

Abstract

DAVIAS, LORI ANNA. A bioenergetics assessment of temperature and food consumption effects on growth of reservoir striped bass. (Under the direction of James A. Rice.)

I examined the influence of temperature and food availability on growth of striped bass *Morone saxatilis* in seven North Carolina reservoirs. Reduced condition and summer mortality events of stocked striped bass in some southern reservoirs have been attributed to the habitat 'squeeze' of high summer temperatures and low dissolved oxygen (DO). However, in a recent study of Lakes Badin and Norman, NC, Thompson et al. (2005) intensively studied striped bass thermal selection, diet, mortality, and energetics, and concluded that food consumption was more important than temperature in explaining the large differences in growth between the systems. Following on this study, I analyzed striped bass growth, diet, predator and prey energy densities, and temperature experience in each of an additional five reservoirs in 2003-2005. Striped bass growth and thermal experience varied widely across all seven reservoirs. Fish growth to age-7 varied from less than 2kg to nearly 6 kg, and fish spent between 0 and 87 days in very warm ($\geq 27^{\circ}\text{C}$) water during summer stratification. Striped bass from lakes that experienced the most severe summer temperature also exhibited relatively fast growth. Simulations of a Wisconsin bioenergetics model parameterized for striped bass estimated that striped bass annual consumption varied between 3,144g for age-2 fish in Lake Gaston and 24,616g for age-5 fish in Jordan Lake. I also used the bioenergetics model to test for the relative effects of water temperature and food

consumption on growth by conducting a series of “habitat exchange simulations.” In this approach I simulated how much the growth of a particular size fish in one reservoir might change if it had experienced the temperature or food consumption of a similar-sized fish in another reservoir. The difference in growth predicted when exchanging consumption was greater than that resulting from exchanging temperature for every pair of lakes compared except for those including Lake Rhodhiss. This lake had an extended period over the summer where striped bass could remain in preferred 20°C habitat, and simulations where these temperatures were combined with high food consumption resulted in the greatest annual growth for striped bass. However, my results stress that regardless of temperature, low food consumption will only yield moderate to slow growth of striped bass. On the other hand, striped bass subjected to very warm temperatures can maintain good growth but only if adequate forage exists. Knowledge of availability and abundance of clupeid prey, in addition to information on thermal conditions, is thus especially important for management of striped bass in southern reservoirs.

**A BIOENERGETICS ASSESSMENT OF TEMPERATURE
AND FOOD CONSUMPTION EFFECTS ON GROWTH OF
RESERVOIR STRIPED BASS**

by
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Biography

Lori Anna Davias was born March 7, 1979 in Hartford, CT to Michael and Sandra Davias. She grew up in a friendly neighborhood of Monroe, CT where she spent much of her free time playing in streams. Her parents encouraged her and her sister Candace in whatever endeavors they chose, and fostered a curiosity about science and the natural world. Lori attended Trumbull High School in Trumbull, CT and was a member of the field hockey and track teams. In 1997 she enrolled at Cornell University in Ithaca, NY. Despite an interest in the arts and writing, her love of science won the bid for a major and she chose to study Natural Resources. As an undergraduate she was always on the water, whether competing in crew or working as an assistant on many ecological research projects that took her from lakes and rivers in New York to streams in Venezuela. Upon graduation in 2002 she worked for one year on a lobster research study at the NOAA/NMFS Sandy Hook Marine Lab in New Jersey.

In August of 2003 she moved south to begin a Master's research assistantship with Dr. James A. Rice in the department of Zoology at North Carolina State University. Lori came to love everything the Land of the Pines has to offer, including warm November afternoons, wandering country roads, friendly people, and lively bluegrass tunes, and will miss it. In June, she will begin work in the lab of Dr. Denise Breitburg at the Smithsonian Environmental Research Center in Edgewater, Maryland. She looks forward to joining the Marine Ecology Lab at SERC, as well as to savoring steamed blue crabs, enjoying cruises on the Chesapeake Bay, and finally, to returning closer to home.

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Introduction

The popularity of striped bass *Morone saxatilis* as a sportfish has resulted in its introduction into hundreds of lakes and reservoirs throughout the southeastern United States (Bailey 1975). Its management also serves the purpose of controlling overabundant clupeid populations (Axon and Whitehurst 1985). However, while some stocking programs have produced successful fisheries (Combs 1980, Nash et al. 1987), reservoir populations of striped bass in the southeast are sometimes typified by poor growth and condition (Matthews 1985, Zale et al. 1990).

Striped bass success depends on a combination of system productivity and environmental conditions that is not completely understood. Striped bass growth is limited by the productivity of the system; more productive reservoirs contain larger populations of forage fish (clupeids) and can sustain larger stocked bass populations (Nash et al. 1987). However, especially in the southeastern US, constraints imposed by temperature and low dissolved oxygen (DO) have been the focus of much striped bass research. Zale et al. (1990) found that striped bass cease feeding at 27°C and have increased mortality above 28°C. These results complement the earlier findings of Coutant (1985), who reported that adult striped bass are intolerant of temperatures above 26–27°C and require a dissolved oxygen concentration of at least 2-3 mg/L.

Especially in summer months, habitat in southern reservoirs can be restricted to temperatures above and dissolved oxygen levels below tolerable limits for striped bass, causing stress, reduced movement and growth, and mortality, including summer die-offs (Matthews 1985). As temperatures warm to the ceiling of thermal tolerance,

theoretically suitable habitat becomes constrained between the warm surface waters and the cooler but often-hypoxic bottom waters.

Following tagged fish with ultrasonic or radio telemetry is a common technique for assessing habitat selection of reservoir striped bass. A tracking study by Cheek et al. (1985) found that movement of striped bass in a Tennessee reservoir was influenced by environmental conditions, with fish preferentially occupying temperatures below 24°C and dissolved oxygen above 4 mg/L. Many other studies have attempted to explain striped bass distribution within the context of suitable temperatures and dissolved oxygen habitat (Matthew et al. 1985, Douglas and Jahn 1987, Zale et al. 1988, Matthews et al. 1989, Coutant et al. 1990, Van den Avyle and Evans 1990, Zale et al. 1990, Matthews et al. 1992, Haeseker 1996, Van Horn 1996, Wilkerson and Fisher 1997, Schaffler et al. 2002, Young and Isley 2002, Baker and Jennings 2005, Bettoli 2005).

These findings led to the expectation that striped bass stocked into very warm and eutrophic southern reservoirs would have poor growth and survival. However, in a recent study on two North Carolina reservoirs, Lakes Norman and Badin, Thompson et al. (2005) found that food availability may be more important than temperature in constraining striped bass growth. The authors used bioenergetics modeling to evaluate the relative role of temperature and food consumption on growth of striped bass. Growth is a complex process that integrates effects of food and temperature, among other variables, and bioenergetics modeling is a powerful way to disentangle these effects. The authors collected intensive, seasonal data on striped bass movement,

temperature selection, diet, predator and prey energy densities, and growth in these two systems from 1999-2003, and revealed two important findings: 1) striped bass will commonly occupy much warmer waters than previously thought ($>29^{\circ}\text{C}$), in order to occupy water with dissolved oxygen levels between 3 and 5 mg/L, and 2) despite the metabolic costs of high temperatures, food consumption was much more important in driving patterns of striped bass growth. Therefore, striped bass can have better growth in a system with poor temperature and DO conditions if a relatively good forage base is available than if environmental conditions are better but forage is less available.

It is important to note that these results are context-dependent. The range of temperature and oxygen conditions that striped bass could potentially inhabit is broad; though native to the Atlantic coast, striped bass and their hybrids have been established in reservoirs across the United States as well as along the west coast. The two North Carolina reservoirs studied by Thompson et al. (2005) are relatively similar to each other in temperature and DO as compared with more northern reservoirs, although they differ from each other on a local scale. Therefore, the relative importance of forage availability and temperature/DO habitat quality may be different depending on the geographic extent of inference. In general, growth of striped bass in southern reservoirs may be limited by temperature and DO, but among southern reservoirs, differences in food may be more relevant than a few degrees difference in temperature that is already warm for the species.

The objective of my thesis is to assess the roles of temperature and food consumption in growth of striped bass and to compare their relative effects among

seven North Carolina reservoirs. This study combines new field data from five additional North Carolina reservoirs collected between 2003 and 2005, with existing data from Lakes Badin and Norman (Thompson et al. 2005) to achieve a broader and more comprehensive understanding of the constraints of temperature and food availability on striped bass growth. As in Thompson et al. (2005), these constraints are evaluated with “habitat exchange simulations” based upon the Wisconsin-style bioenergetics model parameterized for striped bass. I first estimate the amount of food consumption needed to achieve the amount of growth observed from size-at-age data for several age classes in each lake. I then let the model estimate growth using different thermal regimes and amounts of food consumption from similarly-sized fish in other lakes. Differences between observed growth and simulated growth due to exchanging temperature are then compared to the differences due to exchanging consumption to assess the relative importance of each. I discuss simulation results in the context of management of striped bass in southern reservoirs. Because the seasonal intensity of data collected by Thompson et al (2005) on Lakes Badin and Norman was beyond the scope of this study, I used their data to evaluate the potential biases caused by my more limited input data.

Study Systems

The North Carolina Wildlife Resources Commission (NCWRC) currently stocks striped bass in twelve reservoirs in four river basins, ranging from the Appalachian

foothills in the west to the Eastern piedmont. In 2005 more striped bass were stocked in NC reservoirs than any other species, and it is a species of high management priority.

In consultation with NCWRC biologists, I selected five of these reservoirs for this study - Lakes Gaston, Hickory, Jordan, Rhodhiss and Tillery - because they differ in size, levels of forage fish density and species composition, habitat quality (temperature and dissolved oxygen) and productivity (Table 1). I also employ existing data and modeling results from previously-studied Badin Lake and Lake Norman (Thompson et al. 2005). These lakes experience summer stratification with reduced hypolimnetic oxygen concentrations; the degree and stability of this stratification varies with lake depth and hydraulic retention time. Striped bass fingerlings are stocked at about 50 mm total length (TL) in mid-June at five fish per acre (12.4/ha) in all lakes except Badin Lake, which is stocked at twelve fish per acre (29.7/ha), and Gaston Lake, which is stocked at twenty fish per acre (49.4/ha). There is no known natural reproduction of striped bass in these systems, and fingerlings stocked into all reservoirs come from the same broodstock. Broodfish are caught each spring from the Dan and Roanoke Rivers on the North Carolina-Virginia border, with most originating from the Roanoke River (J. Evans, pers. comm.)

In these reservoirs striped bass feed primarily on a pelagic forage community consisting of up to four clupeid species: threadfin shad (*Dorosoma petenense*), gizzard shad (*D. cepedianum*), alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in different proportions. Threadfin and gizzard shad occur in all the lakes, but all four species are found together only in Gaston Lake.

Table 1. Characteristics of study reservoirs.

<i>Lake</i>	<i>River Basin</i>	<i>Area (Ha)</i>	<i>Stocking rate (striped bass/ha)¹</i>	<i>Main forage fish</i>	<i>Mean Depth (m)</i>	<i>Hydraulic retention time (days)</i>	<i>Mean summer Chl-a (µg/L)</i>	<i>Year impounded</i>	<i>Owner</i>
Badin	Yadkin – Pee Dee	5,200	29.7	gizzard, threadfin, blueback	21	28 ²	16.6 ²	1917	ALCOA Power Generating, Inc.
Gaston	Roanoke	8,216	49.4	gizzard, threadfin, alewife, blueback	12.2	29 ²	5.8 ²	1962	Dominion Power
Hickory	Catawba	1,660	12.4	gizzard, threadfin, alewife	9.5	33 ⁴	19.2 ⁴	1927	Duke Energy
Jordan	Cape Fear	5,625	12.4	gizzard, threadfin	4.6	62 ²	38 ²	1983	Army Corps of Engineers
Norman	Catawba	12,943	12.4	gizzard, threadfin, alewife	10.2	239 ⁴	4.2 ⁴	1963	Duke Energy
Rhodhiss	Catawba	1,238	12.4	gizzard, threadfin	6.3	21 ⁴	18.2 ⁴	1925	Duke Energy
Tillery	Yadkin – Pee Dee	2,274	12.4	gizzard, threadfin, blueback	10	15 ³	12 ³	1926	Progress Energy

1. Jeffrey Evans, personal communication. Watha State Fish Hatchery, North Carolina Wildlife Resources Commission. 2. North Carolina Department of Environment and Natural Resources, Division of Water Quality, Environmental Sciences Section, unpublished data. 3. APGI 2002. 4. Duke Energy

Methods and data sources

Bioenergetics modeling approach

Bioenergetics models have been widely used in fisheries (Kitchell and Breck 1980, Rice et al. 1983, Bevelhimer and Adams 1993). The basic model, originally described by Kitchell et al. (1977) has been modified and applied to describe the growth process in dozens of fish species (Hanson et al. 1997). This approach is useful in understanding trophic relationships, such as the impact of a predator on its forage base (Cyterski et al. 2002). It is also an efficient way to tease apart the relative importance of variables that affect fish growth, and to determine factors – such as food and temperature – that may explain differences in growth among systems (Hanson et al. 1997, Railsback and Rose 1999, Yako et al. 2000, Munch and Conover 2002, Dieterman et al. 2004).

