AGE, GROWTH, AND RECRUITMENT OF STRIPED BASS IN LAKE TEXOMA, OKLAHOMA-TEXAS

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Submitted to the Faculty of the
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Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
December, 2005

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STRIPED BASS IN LAKE TEXOMA,

OKLAHOMA-TEXAS

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ACKNOWLEDGEMENTS

I thank my advisor, Dr. Dana Winkelman, for his leadership and advice throughout my studies. He helped me to become a better scientist by allowing me to explore new ideas and learn on my own while being ever vigilant. My graduate experience was greatly enhanced because of his guidance.

I thank my advisory committee for their help through the years, especially Dr. Larry Claypool for his hours of advice on statistical problems. I thank Dr. Mark Payton for additional help with statistics. I thank the staff of the Oklahoma Cooperative Fish and Wildlife Research Unit for making the business end of graduate school much easier to endure.

This work would not have been possible without the aid of my fellow graduate students, namely Matt Mauck, Dan Dauwalter, Maureen Walsh, David Walter, Nick Utrup, Daniel Fenner, and Cliff Sager. I thank the technicians who helped on this project, especially all who spent hours of back-breaking labor running a shop-vac in the mesocosm tanks. I also thank the staff of the University of Oklahoma Biological Station for making my stay there pleasant and for allowing me to borrow equipment to make repairs as needed.

Most of all, I thank my wife, Amy and daughter, Serena for their love and support during my studies. They have made my life much more pleasant during the countless hours of frustration while I completed the vast majority of the requirements for

graduation. I am grateful to my family and in-laws for their help over the years. Without their support, I would have never made it through graduate school.

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CHAPTER I.

TEMPORAL AND SPATIAL VARIABILITY IN TRACE ELEMENT SIGNATURES OF JUVENILE STRIPED BASS OTOLITHS FROM TWO SPAWNING LOCATIONS IN LAKE TEXOMA, OKLAHOMA-TEXAS

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Abstract

We collected juvenile striped bass *Morone saxatilis* from 2002 to 2004 in two tributary arms of Lake Texoma to assess the potential of trace element analysis for identifying spawning locations. There were 16 elements in addition to Calcium present above detection limits in the otoliths of juvenile striped bass during all 3 years. The elemental composition of juvenile striped bass otoliths varied considerably between rivers both within and among years. Overall reclassification rates within each collection year ranged between 74% - 97%; however, reclassification rates among years were much lower (3% - 69%). Although the mechanisms generating spatial and temporal differences in otolith chemistry are not well understood, spatial differences in otolith chemistry indicate that the elemental fingerprints of fish from the different natal rivers in Lake Texoma provide a natural tag of their juvenile habitat. However, annual variability in elemental composition complicates using it to predict recruitment from the juvenile stage to adulthood.

Introduction

In many fisheries, the exploited stock consists of several age classes recruited from various natal and spawning areas (Richards and Rago 1999; Secor 2000b; Berkeley et al. 2004). For instance, many estuarine and ocean fishes are anadromous and the adult stocks consist of individuals spawned in several rivers or inlets (Waldman and Fabrizio 1994; Brown et al. 1999; Secor 2000a). To manage such stocks, it is essential to understand levels of recruitment coming from each potential spawning area, temporal variation in the number of recruits associated with each area, and connectivity among spawning areas (Gillanders 2002a; Kritzer and Sale 2004). To assess the contributions of

spawning areas to fishery stocks, it is necessary to identify an adult's spawning origin. One method is to mark young fish and recapture them as adults (Klar and Parker 1986; Wooley et al. 1990; Johnson 1990), but this methodology has several drawbacks (Buckley and Blankenship 1990). Another approach is to use naturally occurring markers that differ among populations (Waldman et al. 1996; McParland et al. 1999). Genetic markers have been used for population delineation but these markers are not effective when there is movement among populations (Brown et al. 2005). An alternative approach used successfully in marine systems (Campana et al. 1994) and more recently in freshwater systems (Wells et al. 2003) is elemental analyses of calcified structures, typically otoliths (Campana 1999; Campana and Thorrold 2001). This technique is generally referred to as otolith microchemistry or elemental analysis. During growth, trace elements are incorporated into the otolith from the surrounding environment and differences in elemental composition reflect differences in environmental history of the individual (Chesney et al. 1998; Bath et al. 2000; Campana and Thorrold 2001).

Otolith microchemistry has enabled assessment of recruitment, connectivity of populations, and movement of a variety of fish species (Shen et al. 1998, Zlokovitz et al. 2003, Kennedy et al. 2002). Most studies of otolith microchemistry have focused on reconstructing migration between fresh and saltwater environments (Secor 1992, Zimmerman and Reeves 2002, Morris et al. 2003) or distinguishing stocks of fish residing wholly within estuarine or marine environments (Gillanders 2002b, Thorrold et al. 1997, Campana et al. 1994). Few studies have assessed the potential of otolith microchemistry to evaluate recruitment and movement patterns among fishes in freshwater environments (Kennedy et al. 2000, Wells et al. 2003). However, the

freshwater studies that have been completed show promising results. Wells et al. (2003) reported 100% classification accuracy in cutthroat trout (*Oncorhyncus clarki lewisi*) among three streams in Idaho. Kennedy et al. (2000) were able to successfully characterize four major stages in the life cycle of Atlantic salmon (*Salmo salar*), including the freshwater hatchery and rearing stages.

Lake Texoma, formed by the impoundment of the Red and Washita Rivers on the Oklahoma-Texas border, is a nationally recognized striped bass fishery. Striped bass were first introduced to Lake Texoma in 1965 (Harper and Namminga 1986). Since 1974, striped bass have naturally reproduced in both rivers upstream of Lake Texoma and have become an important fishery, generating in excess of $25 million annually to the local economy (Schorr et al. 1995). Water development is also important in the region, and managers are concerned that changes in discharge or water quality in either river could influence striped bass recruitment.

Despite the importance of the fishery and environmental concerns, it is unknown if recruitment differs between the two rivers. A genetic survey indicated no clear genetic differences in spawning adults from the two river systems (Boxrucker 2001). Currently, the Oklahoma Department of Wildlife Conservation (ODWC) is identifying spawning areas in each river and estimating reproduction by collecting striped bass eggs in each river. Egg collection should indicate where the majority of spawning is occurring. However, egg production has not always been correlated with larval and adult recruitment (McGovern and Olney 1996), so it is necessary to assess recruitment at a later stage in life.

Our objectives were to assess elemental differences between otoliths of striped

bass spawned in the Red and Washita River arms of Lake Texoma and determine their usefulness as markers for areas of recruitment. We also assessed annual variation in elemental signatures of juvenile striped bass otoliths.

Methods

Juvenile striped bass *Morone saxatilis* were collected during three consecutive years from 2002 to 2004. In each year, fish were collected from 7 fixed sites on the upper ends of both the Red and Washita River arms of Lake Texoma. Fish were collected by beach seine, stored on ice in the field, and frozen in the laboratory. All juvenile striped bass were collected during the last two weeks of June. Depending on time of spawning, average length ranged from 44.5 mm on the Washita River arm in 2003 to 76.8 mm on the Washita River arm in 2004. We randomly chose 5 fish from each fixed site on each river arm for a total of 35 juvenile striped bass per river arm per year.

In a class 100 clean room, we measured the total length of each fish and removed and cleaned the otoliths (Wells et al. 2003). All tools contacting the otoliths were nonmetallic and acid washed. Once otoliths were extracted, we triple rinsed them with Millipore Milli-Q water, rinsed them for one minute with ultra pure hydrogen peroxide (36%) to remove organics, triple rinsed them again and allowed them to dry for 24 h under a laminar flow hood. The next day we sonicated the left sagital otoliths (or the right sagital if it was the only available otolith) for five minutes in Milli-Q water, triple rinsed them with Milli-Q water, and dried them under a laminar flow hood for another 24 h. We weighed the dry otoliths in a pre-weighed, acid-washed polycarbonate tube on a microbalance to 0.001 mg. We dissolved the whole otolith in nitric acid for at least 1 h

inside a laminar flow hood. Then we diluted the sample to 1% HNO_3 with Milli-Q water. Blank samples were prepared in the same manner, but no otolith was present. Samples were analyzed with a Finnigan MAT Element 2 inductively coupled plasma mass spectrometer (ICP-MS). All elements were analyzed using matrix-matched standards. Limits of detection were calculated as mean blank values plus three standard deviations. Isotopic counts were converted to elemental intensities by multiplying percent natural occurrence of the isotopes. All data were standardized to Ca to account for uncertainty in otolith weight due to difficulty in accurately measuring the weight of juvenile otoliths.

We used multivariate analysis of variance (MANOVA) and canonical discriminant analysis (CDA) to characterize the elemental signatures of the otoliths. All MANOVA significance tests used Pillai's Trace statistic. Confidence ellipses (95%) were calculated around the class means of the first two canonical variates to locate significant differences in otolith chemistries between river arms within years (Payton et al. 2003). Linear discriminant function analysis (LDFA) was used to quantify accuracy of classification of individuals to their resident river arms based on the elemental signatures of the otoliths. We built two linear discriminant functions for each year. One contained all elements detected in the otoliths of juvenile striped bass and the other contained only elements not known to be physiologically regulated (Campana 1999). Additionally, we removed all samples where multiple elements were 3 to 5 standard deviations from the mean background levels (Tukey 1977, Wells et al. 2003). Classification accuracy was determined using a cross validation procedure. Robustness of otolith elemental analysis to account for inter-annual variation was determined by

using the linear discriminant function from each year to classify the remaining two years. All data were $\log_e$ transformed to correct for heteroscedasticity.

Results

One sample was removed from the 2002 data set because it contained multiple outliers resulting in a final sample size of 35 for the Red River and 34 for the Washita River. One sample was removed from the 2003 data set because it contained multiple outliers and one additional sample was lost during the cleaning process resulting in a final sample size of 35 for the Red River and 33 for the Washita River. Three otoliths were removed from the 2004 data set because each sample contained multiple outliers and two additional samples were lost during the cleaning process resulting in a final sample size of 30 for the Red River and 35 for the Washita River.

Sixteen elements (Lithium, Magnesium, Manganese, Rubidium, Yttrium, Barium, Lanthanum, Cerium, Praseodymium, Uranium, Sodium, Phosphorus, Scandium, Iron, Copper, and Strontium) in addition to Calcium were present above detection limits in the otoliths of juvenile striped bass during all 3 years (Figure 1), and 17, 34, and 32 elements were present above detection limits in 2002, 2003, and 2004, respectively. Four of these elements, (Sodium, Magnesium, Phosphorus, and Copper) are known to be physiologically regulated (Campana et al. 2000).

There were significant differences in the elemental signatures of juvenile striped bass spawned in the Red and Washita Rivers during all three years. In 2002, 11 of 16 elements were significantly different between the two rivers (Table 1; Pillai's Trace = 0.89; $F_{16, 52} = 26.50$; $P < 0.0001$). In 2003, 8 of 16 elements were significantly different between the two rivers (Pillai's Trace = 0.70; $F_{16, 51} = 7.60$; $P < 0.0001$). In 2004, 10 of

16 elements were significantly different between the two rivers (Pillai's Trace = 0.73; $F_{16, 48} = 8.07$; $P < 0.0001$).

Cross validation results from the LDFA containing only elements not physiologically regulated revealed a 94% reclassification rate during 2002 (Table 2). A plot of the first and second canonical variates show a strong separation of juvenile striped bass from the Red and Washita Rivers (Figure 2). When we included all elements, this increased to 97% and CVA showed complete separation of fish from the two rivers. Further, 95% confidence intervals around class means of the first two canonical variates did not overlap using either data set. Reclassification rates for juvenile striped bass spawned during 2003 and 2004, using the LDFA developed for 2002, resulted in an overall reclassification rate of 62% and 12%, respectively. When we included all elements and attempted to predict subsequent years, classification accuracy increased slightly (65%) when we predicted fish from 2003 but more than doubled (35%) when we predicted fish from 2004.

Cross validation results from the LDFA revealed a 78% reclassification rate during 2003 (Table 2). A plot of the first and second canonical variates shows some overlap of juvenile striped bass from the Red and Washita Rivers (Figure 2), however, 95% confidence intervals around the class means of the first two canonical variates did not overlap. When we included all elements, this increased to 90% and CVA showed a much stronger separation of fish from the two rivers. Reclassification rates for juvenile striped bass spawned during 2002 and 2004, using the LDFA developed for 2003, resulted in an overall reclassification rate of 69% and 50%, respectively. When we

included all elements and attempted to predict subsequent years, classification accuracy decreased slightly (67%) for 2002 and remained the same (50%) for 2004.

Cross validation results from the LDFA revealed a 74% reclassification rate during 2004 (Table 2). A plot of the first and second canonical variates shows some overlap of juvenile striped bass from the Red and Washita Rivers (Figure 2), but 95% confidence intervals around the class means do not overlap. When we included all elements, this increased to 91% and CVA showed a much stronger separation of fish from the two rivers. Reclassification rates for juvenile striped bass spawned during 2002 and 2003, using the LDFA developed for 2004, resulted in an overall reclassification rate of 13% and 35%, respectively. When all elements were included in the linear discriminant function and it is used to predict subsequent years, classification accuracy decreased (3%) for fish in 2002 and increased slightly (38%) for fish in 2003.

Discussion

The elemental composition of juvenile striped bass otoliths differed between the Washita and Red Rivers, resulting in moderate to high reclassification rates (73.8% - 94.2%). These reclassification rates compared favorably with those obtained in other studies. Juvenile allis shad *Alosa alosa* were classified to their natal river with an 87.8% to 91.1% success rate (Tomas et al. 2005). Westslope cutthroat trout *Oncorhyncus clarki lewisi* from the Coeur d'Alene River, Idaho, were classified to their natal stream with a 100% success rate for each stream (Wells et al. 2003). Adult lake herring *Coregonus artedi* in Lake Superior, were classified to their correct basin with a 68.6% and 62.5% success rate for the eastern and western basins, respectively (Bronte et al. 1996). Also, juvenile yellow perch *Perca flavescens* were correctly classified to their habitat type with

a success rate of 79% for logoonal wetlands and 84% for river-influenced sites (Brazner et al. 1994).

Similar success rates have been reported for juvenile fish in marine systems. Reclassification rates for juvenile American shad *Alosa sapidissima* on the New England coast ranged from 88.1% to 96.2% depending on which river and month was sampled (Thorrold et al. 1998). Similarly, reclassification rates for juvenile trumpeter *Pelates sexlineatus* on the east coast of Australia, ranged from 50% to 100% depending on which estuary and year was sampled (Gillanders and Kingsford 2000). Juvenile rockfish *Sebastes inermis* on the coast of Japan had reclassification rates of 100% for three bays (Guido et al. 2004). Juvenile red drum *Sciaenops ocellatus* could be classified to their natal estuary with a 37% to 100% success rate (Patterson et al. 2004). The general pattern seems to be one of proximity, where fish collected closer together are more likely to be misclassified and fish collected farther apart are more likely to be classified correctly. The close proximity of the Red and Washita River watersheds and resulting high degree of similarity likely contributes to the classification error observed in this study.

In general, reclassification success of adult fish is less than reclassification success of juvenile fish (Edmonds et al 1989; Edmonds et al. 1992; Campana et al. 1994). This is probably due to adults having greater opportunities to reside in water masses of differing chemical composition and consequently the elemental signature reflecting a mixture of all these differing water masses (Campana et al. 2000). However, Patterson et al. (2004) found that adult otolith cores match juvenile elemental signals indicating that

juvenile signatures are stable within the adult otolith and should be useful for identifying spawning and rearing grounds.

Annual variation of the otolith elemental signature within rivers was likely as great as or greater than variability between rivers within a year. Consequently, our ability to build a linear discriminant function for one year and predict subsequent years was low. Our overall correct classification rates ranged between 3% and 69% when we used a discriminant function built for one year to predict subsequent years. This indicates that elemental signatures are temporally variable, as Campana et al. (2000) documented. Reclassification rates ranged from 0% to 90% for juvenile trumpeter (Gillanders and Kingsford 2000) and 25% to 89% for yellow-eye mullet (Edmonds et al. 1992) in both studies when a discriminant function was developed for one year and applied to another year. This indicates that some sites may remain temporally stable for longer periods than other sites. Campana et al. (2000) found that the concentrations of most elements remained stable over periods of 2-3 years. American shad could be reclassified to their natal river with an accuracy of 79.9% to 98.2%, using data from one month to predict a subsequent month (Thorrold et al. 1998).

