

Abstract

THOMPSON, JESSICA SUZANNE. The influence of temperature and forage availability on growth and habitat selection of a pelagic piscivore. (Under the direction of Dr. James A. Rice.)

Habitat characteristics influencing growth of fishes often affect habitat selection because behaviors leading to rapid growth are frequently under strong selective pressure. For a pelagic piscivore such as striped bass *Morone saxatilis* stocked into southern reservoirs, temperature and forage fish density are likely to be the most important factors influencing realized growth, and the spatial distribution of these environmental variables would be expected to influence their spatial distribution. The traditional paradigm used to explain striped bass growth and habitat selection has focused exclusively on physical habitat, specifically unsuitable habitat conditions that may develop during summer stratification when hypolimnetic dissolved oxygen levels are too low and epilimnetic temperatures are too warm to provide suitable conditions for adult fish. This study improves our understanding of reservoir striped bass, and pelagic predators in general, by investigating how prey availability modifies the effects of physical conditions on growth and habitat selection of this species.

Using relocations of striped bass tagged with temperature-sensing sonic transmitters in Badin Lake, NC, I demonstrated that striped bass will occupy temperatures above 27°C for up to two months in order to avoid low dissolved oxygen levels. However, Badin Lake striped bass did not occupy the minimum temperature with at least 2 mg/l dissolved oxygen, the minimum tolerance of the species. Rather, tagged fish of all sizes were consistently found at slightly higher temperatures and higher dissolved oxygen levels just above the oxycline, indicating that reservoir striped bass may not tolerate minimum dissolved oxygen levels for an extended period and may have greater thermal plasticity than originally believed.

even in systems with highly unsuitable summer habitat. Using bioenergetics modeling, I showed that growth is possible even at the high temperatures experienced by the Badin Lake population if fish can attain sufficient consumption rates.

The conclusion that the effects of warm temperatures on growth will be mediated by forage availability was supported by the results of bioenergetics model simulations of the Badin Lake striped bass population, which experienced fairly rapid growth, and the population in Lake Norman, NC, which displayed much slower growth despite experiencing warm temperatures for a shorter period over the summer. High consumption rates allowed Badin Lake striped bass of all sizes to allocate some energy to growth even during the summer and to achieve rapid growth during the fall as temperatures cool. Lake Norman striped bass in older age classes did not consume sufficient prey resources to allocate energy to growth over the summer, and consumption rates of striped bass of all ages declined more over the fall than in Badin Lake, preventing these fish from experiencing any season with conditions conducive to rapid growth. Bioenergetics model simulations in which habitat conditions from Badin Lake and Lake Norman were exchanged indicated that differences in forage availability between the systems had a greater relative effect on growth of striped bass than differences in thermal regime. These results suggest that criteria for determining the suitability of reservoirs for striped bass should incorporate a measure of prey availability, and poor growth and condition should be considered an indicator of imbalance between the predatory demand of the striped bass population and prey supply.

As with growth, habitat selection of Badin Lake striped bass was not solely dependent on temperature. Striped bass were found throughout the range of cooler temperatures just above the oxycline that were available during the summer, rather than selecting the minimum

temperatures available. Growth rate potential (the rate of growth expected for a predator occupying a particular location characterized by temperature and forage fish density) provided a better explanation of the spatial distribution of striped bass in both summers and the first fall of this study than did temperature or forage fish density alone. These results are the first empirical comparison between the distribution of a predator and growth rate potential across an entire aquatic system and provide support for the idea that variation in growth rate potential is a useful way to understand how fish integrate information on temperature and forage fish density. However, growth rate potential was not a perfect predictor of the spatial distribution of Badin Lake striped bass so we cannot assume that fish will optimize their patch choice with respect to this variable under all circumstances.

**THE INFLUENCE OF TEMPERATURE AND FORAGE AVAILABILITY
ON GROWTH AND HABITAT SELECTION OF A PELAGIC PISCIVORE**

by

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Dedication

To my parents, who first taught me to see the wonder in the world

To Matt, whose love lights my way

To Gracie and Mari, who are my greatest joy

And to all the other mamas out there, especially graduate students with twins, remember to take a moment for yourself, and on the many days when that is impossible, remember that you are not alone:

The Marathon Monks

In Japan, Tendai Buddhist monks run some twenty to fifty miles a day along the snowy slopes of Mount Hiei. They do this for one hundred consecutive days, rising at one-thirty in the morning to begin their route. They carry with them a sword and a rope to remind them to commit suicide if they fail. I imagine they entertain great doubt in the beginning, waking in the night, thinking: Maybe those corporate suckers in Tokyo had it right all along.

Over a period of seven years, the marathon monks go on ten such hundred-day runs, covering some twenty-two thousand miles in all. At the end of the seven years, they go without food or sleep for nine days. Those who survive the entire ordeal are considered living Buddhas, wise and awake.

Of course, you cannot join the order if you are a mother. You wouldn't have to.

– Ariel Gore, *The Mother Trip*

Biography

I was born and raised in Austin, Texas, the youngest daughter of Robert and Sandra Finley. I spent much of my time as a child outdoors, taking camping trips with my family and trying to stay cool in the summer, and I attribute my desire to be an ecologist to the encouragement of my father, a geologist, and my mother, a biologist. I attended a magnet high school for math and science but chose a broader education for college, traveling halfway across the country to Bard College, a small liberal arts college in Annandale-on-Hudson, New York. I majored in ecology and conducted my senior thesis quantifying the biomass of fishes utilizing Tivoli Bay, a freshwater tidal marsh along the Hudson River. It was during my time along the river that I gained an appreciation for aquatic systems and for fish, in particular.

After college, I returned to Texas and married my high school sweetheart, Matthew Thompson. We then traveled to Raleigh so I could attend North Carolina State University and pursue my interest in fish ecology. I have had the good fortune to spend my time in graduate school with an amazing group of fellow students and faculty members, many of whom have become my close friends, including my advisor, Dr. Jim Rice. My experiences with teaching during my time at NC State have been particularly gratifying, and teaching figures prominently in my future goals. I currently live in Durham, NC, with Matt and our three year old twins, Graciela and Marisol.

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Chapter 1

Introduction

Animals occupying heterogeneous environments frequently make choices based on the abiotic and biotic characteristics of those environments. While individuals of a species may tolerate a fairly wide range of abiotic and biotic conditions, optimal physiological functioning and highest fitness will be realized over a much narrower range. Habitat selection behaviors that allow individuals to occupy the optimal range of conditions are, therefore, expected to be under strong selective pressure. Patch choice can act upon fitness directly by increasing survival, such as may result from avoiding areas of high predation or temporally unpredictable and extreme physical conditions, or by increasing reproductive success, such as may result from choosing the most suitable breeding sites or maximizing energy available for reproduction by reducing the costs associated with unsuitable habitat conditions. Often, however, habitat selection behaviors act upon fitness indirectly by influencing growth rates. Larger, healthier individuals are more likely to escape predation, and in many species, larger body size results in increased fecundity or increased access to reproductive opportunities.

The benefits of rapid growth are particularly evident among fish because they experience substantial ontogenetic shifts in predation risk (e.g., Ellis and Gibson 1995; Dahlgren and Eggleston 2000; Gibson et al. 2002; Meekan et al. 2006), as well increasing fecundity, reproductive success, and progeny survival as a function of increasing body size (Kamler 2005 and references therein). Temperature and food availability are universal

factors affecting growth rates of fish. Resource density will influence the level of food consumption that can be realized in a particular environment, while temperature will determine the rate of growth resulting from that level of consumption. Depending on the system, additional habitat characteristics can also have a large impact on growth. For example, the rate of encounter with prey will be dependent on water velocity for stream-dwelling fish (Hill and Grossman 1993) and the availability of suitable physical structure for ambush predators (Savino and Stein 1989). All of these habitat characteristics can affect habitat selection among fishes (Kramer et al. 1997 and references therein), emphasizing that those factors influencing growth are often particularly important in habitat selection and that patch choice behavior will mediate the relationship between habitat conditions and growth.

This study examines the relative influence of temperature and forage availability on growth and habitat selection of striped bass *Morone saxatilis* stocked into reservoirs in North Carolina. For a large-bodied, pelagic, freshwater piscivore such as striped bass, temperature and prey density are likely to exert a greater impact on realized growth than any other factor, and spatial variability in these environmental variables would, therefore, be expected to affect their spatial distribution. This system offers a particularly good opportunity to improve our understanding of an economically important species while investigating the effect of temperature and forage availability on growth and spatial distribution of fish. Physical conditions in southern reservoirs are often unsuitable for adult striped bass during periods of summer stratification when the hypolimnion becomes hypoxic and temperatures in the epilimnion are well above preferred temperatures (Coutant 1985). Thermal and dissolved oxygen constraints have been linked to the vertical and horizontal distribution of these fish across numerous reservoirs (Cheek et al. 1985; Coutant 1985; Matthews et al. 1985; Farquhar

and Gutreuter 1989; Van Den Avyle and Evans 1990; Zale et al. 1990; Van Horn et al. 1996; Schaffler et al. 2002; Young and Isely 2002), and the occupation of unsuitably warm temperatures have been implicated in patterns of poor growth and condition (Coutant 1985). Within the limitations imposed by low dissolved oxygen, we may, therefore, expect that temperature has the largest effect on growth and habitat selection of reservoir populations of striped bass. However, little is known about how forage availability modifies these interactions. The hypothesis that warm temperatures lead to poor growth and condition (Coutant 1985) implies that striped bass cannot meet the metabolic demands imposed by those temperatures, but this limitation will clearly be dependent on the energy consumption achieved by these fish. In North Carolina, relatively high quality growth and condition are observed in some productive reservoirs with highly unsuitable summer habitat (Van Horn 1996), suggesting that forage availability can have an important impact on growth. In situations where thermal constraints increase metabolic costs, the ability to track high prey densities and increase consumption rates will be even more critical than in less extreme environments, suggesting that the differential distribution of prey resources will have an important impact on habitat selection of reservoir striped bass.

In Chapter 2, I revisit the traditional paradigm (Coutant 1985) of the influence of unsuitable temperatures and dissolved oxygen conditions on reservoir striped bass. Based on telemetry data, I describe the thermal selection patterns of striped bass in Badin Lake, NC, one of the most unsuitable reservoirs for which such detailed information has been collected. I compare the findings for Badin Lake with those of previous studies on thermal selection of reservoir striped bass and propose general thermal selection rules that should apply across

systems. Such a synthesis had previously been lacking, despite the number of studies conducted on striped bass.

Chapter 3 addresses the question of the relative influence of temperature and forage availability on growth of reservoir striped bass. Using the thermal selection rules developed in Chapter 2, I estimate the thermal experience of striped bass in Badin Lake, NC, which has fairly good striped bass growth, and Lake Norman, NC, which has poor striped bass growth. I then use bioenergetics model simulations to estimate the prey consumption that would result in the observed growth patterns in each system based on experienced temperatures. Using additional bioenergetics model simulations, I exchange the consumption and temperature patterns between the two reservoirs and use the model to estimate growth. The resulting changes in growth due to each habitat exchange indicate the relative effect of temperature and forage availability (as indicated by realized consumption rates) on growth of striped bass in each system.

In Chapter 4, I return to the telemetry data for Badin Lake striped bass to investigate the relationship between striped bass distribution and three environmental characteristics: (i) temperature, based on the application of the thermal selection rules developed in Chapter 2 to temperature and dissolved oxygen profiles interpolated across the reservoir; (ii) forage fish density, based on geostatistical interpolation of hydroacoustic data; and (iii) the integration of temperature and forage fish density as expressed by growth rate potential, the growth rate that would be expected for a striped bass occupying a particular location in the reservoir. The calculation of growth rate potential involves a foraging model using forage fish density to estimate consumption and a bioenergetics model using estimated consumption and temperature to estimate growth. This chapter is the first field test of growth rate potential as

a useful predictor of the spatial distribution of fish, and it is the first time the distribution of reservoir striped bass has been described relative to patterns in both temperature and forage fish density.

Finally, Chapter 5 summarizes the improved understanding of the ecology of reservoir populations of striped bass that has been generated by this study. I also highlight the utility of these methods for future studies of fish populations and how the use of striped bass as a model for investigating the factors influencing growth and spatial distribution of fishes has improved our general understanding of these processes.

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Chapter 2

Thermal selection of striped bass in a southeastern reservoir with unsuitable summer habitat: implications for habitat selection, condition, and mortality

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Manuscript in review at *Transactions of the American Fisheries Society*

Abstract

The cool, oxygenated water preferred by adult striped bass *Morone saxatilis* is unavailable during the summer in many southern reservoirs, causing fish to become squeezed between hypoxic hypolimnetic water and warm epilimnetic water. This temperature-oxygen squeeze has been blamed for poor condition and summer mortality, but the link between these problems and unsuitable summer habitat is not universal across systems. We tracked 64 adult striped bass (425 to 804 mm total length; 0.9 to 6.8 kg wet weight) implanted with sonic transmitters (31 of which were temperature-sensing) over two years in Badin Lake, North Carolina, a reservoir with relatively good striped bass growth and condition despite highly unsuitable summer habitat. Fish showed a strong selection for water temperatures of 20°C in the early summer of the first year when stratification occurred most rapidly, leading most fish to occupy an oxygenated hypolimnetic pocket in the downstream region of the reservoir. Once this pocket disappeared, fish occupied temperatures found just above the oxycline (27 to 31°C), a pattern also observed during the second summer of the study when

thermal conditions were more moderate (occupied temperatures 25 to 28°C). Tagged striped bass were primarily found in the east arm of the reservoir during the mid-summer in both years; the deeper oxycline in this region allowed them to occupy temperatures 1 to 2°C cooler than those above the oxycline in other regions of the reservoir. Bioenergetics-based estimates of potential growth at different temperatures and rations show that growth is still possible at the high temperatures experienced by the Badin Lake population if prey is sufficiently abundant, suggesting that the abundance of forage fish will influence the relationship between habitat conditions and growth and condition of striped bass in similar systems. We also suggest a mechanism for summer mortality related to the occupation of oxygenated hypolimnetic pockets in the early summer that we observed in this study.

Introduction

Habitat use by striped bass *Morone saxatilis* stocked into inland reservoirs has been a topic of great interest to fisheries scientists and managers for over two decades. As interest in recreational fisheries for reservoir striped bass grew (Axon and Whitehurst 1985), so did questions over the precise nature of suitable habitat for adult striped bass in reservoirs, particularly southern reservoirs where the cool, oxygenated habitat preferred by the species was often not available through the summer. These questions were lent additional urgency as patterns of summer mortality and poor growth of adult striped bass were observed in some systems (Matthews 1985). Coutant (1985) hypothesized that these problems were the result of the simultaneous habitat preferences of adult fish for water temperatures 18 to 25°C and dissolved oxygen levels greater than 2 to 3 mg/l. During summer stratification, fish may become squeezed between epilimnetic water with temperatures too warm and hypolimnetic

water with dissolved oxygen levels too low to provide suitable habitat for adult fish. In severe cases, suitable habitat for adult striped bass may be entirely lacking during some portion of the summer.

Studies demonstrating that reservoir populations of striped bass utilize a cool thermal refuge during the summer in order to avoid excessively warm temperatures have supported the thermal preferences identified by Coutant (1985). Thermal refuges may include creek channels and springs (Coutant 1985; Van Den Avyle and Evans 1990), tributaries and tailrace habitats (Cheek et al. 1985; Wilkerson and Fisher 1997; Young and Isely 2002), and deep, downstream regions (Schaffler et al. 2002). These studies have shown that fish generally select water with dissolved oxygen greater than 4 mg/l and temperatures of 19 to 21°C, while avoiding temperatures above 24 to 25°C. These occupied temperatures may actually be higher than those selected by striped bass given a broader range of available temperatures with high dissolved oxygen. Striped bass in Melton Hill Reservoir, TN, which contains oxygenated habitat with a wide range of temperatures, selected a mean summer temperature of 17.5°C with occupied temperatures ranging from 9°C to 24°C (Bettoli 2005). The fundamental thermal niche of reservoir striped bass may, therefore, be even lower than suspected based on studies in systems with thermal refuges.

While striped bass clearly prefer cooler temperatures, many reservoirs stocked with striped bass do not contain an appropriate thermal refuge for adult striped bass during the summer months, and in these systems, telemetry studies have shown that fish typically choose the coolest oxygenated water available. Tagged fish in Lake Whitney, Texas, moved downstream to deep regions near the dam as the reservoir warmed (Farquhar and Gutreuter 1989). Fish generally avoided dissolved oxygen levels lower than 4 mg/l and occupied

temperatures ranging from 24°C in June to 29°C in early September (Farquhar and Gutreuter 1989). Striped bass in Keystone Reservoir, Oklahoma, were found between 26.0 and 29.5°C and from 2.1 to 6.1 mg/l dissolved oxygen in the summer months (Zale et al. 1990). Striped bass occupying downlake areas of Lake Gaston, Virginia-North Carolina, were exposed to temperatures of 27 to 28°C for periods up to one month (Jackson and Hightower 2001).

Studies in systems without a summer thermal refuge show that striped bass are often forced into unsuitable thermal habitat in order to remain in water with dissolved oxygen levels of at least 2 mg/l. However, the hypothesized link between the temperature-dissolved oxygen squeeze and problems with poor fish condition and summer mortality (Coutant 1985) is less clear. Zale et al. (1990) suggested that striped bass cease feeding at temperatures above 27°C and can tolerate temperatures of 27 to 28°C for about a month but die, possibly of malnutrition, if exposed to these temperatures for more than a month or higher temperatures for the same length of time. However, laboratory experiments suggest that adult striped bass can continue to feed up to 30°C (Hartman and Brandt 1995), and striped bass in Lake Whitney, Texas, occupied temperatures of 29°C for at least a month with no observed mortality (Farquhar and Gutreuter 1989). In North Carolina, a habitat suitability index based on the severity of the temperature-dissolved oxygen squeeze is also not a good predictor of striped bass condition. For example, Badin Lake has one of the worst habitat suitability indices in the state (Van Horn 1996), but striped bass are in fairly good condition with relative weights (Anderson and Neumann 1996) in the range of 80 to 100 (Appendix A). Badin Lake represents one of the most unsuitable systems for striped bass that has been studied, with no portion of the water column containing dissolved oxygen levels above 2 mg/l and temperature cooler than 27°C for six to eight weeks in most summers. Minimum

temperatures with 2 mg/l dissolved oxygen can reach 28 to 30°C for three to four weeks (Thompson et al. 2005).

Analysis of striped bass thermal selection in such an extreme environment may shed further light on the behavior of striped bass when habitat conditions are limiting, as well as further elucidating the relationship between habitat conditions and striped bass condition and mortality. Our objectives were, first, to determine the seasonal pattern of thermal selection by striped bass in Badin Lake relative to the temperature and dissolved oxygen values available in the water column at locations occupied by individual fish. Our study spanned two years with widely differing summer habitat conditions, giving us the opportunity to compare thermal selection by fish in the same population under different habitat constraints. We also assessed whether the size of the fish affected its thermal selection pattern. Second, we describe the seasonal spatial distribution of tagged striped bass and relate those distribution patterns to differing thermal conditions across the reservoir. Third, we explore how the severity of thermal conditions may affect striped bass condition by looking at the relationship between food consumption and potential growth of striped bass across a range of summer temperatures. Fourth, while no summer mortality events were observed during the course of our study, we suggest a mechanism by which thermal selection behavior may lead to mortality of striped bass.

Methods

Study site

Badin Lake (also known as Narrows Reservoir) is a 2,165-hectare, moderately eutrophic reservoir located on the Yadkin River, a major tributary of the Pee Dee River, in

the piedmont region of North Carolina (Figure 2.1). Badin Lake was impounded in 1917 for the purpose of hydroelectric power generation and is one of a series of impoundments on the Yadkin River. The reservoir has a mean depth of 21 m and a maximum depth of 54 m and contains areas of littoral habitat, as well as steep-sided regions. The pelagic forage base is composed primarily of threadfin shad *Dorosoma petenense*, with some contribution from gizzard shad *D. cepedianum* and blueback herring *Alosa aestivalis* (Appendix B). An active recreational striped bass fishery exists on the reservoir with a minimum size limit of 406 mm (16 inches) and a daily creel limit of eight fish. The striped bass population does not contain many larger (>650 mm) or older (>age-4) individuals (Appendix A) due primarily to high fishing mortality rates experienced by the population (Thompson et al. In press).

Fish collection and tagging

Information on habitat use by striped bass in Badin Lake was provided by two internal tag types: sonic transmitters and archival data tags. All fish were tagged with one of two sizes of sonic transmitters: Sonotronics IT-95-2, 7 g weight in water; and Sonotronics CTT-83-3, 8 g weight in water. Both transmitters provided information on spatial location, and the larger tag provided additional information on the water temperatures occupied by fish at the time of each relocation. Occupied water temperature was indicated by varying ping interval with an accuracy of $\pm 0.5^{\circ}\text{C}$. This accuracy is greater than the $\pm 2^{\circ}\text{C}$ accuracy reported for this tag model and was obtained by calibrating the tags in the lab prior to use in the field. Calibration involved recording the pulse interval at two known temperatures (room temperature and near freezing) and using a linear relationship between these two recorded intervals to determine the temperature resulting in any given interval heard in the field

(Sonotronics 2004). The model IT-95-2 tag was programmed with a one-week on, one-week off transmitting schedule to extend the battery life to two years, while the model CTT-83-3 tag transmitted continuously with a battery life of three years. A portion of fish were also tagged with an archival data tag (Star-Oddi DST milli, 5 g weight in water) that recorded water temperature ($\pm 0.1^{\circ}\text{C}$) and depth (± 0.1 m) occupied by the tagged fish every hour. This information could only be obtained through recovery of the archival tag.

Collection of fish for tagging began in December 2001. Early fish were captured by angling, but the majority of fish were collected by electrofishing in the tailrace of Tuckertown Dam, at the upstream end of Badin Lake (Figure 2.1), beginning in March 2002. Electrofishing continued through May 2002 and resumed from February 2003 through April 2003 to provide additional fish for the second year of the study. Two fish were also collected by angling in 2003. Captured fish were anesthetized and tagged internally following the methods of Haeseker et al. (1996). All fish were also tagged externally with a Floy internal anchor tag (FM-95W) containing contact information to promote awareness and reporting of fish captured by anglers. After fish recovered from surgery, they were released into the Tuckertown Dam tailrace, where the majority of fish were captured.

Only fish alive (based on the occurrence of movement between relocations) and found in the reservoir for at least a month after tagging were included in the study. Tagged fish were relocated biweekly from March 2002 through January 2004, except during a period of extremely low water in late summer 2002 which necessitated a monthly time period between relocations. On each search date, the entire reservoir was searched by listening for fish at points well within the 1-km range of the transmitters, accounting for bottom topography and noise interference that might block the tag signal. The position of each

tagged fish (as indicated by constant ping volume in each direction) was recorded using a Global Positioning System (GPS) receiver, and for fish tagged with temperature-sensing transmitters, ping interval was also recorded. Because each sonic tag transmitted a unique code, the relocation histories of individual fish could be determined. For each biweekly relocation date, tracking continued until the entire reservoir was searched or until all fish were relocated; this process took two days on some occasions.

Evaluation of temperature and dissolved oxygen selection

Temperatures selected by striped bass were compared to conditions across the reservoir based on temperature and dissolved oxygen profiles taken at sixteen fixed sites across the lake (Figure 2.1). At each site, temperature and dissolved oxygen were measured at one-meter intervals from the surface to the bottom of the water column or a maximum depth of 30 m (due to the limited range of our temperature and dissolved oxygen meter). The only site deeper than 30 m was the site located just above Badin Dam (Figure 2.1).

Observed temperatures of temperature-sensing sonic-tagged fish were used to determine the dissolved oxygen level occupied by each fish based on information from these temperature and dissolved oxygen profiles. For each relocation and corresponding profiling date, the profile site closest to the location of each fish was determined. The depth at which the temperature occupied by the fish occurred was then found and the dissolved oxygen level at that depth was assigned to the fish. The precise depth of the fish could not be determined on dates when the reservoir was not vertically stratified, but dissolved oxygen levels were also uniform throughout the water column at these times so a dissolved oxygen level could still be assigned. The process of assigning a dissolved oxygen level based on the nearest

profile site has the potential to introduce some error due to small-scale spatial variability in the vertical structure of thermal and oxygen conditions, particularly if a fish was relocated at some distance from such a site. However, taking a profile at each site where a tagged fish was relocated would have been prohibitively time-consuming, and because we did not observe high variability between nearby profiles on any date, we feel this method was appropriate. Unfortunately, profiles were not available for two relocation dates in June 2002 due to equipment failure, requiring us to interpolate between temperatures observed at each depth on other dates in order to assign a depth and corresponding dissolved oxygen level to each fish. This process likely introduced more error than was inherent in the estimates for other dates. Temperatures and dissolved oxygen levels occupied by tagged fish were compared to the minimum and maximum values recorded across all profiling sites in the reservoir on each date when such data were available.

The tagging of a subsample of sonic-tagged fish with archival data tags provided additional information on temperatures and depths occupied by striped bass in Badin Lake. On dates when temperature and dissolved oxygen profiles were available and we relocated archival-tagged fish that were subsequently recovered, dissolved oxygen levels could be assigned to these fish in a manner similar to that described above for temperature-sensing sonic-tagged fish, except that their depth could be retrieved directly from the tag and did not have to be estimated based on temperature. The dissolved oxygen level recorded at the fish's depth at the nearest profile site to the fish's location was assigned to the fish.

Temperatures and dissolved oxygen levels selected by Badin Lake striped bass during the summer were frequently found just above the oxycline. We defined the depth just above the oxycline as the depth above the first drop of at least 1 mg/l in one meter of water moving

down from the water surface that resulted in a dissolved oxygen level below 6 mg/l. This last stipulation was necessary because, at certain times during the summer, dissolved oxygen levels dropped from 8 to 10 mg/l at the surface to 6 to 8 mg/l at a depth of a few meters before leveling out and then dropping again. In the few cases when we did not observe a drop of 1 mg/l in one meter of the water column, the depth above the largest dissolved oxygen drop in one meter was used.

Evaluation of the influence of fish size on thermal selection

We assessed the influence of two indices of fish size on observed thermal selection: weight of the fish at tagging and estimated weight on the date of relocation. The estimated weight of each fish for dates when it was relocated was obtained by first estimating length at relocation using a von Bertalanffy growth, based on length at tagging and number of days from tagging to relocation. This growth curve was based on aging of sagittal otoliths taken from 347 Badin Lake striped bass (Appendix A), as well as a subsample of fish randomly selected from each year class for back-calculation using the Fraser-Lee direct proportion method (Carlander 1982). Back-calculation was performed on 27 fish for a total of 79 estimates of length at annulus production (Appendix A). Model fitting was conducted assuming a multiplicative error structure (Quinn and Deriso 1999), giving von Bertalanffy growth curve parameters of $L_{inf} = 797.55$, $k = 0.32$, and $t_0 = -0.25$ (Appendix A). Weight at relocation was then estimated using a significant ($\alpha = 0.05$) multiple regression model fit to seasonal length and weight data for Badin Lake striped bass:

$$\log W = -4.69 + 2.94 \log L - (1.28 \times 10^{-3})D + (3.18 \times 10^{-6})D^2$$

where W = weight at relocation (g), L = estimated length at relocation (mm), and D = day of the year when relocation occurred (Appendix A). The effect of weight at tagging and estimated weight at relocation on occupied temperature was assessed independently for the period from May through September for each year using an analysis of variance model accounting for the non-linear effect of relocation date on occupied temperature. Because our small sample size on any given date may limit the power of this statistical analysis, the data were also examined visually to identify potential trends in occupied temperatures related to fish size. We particularly looked for differences in temperature selection between the smallest tagged fish (less than 2.5 kg), medium-sized tagged fish (2.5 to 5 kg), and the largest tagged fish (over 5 kg), based on size thresholds identified by Coutant (1985).