I used a bioenergetics model to determine the relative contribution of temperature-DO constraints and forage availability to the striped bass growth observed in each reservoir. In a bioenergetics model, fish growth is predicted by a ‘balanced energy budget,’ where growth equals food consumption minus the costs of activity, metabolism and waste products (Hanson et al. 1997):

$$G = C*(1-f-u-s) - (R*ACT)$$

where G is growth, C is consumption, f, u and s are proportional energy loss to egestion, excretion, and specific dynamic action (SDA; the energy associated with digestion). R

is resting metabolism, and ACT is a multiplier of resting metabolism reflecting cost of activity. Consumption is modeled as

$$C=C_{\max} * p * f(T)$$

where C_{\max} is the maximum rate of food consumption at the optimum temperature, as a function of fish size, p is a proportionality constant that adjusts consumption by food availability, and $f(T)$ is a temperature dependence function. R and C_{\max} are both dependent on fish weight, while R is also a function of temperature. Parameters associated with these relationships were determined separately for age-1, age-2, and age-3+ (adult) striped bass by Hartman and Brandt (1995); I used the corresponding set of parameters when modeling different age classes.

I ran model simulations for age-2, age-3, age-4, and age-5 fish from Lakes Jordan, Hickory, Tillery, and Rhodhiss, and for age-2, age-3, and age-4 fish from Lake Gaston. These simulations use daily inputs for temperature experienced, diet composition, predator and prey energy densities, and growth data as explained below. Additionally, I ran simulations on age-3 and age-4 Badin Lake fish and on age-3, age-4, and age-5 Lake Norman fish from data collected by Thompson et al. (2005). The input data for the Badin and Norman Lake simulations were reduced to match the type and frequency of data collected on the other five lakes to facilitate across-lake comparisons, as well as to evaluate any limitations of the less intensive data collection performed on the other lakes (explained below).

Data Needs and Sources

In addition to physiological parameters, a bioenergetics model requires four main kinds of information: 1) daily temperature experienced by the fish, 2) proportions of diet items by size class and species, 3) energy densities of predator and prey, and 4) weight of the fish at the start and end of the simulation, in this case one year.

This study builds on data previously collected for a detailed study of striped bass movement, habitat selection, diet, growth, and energetics in Lake Badin and Norman Lake (Thompson et al. 2005). Three types of new data were collected on each of the five additional reservoirs listed above: 1) comprehensive temperature and dissolved oxygen conditions from vertical profiling done at 4 to 10 locations along each reservoir's main axis spanning the spring to fall period of stratification, supplemented with year-round temperature logger data; 2) an August purse seine sample to determine pelagic forage fish community composition and species-specific length-weight relationships and energy densities; and 3), a November/December striped bass gill net sample, performed by NCWRC biologists, to assess age and size structure, condition, diet, and energy density. Data were collected between December 2003 and October 2005, with two full years of collection only on Lakes Hickory and Rhodhiss. In building lake-specific bioenergetics models, I chose to model the year 2004, meaning that I used temperature, diet, and forage fish data specific to 2004. To increase sample sizes for data input, I pooled 2003 and 2004 striped bass length-at-age and energy density information. In the case of Lake Tillery, I used the December 2004 striped bass

sample and 2005 temperature-oxygen and forage fish data because these were the only dates such data were taken for this reservoir.

Striped bass temperature experience

Temperature and dissolved oxygen conditions were monitored at 1-m depth increments at 4 to 10 locations along the main river channel of each reservoir. Profiles were taken weekly during stratification (approximately May to October) in 2004 and 2005, except for Lake Gaston and Lake Tillery, which were sampled only in 2004 and 2005, respectively. Temperatures for the remainder of the year were taken from TidBit data loggers hung from buoys at approximately 1.5 meter intervals from surface to bottom in two to three locations in each reservoir. Unfortunately, about half of the logger strings disappeared or were washed away by floods from hurricanes, leaving us with data from only the midlake loggers in Lakes Gaston and Hickory and the dam forebay loggers in Lake Rhodhiss. Loggers were deployed in Lakes Tillery and Jordan only in the forebay location, and only in 2005; 2004 Jordan Lake temperature data were supplemented with Army Corps of Engineer data from the dam intake at 2-m depth. The 2002 temperature and dissolved oxygen data from Lakes Norman and Badin were collected in a similar fashion; however more sites were monitored on each reservoir (Thompson et al. 2005).

I determined the temperature experienced by striped bass in each reservoir by integrating the temperature-oxygen conditions from vertical profiling with what was learned about striped bass habitat selection by Thompson et al. (2005). They defined

two behavioral “rules” for temperature selection by striped bass. The “2mg/L” rule was based on literature (e.g. Zale et al. 1990) suggesting that striped bass will not occupy water with dissolved oxygen levels below 2 mg/L. The “above the oxycline” rule was based on detailed telemetry data from striped bass in Badin Lake. According to both rules, fish occupied the warmest water possible during winter and spring until 20°C was reached. Fish then remained at 20°C until hypoxic conditions (DO <2 mg/L) coincided with 20°C, forcing fish into warmer water. By the “above the oxycline” rule, striped bass would remain just above the oxycline until destratification occurred and oxygenated 20°C water again became available. By the “2mg/L” rule, striped bass would occupy the coolest water available with at least 2 mg/L dissolved oxygen until destratification occurred.

The difference in temperature regime estimated using the two rules was relatively small in both Badin Lake and Lake Norman, and never more than 4°C. By the “above the oxycline” rule, striped bass occupied temperatures between 27°C and 29°C in both lakes during the warmest parts of the summer, with one date as high as 30°C. According to the “2mg/L” rule, these fish occupied temperatures of 26°C to 28°C in Badin Lake, and 25°C to 27°C in Lake Norman (Thompson et al. 2005).

While the “above the oxycline” rule was based on observed striped bass behavior, habitat conditions experienced by the fish tracked in Badin Lake differed from those in our other study lakes. Striped bass may occupy different temperatures in a system with a greater range of available temperature and DO conditions than would be seen from behavior of fish in a system with poorer, more constrained habitat conditions (Bettoli

2005). Therefore it is important to also evaluate striped bass thermal experience using the “2mg/L” rule because it provides a conservative lower bound to temperature selection.

I took temperature experience for Lakes Badin and Norman in 2002 directly from Thompson et al. (2005). For the remainder of the lakes, I applied each of the temperature selection rules to the temperature-oxygen data collected in 2004 in Lakes Jordan, Gaston, Hickory and Rhodhiss, and to 2005 data from Lake Tillery (Figure 1). I entered the temperature experience according to each rule into the bioenergetics model, which then interpolated daily temperatures from my bi-weekly data. I then summarized these daily temperature experiences by seven metrics (Table 2): first date that 2mg/L DO and 20°C water was unavailable, number of days striped bass occupied water > 20°C, number of days striped bass occupied water \geq 27°C, average annual temperature (°C), average May 1 – October 31 temperature (°C), average July 15 to Aug 31 temperature (°C), and maximum temperature (°C). I produced a correlation matrix for these metrics to test for significant linear dependence between sets of variables ($\alpha = 0.05$).

I summarized time striped bass spent at 20 and 27°C because according to telemetry studies, 20-22°C is considered the preferred temperature range, and 27°C has been cited as the theoretical ceiling of striped bass thermal tolerance, with many studies reporting fish avoidance of temperatures over 25°C (Coutant and Carroll 1980, Cheek et al. 1985, Coutant 1985, Douglas and Jahn 1987, Van Den Avyle and Evans 1990, Zale et al. 1990, Young and Isely 2002, Baker and Jennings 2005).

Table 2. Selected characteristics of striped bass temperature regime as predicted by the “above the oxycline” rule (top panel) and “2mg/L” rule (middle panel), and the difference between characteristics predicted by each rule (bottom panel).

<i>Lake characteristics using the “above the oxycline” rule</i>	<i>Badin 2002</i>	<i>Gaston 2004</i>	<i>Hickory 2004</i>	<i>Jordan 2004</i>	<i>Norman 2002</i>	<i>Rhodhiss 2004</i>	<i>Tillery 2005</i>
Date 2mg/L DO and 20°C unavailable	24-Jun	13-Jul	8-Jun	13-May	15-Jul	NA	18-May
Number of days > 20°C	121	96	99	165	104	0	134
Number of days ≥ 27°C	54	8	13	50	33	0	87
Average annual temperature (°C)	17.9	16.4	16.8	18.5	18.4	15.2	18.3
Average May 1 – October 31 temperature (°C)	23.2	22.4	22.6	25.3	22.5	19.3	24.9
Average July 15 to Aug 31 temperature (°C)	28.1	26.1	26.5	27.4	27.7	20.0	29.2
Maximum temperature (°C)	29.9	27.5	27.5	29.9	29.9	20.0	30.3

<i>Lake characteristics using the “2mg/L” rule</i>	<i>Badin 2002</i>	<i>Gaston 2004</i>	<i>Hickory 2004</i>	<i>Jordan 2004</i>	<i>Norman 2002</i>	<i>Rhodhiss 2004</i>	<i>Tillery 2005</i>
Date 2mg/L DO and 20°C unavailable	24-Jun	13-Jul	8-Jun	13-May	15-Jul	NA	18-May
Number of days > 20°C	121	96	99	165	104	0	134
Number of days ≥ 27°C	46	0	0	25	25	0	59
Average annual temperature (°C)	17.7	16.1	16.4	18.2	18.3	15.2	17.9
Average May 1 – October 31 temperature (°C)	22.7	20.8	20.9	23.3	22.0	19.1	22.8
Average July 15 to Aug 31 temperature (°C)	27.6	24.5	25.0	26.0	26.4	20.0	28.0
Maximum temperature (°C)	29.8	25.3	25.9	28.9	27.9	20.0	28.8

<i>Difference between two rules</i>	<i>Badin 2002</i>	<i>Gaston 2004</i>	<i>Hickory 2004</i>	<i>Jordan 2004</i>	<i>Norman 2002</i>	<i>Rhodhiss 2004</i>	<i>Tillery 2005</i>
Date 2mg/L DO and 20°C unavailable	0	0	0	0	0	0	0
Number of days > 20°C	0	0	0	0	0	0	0
Number of days ≥ 27°C	8	8	13	25	8	0	28
Average annual temperature (°C)	0.2	0.3	0.4	0.3	0.1	0.0	0.4
Average May 1 – October 31 temperature (°C)	0.5	1.6	1.7	2.0	0.5	0.2	2.1
Average July 15 to Aug 31 temperature (°C)	0.5	1.6	1.5	1.4	1.3	0.0	1.2
Maximum temperature (°C)	0.1	2.2	1.6	0.9	2.0	0.0	1.5

In each case the results showed that the fish would occupy a minimum of 5°C in winter, then follow warming temperatures until 20°C became available in April or May. At this point the temperature experience for each lake differed.

The cooler and better-oxygenated conditions of Lake Rhodhiss allowed striped bass to remain at 20°C from May until the reservoir cooled in October, whereas fish in all other reservoirs were forced into warmer waters at different times in the summer. Lakes Hickory, Tillery, and Gaston all had a period of suitable habitat lasting into late spring before hypoxic conditions intruded far enough into the water column to force fish into less preferred temperatures. In Lake Jordan, however, the shallow depths, extensive hypoxia, and surface waters that warmed early in the spring combined to create conditions where 20°C water with at least 2 mg/L DO was never available during the spring (Figure 1).

The length of time that fish remained in warm ($>20^{\circ}\text{C}$) and very warm ($\geq 27^{\circ}\text{C}$) water also varied by lake (Table 2). Striped bass temperature regimes in Lakes Hickory and Gaston were similar, with just under 100 days above 20°C, and very few days at or above 27°C by the “above the oxycline” rule. By the “2 mg/L” rule, striped bass in these lakes were not forced into water as warm as 27°C (Figure 1). Striped bass in Lakes Jordan, Norman, Badin, and Tillery experienced more than 100 days above 20°C, and from one to three months in very warm ($\geq 27^{\circ}\text{C}$) water by the “above the oxycline rule.” According to the “2mg/L” rule, fish in these lakes were subject to one to two months at or above 27°C (Table 2). Of these four lakes, striped bass in Lake Norman spent the fewest days inhabiting very warm temperatures.