Our data indicated that several elements remained stable for up to two years, however, no elements remained stable for all three years and several elements were different in all three years. One possible explanation for elemental differences in otoliths of juvenile striped bass from Lake Texoma is variation in river flows among years. Concentrations of trace elements in water influences uptake into the otolith (Chesney et al. 1998; Bath et al. 2000; Milton and Cherney 2001). However, we found no patterns between river flow and element concentrations in otoliths of juvenile striped bass.

Another explanation for differences in elemental composition among years is laboratory bias resulting from the analysis of data from different years at different times. Campana et al. (1994) demonstrated that the coefficient of variation for known composition glass is less than 10% for samples analyzed on the same day, but can exceed 100% for samples analyzed on different days. A third possible source of annual variation is dietary differences within and among years (Buckel et al. 2004, Limburg 1995, Gallahar and Kingsford 1996). Diets of Lake Texoma striped bass juveniles were significantly different among years and between rivers within the same year (J. Schaffler, unpublished data). Fish were a greater proportion of the diet at earlier ages during 2004 than during previous years and fish generally accounted for a greater fraction of the diet in the Red River than in the Washita River.

Spatial differences in otolith chemistry suggests that elemental fingerprints of juvenile fish from the Red and Washita Rivers provide a natural tag for assessing recruitment and early residence of striped bass in Lake Texoma. Elemental composition of striped bass otoliths varies over time, and temporal variation must be accounted for when estimating sources of recruitment for adult fish. Although some research on elemental composition of otoliths has addressed temporal variation, many studies only analyze samples from one time period and this could bias interpretation of data collected at later dates. However, we feel that otolith microchemistry deserves further research in freshwater ecosystems and could be a useful tool for management of striped bass in Lake Texoma and other freshwater fishes.

Acknowledgements

Financial support was provided by the Federal Aid in Sport Fish Restoration Act under Project F-56-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University through the Oklahoma Cooperative Fish and Wildlife Research Unit (Cooperators: Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, and the Wildlife management Institute). The authors thank Drs. Bill Fisher, Tony Echelle, and Jason Freund, and David Walter for providing comments that improved this manuscript. We thank Jeff Boxrucker and the staff of the Oklahoma Department of Wildlife Conservation's Oklahoma Fishery Research Lab for providing juvenile striped bass used in this study. We thank Drs. Larry Claypool and Mark Payton for statistical advice. For logistical support with preparing and analyzing otoliths, we thank Dr. Cynthia Jones and the staff of the Center for Quantitative Fisheries Ecology at Old Dominion University.

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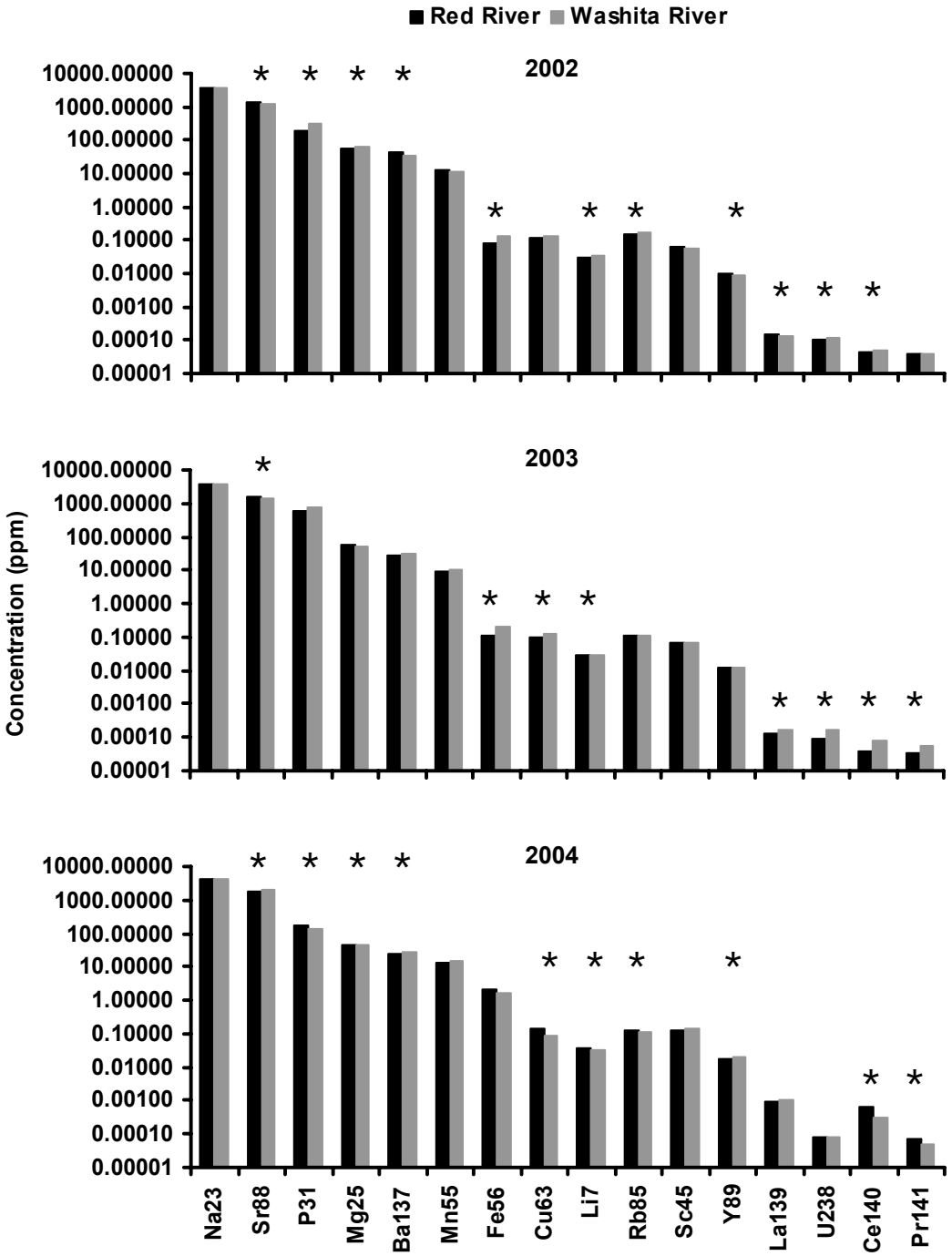
Figure Captions

Figure 1. Mean elemental concentrations (ppm or $\mu g\ g^{-1}$) in the otoliths of juvenile striped bass from the Red (dark bars) and Washita (light bars) Rivers during a) 2002, b) 2003, and c) 2004 for 16 elements that were above detection limits in all three years. Significant differences at $\alpha = 0.05$ level of significance are indicated with an *.

Figure 2. Results of canonical discriminant analysis used to characterize differences in the multivariate elemental signatures of otoliths from juvenile striped bass from the Red (open circles) and Washita (filled circles) Rivers during 2002 (a, b), 2003 (c, d), and 2004 (e, f). Graphs a, c, and e are based on elements that are not under strong physiological regulation, while graphs b, d, and f are based on all elements that were present in all three years. Ellipses represent 95% confidence intervals around class means of the first two canonical variates.


Red River
Washita River
2002
2003
2004
Concentration (ppm)
10000.00000
1000.00000
100.00000
10.00000
1.00000
0.10000
0.01000
0.00100
0.00010
0.00001
Na23
Sr88
P31
Mg25
Ba137
Mn55
Fe56
Cu63
Li7
Rb85
Sc45
Y89
La139
U238
Ce140
Pr141

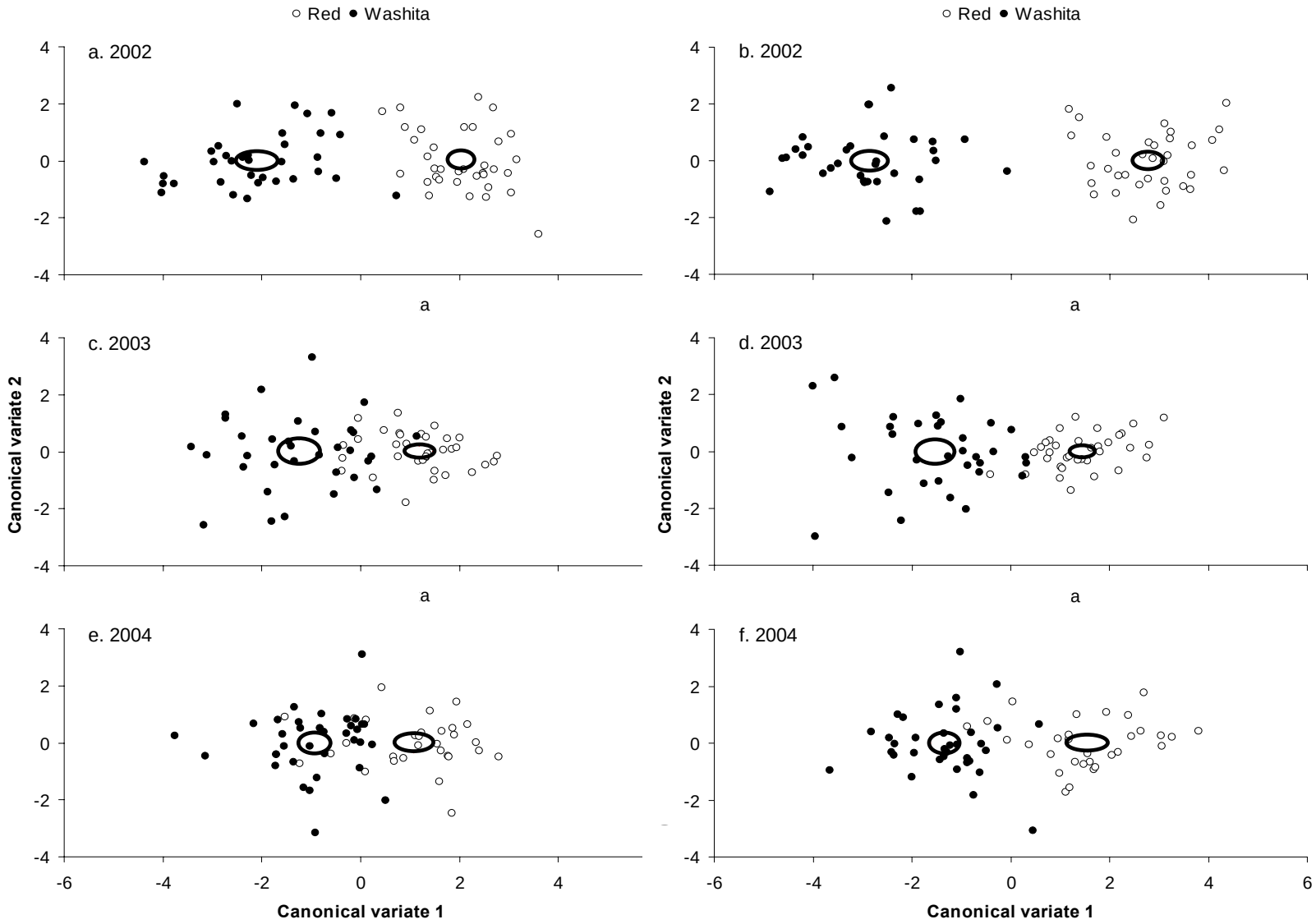

Red Washita
a. 2002
b. 2002
c. 2003
d. 2003
e. 2004
f. 2004
a
Canonical variate 2
Canonical variate 1

Table 1. Results from MANOVA analyses comparing individual elements between the Red and Washita Rivers within each year. Blank cells indicate the comparison was not significant.

	Year					
	2002 (df=67)		2003 (df=66)		2004 (df=63)	
	F	P	F	P	F	P
Strontium	76.98	<0.0001*	11.71	0.0011*	21.00	<0.0001*
Lithium	35.80	<0.0001*	4.75	0.0329	10.12	0.0023*
Cerium	4.97	0.0291*	29.19	0.0001*	4.54	0.0370*
Iron	15.37	0.0002*	15.84	0.0002*	3.19	0.0785
Lanthanum	4.47	0.0383*	13.30	0.0005*	0.89	0.3479
Uranium	6.26	0.0148*	9.60	0.0029*	1.80	0.1847
Phosphorus	111.05	<0.0001*	3.21	0.0778*	8.94	0.0040*
Barium	31.61	<0.0001*	2.11	0.1509	13.00	0.0006*
Rubidium	8.29	0.0054*	0.19	0.6608	9.23	0.0035*
Yttrium	24.35	<0.0001*	1.45	0.2330	6.59	0.0126*
Magnesium	7.72	0.0071*	1.09	0.3010	4.25	0.0432*
Copper	2.11	0.1505	26.95	<0.0001*	22.24	<0.0001*
Praseodymium	0.17	0.6781	23.12	<0.0001*	6.91	0.0107*
Manganese	2.16	0.1460	0.29	0.5919	0.71	0.4019
Sodium	0.26	0.6126	0.01	0.9063	0.46	0.5005
Scandium	2.96	0.0898	2.57	0.1136	0.71	0.4019

Table 2. Results of linear discriminant function analysis based on otolith elemental signatures based on a) only elements that are not under strong physiological regulation and b) based on all elements present in all three years. A discriminant function was developed for each year and used to classify individual fish within that year (values on diagonal), as well as fish from other years (off diagonal). Values indicate the cross-validation accuracy.

a.

		Year Classified		
Year Collected	N	2002	2003	2004
		Red River		
2002	35	91	94	7
2003	35	37	86	0
2004	30	11	6	73
		Washita River		
2002	34	97	30	17
2003	33	100	70	100
2004	35	14	64	74

b.

		Year Classified		
Year Collected	N	2002	2003	2004
		Red River		
2002	35	97	69	63
2003	35	37	94	0
2004	30	3	71	83
		Washita River		
2002	34	97	61	6
2003	33	97	85	100
2004	35	3	3	89

CHAPTER II.

AGE, GROWTH, AND MORTALITY OF LARVAL AND JUVENILE STRIPED BASS IN LAKE TEXOMA, OKLAHOMA-TEXAS.

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Abstract

We quantified growth and mortality rates of larval *Morone* spp. in Lake Texoma and examined associated biotic and abiotic factors of the environment. Zooplankton density was generally greater in the Red River arm of lake than in the Washita River arm. This was due primarily to greater abundances of microplankton in the Red River arm. Mean weekly cohort growth rates ranged from 0.22 – 0.77 $mm \cdot d^{-1}$ and mean instantaneous daily mortality rates ranged from 0.004 – 0.051 d^{-1}. Growth of larval *Morone* spp. was negatively influenced by macroplankton density and salinity and positively influenced by river discharge. Mortality of larval *Morone* spp. increased with increasing larval fish density, discharge, and microplankton density. However, growth and mortality were not significantly correlated with these factors. Growth rates throughout the larval and juvenile phase were best described by a piecewise regression, which was likely because of changes in feeding habits. Individual larval and juvenile striped bass growth rates were positively correlated with temperature and negatively correlated with larval fish density. Food availability was not correlated with growth or mortality.

Introduction

Striped bass *Morone saxatilis* typically are anadromous, found along the Atlantic coast of North America from St. Lawrence, Canada, to the St. Johns River, Florida, and around the Gulf of Mexico to Louisiana that spawn in large freshwater rivers and streams (Pearson 1938; Nichols and Miller 1967). However, they have been extensively stocked as a sport fish into reservoir systems throughout the southeastern United States (Bailey 1974, Axon and Whitehurst 1985). Despite a large economic impact of many reservoir

striped bass fisheries (Schorr et al. 1995), there is little information on the early life history of striped bass from wholly within freshwater systems.

In marine and freshwater systems, growth and survival of striped bass larvae can be influenced by many biotic and abiotic factors. Availability of prey during the first few days of feeding is a critical factor influencing the growth and survival of striped bass larvae (McGovern and Olney 1996; Bulak et al. 1997; North and Houde 2003). In laboratory experiments, larval striped bass growth and survival generally increased with zooplankton density (Chick and Van Den Avyle 1999). Striped bass larvae can grow at prey densities as low as 50 organism/L (Chesney 1989), but densities ≥ 100 organisms/L are optimal (Eldridge et al. 1981; Tsai 1991). In field studies with larval and juvenile striped bass, growth increased following zooplankton blooms (Limburg et al. 1999) and was higher in years of increased zooplankton abundance (Bulak et al. 1997). Evidence for survival has been confounding, however, during a year of high striped bass recruitment, larvae were temporally and spatially matched with high densities of zooplankton, but during a year of low recruitment, there was very little overlap of striped bass larvae and high densities of zooplankton (McGovern and Olney 1996). For other freshwater fish species, zooplankton prey densities are generally unrelated to survival (Bestill and Van Den Avyle 1997; Bunnell et al. 2003).