Evaluation of the influence of temperature and consumption level on potential growth

We evaluated the influence of temperature and consumption on potential growth of a 5-kg Badin Lake striped bass using bioenergetics model simulations. Simulations were conducted using the Wisconsin bioenergetics model format (Kitchell et al. 1977) packaged in the software program Fish Bioenergetics 3.0 (Hanson et al. 1997). The basis of the model is a simple mass balance equation in which growth is set equal to consumption minus metabolic costs and wastes. Each process is described by an additional equation or set of equations using physiological parameters for adult striped bass from Hartman and Brandt (1995). The daily consumption rate is modeled as the product of the allometric maximum consumption rate, a temperature-dependence function, and a proportionality constant, or P -value, which represents the proportion of maximum consumption attained due to ecological constraints such as forage availability and competition. Separate simulations were conducted using P -

values ranging from 0 to 1 in increments of 0.1; these values can be thought of as encompassing a range of ecological situations between the extremes of complete food limitation and unlimited food availability. Temperature affects both consumption and metabolic processes in the model, and simulations were conducted using temperatures ranging from 16°C to 30°C. The potential daily growth of a 5-kg striped bass was estimated at each combination of *P*-value and temperature.

In addition to the *P*-value and occupied temperature, use of the bioenergetics model to estimate potential growth requires information on predator energy density and the total energy density of the diet (based on the proportion of each prey item in the diet and the energy density of each of these respective prey items). These data are needed as model inputs in order to equate the weight gain of the predator with the weight of food consumed; one gram of predator does not necessarily equal one gram of prey in energetic terms, so the ratio of predator energy density to prey energy density is used to make this conversion. We used energy density and diet data collected from Badin Lake striped bass from 2000 through 2002 (Appendix A), and we specifically chose values reflecting average conditions on August 15 across those three years. Striped bass energy density was 7,200 J/g wet weight. Diet was 5% 45 to 55-mm threadfin shad, 16% 55 to 65-mm threadfin shad, 20% 65 to 75-mm threadfin shad, 12% 75 to 85-mm threadfin shad, 2% 85 to 95-mm threadfin shad, 25% threadfin shad larger than 95-mm, 8% gizzard shad larger than 95-mm, 5% blueback herring larger than 95-mm, and 7% non-clupeid fish prey. Size-specific energy density of clupeid prey was measured for Badin Lake prey species (Appendix B) and, again, we chose values reflecting those observed on August 15. Energy density (in J/g wet weight) of threadfin shad was 3,410 for fish 45 to 55-mm, 3,700 for fish 55 to 65-mm, 4,000 for fish 65 to 75-mm,

4,250 for fish 75 to 85-mm, 4,530 for fish 85 to 95-mm, and 6,300 for fish larger than 95-mm. Energy density of gizzard shad larger than 95-mm was 3,900, and energy density of blueback herring larger than 95-mm was 7,600. Because non-clupeid fish prey were primarily bluegill *Lepomis macrochirus*, we used the energy density reported for bluegill in Hanson et al. (1997; 4,186 J/g wet weight) for this prey category.

Results

Sixty-four striped bass tagged and found alive in Badin Lake one month post-surgery were included in the study (Thompson et al. 2005). Thirty-five fish were released between December 2001 and May 2002. The 14 females and 21 males ranged from 473 mm to 804 mm total length (mean 535 mm) and from 1,228 g to 6,408 g wet weight (mean 2,256 g). Sixteen small sonic transmitters and 19 larger, temperature-sensing transmitters were implanted. Twenty of these fish were also implanted with archival data tags; two of these tags were returned by anglers and contained a time series of occupied temperatures and depths during the summer, with one tagged fish at large from May 1 to July 11, 2002, and the other from May 1 to September 13, 2002. An additional 29 fish entered the study between March and May 2003. These 16 females and 13 males ranged from 425 mm to 786 mm total length (mean 627 mm) and from 936 g to 6,810 g wet weight (mean 3,374 g). Seventeen of these newly tagged fish were implanted with small sonic tags and 12 with temperature-sensing tags. Ten fish were also given archival data tags, but all of the tags returned by anglers in this year were from fish harvested within a few weeks of tagging. Sixteen fish survived from 2002 to 2003, bringing the starting sample size in the spring of 2003 to 45 fish (Thompson et al. 2005).

Seasonal thermal selection

In spring 2002, temperature-sensing sonic tagged striped bass generally chose the warmest water available in Badin Lake, ranging from 8°C to 12°C in January through March to 15°C at the beginning of April and nearly 20°C by the end of the month (Figure 2.2). Dissolved oxygen levels were high, typically above 8 mg/l, throughout the water column during this time (Figure 2.2).

The majority of tagged striped bass remained at 20 to 21°C through May and June 2002 (Figure 2.2). This thermal selection pattern required fish to move into deeper water and increasingly low dissolved oxygen levels as summer stratification developed (Figure 2.2). This selection pattern was made even more evident by the temperature and depth data available from the two archival tags recovered from striped bass at large in Badin Lake during the spring and early summer of 2002. Both fish remained at about 20.5°C through late-June (mean daily temperatures from June 18 through June 26, 2002, ranged from 20.2 to 20.8°C) as the depth of the fish increased (Figure 2.3). By June 26, 2002, both fish were occupying a mean depth of about 13.5 m. These results indicate that the fish were occupying a narrow pocket in the hypolimnion with 2 to 2.5 mg/l dissolved oxygen that was observed in the downstream portion of the reservoir close to Badin Dam. As this pocket disappeared, the fish were forced into shallow epilimnetic waters with much warmer temperatures; both archival-tagged fish moved into shallower water (about 6 m) with temperatures above 25°C on June 27, 2002 (Figure 2.3). Fish tagged with temperature-sensing sonic tags displayed the same pattern in the temperatures and dissolved oxygen levels occupied (Figures 2.2, 2.3).

Through July and August 2002, tagged fish remained at very warm temperatures between 27°C and 30°C, with a maximum observed temperature of 30.9°C (Figure 2.2). Fish

occurred at temperatures most closely matching those found just above the oxycline (Figure 2.4), resulting in fairly high dissolved oxygen levels between 4 mg/l and 8 mg/l (Figure 2.2). Occupied temperatures then began to decline through September and October as the reservoir cooled (Figure 2.2a), but fish remained at dissolved oxygen levels above 4 mg/l (Figure 2.2b). Striped bass could have occupied water up to 2°C cooler, and therefore closer to the 20°C preferred in the beginning of the summer, by moving into water with only 2 mg/l dissolved oxygen during this period.

Water temperatures had cooled throughout the water column by mid-November and tagged fish occupied ambient temperatures from about 10°C in mid-November 2002 to a low of about 5°C in late January 2003 (Figure 2.2). Striped bass were found across the range of temperatures on each winter date, ranging from slightly cooler temperatures in the Tuckertown Dam tailrace to slightly warmer temperatures in the remainder of the reservoir. Striped bass typically selected the highest temperatures available as the reservoir began to warm in March. An exception to this pattern occurred in early April when almost all fish were located in the Tuckertown Dam tailrace, where ambient temperatures were cooler (Figure 2.2). Dissolved oxygen levels were above 8 mg/l throughout the reservoir during this period (Figure 2.2). By May 2003, tagged fish occupied water averaging 20°C, matching the temperatures selected by fish in 2002 in this season (Figure 2.2). However, fish moved more gradually into warmer water between 22°C and 23°C through June 2003, in contrast to the abrupt movement into very warm water seen at the end of June 2002. This difference may be due, in part, to the schedule by which the lake stratified in the two years. In 2002, the lake warmed and became stratified rapidly. Temperatures in the epilimnion quickly went above 25°C, and in most regions of the reservoir, all cooler water became hypoxic. Fish were able

to avoid these warm temperatures for a brief period by congregating above Badin Dam in a pocket of cooler, oxygenated water in the hypolimnion. In 2003, the reservoir warmed more gradually and the thermocline was much deeper for a longer period of time, with well-oxygenated epilimnetic water remaining between 20°C and 23°C. This gradual warming may have diminished the thermal cues that would have led fish to search out cooler hypolimnetic water in the deeper regions of the reservoir.

Through July and August 2003, striped bass in Badin Lake were most frequently found just above the oxycline (Figure 2.4), occupying temperatures between 25°C and 28°C and dissolved oxygen levels generally greater than 4 mg/l (Figure 2.2). This pattern compared favorably with observations from the summer of 2002, although thermal conditions were not as severe in 2003 in terms of duration or magnitude of the warmest temperatures occupied. Also, as in 2002, fish did not move deeper into the very coolest water with at least 2 mg/l dissolved oxygen as the reservoir cooled in the early fall, but rather remained closer to the surface in well-oxygenated habitat. Tagged fish generally chose the warmest water available once temperatures dropped below 20°C, reaching a low temperature of 10°C by December 2003 (Figure 2.2).

Influence of fish size on thermal selection

Neither weight at tagging nor estimated weight at relocation had a significant effect on the temperatures occupied by individual striped bass in the summer of 2002 (weight at tagging: ANOVA p-value = 0.98; estimated weight at relocation: ANOVA p-value = 0.67) or 2003 (weight at tagging: ANOVA p-value = 0.62; estimated weight at relocation: ANOVA p-value = 0.88). In 2002, only one tagged fish had an estimated weight above 5 kg. This fish

selected temperatures within the range occupied by all tagged fish and was not found at the lowest observed temperatures. On all dates in July through September when a temperature was obtained for this largest fish, it occupied the temperature just above the oxycline at its individual location. Four fish with estimated weights greater than 2.5 kg were at large in the summer of 2002, and these fish were also consistently located just above the oxycline during these warmest months. In 2003, two tagged fish had estimated weights greater than 5 kg and 13 fish had estimated weights between 2.5 and 5 kg. As in 2002, these fish occupied temperatures above the oxycline at their respective locations and did not display a thermal selection pattern that differed from smaller, tagged fish.

Seasonal spatial distribution

The proportion of tagged striped bass located in different regions of Badin Lake varied seasonally. In both years, fish generally occupied habitat in the west arm of Badin Lake during the winter and spring and habitat in the south and east arms during the summer (Figure 2.1). In April 2002, the majority of fish were located in the Tuckertown Dam tailrace at the upstream end of the west arm of the reservoir. Striped bass are drawn to areas of high flow during the spring due to the urge to move upstream in a spawning migration, and numerous studies have demonstrated that reservoir populations frequently congregate in tributaries and tailrace areas during this time (e.g., Wilkerson and Fisher 1997; Jackson and Hightower 2001; Schaffler et al. 2002; Young and Isely 2002). In May, fish moved progressively further downstream, and by late June, almost all tagged striped bass were congregated in deep water in the south arm of the reservoir, just upstream of Badin Dam

(Figure 2.1). This pattern resulted from the occupation of a small hypolimnetic pocket of cool, oxygenated water found in this region at this time.

As this hypolimnetic pocket disappeared, most fish moved into the east arm of the reservoir, where they remained throughout July 2002. Sites in the east arm typically had an oxycline two to three meters deeper than sites in the west and south arms during July, allowing fish in this region to occupy oxygenated water with temperatures 1 to 2°C cooler than elsewhere in the system. It is possible that the fish were responding to this variation in thermal and dissolved oxygen conditions across the reservoir. Through August and into early September, some tagged fish continued to occupy habitat in the east arm while others began to move into the west arm. This shift began in early August when the depth of the oxycline had become homogeneous at sites throughout the reservoir. Fish utilized primarily west arm habitat from October 2002 through the spring of 2003.

Most striped bass were located in the Tuckertown Dam tailrace in April and May 2003, but by late June, fish had moved into the middle reaches of the west arm and throughout the east arm. Fish did not congregate in deeper regions of the lake in June 2003, in contrast to June 2002. The majority of tagged fish were located in the east arm in July and early-August 2003. This pattern was similar to that observed in 2002, although approximately 20% of tagged fish were still found scattered throughout the west arm during sampling dates in July 2003 while all fish left this region in July 2002. Dissolved oxygen conditions were fairly uniform between the three arms of the reservoir in 2003, so the use of west arm habitat by some fish may reflect the diminished thermal and dissolved oxygen constraints in this year. Occupation of the west arm increased through August and September 2003. Throughout the fall and into the winter, occupation of the west and east

arms of the reservoir remained fairly similar, in contrast to 2002 when the vast majority of tagged striped bass were found in the west arm at this time.

Almost all tagged fish moved widely throughout the reservoir according to these general spatial distribution patterns. Those that remained in particular areas for longer periods of time than were typically observed still had temperature and dissolved oxygen experiences similar to the remainder of tagged fish. We did not observe any fish occupying habitats that would provide a refuge from the thermal experience described for the general tagged population. All fish had habitat usage patterns that varied with season, rather than remaining in a single region of the reservoir throughout the study, indicating that striped bass in Badin Lake do not have annual individual home ranges. Seasonal home ranges were apparent for a few fish tagged in 2002 that were consistently relocated in the same small area (< 5 ha) during the summers of 2002 and 2003, but these fish represented the minority of the Badin Lake striped bass population.

Influence of temperature and consumption level on potential growth

Bioenergetics analysis of a 5-kg striped bass illustrates the interacting effect of temperature and consumption level on growth. Consumption levels do not begin to decline until 28°C and high consumption continues even up to 30°C (Figure 2.5), suggesting that a cessation of feeding at high temperatures is not dictated by physiological constraints. However, even though consumption continues, fish must attain a high proportion of maximum consumption to achieve positive growth at high temperatures. At 30°C, slightly below the maximum observed temperature occupied by Badin Lake striped bass during this study, positive growth is only possible if fish are eating at a rate essentially equal to their

physiological maximum ($P > 0.99$; Figure 2.5), a situation rarely realized in a field environment. At 28°C, positive growth still requires fish to attain a high proportion of maximum consumption ($P > 0.74$; Figure 2.5), but as temperature drops below 26°C, fish may achieve positive daily growth at more ecologically realistic consumption rates ($P \leq 0.62$; Figure 2.5). Even at 20°C, the apparent preferred temperature of Badin Lake striped bass, a 5-kg fish must consume more than 69 g daily ($P > 0.39$) to achieve positive growth rates (Figure 2.5).

The daily growth rate achieved for any given proportion of maximum consumption attained declines substantially with increasing temperature (Figure 2.5). This decline represents a “cost” in terms of lost potential growth that is associated with occupying high temperatures even at relatively high consumption rates. For example, a 5-kg striped bass that consumes 123 g of prey per day will be eating at a rate equivalent to 70% of maximum consumption whether the fish is at 20°C or 26°C (Figure 2.5). However, at 20°C, this consumption rate would allow the fish to gain almost 30 g per day while at 26°C daily growth is limited to about 6 g (Figure 2.5).

The proportion of maximum consumption required for maintenance ration at any given temperature was similar for fish between 2.5 and 7.5 kg. The percent increase in consumption needed to meet metabolic demands as temperature increased was also similar across fish sizes. However, as expected, the absolute consumption rates needed at any given temperature increased with increasing fish size. At maintenance ration, a 5-kg striped bass would have to consume 42% more than a 2.5-kg fish at any particular temperature while a 7.5-kg fish would have to consume 69% more (Figure 2.5).

Discussion

Our results demonstrate that striped bass display the thermal preferences and dissolved oxygen requirements identified by Coutant (1985) even under the most unsuitable summer conditions. Tagged striped bass in Badin Lake, NC, showed a strong selection for 20°C in early summer 2002, leading to occupation of a small, oxygenated hypolimnetic pocket near Badin Dam at a time when rapid stratification and warming led to unsuitable habitat in the remainder of the reservoir. This hypolimnetic pocket contained relatively low dissolved oxygen levels of 2 to 2.5 mg/l, and as dissolved oxygen levels declined below 2 mg/l, fish abruptly moved into shallow epilimnetic water with substantially warmer temperatures above 25 to 26°C. This movement pattern was particularly evident in the detailed depth and temperature information captured by the two archival tags retrieved from fish at large during this time. Therefore, while fish clearly preferred cooler water, they also showed an avoidance of dissolved oxygen levels less than 2 mg/l and chose to occupy oxygenated water at the expense of occupying their preferred temperature.

In contrast to 2002, Badin Lake striped bass moved into water temperatures above 20°C much more gradually through June 2003. Fish still avoided temperatures above 25°C, but they did not move into downstream regions to remain at 20°C. This interannual difference in early summer behavior suggests that the decision to seek out cool water, with its high density of conspecifics and potential segregation from prey, may be triggered as the remaining oxygenated water in the system reaches a critical temperature. Review of published habitat studies on reservoir populations reveals several examples in which striped bass move into thermal refuge habitats with “ideal” temperatures less than 20°C as other oxygenated water in the system reaches 20 to 22°C. Coutant and colleagues (Coutant 1978;

Schaich and Coutant 1980; Waddle et al. 1980) observed tagged fish in Cherokee Reservoir, TN, moving to springs and creek channels with temperatures of 15 to 22°C when the hypolimnion became hypoxic and epilimnetic temperatures were above 22°C. Similarly, striped bass in Watts Bar Reservoir, TN, moved into tributaries when water temperatures in these habitats were 18 to 20°C and other oxygenated water in the system was 20 to 24°C (Cheek et al. 1985). Tagged striped bass in Lake Murray, SC, were concentrated in deep, downstream regions of the reservoir in temperatures of 16 to 18°C when water in the remainder of the reservoir with at least 2.5 mg/l dissolved oxygen was above 22°C (Schaffler et al. 2002).

In other cases, movement of striped bass into thermal refuges was observed as the remaining oxygenated water in the system reached slightly warmer temperatures of 23 to 25°C. Fish in the Flint River-Lake Seminole system, GA, moved into spring-fed areas with temperatures of 19 to 20°C when ambient temperatures in the system were 23 to 25°C (Van Den Avyle and Evans 1990). Movement of tagged striped bass into upstream areas influenced by hypolimnetic discharge with temperatures of 17 to 21.6°C was also observed in J. Strom Thurmond Reservoir, SC-GA, when ambient temperatures reached 23 to 25°C (Young and Isely 2002). The results of these studies correspond well with our observations in June 2002, when fish congregated in the oxygenated hypolimnetic pocket near Badin Dam as the remaining oxygenated water in the reservoir reached 23 to 25°C. In June 2003, tagged fish were occupying water primarily at temperatures of 22 to 23°C, suggesting that these temperatures had not reached the critical point at which fish would begin to search out spatially localized thermal refuges.

The difference in early summer thermal selection between the two years may also have been influenced by the spatial dynamics of prey resources. Sampling of the prey fish community in Badin Lake in summer 2002 indicated that about 18% of forage fish were blueback herring while blueback herring were absent in 2003 samples; the remainder of prey fish were predominantly threadfin shad in both summers (Appendix B). Blueback herring are cool-water fish that may occupy relatively cool, deep water during periods of stratification in southeastern reservoirs (Nestler et al. 2002), suggesting that blueback herring may have occupied the same hypolimnetic oxygen pocket favored by striped bass in 2002. Threadfin shad, on the other hand, are more frequently found in warmer, surface waters during the summer period (Schael et al. 1995). Selection of the coolest oxygenated water available in the early summer of 2003 would, therefore, likely have segregated striped bass from the shallower threadfin shad without providing an alternate, deeper prey in the form of blueback herring. While striped bass have been observed avoiding moving into warmer water to feed on abundant prey (Coutant 1985), the difference in temperature between the surface waters likely occupied by threadfin shad and the preferred temperature of the striped bass may not have been sufficient to drive such a behavioral response over this period.

Once fish were forced into shallower, warmer waters in late June 2002, almost all tagged striped bass moved into the east arm of Badin Lake, probably reflecting differences in the depth of the oxycline between regions of the reservoir. The deeper oxycline in the east arm allowed fish to access water 1 to 2°C cooler than temperatures just above the oxycline in the west or south arms. Therefore, while permanent, localized thermal refuges with preferred temperatures for striped bass are not available in Badin Lake, differences in physical habitat conditions still appeared to influence the spatial distribution of striped bass in the warmest

months of the year. This effect persisted even though the difference between temperatures in habitats occupied by striped bass and those in the remainder of the system was much smaller than in systems where striped bass utilize areas traditionally thought of as thermal refuges. Our results are similar to those of Braschler et al. (1988), who found that striped bass in Lakes Marion and Moultrie, SC, moved into springs, sink holes, and creek beds when temperatures were above 28°C, even though temperatures in those habitats were only 0.3°C cooler than nearby bottom temperatures and 1.0°C cooler than average water column temperatures in the remainder of these unstratified reservoirs. Striped bass in Lake Whitney, TX, occupied downstream habitat during the summer even though the temperatures occupied in this region were only, at most, about 2°C cooler than oxygenated habitat upstream (Farquhar and Gutreuter 1989). Temperature also affected the spatial distribution of striped bass in Lake Norman, NC, with the majority of fish found at locations with oxygenated water less than 26°C (Van Horn et al. 1996). In contrast, Jackson and Hightower (2001) did not find an effect of temperature conditions on the spatial distribution of striped bass in Lake Gaston, VA-NC, even though suitable habitat was only available in uplake regions of the reservoir through the summer months.

Interestingly, occupation of the east arm was also high in July 2003, despite the greater similarity in dissolved oxygen profiles across the reservoir in this year. Temperature and dissolved oxygen profiles from 2000 and 2001 (Thompson et al. 2005) indicate that conditions in 2002, with a deeper oxycline in the east arm, are more characteristic. The use of primarily east arm habitat even in 2003 when physical conditions were similar across the reservoir may, therefore, reflect consistent seasonal habitat usage patterns and suggest that individual fish rely on information on typical conditions accumulated over multiple years.

While the behavior of Badin Lake striped bass in the early summer, particularly in 2002, and the preference for east arm habitat supports a thermal selection pattern in which fish minimize temperature as much as possible while still maintaining adequate dissolved oxygen levels, striped bass did not simply remain at the minimum temperature with at least 2 mg/l dissolved oxygen throughout the remainder of the summer. Instead, temperatures occupied during mid-summer to early fall reflect those just above the oxycline, at dissolved oxygen levels of 4 to 8 mg/l, and these temperatures were typically 0.5 to 2°C warmer than those with only 2 mg/l dissolved oxygen. Therefore, while small differences in temperature appear to affect spatial distribution of striped bass across the surface of the reservoir, leading to occupation of the east arm in July, similar temperature differences did not have the same effect on vertical distribution in the water column. Prey dynamics and dissolved oxygen requirements both have the potential to affect vertical distribution of striped bass during these warmest months of the year. The ability to consume threadfin shad that likely occupy warmer temperatures may outweigh the energetic benefit of micromanaging depth to minimize temperature as much as possible. For example, our estimates of the P -value at maintenance ration for a 5-kg striped bass suggests that a fish at 26°C must attain a P -value of 0.62 while a fish at 28°C must attain a slightly higher P -value of 0.74. While reported P -values greater than 0.65 to 0.70 are uncommon, it is certainly possible that striped bass foraging in a productive system such as Badin Lake may attain such a high value if not spatially segregated from their prey. Largemouth bass *Micropterus salmoides* attained P -values up to 0.75 during seasons with high prey availability (Rice et al. 1983), and saugeye *Sander vitreus* x *Sander canadense* age-1 and older were found to have P -values up to 0.63

during periods of abundant food (Denlinger et al. 2006). Older whitefish *Coregonus lavaretus* were also found to have *P*-values of 0.61 to 0.70 (Tolonen 1999).

Dissolved oxygen requirements may also affect the vertical distribution of striped bass beyond the simple avoidance of dissolved oxygen levels less than 2 mg/l. Other studies of striped bass habitat selection in systems without thermal refuges have reported striped bass occupying dissolved oxygen levels greater than 4 mg/l during stratification (Matthews et al. 1985; Farquhar and Gutreuter 1989), suggesting that striped bass may occupy dissolved oxygen levels of 2 to 3 mg/l only for limited periods of time. Oxygen consumption of striped bass increases with temperature up to 30°C (Hartman and Brandt 1995), and it is possible that at warm temperatures when metabolic activities are high, striped bass may have higher minimum dissolved oxygen requirements. Unfortunately, we are not aware of any data on the duration of low dissolved oxygen tolerance or the relationship between temperature and minimum dissolved oxygen requirements for striped bass. Data on physiological stress indicators show that striped bass experience greater stress responses and slower recovery time at temperatures of 30°C compared with lower temperatures (Davis and Parker 1990), suggesting that the ability of striped bass to deal with stressors such as low dissolved oxygen may be impaired at high temperatures. Detailed information that addresses these dissolved oxygen considerations would be useful in evaluating the suitability of potential habitat for striped bass in systems either under consideration for stocking or where temperature and dissolved oxygen conditions are changing due to anthropogenic influences.

The difference between the temperature above the oxycline and that at 2 mg/l may be larger in other systems with oxygen levels that decline more gradually with depth, leaving open the possibility that striped bass would choose to occupy cooler temperatures at the

expense of higher dissolved oxygen levels in such systems. However, our data suggest that the selection of dissolved oxygen levels above the oxycline may be fairly robust to these differences because the temperatures above the oxycline were actually a better fit to occupied temperatures of tagged fish in 2003, when the oxycline was more gradual and the temperature difference somewhat greater. Matthew et al. (1985) also found the most fish in Lake Texoma, OK-TX, at depths just above the oxycline on five of six dates in July and August. The specific relationship between the vertical distribution of striped bass and the depth of the oxycline is difficult to determine for other studies because authors frequently only reference specific dissolved oxygen levels (such as 2.5 mg/l or 4 mg/l) rather than providing complete profiles. We suggest that future researchers specifically address the vertical distribution of striped bass in relation to the oxycline to determine whether fish most consistently choose temperatures above the oxycline, those at 2 mg/l, or temperatures between these two points. Further delineation of these patterns across systems may allow us to determine how the interaction between selection of temperature and dissolved oxygen levels changes in relation to available temperatures above the oxycline, the temperature difference between the depth at 2 mg/l dissolved oxygen and that above the oxycline, and, potentially, spatial dynamics of prey resources.

In both years of our study, tagged striped bass in Badin Lake remained at temperatures above the oxycline even into the fall, when fish could have moved into 20°C water by occupying lower dissolved oxygen levels of 2 to 3 mg/l as they did in the early summer. This pattern could be influenced by foraging behavior and/or the physiological need to occupy higher dissolved oxygen levels at higher temperatures or after a period of stress related to occupation of warm temperatures. Acclimation to high temperatures may

also affect striped bass thermal selection as the reservoir cools. For many fish species, exposure to high temperatures results in a shift toward warmer preferred temperatures (Kelsch and Neill 1990). A distinction between thermal selection in the beginning of the summer and that observed in the late summer and early fall was also seen in Lake Murray, SC (Schaffler et al. 2002). In July and August, most tagged striped bass were found between 2.5 and 5 mg/l dissolved oxygen at temperatures less than 20°C, but by September, most fish were found at or above 5 mg/l dissolved oxygen at temperatures above 20°C (Schaffler et al. 2002). Van Horn et al. (1996) also found that striped bass in Lake Norman, NC, occupied cooler temperatures (20 to 21.7°C) and lower dissolved oxygen levels (2.3 to 2.5 mg/l) in July but moved into warmer temperatures (25.1 to 26.1°C) and higher dissolved oxygen levels (3.1 to 4.7 mg/l) in August and early-September. These results do not allow us to differentiate between the effects of temperature acclimation and changing dissolved oxygen requirements through time, but they do suggest that other reservoir striped bass populations may also display thermal selection patterns that differ between the early and late summer periods.

Despite the fact that Badin Lake striped bass are squeezed between hypoxic bottom waters and warm surface waters for at least two months over the summer and frequently have no suitable habitat available to them, these fish continue to feed and grow (Appendix A). Our results contrast with those of Zale et al. (1990), who found that striped bass in Keystone Reservoir, OK, ceased feeding at temperatures above 27°C; we are unsure what factors may have caused this difference in feeding behavior, but laboratory experiments certainly support the conclusion that striped bass are physiologically capable of feeding at high temperatures up to 30°C (Hartman and Brandt 1995). While positive growth becomes essentially

impossible for adult striped bass at temperatures of 30°C or greater, our bioenergetics analysis demonstrates that potential growth at lower temperatures is a function of both temperature and the proportion of maximum consumption attainable based on the availability of prey resources. The ability of reservoir striped bass to attain a high proportion of maximum consumption will be dependent on the productivity of the system and resulting forage fish production, as well as the spatial relationship between prey and predator. Perhaps counterintuitively, warm, productive reservoirs without thermal refuges may actually provide better systems for maintaining quality growth and condition of striped bass than systems where the drive to maintain cool temperatures separates striped bass from their prey. In Badin Lake, low dissolved oxygen levels force striped bass into warm surface waters but these depths are also those with the most abundant forage fish, primarily threadfin shad. These fish are, therefore, rarely faced with a choice between cool temperatures and attaining prey resources, a situation in which striped bass may choose cool water (Coutant 1985).