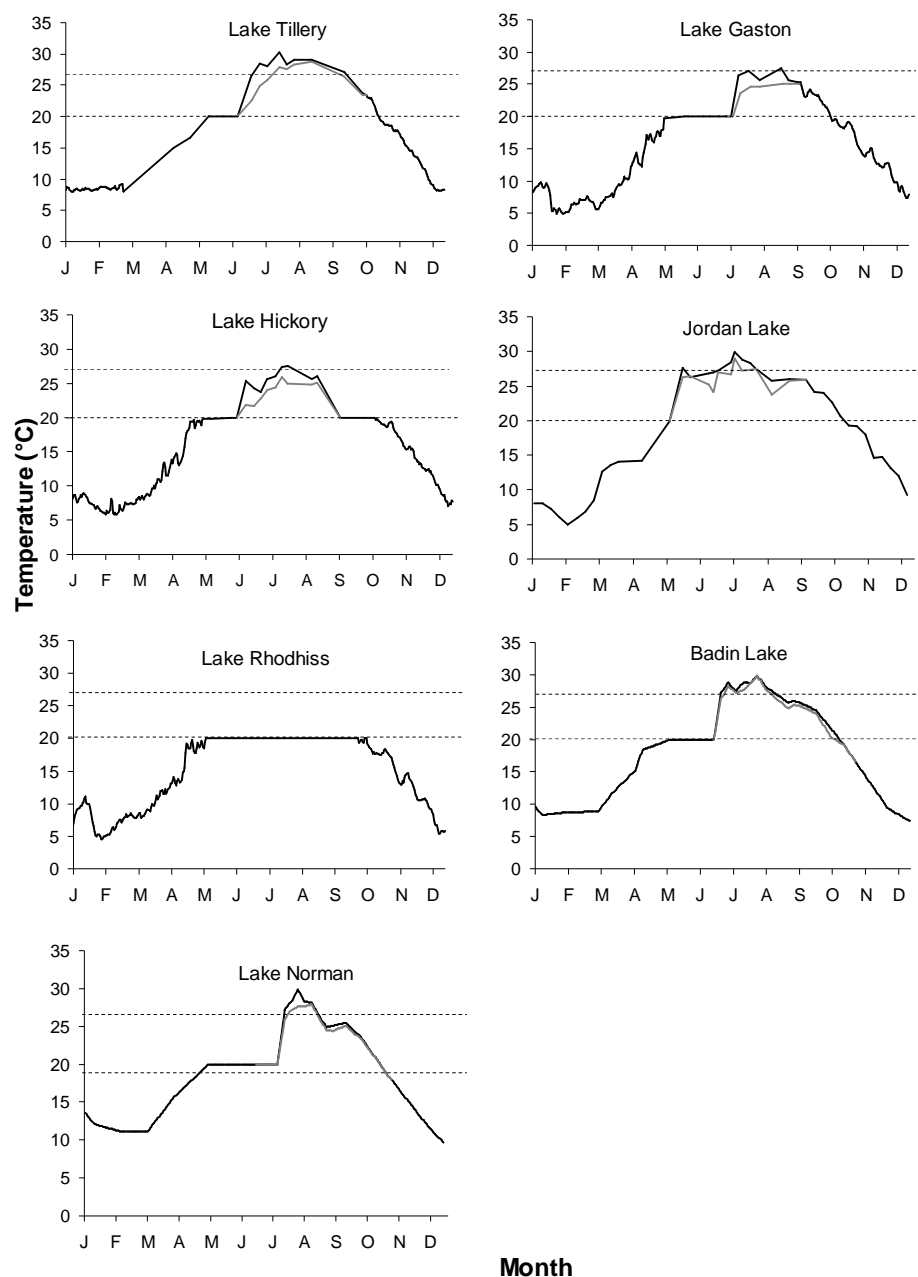


Figure 1. Striped bass temperature regime in each lake as predicted by the "above the oxycline" rule (black line) and the "2 mg/L" rule (grey line). Data presented are from 2004 for all lakes except Tillery, which was only sampled in 2005. Temperatures from January through the start of April 2004 are borrowed from data collected in the same time period in 2005, with the exception of Jordan Lake, for which 2004 Army Corps of Engineers data were used during this time period. Temperatures during stratification are taken from weekly temperature/DO profiling. Outside of the stratification period (October through April), daily temperatures were taken from a temperature logger hung at 1.5-2m depth in the mid to lower lake. In Lake Rhodhiss, there was no difference in temperature regimes predicted by either rule. Dashed lines are drawn at 20°C and 27°C for reference.

Striped bass in Lake Jordan occupied the warmest average temperature between May 1 and October 31 (25.3°C). However, striped bass remained at or above 27°C for the longest duration in Lake Tillery – 87 days by the “above the oxycline” rule” - and occupied an average temperature of 29.2°C during the hottest part of the summer (mid-July to late August). During this time period, striped bass in Lake Norman occupied an average of 27.7 °C, which is warmer than all but Lake Tillery, despite the fact that fish in Lakes Jordan and Badin all sustained many more days above 20°C and at or above 27°C. Maximum temperature was highest in Lake Tillery, reaching 30.3°C (Table 2).

The assessment of severity of summer habitat conditions for striped bass was generally similar among reservoirs regardless of which of these metrics were used to define ‘good’ or ‘poor’ habitat. Thirteen of 21 pairs of metrics had significant correlation coefficients ($P < 0.05$), and the mean temperature between May 1 and October 31 correlated with every other measure (Table 3). Interestingly, the date striped bass were first forced into warm temperatures by hypoxia did not correlate with either the number of days fish spent above 20°C or at or above 27°C. Based on a combination of all metrics (Table 2), I consider striped bass temperature experience to be optimal in Lake Rhodhiss, moderate in Lakes Gaston, Norman, and Hickory and poor in Lakes Badin, Tillery, and Jordan.

As expected, striped bass temperatures during stratification were lower when predicted by the “2mg/L” rule than by the “above the oxycline” rule. Estimates never differed by more than 4°C – seen in Lake Tillery on June 28, 2005 – and generally

Table 3. Correlation coefficients between seven different metrics of striped bass thermal regime (based on the “above the oxycline” rule) for the seven study reservoirs. Values in bold are significant ($P < 0.05$).

	Number of Days > 20°C	Number of Days ≥ 27°C	Mean Annual Temperature	Mean May 1 - Oct 31 Temp.	Mean July 15 - Aug 31 Temp.	Maximum temperature
Day 2mg/L DO & 20°C unavailable	-0.80	-0.61	-0.41	-0.89	-0.43	0.92
Number of Days > 20°C		0.71	0.88	0.97	0.91	0.93
Number of Days ≥ 27°C			0.81	0.80	0.75	0.72
Mean Annual Temperature				0.86	0.88	-0.35
Mean May 1 - Oct 31 Temperature					0.87	0.88
Mean July 15 - Aug 31 Temperature						0.99

differed by only 0.2 – 2°C. This resulted in a difference of only 0.27- 0.41°C in the mean of predicted daily temperature occupied by striped bass across all lakes.

I have presented data for all lakes for one year only; therefore it is important to note that some of the differences in striped bass temperature regimes may be attributable to the fact that sampling occurred in different years for some lakes. However, Thompson et al. (2005) estimated striped bass temperature regime for Lakes Badin and Norman for the entirety of 2001 and 2002, and found that the seasonal differences in temperature regime between lakes were very similar for both years.

Striped bass sampling

Gill net samples were conducted by NCWRC biologists during late November or early December of 2003 (Lakes Gaston, Rhodhiss, and Hickory) and 2004 (Lakes Gaston Rhodhiss, Hickory, Tillery and Jordan). Six to eight 3-m x 61-m gill nets (two each of 3.8, 5.1, 6.4, and 7.6-cm mesh on Lakes Rhodhiss and Hickory, and 2.5, 5.1, and 7.6-cm on all others) were hung opportunistically in one to three areas in each reservoir and fished overnight for five to ten nights. Given the very cool water temperatures at this time of year (approximately 8-12°C) the risk of stomach contents deteriorating before being put on ice was minimal. Between 40 and 150 fish were collected on each reservoir over the entire sampling period. Two to three striped bass in each 100-mm size bin were frozen immediately upon net retrieval and brought to the lab for energy density, age, and stomach content analysis. Additionally, all stomachs and

otoliths of other fish were extracted in the field, placed on ice or in envelopes and returned to the lab.

Striped bass diet

I calculated proportions of major prey items in 10-mm size increments for two periods in the year: summer diet - based on forage composition from August purse seine samples, and winter diet - based on stomach analysis from our late fall striped bass gill net samples. Purse seine forage fish collection procedures are given below. Because not all striped bass consumed the same sizes of prey, I estimated separate diet proportions for two or three size classes of striped bass. I used visual analysis of plots of prey to predator total length to determine lake-specific groupings of striped bass sizes that consumed similar maximum sizes of prey.

In Badin Lake and Lake Norman, striped bass stomach contents generally matched the size and species composition of purse seine forage fish catches, which suggests that they eat in proportion to what is available in the pelagic zone (Thompson et al. 2005). Therefore, I assumed that the summer diet reflects the distribution of species by weight in 10-mm size categories found in August purse seine samples.

November/December diet composition was determined from analysis of striped bass stomachs. Items from a minimum of 40 randomly-selected stomachs from each lake were analyzed to the lowest taxonomic grouping possible and were measured to mm TL when possible. Where items were partially digested, I measured backbone

length and calculated total length from species, genus, or family-specific backbone to total length regressions generated by Thompson et al (2005).

I calculated the percent numeric composition of these stomach items in 10-mm prey size categories, and used length-weight relationships generated in this study (see forage fish section below) to estimate percent composition in the same 10-mm size bins by weight. Where contents could not be identified to species (which was often), individuals identified only to the family and genus level were assigned a species using data from the purse seine sample. For this species assignment, I assumed that items found in stomachs in November/December were consumed in proportion to what was available in the pelagic zone, and that November/December pelagic community had the same species (though not size) composition as the fish captured in the August pelagic purse seine sample.

Due to the more limited sampling performed for this study, no stomach or purse seine samples were taken from the winter or spring. Stomach content data from Badin Lake and Lake Norman showed that during these times shad are largely absent from striped bass diets, presumably because much of the preferred young-of-year prey have been consumed and the adults have moved inshore to spawn. During this time stomachs primarily contained invertebrate or centrarchid prey (Thompson et al. 2005). In light of the uncertainty in estimating spring and summer diets in the five additional reservoirs, I simplified the diet inputs. I entered the August and November/December diet proportions in the model, and used the November/December diet again as the diet on January 1 and December 31 (because the model requires dates to span 365 days), and

then let the model interpolate diet composition between those dates. The consequences of this assumption are evaluated below.

Striped bass in all reservoirs fed on gizzard shad and threadfin shad; gizzard shad were primarily consumed at larger sizes (Figure 2). Blueback herring and alewife were also a significant proportion of striped bass diet in systems where these fish are found. Occasionally stomachs contained invertebrate or centrarchid prey, but I included these items in the striped bass diet for model simulations only for Lakes Hickory, Gaston, and Tillery. No stomachs from Jordan Lake contained invertebrates or centrarchids, and in Lake Rhodhiss invertebrate and centrarchid items were found but comprised less than 1% of all of diet items by weight. In Lakes Badin and Norman, invertebrates and centrarchids were not part of the late summer or December striped bass diet. These items were found in the spring, but I simplified the diet inputs of the Badin and Norman bioenergetics simulations to reflect the more limited sampling done on all other lakes.