In addition to the direct effect of starvation, low zooplankton densities can lead to reduced swimming abilities. Larval striped bass reared under suboptimal prey conditions have slower swimming speeds and are less responsive to simulated predator attacks (Chick and Van Den Avyle 2000). Starved larvae are more vulnerable to attack from potential predators (Rice et al. 1987) and resultant slow growth increases the duration of

vulnerability to gape-limited predators (Crowder et al. 1987). Smaller body size and, thus, smaller gape size also limits the sizes of available prey (Hambright 1991). Conversely, larger body size likely confers a suite of survival advantages to larval fishes through escapement from predation and the benefit of increased foraging opportunities (Miller et al. 1988).

Density of co-occurring larval competitors, particularly gizzard shad *Dorosoma cepedianum*, can reduce larval growth and survival (DeVries and Stein 1992; Dettmers and Wahl 1999). However, other researchers have not documented a relationship between larval gizzard shad abundance and growth or recruitment of larval crappie *Pomoxis* spp. (Pope and DeVries 1994; Bunnell et al. 2003).

Temperature is also an important factor regulating the survival and growth of larval striped bass. Growth is positively correlated with water temperature (Dey 1981; Uphoff 1989; Rutherford and Houde 1995). Episodic mortality of eggs and larvae occurs when water temperature rapidly declines to 12 °C or less (Dey 1981; Uphoff 1989; Rutherford and Houde 1995), but mortality is not otherwise correlated with temperature.

River flow affects both the timing and magnitude of spawning (Turner and Chadwick 1972) as well as mortality of young (Uphoff 1989; North and Houde 2003). In striped bass and white bass *M. chrysops*, a closely related species, spawning activity is closely related to high reservoir inflows (Bulak et al. 1997; Quist et al. 2002). However, the exact relationship is not agreed upon and may vary among systems.

The objectives of our study were to describe patterns in 1) age and growth, 2) mortality and 3) abundance of striped bass in an inland reservoir and relate them to abiotic and biotic factors. We were also interested in whether differences in

environmental conditions in both river arms where striped bass recruitment occurred could lead to differences in vital rates within this population.

Study Site

Lake Texoma is a 36,000 ha impoundment of the Red and Washita Rivers on the Oklahoma-Texas border. Striped bass were initially introduced into this system in 1965 and stockings continued annually through 1973 (Harper and Namminga 1986; Mauck 1991), creating one of only about 10 self-sustaining reservoir populations of striped bass in the U.S. (Bailey 1974; Axon and Whitehurst 1985; Gustaveson et al. 1984). The striped bass fishery on Lake Texoma has become the most valuable recreational fishery in Oklahoma. Striped bass anglers contribute approximately $25 million annually to the local economy, with 77% of these anglers coming from outside of the local region (Schorr et al. 1995).

Methods

Fish collections and sampling

We sampled larval fish with a conical plankton net (0.5 m diameter, 2.0 m length, 500 μm mesh) at one offshore site located near the river mouth and over the old river channel and 5 onshore sites, located within 10 m of shore in the headwaters of the Red and Washita River arms of Lake Texoma from 2002 – 2004 (Figure 1). During 2002, we used two types of sampling gears to capture larval fishes, a conical plankton net and a 1.0 m × 3.0 m larval seine constructed of 500 μm mesh netting. In each year, larval sampling was initiated during the second week of April and continued through at least the third week of May (Table 1). Larval fish collections were made during the day in 2002-2003 and at night in 2004 at 0.5 m below the surface of the water. Diel sampling during 2004

indicated that larval *Morone* spp. abundances were not different during day or night sampling (unpublished data). All tows were 5 minutes in duration and a flowmeter was attached to the mouth of the net to estimate sample volume. Samples were preserved in 95% ethyl alcohol and taken to the lab for identification. From the middle of May through the second week of June, we used a 12.2 m ×1.2 m × 1.6 (or 6.4) mm mesh bag seine to collect late larval and early juvenile striped bass at the same sites where we collected larval fish. Seining began just after dark.

Water temperature, dissolved oxygen, conductivity, and salinity were measured at least once per week at the offshore site on each river arm with a YSI 600QS multi-parameter instrument (Yellow Springs Instruments, Inc.,). Discharge and river temperature data were obtained from U. S. Geological Survey gauging stations located on both the Red and Washita Rivers within 25 km of the headwaters of Lake Texoma.

Zooplankton collection

Zooplankton samples were collected with a Wisconsin-style plankton net (12 cm diameter mouth, 63 μm mesh). All collections were made during the day at the midpoint of the offshore larval fish collection site on both river arms. We lowered the net to the bottom of the reservoir (4-5 m depending on water level), retrieved it, and preserved the contents in 3-5% buffered formalin. In the laboratory, we identified all rotifers to genera, cladocerans to genera (*Daphnia* spp. to species), and classified copepods as calanoid, cyclopoid, or nauplii. At least three zooplankton subsamples were processed from all zooplankton collections in a 5 ml Bogarov tray. For the purposes of this paper, we present these data as microplankton (rotifers and copepod nauplii) and macroplankton (copepods and cladocerans) abundance.

Age and growth

In the laboratory, larval fish were identified to the lowest practical taxon (May and Gassaway 1967). Because larval striped bass and white bass can not be reliably separated (Olney et al. 1983), we combined both species into one group, *Morone* spp. Once larval *Morone* spp. reached about 25 mm, we were able to differentiate species based on morphometric differences. The total length of all *Morone* spp. collected was measured to the nearest 0.1 mm using an image analysis system. We mounted sagital otoliths to glass slides using Cytoseal 60 mounting medium. Otoliths from larvae >10 mm were sanded to the core with 1500-grit sandpaper and polished, then both sagital otoliths were read (nonconsecutively) at 400X magnification. The mean value plus 3 d was used as an estimate of age (Jones and Brothers 1987). Reading pairs were discarded if increment counts differed by more than 10% (McGovern and Olney 1996). Hatch date was estimated by subtracting the estimated age from the day of the year when collection took place. Mean daily growth rate for each fish was calculated by subtracting 2.9 from total length and divided by the estimated age. We used 2.9 mm as an initial estimate of the length of newly hatched striped bass in Lake Texoma because striped bass larvae are 2.9 – 3.7 mm total length at hatching (Doroshev 1970) and in this system, striped bass eggs average 1.45 – 1.66 mm in the Red and Washita Rivers, respectively (Baker 2003; Ryan 2004), over 1 mm smaller than striped bass eggs in their native range (Bergey et al. 2003). Therefore, it seemed likely that newly hatched striped bass would be on the smaller side of this range. The smallest larval *Morone* spp. we captured was 2.9 mm long.

Juvenile striped bass (>25 mm) were measured to the nearest mm and their

otoliths were removed, cleaned in a mild bleach solution, and mounted convex side down in a similar manner to larval *Morone* spp. Otoliths were ground to the core using 600- and 1500-grit sandpaper and polished, then the left (right if it was the only available) sagital otolith was read by two readers. The mean count was used if increment counts differed by <10%. If reading pairs differed by >10% the otolith was reread by both readers. If counts still differed by >10%, the otolith was discarded from the analysis. We limited age analysis to juvenile striped bass collected on or before week 8 to reduce biases that may occur from aging older fish (Jones and Brothers 1987). Age and growth rate determination was identical to that for larval fish.

Initial plots of length versus age suggested a piecewise linear relation in two of the three years examined. The breakpoint of the independent variable was determined by allowing it to change until the model coefficient of determination (R^2) was maximized for each age-class (Neter et al. 1990; Bestill and Van Den Avyle 1997; Toms and Lesperance 2003). The response function fitted for the regression model was

$y = \beta_0 + \beta_1 A + \beta_2 (A - c) X_1 + \beta_3 R + \varepsilon_i$; where y is length (mm), A is age (d), c is a constant representing the breakpoint, $X_1 = 0$ if age is less than or equal to the breakpoint, and R is river (Red = 1, Washita = 0) and ε_i is random error. We applied this model to all three years of data. For years where we had sufficient data (2002 and 2004), we used correlation analysis and stepwise multiple regression analysis to identify factors associated with growth of larval and juvenile striped bass.

Larval growth

We evaluated the influence of abiotic and biotic factors on growth of two age-classes of larval *Morone* spp. To estimate mean daily growth rate, larvae younger than

19 d were grouped by river arm, year, week of hatch, week of collection, and age-class (age-class I, 5-11 days; age-class II, 12-18 days). We chose 5 d as the starting point of our first age class because first feeding generally begins at about 5 d post-hatch (Sandoz and Johnston 1965; Meng and Orsi 1991; Chick and Van Den Avyle 1999). There were at least three larvae in each group and 19 total groups. Within each age-class, we pooled growth rates of groups across river arms and years to evaluate whether variability in mean daily growth rate was explained by mean weekly macroplankton density, microplankton density, larval fish density, salinity, temperature, or discharge.

Larval mortality

We calculated instantaneous daily mortality rates (Z) for each weekly larval cohort in each river arm where we collected at least one individual over three consecutive weeks. We chose not to use data from juvenile collections because we felt that the different sampling methods were not comparable. Instantaneous daily mortality rates were calculated by regressing the natural logarithm of fish abundance in a cohort against week of collection (Ricker 1975). This gave a weekly instantaneous mortality estimate, which was divided by seven to obtain a daily instantaneous mortality rate.

Results

Field collections

During 2002, we captured 87 larval *Morone* spp. on the Red River arm of Lake Texoma where densities ranged between 0-45 *Morone* spp. per 100 m^3 and averaged 9.89. We captured 370 larval *Morone* spp. from the Washita River arm where densities ranged between 0-336 *Morone* per 100 m^3 and averaged 6.51. Additionally, we captured 860 juvenile striped bass on the Red River arm and 70 juvenile striped bass on the

Washita River arm.

During 2003, we captured 10 larval *Morone* spp. on the Red River arm of Lake Texoma where densities ranged between 0-8 *Morone* spp. per 100 m^3 and averaged 0.61. We captured 9 larval *Morone* spp. on the Washita River arm where densities ranged between 0-16 *Morone* spp. per 100 m^3 and averaged 0.52. Additionally, we captured 11 juvenile striped bass on the Red River arm and 16 on the Washita River arm.

During 2004, we captured 556 larval *Morone* spp. on the Red River arm of Lake Texoma where densities ranged between 0-100 *Morone* spp. per 100 m^3 and averaged 9.40. We captured 19 larval *Morone* spp. on the Washita River arm where densities ranged between 0-16 *Morone* spp. per 100 m^3 and averaged 0.44. We captured an additional 348 juvenile striped bass on the Red River arm and 165 on the Washita River arm of Lake Texoma.

Zooplankton collection

Zooplankton was generally more abundant in the Red River arm of Lake Texoma, primarily because of greater abundances of microplankton on this arm. Microplankton density was significantly greater on the Red River arm than on the Washita River arm of Lake Texoma during 2003 (Figure 2a; $F = 28.24$, $df = 1, 10$, $P = 0.0003$) and 2004 ($F = 4.57$, $df = 1,16$, $P = 0.0483$), but not different during 2002 ($F = 1.02$, $df = 1, 10$, $P = 0.3362$). Macroplankton density was significantly greater on the Red River arm than on the Washita River arm of Lake Texoma in 2003 (Figure 2b; $F = 9.85$, $df = 1, 10$, $P = 0.0105$), but not during 2002 ($F = 0.01$, $df = 1, 10$, $P = 0.9099$) or 2004 ($F = 0.11$, $df = 1, 16$, $P = 0.7448$).

Across years within the Red River, microplankton density was similar among all

years in the Red River ($F = 2.91$, $df = 2, 17$, $P = 0.0817$) and Washita River ($F = 1.94$, $df = 2, 19$, $P = 0.1705$) arms of Lake Texoma. Macroplankton density was significantly greater during 2003 than during 2002 ($F = 5.16$, $df = 1, 17$, $P = 0.0177$). No other year combinations were different in the Red River. Macroplankton density was similar among all years in the Washita River ($F = 1.22$, $df = 2, 19$, $P = 0.3163$).

Age and growth

We aged 36 larval and 123 juvenile fish from the Red River arm and 166 larval and 50 juvenile fish from the Washita River arm of Lake Texoma during 2002. Growth rates of larval and juvenile striped bass were best described by a piecewise linear regression where $y = 3.393 + 0.339 \bullet Age + 0.814 \bullet (Age - 14) \bullet X_1 + 1.596 \bullet River$ (Figure 3a; $F = 5753.84$, $P < 0.0001$, $R^2 = 0.9790$). All parameters in the model were significant ($P < 0.0001$). Aged larvae and juveniles from the Red and Washita Rivers appeared to hatch near major rises in flow in both rivers (Figure 4) and larvae may have been produced in greater relative frequency early in the spawning season, whereas the surviving juveniles tended to come from the later spawned individuals in both rivers.

We aged 10 larval and 6 juvenile fish from the Red River arm and 9 larval and 10 juvenile fish from the Washita River arm of Lake Texoma during 2003. Growth rates of larval and juvenile striped bass were best described by a piecewise linear regression where $y = 2.858 + 0.733 \bullet Age + 0.291 \bullet (Age - 19) \bullet X_1 + 0.566 \bullet River$ (Figure 3b; $F = 1688.21$, $P < 0.0001$, $R^2 = 0.9941$). However, the breakpoint ($t = 0.83$, $P = 0.412$) or river ($t = 1.07$, $P = 0.292$ were not statistically significant. There was no apparent relationship between hatch date frequencies of larvae and juveniles from the Red and Washita Rivers and flow in either river in 2003 (Figure 4 c, d).

We aged 283 larval and 114 juvenile fish from the Red River arm and 19 larval and 4 juvenile fish from the Washita River arm of Lake Texoma during 2004. Growth rates of larval and juvenile striped bass were best described by a piecewise linear regression where $y = 2.593 + 0.403 \cdot Age + 0.971 \cdot (Age - 19) \cdot X_1 + 1.012 \cdot River$ (Figure 3c; $F = 3541.48$, $P < 0.0001$, $R^2 = 0.9623$). All parameters in the model were significant ($P < 0.0001$). Aged larvae from the Red and Washita Rivers appeared to hatch near major increases in flow in both rivers and juveniles were produced in greater relative frequency early in the spawning season before either river changed flow characteristics (Figure 4 e, f).

During 2002, temperature ($r = 0.81$, $n = 375$, $P < 0.0001$), microplankton density ($r = 0.73$, $n = 375$, $P < 0.0001$), and macroplankton density ($r = 0.17$, $n = 375$, $P = 0.0012$) were positively correlated and larval fish density ($r = -0.29$, $n = 375$, $P < 0.0001$) was negatively correlated with growth (Figure 5). The model that included temperature and macroplankton density (growth = 0.0596•temperature – 0.0009•macroplankton – 0.6582) explained 65% ($F = 346.96$, $df = 2, 372$, $P < 0.0001$) of the variation in observed growth rates during 2002. During 2004, temperature ($r = 0.51$, $n = 420$, $P < 0.0001$) was positively correlated and microplankton density ($r = -0.51$, $n = 420$, $P < 0.0001$), macroplankton density ($r = -0.53$, $n = 420$, $P < 0.0001$), and larval fish density ($r = -0.56$, $n = 420$, $P < 0.0001$) were negatively correlated with growth (Figure 5). The model that included larval fish, microplankton and macroplankton density (growth = -0.0001•larval – 0.0001•microplankton – 0.0003•macroplankton + 0.8331) explained 39% ($F = 87.86$, $df = 3, 416$, $P < 0.0001$) of the variation in observed growth rates during 2004.