Just as the desire for cool water may lead to segregation from prey and result in poor condition, the same desire may introduce a mechanism for summer mortality of reservoir striped bass. In systems where occupied temperatures are high and prey resources are not sufficient or striped bass are segregated from their prey, mortality may be due to lack of sufficient feeding (Zale et al. 1990). However, the strong selection for cool water that led striped bass to occupy the oxygenated hypolimnetic pocket just upstream of Badin Dam in late June 2002 may also lead to mortality events if fish delay movement from these pockets as dissolved oxygen declines or are unable to successfully navigate the return to oxygenated surface water through the layer of hypoxic water separating them from the epilimnion. While we did not observe mortality in 2002, three summer mortality events involving 175 to

750 fish have occurred on Badin Lake in the past ten years, and all three of these events occurred in late June to mid-July (Lawrence Dorsey, NC Wildlife Resources Commission, unpublished data). We do not have corresponding temperature and dissolved oxygen profiles from these years, but the timing of these mortality events corresponds with the timing of the disappearance of hypolimnetic pockets for the years in which we do have physical habitat data (Thompson et al. 2005). Additionally, these fish kills have been concentrated in the lower end of the reservoir where we have found oxygenated hypolimnetic pockets to be located. This suggests that these events may have been associated with the use of hypolimnetic pockets rather than the occupation of warm temperatures for an extended period, such as might be seen in August or September. While many reported reservoir mortality events occur in the late summer, mortality has also been seen in April, May, and June in some reservoirs (Matthews 1985), suggesting that mortality associated with occupying oxygenated habitat that then becomes depleted could also occur in other systems. Depending on the system, mortality events may, therefore, occur as a result of behavioral habitat selection decisions associated with the preference of striped bass for cooler, oxygenated water, in addition to those that result from fish being forced to occupy warm temperature or being segregated from prey resources. Mortality due to occupation of high temperatures is certainly not a given, as mortality is not consistently observed in many systems, such as Badin Lake, with highly unsuitable summer habitat (Braschler et al. 1988; Farquhar and Gutreuter 1989; Jackson and Hightower 2001).

The results of this study have helped solidify our understanding of striped bass in southeastern reservoirs where suitable habitat may be limited during the summer months. In conjunction with other published habitat studies, we feel some generalizations are possible.

First, striped bass will move into thermal refuge habitats with fairly ideal temperatures (≤ 20 to 22°C) as the remaining oxygenated habitat reaches 22°C to 25°C . These refuges may include temporally ephemeral habitats such as a hypolimnetic dissolved oxygen pocket. Second, in systems without thermal refuges offering preferred temperatures that persist throughout the summer, striped bass will usually occupy the best habitat even if only small temperature differences of 1 to 2°C separate available habitats. These choices will affect the two-dimensional spatial distribution of striped bass across each system. Third, while our results support the idea that striped bass will avoid dissolved oxygen levels below 2 mg/l, it does not appear that striped bass simply remain at the minimum temperature with 2 mg/l dissolved oxygen. Depth distribution may be affected by increased dissolved oxygen requirements during periods of thermal stress or by foraging behavior, and the occupation of higher dissolved oxygen levels occurs even when this choice requires fish to tolerate temperatures above 28°C . Fourth, the relationship between warm temperatures and poor condition will not be universal across systems because growth and condition will also be influenced by the consumption rates attainable in a given reservoir. Striped bass may choose cool temperatures over the ability to eat, but striped bass are physiologically able to eat at warm temperatures if their spatial distribution overlaps with prey. In this way, being forced into shallow water by low dissolved oxygen may actually be energetically advantageous for striped bass in a productive system if it reduces spatial segregation from prey. Finally, summer mortality events may occur by multiple mechanisms, including occupation of high temperatures with insufficient consumption to meet metabolic demands and becoming trapped in habitats such as hypolimnetic dissolved oxygen pockets that then become depleted. Predicting mortality across systems and even across years within a given system

will, therefore, likely require information on the abundance and spatial distribution of prey and the development and depletion of ephemeral oxygenated habitats, in addition to knowledge of the length and severity of the temperature-oxygen squeeze.

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Figures

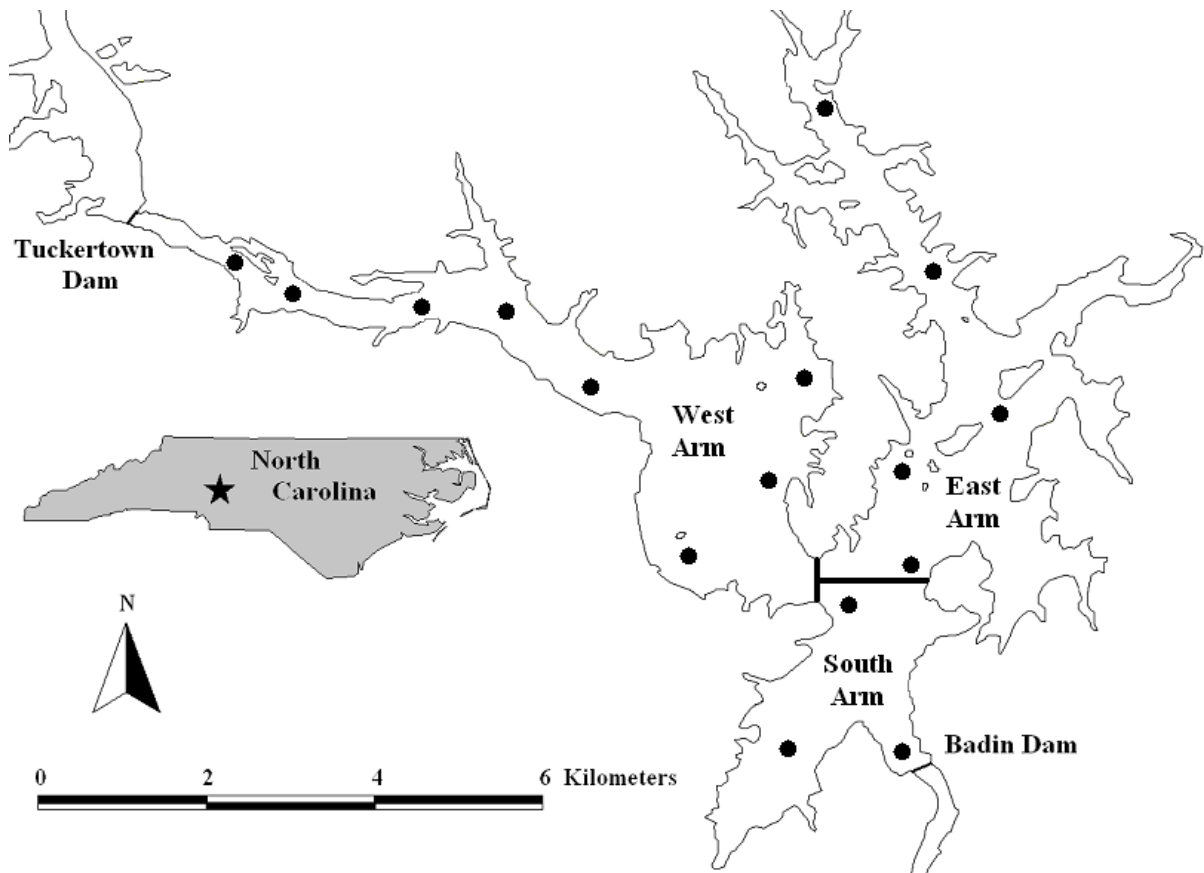


Figure 2.1. Map of Badin Lake, NC, showing sixteen temperature-dissolved oxygen profile sites (solid circles) and the regions of the reservoir (South, East, and West Arms; delineated by solid black lines) referred to in the text.

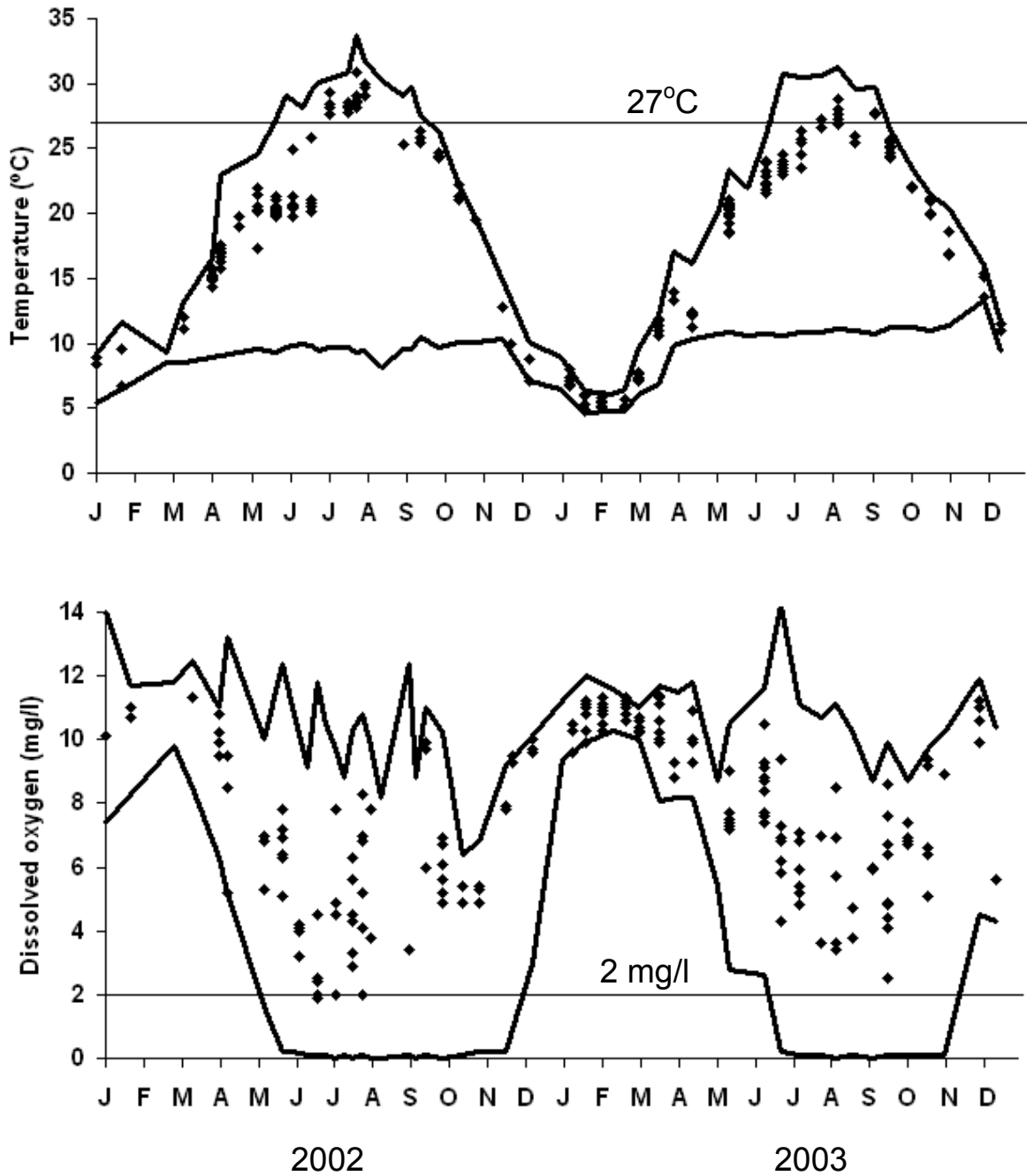


Figure 2.2. Temperatures (top panel) and dissolved oxygen levels (bottom panel) occupied by striped bass tagged with sonic transmitters in Badin Lake, NC, in 2002 and 2003. Points represent conditions chosen by individual fish while the solid lines indicate the minimum and maximum values sampled in the reservoir.

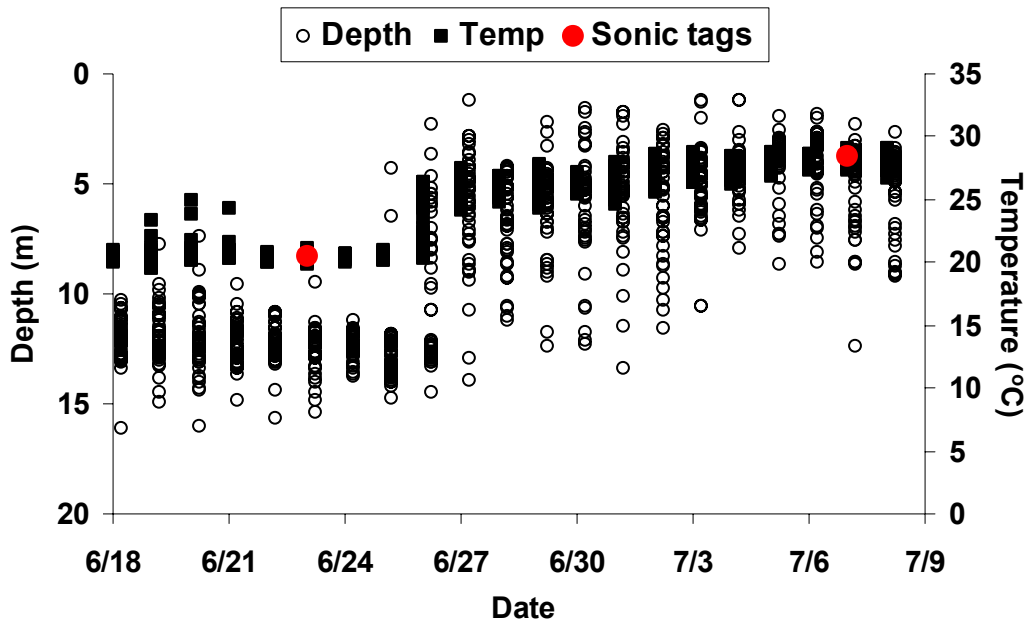


Figure 2.3. Temperatures (solid squares) and depths (open circles) occupied by two striped bass tagged with archival tags in Badin Lake, NC, in summer 2002. Data were recorded every hour; all data collected on a single date are shown at the same point in time to aid in visualization of the general trend. Depth symbols are offset slightly from temperature symbols for the same date. Red circles indicate the mean temperature occupied by striped bass with temperature-sensing sonic tags located on June 23 (N = 5 fish) and July 7 (N = 4 fish).

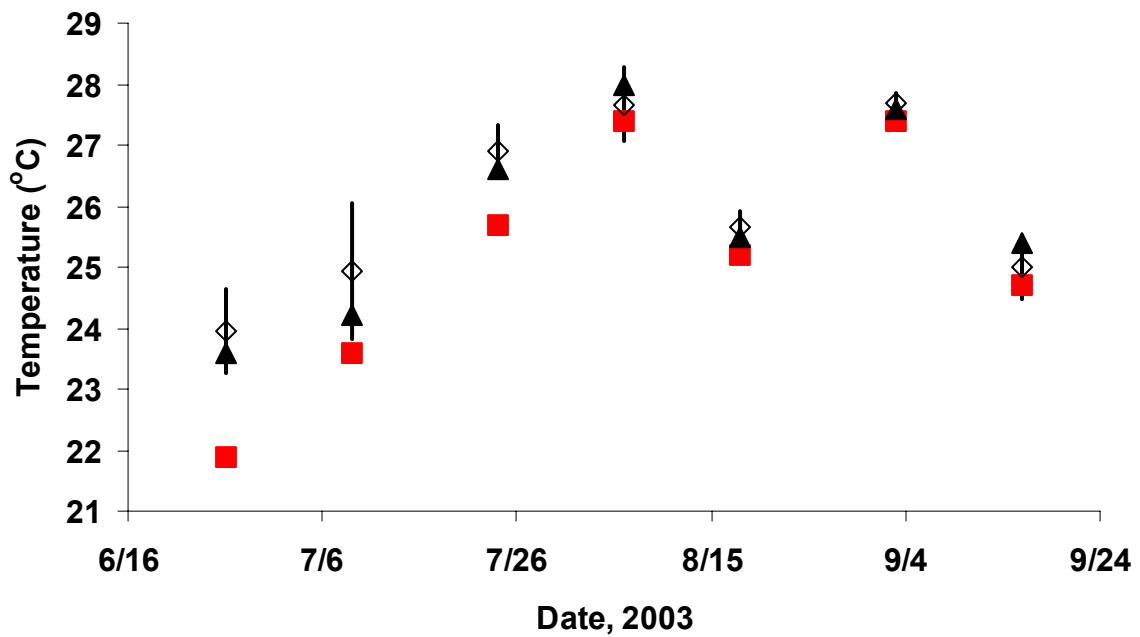
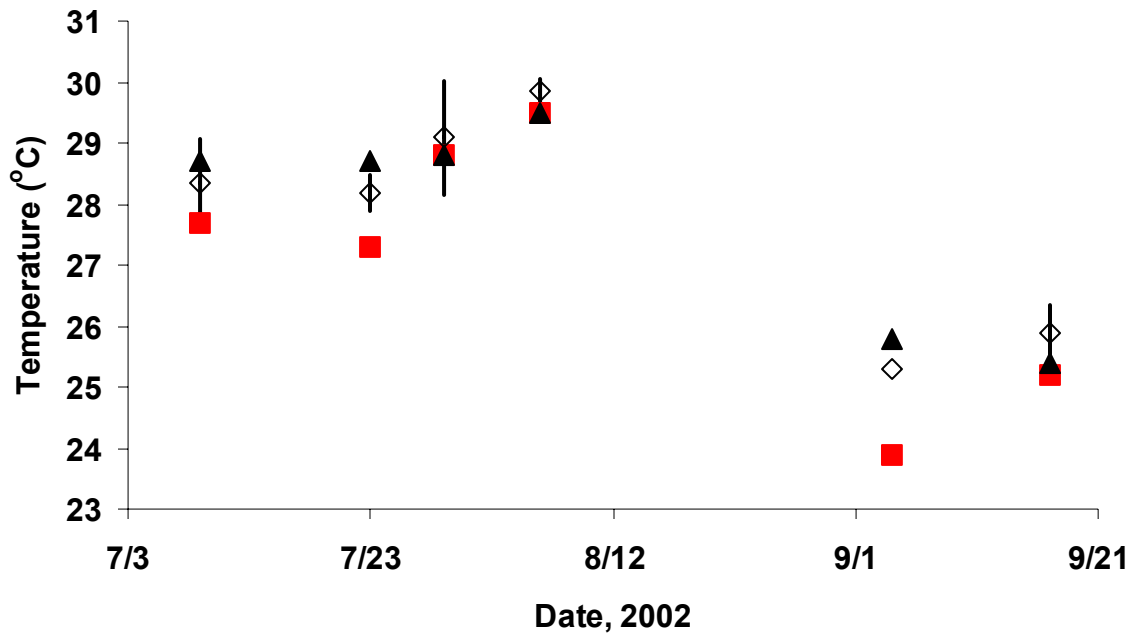


Figure 2.4. The mean temperature occupied by tagged striped bass (open diamonds; error bars are plus and minus one standard deviation) located on each sampling date compared to temperatures at 2 mg/l dissolved oxygen (solid red squares) and just above the oxycline (solid black triangles) in the mid-summer to early fall of 2002 (top) and 2003 (bottom). Temperature and dissolved oxygen profiles are from the deepest site in the east arm of Badin Lake, NC, in the middle of the region most fish were occupying during these time periods.

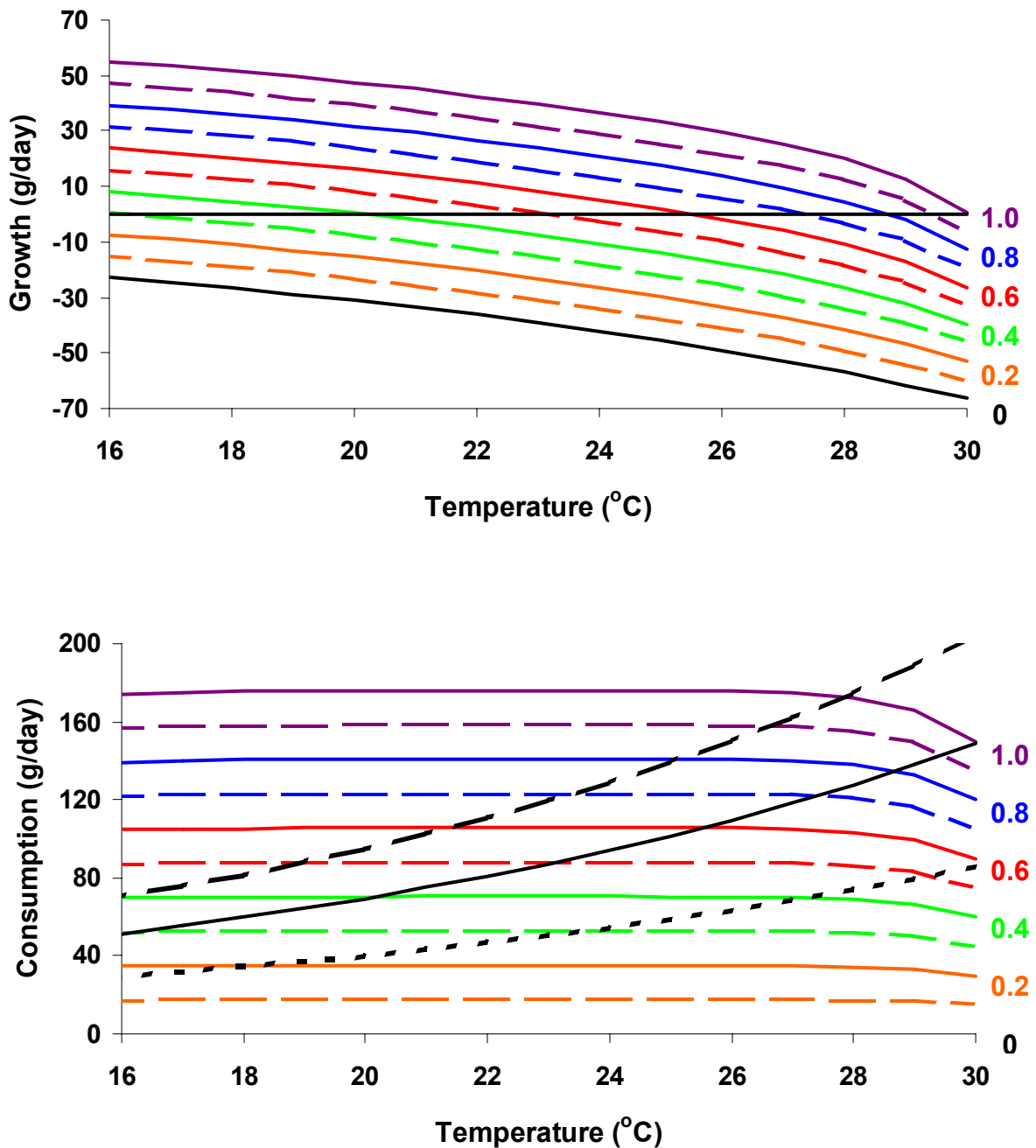


Figure 2.5. Potential growth (g/day; top) and consumption (g/day; bottom) of a 5-kg Badin Lake striped bass across temperatures at P -values ranging from 0 to 1.0 in increments of 0.1. The P -value for each solid line is color-coded and given on the right. Maintenance ration for a 2.5-kg fish (black dotted line), 5-kg fish (black solid line), and 7.5-kg fish (black dashed line) is provided on the graph of consumption.

Chapter 3

The relative influence of temperature and forage availability on growth of striped bass in southeastern reservoirs

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Abstract

The occurrence of warm epilimnetic temperatures and hypolimnetic hypoxia during summer stratification has been linked to poor growth and condition of striped bass *Morone saxatilis* populations in southern reservoirs. However, quality growth has been observed in some productive systems with highly unsuitable physical habitat, suggesting that high forage availability may help mediate the energetic costs associated with warm summer temperatures. We assessed the relative influence of temperature and forage availability on growth of striped bass in Badin Lake and Lake Norman, NC, using bioenergetics model simulations. Badin Lake is highly productive with poor summer conditions but relatively rapid striped bass growth, while Lake Norman is much less productive with suitable habitat for striped bass for a longer period in the summer but poor striped bass growth and condition. Bioenergetics modeling showed that Badin Lake striped bass of all ages achieved high consumption rates close to their physiological maximum rate during the summer, and high consumption continued into the fall when striped bass growth was most rapid. Lake Norman

striped bass experienced lower consumption rates over the summer and fall. Consumption was not sufficient to allow larger striped bass to allocate any energy to growth over the summer, and these fish did not experience any season with the cool temperatures and high consumption rates needed for rapid growth. Habitat exchange simulations, in which the temperature regime or estimated consumption from one reservoir was applied to the other to measure the resulting change in growth, showed that the relative effect of forage availability on striped bass growth was about three times that of temperature in the first year of the study and about 37 times that of temperature in the second year of the study. Our findings suggest that management of reservoir striped bass populations will be improved by considering the important influence of forage availability on striped bass growth and condition.

Introduction

Striped bass *Morone saxatilis* have been stocked into numerous reservoirs across the country, often with the intention of establishing recreational fisheries while controlling overabundant shad *Dorosoma* spp. populations (Axon and Whitehurst 1985). These objectives have been achieved, at least in part, in many cases, but growth and condition of striped bass in some systems have not met the expectations of managers and anglers. The traditional explanation of poor growth and condition of reservoir striped bass has focused on the role of unfavorable environmental conditions that develop during summer stratification events (Coutant 1985). Summer stratification in southern reservoirs can result in epilimnetic water above the maximum temperature preference of adult striped bass and hypolimnetic water below the minimum dissolved oxygen requirement for the species. This temperature-dissolved oxygen squeeze may restrict fish to a small portion of the water column or limit

them to suboptimal temperatures and possibly separate them spatially from their prey (Coutant 1985). In extreme cases, no portion of the water column may have suitable habitat for striped bass (this study, Chapter 2).

However, a simple and consistent relationship between poor summer habitat and poor striped bass growth and condition is not always evident. In North Carolina, several reservoirs with the worst summer habitat for striped bass have faster-growing fish in better condition than those with more moderate conditions (Van Horn 1996). These systems tend to be highly productive, suggesting that high availability of prey fish may offset some of the additional costs associated with the warm temperatures striped bass experience during the summer months. The incongruity between these observations and our previous knowledge of striped bass environmental requirements suggests that a better understanding of the relative importance of temperature and forage availability in dictating growth of reservoir striped bass is needed.

The relationship between temperature, forage availability, and striped bass growth has important implications for optimal management of these populations. Environmental conditions place bounds on potential growth of individual fish, and these limitations should inform decisions regarding which reservoirs to stock and the quality or type of fishery that can reasonably be supported by these stocking operations. However, management decisions regarding stocking and harvesting rates will also have direct impact on realized growth of striped bass by adjusting the relationship between demand for and availability of prey resources. The greater the role of forage availability in limiting predator growth, the more informed these decisions must be in order for the fishery to meet management goals. Striped

bass populations that experience extreme thermal conditions may be particularly reliant on having sufficient forage to meet their metabolic demands.

It is difficult to distinguish the relative role of temperature and forage availability in determining fish growth based solely on observed growth patterns because growth represents the physiological synthesis of an individual's entire environmental history. Fortunately, bioenergetics modeling provides a framework for separating and analyzing the influence of biotic and abiotic conditions on fish growth in a way not possible from observed patterns alone (Kitchell et al. 1977; Rice et al. 1983; Railsback and Rose 1999; Petersen and Paukert 2005; Johnson et al. 2006). Bioenergetics models utilize a balanced energy budget in which consumed energy is set equal to growth plus metabolic and waste costs (Kitchell et al. 1977). With knowledge of the parameters necessary to model these physiological processes, bioenergetics models can be used to estimate consumption based on observed growth and experienced temperatures (recent examples: Michaelson et al. 2001; Baldwin et al. 2003; Irwin et al. 2003; Liao et al. 2004; Sammons and Maceina 2006). The striped bass bioenergetics model (Hartman and Brandt 1995a) has been used to estimate consumption by coastal striped bass (Hartman and Brandt 1995b; Hartman 2003), as well as reservoir populations (Cyterski et al. 2002; Raborn et al. 2002).