Forage fish composition and energy density

Forage fish were collected in early August 2004 on Lakes Gaston, Jordan, Rhodhiss, and Hickory. In August 2005 fish were collected again from Lakes Rhodhiss, Hickory, and Jordan as well as from Lake Tillery. Two locations – forebay and midlake – were sampled on each reservoir, except for Lake Gaston, for which one forebay and two midlake sites were sampled. At each site, one haul of a 76m × 6m purse seine (7.6mm bar mesh) was performed. Total weight of forage fish caught at

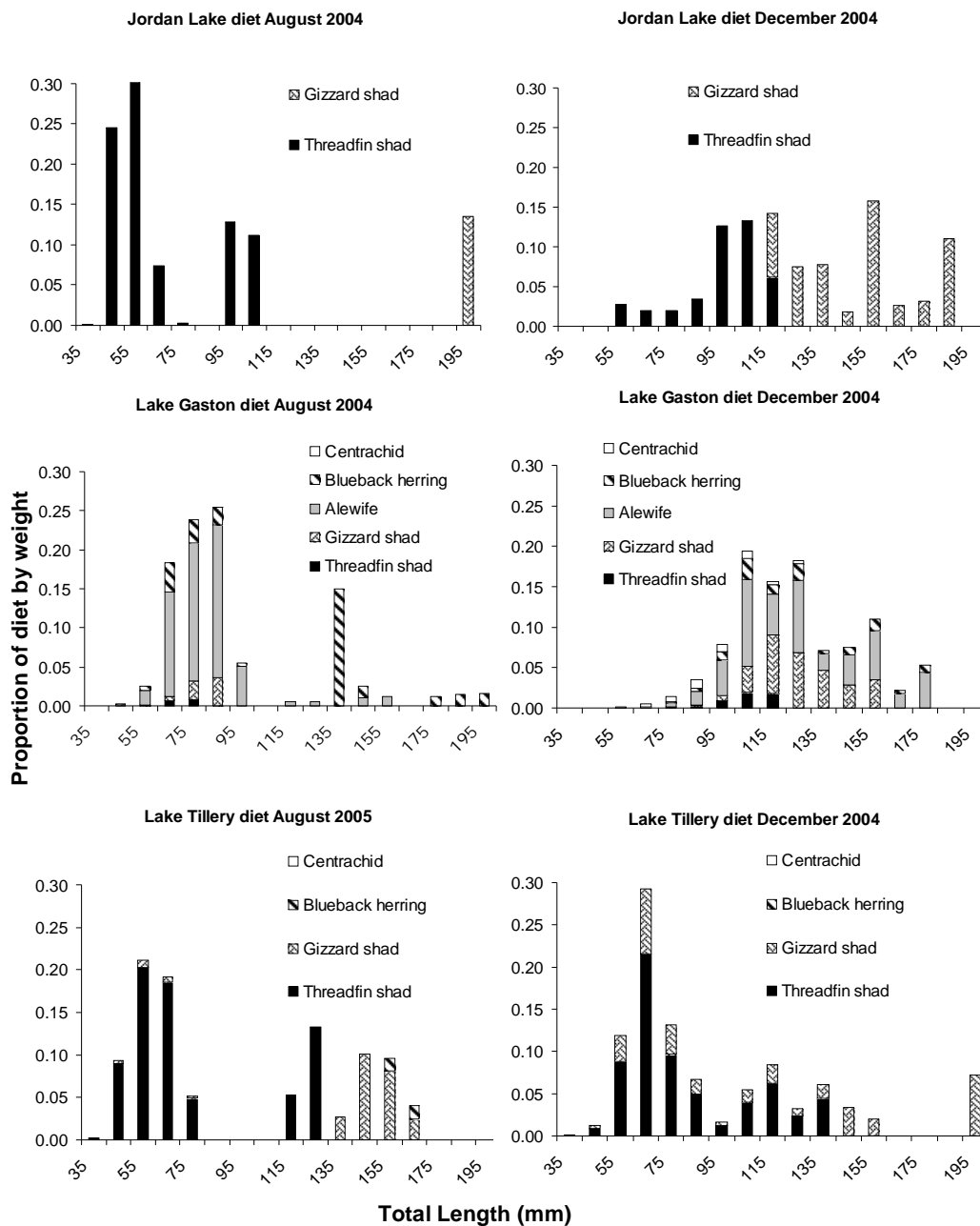
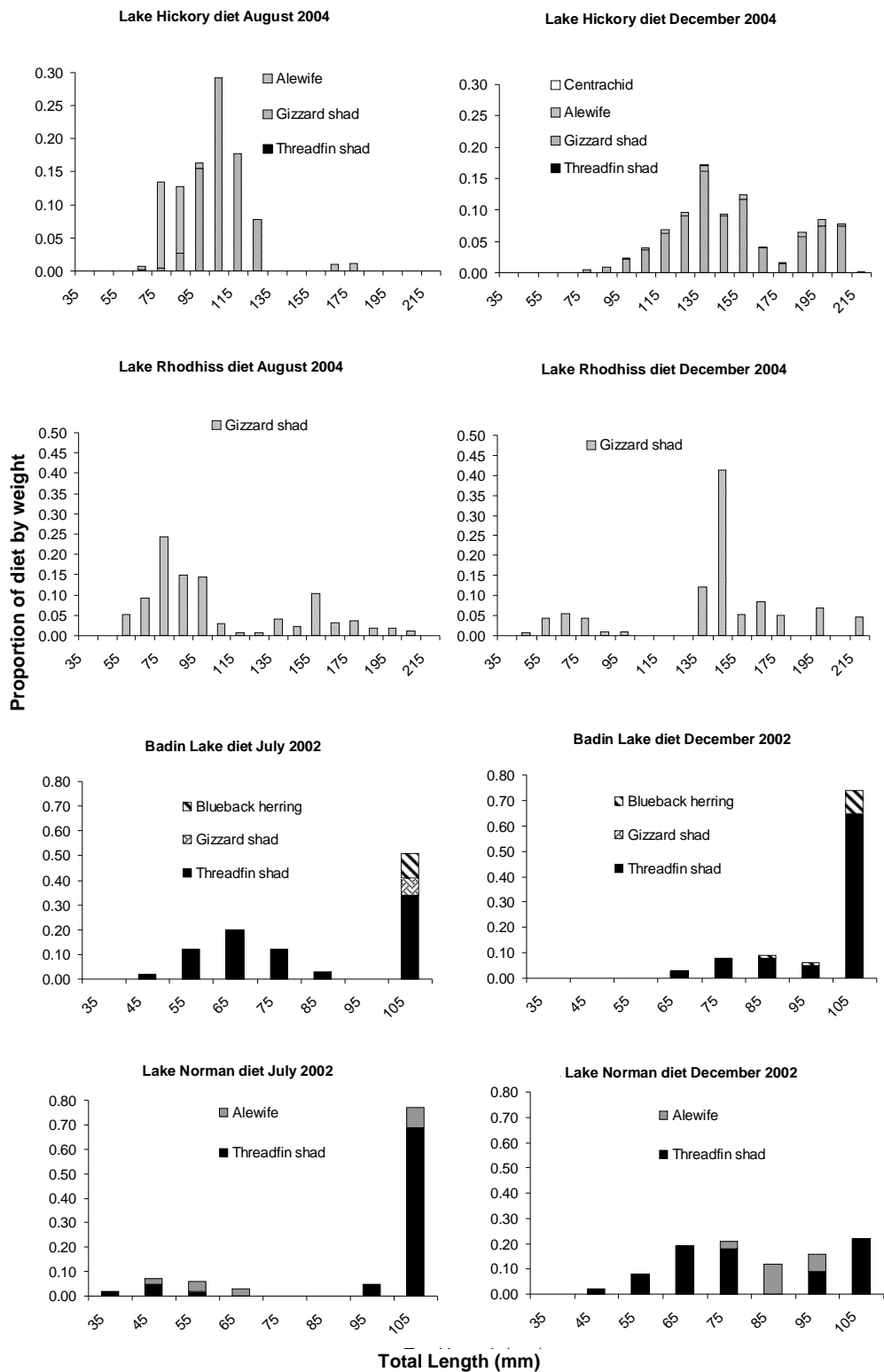


Figure 2. Striped bass diet in July/August and November/December. July/August diet is estimated from purse seine catch data. November/December diet is estimated from stomach contents of gill net-captured striped bass. Where contents were indistinguishable within a taxonomic group, relative proportions as caught in the purse seine were used to partition items to species. Diet proportions by number were converted into proportions by weight using lake- and species-specific length-weight relationships. In the bioenergetics simulations diets were further partitioned into two to three striped bass size categories that captured differences in predator total length to prey size distributions (not shown). Diets for Lakes Badin and Norman came from Thompson et al. (2005).

Figure 2 continued



each site was determined and a representative subsample of at least 2 kg was placed on dry ice and returned to the lab for processing.

For each purse seine haul, total length, weight, and species were recorded for a minimum of 150 randomly selected fish per site, and for at least 200 individuals of the most common species across sites. Fish were randomly selected to assure that species and size distributions were representative of the original sample.

Length-weight relationships were determined for each species for each reservoir (Table 4). Data were log-transformed and relationships for each species were compared across reservoirs using Analysis of Variance (SAS; Proc GLM with lake as class, using a Bonferroni adjustment to control error rate with multiple comparisons; $\alpha=0.05$). Significant effects of reservoir were evident only for alewife between Lakes Gaston and Hickory, gizzard shad between Lakes Norman and Badin and between Lakes Rhodhiss and Hickory, and for threadfin shad between Lakes Tillery and Jordan. However, lake-specific total length to weight relationships were used in estimating proportion by weight of different forage fish species in the striped bass diet (below).

The relationship between total length and weight was about the same for all species up to 60 mm TL. Fish increased in weight with length fastest for gizzard shad and threadfin shad, more slowly for alewife, and slowest for blueback herring (Figure 3).

The relationship between total length and energy density was determined for each forage species for each reservoir to determine size-specific patterns of energy density for the bioenergetics model. Two to three fish in each 5-mm length bin were dried to

Table 4. Equations, R^2 values, and sample sizes relating weight (g) to total length (mm) of forage fish species. Because regression lines did not always differ by lake for a given species (see text), equations are given for species by individual lakes (as used in modeling) and also by pooling data from all lakes. Data from Lakes Norman and Badin are from Thompson et al. (2005).

Lake	Species	Equation	R-squared	N
Lake Norman	Alewife	$Wt=6E*TL^3.0329$	0.99	2,708
Lake Hickory	Alewife	$Wt=1E-05*TL^2.9258$	0.97	421
Lake Gaston	Alewife	$Wt=1E-05*TL^2.9351$	0.89	240
Combined lakes	Alewife	$Wt=1E-05*TL^2.9263$	0.93	690
Lake Gaston	Blueback Herring	$Wt=3E-05*TL^2.7043$	0.98	68
Badin Lake	Blueback Herring	$Wt=1E-05*TL^2.8936$	0.99	173
Combined lakes	Blueback Herring	$Wt=1E-05*TL^2.8839$	0.97	96
Lake Rhodhiss	Gizzard shad	$Wt=1E-05*TL^2.935$	0.99	237
Lake Tillery	Gizzard shad	$Wt=1E-05*TL^2.9234$	0.99	29
Badin Lake	Gizzard shad	$Wt=2E-05*TL^2.8468$	0.99	1,144
Lake Norman	Gizzard shad	$Wt=5E-06*TL^3.1152$	0.99	5,177
Lake Hickory	Gizzard shad	$Wt=2E-05*TL^2.8787$	0.98	298
Combined lakes	Gizzard shad	$Wt=1E-05*TL^2.9173$	0.99	569
Badin Lake	Threadfin shad	$Wt=4E-06*TL^3.1761$	0.99	4,403
Lake Norman	Threadfin shad	$Wt=5E-06*TL^3.1007$	0.98	5,177
Lake Tillery	Threadfin shad	$Wt=8E-06*TL^3.0081$	0.99	402
Lake Hickory	Threadfin shad	$Wt=1E-05*TL^2.9262$	0.97	126
Lake Rhodhiss	Threadfin shad	$Wt=2E-05*TL^2.8016$	0.88	209
Lake Jordan	Threadfin shad	$Wt=1E-05*TL^2.8895$	0.94	607
Combined lakes	Threadfin shad	$Wt=8E-06*TL^3.0081$	0.99	1,348

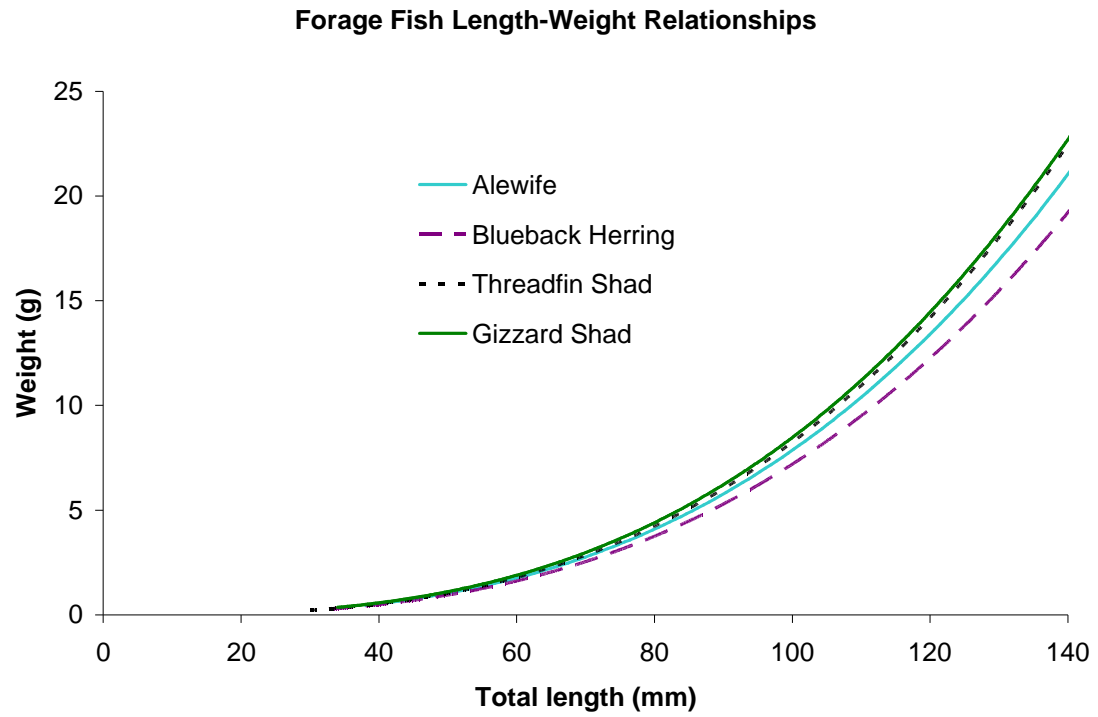


Figure 3. Relationship between weight (g) and total length (mm) for the four major species of forage fish; alewife, blueback herring, threadfin shad, and gizzard shad. The associated equations, R^2 values, and sample sizes are given in Table 4.

constant weight at 70°C. Species-specific energy density to dry weight regressions determined by Thompson et al. (2005) were applied to these data to calculate total energy density in Joules/gram wet weight. Data were log-transformed and regressions of energy density to total length for each species were compared across reservoirs using Analysis of Variance (SAS; Proc GLM with lake as class, using a Bonferroni adjustment to control error rate with multiple comparisons; $\alpha=0.05$). Energy density data from Badin Lake and Lake Norman in 2002 (Thompson et al. 2005) were added to the analysis to compare energy densities of all forage fish sampled. Lake had a significant effect on total length to energy density regressions for all pairwise comparisons of alewife in Lakes Gaston, Norman, and Hickory. Lake also had a significant effect on the regressions for blueback herring between Lakes Badin and Gaston (blueback herring are present in Lake Tillery as well but an insufficient number of fish were sampled to make a regression for this lake). Unique regression equations were found for threadfin shad in Lake Norman, and gizzard shad in Lakes Rhodhiss and Lake Norman. I used lake-specific total length to energy density regressions for individual lakes that differed from every other lake (as stated above), but used a generalized total length to energy density equation to estimate energy density for each size class for all remaining lakes (Table 5).