Larval growth

There was no relationship between larval growth rates and day of hatching for larval *Morone* spp. produced in 2002 (Figure 6a; Slope = 0.005, t = 1.95, P = 0.053), 2003 (Figure 6b; Slope = -0.003, t = -0.41, P = 0.684), or 2004 (Figure 6c; Slope = -0.002, t = -1.25, P = 0.211). Mean daily growth rates of larval *Morone* spp. ranged from 0.42 - 0.51 mm•d^{-1} on the Red River and from 0.22 - 0.77 mm•d^{-1} on the Washita River. For age-class I (5-11 d) none of the measured variables were strongly correlated with growth. Stepwise multiple regression analysis did not result in the construction of any model because all parameters exceeded the significance level of 0.15 for entry into the model. Among older larvae in age-class II (12-18 d), results mirrored that for age-class I larvae. None of the measured variables were highly correlated with growth. Growth of age-class II larvae was marginally correlated with macroplankton density (r = -0.48, n = 9, P = 0.09) and salinity (r = -0.62, n = 9, P = 0.08). The model where growth = -0.0003•macroplankton – 0.5890•salinity – 0.0001•larval + 0.0029•discharge + 1.1044 explained 95% (F = 18.84, df = 4, 4, P = 0.0059) of the most variation in growth of age-class II *Morone* spp.

Larval mortality

Due to highly variable catch rates of larval *Morone* spp. in Lake Texoma we were only able to calculate instantaneous daily mortality rates for six weekly cohorts. In the Washita River during 2002, instantaneous daily mortality rates were 0.050 d^{-1} for larvae hatched during week 15 and 0.004 d^{-1} for larvae hatched during week 16. In the Red River instantaneous daily mortality rate was 0.099 d^{-1} for larvae hatched during week 16. During 2003, we were not able to calculate instantaneous daily mortality rates for any cohort of larvae. During 2004, we were only able to calculate instantaneous daily

mortality rates for larvae hatched in the Red River. Instantaneous daily mortality rates were 0.043 d^{-1} for larvae hatched during week 17, 0.051 d^{-1} for larvae hatched during week 18, and 0.007 d^{-1} for larvae hatched during week 19.

None of the measured parameters were highly correlated with instantaneous daily mortality rates. Larval abundance ($r = 0.70$, $n = 6$, $P = 0.1215$), temperature ($r = 0.70$, $n = 6$, $P = 0.1229$) and discharge ($r = 0.65$, $n = 6$, $P = 0.1648$) approached statistical significance. The model where mortality = 0.00001•larval + 0.00034•discharge + 0.00008•microplankton – 0.06264 explained 96% ($F = 15.51$, $df = 3, 2$, $P = 0.0612$) of the variation in mortality of larval *Morone* spp.

Discussion

Field collections

Abundance of larval *Morone* spp. was highly variable within and between years in both river arms of Lake Texoma. Variability in abundance of young has also been noted for striped bass spawned in the Santee-Cooper Reservoir system (Bulak et al. 1997) and for white bass, a closely related species, in Kansas (Schultz et al. 2002) and Tennessee (Sammons and Bettoli 1998) reservoirs. In marine systems, variability in the abundance of larval and juvenile striped bass has been well documented (Ulanowicz and Polgar 1980; Kernehan et al. 1981; McGovern and Olney). In the Chesapeake and Delaware Canal larval abundance varied from an average of 0 to nearly 100 per 100 m^3 from 1970 – 1977. Larval *Morone* spp. in Lake Texoma varied from 0.44 – 9.89 per 100 m^3 over the three year period we sampled. In the Sacramento-San Joaquin Estuary, juvenile striped bass abundance was highly correlated with inflow, outflow, percent water diverted, and salinity and moderately correlated with temperature (Turner and Chadwick

1972). All of these correlations presumably point to one underlying factor, because all these parameters are interrelated. Most of the larvae that we captured coincided with a major increase in river discharge. This same trend has also been observed for white bass (Quist et al. 2002). Furthermore, rapid fluctuations in temperature can be responsible for mass mortalities of larval striped bass (Dey 1981; Kernehan et al. 1981), which can drastically alter short term abundances and catch rates. We did not find that rapid temperature drops would have resulted in high mortalities in Lake Texoma.

Age and growth

Temperature was positively correlated with growth during 2002 and 2004. It generally has been observed that growth rates of larval *Morone* spp. increase with increasing water temperature. In the Chesapeake Bay and Hudson River Estuary, growth rates of larval striped bass were positively related to temperature (Rutherford and Houde 1995; Limburg et al. 1999). This trend of increasing growth rate with temperature was also observed for larval white perch *Morone americana* in the Hudson River Estuary. It also seems that the growth rate of juvenile striped bass is positively related to temperature. Growth rates increased for weekly cohorts in two years for juvenile striped bass in the Santee-Cooper Reservoir System (Bulak et al. 1997).

Larval fish density was negatively correlated with growth in 2002 and 2004. This is likely because of competitive interactions with other larval fishes for food resources. When predators (larval and juvenile striped bass) and prey (larval fish) are observed to compete for food resources early in life, the growth rate of the predators is reduced (Bystrom et al. 1998). Additionally, growth rates of larval fish are negatively impacted by density (Dettmers and Wahl 1999), because at high densities they are able to drive

preferred zooplankton prey to low densities (DeVries and Stein 1991). However, striped bass growth rates do not always decrease in the presence of a competitor (Buckel and McKown 2002).

We found confounding evidence for macroplankton density and microplankton density. Macroplankton density was not correlated with growth in 2002 and negatively correlated with growth in 2004. This is likely because of the variability in macroplankton densities in the two years examined. Macroplankton density was highly variable during 2002 and there was no apparent trend over our sampling period. During 2004, macroplankton was generally higher early in the spawning season when growth rates were lower and lower later in the season when growth rates were higher. In general, we observed that zooplankton abundance was higher on the Red River arm than on the Washita River arm of Lake Texoma. This pattern occurs in most years (Franks et al. 2001), but likely has little impact on foraging opportunities for larval and juvenile striped bass because zooplankton densities are consistently higher than critical (Chesney 1989) and optimum (Eldridge et al. 1981; Tsai 1991) levels for striped bass growth in both river arms.

We found that a piecewise regression model most closely fit the growth rates of larval *Morone* spp. and juvenile striped bass in Lake Texoma. An abrupt change in the slope of the growth rate indicates a rapid change in growth, probably due to a switch in diet from zooplankton to fish. A switch to piscivory initiates an increase in growth rate of fish (Olson 1996; Mittelbach and Persson 1998; Post 2003). In Lake Texoma, striped bass begin to become piscivorous at 15 mm, and about half of their diet is composed of fish by 25 mm (unpublished data). It is likely that this diet shift is responsible for the

increases in growth observed in 2002 and 2004. Additionally, this corresponds well with our predicted breakpoints in which growth rates changed at 14 mm in 2002and at 19 mm in 2004.

Larval growth

We did not find any differences in growth rates of larval *Morone* spp. hatched early in the spawning season versus those hatched later in the spawning season. The lack of an observed increase in growth with temperature for larval *Morone* spp. was probably due to the relatively short period between sampling periods and resultant small differences in temperature. In Lake Texoma, larval *Morone* spp. hatching occurred over about a 2 week period in two of the three years that we sampled, and in the other year (2003) we collected too few individuals to draw conclusions. In contrast to our research, larval striped bass were captured for about 40 d in Chesapeake Bay (Rutherford and Houde 1995) and Santee-Cooper Reservoir (Bulak et al. 1997) and about 50 d in the Hudson River (Limburg et al. 1999).

We observed back-calculated growth rates of weekly cohorts ranging from 0.22 - 0.77 mm•d^{-1} in Lake Texoma during 2002 and 2004. This is consistent with larval striped bass growth rates from 0.11 - 0.46 mm• d^{-1} in Chesapeake Bay (Rutherford and Houde 1995; Secor and Houde 1995) and from 0.02 - 0.29 mm• d^{-1} in the Hudson River (Limburg et al. 1999). Growth rates of striped bass from Santee-Cooper Reservoir are slightly higher, ranging from 0.78 - 0.91 mm• d^{-1} (Bulak et al. 1997), probably because larger fish were aged.

In general, growth of larval *Morone* spp. increases with macroplankton and microplankton density, temperature, and salinity and decrease with total larval fish

density and flow. We did not observe this pattern in first feeding larvae (age-class I). None of the variables we measured were highly correlated with growth. Growth of older larvae was negatively related to macroplankton abundance and salinity. This was probably because macroplankton density was higher earlier in the season than it was later in the season. Macroplankton densities were almost always greater than critical densities for growth and survival (Chesney 1989; Tsai 1991; Chick and Van Den Avyle 1999). Salinity did not show any consistent patterns, other than it was higher on the Red River than on the Washita River arm and it generally decreased following major inflow events. In general, striped bass survival is higher in low salinities than in freshwater (Bayless 1972; Otwell and Merriner 1975). Optimal growth occurs at a salinity of 6.7 ppt, but optimal survival occurs at 3.4 ppt salinity (Lal et al. 1977). However, Kane et al. (1990) found that the probability of survival was higher at a salinity of 2 ppt than at 3 ppt.

Larval mortality

The mortality rates we observed were within the ranges of observed mortality rates in marine systems. Daily instantaneous mortality rates ranged from 0.003 – 0.086 d^{-1} in the Chesapeake Bay (Rutherford and Houde 1995), and from 0.019 – 0.037 d^{-1} in the Hudson River. Daily instantaneous mortality rates ranged from 0.006 – 0.057 d^{-1} for white perch (Limburg et al. 1999) and from 0.003 – 0.020 d^{-1} for white bass (Quist et al. 2002). Mortality rates of larval cohorts were not significantly correlated to any of the parameters that we measured. This was likely due to a small sample size of cohorts that we used to estimate mortality. However, larval density, river discharge, and microplankton abundance were strong predictors of larval *Morone* spp. mortality. Larval density likely affected mortality through competitive interactions with other larval fishes

for food resources (DeVries and Stein 1992; Dettmers and Wahl 1999). River discharge was correlated with turbidity (personal observation), which likely resulted in reduced foraging opportunities for larval *Morone* spp. (Breitburt 1988; Chesney 1989). Increased river discharge can drastically alter the physical environment resulting in increased or decreased mortality of larval striped bass (Uphoff 1989; North and Houde 2003). In most studies, temperature is the dominant factor influencing mortality in larval striped bass (Uphoff 1989; Secor and Houde 1995; Limburg et al. 1999). We did not observe this pattern in Lake Texoma and the most likely reason is that we captured larval *Morone* spp. over a very narrow range of temperatures.

This study provided new information about the early life history of striped bass that reside within freshwater reservoirs. Further research should focus on whether our findings are consistent with other freshwater reservoirs where striped bass naturally reproduce. Because we were unable to provide strong evidence of a mechanism that may be regulating growth and survival to the juvenile stage, we recommend further research to identify relationships between growth and mortality and the biotic and abiotic factors affecting the early life history of striped bass.

Acknowledgements

Financial support was provided by the Federal Aid in Sport Fish Restoration Act under Project F-56-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University through the Oklahoma Cooperative Fish and Wildlife Research Unit (Cooperators: Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, and the Wildlife management Institute). The authors thank Drs. Bill Fisher, Tony Echelle, and Jason Freund, and Dan Dauwalter for

providing comments that improved this manuscript. We thank numerous graduate students, technicians, and volunteers who assisted in collection of field data, especially Matt Mauck, Mark Nicholson, Zack Thomas, Travis Schaffler, and Stanly Schaffler. We thank Drs. Larry Claypool and Mark Payton for statistical advice and Lee Ann Alf (U.S. Geological Survey, Oklahoma City, Oklahoma) for assistance obtaining provisional hydrograph data for the Red and Washita Rivers.

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Figure Captions

Figure 1. Map of Lake Texoma showing sampling locations (filled circles) on the Red and Washita River arms.

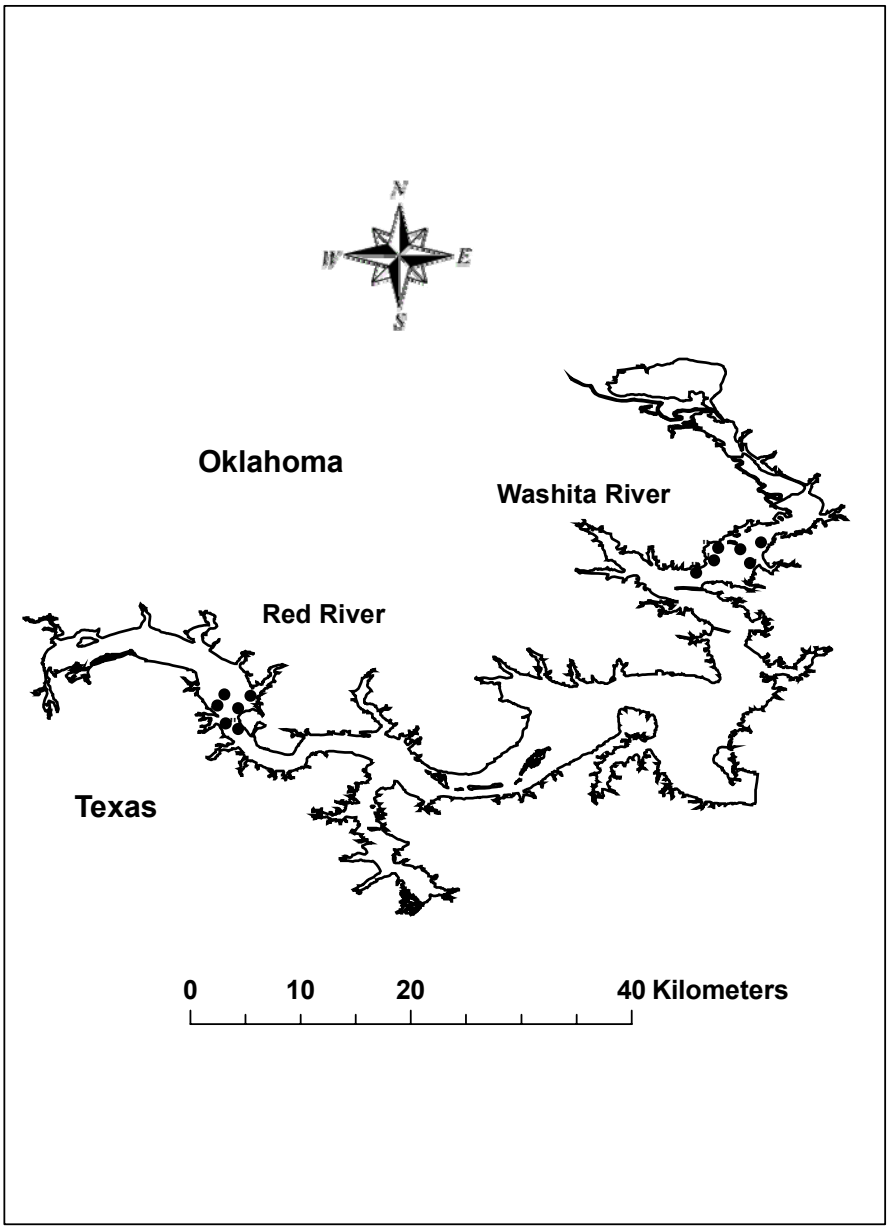
Figure 2. Mean (± 1 SE) a) microplankton and b) macroplankton density from a fixed site on the Red and Washita River arms of Lake Texoma from 2002 – 2004. Pairs with letters in common indicate that mean zooplankton concentrations were not significantly different at $\alpha = 0.05$.