We estimated consumption by striped bass in two North Carolina reservoirs, Badin Lake and Lake Norman, as a function of observed growth and experienced temperatures using bioenergetics modeling. These reservoirs differ in thermal conditions, forage regimes, and the quality of striped bass growth and condition. Badin Lake is a productive system with abundant forage but poor summer conditions with a shallow oxycline, hypoxic hypolimnion, and warm epilimnion. This reservoir is an example of the unexpected relationship between

striped bass growth and environmental conditions that we observe in some North Carolina systems; despite highly unsuitable summer habitat, Badin Lake striped bass display fairly rapid growth with relative weights (Anderson and Neumann 1996) in the range of 80 to 100 (Appendix A). Lake Norman is a relatively unproductive reservoir with more limited forage fish biomass but a more moderate summer stratification event. Sufficiently cool, oxygenated habitat is available for a longer period of time in the early summer, and dissolved oxygen levels decrease more gradually with depth after stratification develops. Despite better environmental conditions, the striped bass population in Lake Norman represents a more typical “problem” population with slow growth and poor condition (relative weights in the range of 70 to 85) that declines with increasing fish length (Appendix A).

Using consumption as a proxy for forage availability, we then conducted additional bioenergetics model simulations in which habitat components (either temperature regime or estimated consumption) were exchanged between these two systems. Comparing the growth patterns estimated in these habitat exchange simulations with our original observed growth patterns from each reservoir allowed us to quantify the relative importance of temperature and forage availability on observed growth. This approach builds on previous applications of bioenergetics modeling that have used these models as a tool to test hypotheses regarding the effects of variation in temperature and food availability on fish growth (Kitchell et al. 1977; Rice et al. 1983; Railsback and Rose 1999; Munch and Conover 2002) by directly comparing simulation results between systems. We discuss the implications of our results for understanding striped bass growth and improving management of stocked populations, as well as providing specific examples of potential management actions for Badin Lake and Lake Norman.

Methods

Study sites

Badin Lake, NC, is a 2,165-hectare, moderately eutrophic reservoir located on the Yadkin River, a major tributary of the Pee Dee River (Figure 3.1). Badin Lake was impounded in 1917 and is one of a series of reservoirs on the Yadkin River. The reservoir has a mean depth of 21 m and a maximum depth of 54 m and contains areas of littoral habitat, as well as steep-sided regions. The pelagic forage base is composed primarily of threadfin shad *D. petenense*, with some contribution from blueback herring *Alosa aestivalis* and gizzard shad *D. cepedianum*. During summer stratification, epilimnetic temperatures commonly reach 28 to 30°C and dissolved oxygen drops below 2 mg/l within 5 m of the surface. While striped bass growth is fairly rapid in this system and condition tends to be relatively high for all sizes of fish (Appendix A), the population does not contain many larger (>650 mm) or older (>age-4) fish (Appendix A), primarily due to high fishing mortality rates (Thompson et al. In press). Striped bass fishery regulations are fairly liberal on Badin Lake, with a minimum size limit of 406 mm (16 inches) and a daily creel limit of eight fish.

Lake Norman, NC, is a 12,634-hectare, relatively unproductive reservoir along the Catawba River, part of the Wateree River drainage (Figure 3.2), and was impounded in 1963. The reservoir has a mean depth of 10 m and a maximum depth of 34 m and is highly dendritic. The pelagic forage base includes threadfin shad and alewife *A. pseudoharengus*, with a small contribution from gizzard shad. During summer stratification, epilimnetic temperatures can reach 27 to 30°C, but hypoxia does not develop throughout the hypolimnion until mid-summer and the oxycline tends to be at a depth of 7 to 10 meters. Striped bass growth slows substantially after age 3 and essentially ceases by age 4 in Lake Norman

(Appendix A). Condition is poor for most striped bass in this system, and condition declines significantly with increasing fish size (Appendix A). At the time of this study, striped bass fishery regulations were fairly restrictive on Lake Norman, with a minimum size limit of 508 mm (20 inches) and a daily creel limit of four fish.

Bioenergetics model format

The Wisconsin bioenergetics model (Kitchell et al. 1977), as packaged in the software program Fish Bioenergetics 3.0 (Hanson et al. 1997), was used in our analysis of the striped bass populations in Badin Lake and Lake Norman, NC. Model simulations estimate the consumption needed to achieve an observed pattern of weight gain or, alternatively, the weight gain that would be expected based on a certain level of consumption. A simple mass balance equation is the basis of the model:

$$C = G_S + G_G + R + S + F + U$$

where C is consumption, G_S is somatic growth, G_G is gonadal growth, R is respiration plus metabolism associated with activity, S is the metabolic cost of digestion, F is egestion, and U is excretion. Each of these processes is modeled by an additional equation or set of equations that incorporates species-specific physiological parameters, temperature, and fish weight. Physiological parameters for the striped bass bioenergetics model are available for age-1, age-2, and age-3+ (adult) fish (Hartman and Brandt 1995a), and these sets of parameters were used in our analysis of the corresponding age classes.

In the striped bass bioenergetics model, the specific consumption rate ($\text{g g}^{-1} \text{day}^{-1}$) is modeled as:

$$C = C_{max} \cdot P \cdot f_C(T)$$

where C_{max} is the maximum specific feeding rate, P is a proportionality constant that accounts for ecological constraints on consumption, and $f_C(T)$ is the temperature dependence function for consumption. C_{max} is further modeled:

$$C_{max} = CA \cdot W^{CB}$$

where CA and CB are species-specific constants and W is fish mass (g). The Thornton and Lessem (1978) algorithm is used to model temperature dependence. When the bioenergetics model is used to estimate consumption based on weight gain, the model solves for the proportionality constant (or P -value) that will adjust consumption to the proportion of C_{max} necessary to result in the observed growth pattern.

Metabolism is also modeled by an additional set of equations. Specific rate of respiration ($\text{g g}^{-1} \text{day}^{-1}$) displays a very similar relationship to that seen for consumption:

$$R = RA \cdot W^{RB} \cdot f_R(T) \cdot ACT$$

where RA and RB are species-specific constants, $f_R(T)$ is an exponential temperature dependence function for respiration, and ACT is an activity multiplier. Activity can be a highly variable component of fish energy budgets and is, unfortunately, very difficult to measure in the field. In the striped bass bioenergetics model, a value is used that was estimated by solving for activity costs for known consumption and growth levels of fish held in the lab (Hartman and Brandt 1995a).

Energy lost to egestion is modeled as a constant proportion of consumed energy while energy lost due to the metabolic cost of digestion and to excretion are modeled as constant proportions of assimilated energy (consumption minus egestion). The proportionality constants governing these processes are fairly consistent among species and introduce little error into simulated consumption estimates (Bartell et al. 1986), so values for these

parameters are often borrowed from other species for which they have been measured (Beamish 1972 in Rice et al. 1983; Beamish 1974 in Rice et al. 1983). This approach is taken in the striped bass model (Hartman and Brandt 1995a).

Developing system-specific bioenergetics model simulations to estimate consumption requires data on the thermal experience of striped bass and the observed pattern of weight gain, as is clear from the form of the model. In addition, the energy density of the predator and prey is required in order to convert consumption to growth in energetically equivalent terms. The total energy density of the prey is dependent on the energy density of each prey item and the proportion of those prey items in the diet. The collection and analysis of these system-specific data are described below. Finally, the amount of weight lost to spawning (G_S) can also be specified in the model (Hanson et al. 1997); however, we chose not to utilize this option in our simulations for several reasons. First, the modeling simulation ideally represents the average individual in the population, and gonadal development, as indicated by changes in gonadosomatic index, was low and variable across the population in both reservoirs (Appendix A). Second, gonadal energy density was lower than somatic energy density for the majority of individuals (Appendix A), so requiring fish to lose a set amount of weight corresponding to the mean observed weight of gonads during the spring period would overestimate the energetic cost of gonadal development. Finally, the lack of observed spawning activity in either reservoir suggests that most individuals do not actually release gametes developed during this time, and reabsorption of this material would help offset the costs of gonadal development.

Bioenergetics model simulations

For each reservoir, bioenergetics model simulations were used to estimate per-capita consumption based on observed growth in 2001 and 2002. For the Badin Lake population, consumption was estimated separately for age-1, age-2, age-3, and age-4 individuals. For the Lake Norman population, estimates were obtained for each of these four age classes, as well as an age-5 fish. These age classes represent the ages of fish captured during the study with sufficient frequency to adequately determine their growth rates. Modeling simulations divided the year into three seasons: spring (January 1 to June 15), summer (June 16 to September 15), and fall (September 16 to December 31). Observed weight gain was then specified for each season. Only a single *P*-value was estimated for each model simulation, so conducting seasonal simulations was advantageous because it allowed the *P*-value to vary between these time periods such that estimated consumption more closely tracked seasonal changes in prey availability. This advantage is particularly important for populations like reservoir striped bass that take advantage of seasonally abundant food resources such as young-of-the-year shad.

Habitat exchange simulations were then used to assess the relative impact of temperature and forage availability (as indicated by realized consumption rates) on growth of striped bass in each reservoir. These simulations used age-3 fish from Badin Lake and age-5 fish from Lake Norman because these fish were approximately the same size at the beginning of each year, minimizing the effects of fish size on consumption and growth. In 2001, both age-3 Badin Lake fish and age-5 Lake Norman fish began the year at 1,729 g; in 2002, age-3 Badin Lake fish began the year at 1,482 g while age-5 Lake Norman fish began the year at 1,514 g. The first temperature exchange simulation applied the temperature regime from

Lake Norman to age-3 Badin Lake fish, constraining them to consume the same amount that was estimated in the per-capita consumption simulations based on observed growth under Badin Lake conditions. Because consumption was fixed, the effect of the change in temperature could be assessed based on the resulting change in growth. The second temperature exchange simulation applied the temperature regime from Badin Lake to age-5 Lake Norman fish, again constraining consumption to reflect the original Lake Norman conditions so that the temperature effect could be assessed through the change in growth. The first consumption exchange simulation then constrained age-3 Badin Lake fish experiencing all Badin Lake conditions, including temperature, to consume as much as was estimated for age-5 Lake Norman fish experiencing Lake Norman conditions. The second consumption exchange simulation constrained age-5 Lake Norman fish to consume the quantity estimated for age-3 Badin Lake fish. Hence, these simulations assessed the effect of these changes in consumption level through the effect on simulated fish growth, using consumption level as a reflection of the forage available to striped bass in each system.

System-specific data sources

The thermal regimes experienced by striped bass in Badin Lake and Lake Norman in 2001 and 2002 were determined by applying thermal selection rules to seasonal temperature and dissolved oxygen profiles collected at 1-m intervals at three sites in each reservoir (Figures 3.1, 3.2). These thermal selection rules were based on the temperature and dissolved oxygen levels occupied by Badin Lake striped bass tagged with temperature-sensing transmitters in 2002 and 2003 (Thompson et al. In review; this study, Chapter 2). According to these rules, through the winter and spring striped bass selected the warmest

water at a depth of 2 m or greater up to 20°C. As the water column stratified, striped bass remained at 20°C as long as water of this temperature was available with at least 2 mg/l dissolved oxygen. Once the dissolved oxygen level at 20°C dropped below 2 mg/l, fish moved up into warmer epilimnetic water and occupying the temperature just above the oxycline, defined as the depth above the first drop of at least 1 mg/l dissolved oxygen in one meter moving down from the water surface that brought the dissolved oxygen level below 6 mg/l (Thompson et al. In review; this study, Chapter 2). Fish remained just above the oxycline until the water temperature at that depth dropped to 20°C, at which point they again occupied the warmest water up to 20°C. For each profile date these rules were applied to the three profile sites and the resulting temperatures were averaged to obtain the temperature input for that date. Profiles were conducted at seasonally appropriate intervals ranging from every three to four weeks in the winter to weekly in the summer (Thompson et al. 2005), and temperatures were linearly interpolated between profile dates to complete the thermal regime for striped bass in each reservoir (Figure 3.3).

The growth data required to estimate consumption in per-capita bioenergetics model simulations were the changes in weight for each age of fish over each seasonal time period modeled. Von Bertalanffy growth models were fit to observed length and age at capture and backcalculation of length-at-annulus formation for fish of each cohort included in bioenergetics model simulations. All ageing was conducted using sagittal otoliths removed from striped bass collected primarily by gill nets (5.1-mm and 7.6-mm mesh) set in June or July, September, and December of 2000 through 2002 (Appendix A). The total number of observations (both length-at-age and length-at-annulus formation) used in fitting growth models for each cohort ranged from 36 to 159 in Badin Lake and from 24 to 60 in Lake

Norman (Appendix A). These growth models were used to determine the length of fish at the beginning and end of each model period. Length was converted to weight based on significant ($\alpha = 0.05$) system-specific regression models relating weight to length and powers of day of the year (Appendix A).

Seasonal patterns in total energy density (somatic plus gonadal; J/g wet wt) of striped bass were determined over the range of fish sizes modeled in bioenergetics simulations of each reservoir. The energy densities of about 30 striped bass from each system were determined directly by calorimetry (Appendix A). These data were used to model the relationship between energy density and percent dry weight of the sample (Hartman and Brandt 1995c). There was no significant difference between the relationship for Badin Lake and Lake Norman, so a single regression model was used to estimate the energy density of all remaining striped bass samples based on their percent dry weight (Appendix A). Striped bass used in energy density analysis were collected in large numbers by gill net at three times (June or July, September, and December) during the years of the study, and small numbers of fish were collected by a variety of sampling techniques about every six weeks between large samples (Appendix A). Seasonal and size-specific energy density inputs to the bioenergetics models were based on the mean energy density observed in each size category over time in each reservoir (Appendix A).

Seasonal, size-specific energy densities were also determined for each species of pelagic forage fish identified in striped bass stomachs. These prey items included threadfin shad and gizzard shad in both reservoirs, blueback herring in Badin Lake, and alewife in Lake Norman. Pelagic forage fish were collected by purse seine (9 m deep by 118 m long net, 4.8-mm mesh size) at two to three sites in each reservoir at three points during the year,

corresponding to the dates of the large striped bass samples, and smaller samples were collected by various sampling methods about every six weeks between large samples (Appendix B). The energy densities of 16 to 20 samples of each forage fish species from each reservoir were determined directly by calorimetry, and these data were used to generate regression models relating energy density to percent dry weight of the samples. No significant differences were found between the Badin Lake and Lake Norman relationships for threadfin shad or gizzard shad (Appendix B), so a single relationship for each species was applied to fish from both systems. The energy densities of additional pelagic prey samples were determined based on these relationships, allowing the seasonal, size-specific pattern in energy density of each pelagic prey species to be determined for each reservoir (Appendix B) for input to the striped bass bioenergetics models.

In addition to clupeid prey fish species, a small proportion of invertebrates and non-clupeid fish were found in the striped bass stomachs (Appendix A), requiring energy densities for these diet items to be specified in the model simulations. The majority of invertebrates identified in striped bass stomachs from both systems were Ephemeroptera, so a constant value of 4,705 J/g wet wt, the mean for Ephemeroptera provided in the prey energy densities in Fish Bioenergetics 3.0 (Cummins and Wuycheck 1971 in Hanson et al. 1997; Driver et al. 1974 in Hanson et al. 1997), was used for all invertebrate prey in all simulations. Non-clupeid prey fish found in striped bass stomachs included bluegill *Lepomis macrochirus*, white perch *M. americana*, and black crappie *Pomoxis nigromaculatus*. The energy density of bluegill reported in Fish Bioenergetics 3.0, 4,186 J/g wet wt (Kitchell et al. 1974 in Hanson et al. 1997), was used for all non-clupeid prey fish in all simulations.

In order for the overall energy density of the striped bass diet to be determined from these various prey energy densities, the striped bass seasonal and size-specific diet composition by weight was also specified in each model simulation. These diet composition data were determined by identifying all prey items in the stomachs of striped bass captured over the course of the study (Appendix A). Items were identified to the lowest taxonomic level possible using standard keys (Jenkins and Burkhead 1993; Voshell 2002), and in the case of prey fish, a backbone length was determined for each item. Backbone lengths were converted to total lengths and then to wet weights (Appendix A) using species-specific regression models determined as part of this study (Appendix B). Diet data were tabulated separately for three size classes of striped bass that differed slightly between reservoirs: less than 425 mm, 425 mm to 600 mm, and greater than 600 mm total length in Badin Lake and less than 475 mm, 475 mm to 575 mm, and greater than 575 mm total length in Lake Norman. The diet compositions of these size classes were distinguished to account for slight differences observed in the most common prey items found in stomachs of striped bass of each size (Appendix A). For each seasonal simulation, the data for the size class in which a particular age striped bass started the simulation were used. Diet composition data were linearly interpolated between the dates for which diet data were specified in the model input (Hanson et al. 1997). Due to this interpolation, diet composition for a date in late-spring had to be specified, even though no striped bass samples had been collected on this date, in order to prevent the simulated diet composition from including a large proportion of young-of-the-year clupeids during a time period when these young fish had not yet appeared in the system. Instead, we used an assumed diet composition reflecting the size and composition of prey fish available in each reservoir at that time.

Results

Seasonal and age-specific consumption patterns in Badin Lake

In Badin Lake, seasonal patterns in cumulative consumption were evident for all age classes (Table 3.1; Figures 3.4a, 3.5a). Consumption was lowest over the spring, particularly among older fish (Table 3.1). The mean percent body weight consumed per day over the spring in 2001 and 2002 ranged from 2.3% to 2.4% for age-1 striped bass, 1.6% to 1.8% for age-2 fish, 1.2% in both years for age-3 fish, and 0.9% to 1.0% for age-4 fish. Weight gain over this time period was also limited compared to the remainder of the year, with age-1 and age-2 fish gaining weight slowly, age-3 fish remaining at almost constant weight, and age-4 fish losing weight (Figures 3.4b, 3.5b). This growth pattern likely reflected a combination of cool spring temperatures (Figure 3.3), which would be expected to lower metabolic costs and maximize possible consumption, and limited consumption due to reduced prey availability. The conclusion that sluggish growth and low consumption over the spring was related to limited food availability can be further evaluated by considering the proportion of maximum consumption attained by striped bass during this period. While maximum consumption itself will be determined by body size and temperature, the proportion of maximum consumption attained will be dictated by ecological conditions such as food availability. Between the two years, this proportion ranged from 0.46 to 0.47 for age-1 fish, 0.40 to 0.48 for age-2 fish, 0.32 to 0.36 for age-3 fish, and 0.30 in both years for age-4 fish. Low food availability in the spring may result from the scarcity of appropriately-sized clupeid forage fish before the young-of-the-year fish become available in the late spring, a conclusion supported by the lack of clupeids in the stomachs of striped bass collected during the spring and very early summer. Striped bass stomachs during this time period were frequently empty or contained

invertebrates (among smaller striped bass) or single large non-clupeid prey fish (among larger striped bass; Appendix A).

Consumption was highest over the summer for all age classes except age-1 striped bass, for which total seasonal consumption was slightly greater in the fall of 2002 (Table 3.1; Figures 3.4a, 3.5a). Mean percent body weight consumed per day over the summer in 2001 and 2002 ranged from 5.0% to 5.2% for age-1 fish, 3.5% to 3.7% for age-2 fish, 3.4% to 3.5% for age-3 fish, and 2.6% to 3.0% for age-4 fish. Compared to the spring and fall periods, high temperatures during the summer (Figure 3.3) increase both metabolic costs and maximum possible consumption, contributing to these higher consumption estimates. Growth over the summer was greater than over the spring time period for all age classes (Figures 3.4b, 3.5b), particularly in 2002 (Figure 3.5b); however, weight gain over the summer was not as great in any year or for any age class as it was over the fall (a period when consumption was lower, as described below). This result suggests that a large proportion of the energy consumed by Badin Lake striped bass during the summer must be used to meet metabolic costs due to high temperatures, rather than being allocated to growth. All ages of Badin Lake striped bass consume a high proportion of maximum consumption based on temperature and body size, suggesting that these fish are able to meet their metabolic costs and achieve moderate growth over the summer due to high food availability. The estimated proportion of maximum consumption attained during this period in 2001 and 2002 ranged from 0.83 to 0.84 for age-1 fish, 0.68 to 0.74 for age-2 fish, 0.76 to 0.78 for age-3 fish, and 0.63 to 0.73 for age-4 fish. Stomachs of striped bass collected during the late summer were full of young-of-the-year clupeids (Appendix A), suggesting that fish of all sizes were taking advantage of this seasonally abundant food resource.

Fall consumption levels were higher than consumption over the spring and typically lower than consumption over the summer (Table 3.1; Figures 3.4a, 3.5a). Mean percent body weight consumed per day during the fall in 2001 and 2002 ranged from 3.3% to 3.4% for age-1 fish, 2.1% to 2.4% for age-2 fish, 1.9% to 2.3% for age-3 fish, and 1.6% to 1.9% for age-4 fish. Fall conditions in Badin Lake appear to be the most conducive to rapid growth of striped bass; growth over the fall was greater than in any other seasonal period for all age classes (Figures 3.4b, 3.5b). The combination of these high growth rates, which would suggest fish are achieving fairly high consumption rates, and cooling temperatures, which would decrease the consumption rate necessary to achieve high growth through a reduction in metabolic costs and maximum possible consumption, likely led to the moderate consumption levels estimated in fall simulations. The proportions of maximum consumption attained by each age class of Badin Lake striped bass in the fall were lower than those attained in the summer period: 0.59 to 0.72 for age-1 fish, 0.51 to 0.53 for age-2 fish, 0.52 to 0.53 for age-3 fish, and 0.46 to 0.49 for age-4 fish. This result suggests that food resources in the system, particularly young-of-the-year clupeids, may become somewhat reduced as the year progresses. However, it is clear that with the lower temperatures experienced during this season forage availability is still sufficient to support high growth rates through the fall.

Total seasonal and annual consumption increased with increasing age for all age classes of Badin Lake striped bass modeled (Table 3.1; Figures 3.4a, 3.5a). Growth continued among all ages commonly observed in this system such that each age class was larger at all points during the year than the previous age class (Figures 3.4b, 3.5b). As body size increased, absolute consumption would also be expected to increase. However, both the mean percent body weight consumed per day and the proportion of maximum consumption

attained in all seasons decreased somewhat with increasing age among Badin Lake striped bass. The majority of the diet of all sizes of striped bass was composed of similarly sized prey items (Appendix A), but because smaller striped bass have a lower body weight and a lower maximum possible consumption, a prey item of a given size will constitute a greater proportion of maximum consumption and a higher percent body weight consumed than for a larger fish. Therefore, smaller prey items will provide proportionally more energy to smaller fish, allowing them to more quickly meet their metabolic needs, leaving energy available to allocate toward growth and giving them a growth advantage over larger fish. However, it is important to note that growth among older striped bass in Badin Lake did not decline very substantially (Figures 3.4b, 3.5b; Appendix A), suggesting that while smaller fish attain a higher proportion of their maximum consumption in all seasons, larger fish are still able to consume sufficient resources to maintain relatively high growth rates.

Seasonal and age-specific consumption patterns in Lake Norman

Consumption by Lake Norman striped bass was more similar between seasons (Table 3.2; Figures 3.6a, 3.7a) than in Badin Lake (Table 3.1; Figures 3.4a, 3.5a), but as in Badin Lake, consumption during the spring period was lower than during the summer or fall (Table 3.2; Figures 3.6a, 3.7a). Between 2001 and 2002, mean percent body weight consumed per day ranged from 2.7% to 3.3% for age-1 striped bass, 1.8% to 1.9% for age-2 striped bass, 1.5% in both years for age-3 striped bass, 1.3% to 1.4% for age-4 striped bass, and 1.3% in both years for age-5 striped bass. As in Badin Lake, the coolest temperatures of the year occurred during the spring period (Figure 3.3) and growth was poor among Lake Norman striped bass over this season (Figures 3.6b, 3.7b), contributing to the low consumption levels

estimated in spring simulations. The proportion of maximum consumption attained by Lake Norman striped bass in the spring of 2001 and 2002 was lower than in other seasons for all age classes and ranged from 0.49 to 0.55 for age-1 fish, 0.40 to 0.41 for age-2 fish, 0.33 to 0.34 for age-3 fish, 0.31 to 0.32 for age-4 fish, and 0.30 to 0.32 for age-5 fish. These values were fairly similar to those attained by Badin Lake striped bass during the spring and suggest that Lake Norman striped bass also experience limited availability of their preferred food, young-of-the-year clupeids, over this season. While the seasonal pattern of stomach fullness was not as pronounced in Lake Norman as in Badin Lake, those stomachs with identifiable contents typically contained invertebrates or single non-clupeid prey fish during the spring (Appendix A).

Consumption was greatest over the summer for all age classes in both years of the study (Table 3.2; Figures 3.6a, 3.7a). Mean percent body weight consumed per day over this season ranged from 4.4% to 4.5% for age-1 fish, 2.9% to 3.6% for age-2 fish, 2.5% to 3.0% for age-3 fish, 2.4% to 2.9% for age-4 fish, and 2.4% to 2.8% for age-5 fish. While younger fish achieved some moderate growth over the summer, growth of age-3 and older fish was negligible (Figures 3.6b, 3.7b), suggesting that almost all of the energy consumed by older Lake Norman striped bass during the summer is used to meet the metabolic demands associated with warm summer temperatures. As in Badin Lake, striped bass in Lake Norman attained the highest proportions of maximum consumption during the summer. However, these proportions were lower and had greater annual variability than in Badin Lake, ranging from 0.74 to 0.75 for age-1 fish, 0.57 to 0.70 for age-2 fish, 0.54 to 0.63 for age-3 fish, 0.52 to 0.62 for age-4 fish, and 0.52 to 0.63 for age-5 fish. Thus, while seasonal availability of prey fish was highest during the summer in Lake Norman, these resources do not appear to

be sufficient to promote growth during this season because they coincide with the warmest temperatures of the year.

Estimates of consumption by Lake Norman striped bass over the fall period fell between the spring and summer seasonal estimates (Table 3.2; Figures 3.6a, 3.7a). The mean percent body weight consumed per day during the fall ranged from 2.8% to 3.3% for age-1 fish, 2.2% to 2.6% for age-2 fish, 1.9% to 2.3% for age-3 fish, 1.8% to 2.3% for age-4 fish, and 1.8% to 2.2% for age-5 fish. The proportions of maximum consumption attained by Lake Norman fish over the fall also fell between those estimated for the spring and summer and ranged from 0.54 to 0.57 for age-1 fish, 0.47 to 0.52 for age-2 fish, 0.42 to 0.48 for age-3 fish, 0.40 to 0.47 for age-4 fish, and 0.40 to 0.48 for age-5 fish. Similar to the results obtained for the summer period, these proportions are lower than those attained by Badin Lake striped bass and suggest that young-of-the-year clupeids may become depleted much more quickly in Lake Norman. While the fall was a period of rapid growth of all age classes in Badin Lake (Figures 3.4b, 3.5b), growth of Lake Norman striped bass was low over the fall, especially among the older fish (Figures 3.6b, 3.7b). These results suggest that Lake Norman striped bass do not experience seasonal conditions with a combination of cooler temperatures and abundant prey resources that are conducive to rapid growth of all size classes of fish at any point during the year.

Total and seasonal consumption estimates increased from age-1 to age-3 fish in Lake Norman, but similar consumption estimates were frequently obtained for fish age-3 through age-5 (Table 3.2; Figures 3.6a, 3.7a). Differences and similarities in consumption were directly correlated with the pattern of weight and growth of these age classes. Growth of Lake Norman striped bass continued until age-3, increasing absolute consumption through

these ages. However, growth diminished considerably after age-3 (Appendix A). In 2001, age-3 and age-4 fish were most similar in terms of both weight and consumption (Figure 3.6). In 2002, age-3, age-4, and age-5 fish were of similar weight throughout most of the year and the cumulative consumption pattern of these ages was almost identical (Figure 3.7).

As in Badin Lake, the percent body weight consumed and the proportion of maximum consumption attained declined with increasing age, although the older age classes were more similar in Lake Norman, presumably due to the similarities in size and consumption of these fish. It is important to note that the differences in size between age-2 fish and fish older than age-3 were considerably smaller than in Badin Lake due to the slower growth of fish in Lake Norman, and yet, the decline in percent body weight consumed and proportion of maximum consumption attained was of a similar magnitude, suggesting a greater relative decline in these measures among older Lake Norman fish. This result suggests that older fish in Lake Norman may have substantially more difficulty consuming resources sufficient to allocate much energy to growth compared to younger fish in the same system and that this contrast between age classes is greater than in Badin Lake. This interpretation is certainly supported by the drastic decline in growth observed among older Lake Norman fish. As in Badin Lake, all sizes of Lake Norman striped bass consume similar sizes of clupeid prey fish (Appendix A) but a prey fish of a given size will provide proportionally less energy for a larger fish. Conditions of prey limitation would be expected to exacerbate this situation because the costs associated with searching for and capturing prey compared to the benefit received from a prey item will also be proportionally greater for larger fish.