I assumed that forage fish energy densities do not vary seasonally. Thompson et al. (2005) found this to be the case for all species except for blueback herring, which exhibited a slightly higher energy density in the summer months. This species was prevalent only in Gaston Lake purse seine hauls; since these hauls were made in August

Table 5. Energy density (J/g wet wt) of threadfin shad, gizzard shad, blueback herring, and alewife. Lake-specific energy density values were calculated only when analysis of variance showed a unique regression of energy density on total length. Energy density is assumed to be constant throughout the year. These energy densities reflect trends described in the text and were used as input to the striped bass bioenergetics model.

Threadfin Shad

<i>TL (mm)</i>	35	45	55	65	75	85	95	105	115	125	150	175	200
Lakes Badin, Hickory, Jordan, Gaston, Tillery, and Rhodhiss combined	2,695	3,132	3,570	4,007	4,445	4,882	5,319	5,757	6,194	6,631	7,725	8,818	9,912
Lake Norman	3,428	3,598	3,768	3,938	4,109	4,279	4,449	4,619	4,789	4,959	5,384	5,809	6,235

Gizzard Shad

<i>TL (mm)</i>	35	45	55	65	75	85	95	105	115	125	150	175	200
Lakes Badin, Hickory, Jordan and Gaston combined	2,717	2,924	3,131	3,338	3,545	3,752	3,960	4,167	4,374	4,581	5,099	5,617	6,135
Lake Rhodhiss	2,798	2,982	3,166	3,351	3,535	3,720	3,904	4,088	4,273	4,457	4,918	5,379	5,840
Lake Norman	3,212	3,451	3,689	3,928	4,166	4,404	4,643	4,881	5,119	5,358	5,954	6,550	7,146

Blueback Herring

<i>TL (mm)</i>	35	45	55	65	75	85	95	105	115	125	150	175	200
Lake Gaston	8,100	7,952	7,804	7,656	7,508	7,360	7,212	7,064	6,916	6,768	6,398	6,028	5,658
Badin Lake	5,060	5,135	5,210	5,285	5,360	5,434	5,509	5,584	5,659	5,734	5,921	6,108	6,295

Alewife

<i>TL (mm)</i>	35	45	55	65	75	85	95	105	115	125	150	175	200
Lake Gaston	5,955	6,182	6,410	6,638	6,866	7,094	7,322	7,550	7,778	8,006	8,576	9,145	9,715
Lake Norman	4,837	4,886	4,935	4,984	5,033	5,082	5,131	5,180	5,229	5,278	5,400	5,523	5,645
Lake Hickory	5,164	5,386	5,608	5,830	6,052	6,274	6,496	6,718	6,940	7,162	7,717	8,272	8,827

my energy density estimates may be slightly overestimated throughout the rest of the year. This potential bias is not a large concern for the Gaston Lake simulations, because stomach data from late fall 2003 and 2004 indicate that blueback herring were not a large proportion of the striped bass diet in this season, when clupeids are expected to be a major part of the diet. For all forage species, the size-specific energy density estimates from the August purse seine samples were assumed to apply at all other times of year as well.

Striped bass energy density

Somatic energy density of striped bass was estimated by drying subsamples of whole fish homogenate and applying a known dry weight to energy density relationship from Thompson et al. (2005). Similarly, gonadal energy density was estimated by drying gonads and applying a known gonad dry weight to energy density relationship. Whole fish energy density was then the weighted mean of these two estimates. I only used whole fish energy density in simulations because striped bass in these systems typically invest little in gonadal growth even in the spring, and do not spawn (Thompson et al. 2005).

The relationship between whole fish energy density and total length was analyzed with Analysis of Variance (SAS; Proc GLM with lake as class, using a Bonferroni adjustment to control error rate with multiple comparisons; $\alpha=0.05$). I included the 2002 striped bass energy density data from Lakes Norman and Badin (Thompson et al. 2005) in the analysis. Lake was a significant effect in the model and several pairwise

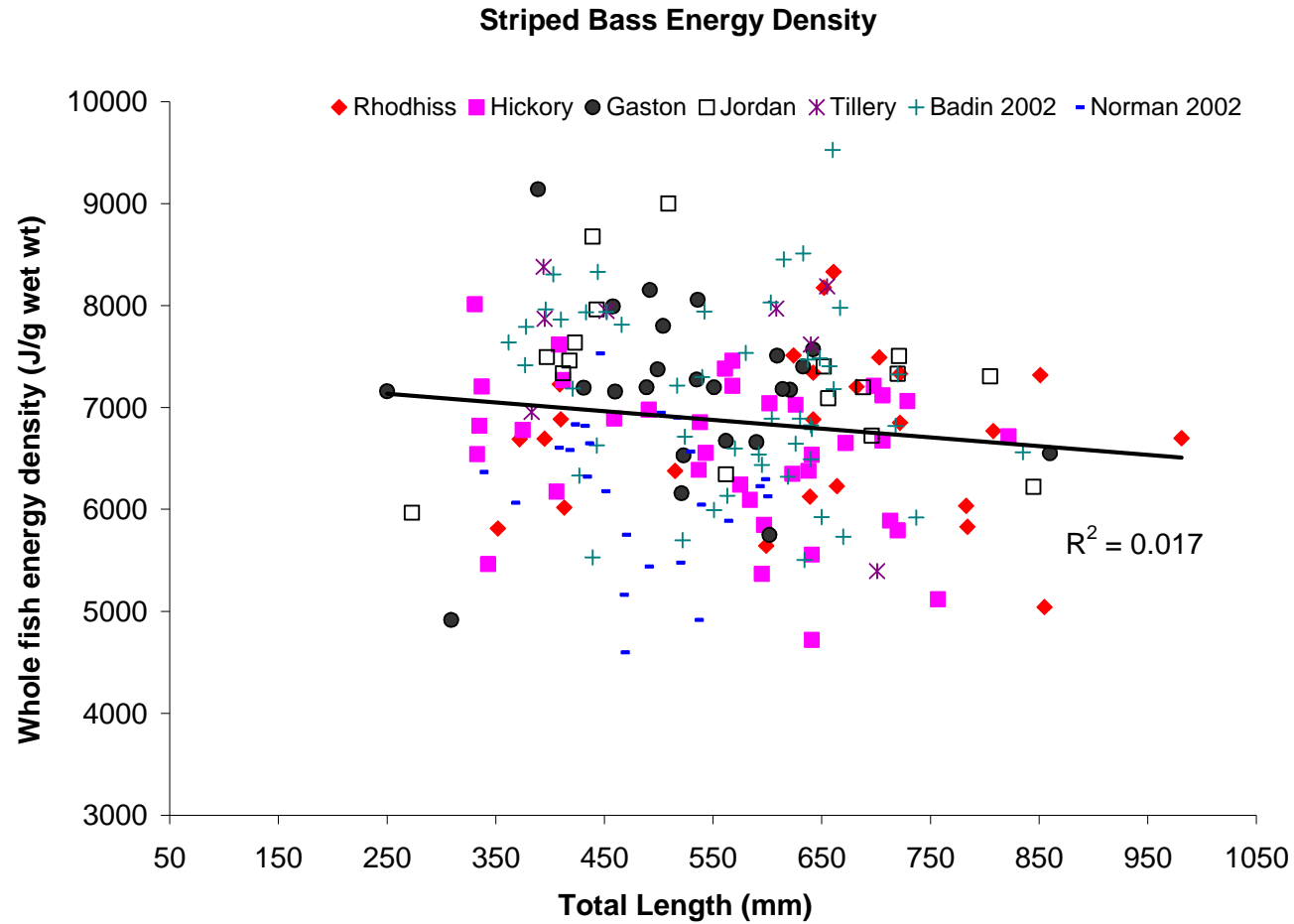


Figure 4. Whole-fish energy density (Joules per gram wet weight) plotted against total length of striped bass in Lakes Rhodhiss, Hickory, Gaston, Jordan, Tillery, Badin, and Norman. The line represents the best fit to data from all lakes except Norman.

comparisons of reservoirs showed differences in total length to energy density regressions. However, only the equation for Lake Norman was unique from those of every other reservoir. Some of this lack of difference may be attributable to the high degree of individual variation in energy density. Therefore, I used one general equation relating total length to energy density for all lakes (Figure 4), excluding Lake Norman. I did not need to employ the regression equation for Lake Norman since I used previous bioenergetics model simulations for Lakes Norman and Badin from Thompson et al. (2005).

Striped bass energy density values varied between 4,500 and 9,500 J/gram wet weight (Figure 4). Although this relationship between total length and energy density is characterized by a high degree of variability and is not highly predictive ($R^2=0.017$), it is significant, with energy density declining slightly with increasing total length;

$$ED = 0.8575*(TL) + 7349,$$

where ED is energy density in J/gram wet weight and TL is in mm. I assume that the relationship of energy density to total length is constant through the year. Thompson et al. (2005) showed that striped bass energy densities varied through the year but were unable to find a predictive model to relate day of year to energy density. Because I have only a December estimate of energy density, I assume no seasonal variation and evaluate this assumption below.

Striped bass growth

Striped bass were aged by reading annuli on saggital otoliths. Otoliths were prepared either by cracking and burning or by sectioning with a low-speed isomet saw and mounting on glass slides using Permount. Two independent readers read otoliths for each lake under 40-100X magnification; any differences in increment counts were resolved by consultation between the readers.

The von Bertalanffy growth curve was fit to observed length-at-age data to generate a growth curve for each lake. The von Bertalanffy growth equation is as follows:

$$L_t = L_{inf} * (1 - e^{-k(t-t_0)})$$

where L_t is the length at time t , L_{inf} is the average maximum length, k is the rate to reach L_{inf} , t is the fractional age assuming a January 1 birthday, and t_0 is the theoretical age at which length is zero (Ricker 1975). Weight-at-age was determined by applying a lake-specific length-weight equation. Von Bertalanffy modeling finds the best fit of a three-parameter growth curve based on observed length-at-age; because these data are from multiple cohorts in one year, growth between specific ages is reflective of general trends in growth averaged over recent years, which should be distinguished from a value of actual growth for a specific age within a specific year. When samples were collected over two years for a particular lake, all data were pooled to create one relationship.

