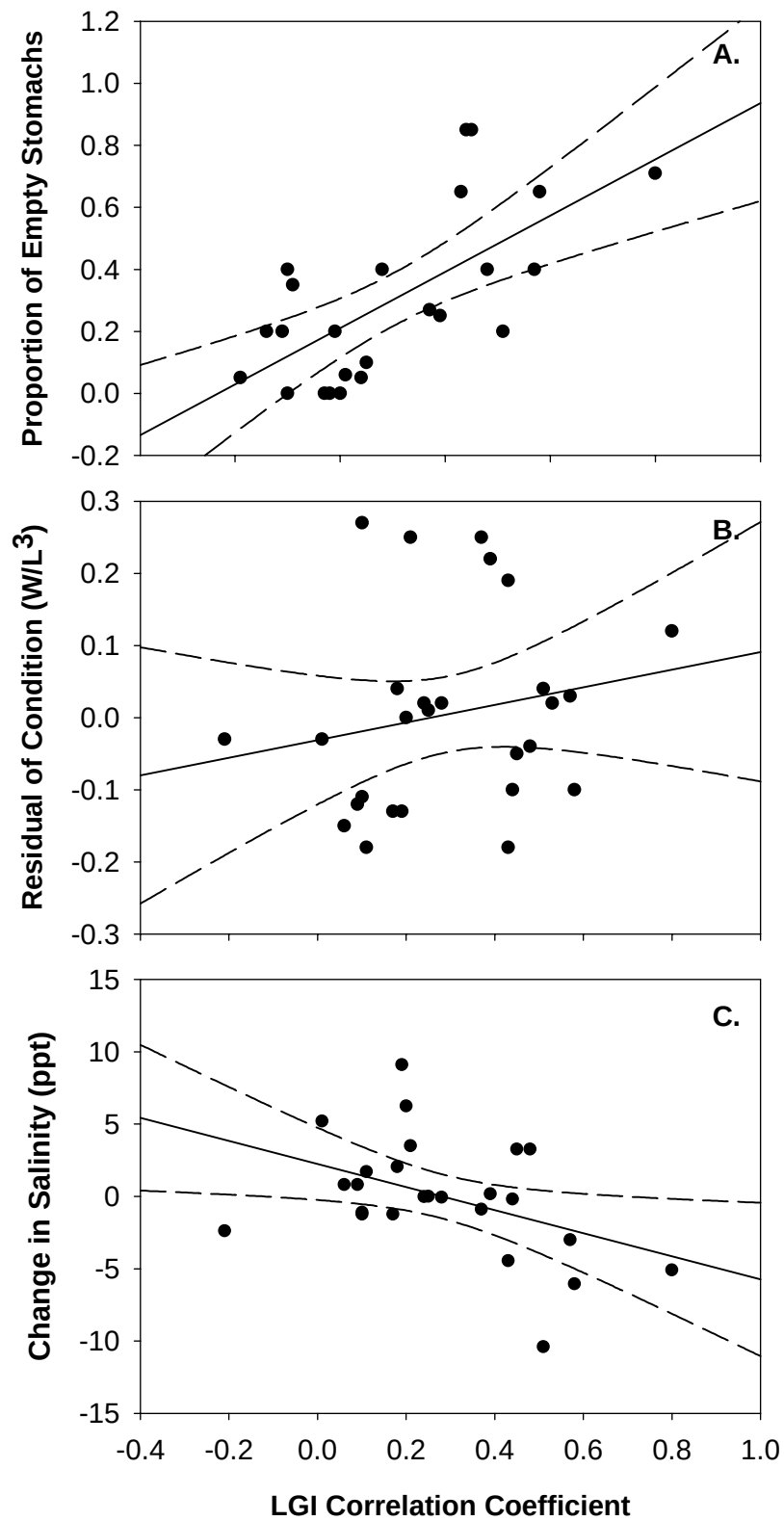


Figure 4.



CHAPTER 3

Is growth a valid indicator of juvenile fish nursery habitat quality?

ABSTRACT

A common assumption throughout the marine ecological and fisheries literature is that growth is a valid indicator of habitat quality and that growth can be used as a criterion for designation of Essential Fish Habitat (EFH). It is critical that prior to assessing habitat quality or assignment of EFH according to growth, factors be considered that may bias growth-based assessment of habitat quality, such as previous growth history, density dependence, and selective mortality. In this study, the validity of growth as an index of habitat quality was tested using early juvenile Atlantic croaker, *Micropogonias undulatus*, a common estuarine-dependent fish along the Atlantic and Gulf coasts of the U.S. as a model species. Juvenile Atlantic croaker were collected using a 1-m beam trawl within juvenile nursery areas of two estuaries in North Carolina, USA, during two seasons, of two recruitment years. Analysis of otolith microstructure from 2,251 croaker provided estimates of individual growth rates and allowed identification of weekly hatch-date-cohorts. There was evidence for density-dependent growth (slower growth at higher conspecific abundance) in the Newport River estuary but not the White Oak River estuary, and selective mortality favoring croaker with faster larval and juvenile growth in both the White Oak River and Newport River estuaries. The results of this study suggest that unless alternative factors such as density dependence and selective mortality are addressed, growth-based assessment of habitat quality and EFH may reach incorrect conclusions regarding the value of different habitats.

INTRODUCTION

Worldwide, coastal development and degradation threaten nearshore and estuarine environments that are vital to the early growth and survival of many coastal fishery species (NRC 1992, Hinrichsen 1998). As a result, the quality of different juvenile nursery habitats must be evaluated accurately, so that the extent to which anthropogenic factors affect habitat quality can be documented and certain habitats can be prioritized for conservation and protection (Able 1999, Beck et al. 2001, Nécaise et al. 2005). Comparison of fish growth rates among habitats is one method that is often used to evaluate habitat quality of different estuarine nursery areas. It is assumed that larger, faster growing fish are healthier and have experienced more favorable abiotic and biotic conditions than smaller, slower growing fish (Guindon and Miller 1995, Baltz et al. 1998, Able et al. 1999, Meng et al. 2000, Phelan et al. 2000, Stunz et al. 2002, Nécaise et al. 2005). Growth may also be used as a criterion for identification of Essential Fish Habitat (EFH, NOAA 1996), with habitats that support rapid growth rates identified as ‘essential’ for maintenance of adult stocks.

Prior to the use of growth as an index of habitat quality or EFH, it is important to recognize that growth rates may be affected by mechanisms other than habitat quality such as selective mortality of slower (or faster) growing individuals, previous growth history, and negative density dependence (i.e., lower growth at higher conspecific densities). Incorporation of selective mortality into growth-based assessment of habitat quality is important because the removal of either slower or faster growing individuals from the population will bias interpretation of overall cohort growth. To date, the importance of fast growth to fish survival is supported in most (e.g., Meekan and Fortier

1996, Searcy and Sponaugle 2001, Bergenius et al. 2002), but not all field studies of larval and juvenile fishes (Litvak and Leggett 1992). Faster growing individuals may gain a survival advantage through a variety of mechanisms including predator avoidance, obtaining food, and withstanding starvation (reviewed in Sogard 1997). Ultimately, unless selective mortality is accounted for, spatial and temporal variations in growth rates may reflect differential loss of slower (or faster) growing individuals rather than environmentally based habitat quality.

Previous growth history may also influence interpretation of juvenile growth rates. For example, a variety of studies examining fish at the larval-juvenile transition have shown that faster growing larvae may continue to grow rapidly as juveniles through competitive advantages gained in size-based dominance hierarchies (Jones 1987, Forrester 1990, Booth 1995, Tupper and Boutilier 1995), developmental advantages associated with relatively faster growth (McCormick and Molony 1992), or because they have a fast-growing genotype (Conover and Present 1990). Alternatively, other studies have shown that some fish species may compensate for periods of reduced growth with a subsequent elevation in growth rates, allowing fish that experienced reduced growth to catch up in body size to individuals that did not experience reduced growth (e.g., compensatory growth, Jobling et al. 1994, Buckel et al. 1998, Sogard and Olla 2002, Hurst et al. 2005). Clearly, studies of growth rates need to be based on a firm understanding of both a species' life history characteristics as well as environmental history.

Finally, density dependent growth may be particularly important to recognize with regard to growth-based assessment of juvenile habitat quality, since high juvenile

densities in nursery areas may result in food limitation and reduced growth rates (reviewed in Cowan et al. 2000). In the context of evaluating habitat quality, however, density dependent growth presents an apparent dichotomy. Although habitats that support higher abundances of juvenile fishes are considered to be important nurseries (Baltz et al. 1993, Minello 1999, Goldberg et al. 2002, Minello et al. 2003, Ross 2003), higher fish densities that lead to a reduction in growth rates will diminish the perception of high habitat quality based solely on growth rate data. Unless alternative mechanisms that can influence growth are accounted for, growth based assessment of habitat quality may prioritize habitats for conservation (EFH) for the wrong reasons.

The objective of this study was to determine if growth is a valid indicator of habitat quality for the common estuarine fish, Atlantic croaker (*Micropogonias undulatus*). Specifically, back-calculated juvenile otolith growth rates were used to determine whether there was evidence for selective mortality influencing growth rates of weekly hatch-date cohorts, and, if so, how much average cohort growth can be altered by differential loss of either slower or faster growing individuals. Next, multiple regression analysis was used (1) to examine how abiotic and biotic factors typically associated with habitat quality (i.e., feeding success, predator abundance, competitor abundance, temperature, salinity) affect juvenile otolith growth of Atlantic croaker, and (2) after accounting for these effects, whether growth-based measures of habitat quality could be biased by previous larval growth history, density dependence, and selective mortality. Results from this study will test the assumption that high growth reflects “good” habitat for Atlantic croaker, and, if necessary, allow us to refine the use of growth as a criterion for identifying habitat quality and EFH.

MATERIALS AND METHODS

Atlantic croaker, *Micropogonias undulatus*, is an economically and ecologically important fish in southeastern United States and Gulf of Mexico estuaries. Along the east coast of the United States adults spawn on the continental shelf, and following offshore pelagic development, late-stage larvae ingress into estuaries and settle in low salinity nursery areas (Weinstein 1979, Ross 2003). Atlantic croaker is an ideal study species with which to investigate processes that influence early juvenile growth because juveniles typically remain in nursery creeks for the first year of development (Miller and Able 2002), and adults have a protracted spawning season along the southeastern U.S. which extends from August to May (Hettler and Chester 1990), allowing for tracking of multiple cohorts over a range of different environmental conditions.

Fish sampling and habitat characterization

Atlantic croaker growth was investigated in two similar, but spatially-distinct estuaries in southeast North Carolina, USA: Newport River and White Oak River (Figure 1). These estuaries were selected because they contain oligohaline nurseries that are isolated from other low-salinity habitats, thereby minimizing the chance of post-settlement immigration and emigration. In both estuaries, Atlantic croaker were tracked from initial ingress through the first month of estuarine residence. Late-stage larval Atlantic croaker entering the Newport River estuary were collected approximately 2 km inside Beaufort Inlet as part of an ongoing NOAA study monitoring larval ingress (Figure 1). At this site, larvae were sampled bi-weekly during maximum nighttime flood tide using a passively-fished 1 x 2 m neuston frame fitted with a 954 μm mesh net for four replicate samples of approximately 100 m³ each. Late-stage larvae entering the White

Oak River estuary were collected weekly from a station located approximately 5 km inside of Bogue Inlet (Figure 1) using the same method described above, but with a 1 x 0.5 m plankton net with 1 mm mesh.

Following inlet collections, juvenile Atlantic croaker (post-ingress individuals) were collected at stations expected to bracket Atlantic croaker nursery areas. Within each estuary, fish were collected weekly from a small boat (~6 m) using a 1 m beam trawl (1 mm mesh upper- and side-panels and a 3 mm mesh bottom-panel) at one mid-estuary and four riverine stations (Figure 1). In the Newport River estuary, collections were made for seven weeks during fall (November-December) and spring (February-April) of two recruitment seasons (2001-2002 and 2002-2003), and in the White Oak River estuary collections were made during spring 2002 and fall-spring 2002-2003. Due to the shallow nature of both estuaries, beam trawl tows were restricted to the last two hours of daytime floodtide and three replicate tows were made at each station, typically for one minute each, covering an area of ~ 60 m². Trawls were always pulled against prevailing currents and tow speed standardized by gauging speed against emergent features in the water (i.e., crab pot buoys and stakes) or the shoreline. Trawl samples were sorted in the field and all fishes were preserved in 95% ethanol. Beam trawl catch efficiency is known to vary according to species and size of the targeted animal (Kuipers 1975, Kuipers et al. 1992, Rozas and Minello 1997), and was not corrected for in this study (but see Searcy Chapter 1 for a discussion of beam trawl efficiency). For reference, density estimates ($\pm$ SE) of fish commonly collected in this study are provided in Appendices 1-10.

Temperature and salinity were measured at each sampling station using a handheld YSI-85 instrument (YSI, Yellow Springs, Ohio, USA). In the spring of 2003,

hourly measures of salinity and temperature were also obtained by deploying YSI-6600 multiparameter dataloggers at the head of each estuary (Figure 1). As a proxy for offshore water temperatures experienced by larvae during pelagic development, average daily water temperature near Beaufort inlet was acquired from records recorded at the NOAA Beaufort Laboratory (Figure 1).

Fish and otolith and processing

In the laboratory, fish collected from each sampling location were identified, and standard length of up to 50 randomly selected individuals of each species was measured to the nearest 0.1 mm. To estimate feeding success on each sampling date, 30 fish from the riverine stations were randomly chosen for stomach content analysis; feeding success for that date was recorded as the proportion of fish from each collection date that had empty stomachs.

For each sampling date, sagittal otoliths were dissected from 30 randomly selected croaker from the mid-estuary stations and a minimum of 30 randomly selected croaker collected from the riverine stations. The right sagitta was attached to a slide with mounting medium and archived. The left sagitta was mounted in epoxy, sectioned along both sides of the frontal plane using a dual blade low-speed ISOMET saw, and polished to the core. The polished otolith section was then examined using a transmitted light microscope at 400x with a rotating polarized filter placed between the light source and the first stage. Unclear otoliths and those with a nonlinear growth axis were discarded. The images of remaining otoliths were captured with a frame grabber and increment count and widths (distance between two sequential increments) were measured using

Image Pro Plus 4.5 image analysis software at 800x. One person read all otoliths twice independently. If the increment counts between the two readings differed by 0 to 2 increments (~5 %), then one reading was randomly chosen for further analysis. If the increment counts between the two readings differed by more than 2 increments, the otolith was read again. If the third reading was less than 2 increment counts away from a previous reading, then one of these two counts was randomly chosen for analysis. If the third reading was greater than two increments away from either previous reading, the otolith was discarded from analysis. In total, 1396 of 1550 (89%) otoliths read were kept from the Newport River estuary, and 855 of 1000 (86%) otoliths read were kept from the White Oak River estuary.

Data Analyses

Daily increment deposition and a positive relationship between otolith and somatic growth has been validated for Atlantic croaker (Searcy et al. in review). However, to avoid any error and assumptions of back-calculating somatic growth from otolith measurements, comparisons of larval and juvenile growth were based solely on otolith growth measurements (i.e., Chambers and Miller 1995, Searcy and Sponaugle 2001). It is also important to recognize that in many fishes otolith increments increase progressively in width as they grow. This ontogenetic increase in otolith width must be accounted for before factors influencing early growth can be examined (Rakocinski et al. 2000). In this study, to ensure that baseline patterns of otolith growth were constant over the ages of fish analyzed, otolith growth was analyzed over periods during which growth exhibited no ontogenetic changes in otolith width. Finally, it is also important to note

that this study utilizes length-based growth measures, which are a conservative measure of actual fish growth, and includes changes in both length and weight (Wootton 1990).

Selective Mortality

To determine whether relatively faster or slower growing Atlantic croaker from each weekly hatch-date cohort had higher mortality, back-calculated otolith growth over the same time period was compared between younger (initial group) and older (survivor group) fish collected. For example, larval otolith growth (growth prior to estuarine ingress) from 11- 30 d post hatch was averaged over two-day intervals and compared between collections from day of peak cohort abundance (initial group) and one week later (survivor group); similarly, daily juvenile otolith growth (growth following estuarine ingress) was measured for the week following peak cohort abundance and compared between collections one week (initial group) and two weeks (survivor group) following peak abundance.

Between-estuary contrasts of larval and juvenile otolith growth were made using the same initial and surviving groups (i.e., initial larval growth group from Newport River vs. initial larval growth group from White Oak River). Although selective mortality at one location can bias growth-based interpretation of habitat quality (difference between ‘real’ and ‘perceived’ growth), comparison of growth rates among locations may also be biased if there is spatial variation in selective mortality (i.e., selective mortality favoring rapid growth in one location and not another).

Otolith increment growth was natural log transformed as preliminary analysis indicated that variance in otolith increment width increased with age. Because otolith

growth measurements taken on individual fish were longitudinal in nature (i.e., sequential measurements were made on each otolith examined), a repeated-measures MANOVA (SAS System version 8.2) was used to test the null hypothesis that there was no difference in growth between initial and survivor groups of croaker (Chambers and Miller 1995). The statistic used for determining whether growth varied between initial and survivor groups in the repeated measures MANOVA analysis was the interaction term for Wilks' λ , which is based on the sample size, number of groups in the comparison, and number of growth intervals being analyzed (Chambers and Miller 1995).

Factors affecting juvenile growth

Separate multiple regression models for juvenile otolith growth were used to determine (1) the relative importance of biotic and abiotic factors that influence growth, and (2) how growth estimates may be biased by selective mortality, previous growth history, and density dependence. The initial multiple regression model included juvenile otolith growth (LN transformed) of each weekly hatch-date cohort as the dependent variable, and biotic explanatory variables of: (1) feeding success (proportion of juvenile croaker with empty stomachs for the week of peak cohort abundance), (2) standard length at ingress (from near inlet collections the week prior to peak cohort abundance in juvenile nurseries), (3) abundance of competitors (early juvenile flounder and spot <20mm) and (4) predators (flounder > 100 mm) the week of peak cohort abundance standardized to 15 minute CPUE in river nursery areas. Abiotic explanatory variables included (5) average water temperature, (6) average salinity, and (7) maximum change in salinity the week following peak cohort abundance. Prior to regression analyses, residual plots were examined for heteroscedasticity; observations that were outliers (Cook's $D < 4/n$ where

n= # of observations) were eliminated from the analysis. Normality was tested by examining the results of Proc Univariate (SAS System), and multicollinearity among independent variables was examined using variance inflation factors (Sokal and Rohlf 1995). To meet model assumptions, competitor and predator abundance were $\log(x+1)$ transformed, salinity and temperature were log-transformed, and feeding success was arcsine-square-root transformed. A stepwise, backwards elimination procedure was then used in the multiple regression analysis to reduce the number of independent variables. Backwards elimination starts with all predictors in the model, removes the variable that is least significant (largest P-value), and refits the model until all remaining variables are significant (in this study $P < 0.10$). The overall significance was tested with the adjusted R^2 value, and squared partial correlation coefficients were calculated to examine the proportion of variance explained uniquely by each independent variable.

To determine whether growth-based interpretation of juvenile croaker habitat quality could be biased by previous growth history (correlations between larval and juvenile growth), density-dependent growth (abundance of conspecifics), and selective mortality (see previous section), a separate multiple regression model was run for each estuary. Prior to statistical analysis, both larval and juvenile otolith growth were standardized across cohorts by taking the residuals of growth on water temperature (near-inlet water temperature for larval growth, and estuarine water temperature for juvenile growth; Figure 2). In the multiple regression analysis, the importance of previous growth history would be indicated by either a significant positive or negative relationship between residual juvenile growth and residual larval growth. Evidence for density-dependent growth would be supported by a negative relationship between residual

juvenile growth and average croaker abundance in riverine stations (standardized to 15 min CPUE between week of peak cohort abundance and week following). The importance of selective mortality (coded 1 for significant selection for faster larval or juvenile growth and 0 if non-significant) would be supported by relatively faster residual juvenile growth occurring for cohorts that had experienced significant selective mortality. As in previous multiple regression analyses, the overall significance was tested with the adjusted R^2 value, and squared partial correlation coefficients were calculated to examine the proportion of variance explained uniquely by each independent variable.

RESULTS

Selective mortality

Surviving-group early-juvenile Atlantic croaker had faster larval otolith growth in the White Oak River estuary for 2 of 15 cohorts (Table 1), and faster juvenile otolith growth in the White Oak River for 2 of 10 cohorts (Table 2) and the Newport River estuary for 3 of 14 cohorts (Table 2). The difference in mean otolith growth between initial and surviving groups ranged between 6 – 8% for larval otolith growth (Table 1), and 7 – 15% for juvenile otolith growth (Table 2). Based on estimates of instantaneous growth (Table 3), these otolith growth differences amount to somatic growth differences between 0.1 and 0.2 mm week⁻¹. Cohorts in which significant selective mortality was detected were not coherent in time between estuaries, suggesting that selective mortality acted independently within each estuary (Table 1, Table 2).

Between-estuary comparisons of larval and juvenile otolith growth for initial and survivor groups indicated that selective mortality of slower growing individuals may

have influenced between-estuary growth comparisons. For example, although larval otolith growth did not differ between initial groups collected in the White Oak and Newport River estuary (Table 4), analysis of the same period of growth from the ‘survivor group’ (collected one week later) had significantly faster larval otolith growth in the White Oak River estuary for two cohorts (23 October 2002 and 21 January 2003; Table 4). This between-estuary difference in larval growth for both cohorts was likely caused by significant selective mortality favoring faster larval growth in the White Oak River estuary but not the Newport River estuary (see Figure 3 for example of 21 January 2003 cohort). Interestingly, there were no between-estuary differences in juvenile ‘survivor group’ growth estimates for any of the cohorts (Table 5), and the only initial growth difference was for the same 21 January 2003 cohort that also exhibited selection for faster larval otolith growth. Therefore, while there is evidence that selective mortality may bias between estuary growth comparisons, overall juvenile growing conditions were likely similar within the White Oak River and Newport River estuaries.

Factors affecting juvenile growth

Juvenile otolith growth was significantly related to temperature and competitor abundance (Table 6). These two factors jointly explained explained 50% of the variability in juvenile otolith growth (Table 6), with temperature independently explaining more variation in juvenile otolith growth than competitor abundance (squared partial correlation coefficients were 39% and 10% for temperature and competitor abundance, respectively; Table 6).

To determine whether estimates of juvenile growth were biased by larval growth history, density dependence, or selective mortality, separate multiple regression analyses

were calculated for each estuary. In the White Oak River estuary, the three-factor multiple regression model was non-significant ($P=0.52$, Table 7, Figure 4). In the Newport River estuary, however, 51% of the variability in residual juvenile growth was explained by a negative relationship with conspecific abundance (squared partial correlation coefficient of 0.37), and a positive relationship with the occurrence of significant selective mortality (squared partial correlation coefficient of 0.43; Table 7, Figure 4). The significant negative relationship between residual juvenile growth and conspecific density suggests that Atlantic croaker growth in the Newport River estuary is density dependent, and the positive relationship with selective mortality suggests that relatively faster growing cohorts were those in which significant selective mortality for faster growth was detected. Ultimately, the dichotomy in multiple regression results between estuaries suggests that although density-dependence and selective mortality may influence juvenile growth, the importance of these factors may vary among nursery areas.

DISCUSSION

The main objective of this study was to determine if growth is a valid indicator of habitat quality using juvenile Atlantic croaker, *Micropogonias undulatus* as a model study species. Individual juvenile growth estimates were obtained from analysis of 2,251 otolith growth records collected during two fall-spring recruitment seasons in the White Oak and Newport River estuaries. Variability in juvenile otolith growth rates was explained by both selective mortality and density dependence, suggesting that growth is not a robust predictor of juvenile habitat quality.