Habitat exchange simulations

The results of the habitat exchange simulations supported the conclusion that forage availability has a strong influence on the growth of reservoir striped bass. In 2001, annual growth of simulated fish in all habitat exchange simulations most closely resembled the growth pattern of fish from the system from which consumption was taken (Table 3.3). In the temperature exchange simulations, simulated annual growth was relatively unchanged, with growth of Badin Lake fish diminishing by 164 g at Lake Norman temperatures and growth of Lake Norman fish increasing by 148 g at Badin Lake temperatures (Table 3.3; Figure 3.8). These temperature differences may seem in the opposite direction of the expected result, but Lake Norman was warmer than Badin Lake over the cooler months of the year (Figure 3.3a), thereby lowering potential growth for a given level of food consumption, while Badin Lake was only warmer than Lake Norman over several weeks in early summer (Figure 3.3a) when cool, oxygenated water disappears from the system more quickly (Thompson et al. 2005). Simulated annual growth in the consumption exchange simulations, however, was substantially influenced by the different consumption levels imposed, with growth of Badin Lake fish diminishing by 461 g given Lake Norman consumption levels and growth of Lake Norman fish increasing by 453 g given Badin Lake consumption levels (Table 3.3; Figure 3.8).

The pattern of differences in growth due to changes in temperature regime and consumption level was somewhat more complex when considered on a seasonal basis. The magnitude of the deviations in growth in both the temperature and consumption exchange simulations were fairly similar for both Badin Lake and Lake Norman in the spring and fall of 2001 (Figure 3.8). During the summer, however, the difference in growth due to changes

in consumption level was substantially greater than differences due to changes in temperature in both systems (Figure 3.8). While the temperature regime for both systems is similar once fish are forced into warm epilimnetic water by diminishing dissolved oxygen levels, fish in Lake Norman were able to remain in the cooler hypolimnetic water for an additional two weeks in 2001 (Figure 3.3a). We would expect this delay in the experience of warm summer temperatures to have energetic consequences, and indeed, Badin Lake fish experiencing Lake Norman temperatures did increase their growth over the summer by 131 g (Table 3.3; Figure 3.8a). However, it is clear from these results that the difference in consumption levels achieved by striped bass in the two systems had even greater repercussions for growth, with Badin Lake fish experiencing Lake Norman consumption showing a 367 g reduction in growth and Lake Norman fish experiencing Badin Lake consumption showing a 418 g improvement in growth over this season (Table 3.3; Figure 3.8).

The results of habitat exchange simulations based on 2002 conditions showed an even more pronounced effect of consumption on striped bass growth relative to the effect of temperature. Annual growth was only diminished by 27 g for Badin Lake fish given Lake Norman temperatures and only increased by 17 g for Lake Norman fish given Badin Lake temperatures (Table 3.3; Figure 3.9). However, using consumption estimated in the other reservoir produced a 1023 g reduction in growth of Badin Lake striped bass and a 974 g improvement in growth of Lake Norman striped bass over the year (Table 3.3; Figure 3.9). As in 2001, the magnitude of the difference in growth due to changes in temperatures versus consumption was similar in the spring in both systems, but changes in consumption had a much greater effect on growth over the summer and, in this year, over the fall as well (Table 3.3; Figure 3.9). In the summer of 2002, Lake Norman striped bass were able to remain in

cooler hypolimnetic water for an additional three weeks beyond the date when Badin Lake fish were forced into warmer water (Figure 3.3b). This difference again set up the potential for substantial temperature effects on growth during this season, but the effect of consumption was even more pronounced. Badin Lake fish experienced a 710 g reduction in growth with Lake Norman consumption levels versus a 217 g increase in growth with Lake Norman temperatures over the summer, while Lake Norman fish showed a 746 g increase in growth with Badin Lake consumption levels versus a 220 g decrease with Badin Lake temperatures over this time period (Table 3.3; Figure 3.9). While temperature and consumption effects were both somewhat reduced in the fall (Figure 3.9), the temperature effect was only about 30% of the consumption effect in both systems over this season, similar to the percentage difference observed over the summer.

Discussion

This study has changed our view of the effects of unsuitable environmental conditions on striped bass in southern reservoirs by illuminating the important role that forage availability can play in mediating the costs of extreme summer conditions. Striped bass in Badin Lake, the more productive reservoir, were able to attain high proportions of their physiological maximum consumption rate in the summer (P -values of 0.63 to 0.84). High consumption rates allowed these fish to achieve modest growth despite experiencing temperatures over 27°C for at least two months. Badin Lake striped bass also attained relatively high proportions of maximum consumption during the fall (P -values of 0.46 to 0.72). In conjunction with a reduction in metabolic costs due to cooling temperatures, these fairly high consumption rates resulted in rapid growth over this season. In contrast, striped

bass in Lake Norman, the less productive reservoir, attained more modest proportions of maximum consumption in the summer (*P*-values of 0.52 to 0.75). While Lake Norman fish experienced temperatures over 27°C for two to three weeks less than Badin Lake fish, increasing the growth achieved for a given level of consumption, these lower consumption rates were not sufficient to allow larger Lake Norman fish to allocate energy to growth. The proportions of maximum consumption attained by Lake Norman striped bass in the fall (*P*-values of 0.40 to 0.57) were also reduced in comparison with Badin Lake, preventing Lake Norman fish from achieving substantial growth even as temperatures cooled. The conclusion that forage availability played a larger role than temperature in dictating patterns of striped bass growth in these two reservoirs was strongly supported by the results of the habitat exchange simulations, which showed that the relative effect of forage availability on annual striped bass growth was about three times that of temperature in 2001 and about 37 times that of temperature in 2002.

Our findings suggest that management of reservoir striped bass should proceed with consideration of the important influence of forage availability on striped bass growth and condition. Highly productive reservoirs need not be automatically excluded from consideration for stocking striped bass because they lack summer habitat meeting Coutant's (1985) suitability requirements of temperatures less than 27°C and dissolved oxygen levels greater than 2 mg/l. Certainly growth for a given forage base will be reduced to some extent as the summer temperatures that fish must occupy increase, but striped bass in Badin Lake occupy water temperatures of 28 to 30°C for extended periods up to two months, and yet they experience fairly rapid growth and maintain high condition. Thompson et al. (In review; this study, Chapter 2) suggested that striped bass in highly productive systems that are forced into

warm epilimnetic waters by low dissolved oxygen levels may actually benefit energetically if those physical conditions increase the spatial overlap between striped bass and pelagic prey. Our results support this conclusion by demonstrating that Badin Lake striped bass experience high consumption rates throughout the summer, indicating no spatial segregation from their prey resources. Summer conditions are also only one component of the total picture that determines striped bass growth. The continuation of high forage availability into the fall as temperatures become cooler may allow striped bass in productive systems to experience the ideal conditions for rapid growth. Therefore, while the quality of a reservoir's physical habitat can be determined relatively easily with a series of temperature and dissolved oxygen profiles through the summer, some means of indexing forage availability may actually provide a more useful indicator of a reservoir's capability to support striped bass.

The importance of forage availability to patterns of striped bass growth and condition also suggests that poor growth and condition should not be considered solely dependent on physical conditions outside the influence of fishery managers. Rather, growth and condition will reflect the ability of the prey community to support the predatory demand of striped bass. This predatory demand will increase as summer temperatures increase, so balancing resource supply and demand will be particularly important for the success of striped bass fisheries in southern reservoirs. Given the low natural mortality and high fishing mortality estimated for reservoir striped bass populations (Hightower et al. 2001; Thompson et al. In press), adjusting harvest regulations and/or stocking rates should provide managers with an effective means of manipulating the structure of these populations and improving growth and condition. Our study provides strong evidence that the poor growth and condition of larger striped bass in Lake Norman are the direct result of insufficient prey resources to support

quality growth given the number and size of fish currently in the system. Almost all consumption by fish age-3 and older is used for maintenance rather than growth, and because harvest regulations do not allow fish to be removed until they reach age-3, most of the forage resources in Lake Norman are being used by fish before they reach harvestable size and then simply to keep the fish alive beyond that point. In Lake Norman age-3 to age-5 striped bass each eat about 160% as much forage each year as an age-1 fish, and about 120% as much as an age-2 fish, while achieving little or no growth.

Based on the results of our study, fishery regulations in Lake Norman have since been adjusted, with the minimum size limit lowered from 508 mm to 406 mm over the fall through spring and no minimum size limit over the summer in order to allow anglers to harvest fish before the size at which growth and condition declines and to allow striped bass remaining in the system greater access to prey resources. Changes in growth rates will provide useful feedback for managers when implementing such modifications to striped bass fisheries. In this context, growth rates can be considered a biological synthesis of information on the availability of food resources for each segment of the population given the current population size structure and number of fish in relation to the energetic costs imposed by the physical environment and the current food web structure. Manipulation of the striped bass population in Badin Lake may also be possible to take greater advantage of the forage resources in this system, and monitoring changes in striped bass growth rates should allow fishery managers to assess the success of management changes in this system, as well. The current rapid growth and high consumption rates of Badin Lake striped bass indicate that forage is not likely limiting, so the system could potentially support a larger number of fish or a greater number of older, larger fish without substantially reducing growth. Increasing stocking rates

could improve angler catch rates, or alternatively, reducing the harvest rate or increasing the size limit could allow for the production of larger fish. Our bioenergetics analysis indicates that the current lack of larger fish in Badin Lake is not due to limits on consumption and growth, and a yield-per-recruit model of this population demonstrated that older fish could be produced with a reduction in the fishing mortality rate (Thompson et al. In press).

The habitat exchange simulation approach used in this study will be useful for assessing the effect of habitat conditions on growth of fish in other populations. Habitat conditions that could be investigated in the bioenergetics framework include the energetic cost of spawning, activity costs such as those associated with migration, the energetic quality of food resources, and, as in this study, temperature and forage availability. The benefit of the habitat exchange simulation method is that it provides a means for comparing the relative importance of two or more of these habitat conditions on growth of fish in multiple populations. In the context of understanding growth of striped bass in southern reservoirs, applying the habitat exchange simulation technique to additional reservoirs with a broader range of thermal constraints and productivities should help us determine how the relative influence of physical conditions and forage availability on striped bass growth changes as physical habitat quality varies. This broader analysis will allow us to continue to refine our understanding of the abiotic and biotic conditions required for successful reservoir striped bass fisheries.

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Tables

Table 3.1. Seasonal per-capita cumulative consumption (g) by age-1, age-2, age-3, and age-4 Badin Lake striped bass in 2001 and 2002 estimated in bioenergetics simulations based on observed seasonal growth of each age class. The spring period refers to Jan. 1 through June 15, the summer period refers to June 16 through Sept. 15, and the fall period refers to Sept. 16 through Dec. 31.

2001:				
	age-1	age-2	age-3	age-4
spring	1,205	2,940	3,538	3,977
summer	2,370	4,044	6,105	7,114
fall	2,200	3,184	5,033	5,541
total	5,775	10,168	14,676	16,632

2002:				
	age-1	age-2	age-3	age-4
spring	1,279	2,479	3,007	4,096
summer	2,328	3,536	5,372	5,900
fall	2,420	3,185	4,567	4,803
total	6,027	9,233	12,946	14,799

Table 3.2. Seasonal per-capita cumulative consumption (g) by age-1, age-2, age-3, age-4, and age-5 Lake Norman striped bass in 2001 and 2002 estimated in bioenergetics simulations based on observed seasonal growth of each age class. The spring period refers to Jan. 1 through June 15, the summer period refers to June 16 through Sept. 15, and the fall period refers to Sept. 16 through Dec. 31.

2001:					
	age-1	age-2	age-3	age-4	age-5
spring	1,507	2,706	3,254	3,226	3,883
summer	2,261	3,646	4,073	4,073	4,933
fall	2,174	3,104	3,437	3,386	4,108
total	5,942	9,456	10,764	10,685	12,924

2002:					
	age-1	age-2	age-3	age-4	age-5
spring	1,796	2,877	3,486	3,599	3,447
summer	2,348	3,014	3,472	3,590	3,457
fall	2,082	2,819	2,948	2,933	2,788
total	6,226	8,710	9,906	10,122	9,692

Table 3.3. Results of habitat exchange simulations for 2001 and 2002 using an age-3 Badin Lake striped bass and an age-5 Lake Norman striped bass. Each row refers to a separate simulation in which all conditions are as in the reservoir listed under Conditions with the exception of the system property noted. The first two rows refer to the original per-capita simulations and are provided for reference. Consumption results are provided for each of the three seasonal periods modeled and for the entire year; values are given in grams followed by the corresponding estimated proportion of maximum consumption (*P*-value) in parentheses. Growth results are given in grams and are provided for each seasonal period modeled, as well as for the entire year. Values in plain type are those input to the model while values in bold are model estimates.

2001:

Conditions	Consumption				Growth			
	spring	summer	fall	total	spring	summer	fall	total
All Badin conditions	3,538 (0.36)	6,105 (0.79)	5,033 (0.53)	14,676	-1	195	596	790
All Norman conditions	3,883 (0.32)	4,993 (0.63)	4,108 (0.47)	12,985	55	8	141	204
Badin conditions except Norman temperatures	3,538 (0.30)	6,105 (0.78)	5,033 (0.52)	14,676	-94	326	394	626
Norman conditions except Badin temperatures	3,883 (0.38)	4,993 (0.63)	4,108 (0.48)	12,985	170	-147	328	352
Badin conditions except Norman consumption	3,883 (0.39)	4,993 (0.67)	4,108 (0.50)	12,985	99	-172	401	329
Norman conditions except Badin consumption	3,538 (0.30)	6,105 (0.74)	5,033 (0.51)	14,676	-53	426	284	657

Table 3.3, continued.

2002:

Conditions	Consumption				Growth			
	spring	summer	fall	total	spring	summer	fall	total
All Badin conditions	3,007 (0.32)	5,373 (0.77)	4,567 (0.52)	12,946	-26	482	749	1,205
All Norman conditions	3,447 (0.30)	3,457 (0.52)	2,789 (0.40)	9,692	-18	-17	81	46
Badin conditions except Norman temperatures	3,007 (0.27)	5,373 (0.74)	4,567 (0.47)	12,946	-127	699	606	1,178
Norman conditions except Badin temperatures	3,447 (0.35)	3,457 (0.53)	2,789 (0.45)	9,692	99	-237	201	63
Badin conditions except Norman consumption	3,447 (0.36)	3,457 (0.53)	2,789 (0.44)	9,692	111	-228	298	182
Norman conditions except Badin consumption	3,007 (0.27)	5,373 (0.73)	4,567 (0.47)	12,946	-153	729	443	1,020

Figures

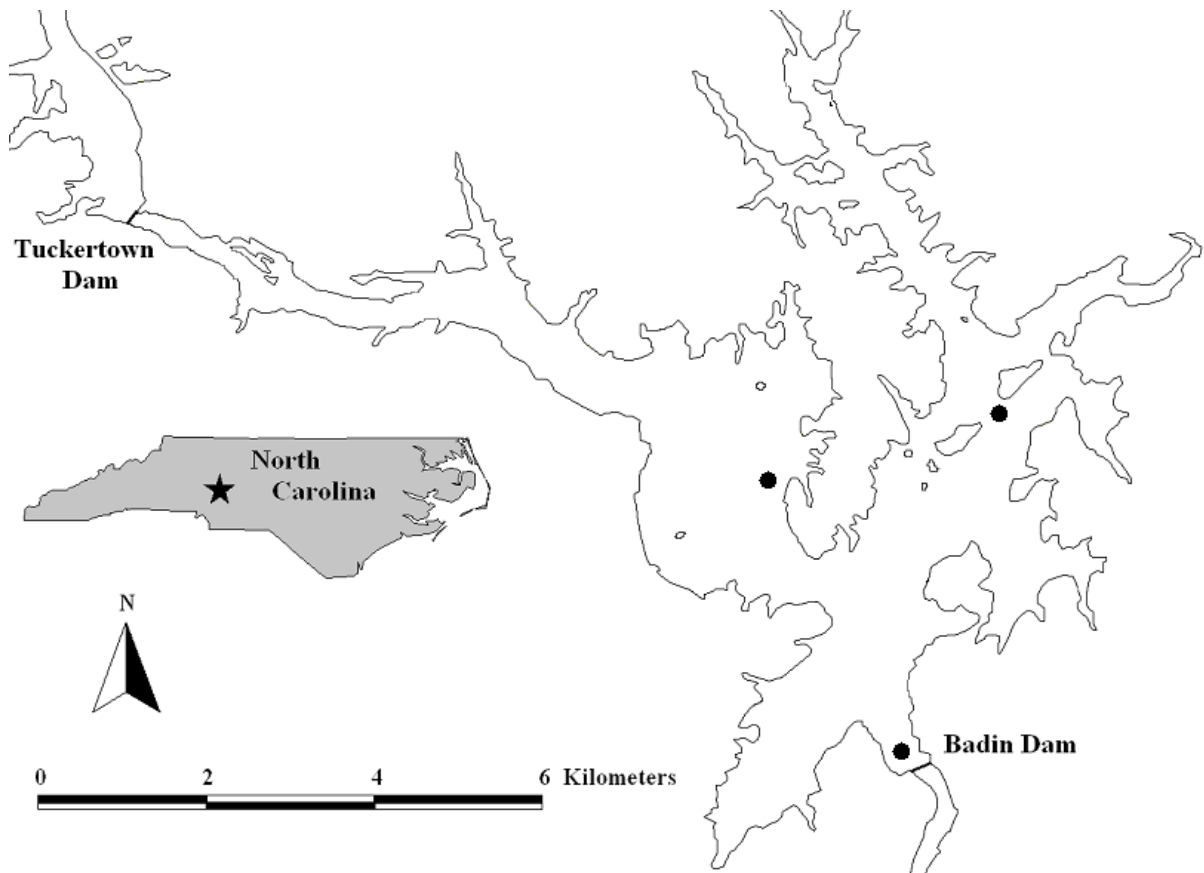


Figure 3.1. Map of Badin Lake, NC, showing sites of temperature and dissolved oxygen profiles (black dots) used in estimating the thermal experience of striped bass.

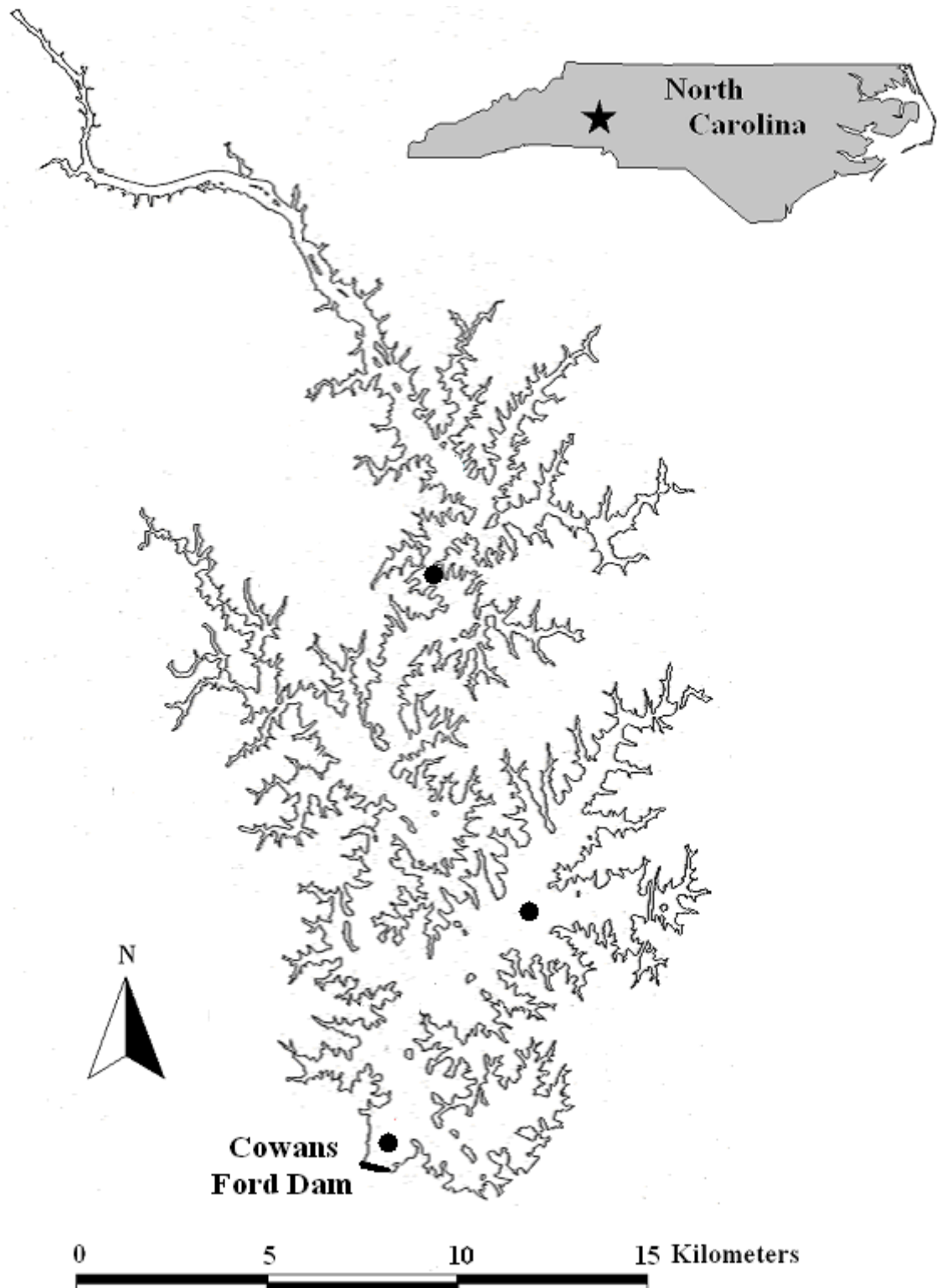


Figure 3.2. Map of Lake Norman, NC, showing sites of temperature and dissolved oxygen profiles (black dots) used in estimating the thermal experience of striped bass.

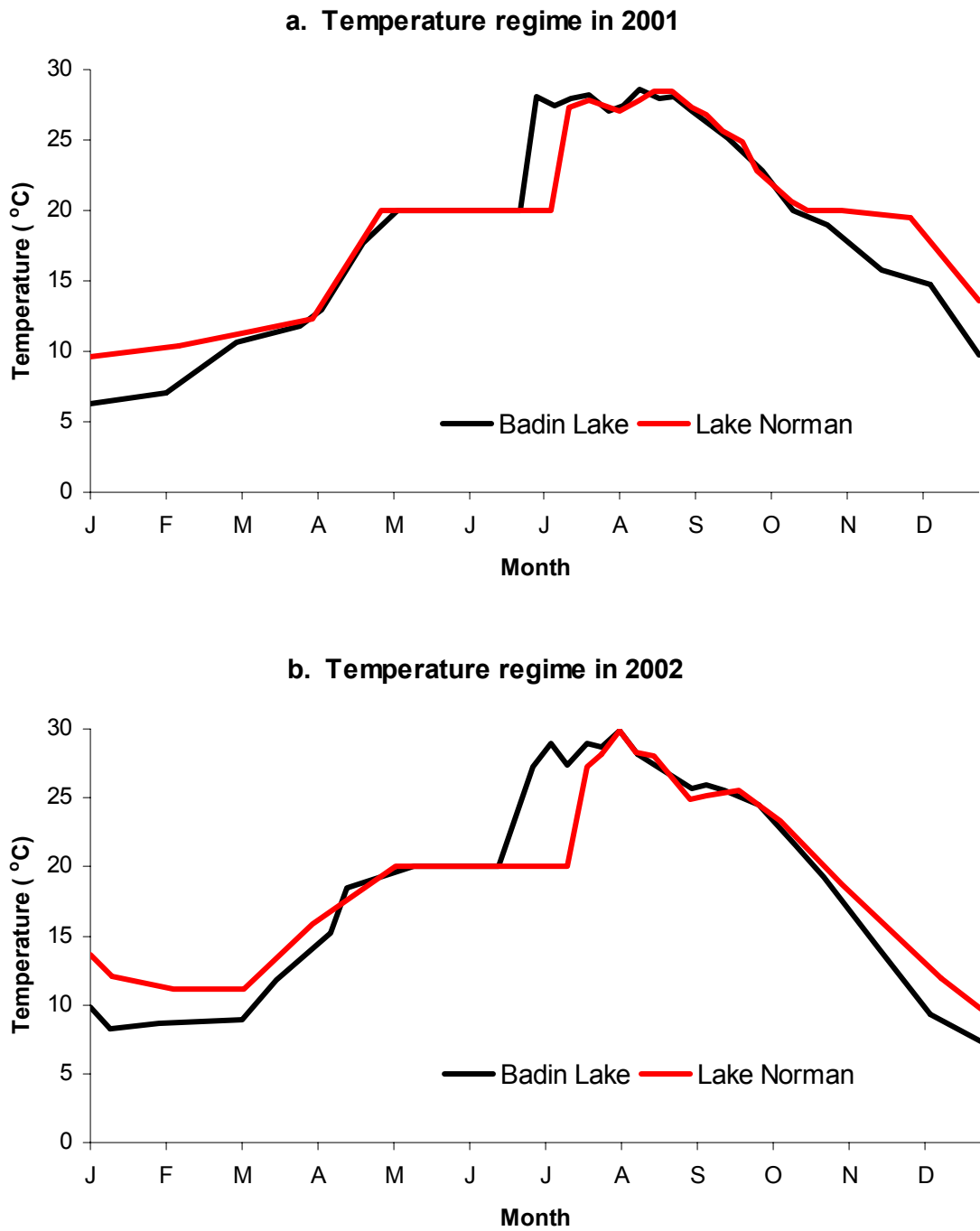


Figure 3.3. Temperature regimes input to striped bass bioenergetics models for Badin Lake (black lines) and Lake Norman (red lines) in (a) 2001 and (b) 2002. Temperatures are based on applying thermal selection rules to temperature and dissolved oxygen profile data, as described in the text.