Patterns of size at age vary substantially among the seven reservoirs (Figure 5). Striped bass achieved the largest sizes in Lakes Rhodhiss and Jordan (over 4kg by age

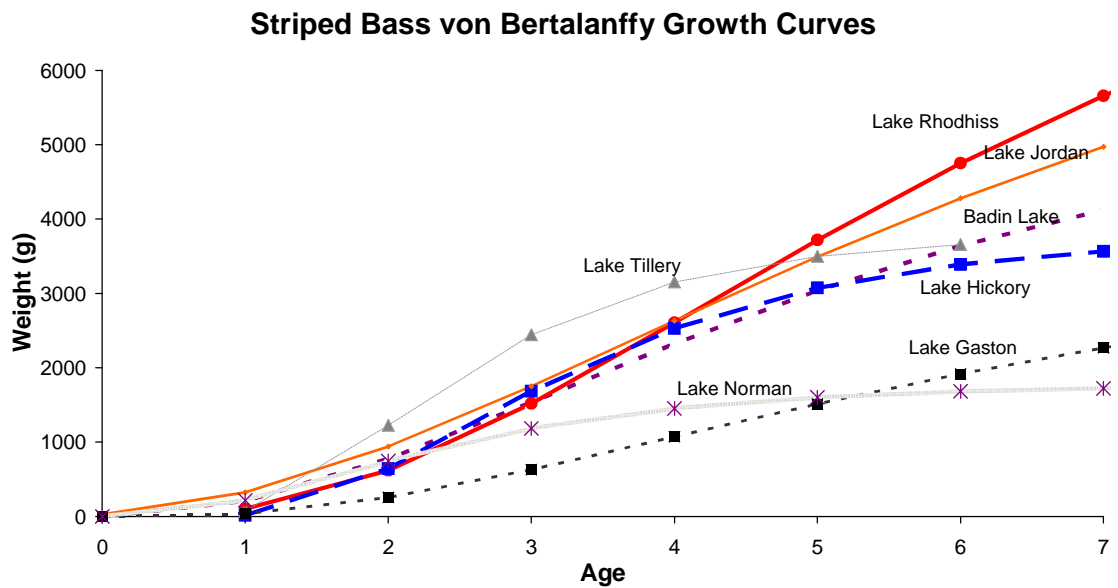


Figure 5. von Bertalanffy growth curves for striped bass. Except for Lake Tillery and Jordan Lake, age data from 2003 and 2004 were combined for the analysis. Badin Lake and Lake Norman models use both actual and backcalculated length-at age for fish collected in 2001 through 2003 from Thompson et al. (2005). Data are displayed as weight-at-age by transforming predicted length to weight using lake-specific length-weight relationships.

7), whereas in Lakes Norman and Gaston striped bass achieved only about half that weight by the same age. Growth was fastest for age 2-4 striped bass in Lake Tillery and slowest for those in Lake Gaston (Figure 5).

Comparing relative effects of temperature and food consumption on growth between reservoirs

The bioenergetics model estimates annual prey consumption (g) from thermal experience, diet, predator and prey energy densities, and observed growth. Using data described above, I ran Wisconsin-type bioenergetics model simulations (Hanson et al. 1997) parameterized for striped bass (Hartman and Brandt 1995) for Lakes Hickory, Gaston, Jordan, Tillery and Rhodhiss to estimate annual consumption of age-2 to age-5 striped bass. I also ran simulations for age-3 and 4 fish in Badin Lake and ages 3-5 Lake Norman striped bass in 2002 using data from Thompson et al. (2005) with the model inputs simplified (described below) to match the level of data collected on the other reservoirs. I ran simulations under both the “above the oxycline” and “2mg/L” temperature selection rules and compared the prey consumption estimated under each temperature regime. I first compared these “baseline” consumption estimates across reservoirs and related them to observed growth. I then evaluated the relative effects of consumption and temperature on striped bass growth in the study reservoirs by taking advantage of the fact that the balanced energy equation can be solved to predict growth given an estimate of annual consumption. This allowed me to simulate how much the growth of a fish in one reservoir might change if it had experienced the temperature or

food consumption of a similar-sized fish from another reservoir. This approach, termed “habitat exchange simulation,” is described more fully below.

First I identified pairs of similarly sized striped bass from two different reservoirs, (i.e., fish that began the calendar year at a similar weight, though not always the same age) to control for allometric effects on growth and consumption. For each pair I evaluated the role of consumption on growth by running a model simulation for one fish using all of its baseline conditions (e.g., diet, energy densities) – except substituting the consumption estimated for the fish in the other reservoir – and letting the model estimate annual growth. Absolute food consumption (in g) was used as a proxy for forage availability, as was done in Thompson et al (2005). I compared this new estimated growth to growth observed from actual length-at-age data, and termed the difference between the two the “consumption effect.”

I next evaluated the role of temperature on growth by repeating the simulation for the first fish, but substituting the temperature experience of the fish from the other lake while leaving consumption unchanged. The difference between baseline growth and growth simulated using the exchanged temperature regime was the “temperature effect.” These habitat exchange simulations were repeated for the second fish in the pair using all its baseline conditions, but substituting first consumption, then temperature experience, of the fish in the first reservoir.

The ratio of the consumption effect to temperature effect (“consumption:temperature effect ratio”) is an index of the relative importance of food availability and food consumption on growth of striped bass for the fish size and lakes being simulated. An absolute value greater than one means that consumption is more

important than temperature in explaining differences in growth of striped bass between the two reservoirs being compared, while an absolute value less than one means that temperature has a greater effect on differences in growth. It is important to note that the directionality of the ratio does not indicate the effect of consumption or temperature. A negative value indicates that each of the two lakes being compared is favorable relative to the other in either temperature or consumption, but not both. A positive ratio, on the other hand, indicates that one lake had both a more favorable temperature regime and better food availability than the other.

I identified fourteen pairs of initial fish sizes in different reservoirs that were suitable for habitat exchange simulations (i.e., differed in weight by no more than 4.5%) and compared the consumption:temperature effect ratio that resulted from each. All simulations presented here used consumption predicted under baseline simulations with the “above the oxycline” temperature regime.

Evaluating potential bias due to limited input data

To evaluate the potential for my limited diet and energy density data to bias the consumption estimates, I re-ran the 2002 Lake Norman and Badin Lake simulations from Thompson et al. (2005) using a data set condensed to reflect the limited nature of the new data collected in the current study. Beginning with the data files for the annual simulations, I eliminated seasonality of predator and prey energy densities. I reduced the data using only August prey energy densities and December striped bass energy densities, and applied these as constant values for the whole year. I also condensed the diet data so that only late summer and late fall diet were represented, and again used the

late fall diet as the January 1 and December 31 diets, interpolating between values throughout the rest of the year. I compared predicted annual consumption from the simulations using full and simplified input data to evaluate the impact of these data constraints.

I also calculated the consumption:temperature effect ratio for habitat exchange simulations based on comprehensive seasonal data from Lakes Norman and Badin (Thompson et al. 2005) and compared these to the consumption:temperature effect ratio resulting from simulations run with more limited data. In this way, I evaluated the effect that simplified data used in this study had on inferences regarding the relative importance of consumption and temperature to striped bass growth.

Results

Consumption estimates from baseline bioenergetics simulations

Annual per capita consumption estimates using the “above the oxycline” temperature selection rule ranged between 3,144 and 24,616 g (Table 6). Consumption was lowest for age-2 striped bass in Lake Gaston and highest for age-5 fish in Jordan Lake. Except for age-5 fish in Lake Norman, consumption estimates increased with fish age in each lake. Between fish of similar starting weight in different reservoirs, there were considerable differences in consumption. For example, age-3 Lake Rhodhiss striped bass and age-4 Lake Norman striped bass both started the year at 1,519g, but fish in Lake Rhodhiss consumed 12,330g while Lake Norman fish consumed only 10,637g. Proportion of maximum consumption achieved (p-value) ranged between 0.32 for age-5 Gaston Lake striped bass and 0.65 for age-2 Lake Rhodhiss striped bass. It

Table 6. Results of bioenergetics modeling simulations. Striped bass start weight and annual weight increment for each simulation were taken from von Bertalanffy growth curves. Consumption values and proportion of maximum consumption (p) are annual estimates. Results are given using temperature experience as determined by the “above the oxycline” rule and the “2 mg/L” rule, and the percent difference in consumption estimates between the two rules is presented where applicable. Lake Norman and Badin Lake are modeled using data from 2002, Lake Tillery is modeled for 2005, and all other lakes are modeled for 2004.

Lake	Age	Jan 1 start weight (g)	Weight increment (g)	Above the Oxycline Rule		2mg/L rule		Consumption difference between rules (%)
				Consumption (g)	p	Consumption (g)	p	
Lake Gaston	2	255	374	2,875	0.37	2,775	0.35	-3.5
	3	629	442	4,559	0.34	4,391	0.33	-3.7
	4	1,071	442	6,092	0.33	5,857	0.32	-3.9
	5	1,513	404	7,398	0.32	7,103	0.31	-4.0
Jordan Lake	2	940	811	10,916	0.57	10,639	0.55	-2.5
	3	1,751	880	16,498	0.56	15,959	0.54	-3.3
	4	2,631	860	20,846	0.56	20,168	0.54	-3.3
	5	3,491	788	24,616	0.55	23,773	0.53	-3.4
Lake Tillery	2	1,223	1,221	15,335	0.59	14,656	0.57	-4.4
	3	2,444	710	19,694	0.52	18,717	0.49	-5.0
	4	3,154	345	21,492	0.5	20,387	0.47	-5.1
	5	3,499	157	22,272	0.49	21,101	0.46	-5.3
Lake Hickory	2	642	1,041	8,988	0.56	8,710	0.54	-3.1
	3	1,683	846	13,005	0.49	12,509	0.47	-3.8
	4	2,529	544	14,808	0.44	14,192	0.42	-4.2
	5	3,073	317	16,019	0.43	15,330	0.41	-4.3
Lake Rhodhiss	2	620	898	9,778	0.65	both habitat selection rules resulted in the same temperature regime		
	3	1,519	1,087	12,330	0.47			
	4	2,606	1,112	16,404	0.45			
	5	3,718	1,034	19,863	0.43			
Lake Norman	3	1,261	341	10,364	0.4	10,086	0.39	-2.7
	4	1,519	126	10,637	0.37	10,325	0.36	-2.9
	5	1,514	46	10,261	0.38	9,975	0.37	-2.8
Badin Lake	3	1,482	1,195	14,697	0.5	14,312	0.49	-2.6
	4	2,519	712	15,724	0.42	15,280	0.41	-2.8

declined with increasing fish age in all lakes. In general, consumption estimates and p-values were greatest for fish that gained the most weight according to von Bertalanffy modeling.

Evaluation of the effect of temperature selection rules on consumption estimates

Consumption estimates did not differ greatly between simulations using the two temperature selection rules. Consumption was in the range of 2.5 to 5.3% higher using the “above the oxycline” rule than using the “2mg/L” rule (Table 6), which is considerably less than the differences in annual consumption by similarly-sized fish in different reservoirs. P-values were also similar between simulations run under the two rules; these were only 0.01 to 0.03 lower for all ages and lakes under the “2 mg/L” rule than under the “above the oxycline” rule (Table 6).

Comparing relative effects of temperature and food consumption among reservoirs

I conducted habitat exchange simulations among lakes characterized by poor striped bass growth (Gaston and Norman), moderate growth (Badin and Hickory), and fast growth (Jordan, Rhodhiss and Tillery). Twelve pairs of lakes had starting weights similar enough (within ~ 100g or 4.5%) to allow comparison.

Poor-growth lakes vs. moderate-growth lakes

Two habitat exchange simulations compared growth of striped bass between lakes with poor striped bass growth (Lakes Gaston or Norman) and lakes with moderate growth (Lakes Hickory or Badin). Substituting the consumption of a 629g Lake Gaston fish

with the higher consumption of a 642g Lake Hickory fish resulted in the Lake Gaston fish tripling its baseline growth, from 442g to 1,529g. The consumption effect was also large for a 1,514g Lake Norman fish receiving Badin Lake consumption. It gained 1,017g more with Badin consumption than under baseline conditions. In each of these simulations, fish from a moderate-growth lake had much smaller weight gain when modeled using consumption from a slow-growth lake. The temperature effect was small for all simulations, resulting in high consumption:temperature effect ratios that were well above 1, (Table 7a.), indicating that consumption had a greater effect than did temperature on explaining differences in growth between the sets of lakes.

Poor-growth lakes vs. fast-growth lakes

Two habitat exchange simulations compared growth of striped bass between poor-growth and fast-growth lakes. Fish from a poor-growth lake (Lakes Gaston and Norman) always gained more weight when grown under consumption from a fast-growth lake (here, Lake Rhodhiss) than under baseline conditions. The largest consumption effects were seen between Lakes Gaston and Rhodhiss. A 629g Lake Gaston fish gained 1,919g more than under baseline conditions using consumption from Lake Rhodhiss. Conversely, when using Lake Gaston consumption, a 620-g Lake Rhodhiss fish actually lost weight over the year simulated, whereas it gained 898g under baseline conditions (Table 7b.) In the comparison between 1,519g fish from

Table 7. Bioenergetics modeling results from striped bass habitat exchange simulations. Start weight is initial (January 1) striped bass weight, growth increment is the predicted annual growth, and difference in increment is annual growth predicted using substituted temperatures or consumption, divided by annual growth increment in the baseline simulation. The consumption:temperature effect ratio is the predicted annual growth increment when consumption is exchanged, divided by the predicted growth increment when temperature regime is exchanged. A ratio with an absolute value greater than one means that consumption is more important than temperature in explaining differences in growth of striped bass between the ages of fish for the two reservoirs being compared. Results in table 7a are from simulations comparing poor to moderate-growth lakes, in 7b from poor to fast-growth lakes, in 7c from moderate to fast-growth lakes, and in 7d from comparisons among fast growth lakes.