Selective Mortality

Selective mortality favoring faster larval and juvenile Atlantic croaker otolith growth was found in both the White Oak and Newport River estuaries. The relationship between faster growth and higher survival is consistent with previous work examining selective mortality for larval and juvenile fishes (Searcy and Sponaugle 2001, Bergenius et al. 2002, Shima and Findlay 2002, Wilson and Meekan 2002, Hoey and McCormick 2004). In the current study, because selective mortality was examined between younger and older juvenile fish, selective mortality refers to the loss of juveniles related to previous larval or juvenile traits. For example, selection on growth rates likely reflects mortality of individuals with a characteristic associated with growth such as length or physiological condition. A variety of studies have shown that faster otolith growth and higher physiological condition are correlated (McCormick and Molony 1992, Suthers et al. 1992, Molony and Sheaves 1998), and both body length (Schmitt and Holbrook 1999) and physiological condition (Booth and Hixon 1999, Hoey and McCormick 2004) can influence the probability of survival of recently settled fishes.

Selective mortality of weekly hatch-date cohorts was not temporally consistent between the Newport and White Oak River estuaries. Thus, higher mortality of slow growing individuals was likely a function of conditions that varied within estuaries over time rather than characteristics associated with each cohort (i.e., range or variability in cohort growth rates). For example, Atlantic croaker entering both estuaries had identical patterns of larval growth (i.e., they experienced the same offshore environment, Table 1), however, rapid larval growth was only selected for in the White Oak River estuary. If slow growing larvae had characteristics that predestined them to higher mortality, it

should have been evident in both estuaries. Therefore, loss of slower growing individuals was likely caused by conditions specific to each estuary such as encounter with patchily distributed prey or predators (e.g., Weinstein et al. 1980, Able et al. 2001).

Regardless of the mechanism underlying selective mortality of juvenile Atlantic croaker, periodic loss of relatively slower growing individuals has important implications for growth-based assessment of habitat quality. The difference in otolith growth between the ‘initial’ and ‘survivor’ groups ranged between 6-15%, which is roughly equivalent to selective mortality results interpreted from previous studies (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Takasuka et al. 2003, Raventos and Macpherson 2005). Therefore, at a minimum, comparisons of growth between habitats that vary by $\leq 15\%$ need to be interpreted cautiously. Alternatively, since selective mortality in this study varied between-estuaries and over-time, direct incorporation of bias associated with selective mortality into growth estimates would need to be conducted for each individual growth comparison (i.e., cohort-by-cohort, or for each habitat).

Factors affecting juvenile growth

Water temperature was the most important environmental factor influencing juvenile Atlantic croaker growth in this study, with a linear relationship between growth and water temperature found within each estuary. This finding is consistent with previous work which has demonstrated that temperature is responsible for both spatial and temporal variations in juvenile fish growth rates (Sogard 1992, Lankford and Targett 1994, McCormick and Molony 1995, Rooker and Holt 1997, Baltz et al. 1998, Planes et

al. 1999). Other factors expected to influence juvenile Atlantic croaker growth such as fish size and feeding success were not significant in the multiple regression analysis. Although fish size is known to be an important factor influencing growth rates (e.g., Baltz et al. 1998), the relatively narrow range in size (i.e., 11-13mm for length at estuarine ingress) for each weekly hatch-date cohort may be one reason why fish size was not a statistically significant determinant in this study. The lack of a statistically significant relationship between juvenile growth and % of empty stomachs may reflect a temporal mismatch between daily growth estimates obtained from individual otolith increments and the once weekly measures of gut contents pooled across multiple individuals (which at best is an integral of feeding success over the previous day, Baltz et al. 1998). Future studies relating juvenile growth to feeding history will be better served by using a longer-term index of previous feeding success, such as total fish lipid content (e.g., Suthers et al. 1992).

After accounting for temperature, juvenile growth was significantly affected by selective mortality and conspecific density in the Newport but not the White Oak River estuary. Lack of a significant relationship between growth and selective mortality in the White Oak River is surprising considering that there was evidence for higher mortality of slower growing individuals in this estuary (previous section). The lack of a positive relationship between growth and selective mortality in the White Oak River estuary does not diminish the importance of selective mortality to interpretation of growth-based assessment of habitat quality, instead, it highlights the relatively coarse nature of including selective mortality as a binary variable in multiple regression analysis.

Ultimately, it is important to recognize that selective mortality can bias growth estimates even if occurrence of selective mortality is relatively rare or statistically supported.

Alternatively, evidence for density dependent growth of juvenile Atlantic croaker in the Newport River and not the White Oak River estuary suggests that the dynamics of factors influencing growth within each estuary should be considered independently.

Density dependent growth is typically associated with resource limitation caused by reduced feeding success (Cowan et al. 2000). Food, however, is not typically considered to be limiting in estuaries (e.g., Miller et al. 1991, Kneib 1993). Indeed, previous field studies of juvenile estuarine fishes (including Atlantic croaker) have failed to find any relationship between fish growth and their density (Ross 1992, Baltz et al. 1998, Eby et al. 2005). These studies, however, were conducted on older juvenile fishes when densities may not have been high enough to elicit a growth response at low food levels. In the current study, densities of juvenile Atlantic croaker were roughly equivalent between the White Oak and Newport River estuaries (Searcy Chapter 1), which suggests that a factor other than density may have led to food limitation. One possibility is that Atlantic croaker nursery habitat within the Newport River estuary was restricted by the presence of a shallow sill near the mouth of the Newport river (Kirby-Smith and Costlow 1989). The sill establishes a firm lower boundary for Atlantic croaker nursery habitat that restricts movement into the upper-estuary (Searcy Chapter 1), which may lead to local depletion of food resources and reduced growth at higher densities.

Finally, although larval growth history was not considered to be an important factor influencing juvenile growth in the current study, it's importance should not be discounted. Juvenile Atlantic croaker may have a positive correlation between larval and

juvenile otolith growth during non-feeding periods following hydrodynamic flushing from estuarine nursery areas (Searcy Chapter 2). Other studies have also found that episodic environmental events may influence subsequent growth rates. For example, compensatory growth is a relatively common phenomenon, whereby fish respond to periods of reduced growth with subsequent accelerated growth (reviewed in, Ali et al. 2003). In a recent laboratory study, juvenile halibut, *Hippoglossus stenolepis* that were exposed to low temperatures were able to compensate for slow growth by having 20% faster growth than a control group (Hurst et al. 2005). Clearly, lack of knowledge of previous environmental conditions that an individual was exposed to can lead to incorrect conclusions about factors influencing growth and growth-based assessment of habitat quality.

Conclusion

Growth is not a robust indicator of habitat quality for juvenile Atlantic croaker. There was evidence for selective mortality in the White Oak and Newport River estuaries that varied both spatially and temporally. Density-dependent growth occurred in the Newport but not the White Oak River estuary. Lack of consistent patterns in factors affecting growth both within and between estuaries suggest that unless alternative factors such as density dependence and selective mortality are addressed, growth-based assessment of habitat quality (and EFH) may reach incorrect conclusions regarding the value of different habitats.

Future studies that use growth-based assessment of habitat quality should either control or directly account for factors that bias estimates of growth rates. For example,

caging studies (e.g., Sogard 1992, Duffy et al. 1996, Phelan et al. 2000, Necaise et al. 2005) may be an appropriate way to control for previous growth history (by using fish of known history), density dependence (by stocking cages at a 'set' amount), and selective mortality (by excluding predators). Despite advantages that caging studies may have to controlling biases listed above, there are also difficulties associated with this experimental approach (reviewed in, Peterson and Black 1994). For example, cages may concentrate or remove nektonic food sources resulting in a corresponding increase or decrease in growth. Artificial confinement of fish to a small area may also reduce perception of growth-based habitat quality if fish typically move over a much larger area to obtain food, or would ordinarily move to avoid poor water quality. Clearly, growth-estimates obtained from caging studies are not universally applicable to all species or habitat types.

Directly accounting for bias associated with field estimates of growth rates may also be difficult. Although density may be used as a covariate to control for density-dependent effects on growth, controlling for selective mortality is more problematic. Selective mortality in this study varied between estuaries and over time, suggesting that to incorporate the effects of differential loss of faster (or slower) growing individuals, selective mortality needs to be investigated on a cohort-by-cohort basis.

Evaluation of habitat quality using fish growth rates may be inadequate to definitively differentiate quality in all but the most extreme conditions (i.e., severe anthropogenic impact, Able 1999). A better approach to investigating juvenile habitat quality is to use a multivariate approach that jointly considers the importance of density, growth, survival, and movement (i.e, habitat-specific juvenile fish production that

contributes to the adult stock). This approach, called the ‘nursery role hypothesis’, states that a habitat has relatively higher quality for juveniles of a particular species if “its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur” (Beck et al. 2001). Although the nursery role of different habitats may be difficult to test empirically (reviewed in Gillanders et al. 2003), misidentification, and failure to protect habitats that are most important may have a detrimental effect on adult populations.

LITERATURE CITED

- Able, K. W. 1999. Measures of juvenile fish habitat quality: Examples from a National Estuarine Research Reserve. Pages 134-147 in L. R. Benaka, editor. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Bethesda, Maryland.
- Able, K. W., J. P. Manderson, and A. L. Studholme. 1999. Habitat quality for shallow water fishes in an urban estuary: the effects of man-made structures on growth. *Marine Ecology Progress Series* **187**:227-235.
- Able, K. W., D. M. Nemerson, R. Bush, and P. Light. 2001. Spatial variation in Delaware Bay (USA) marsh creek fish assemblages. *Estuaries* **43**:441-452.
- Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* **4**:147-190.
- Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental biology of fishes* **53**:89-103.
- Baltz, D. M., C. Rakocinski, and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental biology of fishes* **36**:109-126.
- Beck, M. W., K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, M. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**:633-641.

- Bergenius, M. A., M. G. Meekan, D. R. Robertson, and M. I. McCormick. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**:521-525.
- Booth, D. J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* **76**:91-106.
- Booth, D. J., and M. A. Hixon. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. *Oecologia* **121**:364-368.
- Buckel, J. A., B. H. Letcher, and D. O. Conover. 1998. Effects of a delayed onset of piscivory on the size of age-0 bluefish. *Transactions of the American Fisheries Society* **127**:576-587.
- Chambers, R. C., and T. J. Miller. 1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. Pages 155-175 in D. H. Secor, J. M. Dean, and S. E. Campana, editors. *Recent developments in fish otolith research*. University of South Carolina Press.
- Conover, D. O., and T. M. C. Present. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* **83**:316-324.
- Cowan, J. H., K. A. Rose, and D. R. DeVries. 2000. Is density dependent growth in young-of-the-year fishes a question of critical weight? *Reviews in Fish Biology and Fisheries* **10**:61-89.
- Duffy, J. T., C. E. Epifanio, and J. S. Cope. 1996. Effects of prey density on the growth and mortality of weakfish *Cynoscion regalis* (Bloch and Schneider) larvae:

- experiments in field enclosures. *Journal of Experimental Marine Biology and Ecology* **202**:191-203.
- Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology Progress Series* **291**:249-261.
- Forrester, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**:1666-1681.
- Gillanders, B. M., K. W. Able, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* **247**:281-295.
- Goldberg, R., B. Phelan, J. Pereira, S. Hagan, P. Clark, A. Bejda, A. Calabrese, A. Studholme, and K. W. Able. 2002. Variability in habitat use by young-of-the-year winter-flounder, *Pseudopleuronectes americanus*, in three northeastern U.S. estuaries. *Estuaries* **25**:215-226.
- Guindon, K. Y., and J. M. Miller. 1995. Growth potential of juvenile southern flounder, *Paralichthys lethostigma*, in low salinity nursery areas of Pamlico sound, North Carolina. *Netherlands Journal of Sea Research* **34**:89-100.
- Hettler, W. F., and A. J. Chester. 1990. Temporal distribution of ichthyoplankton near Beaufort inlet, North Carolina. *Marine Ecology Progress Series* **68**:157-168.
- Hinrichsen, D. 1998. Coastal waters of the world: Trends, threats, and strategies. Island Press, Washington D.C.

- Hoey, A. S., and M. I. McCormick. 2004. Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia* **139**:23-29.
- Hurst, T. P., M. L. Spencer, S. M. Sogard, and A. W. Stoner. 2005. Compensatory growth, energy storage and behavior of juvenile Pacific halibut *Hippoglossus stenolepis* following thermally induced growth reduction. *Marine Ecology Progress Series* **293**:233-240.
- Jobling, M., O. H. Meloy, J. d. Santos, and B. Christiansen. 1994. The compensatory growth response of the Atlantic cod: effects of nutritional history. *Aquatics International* **2**:75-90.
- Jones, G. P. 1987. Some interactions between residents and recruits in two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **114**:169-182.
- Kirby-Smith, W. W., and J. D. Costlow. 1989. The Newport River estuarine system. UNC-SG-89-04, UNC Seagrant Publication, Beaufort, NC.
- Kneib, R. T. 1993. Growth and mortality in successive cohorts of fish larvae within an estuarine nursery. *Marine Ecology Progress Series* **94**:115-127.
- Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). *Netherlands Journal of Sea Research* **9**:69-85.
- Kuipers, B. R., B. Maccurrin, J. M. Miller, H. W. Van der Veer, and J. I. J. Witte. 1992. Small trawls in juvenile flatfish research: their development and efficiency. *Netherlands Journal of Sea Research* **29**:109-117.
- Lankford, T. E., and T. E. Targett. 1994. Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): effects of temperature and salinity on feeding, growth, and survival. *Marine Biology* **119**:611-620.

- Litvak, M. K., and W. C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Marine Ecology Progress Series* **81**:13-24.
- McCormick, M. I., and B. W. Molony. 1992. Effects of feeding history on the growth characteristics of a reef fish at settlement. *Marine Biology* **114**:165-173.
- McCormick, M. I., and B. W. Molony. 1995. Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Marine Ecology Progress Series* **118**:59-68.
- Meekan, M. G., and L. Fortier. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. *Marine Ecology Progress Series* **137**:25-37.
- Meng, L., C. Gray, B. Taplin, and E. Kupcha. 2000. Using winter flounder growth rates to assess habitat quality in Rhode Island's coastal lagoons. *Marine Ecology Progress Series* **201**:287-299.
- Miller, J. M., J. S. Burke, and G. R. Fitzhugh. 1991. Early life history patterns of Atlantic North American Flatfish: Likely (and unlikely) factors controlling recruitment. *Netherlands Journal of Sea Research* **27**:261-275.
- Miller, M. J., and K. W. Able. 2002. Movements and growth of tagged young-of-the-year Atlantic croaker (*Micropogonias undulatus* L.) in restored and reference marsh creeks in Delaware Bay, USA. *Journal of Experimental Marine Biology and Ecology* **267**:15-33.
- Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43-75 in L. R.

- Benaka, editor. Fish habitat: Essential fish habitat and rehabilitation. The American Fisheries Society, Bethesda, MD.
- Minello, T. J., K. W. Able, M. P. Weinstein, and C. G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* **246**:39-59.
- Molony, B. W., and M. J. Sheaves. 1998. Otolith increment widths and lipid contents during starvation and recovery feeding in adult *Ambassis vachelli* (Richardson). *Journal of Experimental Marine Biology and Ecology* **221**:257-276.
- Necaise, A. M. D., S. W. Ross, and J. M. Miller. 2005. Estuarine habitat evaluation measured by growth of juvenile summer flounder *Paralichthys dentatus* in a North Carolina estuary. *Marine Ecology Progress Series* **285**:157-168.
- NOAA. 1996. Magnuson-Stevens Fishery Conservation and Management Act amended through 11 October 1996. National Marine Fisheries Service, National Oceanic and Atmospheric Administration technical memorandum NMFS-F/SPO-23. U.S. Department of Commerce. Washington, D.C.
- NRC. 1992. Restoration of aquatic ecosystems: Science, technology, and public policy. National Academy Press, Washington, D.C.
- Peterson, C. H., and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Marine Ecology Progress Series* **111**:289-297.
- Phelan, B. A., R. Goldberg, A. Bejda, J. Pereira, S. Hagan, P. Clark, A. L. Studholme, A. Calabrese, and K. W. Able. 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes*

- americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. Journal of Experimental Marine Biology and Ecology **147**:1-28.
- Planes, S., E. Macpherson, F. Biagi, A. Garcia-Rubies, J. Harmelin, M. Harmelin-Vivien, J.-Y. Jouvenel, L. Tunesi, L. Vigliola, and R. Galzin. 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. Journal of the Marine Biological Association of the United Kingdom **79**:137-143.
- Rakocinski, C. F., B. H. Comyns, and M. S. Peterson. 2000. Relating environmental fluctuation and the early growth of estuarine fishes: ontogenetic standardization. Transactions of the American Fisheries Society **129**:210-221.
- Raventos, N., and E. Macpherson. 2005. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Marine Ecology Progress Series **285**:205-211.
- Rooker, J. R., and S. A. Holt. 1997. Utilization of sub-tropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: patterns of distribution and growth. Marine Ecology Progress Series **158**:139-149.
- Ross, S. W. 1992. Comparisons of population dynamics of juvenile spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and Atlantic menhaden (*Brevoortia tyrannus*) among diverse North Carolina estuarine nursery areas. Dissertation. North Carolina State University, Raleigh.
- Ross, S. W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. Fishery Bulletin **101**:384-404.

- Rozas, L. P., and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* **20**:199-213.
- Schmitt, R. J., and S. J. Holbrook. 1999. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* **80**:35-40.
- Searcy, S., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* **82**:2452-2470.
- Shima, J. S., and A. M. Findlay. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Marine Ecology Progress Series* **235**:303-309.
- Sogard, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* **85**:35-53.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**:1129-1157.
- Sogard, S. M., and B. L. Olla. 2002. Contrasts in the capacity and underlying mechanisms for compensatory growth in two pelagic marine fishes. *Marine Ecology Progress Series* **243**:165-177.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry The Principles and Practice of Statistics in Biological Research*, third edition. W.H. Freeman and Company, New York.
- Stunz, G. W., T. J. Minello, and P. S. Levin. 2002. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. *Marine Ecology Progress Series* **238**:227-236.

- Suthers, I. M., A. Fraser, and K. T. Frank. 1992. Comparison of lipid, otolith and morphometric condition indices of pelagic juvenile cod *Gadus morhua* from the Canadian Atlantic. Marine Ecology Progress Series **84**:31-40.
- Takasuka, A., I. Aoki, and I. Mitani. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Marine Ecology Progress Series **252**:223-238.
- Tupper, M., and R. G. Boutilier. 1995. Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. Journal of Experimental Marine Biology and Ecology **191**:209-222.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fishery Bulletin **77**:339-357.
- Weinstein, M. P., S. L. Weiss, and M. F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear estuary, North Carolina, USA. Marine Biology **58**:227-243.
- Wilson, D. T., and M. G. Meekan. 2002. Growth-related advantages for survival to the point of replenishment in coral reef fish *Stegastes partitus* (Pomacentridae). Marine Ecology Progress Series **231**:247-260.
- Wootton, R. J. 1990. Ecology of Teleost Fishes. Chapman and Hall, New York.

Table 1: Tests for selective mortality of larval otolith growth (11-30 d post-hatch) for Atlantic croaker cohorts within the White Oak River and Newport River estuaries, North Carolina, USA. Results are for repeated-measures MANOVAs between initial (back-calculated growth from day of peak abundance) and surviving groups of fish collected one week later. The symbol, --- indicates no comparison was possible, 'λ' is for Wilk's lambda, ** P<0.01, * P<0.05, NS P>0.05. Where significant, the number within the parentheses indicates the percent difference of average otolith growth between initial and surviving groups of croaker cohorts.

Season	Hatch	White Oak River estuary				Newport River estuary			
		λ	F	df	P (%)	λ	F	df	P (%)
Fall 2001	16-Oct	---	---	---	---	0.83	0.52	9,23	NS
	22-Oct	---	---	---	---	0.79	0.37	9,13	NS
Spring 2002	27-Dec	---	---	---	---	0.52	1.30	9,13	NS
	2-Jan	0.48	1.31	9,11	NS	---	---	---	---
	8-Jan	0.88	0.36	9,25	NS	0.70	1.14	9,24	NS
	14-Jan	0.85	0.29	9,15	NS	0.63	0.96	9,15	NS
	20-Jan	0.66	1.31	9,23	NS	---	---	---	---
	26-Jan	0.23	4.94	9,13	**(6%)	---	---	---	---
Fall 2002	5-Oct	0.64	1.35	9,22	NS	0.75	1.30	9,36	NS
	11-Oct	0.76	0.76	9,22	NS	0.77	1.59	9,47	NS
	17-Oct	0.74	1.20	9,31	NS	0.70	1.25	9,26	NS
	23-Oct	0.76	0.97	9,27	NS	0.74	1.29	9,34	NS
	29-Oct	0.49	1.14	9,10	NS	0.83	0.74	9,33	NS
Spring 2003	9-Jan	---	---	---	---	0.69	0.59	9,12	NS
	15-Jan	0.60	1.82	9,25	NS	---	---	---	---
	21-Jan	0.58	1.94	9,24	*(8%)	0.78	0.69	9,22	NS
	27-Jan	0.88	0.25	9,17	NS	0.53	1.61	9,17	NS
	2-Feb	0.79	0.54	9,18	NS	0.51	1.59	9,15	NS
	8-Feb	0.55	0.90	9,10	NS	0.71	1.07	9,24	NS

Table 2: Tests for selective mortality of juvenile otolith growth for Atlantic croaker cohorts within the White Oak River and Newport River estuaries, North Carolina, USA. Results are for repeated-measures MANOVAs between initial (week following peak abundance) and surviving groups of fish collected one week later. The symbol, --- indicates no comparison was possible, ‘ λ ’ is for Wilk’s lambda, ** $P < 0.01$, * $P < 0.05$, NS $P > 0.05$. Where significant, the number within the parentheses indicates the percent difference of average otolith growth between initial and surviving groups of croaker cohorts.

Season	Hatch	White Oak River estuary				Newport River estuary			
		λ	F	df	P (%)	λ	F	df	P (%)
Fall									
2001	22-Oct	---	---	---	---	0.46	2.97	6,15	*(7%)
Spring	27-Dec	---	---	---	---	0.91	0.18	6,11	NS
2002	8-Jan	---	---	---	---	0.64	0.85	6,9	NS
	14-Jan	---	---	---	---	0.62	1.85	6,18	NS
	20-Jan	0.17	5.58	6,7	*(15%)	---	---		---
	26-Jan	---	---		---	---	---		---
Fall	5-Oct	0.61	1.28	6,12	NS	0.31	4.51	6,12	*(7%)
2002	11-Oct	0.82	1.14	6,32	NS	0.80	0.95	6,23	NS
	17-Oct	0.82	0.49	6,14	NS	0.88	1.7	6,74	NS
	23-Oct	0.93	0.39	6,30	NS	0.71	1.7	6,24	NS
	29-Oct	---	---		---	0.90	0.78	6,42	NS
Spring	9-Jan	---	---		---	0.72	1.14	6,18	NS
2003	15-Jan	0.78	0.37	6,8	NS	---	---		---
	21-Jan	0.83	0.64	6,18	NS	0.83	0.92	6,26	NS
	27-Jan	0.57	3.59	6,29	**(10%)	0.94	0.34	6,34	NS
	2-Feb	0.71	0.87	6,13	NS	0.87	0.79	6,33	NS
	8-Feb	0.46	1.37	6,7	NS	0.46	2.97	6,15	*(10%)

Table 3: Somatic growth estimate for early juvenile Atlantic croaker collected in the White Oak and Newport River estuaries, North Carolina, USA. Regression equations listed for each seasonal collection are for the size-at-age relationship with the corresponding average specific growth. r^2 is the regression coefficient, n is the sample size, SE is standard error of the slope, p is probability, $*** < 0.0001$, and ‘sp. grw.’ is an abbreviation for specific growth.