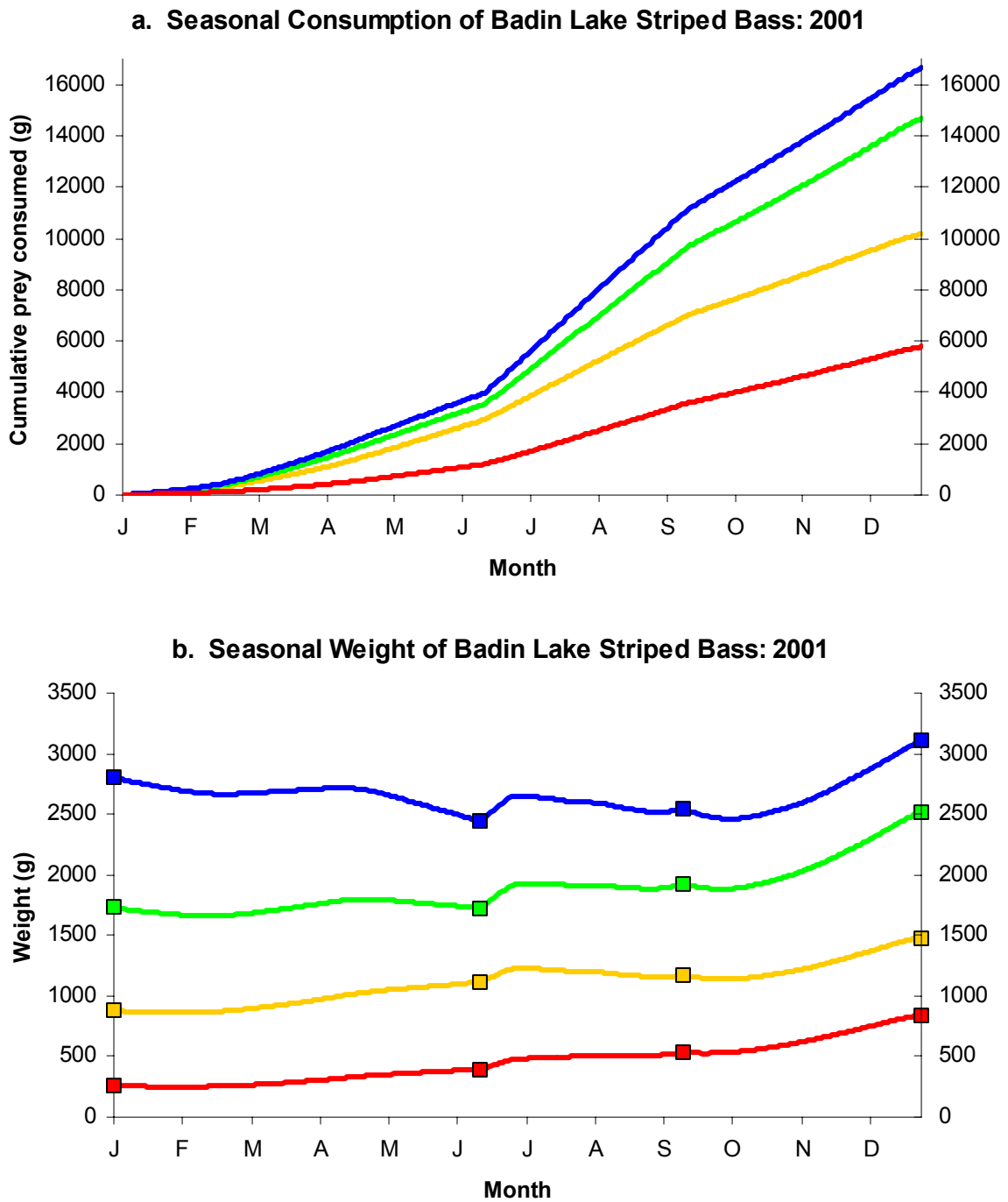
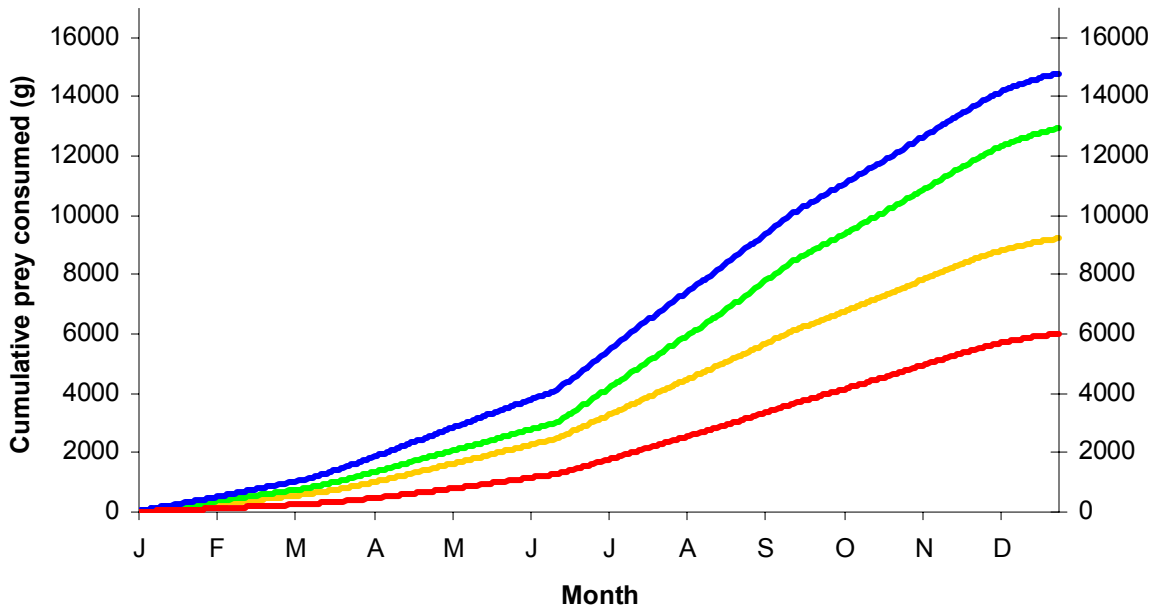


Figure 3.4. Estimates of (a) cumulative consumption (g) and (b) weight (g) of individual age-1 (red), age-2 (yellow), age-3 (green), and age-4 (blue) striped bass in Badin Lake in 2001. Lines indicate values estimated in bioenergetics model simulations, while the points in panel b indicate growth values input to the model based on changes in length predicted by a von Bertalanffy growth curve and the relationship between length and weight and day of the year, as described in the text.

a. Seasonal Consumption of Badin Lake Striped Bass: 2002



b. Seasonal Weight of Badin Lake Striped Bass: 2002

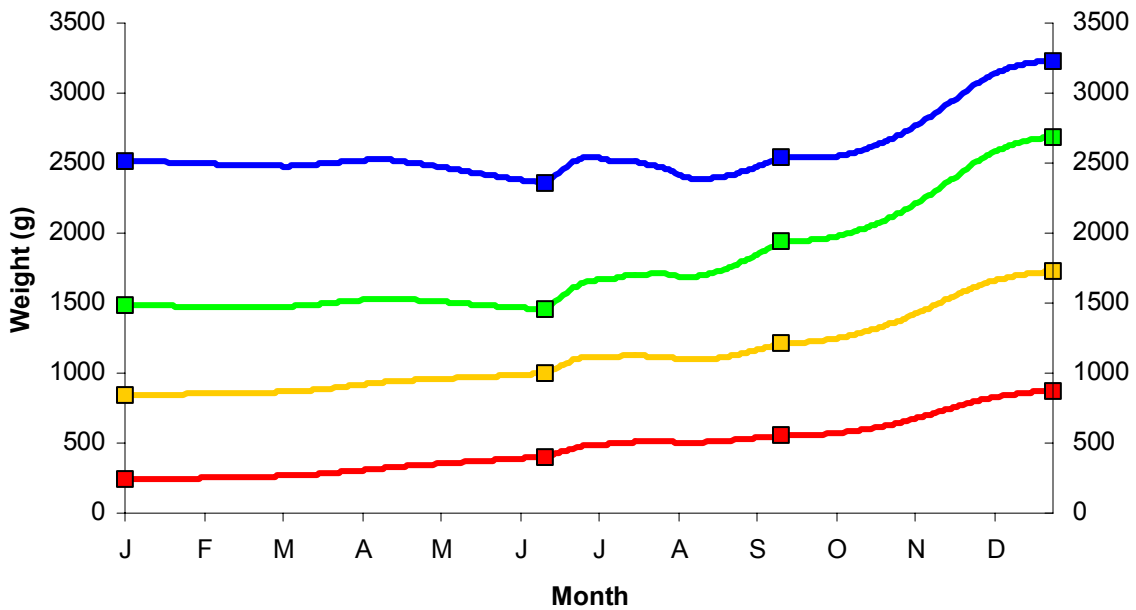
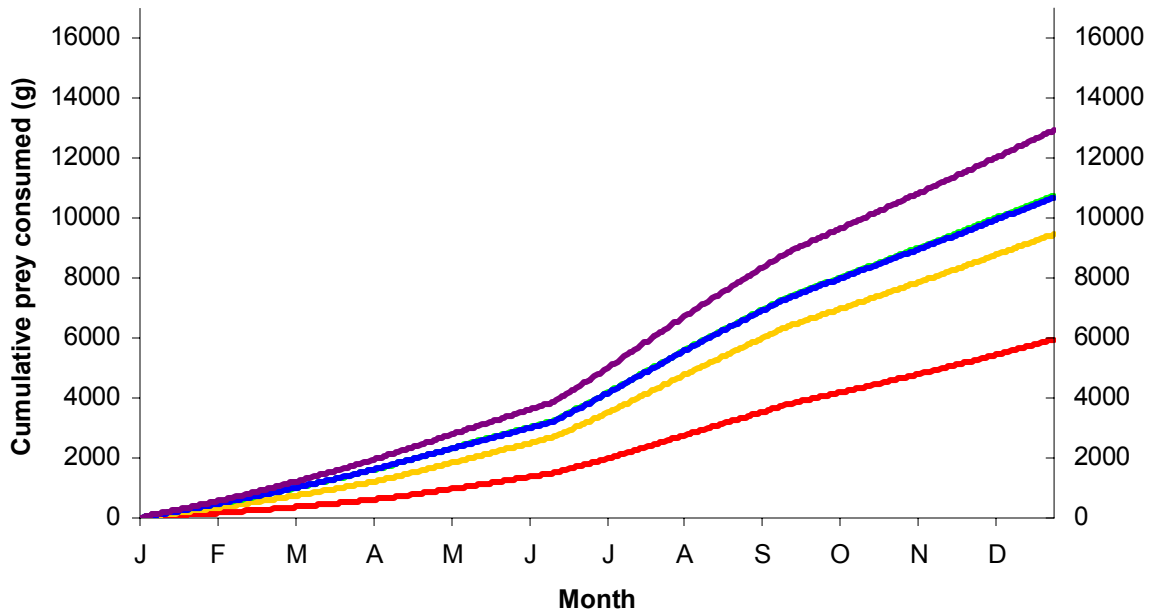


Figure 3.5. Estimates of (a) cumulative consumption (g) and (b) weight (g) of individual age-1 (red), age-2 (yellow), age-3 (green), and age-4 (blue) striped bass in Badin Lake in 2002. Lines indicate values estimated in bioenergetics model simulations, while the points in panel b indicate growth values input to the model based on changes in length predicted by a von Bertalanffy growth curve and the relationship between length and weight and day of the year, as described in the text.

a. Seasonal Consumption of Lake Norman Striped Bass: 2001



b. Seasonal Weight of Lake Norman Striped Bass: 2001

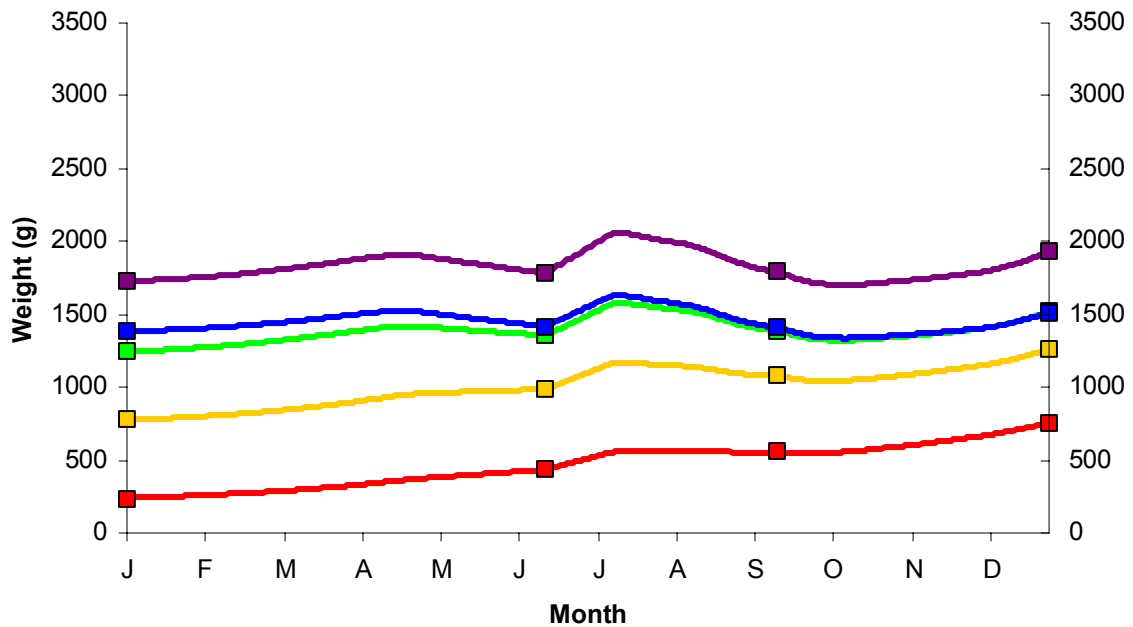
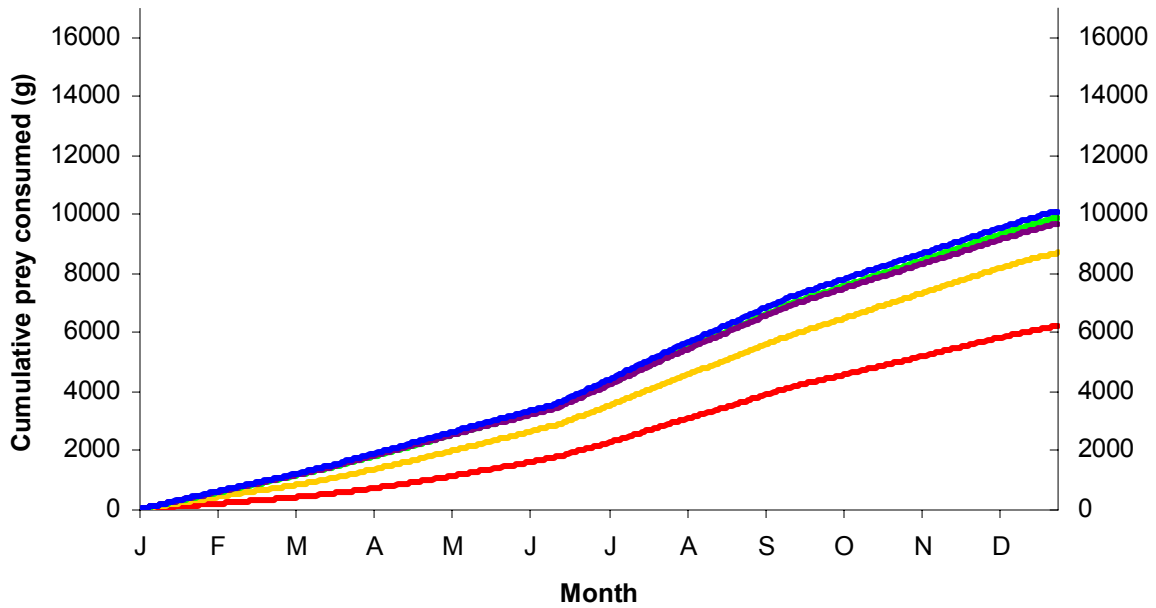


Figure 3.6. Estimates of (a) cumulative consumption (g) and (b) weight (g) of individual age-1 (red), age-2 (yellow), age-3 (green), age-4 (blue), and age-5 (purple) striped bass in Lake Norman in 2001. Lines indicate values estimated in bioenergetics model simulations, while the points in panel b indicate growth values input to the model based on changes in length predicted by a von Bertalanffy growth curve and the relationship between length and weight and day of the year, as described in the text.

a. Seasonal Consumption of Lake Norman Striped Bass: 2002



b. Seasonal Weight of Lake Norman Striped Bass: 2002

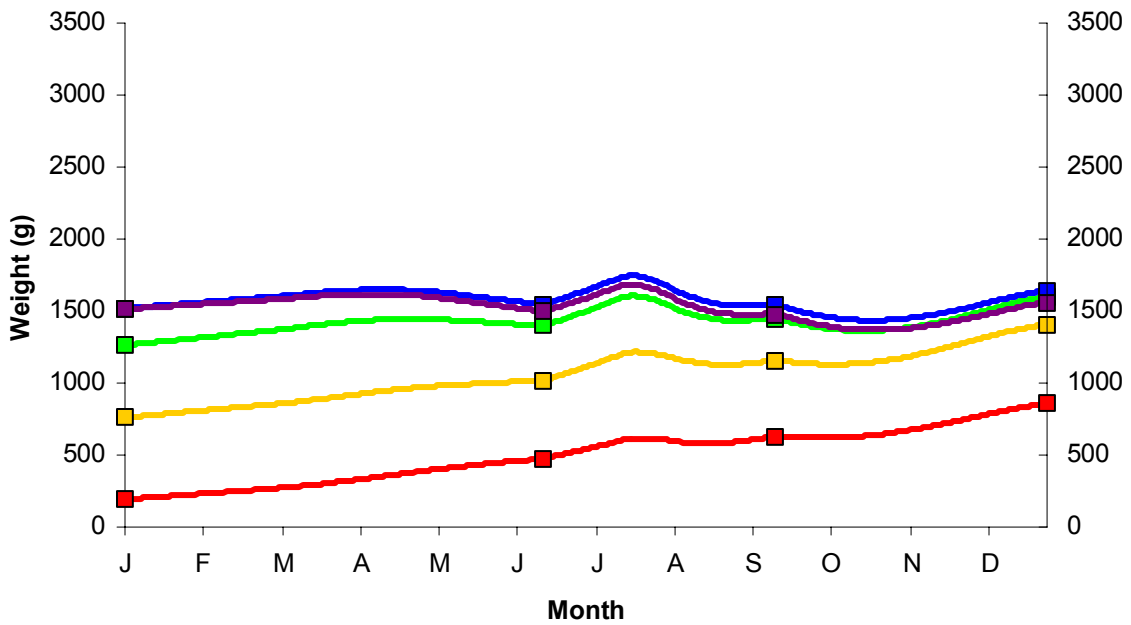


Figure 3.7. Estimates of (a) cumulative consumption (g) and (b) weight (g) of individual age-1 (red), age-2 (yellow), age-3 (green), age-4 (blue), and age-5 (purple) striped bass in Lake Norman in 2002. Lines indicate values estimated in bioenergetics model simulations, while the points in panel b indicate growth values input to the model based on changes in length predicted by a von Bertalanffy growth curve and the relationship between length and weight and day of the year, as described in the text.

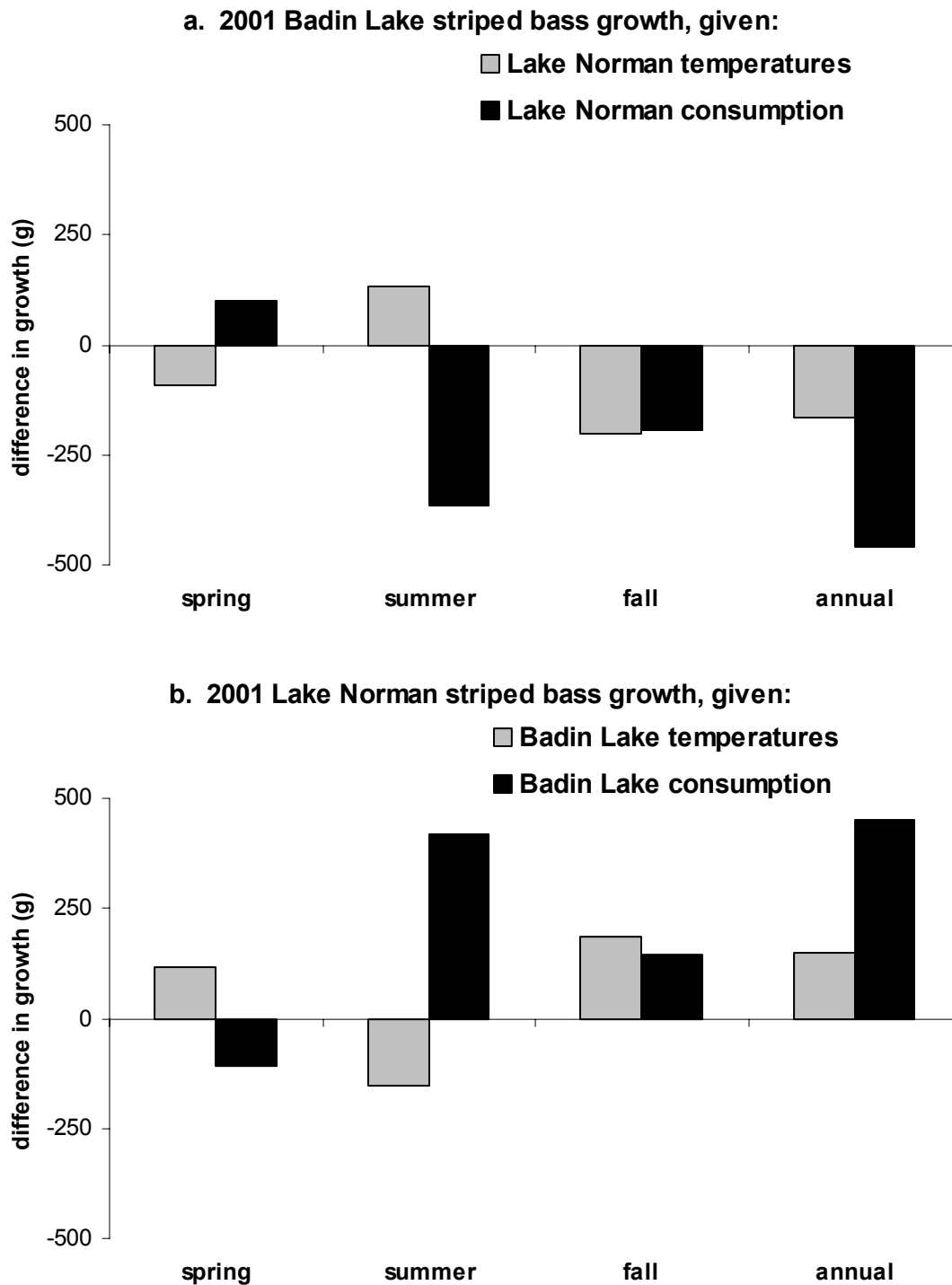


Figure 3.8. Estimated growth (g) in habitat exchange simulations of (a) Badin Lake and (b) Lake Norman striped bass in 2001. Values shown are the differences between the estimated weight gain over the spring, summer, fall, and annual periods and the observed weight gain over those same periods in each system due to substituting the temperature regime (gray bars) or consumption level (black bars) originally estimated in the other system.

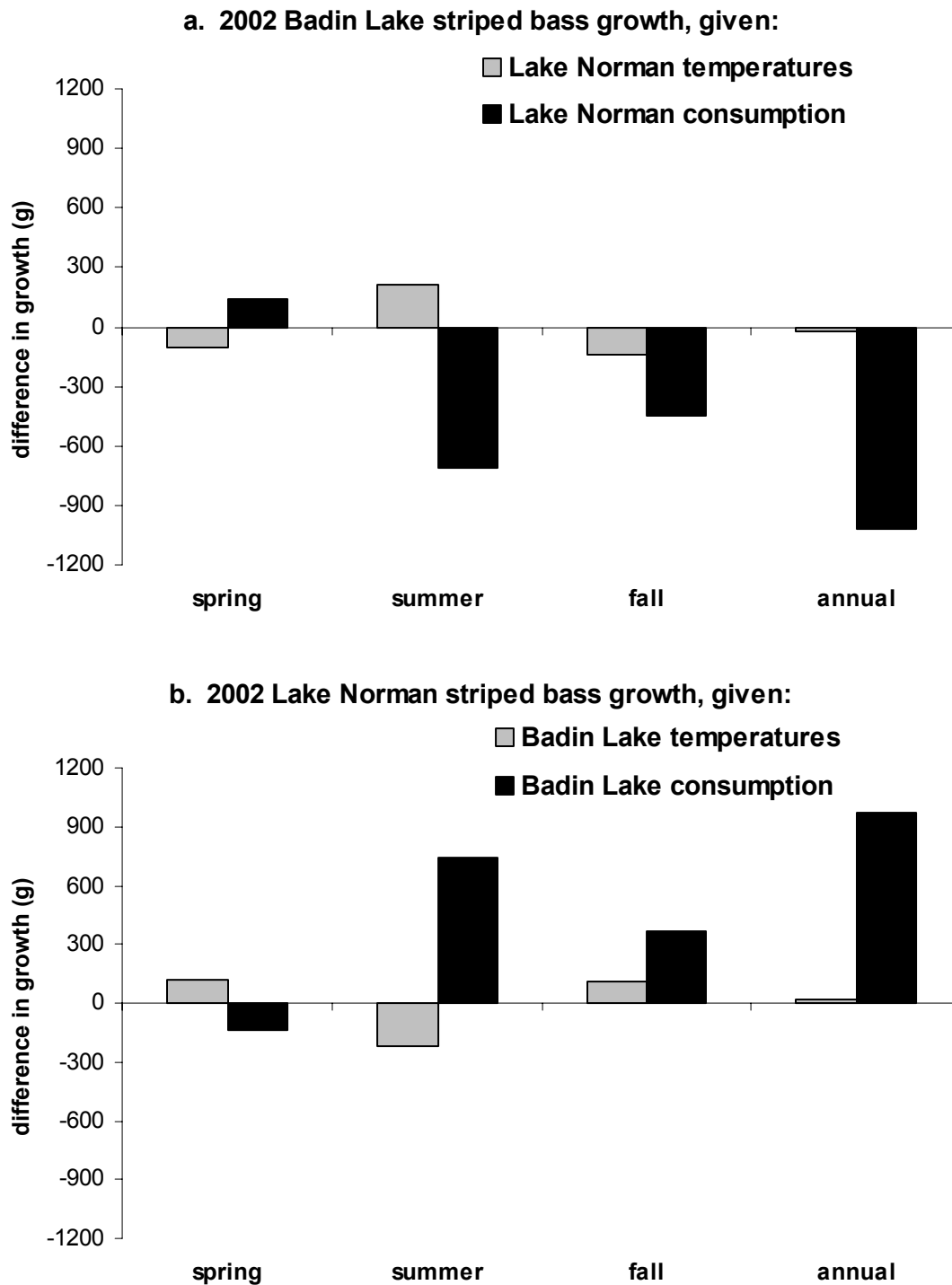


Figure 3.9. Estimated growth (g) in habitat exchange simulations of (a) Badin Lake and (b) Lake Norman striped bass in 2002. Values shown are the differences between the estimated weight gain over the spring, summer, fall, and annual periods and the observed weight gain over those same periods in each system due to substituting the temperature regime (gray bars) or consumption level (black bars) originally estimated in the other system.

Chapter 4

The influence of temperature, forage fish density, and growth rate potential on spatial distribution of a pelagic predator

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Abstract

Temperature and prey resources are important factors influencing habitat selection by fishes. In cases when optimum temperatures and prey densities occur in different patches, the distribution of an integrated measure of habitat quality such as growth rate potential (the rate of growth expected at a particular combination of temperature and food availability) may be a better predictor of habitat selection. Variation in growth rate potential is frequently used as a measure of habitat quality for fishes, but no empirical studies comparing the spatial distribution of a species with the distribution of growth rate potential have been conducted. We evaluated the relationship between the distribution of striped bass *Morone saxatilis* implanted with sonic transmitters and the distribution of temperature, pelagic forage fish density, and growth rate potential in Badin Lake, NC, in the summer and fall of two consecutive years. Temperatures and forage fish densities were interpolated across the system based on vertical profile measurements and hydroacoustic surveys, respectively. Growth rate potential was based on bioenergetics model predictions using observed

temperatures and consumption rates estimated by applying a foraging model to observed prey densities. Significant correlations between striped bass abundance and growth rate potential, based on the results of partial Mantel tests, were found in both summers and in the fall of the first year. Temperature also appeared to have a hierarchical influence on habitat selection. Striped bass avoided regions with the warmest temperatures but high forage fish densities and growth rate potential during the summer sampling periods, and in the fall, one-third to one-half of tagged fish selected cool temperatures at the upstream end of Badin Lake despite the lack of forage fish in this region. This latter pattern may be related to simple selection for temperatures optimizing growth or it may be related to an energetic advantage gained by occupying cool temperatures during non-feeding periods. These results suggest that the distribution of growth rate potential can offer insight into habitat selection, particularly when temperatures are highly heterogeneous such that growth rate potential does not correspond closely with the density of food resources. However, the results of this study also highlight the complexity of habitat selection processes. The spatial distribution of a species such as striped bass is likely to result from a combination of behaviors, including optimization of potential growth under the constraints imposed by environmental variables such as temperature.

Introduction

Evolutionary adaptation should favor the ability of animals foraging in a patchy environment to respond to variation in resource density because a forager's energy intake will affect lifetime fitness, dependent on the animal's ability to either maximize energy intake over time or to minimize the time or risk associated with foraging (Schoener 1971).