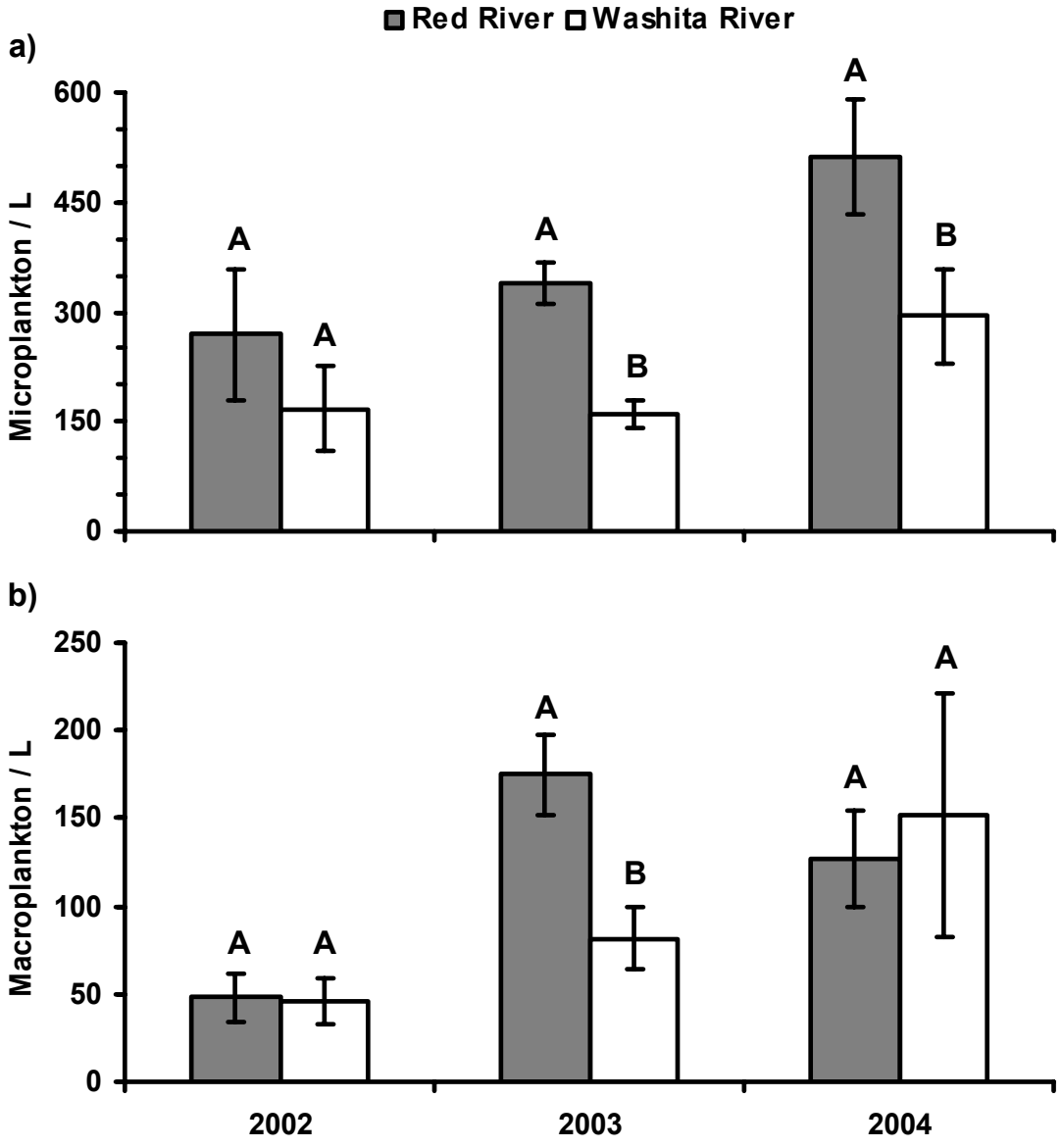
Figure 3. Back-calculated growth rate of larval *Morone* spp. and juvenile striped bass hatched in the Red (open circles) and Washita (open triangles) Rivers during a) 2002, b) 2003, and c) 2004. The segmented regression line is black for fish hatched in the Red River and gray for fish hatched in the Washita River. During 2003, there was no difference in growth rates of fish in either river.

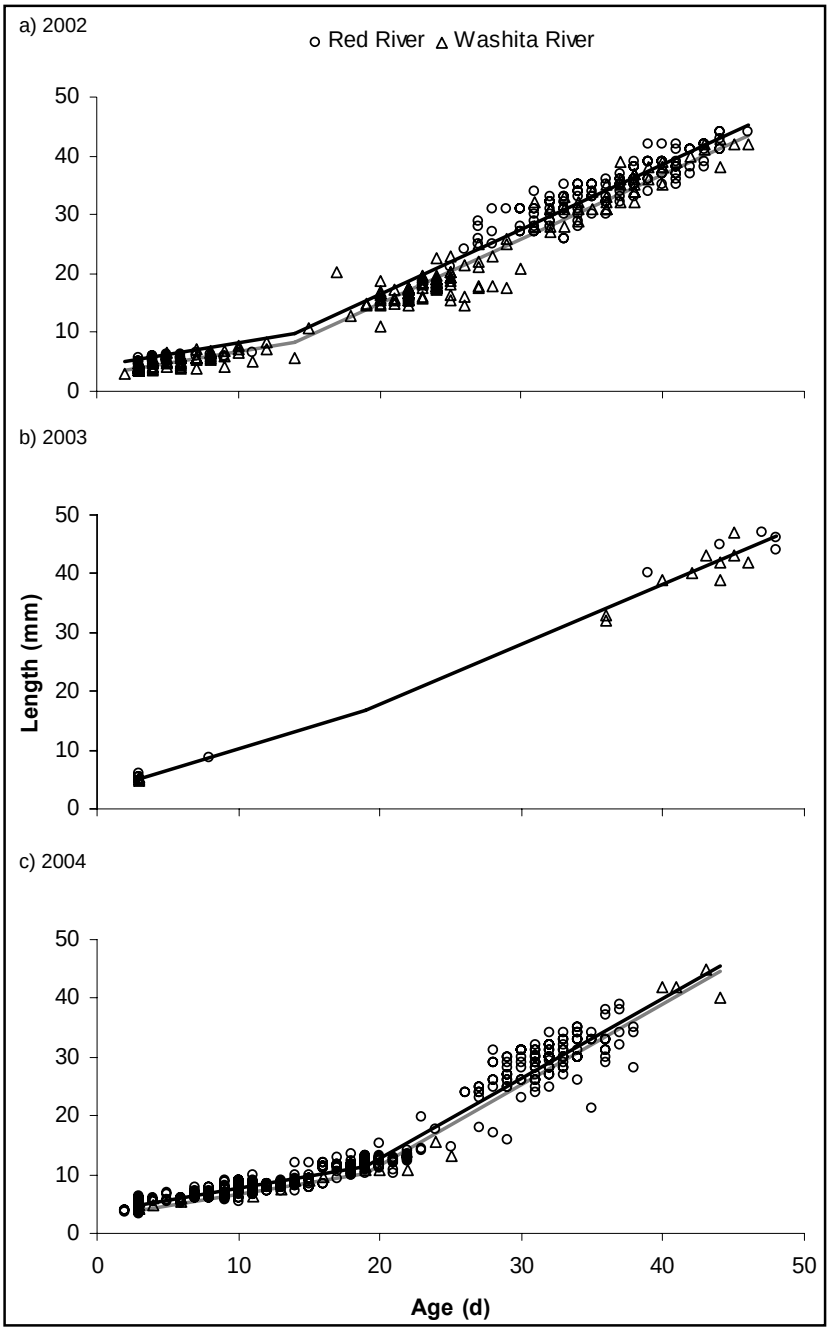
Figure 4. Relative frequencies of back-calculated hatch dates of larval *Morone* spp. (open triangles) and juvenile striped bass (closed circles) versus river discharge and temperature in the Red (a, c, e) and Washita Rivers (b, d, f) above Lake Texoma during 2002 (a, b), 2003 (c, d), and 2004 (e, f).

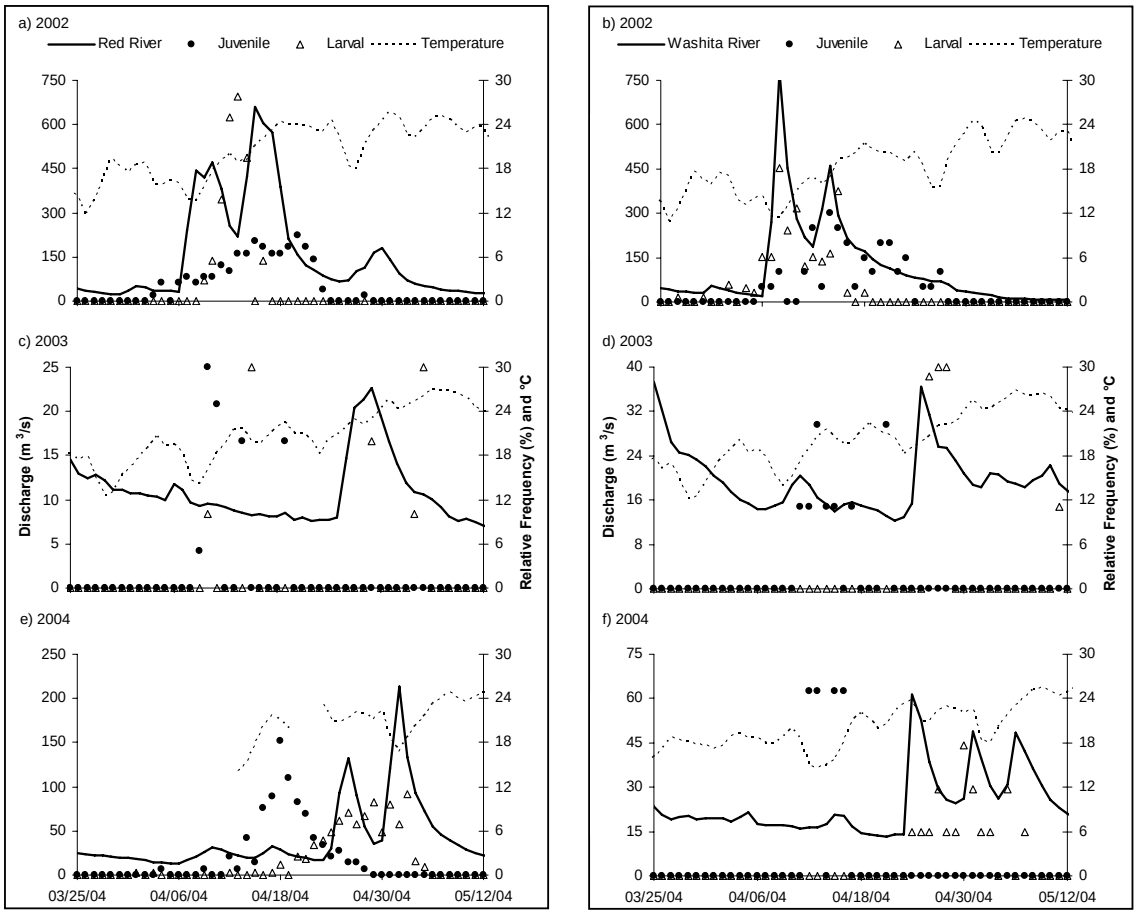
Figure 5. Relationship between mean weekly growth rate and mean weekly temperature, microplankton density, macroplankton density, and larval fish density during 2002 and 2003 for all larval and juvenile striped bass captured in the Red and Washita River arms of Lake Texoma.

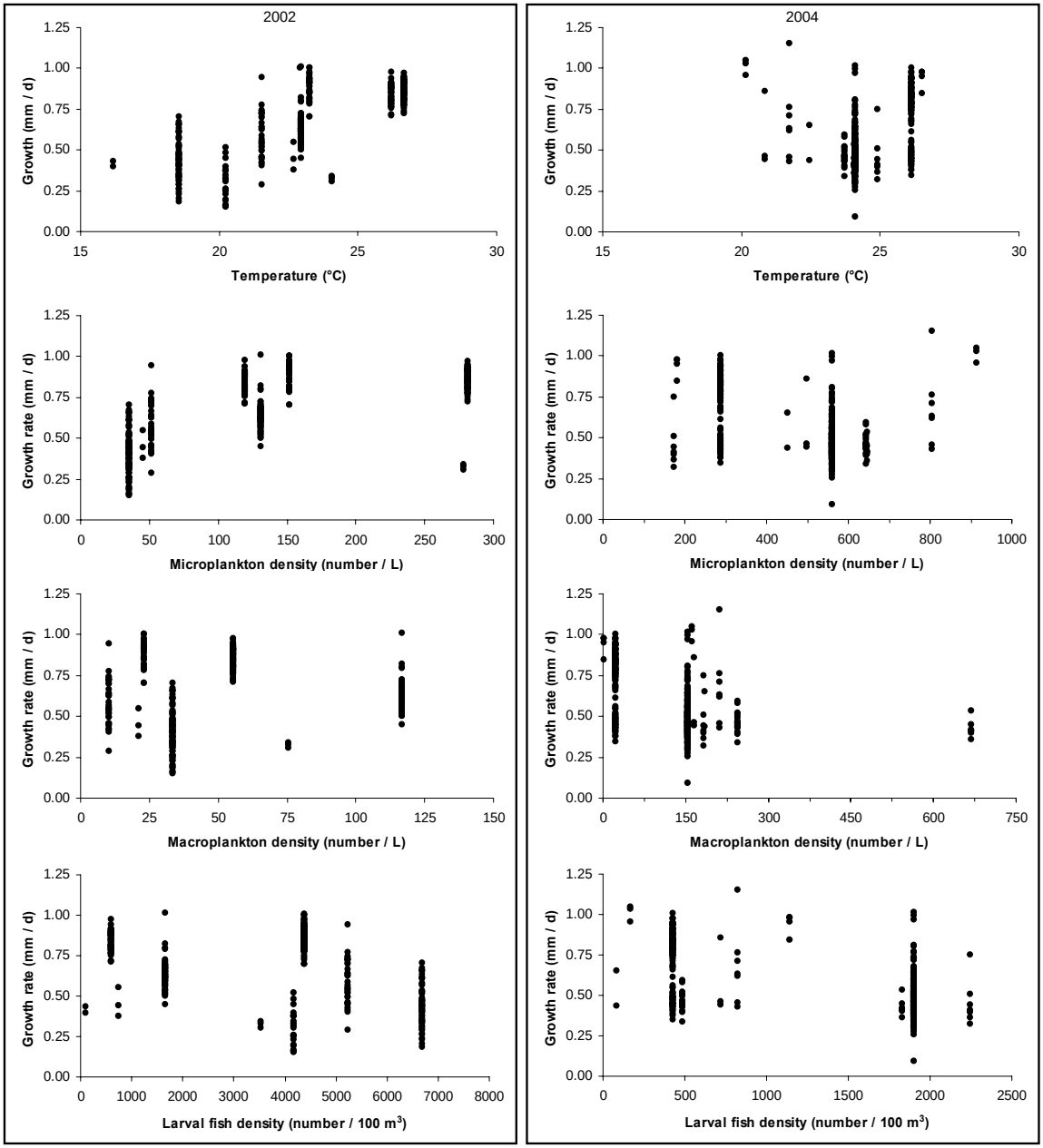
Figure 6. Growth versus hatch day for larval *Morone* spp. collected in Lake Texoma during a) 2002, b) 2003, and c) 2004.


N
W
E
S
Oklahoma
Washita River
Red River
Texas
0
10
20
40 Kilometers


Red River
Washita River
a)
Microplankton / L
600
450
300
150
0
A
A
A
B
A
B
b)
Macroplankton / L
250
200
150
100
50
0
A
A
A
B
A
A
2002
2003
2004


a) 2002
Red River
Washita River
b) 2003
c) 2004
Length (mm)
Age (d)
0
10
20
30
40
50


a) 2002
Red River
Juvenile
Larval
Temperature
b) 2002
Washita River
c) 2003
d) 2004
e) 2004
f) 2004
Discharge (m 3/s)
Relative Frequency (%) and °C
03/25/04
04/06/04
04/18/04
04/30/04
05/12/04


2002
2004
Growth (mm / d)
Temperature (°C)
Growth rate (mm / d)
Microplankton density (number / L)
Macroplankton density (number / L)
Larval fish density (number / 100 m3)

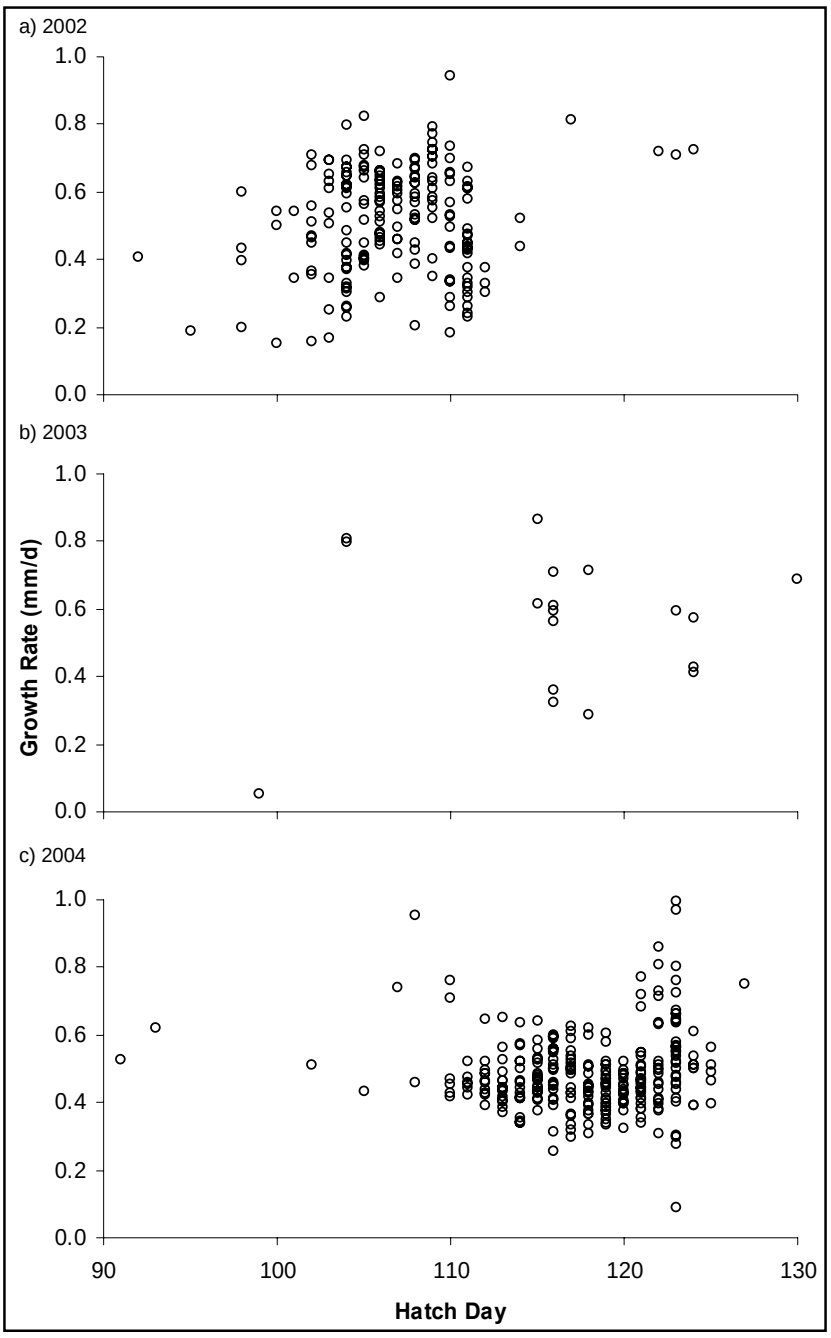

a) 2002
b) 2003
c) 2004
Growth Rate (mm/d)
Hatch Day
0.0
0.2
0.4
0.6
0.8
1.0
90
100
110
120
130

Table 1. Week samples were collected. Sample collection was always initiated the fourteenth week of the year. We designated this as week 1.