Season	Regression	r^2	n	SE	p	sp. grw. (mm d ⁻¹)
A. White Oak River Estuary						
Spring 2002	$y = 0.215x + 2.353$	0.82	153	0.008	***	0.185
Fall 2002	$y = 0.229x + 2.837$	0.93	262	0.004	***	0.196
Spring 2003	$y = 0.173x + 3.868$	0.92	313	0.003	***	0.148
B. Newport River estuary						
Fall 2001	$y = 0.222x + 2.159$	0.72	93	0.015	***	0.190
Spring 2002	$y = 0.239x + 1.116$	0.74	119	0.013	***	0.205
Fall 2002	$y = 0.213x + 3.226$	0.79	408	0.005	***	0.183
Spring 2003	$y = 0.152x + 5.307$	0.90	320	0.003	***	0.130

Table 4: Repeated measures MANOVA results for between-estuary (White Oak River and Newport River estuaries, North Carolina, USA) comparisons of ‘initial’ and ‘survivor’ group larval otolith growth. The symbol ‘ λ ’ is for Wilk’s lambda, * $P < 0.05$, NS $P > 0.05$. Where significant, the text in parentheses indicates whether otolith growth was faster in the White Oak River (W) or Newport River (N) estuary.

Initial Group						Survivor Group				
Season	Hatch	λ	F	df	P		λ	F	df	P
Spring	8-Jan	0.71	1.58	9,34	NS		0.80	0.41	9,15	NS
2002	14-Jan	0.90	0.24	9,19	NS		0.63	0.73	9,11	NS
Fall	5-Oct	0.90	0.59	9,48	NS		0.39	1.73	9,10	NS
2002	11-Oct	0.71	1.14	9,25	NS		0.78	1.46	9,46	NS
	17-Oct	0.83	0.64	9,29	NS		0.76	1.01	9,29	NS
	23-Oct	0.85	0.49	9,26	NS		0.65	2.16	9,36	*(W>N)
	29-Oct	0.72	1.46	9,34	NS		0.69	1.40	9,28	NS
Spring	21-Jan	0.67	1.16	9,21	NS		0.53	2.42	9,25	*(W>N)
2003	27-Jan	0.60	0.94	9,13	NS		0.60	1.55	9,21	NS
	2-Feb	0.66	1.14	9,20	NS		0.63	1.51	9,23	NS
	8-Feb	0.69	1.13	9,23	NS		0.42	1.38	9,9	NS

Table 5: Repeated measures MANOVA results for between-estuary (White Oak River and Newport River estuaries, North Carolina, USA) comparisons of ‘initial’ and ‘survivor group’ juvenile otolith growth. The symbol ‘ λ ’ is for Wilk’s lambda, * $P < 0.05$, NS $P > 0.05$. Where significant, the text in parentheses indicates whether otolith growth was faster in the White Oak River (W) or Newport River (N) estuary.

Season	Hatch	Initial Group				Survivor Group			
		λ	F	df	P	λ	F	df	P
Fall 2002	5-Oct	0.80	0.52	6,13	NS	0.54	1.54	6,11	NS
	11-Oct	0.90	0.72	6,37	NS	0.87	0.44	6,18	NS
	17-Oct	0.93	0.68	6,57	NS	0.82	1.08	6,31	NS
	23-Oct	0.71	1.83	6,27	NS	0.95	0.24	6,27	NS
Spring 2003	21-Jan	0.68	2.15	6,28	*W>N	0.82	0.59	6,16	NS
	27-Jan	0.75	1.80	6,33	NS	0.87	0.72	6,30	NS
	2-Feb	0.76	1.95	6,37	NS	0.58	1.10	6,9	NS
	8-Feb	0.50	1.98	6,12	NS	0.62	1.01	6,10	NS

Table 6. Factors selected as significant ($P < 0.10$) for multiple regression analysis of juvenile croaker otolith growth with data from the White Oak and Newport River estuaries pooled. Listed are regression parameters (par.) and squared partial correlation coefficients for the independent variables of temperature, and log (x+1) transformed competitor abundance.

Model	Par.	df	Par. estimate	Std. error	t	P > t 	Partial corr²
Adj. $R^2 = 0.50$	Intercept	1	1.700	0.056	30.45	< 0.0001	.
$F_{2,27} = 15.78$	Temperature	1	0.019	0.005	4.18	< 0.001	0.39
$P < 0.0001$	Competitor	1	0.019	0.011	1.75	= 0.09	0.10

Table 7. Regression parameters (par.) and squared partial correlation coefficients for multiple regression analysis of residual juvenile croaker otolith growth (corrected for water temperature) within the White Oak and Newport River estuaries, North Carolina, USA. Independent variables included the abundance of juvenile Atlantic croaker averaged between one and two weeks following peak cohort abundance (15 minute CPUE, log transformed), residual larval otolith growth (larval grw., corrected for offshore water temperature), and the occurrence of significant selective mortality (sel. mort.) on juvenile growth evident the first week following peak abundance.

Model	Par.	df	Par. estimate	Std. error	t	P > t	Partial corr ²
White Oak River Estuary							
Adj. R ² = -0.05	Intercept	1	-0.019	0.252	-0.08	= 0.94	.
F _{3,9} = 0.79	Croaker	1	0.006	0.041	0.15	= 0.88	.
P = 0.52	Larval grw.	1	-0.714	0.467	-1.53	= 0.16	.
	Sel. Mort.	1	-0.004	0.004	-0.86	= 0.41	.
Newport River Estuary							
Adj. R ² = 0.51	Intercept	1	0.099	0.051	1.94	= 0.08	.
F _{3,10} = 5.90	Croaker	1	-0.022	0.009	-2.42	< 0.05	0.37
P < 0.05	Larval grw.	1	-0.35	0.219	-1.60	= 0.14	.
	Sel. Mort.	1	0.045	0.017	2.74	< 0.05	0.43

FIGURE LEGENDS

Figure 1. Location of White Oak and Newport River estuaries, North Carolina, USA.

Inset shows location of beam-trawl stations (triangles) and deployment site of YSI-6600 multiparameter dataloggers (crosses).

Figure 2. Relationship between (A) nearshore water temperature and average natural log transformed larval Atlantic croaker otolith growth (11-30d post-hatch), and (B) estuarine water temperature and average natural log transformed Atlantic croaker juvenile otolith growth (first week following peak croaker abundance).

Figure 3. Comparison of (A) larval Atlantic croaker otolith growth between initial groups (collected at peak abundance) and survivor groups (collected one week later) within the White Oak and Newport River estuaries, North Carolina, USA; and (B) between-estuary comparisons of initial and survivor groups. For reference, significance of repeated measures MANOVA for each comparison is noted within the text of each figure.

Figure 4. Relationship between dependent (residual juvenile growth corrected for estuarine water temperature) and independent variables used in multiple regression analyses. Atlantic croaker abundance (15 min CPUE) of weekly hatch-date cohorts corresponds to average total number of croaker collected between peak and the week following peak abundance in riverine nursery areas. Residual larval growth was corrected for offshore water temperature. Bottom panels indicate whether significant

selective mortality was found for either larval (11-30 d post hatch) or juvenile (week following peak ingress) periods. See Table 7 for regression parameters.

Figure 1.

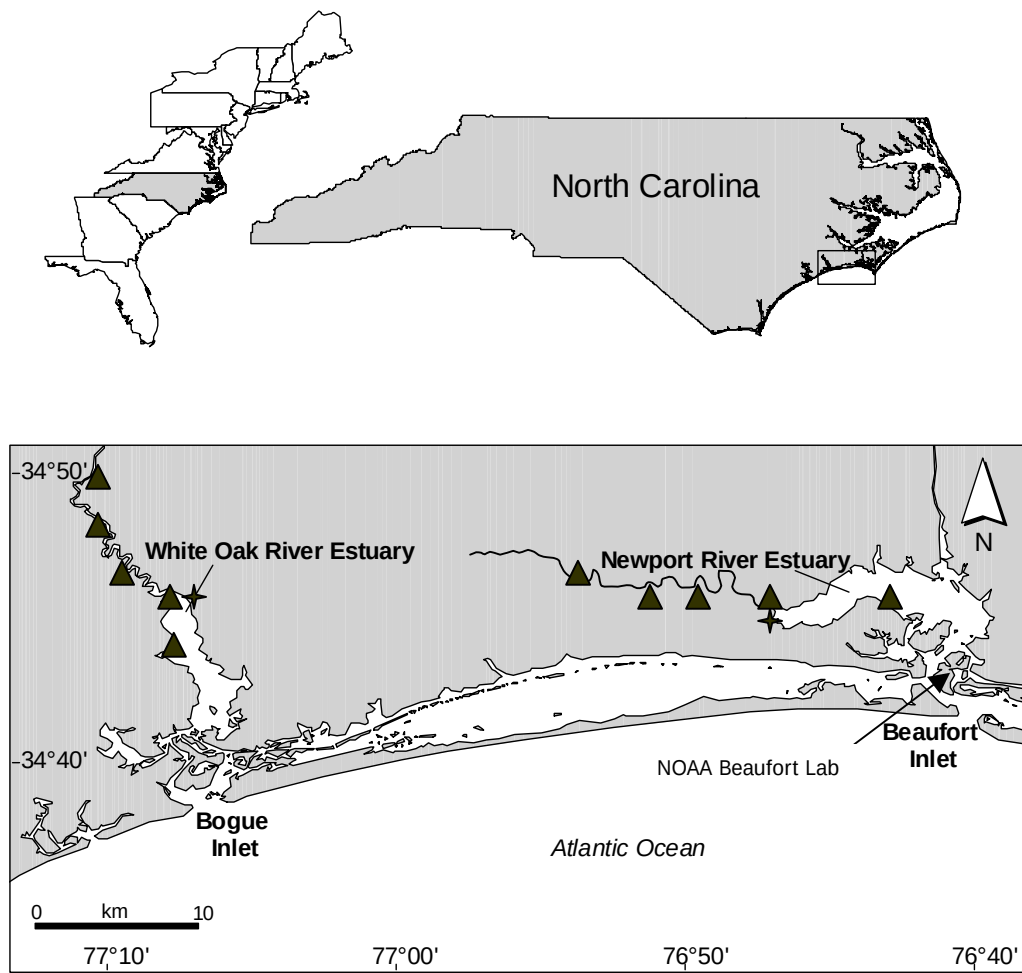


Figure 2.

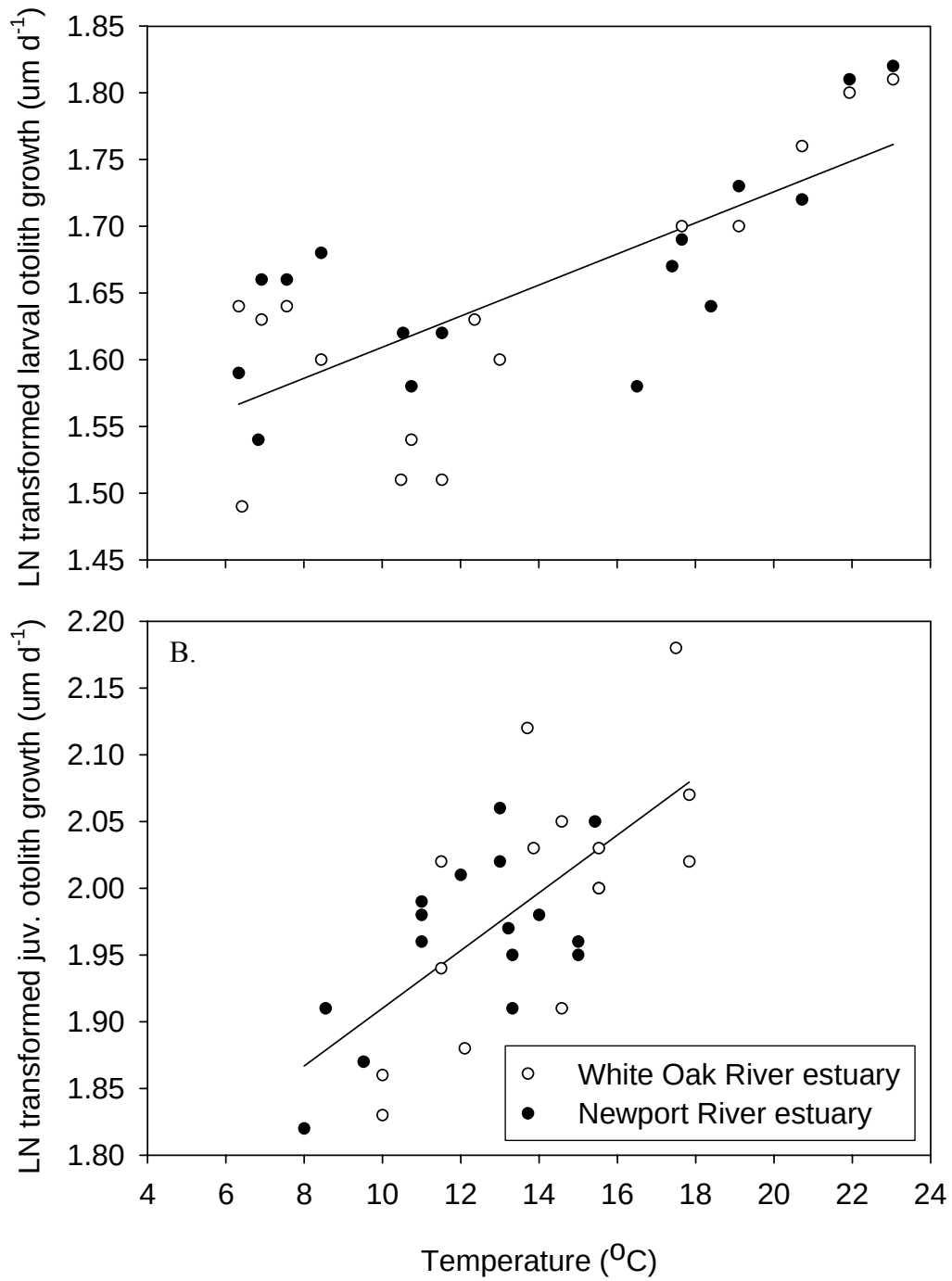
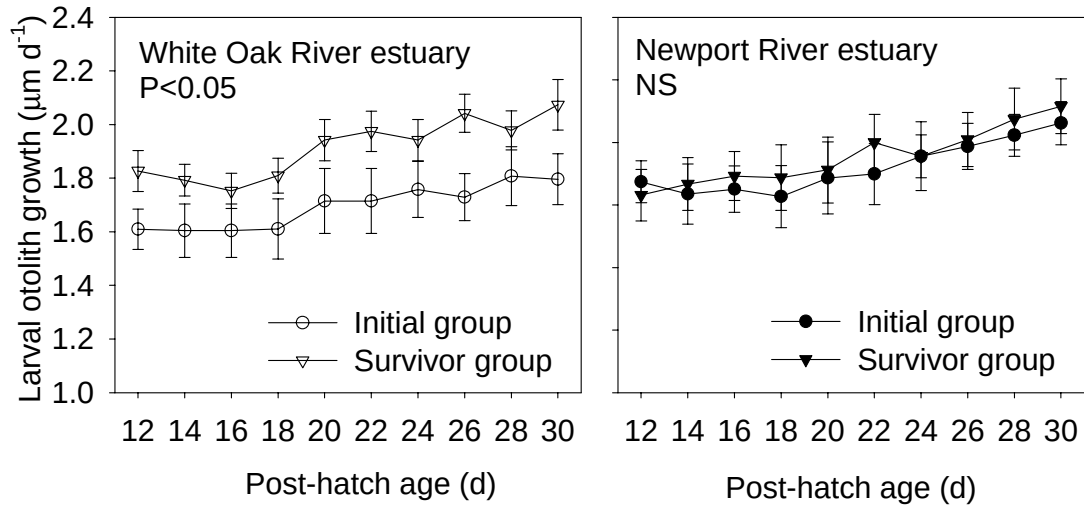


Figure 3.

A. Within estuary comparison of initial and survivor groups



B. Between estuary comparisons of initial group and survivor groups

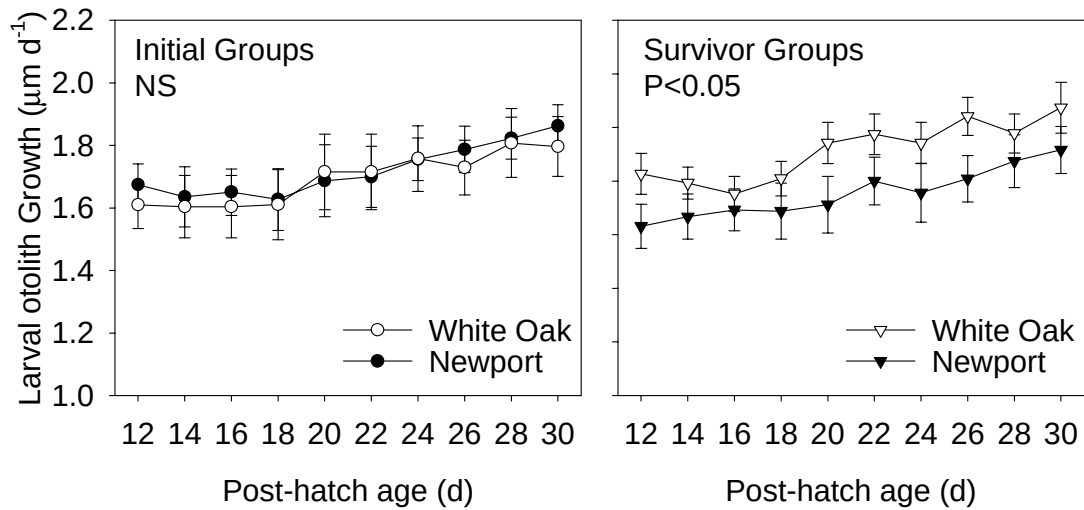
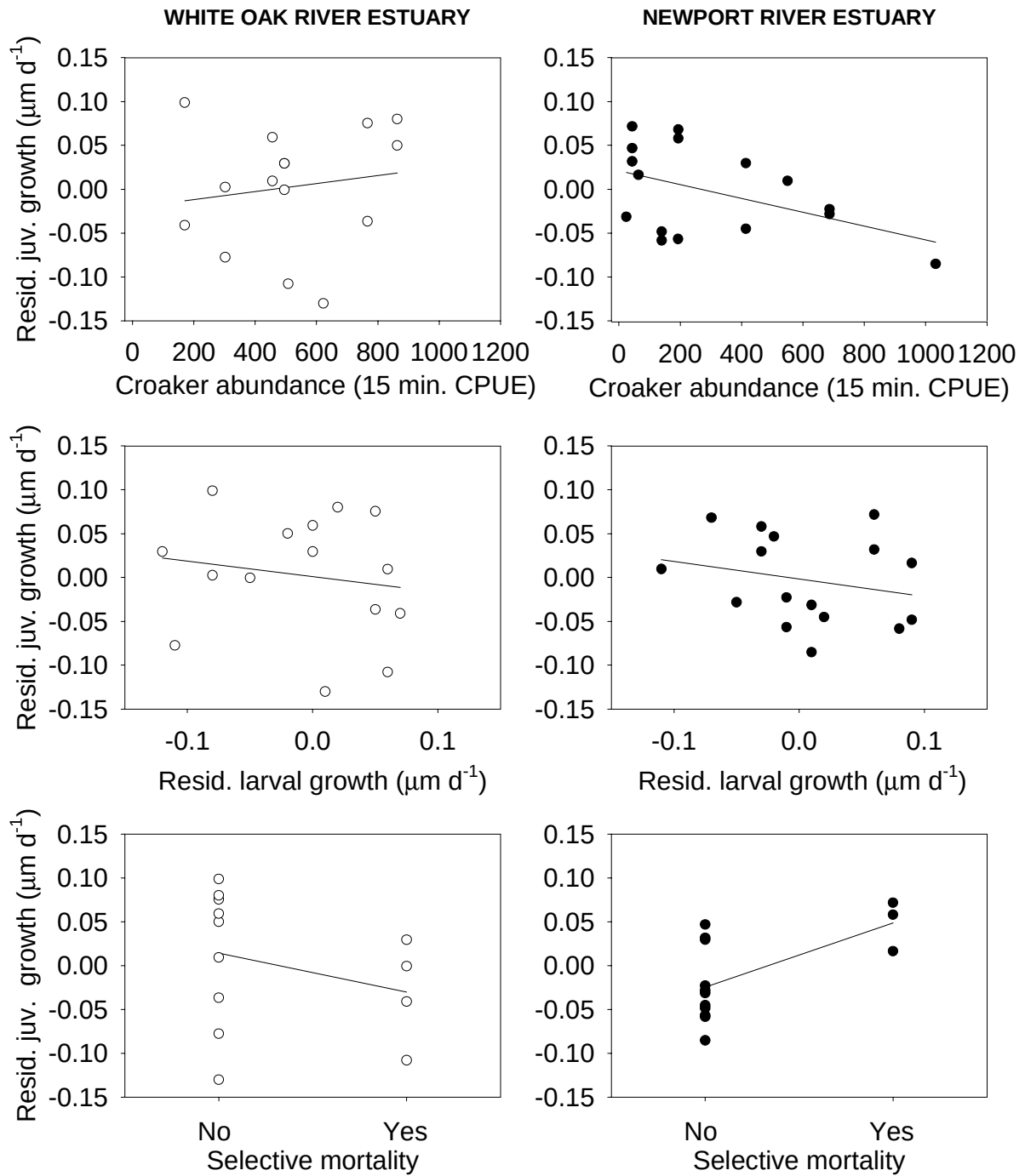


Figure 4.



CHAPTER 4

**Estuarine-specific early juvenile survival and
the importance of post-settlement density-dependent mortality**

ABSTRACT

The nursery-role of estuarine habitats has been recognized for nearly a century; however, understanding the relative importance of factors that influence early recruitment success of juvenile estuarine fishes remains a subject of debate. Here we examine how mortality within two similar estuaries is influenced by abiotic (temperature, salinity, change in salinity), and biotic (feeding success, predator abundance) factors, as well as conspecific density (density-dependence), and individual characteristics (larval and juvenile growth rates). Juvenile Atlantic croaker, *Micropogonias undulatus*, were collected weekly using a 1-m beam trawl in oligohaline nurseries of the White Oak River and Newport River estuaries, North Carolina, USA, in both fall and spring of 2001-2002 and 2002-2003 (fall 2001 was not sampled in the White Oak River estuary). Growth, abundance, and mortality of weekly hatch-date croaker cohorts were estimated from interpretation of otolith microstructure. Mortality estimates for weekly hatch date cohorts during the first three weeks of estuarine residence was high, ranging from 74-100%. Although individual growth rates were not an important determinant of early recruitment success in this study, conspecific abundance was, suggesting that density-dependent mortality (likely caused by predatory flounders) was an important factor controlling abundance of early juvenile Atlantic croaker. A better understanding of how the nursery environment, density dependence, and individual characteristics interact to control recruitment success, is critical for making effective decisions regarding Essential Fish Habitat and fishery and habitat management plans.