Numerous studies across a range of species and habitats have shown that foragers respond to the differential distribution of prey resources (recent examples: Thompson et al. 2001; Harwood et al. 2003; Mori and Boyd 2004; Klaassen et al. 2006; Searle et al. 2006). Habitat characteristics other than resource density may also strongly influence fitness, suggesting that animals will respond to multiple relevant habitat characteristics simultaneously. Theoretical models and empirical studies have demonstrated that animals integrate information on resource density and biotic habitat characteristics such as the density of competitors (e.g., Rosenzweig 1991; Sandlin 2000; Alanara et al. 2001; Gerhardt and Talliaferro 2003) and the presence of predators (e.g., Werner et al. 1983; Gilliam and Fraser 1987; Abramsky et al. 2002; Verdolin 2006; reviewed by Lima and Dill 1990).

Comparatively little is known about how ectotherms integrate and respond to the differential distributions of resource density and temperature, both of which will impact net energy intake and realized growth rates. Thermoregulation has been modeled in the context of optimality theory (Huey and Slatkin 1976), and fish are known to respond to variation in temperature by spending most of their time within a narrow range (*c.* 4°C) of preferred temperatures when those temperatures are available and other habitat characteristics are constant (Magnuson et al. 1979). Animals occupying heterogeneous environments, however, may not be able to optimize temperature and foraging choices simultaneously. Crowder and Magnuson (1983) suggested that an estimate of potential growth that integrates both temperature and food availability, such as might be generated by a bioenergetics model (Kitchell et al. 1977), may be a more appropriate measure of patch quality for fish than prey density or temperature alone. If fish are able to integrate information on temperature and food availability in the environment, then they would be expected to select patches providing

the highest growth rates (Crowder and Magnuson 1983). The intuitive nature of this behavioral energetics hypothesis has led to the use of growth rate potential (Brandt et al. 1992) as an index of habitat quality. Growth rate potential models integrate effects of temperature and food availability on growth in a spatially-explicit context by dividing a system into cells each characterized by forage density, prey size, and temperature. Within each cell, forage density and prey size provide inputs to a foraging model, which predicts consumption, and temperature and estimated consumption then provide inputs to a bioenergetics model, which predicts the growth rate a predator would experience if it occupied that cell (Brandt et al. 1992). Growth rate potential has been used to describe habitat quality for species in both freshwater and estuarine systems (Brandt and Kirsch 1993; Goyke and Brandt 1993; Mason et al. 1995; Luecke et al. 1999; Nislow et al. 2000; Höök et al. 2003; Roy et al. 2004), and estimates of growth rate potential have been used in calculating carrying capacity (Luo et al. 2001) and production (Luo and Brandt 1993; Logerwell et al. 2001).

Authors using growth rate potential as a measure of habitat quality frequently suggest that understanding habitat quality in this context is useful even if it is independent of the occupation of high growth rate potentials by the species of interest (e.g., Brandt and Kirsch 1993; Mason et al. 1995; Höök et al. 2003). However, we contend that such a description of habitat quality has little biological significance if fish do not respond to variation in growth rate potential when making habitat selection decisions. If temperature or prey density alone or some other habitat characteristic such as cover (Bevelhimer 1996) most strongly influences patch choice, then those variables will contribute more to our understanding of habitat selection and will be the most appropriate measure of habitat suitability in

applications such as comparing systems for stocking sport fish (Mason et al. 1995) or potentially developing the most appropriate reserve design (Roy et al. 2004).

The limited information available on the importance of growth rate potential in influencing patch choice of fishes is mixed. In the field, microhabitats occupied by age-0 Atlantic salmon *Salmo salar* had a significantly higher mean growth rate potential than randomly selected available microhabitats (Nislow et al. 2000), but the authors did not describe the overall spatial distribution of fish in relation to the distribution of growth rate potential across the system. In the laboratory, schools of roach *Rutilus rutilus* selected warm temperatures closer to their preferred range, even when food availability at cooler temperatures was up to four times higher (Krause et al. 1998). However, the authors did not discuss the difference in growth rates resulting from these combinations of temperature and food, and they note that feeding occurred on a shorter time scale than their measurements of distribution, with fish waiting in the warmer experimental chamber just until food appeared in the cooler chamber, moving into the cooler chamber to feed rapidly, then returning to the warmer chamber (Krause et al. 1998). Short-term patch choice behavior by juvenile bluegill *Lepomis macrochirus* in the laboratory was based on preferred temperatures rather than optimizing growth rate potential (Wildhaber and Crowder 1990). This result led Wildhaber (2001) to suggest that growth rate potential would not provide a useful predictor of patch choice in fishes, but rather patch choice would be dependent on a hierarchical trade-off between temperature and food where the quality of a patch based on food availability is reduced as the temperature of the patch diverges from the final temperature preferendum of the predator. The relevance of these laboratory observations to behavior of fishes in natural environments, however, is unknown.

We present the first study we are aware of that compares the spatial distribution of a predator with the distribution of temperature, prey density, and growth rate potential across an entire aquatic system. The most insight may derive from such a comparison in a system where trade-offs between regions offering preferred temperatures and high prey availability are likely to exist, as is the case for striped bass *Morone saxatilis* stocked into southern reservoirs. Adult striped bass may experience unsuitable habitat conditions during summer stratification when the cool (20 to 22°C), oxygenated (>2 mg/l dissolved oxygen) water preferred by adult fish is unavailable (Coutant 1985). During these periods, low dissolved oxygen levels in the hypolimnion can force striped bass into epilimnetic water with temperatures well above their preferred range (Chapter 2). The differential distribution of minimum oxygenated temperatures across a reservoir can influence the spatial distribution of striped bass in systems with thermal refuges (Cheek et al. 1985; Coutant 1985; Van Den Avyle and Evans 1990; Schaffler et al. 2002; Young and Isely 2002), as well as those without (Braschler et al. 1988; Farquhar and Gutreuter 1989; Van Horn et al. 1996; this study, Chapter 2). These observations suggest that thermal conditions will have the strongest influence on habitat selection of striped bass during the summer, but the effect of pelagic prey distribution on habitat selection has yet to be investigated. Bioenergetics analysis of reservoir striped bass populations has shown that consumption rates can have a larger impact on realized growth rates than do thermal regimes in some systems (this study, Chapter 3), suggesting that habitat selection based on prey resources or growth rate potential may also be important.

We investigated the relationship between the spatial distribution of striped bass and the distributions of temperature, forage fish density, and growth rate potential in Badin Lake,

North Carolina. In addition to the potential trade-off between minimizing experienced temperatures and occupying areas of high forage fish density during the summer, this system offers a good test of habitat selection based on these three habitat characteristics for several reasons. First, striped bass are pelagic so the effect of physical structure (e.g., woody debris) on fish distribution is likely low. Previous laboratory experiments have shown that the availability of cover can be more important than the energetic quality of a habitat for species strongly oriented towards physical structure (Bevelhimer 1996). Second, because adult striped bass are at the top of the aquatic food web in Badin Lake, the influence of predator avoidance behavior on spatial distribution (Werner et al. 1983; Gilliam and Fraser 1987) is likely negligible. Third, tracking of striped bass tagged with ultrasonic transmitters in this system indicated that striped bass are highly mobile, even within a daily time frame (J. S. Thompson, unpublished data), suggesting that these fish are able to integrate information on the distribution of environmental variables across the reservoir. Fourth, movement of adult striped bass into preferred spawning habitat (although natural reproduction is not successful in most reservoirs, including Badin Lake) is limited to the spring, so habitat selection in other seasons will not be influenced by reproductive behavior. Finally, while growth is often assumed to be related to fitness through the link between rapid growth and higher survival or higher fecundity, these linkages have been directly studied for striped bass. Larger female striped bass are known to produce a greater number of larger eggs resulting in larger, faster-growing larvae (Monteleone and Houde 1990) and striped bass are often prey to gape-limited predators in their natural environment (e.g., Gartland et al. 2006), so behaviors resulting in faster growth rates have been under strong selective pressure in this species.

Comparisons between striped bass distribution and habitat characteristics were conducted on dates in the summer and fall of two consecutive years in order to assess the relative influence of these variables during periods of differing thermal constraints. In addition, forage fish densities were higher over a greater portion of Badin Lake in the summer and fall of the first year compared with the second year, allowing us to compare the strength of the correlation between striped bass and forage fish density or growth rate potential when prey availabilities differed. All analyses were conducted at several spatial scales to account for the potential effect of the scale of observation on interpretation of predator-prey correlations (e.g., Rose and Leggett 1990; Thompson et al. 2001; Stenberg and Persson 2006).

Methods

Study site

Badin Lake is one of a series of impoundments located on the Yadkin River in the piedmont region of North Carolina (Figure 4.1). Badin Lake is 2,165 hectares, moderately eutrophic, and has a mean depth of 21 m and a maximum depth of 54 m. The reservoir is generally stratified from June through early September, with a hypoxic hypolimnion through most of that period. The pelagic forage base is composed primarily of threadfin shad *Dorosoma petenense*, with a small contribution from gizzard shad *D. cepedianum* and blueback herring *Alosa aestivalis* (Appendix B). An active recreational striped bass fishery exists on the reservoir, and the striped bass population is composed of relatively small (< 650 mm) and young (\leq age-4) individuals (Appendix A) due primarily to high fishing mortality rates (Thompson et al. In press).

Spatial distribution of striped bass

The spatial distribution of striped bass in Badin Lake was determined by tagging fish with internal sonic transmitters and relocating tagged fish on August 5 and October 29, 2002, and July 24 and October 1, 2003. Fish located in 2002 were collected and tagged in December 2001 through May 2002. Several fish were collected by angling, but most were obtained by electrofishing in the tailrace of Tuckertown Dam, at the upstream end of Badin Lake (Figure 4.1). Fish located in 2003 included those surviving from 2002, as well as additional fish collected and tagged in February through April 2003. Two of these fish were obtained from anglers, but the remaining fish tagged in the second year were collected using electrofishing below Tuckertown Dam.

Striped bass of legal harvest size (≥ 406 mm) were anesthetized and tagged internally with one of two sizes of ultrasonic transmitters following the methods of Haeseker et al. (1996). The smaller transmitter (Sonotronics IT-95-2; 7 g weight in water) was used for fish less than 1 kg. In addition, some larger fish were tagged with the smaller transmitter so that they could also be implanted with an archival temperature and depth tag (Star-Oddi DST milli; 5 g weight in water) without the total tag weight exceeding 1.5% of their body weight. The Sonotronics IT-95-2 tags were programmed with a one-week on, one-week off transmit schedule to extend the battery life to two years. The larger tag (Sonotronics CTT-83-3; 8 g weight in water) was temperature-sensing and had a continuous transmit state with a battery life of three years. All fish were also tagged externally with a Floy internal anchor tag (FM-95W) containing contact information to encourage anglers to report harvests of tagged fish. After fish recovered from surgery, they were released into the Tuckertown Dam tailrace (Figure 4.1), where most fish had been captured.

The locations of tagged fish known to be alive (based on the occurrence of movement between relocations) were determined on each of the four seasonal search dates by searching the entire reservoir and listening for fish at points well within the 1-km range of the transmitters, accounting for bottom topography and noise interference that might block the tag signal. The position of each tagged fish (as indicated by constant ping volume in all directions) was recorded using a Global Positioning System (GPS) receiver. For each date, tracking continued until the entire reservoir was searched or until all tagged fish were found.

Striped bass locations and all environmental variables were analyzed and compared in two dimensions (latitude and longitude) for all dates. While temperature varied vertically, especially during the summer, the temperatures occupied by striped bass were actually quite predictable based on the vertical distributions of temperature and dissolved oxygen concentration (Thompson et al. In review; this study, Chapter 2). Using the thermal selection rules Thompson et al. (In review) derived from extensive observations of Badin Lake striped bass carrying temperature-sensing transmitters, we were able to map temperature in two dimensions in a biologically meaningful way (see below). In addition, during the summer period, forage fish were distributed in a tight layer from the surface to a depth of 3 to 5 m (J. S. Thompson and J. C. Taylor, unpublished data) due to the shallow depth of the oxycline. We believe it is reasonable to assume that striped bass would respond to the range of prey densities in this layer, rather than the density at any one specific depth. Integrating density throughout this layer allowed us to map prey density in two dimensions (see below). In the fall, the reservoir was essentially isothermal with depth, eliminating the depth component of temperature distribution. While forage fish were distributed in a thicker layer (generally oriented from near the surface to a depth of 9 to 12 m) in the fall (J. S. Thompson and J. C.

Taylor, unpublished data), the lack of thermal constraints makes it even more likely that striped bass would integrate information on forage fish density throughout the water column.

Spatial distribution of temperature

Temperature and dissolved oxygen values were recorded at each 1-m depth interval from the water surface to the bottom at sixteen fixed sites across the reservoir (Figure 4.1) within one to two days of each of the four striped bass relocation dates. For the dates in August 2002 and July 2003, temperature and dissolved oxygen values were then interpolated horizontally across the reservoir at each 1-m depth interval at each point on a 20-m by 20-m grid with a depth of at least 4 m (a total of 33,448 points) using the spline interpolation technique available in the Excel (Microsoft Corporation 2000) Add-In Xlxfun (Advanced Systems Design and Development 2005). The interpolation grid was constrained to points at least 4 m deep because this grid was also used in interpolation of forage fish density, and we were not able to sufficiently sample the shallowest regions of the reservoir with the hydroacoustics gear (see below). Only two striped bass locations were at positions outside of the interpolation grid over the course of the study. These depth-specific interpolations allowed us to create temperature and dissolved oxygen profiles at each point on the interpolation grid. Then using the thermal selection rules developed by Thompson et al. (In review), which indicated that during the summer striped bass occupied temperatures just above the oxycline, we determined the temperature a striped bass would occupy if it was found at that particular location in the reservoir. This approach allowed us to reduce three-dimensional temperature data to two dimensions (latitude and longitude) in a way specifically relevant to the thermal selection patterns of Badin Lake striped bass. It is

important to reiterate that low dissolved oxygen has the greatest influence on the vertical distribution of striped bass during the summer; our two-dimensional maps of temperature reflect the options available to striped bass considering the constraints imposed by dissolved oxygen.

By October of each year the reservoir was no longer thermally stratified and dissolved oxygen was high throughout the water column at each profile site, so for the October dates we interpolated temperature across the reservoir based on the temperature at a depth of 2 m at each profile site. This depth reflected the temperature in the entire water column with the exception of the last one to two meters above the bottom, which were cooler at some of the deepest profile sites.

Spatial distribution of forage fish density

Hydroacoustic surveys to determine forage fish density were conducted within one to four days of each of the four striped bass relocation dates. Both longitudinal and cross-sectional transects (Figure 4.1) were sampled at night when schooling species are typically more disaggregated than during the day (Weston and Andrews 1990; Boudreau 1992; Fréon et al. 1996). Details of hydroacoustic data collection and processing can be found in Taylor et al. (2005). In brief, we used a 200-kHz, Model 241 split-beam echosounder (Hydroacoustic Technology, Inc. [HTI], Seattle, Washington) operating two split-beam transducers. An elliptical transducer (4° by 10° nominal beam dimensions) was oriented horizontally to collect data in the top 2 m of the water column from 1 m to 30 m perpendicular to the path of the boat. A circular transducer (15° nominal beam dimension) was oriented downward to collect data from a depth of 2 m to the bottom. Data were

processed and stored during collection (Digital Echo Processor 3.54, HTI) and then analyzed using split-beam and echo integration techniques (Echoscape 2.10, HTI). Split-beam analysis was used to determine the mean target strength (decibels, dB) of individual fish targets based on the echo level returned to the transducer and the position of the fish relative to the acoustic beam. Echo integration was used to determine the total reflected energy of all targets in the acoustic beam. For each 20 m along the transect, the water column was divided into vertical strata corresponding to the top 2 m (sampled by the side-oriented transducer) and each meter from 2 m to the bottom (sampled by the downward-oriented transducer). For each of these 20-m by 2-m or 20-m by 1-m cells, the total reflected energy was divided by the mean target strength in that cell to obtain a measure of volumetric density (fish/m³). Volumetric densities were then summed across the water column to produce two-dimensional densities (fish/m²) for each 20-m section of each transect. Fish size did not differ substantially between cells.

The spatial structure of these forage fish densities was modeled using a geostatistical approach (Taylor et al. 2005) implemented in S-PLUS 6.1 (Insightful Corp.). Densities were first log-transformed because the data were skewed with a large number of small values and a small number of larger values. The reservoir was divided into five regions (Figure 4.1), and a three-step analysis was then conducted on the log-transformed observed fish densities in each region. First, a generalized additive model (GAM) was used to describe the large-scale trend in fish density as a function of spatial position, expressed in terms of latitude (or northing, km) and longitude (or easting, km). Second, the residuals of the GAM were analyzed for small-scale spatial structure using a variogram model. Because the large-scale trend was removed, the GAM residuals met the requirement of stationarity of the mean

necessary for spatial structure analysis (Cressie 1993). The robust variogram estimator of Cressie and Hawkins (1980) was used to calculate empirical directional variograms that were then assessed for the presence of anisotropy. No anisotropy was observed in any region for any date, so omnidirectional empirical variograms were calculated. The behavior of the empirical variograms indicated that a spherical theoretical variogram model would best fit the data for all dates. The spherical variogram model is described by three parameters: the range, or the distance beyond which points are no longer spatially autocorrelated; the sill, or the total variance in the data set; and the nugget, or the variability that occurs at a scale finer than the spatial analysis. These parameters were fit using weighted, nonlinear least squares (Cressie 1985). Finally, ordinary kriging based on the spherical variogram model was conducted to determine the predicted residual fish density at each point on the same 20-m by 20-m grid used in interpolation of temperature values, with the grid divided into the five regions used in the spatial analysis. Predictions of the GAM at each of the grid points were then added to the predictions from kriging to produce the final fish density estimates.

The species and size composition of the forage fish community was assessed on each of the hydroacoustic survey dates using purse seine hauls in 2002 and mid-water trawls in 2003. Two purse seine hauls (9 m deep by 118 m long net, 4.8-mm mesh size) were taken on each 2002 sampling date: one just south of the confluence of the east and west arms and one in the northwest portion of the west arm basin (Figure 4.1). Trawling (2.4 m by 1.2 m frame, 10 m long net, 5-mm minimum mesh size) was conducted at sites throughout the reservoir. All sampling was conducted just after dark. For each date the length, weight, and species of randomly chosen fish were recorded until at least two hundred of the most common species were measured (Appendix B).

Spatial distribution of growth rate potential

For the calculation of growth rate potential, each point on the 20-m by 20-m grid used in interpolation of environmental variables was considered to be the centroid of a 400 m² cell characterized by the temperature and forage fish density estimated at that point on the grid. A foraging model was used to estimate consumption based on forage fish density. The average number of prey consumed per day (C_{number}) was calculated as the product of the probability of successful attack and capture given an encounter ($p_{attack} \cdot p_{capture} = p$), the volume searched per day (a ; m³), and the prey density (D ; fish/m³):

$$C_{number} = p \cdot a \cdot D$$

(Breck 1993). For each cell, forage fish density (fish/m²) summed over the water column based on hydroacoustic data was converted into average volumetric density (D) by dividing by the average thickness of the forage fish layer in each region of the reservoir used in spatial analysis of forage fish density (Figure 4.1). For sites shallower than this thickness, forage fish density (fish/m²) was divided by the depth of the site.

The effects of prey swimming speed and turbulence were assumed to be negligible compared to the swimming speed of striped bass, so the volume searched per day was modeled by the cylinder model:

$$a = \pi \cdot RD^2 \cdot SS \cdot TF$$

where RD is the reaction distance of the predator, SS is the swim speed of the predator, and TF is the length of time spent foraging per day (Giske et al. 1998). Empirical measures of reaction distance are not available for striped bass. Reaction distance has been assumed to be 0.5 m in many applications of the spatially-explicit growth rate potential model applied to piscivores (Goyke and Brandt 1993; Mason et al. 1995; Mason and Brandt 1996; Luecke et

al. 199). A model of reaction distance of salmonid predators based on light levels and turbidity estimated lower reaction distances (0 to 0.18 m) in a mesoeutrophic system (Beauchamp et al. 1999). However, this model was partially parameterized using laboratory experiments in which predators were allowed to orient to prey based solely on visual stimuli (Vogel and Beauchamp 1999), whereas pelagic predators may rely on a suite of senses when foraging (Giske et al. 1998). The reaction distance of fishes foraging in periods of darkness has been assumed to be equal to the total length of the predator under the assumption that foraging occurs by means of these other senses, particularly the lateral line system (Tyler 1998). In the absence of a better estimate, we modeled reaction distance as a constant 0.5 m, just under the total length of most tagged striped bass in Badin Lake. The value chosen for this parameter will affect the quantitative estimates of growth rate potential but will not affect the relative relationship in growth rate potential between cells because this value is constant across the reservoir.

The swim speed of striped bass during foraging and the length of time spent foraging per day are also unknown. We assumed that striped bass would swim at one body length per second, independent of water temperature. A swim speed of one body length per second has been identified as a good approximation of optimal cruising speed for pelagic predators (Weihs 1973; Ware 1978) and is well within the critical swim speed of striped bass at 15°C (Freadman 1979). The mean estimated length of striped bass relocated on each analysis date was used in calculating swim speed. Length at relocation was estimated by projecting fish along a von Bertalanffy growth curve from its length at tagging for the number of days from tagging to relocation. This growth curve was based on ageing of sagittal otoliths taken from 347 Badin Lake striped bass in 2000 through 2002 (Appendix A). We assumed striped bass

forage primarily during crepuscular periods, so the length of time spent foraging per day was set to two hours. As with reaction distance, any error in assumed swim speed or length of time spent foraging will affect the quantitative values of growth rate potential but not the qualitative relationship between cells because these values did not vary between cells.

The probability of a successful capture given an attack has been determined for striped bass in relation to the prey-to-predator size ratio (PPR):

$$p_{capture} = 0.861 - 1.82PPR$$

(Hartman 2000). We calculated $p_{capture}$ using the ratio of the mean total length of forage fish collected in physical sampling of the prey fish community (by purse seine or trawl; see above) to the mean length of tagged striped bass relocated on each sampling date (see above). Striped bass in Badin Lake feed on prey fish in proportion to their availability, as determined by purse seine sampling, during periods when young-of-year clupeids are abundant (Appendix A), as they would be on both the summer and fall dates analyzed in this study. Assuming that Badin Lake striped bass attacked all prey fish encountered (i.e., $p_{attack} = 1$ such that $p = p_{capture}$) resulted in uniformly high growth rate potential across the entire reservoir for most analysis dates, with no discrimination between regions based on forage fish density or temperature. Based on initial analyses investigating the relationship between values of p_{attack} and resulting measures of growth rate potential over the system, we chose to set p_{attack} equal to 0.10 in order to produce reasonable estimates of growth rate potential that could be used to infer patterns of variation across the system.

For each cell, C_{number} estimated using the foraging model was multiplied by the mean weight of prey fish in physical samples to estimate the mass of prey consumed (C_{mass}). However, the maximum consumption rate of a predator over a unit of time (C_{max}) will be

limited by physiological processes (such as digestion and gut evacuation) whose rates depend on temperature and body size. For each cell, C_{max} was calculated based on the temperature in that cell and the mean weight of relocated striped bass (based on estimated length at relocation and the relationship between weight and length as a function of day of the year; Appendix A) using physiological parameters from Hartman and Brandt (1995). If C_{mass} was greater than C_{max} , then consumption ($C_{predict}$) for that cell was set to C_{max} ; if C_{mass} was less than C_{max} , then $C_{predict}$ was set to C_{mass} .

The final consumption estimate for each cell ($C_{predict}$) was divided by mean striped bass weight to produce a specific rate (C ; $\text{g g}^{-1} \text{ day}^{-1}$) and then input to the Wisconsin bioenergetics model (Kitchell et al. 1977; Hanson et al. 1997) to determine potential growth using physiological parameters for adult striped bass (Hartman and Brandt 1995). Specific growth (G ; $\text{g g}^{-1} \text{ day}^{-1}$) was estimated by a mass balance equation:

$$G = C - (R + F + U)$$

where R is metabolic costs (including those associated with digestion and activity), F is egestion, and U is excretion. Metabolic and waste costs are temperature- and weight-dependent (Hartman and Brandt 1995); the temperature for each cell and the mean weight of relocated striped bass were used in these calculations. The energy densities of predator and prey are also required to convert consumption to growth in energetically equivalent terms. Appropriate size-, season- and year-specific values of striped bass energy density based on sampling of the Badin Lake population (Appendix A) were used for the predator energy densities. Overall prey energy density was calculated based on the size- and season-specific energy densities of each prey item sampled in Badin Lake (Appendix B) and the proportion of each prey type in Badin Lake striped bass stomachs (Appendix A).

Correlation between distribution of striped bass and habitat characteristics

The correlation between the distribution of striped bass and environmental variables was assessed using partial Mantel tests (Smouse et al. 1986). Mantel's test (Mantel 1967) is a regression technique that examines the relationship between two distance matrices describing the pairwise similarities between variables at particular sample locations. The normalized Mantel statistic, r , varies from -1 to 1 , and the significance of this statistic is typically assessed using a permutation test in which the statistic calculated on the original distance matrices is compared to values generated when elements of the matrices are rearranged at random. If a strong relationship exists between the matrices, then the original statistic will be higher (if positive) or lower (if negative) than most of the statistics calculated by random permutations (Fortin and Gurevitch 1993). The partial Mantel test (Smouse et al. 1986) extends this regression technique to three or more distance matrices by calculating the partial correlation between two matrices while controlling for the effects of all others.

Partial Mantel tests were conducted to test for correlation between striped bass abundance and environmental variables at five spatial scales based on the 20-m by 20-m grid used in forage fish density and temperature interpolations. Each point on the grid was considered to be the centroid of a 400 m^2 cell. At the smallest spatial scale analyzed, the reservoir was divided into 60 bins of 22.28 to 22.32 hectares, each containing 557 to 558 of these 400 m^2 cells. The original 60 bins were then combined in groups of two (for 30 bins of 44.56 to 44.64 hectares), three (for 20 bins of 66.84 to 66.96 hectares), four (for 15 bins of 89.12 to 89.28 hectares), and five (for 12 bins of 111.40 to 111.60 hectares). At each spatial scale the minimum over-water distance between the centroid of each bin and all others was measured in a geographical information system (ArcGIS 9, ESRI) to create a distance matrix

describing the spatial relationship between bins. At each spatial scale distance matrices for forage fish density, temperature, growth rate potential, and striped bass abundance were also calculated. While these matrices are also termed “distance” matrices, they simply describe the similarity or dissimilarity between conditions in each bin. Forage fish density, temperature, and growth rate potential distance matrices described the pairwise absolute differences between the mean values (measured at each point on the original interpolation grid) in each bin. Striped bass distance matrices described the pairwise absolute differences between the number of tagged striped bass located in each bin; the actual location of each fish within the bin was not considered, only which bin the fish was located within.

For each sampling date and each spatial scale, three partial Mantel tests were conducted. In the first, the correlation between striped bass abundance and forage fish density was calculated while controlling for the effect of spatial location and temperature. In the second, the correlation between striped bass abundance and temperature was calculated while controlling for the effect of spatial location and forage fish density. In the third, the correlation between striped bass abundance and growth rate potential was calculated while controlling for the effect of spatial location. For the October sampling dates, a fourth test was conducted to calculate the correlation between striped bass abundance and growth rate potential while controlling for the effects of both spatial location and temperature. This last test was used to evaluate the relationship between striped bass and growth rate potential while accounting for the fact that a moderately high proportion of fish were found at cooler temperatures in the Tuckertown Dam tailrace on these dates. The significance of each partial Mantel statistic was calculated based on 10,000 permutations. One-tailed probability levels were used, with the right-hand tail probability being used for positive observed statistics and

the left-hand tail probability being used for negative observed statistics. All partial Mantel tests were conducted in S-PLUS 6.1 (Insightful Corp.).

Results

Early August 2002

Temperatures just above the oxycline varied from 28.4 to 31.4°C in early August 2002 (Figure 4.2a). The upper east and west arms contained the warmest temperatures, typically greater than 29.5°C, while temperatures in the lower east and west arms ranged from 28.7 to 29.3°C. The coolest temperatures on this date were found in the southernmost section of the reservoir (Figure 4.2a).