			Week									
River	Year	Type	1	2	3	4	5	6	7	8	9	10
Red	2002	Larval	X	X	X	X		X	X			
		Juvenile							X	X	X	X
		Zooplankton			X	X		X		X	X	
Washita	2002	Larval	X	X	X	X	X	X	X	X		
		Juvenile								X	X	X
		Zooplankton			X	X	X	X		X	X	X
Red	2003	Larval	X	X	X	X	X	X				
		Juvenile						X		X		
		Zooplankton	X	X	X	X	X	X				
Washita	2003	Larval	X	X	X	X	X	X				
		Juvenile						X		X		
		Zooplankton	X	X	X	X	X	X				
Red	2004	Larval	X	X	X	X	X	X	X			
		Juvenile							X	X		X
		Zooplankton	X	X	X	X	X	X	X	X		X
Washita	2004	Larval	X	X	X	X	X	X	X			
		Juvenile							X	X		X
		Zooplankton	X	X	X	X	X	X	X	X		X

CHAPTER III.

GAPE LIMITATION AND PISCINE PREY SIZE-SELECTION OF LARVAL AND JUVENILE STRIPED BASS IN LAKE TEXOMA, OKLAHOMA-TEXAS

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Abstract

We investigated larval and juvenile striped bass *Morone saxatilis* piscivory in Lake Texoma, Oklahoma-Texas. Shad *Dorosoma* spp. were the primary prey species consumed by larval and juvenile striped bass, but they also ate silverside. The proportion of shad and silverside *Menidia* spp. consumed did not differ from that available in the reservoir. The lengths of shad and silversides consumed were similar in size and increased with striped bass length. In mesocosm feeding experiments, striped bass tended to select the smallest individuals available. Striped bass consumed the same number of prey in 5 h experiments as in 9 h experiments. In reservoirs, striped bass are highly predatory at a small size. This may have important implications for stocking programs where growth of predatory species may be enhanced where juveniles are stocked at a larger size than their primary forage species.

Introduction

Most piscivorous fish show ontogenetic shifts in feeding, typically consuming smaller food items such as zooplankton and benthic invertebrates before switching to a diet dominated by fishes (Mittelbach and Persson 1998). Ontogenetic diet shifts help maximize fitness by maximizing growth during the early life stages (Shelton et al. 1979; Olson 1996; Robichaud-LeBlanc et al. 1997). Faster growth rates are thought to confer a suite of survival advantages, including reduced predation rates by larger individuals (Post and Evans 1989) as well as allowing access to a wider range of potential prey through reduced gape limitations (Hambright 1991; Juanes 1994). Larger individuals may also be responsible for much of the recruitment observed because they are able to survive their first winter due to higher lipid reserves (Ludsin and DeVries 1997).

Numerous studies have examined the ontogeny of piscivory in juvenile striped bass *Morone saxatilis* during the first year of life (Gomez 1970; Robichaud-LeBlanc et al. 1997; Sutton and Ney 2002). However, none of these studies examined the sizes of prey consumed relative to prey sizes available in the environment. Piscivores can ingest prey up to 50% of their length, but prefer prey that average 20-30% of their length (Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987) or about 60% of their gape width (Hambright 1991; Gill and Hart 1994; Einfalt and Wahl 1997). For striped bass, prey 7-18% of their length are most profitable (Hartman 2000a).

Often, juvenile and adult fish predators are implicated as preying on larval and juvenile fishes (Kohler and Ney 1980; Adams and DeAngelis 1987; Sutton and Ney 2002). Stomach content analysis underestimates both the frequency of occurrence and intensity of adult and juvenile fish consumption of larvae and juveniles owing to the rapid digestion of soft-bodied larvae and juveniles (Crowder 1980; Bowen 1996; Kim and DeVries 2001). Mesocosms represent a novel method to detect the effect of predators on prey fishes (Kim and DeVries 2001).

We conducted feeding experiments to determine if juvenile striped bass (<75mm) were size selective piscivores. We compared sizes of prey eaten in feeding experiments with prey sizes observed during concurrent field studies in Lake Texoma, Oklahoma-Texas. We also determined whether stomach content analysis of field-caught fish accurately reflect the pattern of piscivory in juvenile striped bass.

Methods

Striped bass fry were obtained from the Oklahoma Department of Wildlife Conservation's (ODWC) Byron Fish Hatchery and stocked into 6 m^3 mesocosm tanks.

Striped bass were reared to a mean size of 30.2 mm on a natural zooplankton diet. Striped bass were held for 24 h without food before they were used in any experiments. We conducted two predation experiments in the mesocosms during 2003 and one predation experiment during 2004. The mesocosm tanks were equipped with drains approximately 1 inch above the bottom and arranged in a manner that allowed us to simultaneously drain 3 tanks without cross contamination. The mean time to drain a mesocosm tank and remove all of its contents was 1 h 9 min. Throughout all experiments, we drained each tank into 500 μm mesh conical plankton nets to avoid any loss of prey fish. The remaining water that did not drain out, was pumped out and filtered through another 500 μm mesh conical plankton net and the contents of both nets were preserved in 95% ethyl alcohol.

The first experiment consisted of 4 treatments: a short duration control without striped bass (4 h), a short duration treatment (4 h), a long duration control (8 h) and a long duration treatment (8 h). Eleven mesocosms were filled with approximately 5.3 m^3 of lake water from Lake Texoma and stocked with approximately 100 silversides *Menidia* spp. ranging in length from 8.8 – 24.5 mm and averaging 14.2 mm over all tanks. The following morning, we stocked 10 juvenile striped bass (range, 24 – 33 mm) each into six mesocosm tanks. The remaining five tanks were used as controls. We set this experiment up in a randomized block design where we staggered the start times so that we were able to drain one short duration control and short duration treatment simultaneously. Upon completion of the short duration experiments, we began to drain a long duration control and long duration treatment. For this part of the experiment we were only able to use 2 long duration controls because of tank limitations. The three

short duration experiments were run for an average of 4 h 58 min. The three long duration experiments were run for an average of 9 h 6 min. Striped bass from this experiment were transferred to an unused mesocosm tank immediately after the experiment was terminated and used in the second experiment.

The second experiment was conducted 1 week later in a manner nearly identical to the first experiment, except we did not use a long duration treatment because we observed treatment effects in the short duration (4 h) treatments during the first experiment and we wanted to minimize any tank effects. Six mesocosm tanks were filled with lake water and stocked with 100 silversides ranging in length from 12.0 – 42.0 mm and averaging 23.2 mm over all tanks. We also counted 100 silversides into each of three jars (count) and preserved them to determine our variability in stocking rates and our ability to recover prey from the mesocosm tanks. This was done because of the difficulties in accurately stocking silversides into the mesocosm tanks. Striped bass averaged 39.4 mm (31 – 52 mm) and were stocked at a rate of 9 fish per tank into three tanks. Three additional tanks served as controls. All six tanks were run for an average of 4 h 32 min and tanks were drained in randomized pairs consisting of a treatment and a control.

The third experiment was conducted during 2004. We obtained striped bass fry from ODWC's Byron Fish Hatchery and reared them to an average length of 50.5 mm. We also collected the largest striped bass that we were able to find in Lake Texoma and used them so that we would have two size classes of predators. These fish averaged 68.4 mm in length and were held in a mesocosm tank for 9 d before being used in the predation experiment. This experiment was conducted in a similar manner to the

previous two experiments. Striped bass were deprived of food for 24 h before they were used. In this experiment, mesocosms were filled with approximately 5.3 m^3 of city water and mixed with an appropriate amount of sodium chloride to bring salinities up to the same level (0.8 – 0.9 ppt) as fish collection sites in Lake Texoma. The mesocosms were allowed to set for 5 d for dechlorination. The change from lake water was necessary because the pumps that provided lake water broke and could not be immediately repaired. Silversides were stocked into 12 mesocosms at a rate of 100 per tank ranging in length from 27 – 44 mm and averaging 34.8 mm over all tanks. We also counted 100 silversides each into 4 jars (count) and preserved them. The following morning, we stocked four tanks with 10 striped bass ranging in length from 40 – 61 mm and four tanks with 7 striped bass ranging in length from 58 – 87 mm. We only stocked 7 of the large size class striped bass into each of the large predation treatment mesocosms because we were only able to capture 28 striped bass in Lake Texoma that were larger than the striped bass we already had. The four remaining tanks were used as controls. Experiments were run for a similar duration as the previous predation experiments. Mesocosm tanks were drained in randomized groups of threes.

We collected larval and juvenile striped bass from Lake Texoma from 2002 – 2004. All striped bass were preserved in 95% ethyl alcohol upon capture. Larval striped bass were measured to the nearest 0.1 mm and juvenile striped bass were measured to the nearest 1 mm. We removed the stomach contents from all fish. When we encountered fish in the stomach contents, we identified it to the lowest practical taxon (usually genera) and measured its length to the nearest 0.1 mm using an image analysis system.

To estimate the maximum width of prey that could be swallowed by larval and juvenile striped bass, we measured the external mouth width (the distance between the outer edges of the maxillary bones just beneath the eyes) of preserved striped bass. This measurement is a good estimate of the distance between the cleithrum bones, which limit maximum sizes of prey consumed by largemouth bass (Lawrence 1958; Hambright 1991). Because we used preserved striped bass and not live fish, this could have introduced an unknown amount of error into our estimated mouth width. We also measured the length and body depth (maximum width) of larval and juvenile shad *Dorosoma* spp. and silversides to estimate the maximum sizes that could be ingested by larval and juvenile striped bass.

We used analysis of variance to examine differences in the numbers of fish recovered from experimental mesocosms with predators and controls without predators present. In experiment 1 and 2 we used the Kolmogorov-Smirnov 2-sample test to identify differences in the distributions of lengths of silversides in treatment tanks and control tanks. For experiment 3, we used Chesson's alpha (Chesson 1978, 1983) to evaluate selectivity. For this analysis we categorized prey into three length-classes, small ($\leq$ 30 mm), intermediate (31 – 35 mm) and large ($\geq$ 36 mm). With this index, a value of $\alpha = 1/3$ indicates that a length-class was eaten in proportion to its abundance in the controls, while values greater than 1/3 indicate positive selection and values less than 1/3 indicate negative selection. Linear regression was used to examine the relationship between striped bass length and prey length consumed for striped bass collected from 2002 – 2004 in Lake Texoma. We used logistic regression to model the probability that

the frequency of shad consumed changed with increasing length. All statistical tests were considered significant at $\alpha = 0.05$.

Results

Models were created to predict the theoretical maximum size of ingestible prey items based on the length of larval and juvenile striped bass. This equation was $GW = 0.065 \cdot L - 0.1747$, where GW is gape width (mm) and L is length (mm). The equation that best described the relationship between shad length and body depth was $BD = 0.3884 \bullet L - 4.9562$. The equation that best described the relationship between silverside length and body depth was $BD = 0.1376 \bullet L - 0.5046$.

In experiment 1, there was a significant effect due to the experimental combinations (Figure 1a; $F = 37.16$, $df = 3, 7$, $P < 0.001$). Short duration treatments were not significantly different from long duration treatments (Tukey's 0.05). Both striped bass predation treatments contained significantly fewer prey than controls (Tukey's 0.05). We did not directly measure the lengths of prey consumed in experiment 1. All of the silverside stocked into the mesocosm tanks came from the same initial distribution and we measured the lengths of all silverside recovered from the mesocosm tanks. Because there were no differences in the numbers of silverside consumed between striped bass predation treatments, we pooled data to examine differences in lengths of prey fish in treatment and control tanks. There was no difference in the size distribution of silverside remaining in the mesocosm tanks where striped bass were present (treatment) and where they were not present (control) (Figure 2; $D = 0.05$, $P = 0.4986$).

In experiment 2, there was no significant treatment effect (Figure 1b; $F = 3.61$, $df = 2, 6$, $P = 0.0934$). Based on stomach content analysis, there were 15 silversides eaten

in tank 15, 6 eaten in tank 14, and only 1 eaten in tank 13. Visually, there was much more zooplankton eaten by striped bass in tank 13 than either tank 14 or 15. Also, when striped bass consumed silverside, zooplankton were virtually absent from their stomachs. Like experiment 1, we did not directly measure lengths of silverside consumed by striped bass juveniles in experiment 2, but we measured lengths of silverside recovered from mesocosm tanks. There was a significant difference in the distribution of lengths of silverside recovered from mesocosm tanks with and without striped bass present ($D = 0.16$, $P = 0.0011$).

In experiment 3, there was a significant treatment effect (Figure 3a; $F = 19.01$, $df = 3, 12$, $P < 0.0001$). There was no significant difference between treatments with small or large striped bass (Tukey's 0.05). However, both of these treatments had significantly fewer prey than the controls (Tukey's 0.05) and the count (Tukey's 0.05), prey counted into a jar which were used to evaluate our variability in stocking the mesocosm tanks. The control and count were not significantly different (Tukey's 0.05). Large striped bass consumed an average of 1.2 (range, 0 – 2) prey per predator and small striped bass consumed an average of 0.4 (range, 0 – 1) prey per predator. After we corrected for the number of prey recovered from the striped bass stomachs, there was still a treatment effect (Figure 3b; $F = 4.60$, $df = 3, 12$, $P = 0.0230$). Treatments were not significantly different than the control (Tukey's 0.05), the large predator treatment was not significantly different than the count (Tukey's 0.05), but the small predator treatment was still significantly different than the count (Tukey's 0.05). There were no differences in the lengths of silversides among the different treatments (Figure 4; $F = 1.39$, $df = 2, 610$, $P = 0.2491$). There was a significant difference among the lengths of predators used in

experiment 3 ($F = 158.86$, df = 1, 67, $P < 0.0001$). However, there was no difference among the sizes of silversides consumed among the two sizes of predators ($F = 1.34$, df = 7, 38, $P = 0.2567$). Both large and small striped bass showed a strong preference for the smallest striped bass available (mean $\alpha = 0.925$ and $\alpha = 0.963$ for large and small striped bass, respectively), and there was no difference among Chesson's α for large and small striped bass preying on small silversides (Figure 5; $F = 2.17$, df = 1, 6, $P = 0.1911$), intermediate silversides ($F = 0.98$, df = 1, 6, $P = 0.3596$), or large silversides ($F = 0.24$, df = 1, 6, $P = 0.6423$).