INTRODUCTION

Fish populations often exhibit large variations in recruitment and subsequent abundance (Rothschild 1986, Fogarty et al. 1991). Although such variations may be caused by mortality during both larval and juvenile periods (e.g., Caley et al. 1996), there is increasing evidence that high mortality rates following settlement of larvae to juvenile habitats is a key determinant of future recruitment success (Jones 1991, Bailey 1994, Carr and Hixon 1995, McCormick 1998). Early juvenile mortality may result from abiotic (i.e., temperature, salinity, and dissolved oxygen: Breitburg 1992, Rutherford and Houde 1995, Gillanders and Kingsford 2002, Miller et al. 2003), and biotic conditions (i.e., food availability and predator abundance: Phillips et al. 1995, Tupper and Boutilier 1995a, Rilling and Houde 1999, Rooker et al. 1999), the importance of which can be mediated by cohort (i.e., density-dependent mortality, Hixon and Carr 1997, Anderson 2001, Webster 2003), and individual characteristics (selective mortality acting on phenotypic traits, Campana 1996, Ottersen and Loeng 2000). Although abiotic, biotic, cohort, and individual characteristics can all influence early recruitment success, the relative importance of these factors has not been jointly considered.

Density-dependent mortality, which describes mortality that changes as a function of abundance or density, is a fundamental concept in the study of fish population dynamics (Rose et al. 2001). To date, most studies investigating density-dependent mortality have found that it acts in a stabilizing fashion with higher mortality at higher population densities and reduced mortality at lower population densities (Van der Veer 1986, Tanaka et al. 1989, Eggleston and Armstrong 1995, Hixon and Carr 1997, Steele 1997, Anderson 2001, Webster 2002, Forrester and Steele 2004). Greater mortality at higher densities may occur as the

result of a variety of mechanisms including disease, parasitism, increased predation (i.e., aggregative and functional feeding responses) or greater competition for food and space (reviewed in Rose et al. 2001). Recognition that density-dependent processes can influence mortality is important, as occurrence of density dependence can provide a framework from which to investigate temporal variations in mortality, as well as how the relative importance of factors that influence mortality change at high vs. low population densities.

Variability in mortality may also be influenced by selective mortality that increases probability of mortality for individuals with certain phenotypic characteristics. For example, modeling studies suggest that relatively small differences in individual larval and juvenile growth can cause order of magnitude differences in the number of individuals surviving to the next life history stage (Houde 1987, Pepin 1990, Rice et al. 1993). Larger-faster growing individuals are assumed to be better at avoiding gape limited predators and surviving stressful abiotic conditions and periods of reduced feeding success, than smaller-slower growing individuals (e.g., Sogard 1997). A variety of field studies have shown that survival is higher for individuals that grow faster as larvae (Searcy and Sponaugle 2001, Bergenius et al. 2002), settle at a larger size (McCormick and Hoey 2004), or with greater body condition (Booth and Hixon 1999, Hoey and McCormick 2004). Unless mortality that can be attributed to density dependence and individual characteristics is considered, studies of early recruitment success may miss important regulatory processes.

Relating cohort survival to environmental variability (food, predator, and abiotic variables), as well as conspecific density and individual characteristics, requires tracking individuals through time. Typically, insight into such processes is gained through individually based models (e.g., Rice et al. 1993) that, due to logistical difficulties, are rarely

validated with field studies. Analysis of otolith microstructure (fish ear stones) provides an empirical means of studying individual fish growth and survival, and linking recruitment dynamics to concurrent measures of abiotic and abiotic variables (e.g., Rice et al. 1987). Daily otolith ring deposition yields information on growth rates, size-at-age, and population age structure, which, when combined with capture date, allows for estimates of mortality and selective processes (by comparing otolith characteristics between earlier and later collections of the same cohort, Searcy and Sponaugle 2001).

The overall objective of this study was to determine if temporal (year, season) and spatial (between estuary) trends in early juvenile mortality and abundance of estuarine-dependent Atlantic croaker (*Micropogonias undulatus*) exist, and if so, to quantify the mechanistic basis underlying this variability. Specifically, we examined (1) the extent to which mortality of weekly hatch-date cohorts was determined by abiotic and biotic components of the juvenile nursery, as well as cohort (juvenile abundance) and individual characteristics (larval and juvenile growth), and (2) whether the relative importance of these factors varied between estuaries. Such information is critical to making informed decisions regarding habitat conservation, identifying feasible sites for introduction of hatchery-reared organisms for stock enhancement purposes, and understanding factors influencing variable recruitment success (e.g., Grimes 1998, Beck et al. 2001).

MATERIALS AND METHODS

Study species

Atlantic croaker, *Micropogonias undulatus*, is an economically and ecologically important fish in southeastern United States and Gulf of Mexico estuaries. Along the east coast of the United States, adults spawn on the continental shelf, and following offshore pelagic development, late-stage larvae ingress into estuaries and settle in low salinity nursery areas (Ross 2003). Atlantic croaker is an ideal study species with which to investigate early population dynamics of estuarine dependent fish because: (1) croaker are relatively common in our study area; (2) life history characteristics are similar to other fishes that use estuaries as nursery areas such as red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), weakfish (*Cynoscion regalis*), spot (*Leiostomus xanthurus*), Atlantic menhaden (*Brevoortia tyrannus*), flounders (*Paralichthys sp.*), and mullet (*Mugil sp.*); (3) juveniles are relatively site attached (Miller and Able 2002); and (4) adults have a protracted spawning season south of Cape Hatteras, N.C. which extends from August to May (Hettler and Chester 1990) allowing for tracking of multiple cohorts and hypothesis testing that would not be possible for a less abundant species.

Tracking weekly cohorts in the field

Late-stage larval and early juvenile Atlantic croaker were collected in the White Oak and Newport River estuaries, North Carolina, USA (Figure 1). The White Oak and Newport River estuaries were chosen because they are spatially distinct with separate inlets, however, they share many physical characteristics: both estuaries are small (28 km² and 31 km² respectively), shallow (~1 m at mean low water), tidal, and well-mixed. Moreover, Atlantic

croaker nursery areas (deep oligohaline channels, Weinstein 1979) within each estuary have a similar mud bottom, and are isolated from other potential nursery habitats, minimizing the likelihood of immigration and emigration among nursery areas.

Weekly hatch-date cohorts of Atlantic croaker were tracked from initial ingress into juvenile nursery areas for a period of one month during fall (November-December) and spring (February-April) of two recruitment seasons (2001-2002 and 2002-2003) in the Newport River estuary, and spring 2002 and fall-spring 2002-2003 in the White Oak River estuary (Figure 1). Collection stations bracketed expected Atlantic croaker nursery habitat with four sampling stations in riverine areas and one mid-estuary site (Figure 1). Samples were collected from a small boat using a 1 m beam trawl with 1 mm mesh upper- and side-panels and a 3 mm mesh bottom-panel. Due to the shallow nature of both estuaries, beam trawl tows were restricted to the last two hours of daytime flood tide, and each station was sampled with three replicate tows, typically of one minute each covering an area of approximately 60 m². Trawls were always pulled against prevailing currents at a tow speed standardized by gauging speed against emergent features in the water (i.e., crab pot buoys and stakes) or the shoreline. Trawl samples were sorted in the field and all fishes were preserved in 95% ethanol. Beam trawl catch efficiency is known to vary according to species and size of the targeted animal (Kuipers 1975, Kuipers et al. 1992, Rozas and Minello 1997), and was not corrected for in this study (see Searcy Chapter 1 for a discussion of beam trawl efficiency). For reference, density estimates ($\pm$ SE) of fish commonly collected in this study are provided in Appendices 1-10. Temperature and salinity were measured at each sampling station using a handheld YSI-85 instrument (YSI, Yellow Springs, Ohio, USA). In the spring

of 2003, hourly measures of salinity and temperature were also obtained by deploying YSI-6600 multiparameter dataloggers at the head of each estuary (Figure 1).

Age, growth, and stomach content analysis

In the laboratory, fish collected from each sampling location were identified and standard length of up to 50 randomly selected individuals of each species measured to the nearest 0.1 mm. To provide a measure of Atlantic croaker feeding success on each sampling date, 30 fish collected from the riverine stations were randomly chosen for stomach content analysis (recorded as the proportion of fish from each collection date that had empty stomachs).

For age and growth analysis, sagittal otoliths were dissected from 30 randomly selected ingress-age fish (late-larvae) from the mid-estuary stations and a minimum of 30 randomly selected juvenile fish collected from the riverine stations. The right sagitta was attached to a slide with mounting media and archived. The left sagitta was mounted in epoxy, sectioned along both sides of the frontal plane using a dual blade low-speed ISOMET saw, and polished to the core. The polished otolith section was then examined using a transmitted light microscope at 400x with a two-part rotating polarized filter placed between the light source and the first stage. Otolith images were captured with a frame grabber and increment count and widths (distance between two sequential increments) were measured using Image Pro Plus 4.5 image analysis software at 800x. One person read all otoliths twice independently. If the increment counts between the two readings differed by 0 to 2 increments, then one reading was randomly chosen for further analysis. If the increment counts between the two readings differed by more than 2 increments, the otolith was read

again. If the third reading was less than 2 increment counts away from a previous reading, then one of these two counts was randomly chosen for analysis. If the third reading was greater than two increments away from either previous reading, the otolith was discarded from further analysis. In total, 1396 of 1550 (89%) otoliths read were kept for Atlantic croaker from the Newport River estuary, and 855 of 1000 (86%) otoliths read were kept for Atlantic croaker from the White Oak River estuary.

Data Analysis

Mortality

To estimate age of all croaker collected, separate age-length keys (3-d bins for age and 1-mm bins for length) were created for each weekly collection of Atlantic croaker from each estuary. The use of age-length keys allowed us to incorporate variability in size-at-age (Campana and Jones 1992) and assign a weekly hatch-date cohort to each fish collected based on length and date of capture. Weekly abundance of each hatch-date cohort was calculated as the total number of fish collected from the river sampling stations and standardized to a total tow duration of 15 minutes (catch per unit effort, CPUE = 15 minutes).

Mortality rates were estimated using (1) regressions of the decline in $\log_e$ transformed abundance on age (e.g., Rooker et al. 1999), as well as (2) - $\log_e (N_3/N_0)$, where N_0 is the total peak abundance for that hatch-date cohort and N_3 is 'final abundance' three weeks later. Both estimates of mortality produced similar results, therefore, to be consistent with previous research on mortality of early juvenile fishes (e.g., Shima 2001), the later analysis was used to estimate mortality. The main assumptions in the mortality analysis were that gear efficiency was constant between estuaries and for all size classes and cohorts, and that

following peak abundance there was no immigration or emigration from the nursery areas. These assumptions were likely valid as habitat type and hence gear efficiency were similar between estuaries, a relatively narrow range of early juveniles were targeted (10-20 mm), and previous work suggests that emigration of juvenile Atlantic croaker from nursery areas is negligible (Miller and Able 2002), except during periods of high freshwater runoff (Searcy Chapter 1), which were excluded from this study.

Spatiotemporal variations in patterns of Atlantic croaker mortality and abundance

The null hypothesis that instantaneous mortality, peak abundance, and final abundance were the same between year, season, and estuary was tested with analysis of variance. Although there were no specific *a priori* alternative hypotheses for estuary or year, the alternative hypothesis for season was that Atlantic croaker mortality would be lower for earlier spawned (fall) cohorts than later spawned (spring) cohorts. This hypothesis was based on the assumption that continued ingress of Atlantic croaker from fall through the winter months would result in increased competition for food (and higher mortality) for cohorts ingressing later during the spring.

Prior to analyses, all data were examined for normality and homogeneity of variance. The Newport River had a balanced sampling design for estimates of mortality and abundance (2 seasons within each of two years); therefore, a two-way ANOVA model was used to examine year, season, and year x season interaction effects on croaker mortality and abundance. In the White Oak River, no sampling was conducted in Fall 2001, consequently, mortality and abundance were tested using one-way ANOVA models to examine the effect of year (Spring 2002 and 2003) and season (Fall 2002 and Spring 2003). Next, between-

estuary comparisons were used to determine (1) if weekly trends in early juvenile Atlantic croaker mortality were similar between estuaries (correlation between weekly hatch-date mortality estimates), and (2) whether there were general between-estuary differences in instantaneous mortality, peak abundance and final abundance (one-way ANOVA with Spring 2002, Fall 2002, Spring 2003 pooled) and estuary (White Oak River and Newport River estuary) as factors.

To further examine between-estuary differences in Atlantic croaker mortality and abundance, separate multiple regression analyses were used to determine whether greater variability in Atlantic croaker (1) instantaneous mortality and (2) final abundance could be explained by including characteristics of individual fish (larval and juvenile growth) and conspecific density (density dependence) over standard measures of abiotic and biotic conditions recorded within each estuary. Characteristics of individual fish included average larval (10-30 d post-hatch) and juvenile otolith growth (week following peak cohort abundance) corrected for water temperature by taking the residuals of larval otolith growth on nearshore water temperature (average daily temperature from NOAA Beaufort lab, Figure 1) and residuals of juvenile otolith growth on estuarine water temperature. Mortality was assumed to follow a general exponential decline with highest mortality occurring on the youngest juveniles (i.e., type III mortality, Hixon 1991). Therefore, the abiotic explanatory variables of average water temperature, average salinity, and maximum change in salinity were averaged over the week following peak abundance, and the biotic explanatory variables of proportion of juvenile croaker with empty stomachs (feeding success), and abundance of competitors (early juvenile flounder and spot <20mm), predators (flounder), and juvenile conspecifics (croaker <20 mm; all standardized to 15 minute CPUE in riverine nursery areas)

were measured to coincide with peak abundance of weekly hatch-date cohorts. The only difference in multiple regression models estimating the effects of various factors on the dependent variables of instantaneous mortality and final abundance was that the instantaneous mortality multiple regression model used 'total' abundance of juvenile Atlantic croaker present in riverine nursery areas, whereas the final abundance multiple regression model used 'peak cohort' Atlantic croaker abundance (maximum abundance of weekly hatch-date cohort). Peak abundance was chosen for use in the final abundance multiple regression model as a proxy for larval supply, thereby allowing for comparisons of the relative importance of pre-settlement (larval growth, peak abundance) and post-settlement (juvenile growth, abiotic and biotic conditions within the juvenile nursery) factors on final croaker abundance.

Prior to regression analyses, residual plots were examined for heteroscedasticity; observations that were outliers (Cook's $D < 4/n$ where $n = \#$ of observations) were eliminated from the analysis, and normality was tested by examining the results of Proc Univariate (SAS System). To meet model assumptions, croaker, competitor and flounder abundance were $\log(x+1)$ transformed, salinity and temperature were log-transformed, and feeding success was arcsine-square-root transformed. Finally, as strong correlations among independent variables can exaggerate outcomes of regression models, independent variables were examined for multicollinearity using variance inflation factors (Sokal and Rohlf 1995). For both dependent variables, temperature and flounder abundance were determined to be collinear ($VIF > 2$) and therefore temperature was excluded from further analysis.

Due to the large number of independent variables (8) compared to the number of cohorts tracked (Newport=16 and White Oak=15; Table 1), separate multiple regressions for

each estuary with inclusion of all explanatory variables ran the risk of experimentwise Type I error (achieving statistical significance due to chance alone, Sokal and Rohlf 1995).

Consequently, prior to regression analyses for both instantaneous mortality and final abundance the number of independent variables was reduced by combining data from both estuaries and using stepwise backwards elimination. Backwards elimination starts with all predictors in the model, removes the variable that is least significant (largest P-value), and refits the model until all remaining variables are significant (in this study $P < 0.10$). In this study, the backwards elimination procedure reduced the initial model to a subset of independent variables (salinity, croaker abundance, and flounder abundance), which explained 46% of the variance in instantaneous mortality in both estuaries (Table 3) and 66% of the variability in final abundance (Table 4). The reduced multiple regression models for each dependent variable was then run for each estuary separately; the overall significance was tested with the adjusted R^2 value, and squared partial correlation coefficients were calculated to examine the proportion of variance explained uniquely by each independent variable.

Density dependence

Mortality is density-dependent if per capita mortality increases with population density (e.g., Hixon and Carr 1997). Mean per capita loss rates were estimated as $(N_0 - N_3)/N_0$ where N_0 was the peak CPUE for that hatch-date cohort and N_3 was the total CPUE of the same cohort three weeks later. The significance of the linear regression was used to determine whether per capita croaker mortality was related to peak abundance of the specific hatch-date cohort or total-conspecific abundance (all juvenile Atlantic croaker $< 20\text{mm}$).

Finally, to qualitatively determine the maximum carrying capacity of each estuary, plots of final versus peak abundance were examined.

RESULTS

Mortality

Mortality estimates of weekly hatch-date cohorts of Atlantic croaker for the first three weeks within each estuary was extremely high, ranging from 74-99% in the White Oak River estuary and 87-100% in the Newport River estuary (Table 1). In total, mortality estimates of Atlantic croaker were calculated for five cohorts in each Spring 2002, Fall 2002, and Spring 2003 in the White Oak River estuary (Table 1), and three cohorts of Atlantic croaker collected in both Fall 2001 and Spring 2002, and five cohorts collected in both Fall 2002 and Spring 2003 in the Newport River estuary (Table 1).

Spatiotemporal variations in patterns of Atlantic croaker mortality and abundance

In the Newport River estuary, instantaneous mortality, peak abundance, and final abundance of early juvenile Atlantic croaker hatch-date cohorts did not vary significantly with year, season, or the interaction between year and season (Figures 2,3; two-way ANOVA all $p > 0.21$). In the White Oak River estuary, similar analyses to those conducted for the Newport River estuary were not possible because sampling was not conducted in Fall 2001. Instead, pairwise comparisons indicated that although peak abundance of early juvenile hatch date cohorts did not differ significantly between year (Spring 2002 and 2003) or season (Fall 2002 and Spring 2003), both instantaneous mortality and final abundance did (although the seasonal effect for both comparisons was marginally non-significant $p = 0.07$, Table 2). The

hypothesis that later-recruiting juvenile Atlantic croaker (spring cohorts) would have higher mortality than earlier recruits (fall cohorts) was not supported in either estuary, because fall cohorts suffered higher (but not statistically significant) average mortality than spring cohorts (Table 2, Figure 2).

Distinct between-estuary differences in early Atlantic croaker recruitment dynamics were suggested by between-estuary comparisons of peak abundance, final abundance, and instantaneous mortality. For example, peak croaker abundance and final abundances were significantly higher in the White Oak than the Newport River estuary (1-way ANOVA, $df = 1,26$, both $p < 0.001$; Figure 3); however, instantaneous mortality did not vary significantly between estuaries (1-Way ANOVA, $df = 1,26$, $p = 0.16$, Table 1, Figure 2). Similarly, mortality was not correlated between estuaries ($r = 0.14$, $p = 0.69$), suggesting that early recruitment dynamics within each estuary should be considered independently.

To explore potential mechanisms underlying spatiotemporal variation in Atlantic croaker mortality and abundance, multiple regression analyses were used. For the White Oak River estuary, there was a positive relationship between instantaneous mortality of early juvenile Atlantic croaker with total croaker abundance, flounder abundance, and salinity (the relationship with flounder abundance was moderately non-significant; Table 3). These three factors jointly explained 74% of the variation in instantaneous Atlantic croaker mortality (Table 3) with squared partial correlations revealing that salinity explained most of the variability in instantaneous mortality (48%), followed by total croaker (36%) and flounder abundance (24%; Table 3). Likewise, in the Newport River estuary, a high proportion of variability in instantaneous croaker mortality (72%) was positively related to total croaker abundance and flounder abundance (squared partial correlation coefficients of 73% and 64%

respectively, Table 3); however, in contrast to results from the White Oak River estuary, there was a non-significant relationship between instantaneous mortality and salinity.

Variability in final abundance of Atlantic croaker within each estuary was also significantly related to indices of croaker abundance (peak abundance of weekly hatch-date cohort), flounder abundance, and salinity. In the White Oak River estuary, 80% of the variability in final croaker abundance was explained by a significant negative relationship with both flounder abundance and salinity (squared partial correlation coefficients of 0.58 and 0.63, respectively; Table 4). In the Newport River estuary, 70% of the variability in final croaker abundance was explained by a significant negative relationship between final croaker abundance and flounder abundance as well as a positive relationship between final croaker abundance and peak croaker abundance (squared partial correlation coefficients of 0.75 and 0.45, respectively; Table 4). Overall, flounder abundance was the only explanatory variable that was consistently important in explaining variation in both instantaneous mortality and final croaker abundance within each estuary (Tables 3 and 4), suggesting that within the study system flounder abundance is a dominant factor controlling early recruitment dynamics of Atlantic croaker.

Density Dependence

Density-dependent mortality of juvenile Atlantic croaker within both the White Oak and Newport River estuaries was supported by a positive relationship between per capita mortality and total juvenile Atlantic croaker abundance (Figure 5A,B). Furthermore, lack of a significant relationship between per capita mortality and peak cohort abundance (linear regression; both estuaries $p > 0.12$), suggests that density-dependent mortality is the result of

all juvenile Atlantic croaker present (total abundance) within each nursery area and not simply the abundance of a specific weekly hatch-date cohort (peak abundance).

Finally, relatively large differences in carrying capacity between the White Oak and Newport River estuaries is suggested from visual interpretation of the relationship between peak and final cohort abundance within each estuary. In the White Oak River estuary, the estimated maximum CPUE was approximately 30 Atlantic croaker collected in a 15 minute tow (Figure 6A), which, when based on an average tow speed of 60m min^{-1} , is roughly equivalent to a density of 3 individuals per 100m^2 . Likewise, in the Newport River estuary, the estimated carrying capacity of 10 Atlantic croaker collected in a 15 minute tow (Figure 6B) is equivalent to 1 individual per 100m^2 . This consistent three-fold difference in carrying capacity between estuaries suggests that the White Oak River estuary may be a relatively more important nursery than the Newport River estuary.

DISCUSSION

Understanding processes that influence mortality and abundance of fishes within juvenile nursery areas is a critical component of fishery and habitat management plans (Gibson 1994, Minello 1999, Beck et al. 2001). In this study, otolith analysis and intensive field surveys were used to identify and estimate mortality of weekly hatch-date cohorts. A unique aspect of this work is consideration of how mortality within two similar estuaries is influenced by abiotic and biotic factors, as well as density dependence and individual characteristics (larval and juvenile growth rates). Overall, results suggest that early juvenile Atlantic croaker recruitment dynamics acted independently in the White Oak and Newport River estuaries, as was evident from a lack of between-estuary correlation in weekly cohort

mortality, and no between-estuary similarities in seasonal or annual estimates of instantaneous mortality, peak abundance, and final abundance. Although, individual growth rates were not an important determinant of recruitment success in this study, conspecific abundance was, suggesting that density-dependent mortality (likely caused by predatory flounders) is an important factor controlling abundance of early juvenile Atlantic croaker within nursery areas.

Mortality

Mortality estimates for weekly hatch-date cohorts of Atlantic croaker during the first three weeks of estuarine residence ranged from 74-100% in the White Oak River estuary, and 87-100% within the Newport River estuary (Table 1). Similarly, high mortality has been observed for early juvenile fishes in a variety of environments, including, temperate and tropical reefs (Shulman and Ogden 1987, Sale and Ferrel 1988, Levin 1994, Caselle 1999, Schmitt and Holbrook 1999, Steele and Forrester 2002), seagrass and macroalgal beds (Dahlgren and Eggleston 2001, Watson et al. 2002), estuaries (Rooker et al. 1999, Manderson et al. 2003), and temperate coastal regions (Tupper and Boutilier 1995b, Van der Veer et al. 1997). As such, the larval-juvenile transition of many fish species including Atlantic croaker is a critical period and studies that begin sampling after this transitional period may miss important regulatory processes (Cowen and Sponaugle 1997).