Table 7a. Poor-growth lakes vs. moderate-growth lakes

Age 3 Gaston vs. Age 2 Hickory:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Gaston conditions	629	442		
Gaston conditions except Hickory temperatures	629	432	-10	
Gaston conditions except Hickory consumption	629	1,971	1,529	-152.90
All Hickory conditions	642	1,041		
Hickory conditions except Gaston temperatures	642	1,035	-6	
Hickory conditions except Gaston consumption	642	12	-1,029	171.50
Age 5 Norman vs. Age 3 Badin:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Norman conditions	1,514	46		
Norman conditions except Badin temperatures	1,514	90	44	
Norman conditions except Badin consumption	1,514	1,063	1,017	23.11
All Badin conditions	1,482	1,205		
Badin conditions except Norman temperatures	1,482	1,154	-51	
Badin conditions except Norman consumption	1,482	257	-948	18.59

Table 7b. Poor-growth lakes vs. fast-growth lakes

Age 3 Gaston vs. Age 2 Rhodhiss	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Gaston conditions	629	442		
Gaston conditions except Rhodhiss temperatures	629	659	217	
Gaston conditions except Rhodhiss consumption	629	2,361	1,919	8.84
All Rhodhiss conditions	620	898		
Rhodhiss conditions except Gaston temperatures	620	666	-232	
Rhodhiss conditions except Gaston consumption	620	-57	-955	4.12

Age 4 Norman vs. Age 3 Rhodhiss:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Norman conditions	1,519	126		
Norman conditions except Rhodhiss temperatures	1,519	1,079	953	
Norman conditions except Rhodhiss consumption	1,519	513	387	0.41
All Rhodhiss conditions	1,519	1,087		
Rhodhiss conditions except Norman temperatures	1,519	163	-924	
Rhodhiss conditions except Norman consumption	1,519	662	-425	0.46

Table 7c. Moderate-growth lakes vs. fast-growth lakes

Age 4 Hickory vs. Age 4 Jordan:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Hickory conditions	2,529	544		
Hickory conditions except Jordan temperatures	2,529	-65	-609	
Hickory conditions except Jordan consumption	2,529	2,201	1,657	-2.72
All Jordan conditions	2,631	860		
Jordan conditions except Hickory temperatures	2,631	1,606	746	
Jordan conditions except Hickory consumption	2,631	-451	-1,311	-1.76

Table 7c. continued

Age 4 Hickory vs. Age 4 Rhodhiss:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Hickory conditions	2,529	544		
Hickory conditions except Rhodhiss temperatures	2,529	1,139	595	
Hickory conditions except Rhodhiss consumption	2,529	974	430	0.72
All Rhodhiss conditions	2,606	1,112		
Rhodhiss conditions except Hickory temperatures	2,606	483	-629	
Rhodhiss conditions except Hickory consumption	2,606	697	-415	0.66
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Age 4 Badin vs. Age 4 Rhodhiss:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Badin conditions	2,519	712		
Badin conditions except Rhodhiss temperatures	2,519	2,039	1,327	
Badin conditions except Rhodhiss consumption	2,519	892	180	0.14
All Rhodhiss conditions	2,606	1,112		
Rhodhiss conditions except Badin temperatures	2,606	-122	-1,234	
Rhodhiss conditions except Badin consumption	2,606	933	-179	0.15
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Age 2 Hickory vs. Age 2 Rhodhiss:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Hickory conditions	642	1041		
Hickory conditions except Rhodhiss temperatures	642	1309	268	
Hickory conditions except Rhodhiss consumption	642	1242	201	0.75
All Rhodhiss conditions	620	898		
Rhodhiss conditions except Hickory temperatures	620	669	-229	
Rhodhiss conditions except Hickory consumption	620	745	-153	0.67

Table 7c. continued

Age 4 Badin vs. Age 3 Tillery:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Badin conditions	2,519	712		
Badin conditions except Tillery temperatures	2,519	358.64	-353.36	
Badin conditions except Tillery consumption	2,519	1,795.5	1,083.5	-3.07
All Tillery conditions	2,444	710		
Tillery conditions except Badin temperatures	2,444	986	276	
Tillery conditions except Badin consumption	2,444	-133	-843	-3.05

Age 4 Hickory vs. 3 Tillery:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Hickory conditions	2,529	544		
Hickory conditions except Tillery temperatures	2,529	-294	-838	
Hickory conditions except Tillery consumption	2,529	1,875	1,331	-1.59
All Tillery conditions	2,444	710		
Tillery conditions except Hickory temperatures	2,444	1,743	1,033	
Tillery conditions except Hickory consumption	2,444	-320	-1,030	-1.00

Age 4 Badin vs. Age 4 Jordan:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Badin conditions	2,519	712		
Badin conditions except Jordan temperatures	2,519	723	11	
Badin conditions except Jordan consumption	2,519	2,120	1,408	128.00
All Jordan conditions	2,631	860		
Jordan conditions except Badin temperatures	2,631	815	-45	
Jordan conditions except Badin consumption	2,631	-258	-1,118	24.84

Table 7d. Comparisons among fast-growth lakes

Age 4 Jordan vs. Age 4 Rhodhiss:	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All Jordan conditions	2,631	860		
Jordan conditions except Rhodhiss temperatures	2,631	2,317	1,457	
Jordan conditions except Rhodhiss consumption	2,631	-121	-981	-0.67
All Rhodhiss conditions	2,606	1,112		
Rhodhiss conditions except Jordan temperatures	2,606	-142	-1,254	
Rhodhiss conditions except Jordan consumption	2,606	2,296	1,184	-0.94

Lakes Norman and Rhodhiss, the temperature effect was actually greater than the consumption effect, resulting in a consumption:temperature effect ratio of about 0.4.

Moderate-growth lakes vs. fast-growth lakes

Seven habitat exchange simulations were performed between lakes with moderate striped bass growth (Lakes Hickory and Badin) and lakes on the higher end of the growth spectrum (Lakes Rhodhiss, Tillery and Jordan). I ran habitat exchange simulations between all six combinations of these two sets of lakes for age-3 or age-4 striped bass weighing between 2,444 to 2,631g, and also between Lakes Hickory and Rhodhiss for age-2 fish weighing approximately 600g. As with the simulations involving fish from the slowest-growth lakes (Lakes Gaston and Norman), exchange of consumption from a faster-growth lake into the simulation of a moderate-growth lake always resulted in an increase in growth increment over the baseline simulation. The growth increment for age-4 Lake Hickory fish doubled from 544 to 974g using Lake Rhodhiss consumption (Table 7c), and quadrupled with Lake Jordan consumption. Over all seven comparisons, substituting consumption from a faster-growth lake to a slower-growth lake resulted in an additional growth gain of 180 to 1,657g relative to the baseline simulation.

Simulations where fish from a moderate-growth lake were grown under temperatures experienced by fish in a faster-growth lake resulted in an increase of growth increment relative to the baseline simulation for five of these seven scenarios. In the other two simulations, the growth increment due to exchanging temperature from

a faster-growth lake was less than under the baseline simulation. These were the comparisons where Lakes Badin and Hickory (moderate growth) were grown under temperatures experienced by fish in Lake Tillery.

Over these seven comparisons, the consumption:temperature effect ratios ranged from 0.14 (Badin simulations with Rhodhiss temperature or consumption) to 128 (Badin simulations with Jordan temperature or consumption, Table 7.) Each of the three simulations involving Lake Rhodhiss had consumption:temperature effect ratios below 1, meaning the effect of temperature was stronger than consumption in explaining differences in growth between Lake Rhodhiss and Lakes Badin or Hickory. Consumption affected growth about twice as much as did temperature in the comparison between Lakes Hickory and Jordan, and about three times as much between Lakes Hickory and Tillery (Table 7). In the comparison between Lakes Badin and Jordan, the small differences in temperature experience resulted in minimal changes to growth in habitat exchange simulations, and the effect of consumption was many times higher than the effect of temperature.

Comparisons among fast-growth lakes

One simulation compared age-4 fish from the two lakes with the highest striped bass growth and very different temperature regimes: Lakes Jordan and Rhodhiss. The effects of substituting temperature and consumption from Lake Jordan on growth of Lake Rhodhiss striped bass were only marginally different, with temperature slightly more important (consumption:temperature effect ratio of -0.94). However, when substituting Lake Rhodhiss conditions into Lake Jordan simulations, the more favorable

Rhodhiss temperatures resulted in a growth increment increase that was more than nine times greater than the decrease due to the slightly more limited Lake Rhodhiss consumption. This resulted in a temperature consumption effect of -0.67 (Table 7).

Evaluation of effects of limited data inputs on bioenergetics simulations and habitat exchange simulations

Consumption estimates for Lake Norman and Badin Lake bioenergetic simulations that were based on more limited data inputs did not differ much from consumption estimates of simulations based on more comprehensive seasonal diet and energy density data (from Thompson et al. 2005). Consumption estimates using limited data differed by only 0.6- 6.1% from simulations based on more comprehensive seasonal data (Table 8).

Habitat exchange simulations using limited data gave similar results to the same comparisons using more comprehensive data (Table 9). The consumption:temperature effect ratio for each lake was about twice as large for simulations using the more detailed input data. However, the ratio values were very high in both cases, indicating that differences in consumption accounted for much more of the difference in growth between reservoirs than did temperature whether the more detailed or simplified input data were used (Table 9).

Table 8. Total annual consumption (g) by Badin Lake and Lake Norman striped bass estimated in bioenergetics simulations using detailed seasonal diet and energy density data (full) from Thompson et al. (2005), the same simulations using diet and energy density data restricted to the same frequency of collection as in the this study (simplified), and the percent differences between consumption estimated using the simplified and full data inputs (% difference). All simulations use the “above the oxycline” temperature selection rule.

Badin Lake 2002			
	full	simplified	% difference
age-3	14,782	14,697	-0.6
age-4	16,687	15,724	-6.1
Lake Norman 2002			
	full	simplified	% difference
age-3	10,736	10,364	-3.6
age-4	11,078	10,748	-3.1
age-5	10,665	10,283	-3.7

Table 9. Results of “habitat exchange simulations” for age-3 Badin Lake and age-5 Lake Norman striped bass using comprehensive seasonal data from Thompson et al. (2005) and using data simplified to the type and frequency collected on the other lakes in this study.

Simulations based on comprehensive seasonal data	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All age-3 Badin conditions	1,482	1,205		
Badin conditions except Norman temperatures	1,482	1,178	-27	
Badin conditions except Norman consumption	1,482	182	-1,023	37.89
All age-5 Norman conditions	1,514	46		
Norman conditions except Badin temperatures	1,514	63	17	
Norman conditions except Badin consumption	1,514	1,020	974	57.29

Simulations based on simplified data	Start weight (g)	Growth increment (g)	Difference in increment (g)	Consumption: temperature effect ratio
All age-3 Badin conditions	1,482	1,205		
Badin conditions except Norman temperatures	1,482	1,154	-51	
Badin conditions except Norman consumption	1,482	257	-948	18.59
All age-5 Norman conditions	1,514	46		
Norman conditions except Badin temperatures	1,514	90	44	
Norman conditions except Badin consumption	1,514	1,063	1,017	23.11

Discussion

Thompson et al. (2005) applied bioenergetics modeling to compare growth of striped bass in two North Carolina reservoirs, and found that food consumption was more important than temperature in explaining differences in fish growth between these systems. I extended this approach to a broader range of reservoirs differing substantially in temperature-DO conditions, forage availability, and other characteristics to test the generality of this finding. My results corroborated those of Thompson et al. (2005) indicating that striped bass can grow well under warm conditions if they have enough food to sustain the increased metabolic demands of high temperatures, and further stress the need to incorporate the role of forage availability in striped bass management in southern reservoirs.

In contrast to literature stating that striped bass suffer reduced condition and increased mortality at temperatures $\geq 27^{\circ}\text{C}$ (Coutant 1985, Matthews et al. 1985, Zale et al. 1990, McDaniel et al. 1993), size-at age data and temperature/DO monitoring from this study showed that the systems where striped bass occupied the warmest summer conditions supported relatively good growth of striped bass. Zale et al. (1990) noted from angler surveys that striped bass ceased feeding at 27°C , as did Coutant (1985), and that such temperature-induced malnutrition was the ultimate cause of late summer mortality. However, Thompson et al. (2005) did not find this to be the case in their study.

Striped bass in Lakes Norman and Gaston exhibited very slow growth, achieving only half the weight by age-7 of striped bass in other study reservoirs. Temperatures experienced by striped bass in these systems, whether predicted by the “above the oxycline” rule or the more conservative “2mg/L” rule, were only moderate in severity relative to conditions experienced by striped bass in the five other reservoirs. This, along with the observation that both lakes are also the lowest in Chlorophyll-a, an indicator of productivity that has been positively correlated to clupeid biomass (Allen et al. 2000), suggests that inadequate food may have limited growth of striped bass in these lakes more so than warm temperatures.

Bioenergetics modeling further corroborated this finding. In the baseline simulations, striped bass from lakes with the best growth had the highest annual consumption, as might be expected. Habitat exchange simulations then showed that if striped bass from poor-growth lakes (Norman and Gaston) could achieve the same food consumption as did the fish with better growth, they would always grow more than they did under their own consumption. In many cases, food consumption (the proxy for prey availability) was more important than temperature in explaining differences in growth among reservoirs.