In Lake Texoma, fish dominated the diet of juvenile striped bass longer than 35 mm. When larval and juvenile striped bass consumed fish, shad were the primary prey species accounting for 87% (range = 80 – 92%) of the fish consumed. Silversides made up the remaining 13% (range = 8 – 20%). Over the three year period that we sampled fish, we found only two instances where striped bass consumed a fish other than shad or silversides. One was a juvenile mosquito fish *Gambusia affinis* and the other was a larval drum *Aplodinotus grunniens*. There were also several instances where fish were present in the diet, but were unidentifiable because of digestion. However, there is no reason for us to believe that these fish were not shad or silversides. Based on larval fish sampling, shad made up 94% (range = 90 – 97%) of the larval fish community while silversides made up approximately 6% (range = 2 – 9%) of the larval fish community. Overall, shad and silverside generally accounted for 95 – 98% of all larval fish captured. There was no difference between the composition of striped bass diets and the larval fish community ($t = 0.39$, $P = 0.7116$). There was also no trend in preference for shad or silversides with increasing length in striped bass (Wald $\chi^2 = 1.6040$, $P = 0.2053$). The prey species did

not make any difference in the length of prey consumed versus the length of the predator ($t = 1.41$, $P = 0.1595$), however, we analyzed species separately. The length of shad consumed increased linearly with increasing striped bass length (Figure 6; $F = 133.72$, $df = 2, 733$, $P < 0.0001$), and there was also a significant effect due to collection year ($t = 3.23$, $P = 0.0013$). The length of silversides consumed also increased linearly with increasing striped bass length ($F = 34.42$, $df = 2, 99$, $P < 0.0001$). There was also a significant effect due to collection year for silverside ($t = 3.29$, $P = 0.0014$). Striped bass consumed shad as small as 4% of their body length to as large as 71% of their body length. The average size shad consumed was 27% of the striped bass's body length. Striped bass consumed silverside that ranged from 12 – 44% of their body length, and averaged 28%.

Discussion

Our field results from Lake Texoma indicate that, larval and juvenile striped bass foraged on the two most abundant fish prey species in the same proportions as they were found in the environment. In general striped bass juveniles are nonselective in their feeding habits (Heubach et al. 1963; Markle and Grant 1970; Boynton 1981). Most of the variation in estuarine juvenile striped bass diets was due to the location within the estuary (Markle and Grant 1970; Boynton et al. 1981; Robichaud-LeBlanc et al. 1997). Contrary to our observation in Lake Texoma, Matthews et al. (1992) found that silversides accounted for most of the diet of striped bass less than 150 mm total length. Matthews et al. (1992) collected juvenile striped bass later in the year and it is possible this discrepancy is due to forage availability or size of the striped bass examined. In another Oklahoma reservoir, juvenile striped bass consumed a variety of fish and large

invertebrates (Gomez 1970).). In a Tennessee reservoir, juvenile striped bass diets were dominated by shad throughout summer (Van Den Avyle et al. 1983). In a Virginia reservoir, juvenile striped bass diets were dominated by fish, primarily cyprinids, as early as 50 mm in length, but transitioned to alewives at about 120 mm (Sutton and Ney 2002). Despite many studies that have examined diets of striped bass, few have collected forage availability data so it is difficult to draw definitive conclusions about prey selection or make comparisons to out study

Striped bass consumed prey in all mesocosm experiments and consumed the same number of silverside in short duration treatments as they did in longer duration treatments, indicating that striped bass were satiated by 5 h and had stopped eating. The lack of difference between the treatments indicates that mesocosm predation experiments yield informative results in about 4 – 5 hours, which was consistent with another predation study (Kim and DeVries 2001). Such short duration experiments minimize tank effects that can be problematic with longer experiments. The lack of differences between short and long duration treatments was a somewhat unexpected based on feeding experiments that found 50% of the stomach contents would be evacuated by 5.87 h and by 9 h only about 33% would remain (Hartman 2000b). Hartman's experiments were conducted at 17 °C using cut bay anchovies as prey. Our experiments were conducted at 22 – 24 °C and, at these temperatures, the digestive rate of striped bass should be faster. Satiation level of a fish can significantly affect the feeding behaviour of a fish when encountering large prey (Hart and Gill 1992; Gill and Hart 1994). Given the large sizes of prey relative to the striped bass in our experiments, it is likely that hunger levels had

not increased to the point to motivate predators to feed a second time in the 8 h experiments.

In the second experiment, we did not find a difference in the numbers of silverside recovered from mesocosm tanks with and without striped bass present. The lack of differences was likely due to prey size. Prey in experiment 2 averaged 64% of the striped bass length, while in experiment 1 prey averaged 47% of the striped bass length. In the field, the largest silverside we observed in the stomach of a striped bass was 44% of the striped bass length. It is likely that striped bass in the second experiment had very few foraging opportunities and the differences in distributions between silverside recovered from mesocosm tanks with and without striped bass was due to striped bass consuming those relatively few silverside that were small enough to consume. Similarly, Campbell (1998) found that walleye selectively consume the smallest prey available when they are presented with prey that average 40 – 50% of their length. In the third experiment, striped bass consumed the smallest prey available. Prey consumed averaged 38% (range, 25 – 52%) of the striped bass length in the large predator treatment and 54% (range (41 – 70%) of the striped bass length in the small predator treatment. This further illustrates the size selective predatory nature of juvenile striped bass.

In mesocosm experiments 2 and 3, stomach content analysis reflected the number of prey that was missing. In contrast, Kim and DeVries (2001) that stomach content analysis of adult freshwater predators did not accurately reveal the pattern of observed predatory of mortality in limnetic fish larvae. Predation would have been drastically underestimated in the field. Based on what we found, stomach content analysis is likely an accurate predictor of juvenile striped bass diets in Lake Texoma.

Most of the prey consumed by larval and juvenile striped bass were less than 40% of striped bass total length. However, 11% of the shad and 3% of the silverside that juvenile striped bass consumed were greater than 40% of the striped bass's total length. In one instance a striped bass consumed a prey that was 71% of its total length (a 20 mm larval striped bass consumed a 14.2 mm larval shad. Larval and juvenile striped bass consumed prey up to 71% of their total length. This was the only instance where a prey fish was consumed that was greater than 59% of the striped bass total length. In this particular case, it was a 20 mm larval striped bass that consumed a 14.2 mm larval shad. Hartman (2000a) found that striped bass could not successfully feed on prey larger than about 40% of their total length. Conversely, we found that 11% of the shad and 3% of the silverside that juvenile striped bass consumed were greater than 40% of the striped bass' total length. This may be explained by the sizes of striped bass we examined versus the sizes examined by Hartman (2000a). Striped bass in Hartman's (2000a) study were 300 – 400 mm, whereas the maximum size striped bass we examined was 81 mm. Additionally, our fish were preying on larval and early juvenile fish whose swimming and escapement ability is likely much less than that of adult prey fish used in the previous study. Yellow perch consume round gobies that are 7 – 47% of their total length and alewives that are 18 – 46% of their total length (Truemper and Lauer 2005). Walleye can consume golden shiner up to 55%, gizzard shad up to 41%, and bluegill up to 38% of their total length (Einfalt and Wahl 1997).

Gape width is a more appropriate indicator of maximum prey size for striped bass than mouth part size (Dennerline and Van Den Avyle 2000). In studies of striped bass and hybrid striped bass, prey sizes ingested are usually less than the theoretical maximum

sizes predicted from gape width. Dennerline and Van Den Avyle (2000) found that only 4 % of prey exceeded the theoretical maximum size for striped bass and 8% of prey exceeded the theoretical maximum size for hybrid striped bass. We found that 5% of the shad ingested by juvenile striped bass exceeded our predicted theoretical maximum ingestible size whereas no silverside ingested exceeded our predicted theoretical maximum ingestible size. Our results compare favorably with what was found for larger striped bass and other *Morone* spp. The discrepancy that we found between the theoretical maximum ingestible size of prey and the observed maximum prey size was likely because our regressions represented the average relationships between gape width and striped bass length and for shad length and body depth. In a review of piscivore feeding studies, Juanes (1994) found that the size of prey ingested was often in the lower range of sizes possible. Our results fit this general pattern despite our observations that larval and juvenile striped bass consumed prey as large as and occasionally larger than our predicted theoretical maximum size. The average size chosen was about half that of what we would have predicted as the maximum possible size of ingestible prey.

There was a tendency for larger striped bass to consume larger prey and the relationship was the same irregardless of the species consumed. The same basic trend has been observed for larger striped bass and hybrid striped bass (Dennerline and Van Den Avyle 2000). However, there was only one reservoir where prey sizes increased at about the same rate as in our study. This is probably because of the larger sizes of predators observed and prey availability within those systems. Prey length has also been shown to increase with predator length for walleye feeding on three species of fish

(Einfalt and Wahl 1997). It also appeared from our data that lengths of both prey species increased at about the same rate.

Our results indicate that in Lake Texoma striped bass juveniles are highly piscivorous at an early age. Early piscivory could have important implications for recruitment and survival in other naturally spawning and stocked inland populations of striped bass. Sutton and Ney (2002) advocated stocking striped bass earlier in the season and at a larger size so they could begin piscivorous feeding earlier. Our results seem to indicate that if striped bass are present in the system before the peak in larval fish abundance and are sufficiently larger, they will become piscivorous.

Our results also show the usefulness of mesocosms in quantifying short term impacts of piscivorous fishes on prey fish populations. This was similar to another mesocosm study that documented the importance of adult fish predation on larval fishes (Kim and DeVries 2001). Although we were able to accurately detect and quantify the extent of predation in the field, mesocosms can give more detailed insight into the impact of piscivorous fishes on prey fish populations.

Acknowledgements

Financial support was provided by the Federal Aid in Sport Fish Restoration Act under Project F-56-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University through the Oklahoma Cooperative Fish and Wildlife Research Unit (Cooperators: Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, and the Wildlife management Institute). The authors thank Drs. Bill Fisher, Tony Echelle, and Jason Freund for providing comments that improved this manuscript. We thank Drs. Larry Claypool and Mark Payton for statistical

advice. We thank numerous graduate students, technicians, and volunteers who assisted in collection of field data, especially Matt Mauck, Mark Nicholson, Zack Thomas, Travis Schaffler, and Stanly Schaffler.

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Figure Captions

Figure 1. Numbers (mean ± 1 SE) of prey recovered from mesocosm tanks from a) experiment 1 and b) experiment 2. Different letters indicate significant differences (Tukey's multiple comparison procedure) among predator treatments and the predator free controls.

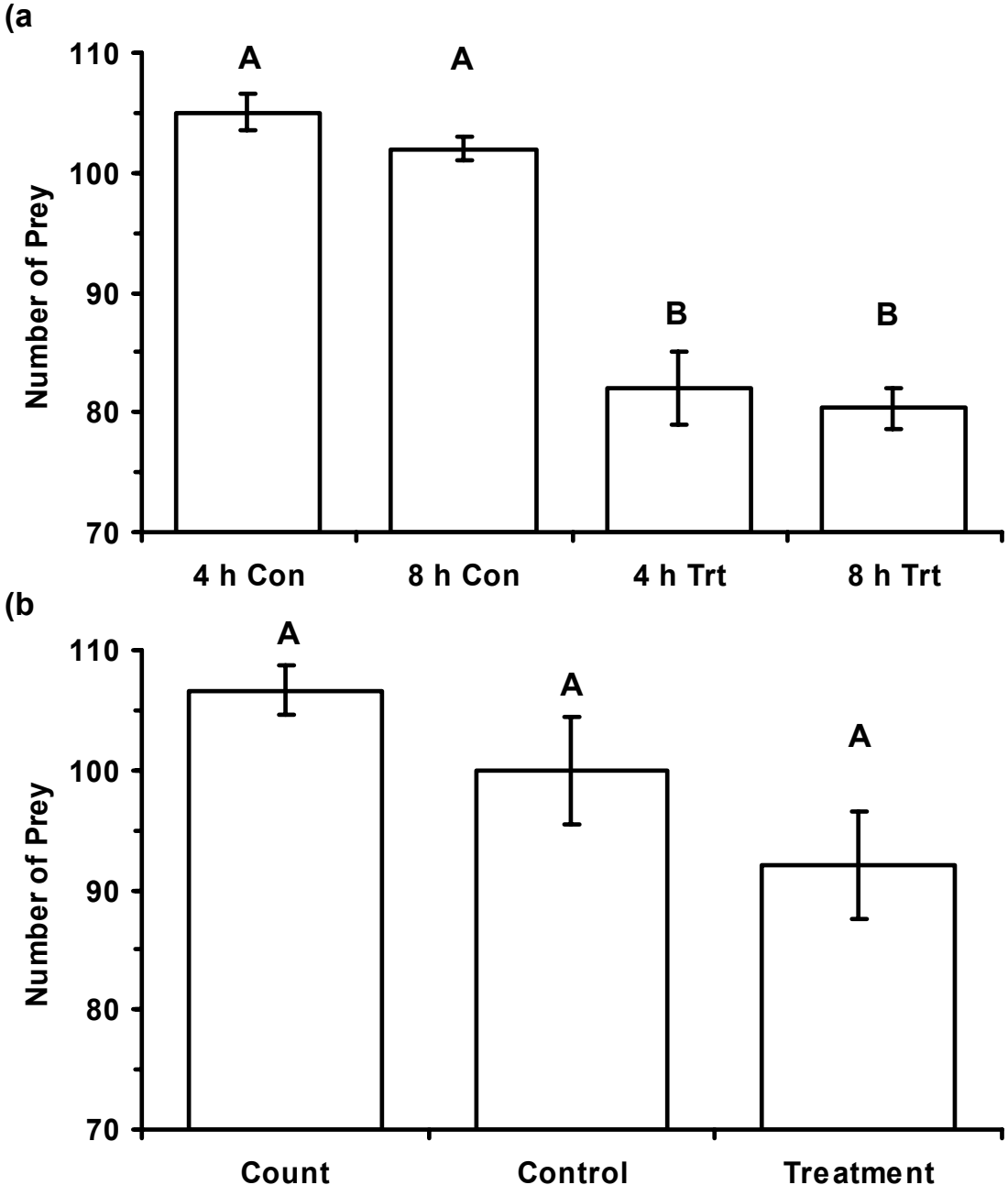
Figure 2. Length of striped bass (mm) and silversides (mm) recovered from control tanks and treatment tanks from experiment 1 and experiment 2. Error bars depict the 95% confidence interval.

Figure 3. Numbers (mean ± 1 SE) of prey recovered from mesocosm tanks in a) experiment 3 and b) experiment 3 corrected for the number of prey in the predators stomachs. Means with the same letter are not significantly different (Tukey's multiple comparison procedure).

Figure 4. Lengths of silverside (mm ± 1 SE) recovered from control and experimental (small and large) tanks, lengths (mm ± 1 SE) of silversides in stomach contents of small and large striped bass stomachs, and lengths (mm ± 1 SE) of small and large striped bass in experiment 3.

Figure 5. Prey selection by small and large striped bass in experiment 3. The dashed line indicates neutral selection.