Spatiotemporal variations in patterns of Atlantic croaker mortality and abundance

Estimates of weekly mortality of juvenile Atlantic croaker were not spatially coherent between estuaries, which suggests that mortality rates were primarily affected by intra-

estuary processes rather than large-scale environmental variables that could simultaneously affect both estuaries (i.e., rainfall, storm surge, atmospheric frontal passages). Likewise, there were no significant seasonal trends in mortality (contrary to the expectation of higher springtime mortality) suggesting that processes that influence mortality likely remain relatively constant (or equally variable) throughout the year.

Mortality of weekly hatch-date cohorts within the White Oak and Newport River estuaries had a significant positive relationship with both croaker and flounder abundance, whereas a significant positive relationship between mortality and salinity was only found in the White Oak River estuary. As croaker larvae and juveniles are euryhaline (Peterson et al. 1999), salinity likely does not directly influence mortality, but may be correlated with other factors that do influence mortality. For example, in the White Oak River estuary, salinity may be associated with the delivery of transient predators into oligohaline nursery areas that are blocked in the Newport River estuary by a shallow (<0.25 m at low tide) and broad (~1 km) sill that occurs at the entry to the riverine nursery (Kirby-Smith and Costlow 1989). Regardless of the mechanism, salinity is clearly not a robust predictor of early juvenile Atlantic croaker mortality across the two study systems.

The general observation that predation is a major cause of mortality for newly settled fishes (Van der Veer and Bergman 1987, Hixon and Carr 1997, Dahlgren and Eggleston 2000, Manderson et al. 2003) is supported in the current study by both a positive relationship between juvenile Atlantic croaker mortality and flounder abundance, and a negative relationship between final croaker abundance and flounder abundance. In the current study, most flounder collected were southern flounder (*Paralichthys lethostigma*), which are well suited to prey on juvenile Atlantic croaker, as they are abundant in oligohaline nursery areas

(Guindon and Miller 1995, Walsh et al. 1999) and have enhanced feeding success in turbid waters (Minello et al. 1987). Interestingly, the likelihood that predation by flounders was responsible for the high early juvenile mortality of Atlantic croaker counters the assumption that oligohaline nursery areas are predator refuges (see also, Ross 2003); however, future work is required to determine if low-salinity habitats are refuges relative to other estuarine habitats such as higher salinity tidal creeks (Sheaves 2001, Manderson et al. 2004).

Despite evidence for selective mortality favoring rapid larval and juvenile growth within each estuary (or factors correlated to growth such as length or condition, Searcy Chapter 3), there was no evidence that the individual characteristics of larval and juvenile growth were valid predictors of either instantaneous mortality or final juvenile abundance. The lack of a significant relationship between mortality and growth characteristics may reflect that within this study system the strength or frequency of selective pressures on growth were too low to be detected. In systems that have a larger proportion visual predators and therefore potentially greater selection on phenotypic traits (i.e., coral reef environments), individual fish growth rates may be relatively more important in explaining variability in cohort survival than in estuaries.

Density Dependence

Mortality of juvenile Atlantic croaker within each estuary was density-dependent, with a positive relationship between per capita mortality and abundance. Density-dependent mortality of early juvenile fish is consistent with most studies investigating mortality of fish immediately following settlement (Modin and Pihl 1994, Tonn et al. 1994, Forrester 1995, McBride et al. 1995, Tupper and Boutilier 1995a, Bailey et al. 1996, Hixon and Carr 1997,

Sano 1997, Steele 1997, Schmitt and Holbrook 1999, Forrester and Steele 2000), but not all (Victor 1986, Robertson 1992). Interestingly, density-dependent mortality of juvenile Atlantic croaker was the result of all juvenile conspecifics present within each nursery area and not simply the abundance of a specific weekly hatch-date cohort. This finding may be due to the fact that Atlantic croaker do not ingress into estuaries as distinct pulses (Hettler and Chester 1990), and weekly-cohort designations were based on otolith aging and not any obvious phenotypic traits. For other fishes with continuous larval supply (non-pulsed settlement patterns), density-dependent interactions may also be the additive result of previous settlement history within a recruitment season rather than cohort-specific processes.

Overall, the mechanistic basis for the observed patterns of density-dependent mortality is likely predation; however, competitive interactions leading to higher mortality must also be considered. Density-dependent resource competition leading to starvation has been suggested for a variety of different fishes (Rubenstein 1981, Forrester and Steele 2000, Craig et al. in review). In the current study, feeding was unlikely limited since there was no significant relationship between % of empty stomachs and mortality (Figure 4), however, due to the fact that starving fish may have died prior to weekly beam-trawl sampling, starving fish may not have been evident in collections. In contrast, the importance of density-dependent predation is supported by both a positive relationship between juvenile Atlantic croaker mortality and flounder abundance (i.e., an aggregative response), and previous experimental work that has shown that southern flounder consumption rates increase with increased prey abundance (i.e., a type II functional response, Wright et al. 1993).

Finally, although higher density estimates of juvenile Atlantic croaker within the White Oak River than the Newport River estuary suggest that the White Oak River estuary

has a relatively higher nursery value (value assigned according to density, Baltz et al. 1993, Minello 1999), this result should be interpreted cautiously. As previously discussed, differences in juvenile Atlantic croaker abundance in the current study were likely determined by predation (which may vary in time and space) rather than any intrinsic property of the estuaries themselves. As such, abundance of Atlantic croaker within juvenile nursery habitats may ultimately be more dependent on the indirect effects of factors controlling flounder distribution and abundance rather than direct affects associated with abiotic or biotic conditions within each nursery area.

Conclusion

Between-estuary differences in mortality and abundance of juvenile Atlantic croaker support the observation that factors influencing early recruitment dynamics act separately within each estuary (e.g., Sogard 1992, Scharf 2000, Goldberg et al. 2002). Although spatially independent, variability of Atlantic croaker mortality within each estuary was significantly related to conspecific abundance (i.e., it was density-dependent). Evidence for density-dependent mortality of juvenile Atlantic croaker has important implications for fisheries and habitat management. For example, studies investigating early demographic rates that fail to consider density-dependence may misinterpret the importance of factors influencing early recruitment success. Next, from a stock enhancement perspective, the occurrence of density-dependence suggests that continued supply of juvenile fish to a habitat will result in a diminishing increase in later abundance. Finally, occurrence of density dependence suggests that any reduction in nursery area size due to habitat loss or degradation

will increase densities of remaining fish, resulting in movement of juveniles to potentially less favorable habitats, or a decline in early juvenile abundance and recruitment success.

LITERATURE CITED

- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* **82**:245-257.
- Bailey, K. M. 1994. Predation on juvenile flatfish and recruitment variability. *Netherlands Journal of Sea Research* **32**:175-189.
- Bailey, K. M., R. D. Brodeur, and A. B. Hollowed. 1996. Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: A critical factor analysis. *Fisheries Oceanography* **5**:179-189.
- Baltz, D. M., C. Rakocinski, and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental biology of fishes* **36**:109-126.
- Beck, M. W., K. L. J. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51**:633-641.
- Bergenius, M. A., M. G. Meekan, D. R. Robertson, and M. I. McCormick. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**:521-525.
- Booth, D. J., and M. A. Hixon. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. *Oecologia* **121**:364-368.
- Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. *Ecological monographs* **62**:525-546.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual review of ecology and systematics* **27**:477-500.

- Campana, S. E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Marine Ecology Progress Series **135**:21-26.
- Carr, M. H., and M. A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. Marine Ecology Progress Series **124**:31-42.
- Caselle, J. E. 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. Ecological monographs **69**:177-194.
- Cowen, R. K., and S. Sponaugle. 1997. Relationships between early life history traits and recruitment among coral reef fishes. Pages 423-450 in R. C. Chambers and E. A. Trippel, editors. Early life history and recruitment in fish populations. Chapman and Hall, New York.
- Craig, J. K., J. A. Rice, L. B. Crowder, and D. A. Nadeau. in review. Density-dependent growth and mortality in juvenile estuarine fishes: an experimental approach with spot *Leiostomus xanthurus*. Estuaries.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology **81**:2227-2240.
- Dahlgren, C. P., and D. B. Eggleston. 2001. Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system.
- Eggleston, D. B., and D. A. Armstrong. 1995. Pre- and Post-settlement determinants of estuarine dungeness crab recruitment. Ecological monographs **65**:193-216.
- Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology and Evolution **6**:241-246.

- Forrester, G. E. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia* **103**:275-282.
- Forrester, G. E., and M. A. Steele. 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. *Ecology* **81**:2416-2427.
- Forrester, G. E., and M. A. Steele. 2004. Predators, prey refuges, and the spatial scaling of density dependent mortality. *Ecology* **85**:1332-1342.
- Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**:191-206.
- Gillanders, B. M., and M. J. Kingsford. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology* **40**:233-309.
- Goldberg, R., B. Phelan, J. Pereira, S. Hagan, P. Clark, A. Bejda, A. Calabrese, A. Studholme, and K. W. Able. 2002. Variability in habitat use by young-of-the-year winter-flounder, *Pseudopleuronectes americanus*, in three northeastern U.S. estuaries. *Estuaries* **25**:215-226.
- Grimes, C. B. 1998. Marine stock enhancement: sound management or techno-arrogance? *Fisheries* **23**:18-23.
- Guindon, K. Y., and J. M. Miller. 1995. Growth potential of juvenile southern flounder, *Paralichthys lethostigma*, in low salinity nursery areas of Pamlico sound, North Carolina. *Netherlands Journal of Sea Research* **34**:89-100.
- Hettler, W. F., and A. J. Chester. 1990. Temporal distribution of ichthyoplankton near Beaufort inlet, North Carolina. *Marine Ecology Progress Series* **68**:157-168.

- Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. *in* P. F. Sale, editor. The Ecology of Fishes on Coral Reefs. Academic Press, New York.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946-949.
- Hoey, A. S., and M. I. McCormick. 2004. Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia* **139**:23-29.
- Houde, E. D. 1987. Fish life dynamics and recruitment variability. American Fisheries Society Symposium **2**:17-29.
- Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective. Pages 294-328 *in* P. F. Sale, editor. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego.
- Kirby-Smith, W. W., and J. D. Costlow. 1989. The Newport River estuarine system. UNC-SG-89-04, UNC Seagrant Publication, Beaufort, NC.
- Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). *Netherlands Journal of Sea Research* **9**:69-85.
- Kuipers, B. R., B. Maccurrin, J. M. Miller, H. W. Van der Veer, and J. I. J. Witte. 1992. Small trawls in juvenile flatfish research: their development and efficiency. *Netherlands Journal of Sea Research* **29**:109-117.
- Levin, P. S. 1994. Fine-scale temporal variation in recruitment of a temperate demersal fish. The importance of settlement versus postsettlement loss. *Oecologia* **97**:124-133.
- Manderson, J. P., J. Pessutti, J. G. Hilbert, and F. Juanes. 2004. Shallow water predation risk for a juvenile flatfish (winter flounder; *Pseudopleuronectes americanus*, Walbaum) in

- a northwest Atlantic estuary. *Journal of Experimental Marine Biology and Ecology* **304**:137-154.
- Manderson, J. P., J. Pessutti, C. Meise, D. Johnson, and P. Shaheen. 2003. Winter flounder settlement dynamics and the modification of settlement patterns by post-settlement processes in a NW Atlantic estuary. *Marine Ecology Progress Series* **253**:253-267.
- McBride, R. S., M. D. Scherer, and J. C. Powell. 1995. Correlated variations in abundance, size, growth, and loss rates of age-0 bluefish in a southern New England estuary. *Transactions of the American Fisheries Society* **124**:898-910.
- McCormick, M. I. 1998. Condition and growth of reef fish at settlement: Is it important? *Australian Journal of Ecology* **23**:258-264.
- McCormick, M. I., and A. S. Hoey. 2004. Laval growth history determined juvenile growth and survival in a tropical marine fish. *Oikos* **106**:225-242.
- Miller, M. J., and K. W. Able. 2002. Movements and growth of tagged young-of-the-year Atlantic croaker (*Micropogonias undulatus* L.) in restored and reference marsh creeks in Delaware Bay, USA. *Journal of Experimental Marine Biology and Ecology* **267**:15-33.
- Miller, M. J., D. M. Nemerson, and K. W. Able. 2003. Seasonal distribution, abundance, and growth of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay and adjacent marshes. *Fishery Bulletin* **101**:100-115.
- Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43-75 in L. R. Benaka, editor. *Fish habitat: Essential fish habitat and rehabilitation*. The American Fisheries Society, Bethesda, MD.

- Minello, T. J., R. J. Zimmerman, and E. X. Martinez. 1987. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: effects of turbidity and substratum on predation rates. Fishery Bulletin **85**:59-70.
- Modin, J., and L. Pihl. 1994. Differences in growth and mortality of juvenile plaice, *Pleuronectes platessa* L., following normal and extremely high settlement. Netherlands Journal of Sea Research **32**:331-341.
- Ottersen, G., and H. Loeng. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES Journal of Marine Science **57**:339-348.
- Pepin, P. 1990. Predation and starvation of larval fish: a numerical experiment of size- and growth-dependent survival. Biological Oceanography **6**:23-44.
- Peterson, M. S., B. H. Comyns, C. F. Rakocinski, and G. L. Fulling. 1999. Does salinity affect somatic growth in early juvenile Atlantic croaker, *Micropogonias undulatus* (L.)? Journal of Experimental Marine Biology and Ecology **238**:199-207.
- Phillips, J. M., J. R. Jackson, and R. L. Noble. 1995. Hatching date influence on age-specific diet and growth of age-0 largemouth bass. Transactions of the American Fisheries Society **124**:370-379.
- Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society **116**:703-718.
- Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an

- individual-based size-dependent predation model. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:133-142.
- Rilling, G. C., and E. D. Houde. 1999. Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. *Fishery Bulletin* **97**:555-569.
- Robertson, D. R. 1992. Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panama. *Marine Biology* **114**:527-537.
- Rooker, J. R., S. A. Holt, G. J. Holt, and L. A. Fuiman. 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. *Fishery Bulletin* **97**.
- Rose, K. A., J. H. Cowan, K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2**:293-327.
- Ross, S. W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin* **101**:384-404.
- Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts.
- Rozas, L. P., and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* **20**:199-213.
- Rubenstein, D. I. 1981. Individual variation and competition in the Everglades pygmy sunfish. *Journal of Animal Ecology* **50**:337-350.

- Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fishery Bulletin* **93**:315-332.
- Sale, P. F., and D. L. Ferrel. 1988. Early survivorship of juvenile coral reef fishes. *Coral Reefs* **7**:117-124.
- Sano, M. 1997. Temporal variation in density dependence: recruitment and postrecruitment demography of a temperate zone sand goby. *Journal of Experimental Marine Biology and Ecology* **214**:67-84.
- Scharf, F. S. 2000. Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast with implications for recruitment and stock enhancement. *Transactions of the American Fisheries Society* **129**:1207-1222.
- Schmitt, R. J., and S. J. Holbrook. 1999. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* **80**:35-40.
- Searcy, S., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* **82**:2452-2470.
- Sheaves, M. 2001. Are there really few piscivorous fishes in shallow estuarine habitats. *Marine Ecology Progress Series* **222**:279-290.
- Shima, J. S. 2001. Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality. *Oecologia* **126**:58-65.
- Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series* **39**:233-242.

- Sogard, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* **85**:35-53.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**:1129-1157.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry The Principles and Practice of Statistics in Biological Research*, third edition. W.H. Freeman and Company, New York.
- Steele, M. A. 1997. Population regulation by post-settlement mortality in two temperate reef fishes. *Oecologia* **112**:64-74.
- Steele, M. A., and G. E. Forrester. 2002. Early postsettlement predation on three reef fishes: effects on spatial patterns of recruitment. *Ecology* **83**:1076-1091.
- Tanaka, M., T. Goto, M. Tomiyama, and H. Sudo. 1989. Immigration, settlement and mortality of flounder (*Paralichthys olivaceus*) larvae and juveniles in a nursery ground, Shijiki bay, Japan. *Netherlands Journal of Sea Research* **24**:57-67.
- Tonn, W. M., I. J. Holopainen, and C. A. Paszkowski. 1994. Density-dependent effects and the regulation of crucian carp populations in single species ponds. *Ecology* **75**:824-834.
- Tupper, M., and R. G. Boutilier. 1995a. Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. *Journal of Experimental Marine Biology and Ecology* **191**:209-222.
- Tupper, M., and R. G. Boutilier. 1995b. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**:1834-1841.

- Van der Veer, H. W. 1986. Immigration, settlement, and density-dependent mortality of a larval and early post-larval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Marine Ecology Progress Series **29**.
- Van der Veer, H. W., and M. J. N. Bergman. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. Marine Ecology Progress Series **35**:203-215.
- Van der Veer, H. W., T. Ellis, J. M. Miller, L. Pihl, and A. D. Rijnsdorp. 1997. Size-selective predation on juvenile North Sea flatfish and possible implications for recruitment. Pages 279-303 in R. C. Chambers and E. A. Trippel, editors. Early life history and recruitment in fish populations. Chapman and Hall, London.
- Victor, B. C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecological monographs **56**:145-160.
- Walsh, H. J., D. S. Peters, and D. P. Cyrus. 1999. Habitat utilization by small flatfishes in a North Carolina estuary. Estuaries **22**:803-813.
- Watson, M., J. L. Munro, and F. R. Gell. 2002. Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. Marine Ecology Progress Series **237**:247-256.
- Webster, M. S. 2002. Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia **131**:52-60.
- Webster, M. S. 2003. Temporal density dependence and population regulation in a marine fish. Ecology **84**:623-628.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fishery Bulletin **77**:339-357.

Wright, R. A., L. B. Crowder, and T. H. Martin. 1993. The effects of predation on the survival and size-distribution of estuarine fishes: an experimental approach. *Environmental biology of fishes* **36**:291-300.

TABLE 1. *Micropogonias undulatus*. Estimates of instantaneous mortality (Inst. Z) and Per capita mortality (Per capita Z) for weekly hatch-date croaker cohorts collected in the Newport and White Oak River estuaries, North Carolina, USA. Mortality estimates were based on the difference between peak abundance and final abundance three weeks later (standardized to 15 minute CPUE). No cohorts were collected in Fall 2001 in the White Oak River estuary (N/A), and the symbol --- refers to the inability to track a cohort for three weeks due to insufficient collection of individuals to base a mortality estimate.

Season	Hatch	White Oak River		Newport River	
		Inst. Z	Per capita Z	Inst. Z	Per capita Z
Fall 01	16 Oct 01	N/A	N/A	3.25	1.00
	22 Oct 01	N/A	N/A	3.68	0.98
	28 Oct 01	N/A	N/A	2.94	0.95
Spring 02	27 Dec 01	---	---	2.71	0.97
	02 Jan 02	3.04	0.96	---	---
	08 Jan 02	3.13	0.96	1.93	0.87
	14 Jan 02	4.13	0.99	2.46	0.93
	20 Jan 02	4.07	0.99	---	---
	26 Jan 02	3.35	0.97	---	---
Fall 02	05 Oct 02	2.59	0.93	2.40	0.94
	11 Oct 02	1.69	0.82	4.54	1.00
	17 Oct 02	3.33	0.96	2.91	0.96
	23 Oct 02	1.85	0.85	2.98	0.96
	29 Oct 02	4.19	0.99	4.95	1.00
Spring 03	09 Jan 03	---	---	4.72	1.00
	15 Jan 03	1.32	0.74	---	---
	21 Jan 03	2.21	0.90	4.59	0.99
	27 Jan 03	1.35	0.75	2.18	0.90
	02 Feb 03	1.72	0.83	2.67	0.94
	08 Feb 03	1.88	0.85	2.35	0.93

TABLE 2. *Micropogonias undulatus*. Results of one-way ANOVA for the White Oak River estuary examining differences in instantaneous mortality, peak and final Atlantic croaker abundance between year (Spring 2002 – Spring 2003) and season (Fall 2002 – Spring 2003). Prior to analyses, final croaker abundance was ($\log x + 1$) transformed to meet ANOVA assumptions.

Parameter	Factor	DF	SS	MS	F	P
Instantaneous mortality	Year	1	8.547	8.547	41.58	<0.001
	Error	8	1.644	0.206		
	Season	1	2.67	2.67	4.31	0.07
	Error	8	0.1172	0.015		
Peak abundance ($\log x + 1$)	Year	1	0.0008	0.0008	0.04	0.85
	Error	8	0.179	0.022		
	Season	1	0.006	0.006	0.16	0.70
	Error	8	0.284	0.036		
Final abundance ($\log x + 1$)	Year	1	1.781	1.781	90.28	<0.0001
	Error	8	0.158			
	Season	1	0.534	0.534	4.2	0.07
	Error	8	1.017	0.127		

TABLE 3. *Micropogonias undulatus*. Regression parameters and squared partial correlation coefficients for instantaneous mortality of weekly hatch-date croaker cohorts as the dependent variable, and log (x+1) transformed flounder (predator) and croaker (competitor) abundance, and log transformed salinity as independent variables.

Model	Parameter	df	Parameter estimate	Std. error	t value	P > t	Partial corr ²
Both Estuaries Adj. R ² = 0.46 F _{3,25} = 8.87 P < 0.001	Intercept	1	0.01	1.00	0.01	0.99	.
	Total croaker	1	0.73	0.37	1.99	<0.05	0.14
	Flounder	1	1.79	0.44	4.10	<0.001	0.40
	Salinity	1	0.83	0.34	2.46	<0.05	0.19
White Oak Adj. R ² = 0.74 F _{3,10} = 13.34 P < 0.001	Intercept	1	-6.83	3.54	-1.93	0.08	.
	Total croaker	1	3.04	1.29	2.35	<0.05	0.36
	Flounder	1	1.03	0.57	1.79	0.10	0.24
	Salinity	1	1.57	0.52	3.03	<0.05	0.48
Newport Adj. R ² = 0.72 F _{3,11} = 12.76 P < 0.001	Intercept	1	-1.47	0.96	-1.53	0.16	.
	Total croaker	1	1.69	0.38	4.39	<0.001	0.64
	Flounder	1	2.64	0.49	5.42	<0.001	0.73
	Salinity	1	0.06	0.35	0.18	0.86	0.00

TABLE 4. *Micropogonias undulatus*. Regression parameters and squared partial correlation coefficients for final abundance (3 weeks after peak abundance) of weekly hatch-date croaker cohorts as the dependent variable, and log (x+1) transformed flounder (predator) and peak croaker (competitor) abundance, and log transformed salinity as independent variables.

Model	Parameter	df	Parameter estimate	Std. error	t value	P > t	Partial corr ²
Both Estuaries Adj. R ² = 0.66 F _{3,25} = 19.10 P < 0.0001	Intercept	1	-0.49	0.46	-1.07	0.29	.
	Peak croaker	1	0.87	0.21	4.15	<0.001	0.41
	Flounder	1	-0.10	0.19	-5.16	<0.0001	0.51
	Salinity	1	-0.42	0.15	-2.71	<0.01	0.23
White Oak Adj. R ² = 0.80 F _{3,10} = 18.48 P < 0.001	Intercept	1	2.18	0.90	2.42	<0.05	.
	Peak croaker	1	-0.23	0.40	-0.57	0.58	0.00
	Flounder	1	-0.73	0.19	-3.75	<0.01	0.58
	Salinity	1	-0.84	0.20	-4.15	<0.01	0.63
Newport Adj. R ² = 0.70 F _{3,11} = 12.15 P < 0.001	Intercept	1	-0.32	0.41	-0.79	0.45	.
	Peak croaker	1	0.62	0.21	2.99	<0.01	0.45
	Flounder	1	-1.20	0.21	-5.70	<0.0001	0.75
	Salinity	1	-0.13	0.16	-0.85	0.42	0.00

FIGURE LEGENDS

Figure 1. Location of White Oak River and Newport River estuaries, North Carolina, USA.