Bioenergetics modeling simulations showed that temperature was more important than consumption in explaining differences in striped bass growth only when comparisons were made against Lake Rhodhiss, which offered optimal temperature habitat for striped bass. In the year I simulated, temperatures experienced by striped bass in this lake never exceeded 20°C. In all but one habitat exchange simulation involving this lake, the effect of temperature on growth was greater than that of

consumption. This result helps evaluate the context-dependency of the role of food and temperature constraints on growth: when comparing lakes that are already warmer than preferred by striped bass, differences in consumption will be very important in determining how well striped bass will grow. However, when comparisons include a lake that has ideal thermal conditions, temperature may be the most important driver of differences in striped bass growth.

There were limitations to the approach I used; however where possible limitations were controlled or accounted for. I compared results of existing bioenergetics simulations that used very comprehensive seasonal diet and energy density information against results from simulations based on the same data set reduced to the type and frequency of data collected in this study, and found that my data limitations had a minimal effect on both the absolute consumption estimates or the interpretation of the relative roles of consumption and temperature. Temperature selection might be influenced differently in other systems due to vertical segregation of striped bass from their prey (Lewis 1983, Cyterski et al. 2005). However, the two temperature selection rules placed reasonable upper and lower bounds on temperatures that striped bass theoretically could occupy, and consumption estimates under each rule were very similar.

One final limitation was that the twelve pairs of habitat exchange simulations were not arranged in a balanced design. I could only compare pairs of fish for which there were similar start weights (within 4.5%) to account for allometric effects on consumption and growth. A disproportionate number of simulations involved Lakes Rhodhiss, Hickory and Badin, and this should be considered when interpreting the list

of consumption:temperature effect ratios. The approach used to make comparisons of growth among lakes isn't amenable to statistical tests; however the simulation results are still informative.

An enormous amount of effort has been given to tracking striped bass in reservoirs and rivers to determine preferred and achieved temperature and dissolved oxygen conditions, the presence of thermal refuges, and evidence for striped bass site fidelity (e.g., Betolli 2005 and references therein). Fewer studies have investigated the consequences of habitat constraints on growth, condition, and survival of striped bass. Matthews (1985) reported widespread mortality of striped bass in 27 of 80 impoundments across the southeast. Wooley and Crateau (1983) found that condition factors, survival rates beyond age-7, average weights, and lengths were all lower for the Atlantic strain striped bass than for native (and presumably more warm-water tolerant) Gulf-strain fish in the Apalachicola River, FL. Baker and Jennings (2005) reported high mortality for Atlantic-strain striped bass introduced into Lake Blackshear, GA, where summer temperatures exceeded 27°C for 13 weeks and drought made thermal refuges scarce; however I question the implications of these results given that non-native, tagged adult fish were introduced to the system without first being acclimated to conditions as juveniles.

Other telemetry studies have found very low rates of natural mortality for landlocked striped bass. Jackson and Hightower (2001) found that telemetered striped bass in Lake Gaston occupied 27-28°C water, but not for more than a month. Modified tag-return models for these same fish (Hightower et al. 2002) showed that natural mortality was a very small component of total mortality. Young and Isely (2004) also

found very low rates of natural mortality of telemetered striped bass in J. Strom Thurmond Reservoir, South Carolina-Georgia, and attributed the few summer deaths to fish being trapped in unsuitable habitat. Thompson et al. (submitted) also found very low rates of natural mortality for striped bass in Badin Lake from telemetry tag-return data.

To my knowledge, this study and Thompson et al. (2005) are the only studies to investigate the combined effects of temperature and food consumption on growth of striped bass in reservoirs. Cyterski et al. (2002) ran bioenergetics simulations on all age classes of striped bass in Smith Mountain Lake, Virginia, however their objective was to quantify annual prey consumption by striped bass and largemouth bass *Micropterus salmoides*, and did not discuss the effects of consumption on striped bass growth. Through continued research in this system, Cyterski and Ney (2005) concluded that an increase in predator demand on clupeids would lead to prey shortages for striped bass and largemouth bass. Dieterman et al. (2004) used bioenergetics modeling in a similar fashion to the comparisons done in this study to investigate the influence of temperature, food type, and food availability on growth of brown trout *Salmo trutta* in Minnesota streams. They found that differences in growth between fast and slow-growth streams were due to differences in diet and prey availability, and that temperature mediated these effects.

One important consideration when explaining growth of any fish population is genetic capacity for such growth. Like many other fishes including the Atlantic silverside (*Menidia menidia*), capacity for growth in young of year striped bass is positively related to latitude (Conover et al 1997). By this phenomenon, termed

countergradient growth variation, fish from northern latitudes with shorter growing seasons (northern strain) achieve similar growth as fish of the same species from systems with a longer growing season (southern strain; see Conover et al. 2005 for discussion). Furthermore, northern-strain young of year striped bass growth capacity is not related to temperature, meaning that under identical conditions of food and growing season, northern strain fish achieve greater growth than southern strain fish at low (17 °C) and high (up to 29°C) temperatures (Conover et al 1997). Given this knowledge, agencies may question whether northern strain striped bass would achieve greater growth when stocked in southern reservoirs than would their southern counterparts. I would advise against this stocking scenario. Although the potential exists for northern strain striped bass to have better growth over the first year, there is no guarantee that faster growth will continue at larger sizes. Genetic differences in growth capacity are realized only if food consumption or gross growth efficiency are increased (Present and Conover 1992). Therefore, reduced food availability in some systems (such as Lake Norman) may still limit growth of fish at harvestable sizes, despite a genetic capacity for fast growth realized by young fish. Furthermore, and more importantly, northern strain fish cannot be contained in reservoirs. In North Carolina, reservoirs on the Cape Fear and Roanoke Rivers are close enough to the coast that fish migrating over dams can easily mix with spawning wild fish and reproduce, threatening the genetic integrity of the native stocks.

My results suggest that some basic information on temperature-dissolved oxygen habitat condition and on forage availability might allow striped bass management strategies to be designed based on growth potential of the environment. Gathering

temperature-dissolved oxygen data and estimating striped bass thermal experience from a set of rules is relatively straightforward, but estimation of forage abundance is not as simple. Quantitative sampling of shad populations by hydroacoustics, electrofishing, gillnetting, trawling, cove-rotoning, and seining is labor-intensive and methods vary in precision (see Van Den Avyle et al. 1995 for comparison of these gears). As an alternative to directly sampling pelagic forage communities, limnological characteristics, especially such as Chlorophyll-a (Chl-a) values, morphoedaphic index (MEI) (Oglesby and Jenkins 1982), or trophic state index (Clayton and Maceina 2002), might serve as useful proxies for forage abundance. Density and biomass of gizzard shad and threadfin shad were both related to Chl-a and lake area in lakes in Florida (Allen et al. 2000). I compared lakewide mean summer Chl-a values (Table 1; Figure 6) to annual growth increments and age-specific consumption estimates for each lake. I used only summer (May through August) Chl-a values (May through August) in order to standardize the most recent data collected for each lake by the North Carolina Division of Water Quality since not all lakes were sampled on the same time intervals, but were sampled frequently in these months. Cursory analysis of annual consumption estimates by age of striped bass from this study shows a moderately strong correlation between annual consumption and lakewide mean summer Chl-a values (Table 1; Figure 6). Striped bass annual growth increment (uncontrolled for age or starting weight) is weakly related to the same measure of Chl-a (Figure 7).

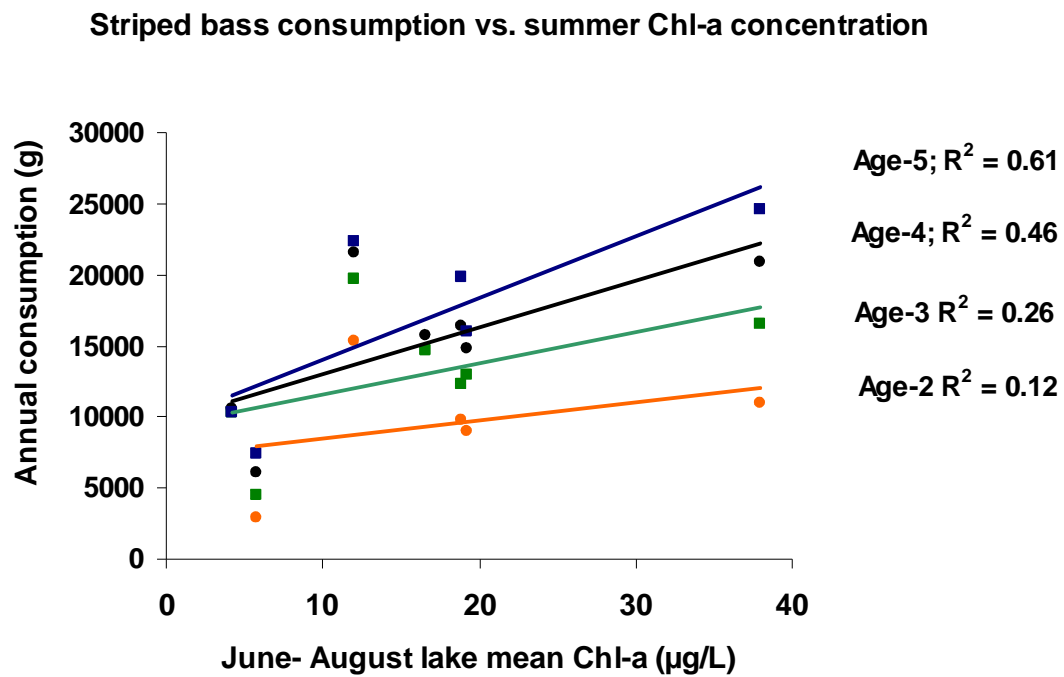


Figure 6. Relationship of striped bass consumption and the lake mean summer chlorophyll-a concentration, by age. Sources for Chl-a are given in Table 1.

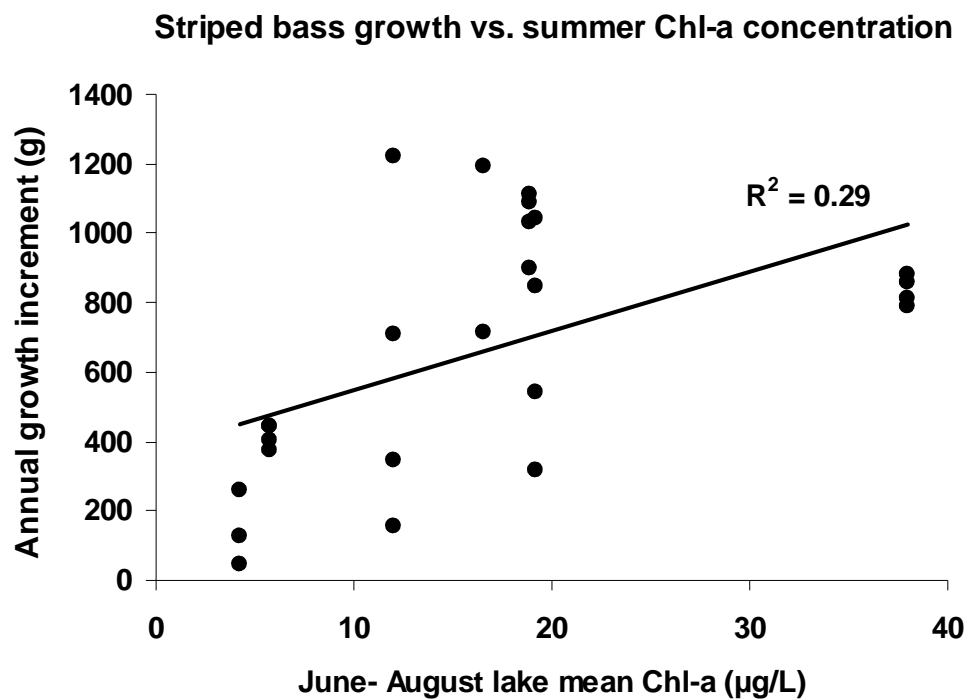


Figure 7. Relationship of striped bass annual growth increment and the lake mean summer chlorophyll-a concentration. Sources for Chl-a are given in Table 1.

The results of this study, along with those of Thompson et al. (2005), strongly identify the need for striped bass management to incorporate information on both forage availability and temperature-dissolved oxygen conditions. Knowledge of availability and abundance of clupeid prey items is especially important for management of striped bass in southern reservoirs, because striped bass can maintain relatively good growth under severe summer temperature-dissolved oxygen conditions only if consumption is adequate to meet the increased metabolic demands of high temperature. This may mean that some systems previously thought to be too warm to support striped bass could be considered if productivity or clupeid biomass is high. Conversely, in reservoirs known to produce poor striped bass growth, managers should investigate food availability, and target management effort on sizes and/or stocking rates of striped bass that can best capitalize on the limited prey resource

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