Figure 6. Shad (top panel) and silverside (bottom panel) total length eaten by striped bass in Lake Texoma from 2002 – 2004. The dashed line is the theoretical maximum size prey that could be ingested by striped bass based on gape width and prey maximum morphological measurements.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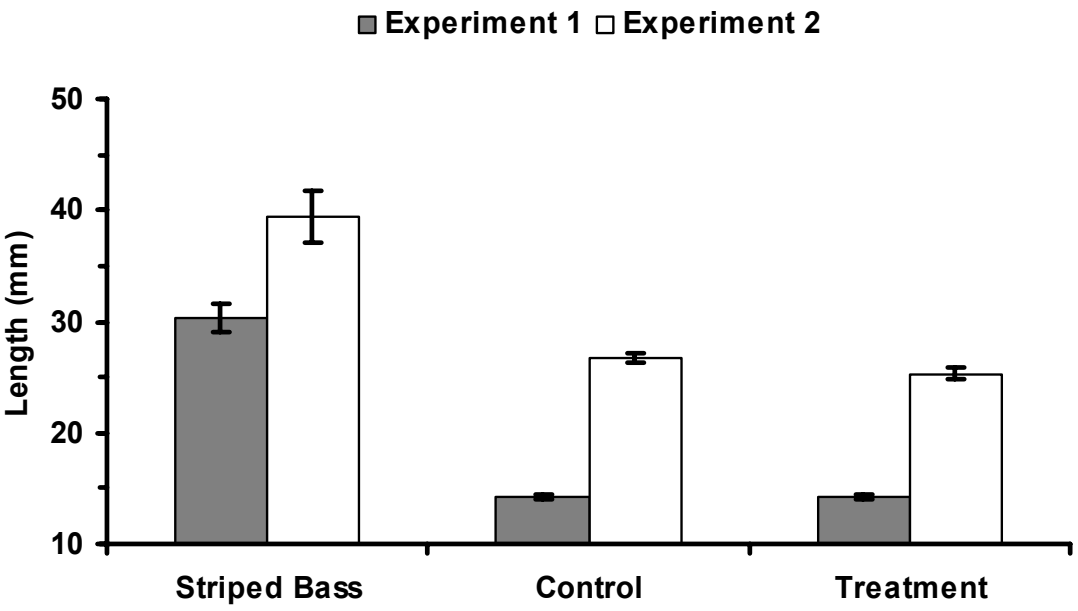
Experiment 1
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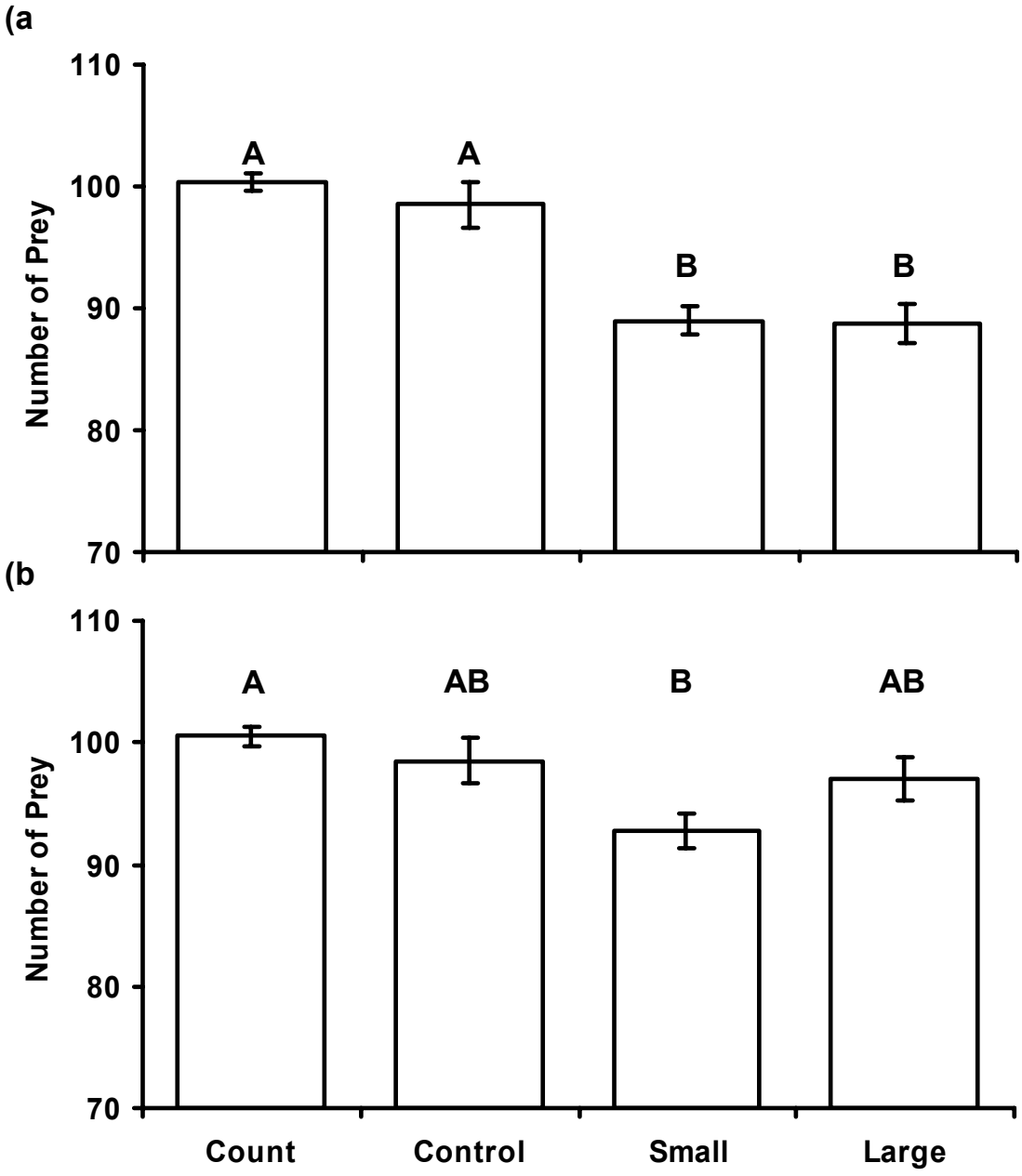
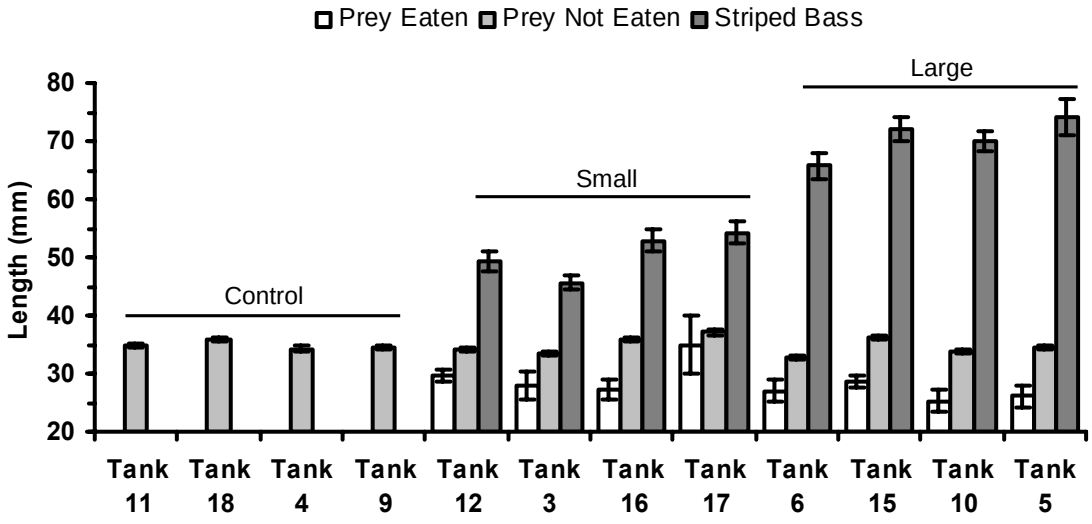
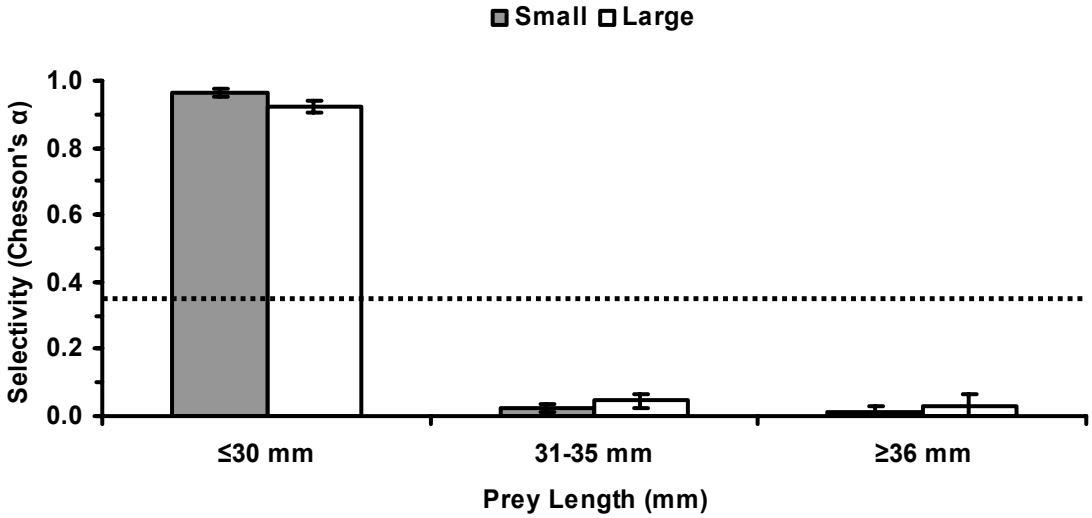
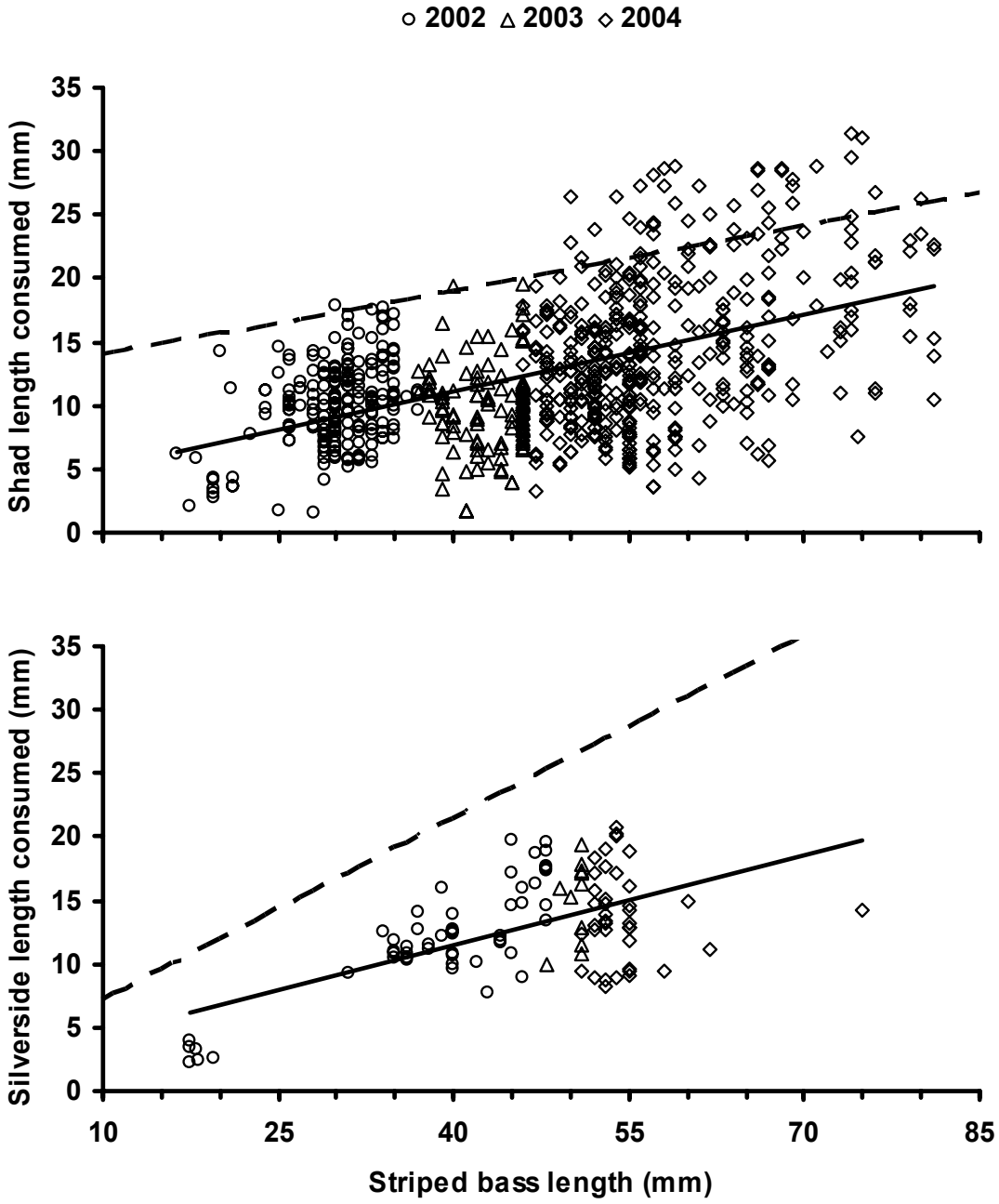
Length (mm)
Striped Bass
Control
Treatment


(a
110
100
90
80
70
Number of Prey
A
A
B
B
(b
110
100
90
80
70
Number of Prey
A
AB
B
AB
Count
Control
Small
Large


Prey Eaten
Prey Not Eaten
Striped Bass
Large
Small
Control
Length (mm)
80
70
60
50
40
30
20
Tank 11
Tank 18
Tank 4
Tank 9
Tank 12
Tank 3
Tank 16
Tank 17
Tank 6
Tank 15
Tank 10
Tank 5


Small
Large
1.0
0.8
0.6
0.4
0.2
0.0
Selectivity (Chesson's α)
≤30 mm
31-35 mm
≥36 mm
Prey Length (mm)


○ 2002 △ 2003 ◇ 2004
Shad length consumed (mm)
0
5
10
15
20
25
30
35
Silverside length consumed (mm)
0
5
10
15
20
25
30
35
10
25
40
55
70
85
Striped bass length (mm)

VITA

Jason Jeremy Schaffler

Candidate for the Degree of

Doctor of Philosophy

Dissertation: AGE, GROWTH, AND RECRUITMENT OF STRIPED BASS IN LAKE TEXOMA, OKLAHOMA-TEXAS

Major Field: Zoology

Biographical:

Education: Received Bachelor of Science degree in Biology with fish and wildlife emphasis from Northeastern State University, Tahlequah, Oklahoma in May 1999. Received Master of Science degree in aquaculture, fisheries, and wildlife biology from Clemson University, Clemson, South Carolina in May 2001. Completed the requirements for the Doctor of Philosophy degree with a major in Zoology at Oklahoma State University in December 2005.

Experience: Employed by Northeastern State University, as an undergraduate research assistant from 1998 – 1999; employed by Clemson University as a graduate research assistant from 1999 – 2001; employed by Oklahoma State University as a graduate research associate from 2001 – 2005.

Professional Memberships: American Fisheries Society, Oklahoma Chapter of the American Fisheries Society, Oklahoma Academy of Science.

Name: Jason Jeremy Schaffler Date of Degree: December, 2005

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: AGE, GROWTH, AND RECRUITMENT OF STRIPED BASS IN LAKE TEXOMA, OKLAHOMA-TEXAS

Pages in Study: 91 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: Our study was initiated to provide baseline information on the early life history of striped bass *Morone saxatilis* in Lake Texoma, Oklahoma-Texas. We sampled larval fishes in Lake Texoma using 500 μm mesh plankton nets in the spring of 2002 – 2004. We aged larval and juvenile striped bass to determine growth rates the reproductive period of striped bass. We also evaluated daily mortality rates based on capture data. Striped bass become piscivorous at an early age and stomach content analysis may under represent the true fraction of fish present in their diet. To examine this, we compared predation rates in mesocosms with field data. Because striped bass spawn in the Red and Washita River arms of Lake Texoma, we need to be able to reliable differentiate recruits originating in these two systems. We examined otolith elemental analysis as a means to differentiate these tow stocks of striped bass.

Findings and Conclusions: Striped bass growth and daily instantaneous mortality rates were highly variable. Growth rates ranged from 0.22 – 0.77 $mm \cdot d^{-1}$ and instantaneous daily mortality rates ranged from 0.004 – 0.051 d^{-1}. Growth of larval *Morone* spp. was negatively influenced by macroplankton density and salinity and positively influenced by river discharge. Mortality of larval *Morone* spp. was increased by increases in larval fish density, discharge, and microplankton density. Growth rates throughout the larval and juvenile phase were best fit wit a piecewise regression. This was likely due to changes in feeding habits. Temperature was positively correlated and larval fish density was negatively correlated with individual larval and juvenile striped bass growth rates. Results for food availability did not follow any pattern. Stomach content analysis was a good predictor of juvenile striped bass diets. The elemental composition of juvenile striped bass otoliths varied considerably between rivers both within and between years. Overall reclassification rates within each collection year ranged between 73.8% - 97.1%. Reclassification rates between years were much poorer (11.9% - 62.3%). Although the mechanisms generating spatial and temporal differences in otolith chemistry are not well understood, spatial differences in otolith chemistry suggests that the elemental fingerprints of fish from the different natal rivers in Lake Texoma do provide a natural tag of their juvenile habitat.

ADVISER'S APPROVAL: Bill Fisher