Inset shows location of beam-trawl stations (triangles) and deployment site of YSI-6600 multiparameter dataloggers (crosses).

Figure 2. *Micropogonias undulatus*. Comparison of instantaneous mortality for early juvenile Atlantic croaker in the Newport and White Oak River estuaries (means $\pm$ 1 SE). The White Oak River estuary was not sampled in Fall 2001.

Figure 3. *Micropogonias undulatus*. Seasonal average peak croaker abundance and final croaker abundance three weeks later measured by Catch-Per-Unit-Effort (standardized to 15 minute tow duration, means $\pm$ SE). White Oak River was not sampled in Fall 2001 (N/A).

Figure 4. Relationship between instantaneous mortality and three independent variables used in multiple regression analyses (croaker and flounder abundance, and salinity). Croaker and flounder abundance were standardized to 15 min CPUE (log x + 1 transformed) and salinity was log transformed. For reference, the linear regression line is plotted within each figure. See Table 3 for the results of statistical tests.

Figure 5. Relationship between per capita mortality rate and total juvenile Atlantic croaker abundance (all croaker < 20mm standard length collected at time of peak cohort abundance) in the (A) White Oak and (B) Newport River estuaries. Embedded results are for linear regression analysis. Regression line is plotted with 95% confidence intervals.

Figure 6. Relationship between final (3 weeks following peak abundance) and peak abundance in the (A) White Oak River estuary, and (B) Newport River estuary. CPUE for abundance estimates was standardized to a 15 minute tow duration.

Figure 1.

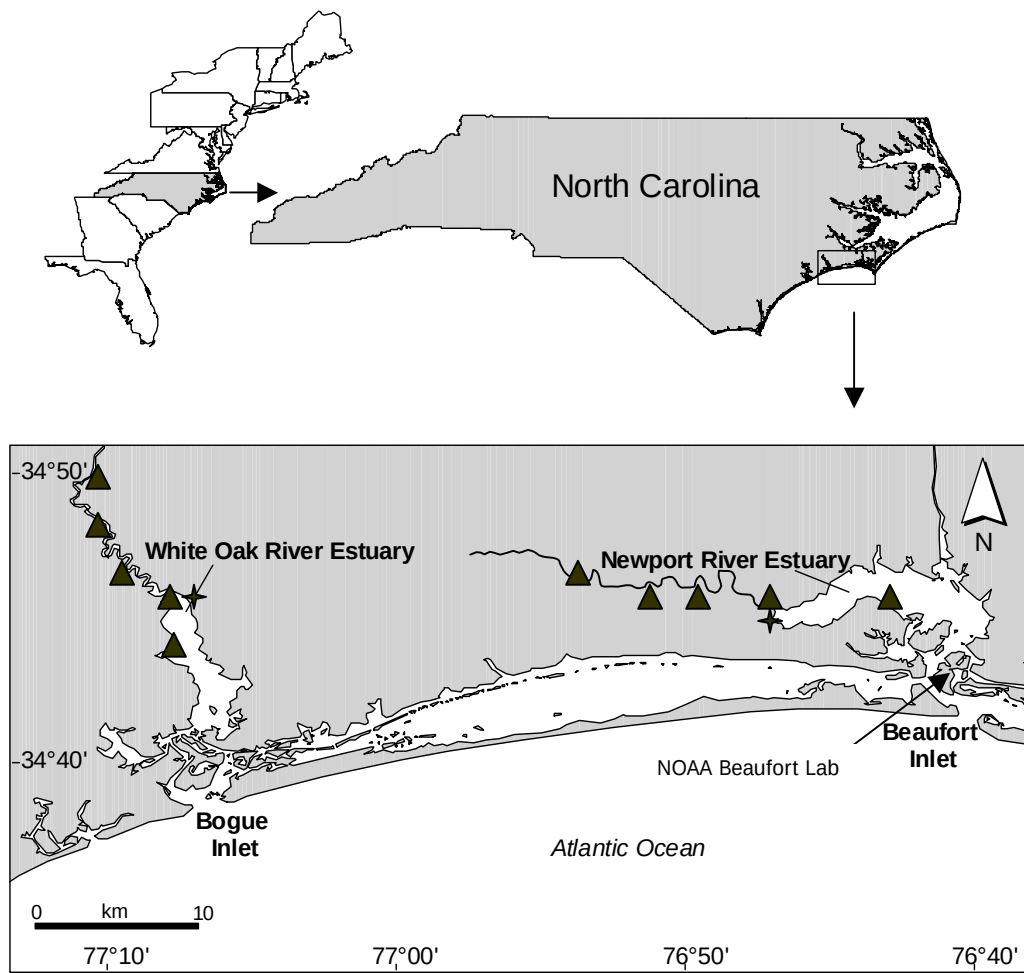


Figure 2.

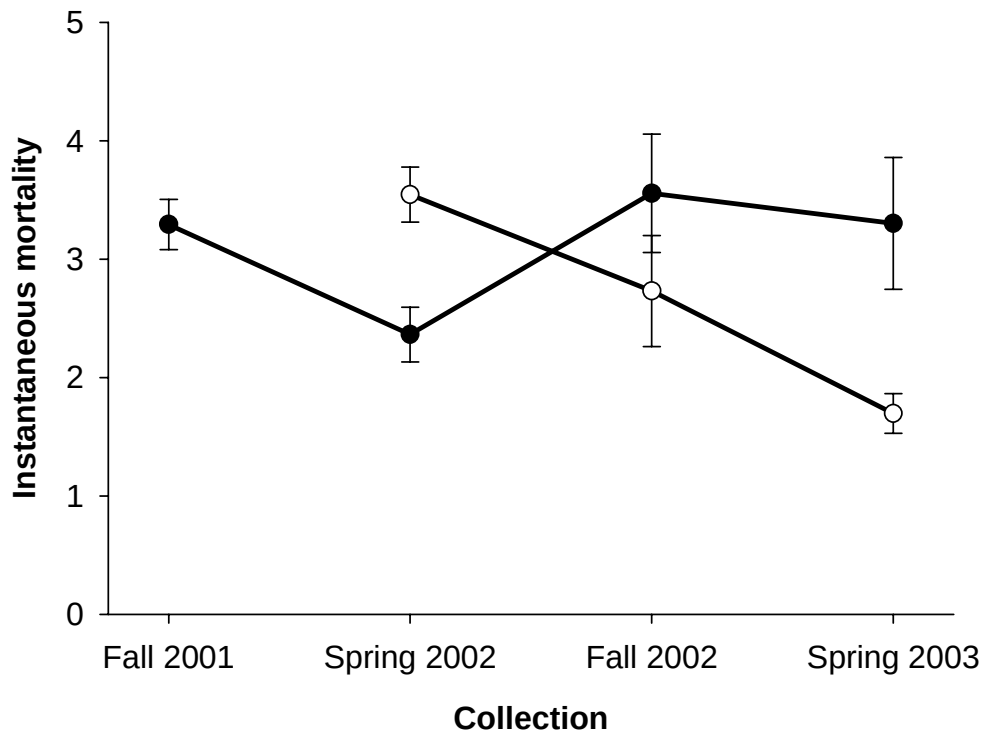


Figure 3.

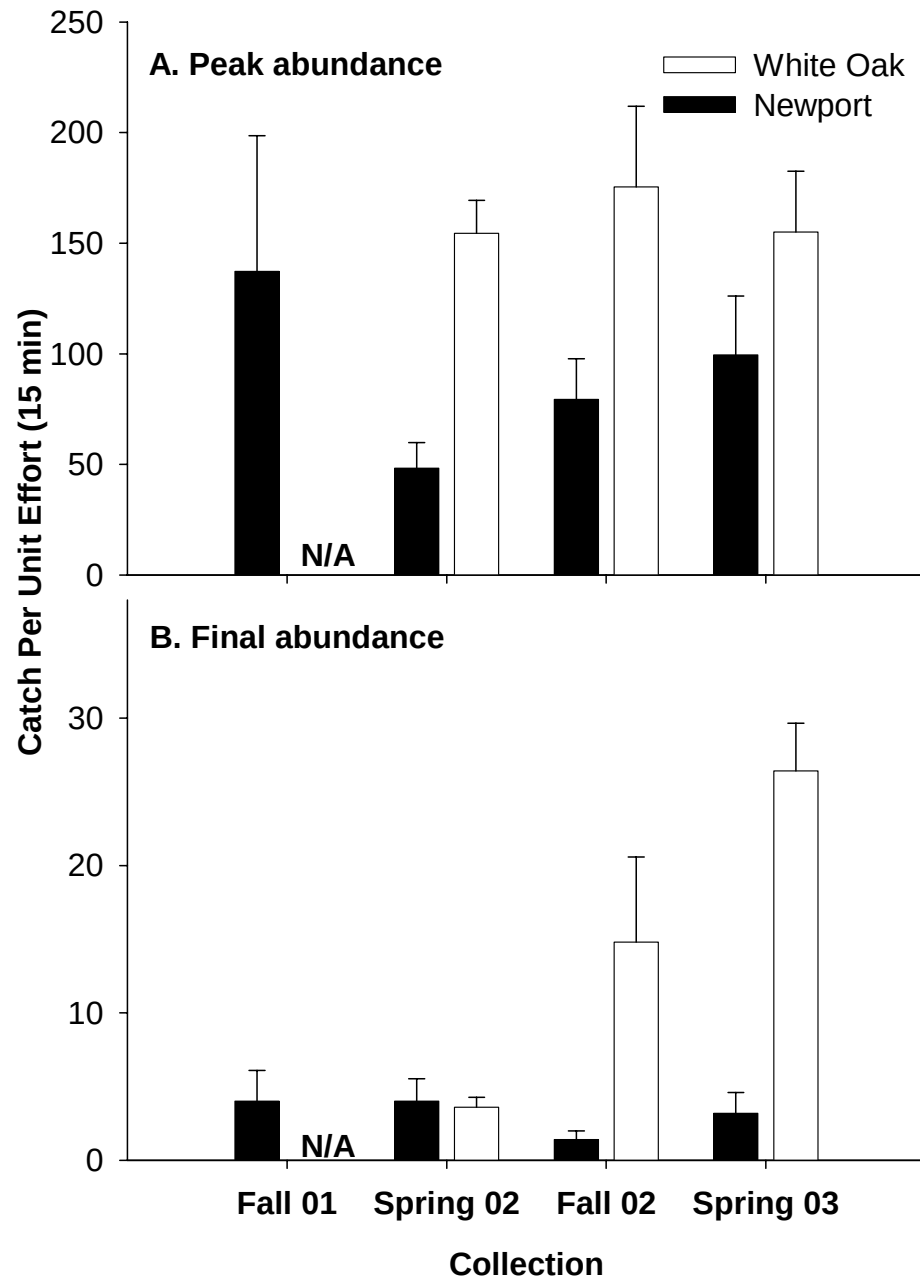


Figure 4.

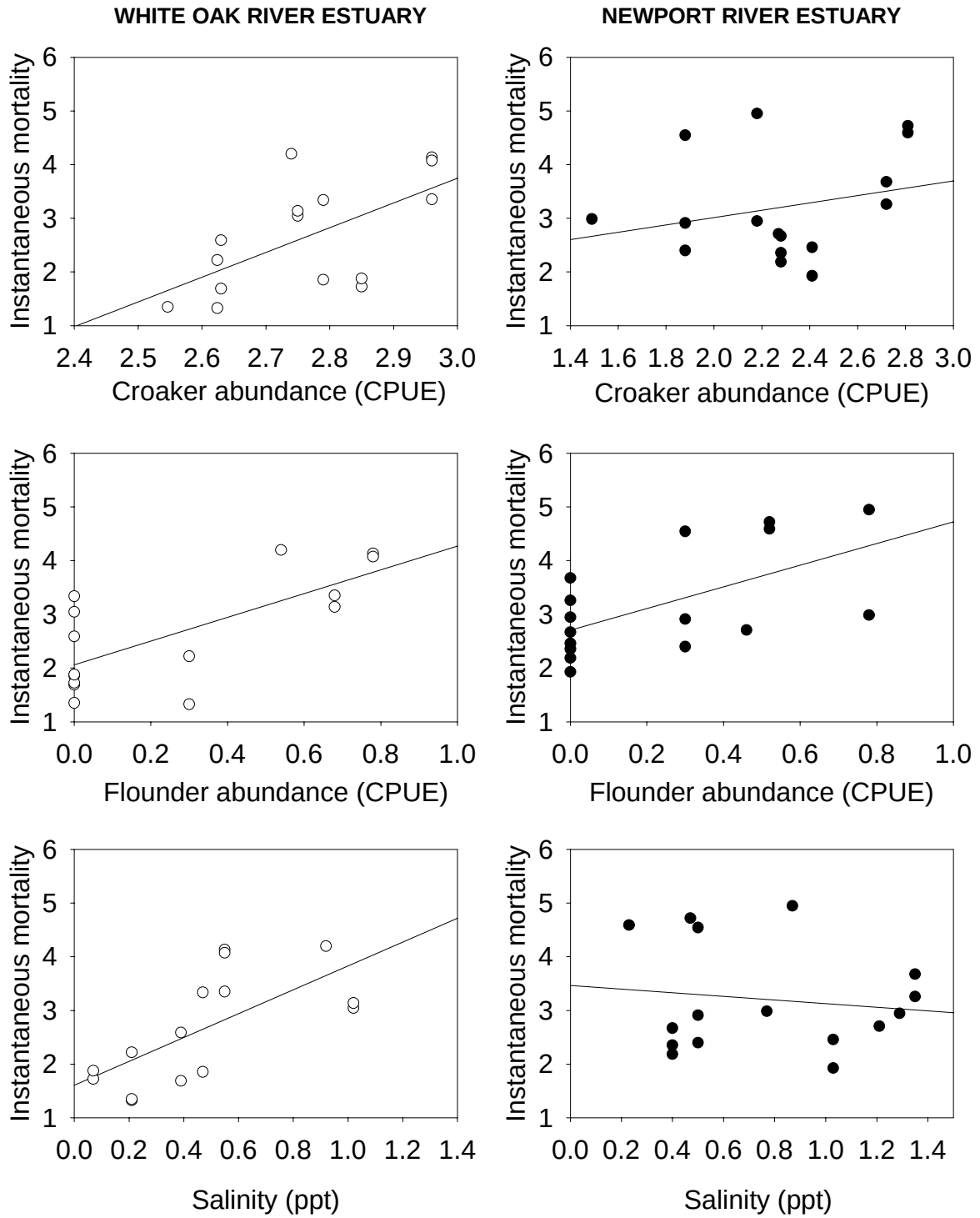


Figure 5.

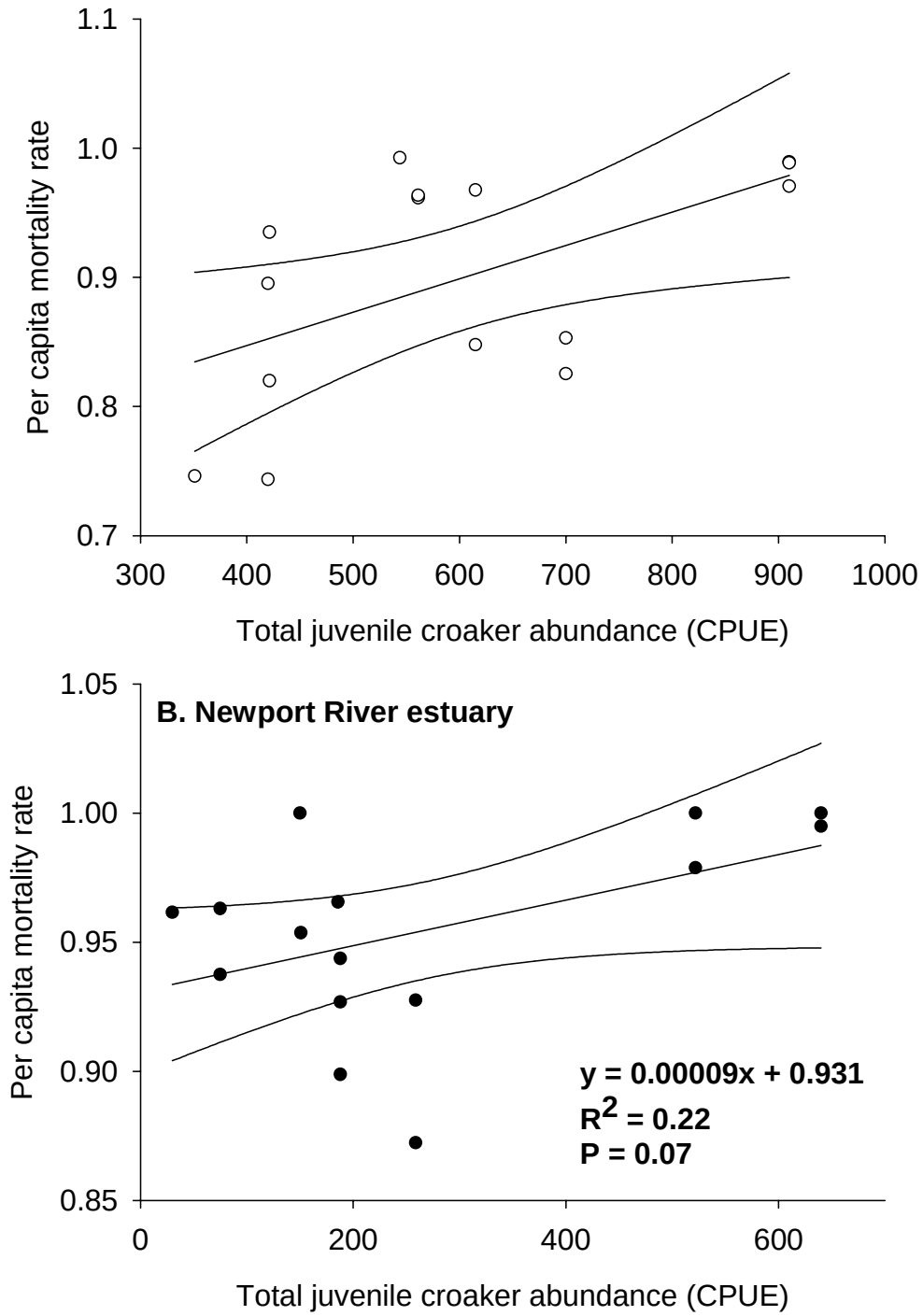
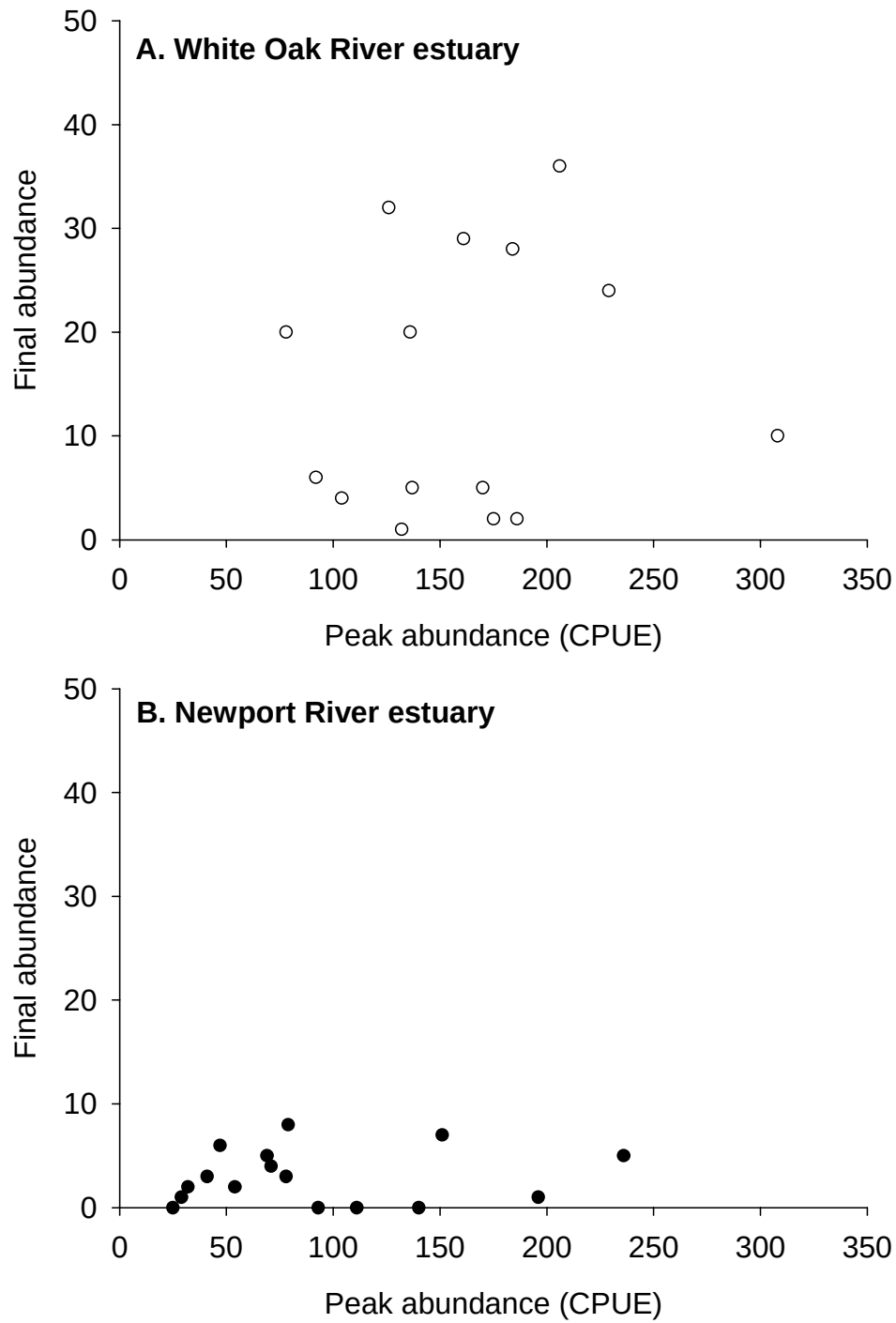


Figure 6.



CONCLUSION

Estuarine habitats serve as important nurseries for many species of juvenile fishes and invertebrates. Due to concerns about habitat destruction and alteration, the U.S. National Marine Fisheries Service identified four levels of criteria by which to evaluate habitats and prioritize Essential Fish Habitats 'EFH' for protection: 1) presence-absence, 2) distribution and abundance, 3) habitat-specific growth, reproduction and survival, and 4) per capita production of juveniles (NMFS 1997). This dissertation addressed classification of EFH levels 2 and 3 by identifying patterns of nursery habitat use for early juvenile Atlantic croaker (*Micropogonias undulatus*), examining factors that influenced growth and mortality, and testing the widely held assumption that 'growth is a valid indicator of habitat quality'.

EFH Level-2 (Distribution and Abundance)

Juvenile Atlantic croaker abundance patterns in the White Oak and Newport River estuaries, NC was consistently higher in river than upper-estuary creek habitats. Within river areas, freshwater runoff was an essential component determining spatial patterns of Atlantic croaker nursery habitat use. In both estuaries, juvenile Atlantic croaker move up- and down-river in relation to changes in salinity, with highest croaker abundances found in salinities ranging from 0-13 ppt. Following periods of high freshwater runoff, croaker distributions moved downstream from river nursery areas into alternative nursery habitats located in the upper-estuary. The dynamic nature of Atlantic croaker nursery habitat should be considered in fishery and habitat management plans (i.e., time and area closures in the upper-estuary to shrimp trawling following periods of high freshwater runoff). Furthermore, it is important to recognize that changes in

estuarine hydrodynamics that alter runoff and seawater exchange (i.e., bulkheading, channelization, dredging) may have corresponding impacts on patterns of Atlantic croaker nursery habitat use and potentially survival. Classification of juvenile Atlantic croaker EFH should incorporate a sliding scale that considers both the relative spatial position of abiotic (salinity, runoff) and habitat (deep channels) components of the nursery environment. For example, although deep oligohaline channels should be protected as the primary nursery habitat utilized by juvenile Atlantic croaker, during conditions when low salinity extends into the upper-estuary (i.e., croaker distribution shifts downstream following large rainfall events), the upper-estuary should also be protected.

EFH Level-3 (mortality)

Between-estuary differences in cohort-specific mortality and abundance of juvenile Atlantic croaker support the observation that factors influencing early recruitment dynamics act independently within different estuaries (e.g., Sogard 1992, Scharf 2000, Goldberg et al. 2002). Although spatially independent, variability of Atlantic croaker mortality within each estuary was significantly related to conspecific abundance (i.e., it was density-dependent). Evidence for density-dependent mortality of juvenile Atlantic croaker has important theoretical implications for studies of recruitment dynamics (i.e., population stability; Rose et al. 2001), as well as applied implications for fisheries and habitat-management. For example, studies investigating early demographic rates that fail to consider density-dependence may misinterpret the importance of other factors such as food availability and abiotic conditions in influencing early recruitment

success. From a stock enhancement perspective, the occurrence of density-dependence suggests that continued supply of juvenile fish to a habitat will not necessarily result in a corresponding increase in later abundance of sub-adults, and any reduction in nursery area size due to habitat loss or degradation will increase densities of remaining fish, resulting in movement of juveniles to potentially less favorable habitats, or a decline in early juvenile abundance and recruitment success. The occurrence of density dependent mortality also cautions against density-based estimates of EFH. For example, lack of variability in fish densities among habitats does not necessarily suggest that habitats are equivalent (i.e. same larval supply, growth, etc...), but simply that density dependent mortality keeps densities relatively invariant.

EFH level 3 (growth)

Growth is not a robust indicator of habitat quality for juvenile Atlantic croaker. Selective mortality favoring faster larval and juvenile Atlantic croaker otolith growth was found in both the White Oak and Newport River estuaries. Periodic loss of relatively slower growing individuals has important implications for growth-based assessment of habitat quality. The difference in otolith growth between the 'initial' and 'survivor' groups ranged between 6-15%, which is roughly equivalent to selective mortality results interpreted from previous studies (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Takasuka et al. 2003, Raventos and Macpherson 2005), and suggests that at a minimum, comparisons of growth rates between groups (spatial or temporal) that vary by $\leq 15\%$ need to be interpreted cautiously.

Potential bias associated with growth-based assessment of habitat quality was found in density dependent growth that occurred in the Newport but not the White Oak River estuary. Between estuary differences in the occurrence of density-dependent growth was likely caused by differences in geomorphology between estuaries (more restricted nursery habitat in the Newport than in the White Oak River estuary). Finally, a positive correlation between larval and juvenile growth was found in only some of the cohorts of Atlantic croaker and was most likely associated with high levels of freshwater runoff (as evidenced by a rapid decline in salinity to near 0 ppt), leading to poor feeding success in downstream juvenile nursery areas. Unless alternative factors such as previous environmental history, density-dependence, and selective mortality are addressed, growth-based assessment of habitat quality may reach incorrect conclusions regarding the value of different habitats.

Future studies that use growth-based assessment of habitat quality should either control or directly account for factors that bias estimates of growth rates. For example, caging studies (e.g., Sogard 1992, Duffy et al. 1996, Phelan et al. 2000, Necaie et al. 2005) may be an appropriate way to control for growth biases discussed in this dissertation (previous growth history, density dependence, and selective mortality). However, despite the advantages of caging studies in controlling recent environmental history, excluding predators, and controlling density, there are also difficulties associated with this experimental approach (reviewed in Peterson and Black 1994). For example, cages may concentrate or remove nektonic food sources resulting in a corresponding increase or decrease in growth. Artificial confinement of fish to a small area may also reduce perception of growth-based habitat quality if fish typically move over a much

larger area to obtain food, or would ordinarily move to avoid poor water quality.

Alternatively, directly accounting for bias associated with field estimates of growth rates presented in this dissertation may also be difficult. Although density of conspecifics may be used as a covariate to control for density-dependent effects on growth, controlling for selective mortality is more problematic because selective mortality varied both spatially and temporally. For example, selective mortality of croaker in this study varied between-estuaries and over-time, suggesting that incorporation of selective mortality into growth estimates needs to be investigated on a cohort-by-cohort basis. Ultimately, caution should be used when applying growth-based evaluation of habitat quality from either caging experiments or back-calculated otolith growth from field studies.

Future Research

Evaluation of habitat quality using univariate methods such as comparisons of fish growth among habitats is likely insufficient to rigorously evaluate the relative importance of different habitats. A better approach to investigating juvenile habitat quality may be to use a multivariate approach that jointly considers the importance of density, growth, survival, and movement (i.e, habitat specific juvenile fish production that contributes to the adult stock). This approach, called the ‘nursery role hypothesis’, states that a habitat has relatively higher quality for juveniles of a particular species if “its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur” (Beck et al. 2001). Although the nursery role of different habitats may be difficult to test empirically without an extensive tagging study or otolith microchemistry techniques

(reviewed in, Gillanders et al. 2003), the danger in not correctly prioritizing habitats for protection is that habitat management plans will have wasted money, time, and effort, and may fail to protect habitats that are most important to a species survival.

LITERATURE CITED

- Beck, M. W., K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, M. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**:633-641.
- Duffy, J. T., C. E. Epifanio, and J. S. Cope. 1996. Effects of prey density on the growth and mortality of weakfish *Cynoscion regalis* (Bloch and Schneider) larvae: experiments in field enclosures. *Journal of Experimental Marine Biology and Ecology* **202**:191-203.
- Gillanders, B. M., K. W. Able, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* **247**:281-295.
- Goldberg, R., B. Phelan, J. Pereira, S. Hagan, P. Clark, A. Bejda, A. Calabrese, A. Studholme, and K. W. Able. 2002. Variability in habitat use by young-of-the-year winter-flounder, *Pseudopleuronectes americanus*, in three northeastern U.S. estuaries. *Estuaries* **25**:215-226.
- Meekan, M. G., and L. Fortier. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. *Marine Ecology Progress Series* **137**:25-37.

- Necaise, A. M. D., S. W. Ross, and J. M. Miller. 2005. Estuarine habitat evaluation measured by growth of juvenile summer flounder *Paralichthys dentatus* in a North Carolina estuary. Marine Ecology Progress Series **285**:157-168.
- NMFS. 1997. Magnuson-Stevens Act provisions: essential fish habitat: interim final rule and request for comments. Federal Register [Docket 96103033-7238-04; I.D. 120996A]: 66-66559.
- Peterson, C. H., and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. Marine Ecology Progress Series **111**:289-297.
- Phelan, B. A., R. Goldberg, A. Bejda, J. Pereira, S. Hagan, P. Clark, A. L. Studholme, A. Calabrese, and K. W. Able. 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. Journal of Experimental Marine Biology and Ecology **147**:1-28.
- Raventos, N., and E. Macpherson. 2005. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Marine Ecology Progress Series **285**:205-211.
- Scharf, F. S. 2000. Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast with implications for recruitment and stock enhancement. Transactions of the American Fisheries Society **129**:1207-1222.
- Searcy, S., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecology **82**:2452-2470.

- Shima, J. S., and A. M. Findlay. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Marine Ecology Progress Series* **235**:303-309.
- Sogard, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* **85**:35-53.
- Takasuka, A., I. Aoki, and I. Mitani. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology Progress Series* **252**:223-238.

APPENDICES

Appendix 1: Atlantic croaker, *Micropogonias undulatus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the Newport River estuary, NC. Stations are organized up- to down-river (N1 – N4), mid-estuary (N5), and creek sampling stations (O1 – O2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2001	02 Dec	Density	171.7 (35.6)	52.3 (30.8)	1.9 (0.3)	6.4 (1.2)	2.8 (0.3)	N/A	N/A
		Length	11.1 (0.1)	11.4 (0.2)	12.3 (1.1)	14.5 (1.7)	10.7 (0.2)		
	10 Dec	Density	—	2.2 (0.0)	—	62.0 (15.1)	9.6 (2.0)	N/A	N/A
		Length		17.3 (5.5)		12.1 (0.1)	11.1 (0.2)		
	17 Dec	Density	201.1 (45.3)	86.1 (36.1)	11.1 (1.3)	18.9 (14.5)	35.3 (1.3)	N/A	N/A
		Length	12.1 (0.1)	11.6 (0.1)	11.1 (0.1)	10.9 (0.1)	10.8 (0.1)		
Spring 2002	13 Feb	Density	1.8 (0.5)	71.9 (8.1)	48.1 (8.7)	25.5 (8.0)	1.8 (0.4)	—	—
		Length	15.4 (1.0)	14.0 (0.1)	15.4 (0.1)	15.2 (0.1)	10.9 (0.1)		
	18 Feb	Density	16.7 (0.8)	13.6 (7.8)	57.3 (10.6)	12.2 (3.6)	39.5 (0.6)	5.0 (0.8)	—
		Length	21.6 (4.8)	45.4 (18.7)	19.6 (0.7)	20.1 (1.8)	11.8 (0.3)	10.4 (0.2)	
	25 Feb	Density	7.2 (0.6)	5.6 (1.4)	12.0 (1.4)	933.8 (299.5)	11.4 (4.5)	—	—
		Length	21.3 (6.0)	11.6 (0.4)	12.1 (0.3)	25.4 (0.1)	12.0 (0.4)		
	04 Mar	Density	1.9 (0.6)	0.4 (0.0)	34.2 (9.2)	101.9 (15.9)	14.5 (5.3)	0.6 (0.3)	0.6 (0.3)
		Length	28.3 (6.2)	12.0 (0.0)	12.6 (0.4)	13.4 (0.3)	10.1 (0.1)	12.0 (0.0)	14.0 (0.0)
	10 Mar	Density	12.5 (3.3)	5.3 (1.4)	410.5 (74.9)	6.4 (0.6)	25.6 (10.6)	1.1 (0.6)	—
		Length	15.4 (0.5)	12.9 (0.5)	13.0 (0.1)	16.4 (1.7)	11.2 (0.4)	10.0 (0.0)	
	16 Mar	Density	23.9 (2.8)	0.6 (0.3)	37.3 (5.3)	18.6 (3.9)	15.6 (8.9)	—	—
		Length	22.3 (1.8)	17.0 (0.0)	14.5 (0.3)	15.4 (0.6)	16.5 (1.5)		

Appendix 1 continued

Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2002	16 Nov	Density Length	3.9 (2.2) 35.0 (3.9)	16.1 (7.8) 14.1 (1.2)	—	13.3 (4.4) 24.4 (2.4)	1.1 (1.1) 10.0 (0.0)	—	76.1 (16.4) 11.2 (0.1)
	22 Nov	Density Length	0.6 (0.6) 42.2 (0.0)	0.6 (0.56) 50.0 (0.0)	1.7 (1.0) 11.7 (0.2)	2.2 (1.1) 10.9 (0.6)	51.7 (17.3) 10 (0.1)	3.3 (1.0) 11.7 (0.7)	33.9 (15.6) 11.3 (0.1)
	28 Nov	Density Length	10.0 (1.9) 40.0 (0.0)	5.6 (3.1) 28.8 (3.8)	—	1.1 (0.6) 20.0 (5.0)	—	0.6 (0.6) 25.0 (0.0)	12.2 (1.1) 13.3 (0.3)
	07 Dec	Density Length	—	5.6 (2.9) 16.2 (2.9)	14.5 (1.5) 11.5 (0.6)	84.5 (9.8) 10.5 (0.1)	1.7 (1.0) 10.0 (0.0)	—	—
	13 Dec	Density Length	0.6 (0.6) 10.0 (0.0)	33.3 (6.0) 12.1 (0.7)	27.2 (6.8) 20.0 (3.3)	5.6 (1.5) 18.2 (3.8)	41.7 (21.5) 10.7 (0.1)	0.6 (0.6) 13.0 (0.0)	—
	20 Dec	Density Length	60.6 (17.7) 13.3 (0.8)	17.8 (12.4) 12.8 (1.0)	11.1 (2.9) 12.4 (0.7)	11.1 (0.6) 10.9 (0.4)	17.8 (1.1) 10.1 (0.2)	114.1 (30.8) 10.3 (0.1)	10.8 (1.7) 10.5 (0.2)
	27 Dec	Density Length	—	—	66.1 (14.5) 12.0 (0.7)	20.0 (9.8) 20.0 (2.5)	17.8 (2.2) 10.0 (0.2)	12.2 (5.3) 10.1 (0.2)	1.5 (1.5) 10.9 (0.3)
Spring 2003	04 Mar	Density Length	—	—	—	479.0 (174.5) 12.0 (0.2)	12.8 (0.6) 11.9 (0.2)	—	—
	11 Mar	Density Length	—	—	—	—	171.2 (15.0) 12.4 (0.2)	15.6 (4.5) 11.2 (0.5)	—
	18 Mar	Density Length	—	60.6 (10.7) 13.1 (0.2)	11.1 (6.1) 13.4 (0.4)	22.8 (13.1) 14.2 (0.2)	27.8 (4.6) 11.3 (0.2)	12.2 (1.1) 11.8 (0.3)	3.3 (1.9) 12.4 (0.6)
	25 Mar	Density Length	—	—	—	—	16.11 (12.0) 12.2 (0.4)	—	—
	01 Apr	Density Length	—	—	1.1 (1.1) 12.2 (0.6)	39.5 (10.7) 13.8 (0.2)	6.1 (2.8) 12.6 (0.5)	—	—
	08 Apr	Density Length	—	—	—	44.5 (5.5) 16.2 (0.4)	56.7 (6.7) 12.4 (0.2)	—	—
	15 Apr	Density Length	—	—	—	28.3 (13.0) 16.3 (0.3)	1.1 (0.6) 12.5 (0.5)	—	—

Appendix 2: Spot, *Leiostomus xanthurus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the Newport River estuary, NC. Stations are organized up- to down-river (N1 – N4), mid-estuary (N5), and creek sampling stations (O1 – O2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2001	02 Dec	Density Length	—	—	—	—	—	N/A	N/A
	10 Dec	Density Length	—	—	—	—	—	N/A	N/A
	17 Dec	Density Length	—	—	—	—	—	N/A	N/A
Spring 2002	13 Feb	Density Length	0.1 (0.1) 18.0 (4.0)	1.1 (0.3) 15.8 (0.4)	3.9 (0.8) 15.9 (0.3)	8.0 (2.6) 16.7 (0.1)	17.6 (4.8) 15.6 (0.1)	3 (1.7) 20.7 (0.3)	0.2 (0.1) 21.0 (0.3)
	18 Feb	Density Length	—	0.6 (0.3) 68.0 (0.0)	26.2 (5.6) 19.9 (0.5)	6.1 (1.1) 16.7 (0.7)	52.3 (29.8) 15.1 (0.1)	66.9 (4.1) 14.8 (0.1)	43.4 (6.7) 15.0 (0.2)
	25 Feb	Density Length	—	—	0.5 (0.0) 80.0 (0.0)	5.0 (0.0) 26.3 (0.5)	62.9 (19.5) 14.4 (0.1)	11.4 (2.8) 14.4 (0.3)	43.7 (3.6) 17.0 (0.1)
	04 Mar	Density Length	—	—	6.1 (3.1) 16.5 (1.1)	47.6 (7.5) 17.1 (0.3)	614.0 (95.7) 16.3 (0.1)	20.3 (3.9) 20.9 (0.4)	69.0 (2.2) 17.1 (0.1)
	10 Mar	Density Length	0.6 (0.3) 16.0 (0.0)	—	0.6 (0.3) 14.0 (0.0)	5.0 (5.0) 15.0 (0.0)	485.4 (30.6) 15.8 (0.0)	106.3 (12.2) 19.2 (0.4)	113.0 (31.2) 19.7 (0.2)
	16 Mar	Density Length	—	—	8.4 (1.7) 16.6 (0.3)	35.6 (2.2) 18.6 (0.2)	629.0 (121.4) 16.5 (0.1)	47.3 (0.6) 22.3 (0.7)	113.6 (26.7) 20.1 (0.2)

Appendix 2 continued

Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2002	16 Nov	Density Length	—	—	—	—	—	—	—
	22 Nov	Density Length	—	—	—	—	—	—	—
	28 Nov	Density Length	—	—	—	—	—	—	—
	07 Dec	Density Length	—	—	—	—	—	—	—
	13 Dec	Density Length	—	—	—	0.6 (0.6) 50 (0.0)	—	—	—
	20 Dec	Density Length	—	—	—	—	—	—	—
	27 Dec	Density Length	—	—	—	—	—	1.1 (1.1) 12 (0.8)	1.3 (0.2) 12 (0.8)
Spring 2003	04 Mar	Density Length	—	—	—	61.1 (28.1) 17.1 (0.2)	103.4 (7.7) 17.5 (0.2)	84.5 (17.3) 19.3 (0.1)	118.4 (44.2) 17.6 (0.2)
	11 Mar	Density Length	—	—	—	3.3 (2.5) 17.3 (0.4)	430.6 (100.1) 18.0 (0.2)	1668.1 (1.1) 19.7 (0.2)	3338.4 (335.6) 20.1 (0.2)
	18 Mar	Density Length	—	63.9 (13.5) 17.3 (0.2)	8.5 (4.1) 18.3 (0.5)	11.9 (1.8) 17.9 (0.4)	151.7 (43.2) 17.0 (0.2)	425.6 (13.5) 19.5 (0.5)	785.7 (192.5) 19.2 (0.3)
	25 Mar	Density Length	—	—	—	—	493.4 (29.0) 19.9 (0.4)	120.6 (55.1) 22.5 (0.4)	913.5 (116.5) 19.8 (0.3)
	01 Apr	Density Length	—	—	1.7 (0.0) 18.0 (0.0)	315.1 (101.5) 18.7 (0.3)	445.6 (164.7) 21.1 (0.4)	110.0 (6.9) 23.7 (0.6)	413.4 (58.4) 21.3 (0.4)
	08 Apr	Density Length	—	4.4 (0.6) 20.3 (0.8)	4.4 (2.4) 18.1 (0.8)	48.3 (18.6) 19.4 (0.3)	472.9 (82.0) 19.8 (0.6)	145.6 (39.5) 26.8 (0.7)	402.3 (67.6) 21.3 (0.4)
	15 Apr	Density Length	—	—	—	84.5 (18.5) 20.6 (0.6)	108.9 (18.5) 24.2 (0.9)	309.0 (44.8) 27.9 (0.8)	954.6 (239.0) 21.0 (0.2)

Appendix 3: Pinfish, *Lagodon rhomboides*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the Newport River estuary, NC. Stations are organized up- to down-river (N1 – N4), mid-estuary (N5), and creek sampling stations (O1 – O2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2001	02 Dec	Density Length	—	—	—	—	—	N/A	N/A
	10 Dec	Density Length	—	—	—	—	—	N/A	N/A
	17 Dec	Density Length	—	—	—	—	—	N/A	N/A
Spring 2002	13 Feb	Density Length	—	0.1 (0.1) 15.0 (0.0)	0.3 (0.1) 16.0 (0.0)	1.9 (0.7) 14.7 (0.1)	1.2 (0.4) 14.3 (0.1)	0.1 (0.1) 13.5 (0.5)	0.4 (0.1) 13.7 (0.3)
	18 Feb	Density Length	—	—	0.2 (0.3) 15.0 (0.0)	—	30.3 (9.7) 13.7 (0.2)	1.7 (0.0) 13.8 (0.6)	9.2 (3.3) 14.6 (0.2)
	25 Feb	Density Length	—	—	—	—	31.7 (8.4) 13.0 (0.1)	1.1 (0.6) 13.0 (0.0)	2.2 (0.0) 14.2 (0.5)
	04 Mar	Density Length	—	—	—	5.0 (2.5) 15.2 (0.3)	76.8 (10.0) 15.0 (0.0)	1.3 (0.3) 15.3 (0.3)	24.2 (0.8) 14.8 (0.1)
	10 Mar	Density Length	—	—	—	1.9 (0.6) 14.8 (0.3)	44.0 (9.5) 14.1 (0.1)	10.6 (8.9) 14.5 (0.5)	9.5 (2.2) 14.3 (0.5)
	16 Mar	Density Length	—	—	—	—	5.6 (2.2) 14.5 (0.3)	—	—

Appendix 3 continued

Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2002	16 Nov	Density Length	—	—	—	—	—	—	—
	22 Nov	Density Length	—	—	—	—	—	—	—
	28 Nov	Density Length	—	—	—	—	—	—	—
	07 Dec	Density Length	—	—	—	—	—	—	—
	13 Dec	Density Length	—	—	2.2 (1.5) 13.4 (0.2)	0.6 (0.6) 12.6 (0.0)	3.3 (1.7) 13.1 (0.1)	2.2 (0.6) 12.6 (0.2)	—
	20 Dec	Density Length	3.3 (1.0) 13.0 (0.4)	—	—	0.6 (0.6) 12.9 (0.0)	1.1 (0.6) 13.2 (0.5)	25.9 (7.9) 12.3 (0.1)	13.1 (4.3) 12.7 (0.1)
	27 Dec	Density Length	—	—	—	—	13.3 (0.0) 12.2 (0.2)	26.7 (8.8) 12.4 (0.1)	25.4 (10.9) 12.3 (0.1)
Spring 2003	04 Mar	Density Length	—	—	—	2.2 (1.1) 16.6 (0.0)	18.3 (1.7) 14.7 (0.1)	1.7 (1.0) 15.7 (0.4)	47.8 (17.5) 14.9 (0.1)
	11 Mar	Density Length	—	—	—	0.6 (0.6) 15.1 (0.0)	2.8 (1.5) 13.2 (0.6)	5.6 (1.1) 14.2 (1.4)	42.2 (5.9) 14.8 (0.3)
	18 Mar	Density Length	—	1.1 (1.1) 13.9 (0.1)	—	0.4 (0.4) 13.9 (0.1)	21.7 (5.1) 13.5 (0.1)	—	8.9 (2.2) 14.2 (0.3)
	25 Mar	Density Length	—	—	—	—	—	—	5.6 (4.0) 14.3 (0.5)
	01 Apr	Density Length	—	—	—	1.7 (1.7) 13.6 (0.6)	—	—	1.1 (1.1) 13.5 (0.0)
	08 Apr	Density Length	—	—	—	—	—	1.1 (1.1) 13.5 (0.0)	1.1 (1.1) 13.5 (0.0)
	15 Apr	Density Length	—	—	—	—	—	—	—

Appendix 4: Southern flounder, *Paralichthys lethostigma*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the Newport River estuary, NC. Stations are organized up- to down-river (N1 – N4), mid-estuary (N5), and creek sampling stations (O1 – O2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2002	16 Nov	Density Length	—	—	—	—	—	—	—
	22 Nov	Density Length	—	—	—	—	—	—	—
	28 Nov	Density Length	—	—	—	—	—	—	—
	07 Dec	Density Length	—	—	—	—	—	—	—
	13 Dec	Density Length	—	—	—	—	—	—	—
	20 Dec	Density Length	—	—	—	—	—	0.6 (0.4) 11.8 (0.0)	—
	27 Dec	Density Length	—	—	2.2 (0.6) 12.3 (0.4)	46.7 (1.7) 12.2 (0.1)	—	3.3 (1.0) 11.8 (0.1)	0.4 (0.4) 10.7 (0.0)

Appendix 4 continued

Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Spring 2003	04 Mar	Density Length	10.0 (4.8) 13.6 (0.1)	—	—	214.5 (37.4) 13.6 (0.1)	2.8 (2.0) 13.6 (0.2)	1.1 (1.1) 13.2 (0.3)	—
	11 Mar	Density Length	—	5.6 (2.8) 11.8 (0.1)	13.9 (10.0) 11.8 (0.1)	238.4 (93.3) 13.3 (0.1)	20.0 (1.9) 13.0 (0.2)	38.9 (22.3) 15.0 (0.3)	—
	18 Mar	Density Length	2.8 (1.1) 13.7 (0.4)	2.8 (1.5) 13.7 (0.2)	—	1.5 (1.5) 13.5 (0.2)	0.7 (0.6) 12.9 (0.0)	13.3 (6.9) 15.5 (0.5)	1.1 (1.1) 16.8 (0.0)
	25 Mar	Density Length	—	—	—	1.2 (1.4) 16.5 (0.1)	—	0.8 (0.6) 20.0 (0.0)	—
	01 Apr	Density Length	—	—	—	10.0 (1.0) 15.1 (0.5)	—	1.1 (1.1) 20.1 (0.0)	2.2 (1.1) 22.0 (3.7)
	08 Apr	Density Length	3.3 (1.9) 17.5 (0.8)	0.9 (0.6) 13.2 (0.0)	0.6 (0.6) 18.3 (0.0)	—	0.6 (0.6) 15.3 (0.0)	1.1 (1.1) 32.4 (0.0)	—
	15 Apr	Density Length	—	—	—	1.1 (0.6) 14.8 (1.4)	—	1.1 (1.1) 43.6 (0.0)	—

Appendix 5: Summer flounder, *Paralichthys dentatus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the Newport River estuary, NC. Stations are organized up- to down-river (N1 – N4), mid-estuary (N5), and creek sampling stations (O1 – O2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Fall 2002	16 Nov	Density Length	—	—	—	—	—	—	—
	22 Nov	Density Length	—	—	—	—	—	—	—
	28 Nov	Density Length	—	—	—	—	—	—	—
	07 Dec	Density Length	—	—	—	—	—	—	—
	13 Dec	Density Length	—	—	—	—	—	—	—
	20 Dec	Density Length	—	—	—	—	—	—	—
	27 Dec	Density Length	—	—	—	—	—	—	—

Appendix 5 continued

Season	Date	Measure	N1	N2	N3	N4	N5	O1	O2
Spring 2003	04 Mar	Density Length	—	—	—	7.2 (0.6) 15.6 (0.3)	2.8 (0.6) 17.5 (1.2)	—	0.6 (0.6) 17.3 (0.0)
	11 Mar	Density Length	—	—	—	—	10.6 (2.0) 15.0 (0.3)	—	—
	18 Mar	Density Length	—	—	—	0.2 (0.2) 15.0 (0.0)	0.6 (0.6) 16.8 (0.0)	2.2 (2.2) 17.5 (0.3)	—
	25 Mar	Density Length	—	—	—	—	—	1.7 (1.7) 16.7 (2.3)	11.1 (5.9) 20.1 (1.3)
	01 Apr	Density Length	—	—	—	1.1 (0.6) 14.6 (0.2)	—	—	1.1 (1.1) 19.2 (0.0)
	08 Apr	Density Length	—	—	2.8 (2.8) 13.5 (0.5)	1.1 (0.6) 14.7 (2.0)	1.7 (1.7) 13.8 (0.6)	3.3 (1.9) 27.1 (0.9)	1.1 (1.1) 19.2 (0.0)
	15 Apr	Density Length	—	—	—	—	—	2.8 (2.8) 20.2 (1.7)	3.3 (1.9) 23.0 (5.7)

Appendix 6: Atlantic croaker, *Micropogonias undulatus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the White Oak River estuary, NC. Stations are organized up- to down-river (W1 – W4), mid-estuary (W5), and creek sampling stations (H1 – H2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2002	19 Feb	Density	150 (2.5)		29.2 (12.5)	0.6 (0.3)	5.8 (4.2)	0.6 (0.3)	—
		Length	13.7 (0.3)		11.9 (0.3)	12.0 (0.0)	16.5 (0.5)	15.0 (0.0)	
	26 Feb	Density	8.6 (1.4)		0.8 (0.8)	5.6 (0.6)	3.9 (2.2)	1.1 (0.6)	1.1 (0.6)
		Length	22.3 (1.6)		16.5 (0.0)	16.3 (2.4)	21.0 (0.0)	14.0 (1.0)	12.0 (0.0)
	05 Mar	Density	13.4 (4.2)		283.9 (47.6)	5.0 (5.0)	10.6 (2.8)	4.5 (1.1)	1.1 (0.6)
Fall 2002		Length	16.0 (1.8)		13.8 (0.2)	12.5 (0.3)	11.8 (1.8)	23.0 (0.0)	24.0 (0.0)
	10 Mar	Density	10.0 (5.0)		15.9 (4.2)	3.6 (0.3)	27.3 (4.5)	6.7 (6.7)	—
		Length	14.3 (1.2)		14.2 (0.6)	12.5 (0.5)	20.4 (1.2)	12.5 (0.3)	
	18 Mar	Density	0.8 (0.0)		11.7 (3.3)	7.8 (2.2)	22.3 (6.1)	10.6 (2.8)	—
		Length	21.0 (0.0)		24.3 (6.5)	13.8 (0.8)	22.2 (1.2)	15.3 (1.2)	
	15 Nov	Density	26.2 (6.4)	71.8 (31.6)	49.0 (42.4)	27.3 (22.5)	94.1 (14.2)	—	0.6 (0.6)
		Length	18.7 (1.0)	17.9 (1.0)	11.7 (0.5)	13.9 (1.1)	11.5 (0.4)		10.0 (0.0)
	21 Nov	Density	20.0 (5.1)	119.1 (49.6)	101.3 (50.7)	203.2 (175.2)	20.6 (12.2)	2.8 (0.6)	3.9 (2.2)
		Length	31.5 (2.8)	21.5 (1.3)	18.1 (1.3)	11.9 (0.9)	11.1 (0.4)	12.3 (0.7)	12.1 (1.0)
	27 Nov	Density	13.4 (1.9)	51.2 (4.3)	114.1 (58.6)	95.2 (39.8)	33.4 (11.0)	—	—
		Length	20.2 (1.5)	26.4 (0.9)	16.2 (0.7)	11.3 (0.2)	11.3 (0.2)		
	05 Dec	Density	10.0 (8.4)	116.3 (34.8)	101.9 (20.3)	13.9 (20.3)	13.4 (1.9)	1.7 (0.0)	1.1 (1.1)
		Length	25.9 (2.8)	17.6 (0.9)	17.2 (2.9)	11.8 (0.5)	11.9 (1.2)	11.0 (0.0)	10.0 (0.0)
	12 Dec	Density	47.3 (19.9)	2.8 (0.6)	96.9 (1.7)	160.3 (72.6)	3.3 (1.0)	—	15.0 (5.8)
		Length	15.7 (1.0)	16.7 (2.6)	23.2 (1.6)	12.5 (0.8)	10.7 (0.5)		12.1 (0.4)
	19 Dec	Density	12.8 (0.6)	528.3 (246.1)	23.9 (10.6)	2.2 (1.5)	62.3 (11.6)	3.3 (0.0)	24.5 (6.8)
		Length	17.7 (1.6)	22.6 (1.5)	11.5 (0.7)	11.3 (1.5)	11.5 (0.3)	12.4 (0.7)	12.9 (0.2)
	26 Dec	Density	7.2 (2.9)	6.1 (1.5)	19.5 (1.5)	3.3 (0.0)	25.6 (9.7)	12.8 (2.2)	199.3 (88.2)
		Length	22.8 (3.5)	21.8 (3.4)	29.4 (1.4)	23.8 (8.8)	10.8 (0.2)	12.6 (0.3)	11.0 (0.2)

Appendix 6 continued

Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2003	07 Mar	Density Length	—	1.7 (0.0) 32.1 (5.0)	2.2 (1.1) 31.5 (5.6)	6.7 (1.9) 13.3 (0.4)	415.3 (174.1) 12.3 (0.2)	—	—
	14 Mar	Density Length	—	—	8.4 (5.1) 21.0 (2.1)	132.5 (27.1) 11.9 (0.1)	54.6 (16.4) 13.2 (0.6)	—	—
	21 Mar	Density Length	1.7 (0.0) 13.5 (0.3)	15.6 (2.9) 15.0 (0.6)	32.3 (12.3) 14.9 (1.0)	262.2 (163.0) 12.4 (0.2)	22.8 (4.8) 22.0 (1.7)	6.7 (0.0) 13.6 (1.4)	1.1 (1.1) 13.2 (0.0)
	28 Mar	Density Length	—	1.7 (1.0) 15.2 (0.3)	38.1 (17.4) 14.0 (0.2)	41.5 (19.5) 13.2 (0.4)	52.3 (4.5) 15.8 (0.8)	28.9 (15.6) 13.6 (0.5)	25.6 (9.5) 14.1 (0.4)
	04 Apr	Density Length	3.9 (1.5) 23.4 (3.2)	1.1 (0.6) 14.7 (0.2)	43.2 (24.0) 14.6 (0.4)	12.2 (7.5) 16.2 (0.9)	2.2 (1.5) 16.1 (0.9)	—	6.7 (3.9) 14.8 (3.5)
	11 Apr	Density Length	1.7 (1.7) 24.4 (3.3)	4.5 (1.1) 21.9 (1.8)	—	173.7 (112.9) 14.1 (0.3)	27.8 (1.5) 19.2 (1.4)	5.6 (5.6) 15.2 (2.0)	—
	18 Apr	Density Length	2.8 (0.6) 31.5 (8.5)	—	7.1 (2.3) 17.8 (1.3)	46.4 (15.6) 15.7 (0.2)	45.6 (6.4) 22.7 (0.7)	1.1 (1.1) 68.0 (0.0)	3.3 (1.9) 18.8 (0.6)

Appendix 7: Spot, *Leiostomus xanthurus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the White Oak River estuary, NC. Stations are organized up- to down-river (W1 – W4), mid-estuary (W5), and creek sampling stations (H1 – H2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2002	19 Feb	Density	2.8 (1.7)		44.8 (36.0)	13.1 (6.7)	68.7 (34.9)	47.3 (23.8)	51.2 (31.8)
		Length	19.3 (0.9)		17.3 (0.4)	15.5 (0.3)	15.1 (0.3)	16.5 (0.2)	16.0 (0.1)
	26 Feb	Density	7.8 (3.9)		30.1 (16.9)	36.7 (19.9)	128.6 (72.8)	191.2 (100.2)	285.3 (142.7)
		Length	17.5 (0.5)		16.5 (0.3)	15.8 (0.2)	16.0 (0.1)	16.8 (0.1)	16.3 (0.1)
	05 Mar	Density	0.8 (0.8)		77.9 (57.6)	49.5 (28.4)	93.0 (51.7)	61.2 (31.0)	177.0 (88.6)
Fall 2002		Length	17.0 (0.6)		16.4 (0.2)	16.6 (0.2)	16.9 (0.2)	17.7 (0.3)	16.7 (0.1)
	10 Mar	Density	—		0.3 (0.3)	60.4 (33.0)	374.1 (190.4)	218.2 (127.3)	280.6 (215.7)
		Length			23.0 (0.0)	16.6 (0.2)	18.1 (0.2)	20.5 (0.5)	17.7 (0.3)
	18 Mar	Density	—		8.4 (4.3)	68.2 (41.3)	285.0 (184.8)	169.2 (96.9)	295.6 (148.1)
		Length			16.6 (0.5)	16.2 (0.2)	20.7 (0.2)	20.9 (0.4)	18.9 (0.3)
	15 Nov	Density	—	—	—	—	0.6 (0.6)	1.1 (0.6)	—
		Length					40.0 (0.0)	40.0 (0.0)	
	21 Nov	Density	—	—	—	—	—	—	—
		Length							
	27 Nov	Density	—	—	—	—	—	2.2 (0.6)	—
		Length						45.0 (0.0)	
	05 Dec	Density	—	—	—	7.2 (4.3)	—	—	—
		Length				45.0 (0.0)			
	12 Dec	Density	—	—	0.0 (3.5)	1.7 (1.7)	—	—	—
		Length			55.6 (2.9)	60.0 (0.0)			
	19 Dec	Density	—	—	—	—	—	—	—
		Length							
	26 Dec	Density	—	1.7 (1.0)	—	—	—	—	—
		Length		60.0 (0.0)					

Appendix 7 continued

Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2003	07 Mar	Density Length	—	—	—	0.6 (0.6) 19.3 (0.3)	362.9 (24.9) 19.3 (0.3)	122.5 (14.6) 20.8 (0.3)	843.9 (47.6) 19.2 (0.3)
	14 Mar	Density Length	—	—	—	—	384.1 (35.3) 20.5 (0.3)	1754.6 (24.8) 20.5 (0.3)	4707.2 (258.9) 21.2 (0.4)
	21 Mar	Density Length	—	6.1 (1.5) 20.8 (0.6)	8.4 (4.4) 20.8 (0.6)	27.8 (14.0) 19.8 (0.3)	296.1 (90.8) 21.1 (0.3)	73.5 (17.7) 18.6 (0.7)	43.4 (11.7) 25.1 (2.4)
	28 Mar	Density Length	—	—	5.3 (4.5) 22.5 (0.4)	2.2 (1.5) 20.2 (1.6)	900.7 (129.3) 21.7 (0.4)	53.4 (30.9) 17.8 (1.0)	399.7 (137.8) 20.2 (0.4)
	04 Apr	Density Length	—	3.3 (1.0) 22.3 (0.8)	3.3 (1.9) 22.2 (1.7)	30.1 (14.6) 22.4 (0.6)	108.0 (36.1) 22.5 (0.4)	423.1 (264.1) 20.3 (0.5)	1215.8 (223.9) 20.2 (0.2)
	11 Apr	Density Length	—	—	—	17.8 (5.3) 20.2 (0.8)	508.8 (84.1) 25.1 (0.5)	116.9 (27.3) 28.5 (1.0)	89.1 (20.6) 28.7 (0.7)
	18 Apr	Density Length	—	—	0.2 (0.2) 22.1 (0.9)	2.2 (0.6) 23.9 (0.6)	449.2 (37.8) 30.1 (0.8)	109.1 (41.5) 30.1 (0.8)	285.0 (99.6) 26.4 (0.8)

Appendix 8: Pinfish, *Lagodon rhomboides*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the White Oak River estuary, NC. Stations are organized up- to down-river (W1 – W4), mid-estuary (W5), and creek sampling stations (H1 – H2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2002	19 Feb	Density	—		1.4 (1.0)	0.8 (0.8)	2.5 (2.1)	8.1 (4.1)	28.9 (14.6)
		Length			15.0 (0.0)	14.3 (0.3)	14.8 (0.1)	17.3 (0.7)	14.8 (0.1)
	26 Feb	Density	—		—	0.6 (0.6)	29.5 (15.4)	11.4 (6.0)	51.8 (26.1)
		Length				15.0 (0.0)	14.8 (0.1)	15.0 (0.1)	15.2 (0.3)
	05 Mar	Density	—		1.7 (1.0)	3.3 (1.7)	11.1 (5.9)	6.1 (3.1)	72.4 (39.7)
Fall 2002		Length			15.0 (0.0)	15.0 (0.0)	14.9 (0.2)	17.0 (0.6)	15.4 (0.1)
	10 Mar	Density	—		—	0.8 (0.5)	55.7 (30.1)	3.3 (19)	165.3 (148.1)
		Length				15.0 (0.0)	15.4 (0.1)	17.3 (2.3)	15.1 (0.1)
	18 Mar	Density	—		0.6 (0.6)	1.9 (1.5)	34.0 (24.6)	9.5 (7.1)	115.8 (60.4)
		Length			15.0 (0.0)	14.9 (0.1)	15.6 (0.2)	18.2 (0.7)	15.6 (0.1)
	15 Nov	Density	—	—	—	—	—	—	—
		Length							
	21 Nov	Density	—	—	—	—	—	—	—
		Length							
	27 Nov	Density	—	—	—	—	—	—	1.7 (1.7)
		Length							40.0 (0.0)
	05 Dec	Density	—	—	—	8.9 (8.1)	—	—	—
		Length				45.0 (0.0)			
	12 Dec	Density	—	—	10.0 (5.4)	2.2 (2.2)	—	—	—
		Length			47.8 (2.4)	60.0 (0.0)			
	19 Dec	Density	—	—	—	—	3.3 (0.0)	15.6 (11.5)	10.0 (0.0)
		Length					12.9 (0.2)	13.6 (0.1)	14.1 (0.3)
	26 Dec	Density	—	—	—	2.8 (0.6)	3.3 (0.0)	8.9 (2.4)	14.5 (3.1)
		Length				34.8 (9.3)	12.9 (0.2)	13.8 (0.2)	13.6 (0.1)

Appendix 8 continued

Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2003	07 Mar	Density Length	—	—	—	—	9.5 (9.5) 15.0 (0.2)	416.4 (79.1) 16.0 (0.2)	1358.3 (58.9) 15.4 (0.1)
	14 Mar	Density Length	—	—	—	—	11.7 (2.6) 14.9 (0.2)	3647.3 (1669.3) 16.5 (0.2)	4034.7 (108.8) 16.2 (0.2)
	21 Mar	Density Length	—	—	—	0.6 (0.6) 14.0 (0.0)	0.6 (0.6) 13.5 (0.0)	741.5 (160.5) 15.6 (0.2)	40.1 (30.6) 15.9 (0.2)
	28 Mar	Density Length	—	—	—	0.6 (0.3) 15.4 (1.2)	1.7 (1.0) 16.6 (1.0)	1531.9 (831.7) 15.1 (0.2)	15.6 (2.9) 16.4 (0.3)
	04 Apr	Density Length	—	—	—	0.6 (0.6) 18.3 (0.0)	3.9 (2.2) 16.6 (0.8)	953.0 (576.2) 15.5 (0.2)	113.6 (46.8) 14.8 (0.2)
	11 Apr	Density Length	—	—	—	2.8 (0.6) 12.8 (0.0)	3.3 (0.0) 16.6 (0.8)	131.4 (21.3) 17.0 (0.3)	2.2 (2.2) 17.1 (0.4)
	18 Apr	Density Length	—	—	—	—	1.0 (1.9) 21.0 (0.0)	21.2 (12.5) 20.2 (0.3)	—

Appendix 9: Southern flounder, *Paralichthys lethostigma*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the White Oak River estuary, NC. Stations are organized up- to down-river (W1 – W4), mid-estuary (W5), and creek sampling stations (H1 – H2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Fall 2002	15 Nov	Density Length	—	—	—	—	—	—	—
	21 Nov	Density Length	—	—	—	—	—	—	—
	27 Nov	Density Length	—	—	—	—	—	—	—
	05 Dec	Density Length	—	—	—	—	—	—	—
	12 Dec	Density Length	—	—	—	—	—	—	—
	19 Dec	Density Length	—	—	—	—	—	—	—
	26 Dec	Density Length	—	—	—	—	—	—	—

Appendix 9 continued

Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2003	07 Mar	Density Length	—	56.8 (37.1) 13.5 (0.2)	45.1 (39.3) 13.9 (0.2)	0.6 (0.6) 13.0 (0.0)	114.7 (17.5) 13.9 (0.2)	64.6 (2.2) 17.0 (0.3)	15.6 (15.6) 15.3 (0.6)
	14 Mar	Density Length	—	—	10.6 (3.7) 14.2 (0.2)	90.7 (30.4) 13.4 (0.1)	64.0 (23.7) 13.6 (0.4)	191.5 (93.3) 17.8 (0.4)	237.6 (18.0) 17.2 (0.4)
	21 Mar	Density Length	2.2 (0.6) 13.6 (0.2)	6.1 (6.1) 14.0 (0.4)	44.5 (12.6) 13.9 (0.3)	2.0 (1.7) 14.1 (0.6)	72.4 (12.5) 17.0 (0.5)	20.0 (6.7) 17.6 (0.7)	91.3 (64.6) 16.2 (0.4)
	28 Mar	Density Length	10.6 (10.6) 15.1 (0.5)	15.0 (9.8) 15.1 (0.3)	4.5 (2.4) 15.2 (0.3)	—	95.7 (4.8) 18.4 (0.8)	—	103.5 (17.1) 16.6 (0.4)
	04 Apr	Density Length	—	23.9 (5.3) 16.5 (0.4)	3.5 (3.5) 16.5 (0.5)	31.7 (20.2) 16.5 (0.4)	17.3 (9.8) 18.6 (0.5)	17.8 (8.9) 18.7 (1.7)	91.3 (25.7) 18.6 (0.8)
	11 Apr	Density Length	3.9 (3.9) 17.5 (0.8)	78.5 (27.2) 17.1 (0.4)	—	—	88.0 (5.3) 22.0 (1.2)	14.5 (8.7) 21.0 (1.1)	23.4 (8.8) 21.5 (1.5)
	18 Apr	Density Length	1.1 (1.1) 17.6 (1.4)	28.4 (12.0) 19.1 (0.6)	0.3 (0.3) 18.4 (0.0)	0.2 (0.2) 18.0 (0.0)	84.1 (2.8) 21.3 (1.1)	5.6 (5.6) 20.7 (1.1)	43.4 (1.9) 19.5 (0.4)

Appendix 10: Summer flounder, *Paralichthys dentatus*. Density (standardized to # 100m²) and standard length (mm) measures with associated standard error (number in parentheses) from 1-m beam trawl collections in the White Oak River estuary, NC. Stations are organized up- to down-river (W1 – W4), mid-estuary (W5), and creek sampling stations (H1 – H2). N/A indicates that the station was not sampled and ‘—’ indicates that no fish were collected.

			River				Estuary	Creek	
Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Fall 2002	15 Nov	Density Length	—	—	—	—	—	—	—
	21 Nov	Density Length	—	—	—	—	—	—	—
	27 Nov	Density Length	—	—	—	—	—	—	—
	05 Dec	Density Length	—	—	—	—	—	—	—
	12 Dec	Density Length	—	—	—	—	—	—	—
	19 Dec	Density Length	—	—	—	—	—	—	—
	26 Dec	Density Length	—	—	—	—	—	—	—

Appendix 10 continued

Season	Date	Measure	W1	W2	W3	W4	W5	H1	H2
Spring 2003	07 Mar	Density Length	—	1.4 (1.1) 16.4 (0.9)	0.6 (0.6) 15.4 (0.0)	—	10.0 (1.9) 15.9 (0.3)	—	—
	14 Mar	Density Length	—	—	—	8.4 (3.5) 15.4 (0.2)	3.9 (1.5) 15.5 (0.4)	4.5 (4.5) 17.2 (0.0)	26.7 (0.0) 16.4 (0.5)
	21 Mar	Density Length	—	—	6.7 (1.0) 15.6 (0.3)	4.5 (4.5) 15.2 (0.3)	1.7 (1.0) 16.4 (0.7)	—	2.2 (2.2) 16.5 (0.0)
	28 Mar	Density Length	—	—	—	—	—	—	—
	04 Apr	Density Length	—	—	—	—	—	—	—
	11 Apr	Density Length	—	—	—	—	1.7 (0.0) 21.7 (1.9)	—	—
	18 Apr	Density Length	—	—	—	—	—	—	—