Interpolated forage fish densities ranged from 0.28 to 6.12 fish/m² (Figure 4.2b), with a mean of 2.52 fish/m² (standard deviation [SD] = 1.08 fish/m²). The large-scale GAM trend explained 18 to 69% of the variability in observed forage fish density, depending on the region of the reservoir (Table 4.1). Small-scale spatial structure was present in the GAM residuals for all regions. While clupeids disaggregate during the night compared with daytime conditions, patchiness related to schooling has been seen in nighttime sampling in other systems (Schael et al. 1995; Fréon et al. 1996; Taylor 2004), and such patchiness would lead to small-scale structure of the type observed in our study. The parameters fit to the variograms describing that structure varied between regions (Table 4.1, Figure 4.3). The range parameter, which can be visualized as the distance (km) at which the modeled variogram reaches its asymptote (Figure 4.3), was fairly similar for all regions except region 2, which had a range more than twice that of any other region (Table 4.1, Figure 4.3). This longer range resulted from a large patch of fish present in the upper section of the west arm

basin (Figure 4.2b). Forage fish densities were generally highest (> 3.5 fish/m²) in the west arm basin, the uppermost portion of the east arm, and the southernmost tip of the reservoir (Figure 4.2b). Moderately high densities between 2 and 3.5 fish/m² were also found in the central portion of the west arm, just east of the islands located in the middle section of the east arm, and throughout the southern section of the reservoir (Figure 4.2b).

Growth rate potential varied from -0.0116 to 0.0068 g g⁻¹ day⁻¹ (Figure 4.2c), with a mean of 0.0041 g g⁻¹ day⁻¹ (SD = 0.0031 g g⁻¹ day⁻¹). The highest growth rate potential values were seen in portions of the lower east arm and in the southern section of the reservoir (Figure 4.2c). Fairly high growth rate potential was also found in the west arm basin, while low growth rate potential values occurred in the upper east and west arms and at the confluence of the east and west arms (Figure 4.2c).

In early August 2002, 19 tagged striped bass (mean total length \pm SD: 596 ± 77 mm; mean weight \pm SD: 2299 ± 977 g) were located. Fish were found in an aggregation in the central portion of the east arm, as well as in the lower portion of the east arm, the upper portion of the southern region of the reservoir, and the upper portion of the west arm basin (Figure 4.2). With the exception of one fish in the upper east arm, tagged striped bass were found at or below the median temperature of 29.1°C (Figure 4.2a). However, striped bass were distributed throughout the lower range of temperatures, and no significant correlation between striped bass abundance and temperature was found at any spatial scale. A marginally significant negative correlation was found at the smallest spatial scale (Table 4.2), but in the context of the partial Mantel tests used in this study, a negative correlation indicates that locations more similar in striped bass abundance were more dissimilar in temperature, again reflecting the range of temperatures occupied. In addition, striped bass

were found across the range of forage fish densities observed. Three fish overlapped with high forage fish densities in the northwest portion of the west arm basin, but striped bass were also found at moderate densities in the southern portion of the reservoir and the southeast portion of the east arm and at low densities in the central section of the east arm and the confluence of the east and west arms (Figure 4.2b). No significant correlation between striped bass abundance and forage fish density was found at any spatial scale on this date. Thirteen of nineteen (68%) tagged striped bass were found at or just below the maximum growth rate potential observed on this date (0.005 to $0.007 \text{ g g}^{-1} \text{ day}^{-1}$) in the west arm basin, the upper portion of the southern region, and the eastern edge of the lower east arm (Figure 4.2c). An additional three fish were found just adjacent to an area of high growth rate potential, and only one fish was located at a negative growth rate potential value (Figure 4.2c). Reflecting these observations, a marginally significant correlation between striped bass abundance and growth rate potential was found in the middle range of spatial scales tested (Table 4.2).

Late July 2003

Temperatures just above the oxycline in late July 2003 were cooler than those observed in the previous summer, ranging from 26.7 to 28.9°C across the reservoir (Figure 4.4a). Temperatures above 28°C were located only in the upper region of the east arm, while temperatures in most of the west arm and the lower portion of the east arm varied from 27 to 27.6°C . Slightly cooler temperatures below 27°C were found in the southern portion of the reservoir and the Tuckertown Dam tailrace (Figure 4.4a).

Interpolated forage fish density in late July 2003 varied from 0.01 to 5.50 fish/m² (Figure 4.4b). While maximum fish density was similar to that observed in the summer of 2002, patches of high density were smaller and less common in 2003 (Figure 4.4b), resulting in a much lower mean fish density of 0.88 fish/m² (SD = 0.66 fish/m²). Large-scale trends were particularly pronounced on this date, and the GAM explained 38 to 73% of the spatial variability in fish density in each region of the reservoir (Table 4.3). The range parameters of the spherical variogram models fit to the GAM residuals were higher than in previous dates for all regions except region 2, which had the lowest range on this sampling date (Table 4.3, Figure 4.5). The sill, which can be visualized as the value of the semivariance at the asymptote of the model variogram (Figure 4.5), was quite high in region 4 (Table 4.3, Figure 4.5). While it is unclear what factors may have increased the variability in densities in this area, the theoretical variogram model provided a reasonable fit to the empirical variogram, particularly at short distances, so kriging should provide valid predictions of fish density in this region. Both observed and predicted forage fish densities were low (< 0.5 fish/m²) throughout region 4 (Figure 4.4b). Four distinct patches of high density (> 2 fish/m²) were observed on this date: in the uppermost region of the east arm, in the central section of the east arm, at the confluence of the east and west arms, and in the central portion of the southern section of the reservoir (Figure 4.4b). Moderate fish densities between 1 and 2 fish/m² were also found throughout most of the east arm, above Badin Dam, and in the eastern portion of the west arm basin (Figure 4.4b).

Growth rate potential ranged from -0.0124 to 0.0083 g g⁻¹ day⁻¹ (Figure 4.4c), with a mean value of -0.0067 g g⁻¹ day⁻¹ (SD = 0.0041 g g⁻¹ day⁻¹). Regions of positive growth rate potential were very limited on this date. The highest growth rate potential values were seen

in four small patches (Figure 4.4c) corresponding to the four areas of highest forage fish density (Figure 4.4b). A larger region of low, positive growth rate potential was seen in the lower portion of the east arm (Figure 4.4c).

Twenty-two tagged striped bass (mean total length \pm SD: 631 \pm 71 mm; mean weight \pm SD: 2674 \pm 890 g) were located on the summer sampling date in 2003. All tagged striped bass were found at or below the median temperature (27.1°C) just above the oxycline on this date (Figure 4.4a), although as in the previous summer (Figure 4.2a), striped bass were found throughout the cooler range of temperatures (Figure 4.4a). A significant correlation between striped bass abundance and temperature was found at the largest spatial scale tested (Table 4.4), likely because many of the fish found in the coolest temperatures in the lower east arm and the confluence of the east and west arms (Figure 4.4a) were grouped at this largest scale. Tight groups of striped bass overlapped with dense forage fish patches at the confluence of the east and west arms and in the middle portion of the east arm, and over 75% of tagged striped bass were found at forage fish densities of at least 1 fish/m² on this date (Figure 4.4b). The correlation between striped bass abundance and forage fish density was significant or marginally significant at all spatial scales tested (Table 4.4). Tagged striped bass at the confluence of the east and west arms and in the middle portion of the east arm were located at high growth rate potentials, and fish in the lower portion of the east arm were also found at positive growth rate potentials (Figure 4.4c). As for forage fish density, the correlation between striped bass abundance and growth rate potential was significant or marginally significant at all spatial scales (Table 4.4).

Late October 2002

Temperatures were isothermal with depth and varied from 17.2 to 19.6°C across Badin Lake in late October 2002 (Figure 4.6a). The majority of the lake had temperatures above 19°C with the exception of the uppermost portion of the west arm in the tailrace of the Tuckertown Dam (Figure 4.6a), which contained cooler water as a result of water discharge from the deepest region of Tuckertown Reservoir.

Interpolated forage fish density ranged from 0.11 to 3.65 fish/m² (Figure 4.6b), with a mean density of 1.01 fish/m² (SD = 0.54 fish/m²). Depending on the region of the reservoir being analyzed, the large-scale GAM trend explained 17 to 66% of the variability in observed forage fish density (Table 4.5). Small-scale spatial structure was modeled by a spherical variogram model for all regions (Table 4.5, Figure 4.7). As in early August 2002, the range parameter was greatest in region 2, but the sill parameters were generally higher on this date (Table 4.5) than in the summer (Table 4.1), indicating greater global variances in the fall hydroacoustic data (Table 4.5). The highest forage fish densities (>2 fish/m²) were found primarily in the central section of the west arm, as well as small patches in the upper portion of the east arm (Figure 4.6b). Densities of at least 0.5 fish/m² were observed throughout most of the reservoir in late October, with the exception of the upper section of the west arm and small patches of low density primarily in the central section of the east arm (Figure 4.6b).

In late October 2002, mean growth rate potential was 0.0039 g g⁻¹ day⁻¹ (SD = 0.0048 g g⁻¹ day⁻¹), and growth rate potential values ranged from -0.0056 to 0.0114 g g⁻¹ day⁻¹ (Figure 4.6c). The highest growth rate potential values were found in the upper portion of the west arm basin and throughout the middle portion of the west arm (Figure 4.6c). Patches

of moderate to high growth rate potential were also seen in the upper east arm, near the confluence of the east and west arms, and in small patches in the southern portion of the reservoir (Figure 4.6c).

Sixteen tagged striped bass (mean total length \pm SD: 602 \pm 54 mm; mean weight \pm SD: 2484 \pm 684 g) were located in late October 2002. Seven of these were found in cool, flowing water in the Tuckertown Dam tailrace at the lowest temperatures observed on this date (Figure 4.6a), and a highly significant correlation between striped bass abundance and temperature was found at all spatial scales tested (Table 4.6), indicating a high degree of dependency between striped bass abundance and temperature. Forage fish density (Figure 4.6b) and growth rate potential (Figure 4.6c) were low in the upper west arm. For those striped bass not located in the tailrace, six of nine tagged fish (67%) were found in the patch of high forage fish density (1.5 to 3 fish/m²; Figure 4.6b) and high growth rate potential (\geq 0.009 g g⁻¹ day⁻¹; Figure 4.6c) located in the central portion of the west arm on this date. Similar to the summer dates (Figures 4.2, 4.4), regions of high growth rate potential in the upper east arm and southernmost portion of the reservoir were unoccupied by tagged striped bass (Figure 4.6). Occupation of the west arm may have been related to the slightly cooler temperatures (0.1 to 0.4°C; Figure 4.6a) or the larger patch size (Figure 4.6c) in the west arm compared with other regions of high growth rate potential or due to the proximity of this region to the Tuckertown Dam tailrace. Marginally significant correlations were found between striped bass abundance and forage fish density and between striped bass abundance and growth rate potential after controlling for the effect of temperature at the smallest three spatial scales tested (Table 4.6).

Early October 2003

In early October 2003, temperatures were generally isothermal with depth and ranged from 21.9 to 23.4°C (Figure 4.8a). Most of the reservoir contained temperatures above 23°C, with slightly cooler temperatures in the uppermost section of the east arm and the coolest temperatures in the uppermost portion of the west arm (Figure 4.8a). As in the fall of 2002, the cool water in the tailrace on this date was the result of water discharge from the upstream reservoir.

Mean interpolated forage fish density was 0.55 fish/m² (SD = 0.68 fish/m²) and varied from 0.01 to 7.02 fish/m² in early October 2003 (Figure 4.8b). The GAM trend explained 18 to 64% of the variability in forage fish density, depending on the region of the reservoir being analyzed (Table 4.7). The sill parameter of the spherical variogram model was highest in region 4 (Table 4.7), similar to the summer date in this year. The empirical variogram for region 5 was more variable about the sill than for the other regions and dates modeled (Figure 4.9), and alternate forms of large-scale trend model did not improve the stability of the variogram. However, the theoretical variogram fit the empirical values closely at distances smaller than the range, which is most critical for the success of interpolation techniques such as kriging (Fortin and Dale 2005). Very dense patches of forage fish were observed at the upper end of the east arm and in the center of the west arm basin, as well as high density patches in the northern portion of the west arm basin and the central section of the west arm (Figure 4.8b). Moderate densities of 0.5 to 1.5 fish/m² were also observed in the central section of the east arm and near the confluence of the east and west arms (Figure 4.8b).

Growth rate potential ranged from -0.0081 to $0.0112 \text{ g g}^{-1} \text{ day}^{-1}$ (Figure 4.8c), with a mean value of $-0.0021 \text{ g g}^{-1} \text{ day}^{-1}$ (SD = $0.0054 \text{ g g}^{-1} \text{ day}^{-1}$). Regions of highest growth rate potential were seen in the upper east arm, portions of the west arm basin, and the middle section of the west arm (Figure 4.8c). Fairly high growth rate potential was also found in the middle portion of the east arm, while a large region of low but positive growth rate potential was seen near the confluence of the east and west arms (Figure 4.8c).

Twenty-six tagged striped bass (mean total length \pm SD: $659 \pm 71 \text{ mm}$; mean weight \pm SD: $3155 \pm 991 \text{ g}$) were located in early October 2003. Ten striped bass were located in cool, flowing water in the Tuckertown Dam tailrace and one additional fish was found in the upper west arm at the coolest temperatures observed in the reservoir on this date (Figure 4.8a). The correlation between striped bass abundance and temperature was significant or marginally significant at all spatial scales tested (Table 4.8). Thirteen of the fifteen striped bass not located in the upper west arm were found at moderate forage fish densities of 0.5 to 1.5 fish/m^2 (Figure 4.8b). These forage fish densities were substantially lower than the highest densities observed on this date, but they were also higher than the very low densities seen throughout much of the system (Figure 4.8b). Growth rate potential was positive for these thirteen striped bass and was relatively high for a group of fish located in the middle portion of the east arm (Figure 4.8c). However, the regions of highest growth rate potential in the upper east arm, the west arm basin, and the middle portion of the west arm were unoccupied by tagged striped bass (Figure 4.8c). No significant correlations between striped bass and forage fish density or growth rate potential were found on this sampling date, even after controlling for the effect of temperature.

Discussion

Our study demonstrates that the distribution of growth rate potential can improve our understanding of the spatial distribution of a pelagic predator, particularly when thermal conditions are highly heterogeneous. This result was especially evident in the summer of 2002, when thermal conditions were highly unsuitable but striped bass in Badin Lake did not optimize patch choice with respect to temperature or forage fish density. On this sampling date, striped bass were found across the cooler range of temperatures but did not occupy the coolest temperatures available despite all temperatures being substantially higher than the optimum value for growth (14.2°C; based on parameters in Hartman and Brandt 1995), the mean occupied summer temperatures of adult striped bass in a Tennessee reservoir with a wide range of available temperatures (17.5°C; Bettoli 2005), or the preferred temperatures displayed by striped bass seeking thermal refuges during the summer (20 to 22°C; Coutant 1985). Similarly, while some striped bass were located at very high forage fish densities in the west arm basin, most tagged fish were found at more moderate forage fish densities despite higher densities being available at similar or even lower temperatures. Striped bass did not, therefore, optimize patch choice with respect to resource density, either alone or in conjunction with a trade-off with temperature. The distribution of growth rate potential explains many of these seemingly unexpected spatial patterns. The west arm basin, where forage fish densities were highest, actually had slightly lower growth rate potential values than some areas of the lower east arm and southern region of the reservoir. The west arm forage fish densities resulted in potential consumption above C_{max} , the physiological maximum consumption rate, so these high forage fish densities were not physiologically available and the slightly higher temperatures in the west arm reduced potential growth at the

maximum consumption rate. In contrast, striped bass occupying more moderate forage fish densities at slightly cooler temperatures were able to maximize their growth rate. Regions of high and moderate forage fish densities in the upper east and west arms that were unoccupied by tagged striped bass had low growth rate potential due to the very high temperatures in those areas. Positive growth of adult striped bass requires consumption at or close to C_{max} at temperatures above 29.5°C (Thompson et al. In review; this study, Chapter 2).

The spatial distribution of growth rate potential also provided insight into the pattern of striped bass distribution in the summer of 2003. Forage fish were generally less abundant and occurred in smaller patches on this sampling date, and in contrast to the previous summer, variation in forage fish density had a greater effect on growth rate potential than did variation in temperature. Patches with the highest growth rate potential corresponded directly to the densest patches of forage fish. Groups of striped bass occupied two of the four patches in the reservoir with the highest forage fish densities and highest growth rate potential. The largest group of tagged striped bass on this date, located in the southern portion of the east arm, was found at moderate forage fish densities similar to those available in other regions of the reservoir. The cooler temperatures in this region, however, resulted in this area having the highest growth rate potential of any region outside the four small patches of highest growth rate potential. Therefore, while these fish were not optimizing their patch choice based on growth rate potential, i.e., occupying the highest growth rate potential available, an explanation for the occupation of this particular region is more evident based on the distribution of growth rate potential than on the distribution of forage fish alone.

Unlike in the summer of 2002, the patch of high forage fish density in the upper east arm did correspond to an area of high growth rate potential in 2003 because temperatures in

this region, while the warmest observed on this date, were cooler than in the previous summer. The absence of tagged striped bass in the upper east arm suggests that temperature may have a hierarchical role in habitat selection under some circumstances, and while fish were not found at the absolute minimum temperatures available, they may still be responding to the relative relationship of thermal constraints across the system. The patch of high growth rate potential in the southern portion of the reservoir was also unoccupied by tagged striped bass, a pattern that was more surprising given the relatively cool temperatures in this region and the limited availability of high growth rate potential across the system on this date. While the relatively low sample size of tagged striped bass in this study precludes identification of all regions of the reservoir occupied by the striped bass population, the smaller patch size on this sampling date may also have made it more difficult for striped bass to track growth rate potential closely. Biweekly relocations of tagged striped bass in Badin Lake associated with estimating mortality (Thompson et al. In press) and thermal selection (Thompson et al. In review; Chapter 2) showed that striped bass generally avoided both the far southern region of the reservoir and the upper end of the east arm. Fish may avoid these regions or prefer other regions of the reservoir based on habitat characteristics we have not identified. If fish rarely search these areas, it will likely be more difficult for them to locate isolated resources in these regions.

On both fall sampling dates, a fairly substantial proportion (2002: 44%; 2003: 38%) of tagged striped bass were located in the uppermost portion of the west arm just below Tuckertown Dam despite the lack of forage fish and the low growth rate potential estimated in this area. Many fish species are drawn to regions of high flow and this has been demonstrated for striped bass in the spring (Wilkerson and Fisher 1997; Jackson and

Hightower 2001; Schaffler et al. 2002; Young and Isely 2002; this study, Chapter 2). Striped bass may also respond to variation in flow at other times during the year, and the occupation of the Tuckertown Dam tailrace when water is being released from the dam may reflect this inclination. There are also two possible explanations for the relatively high occupation of this habitat based on the presence of cool temperatures in this area. First, behavioral thermoregulation suggests that fish will occupy the temperature that maximizes growth when consumption is at the maximum consumption rate possible within physiological limits. Striped bass displaying this form of patch choice behavior would select the coolest temperatures down to 14.2°C, such that habitat selection may be influenced by the distribution of temperature even in the fall months. However, tagged striped bass were found in the Tuckertown Dam tailrace on most tracking dates in the late fall and winter of 2002 and 2003, even after the cooler temperatures of the tailrace dropped well below 14.2°C (J. S. Thompson, unpublished data). This result supports a second possible explanation for this behavior. Striped bass may gain an energetic advantage by occupying these cooler temperatures, where metabolic rates are reduced, during non-feeding periods. This hypothesis has been suggested to explain diel vertical migrations of fish between warmer depths with abundant food and cooler, deeper depths (Brett 1971; Bevelhimer and Adams 1993; Rosland and Giske 1994; Sims et al. 2006). While a few tagged striped bass remained in the tailrace during successive biweekly relocations, most fish that utilized tailrace habitat in the fall and winter were found in the tailrace and then in the main body of the reservoir on alternating relocation dates. This pattern suggests that fish move out of the tailrace and into more productive areas for feeding bouts, although this behavior could also occur if fish were drawn into the upper west arm simply by selection for the coolest temperatures available

during the period when those temperature are still above 14.2°C. Striped bass were only located in the tailrace in substantial numbers (> 15% of tagged fish) on relocation dates when temperatures were cooler than the remainder of the reservoir (J. S. Thompson, unpublished data).

As expected due to the greater homogeneity of temperatures, the distribution of growth rate potential and forage fish densities were similar on the fall sampling dates so the distribution of growth rate potential did not provide as much additional insight into striped bass distribution as in the summer. In the fall of 2002, 67% of tagged striped bass not located in the upper west arm were found in a dense patch of forage fish at or close to the maximum growth rate potential available in the system. The spatial distribution of striped bass not located in the upper west arm of the reservoir in the fall of 2003, however, was not as clearly associated with high forage fish densities or high growth rate potentials. The largest group of striped bass, located in the middle portion of the east arm, occupied a region of relatively high growth rate potential, and all but two tagged striped bass not in the upper west arm were found at positive growth rate potentials even though a large proportion of the reservoir was estimated to have negative growth rate potentials on this date. However, patches with the highest growth rate potential, corresponding to areas of high forage fish density, were unoccupied by tagged striped bass on this sampling date.

Better parameterization of foraging models for piscivorous fishes may improve our ability to evaluate spatially-explicit growth rate potential models as predictors of spatial distribution and will be necessary to move from relative comparisons across or between systems to estimating expected growth based on habitat characteristics. In our application, most of the parameters included in the foraging model used to estimate consumption,

including reaction distance, swim speed of the predator, length of time spent foraging, and the probability that a prey item was attacked once detected, had a large impact on values of estimated growth rate potential. Because these parameters were held constant across the system, they will not affect the relative relationship between growth rate potential in different cells (Brandt and Kirsch 1993). However, depending on the parameters chosen, we found that the range of forage fish densities we observed could result in growth rate potential values that were almost uniformly high to almost uniformly low across the system. We believe the foraging model parameters that we used are reasonable, but further laboratory and field studies aimed at improving estimates of foraging model parameters will improve our confidence in these results. This improved parameterization may be particularly useful in understanding habitat selection during periods when fish appear to occupy marginal growth rate potential habitat, such as the fall 2003 sampling date in our study, because these parameters will affect how quickly growth rate potential increases with small increases in forage fish density.

The spatial scale of analysis is frequently important in studies of correlations between predators and their prey (e.g., Rose and Leggett 1990; Thompson et al. 2001; Stenberg and Persson 2006). For each of the four sampling dates in our study, the significance of the correlation between striped bass distribution and the distribution of one or more environmental variables depended on the spatial scale being tested. The relationship between spatial scale and the significance of these correlations was not, however, consistent across dates and did not appear to be dependent on the scale of spatial heterogeneity of environmental conditions. In general, when significant or marginally significant relationships were found, these correlations occurred across the smaller range of spatial

scales tested, as was seen for temperature and growth rate potential in early August 2002 and forage fish density and growth rate potential in late October 2002. In late July 2003, however, the relationship between the distributions of striped bass and temperature was only significant at the largest spatial scale, and the relationships between striped bass and forage fish density and growth rate potential were significant at the smallest scales and the largest scale but not at the middle range of scales tested. Studies finding a consistent scale-dependent relationship between mobile predators and prey have frequently included a wider range of spatial scales (e.g., Rose and Leggett 1990) than we were able to include in our study due to the small size of Badin Lake. Given the high mobility of striped bass, it is perhaps not surprising that we did not see consistent scale-dependency over the range of scales we tested. However, it is important to note that we may not have identified all of the relevant correlations between striped bass and environmental variables if we had chosen only one arbitrary spatial scale for our analysis, emphasizing the importance of studying habitat selection at multiple scales.

Overall, patch choice based on variation in growth rate potential provided the single best rule to explain the spatial distribution of tagged striped bass in Badin Lake, NC, across our sampling dates. The correlation between striped bass abundance and growth rate potential was significant or marginally significant for three of the four dates in our study, suggesting that growth rate potential may provide a biologically meaningful measure of habitat quality for similar pelagic, apex predators whose patch choice behavior is unlikely to be strongly influenced by physical structure (Bevelhimer 1996) or predator avoidance (Werner et al. 1983; Gilliam and Fraser 1987). However, our study also illustrates the complexity common in empirical studies of habitat selection (Perry and Pianka 1997). While

we can reasonably explain the patterns of striped bass distribution we observed in relation to habitat characteristics, these distributions would have been difficult to predict in their entirety because striped bass did not consistently optimize their patch choice behavior with respect to temperature, forage fish density, or growth rate potential. In the summer, temperature seemed to exert a hierarchical influence on habitat selection, causing striped bass to avoid regions of high growth rate potential that occurred at particularly warm temperatures, even when regions of high growth rate potential were limited across the system. In the fall, some striped bass were found at cool temperatures with limited prey resources, suggesting that striped bass may prefer to occupy cooler temperatures during non-feeding periods and spatial distributions may shift over finer time-scales than were analyzed in this study. Across both seasons, tagged striped bass were absent from some regions of high growth rate potential. Of course, the value in optimality theory is not in proving that animals' behavior is optimal, but rather in providing a framework to help us understand how animals experience their environment within their own set of evolutionary adaptations. We do not presume that striped bass can estimate growth rate potential, *per se*, but our study provides evidence that variation in growth rate potential is a useful way to investigate how fish integrate information on temperature and prey availability. Further comparisons between the distributions of fish and growth rate potential in heterogeneous systems should help us determine the range of conditions over which growth rate potential continues to be a useful way to understand patch choice behavior.

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Tables

Table 4.1. Percent of variability in forage fish density explained by GAM trend and spherical variogram parameters fit to GAM residuals for forage fish densities measured by hydroacoustics in early August 2002. Results are provided for the five regions of Badin Lake identified in Figure 4.1.

	% of variability explained by GAM	spherical variogram model parameters		
		range (km)	sill	nugget
Region 1	39%	0.1219	0.0728	0.0444
Region 2	69%	0.6808	0.0911	0.0403
Region 3	18%	0.1897	0.1895	0.0630
Region 4	61%	0.2903	0.1971	0.1481
Region 5	63%	0.1446	0.1016	0.0473

Table 4.2. Results of partial Mantel tests examining correlation between the spatial distribution of striped bass abundance and the distributions of forage fish density, temperature, and growth rate potential in early August 2002. Results are given for five spatial scales ranging from the reservoir being divided into 60 spatial bins to 12 spatial bins; further description of spatial scales is given in the text. Partial normalized Mantel statistics, r , and p-values are given for tests significant at $\alpha \leq 0.10$. All tests accounted for the effect of spatial location on striped bass abundance; additional details are provided in the text.

	60 bins	30 bins	20 bins	15 bins	12 bins
forage fish density	--	--	--	--	--
temperature	$r = -0.083$ $p = 0.061$	--	--	--	--
growth rate potential	--	$r = 0.119$ $p = 0.061$	$r = 0.163$ $p = 0.060$	--	--

Table 4.3. Percent of variability in forage fish density explained by GAM trend and spherical variogram parameters fit to GAM residuals for forage fish densities measured by hydroacoustics in late July 2003. Results are provided for the five regions of Badin Lake identified in Figure 4.1.

	% of variability explained by GAM	spherical variogram model parameters		
		range (km)	sill	nugget
Region 1	38%	0.3586	0.5641	0.0339
Region 2	58%	0.1474	0.1712	0.0619
Region 3	41%	0.3512	0.0901	0.0268
Region 4	49%	0.4827	1.1076	0.4617
Region 5	73%	0.1730	0.1819	0.0513

Table 4.4. Results of partial Mantel tests examining correlation between the spatial distribution of striped bass abundance and the distributions of forage fish density, temperature, and growth rate potential in late July 2003. Spatial scales and tests are as described for Table 4.2.

	60 bins	30 bins	20 bins	15 bins	12 bins
forage fish density	$r = 0.125$ $p = 0.027$	$r = 0.209$ $p = 0.017$	$r = 0.163$ $p = 0.045$	$r = 0.144$ $p = 0.096$	$r = 0.659$ $p = 0.001$
temperature	--	--	--	--	$r = 0.389$ $p = 0.002$
growth rate potential	$r = 0.137$ $p = 0.009$	$r = 0.214$ $p = 0.022$	$r = 0.166$ $p = 0.047$	$r = 0.141$ $p = 0.097$	$r = 0.621$ $p = 0.002$

Table 4.5. Percent of variability in forage fish density explained by GAM trend and spherical variogram parameters fit to GAM residuals for forage fish densities measured by hydroacoustics in late October 2002. Results are provided for the five regions of Badin Lake identified in Figure 4.1.

	% of variability explained by GAM	spherical variogram model parameters		
		range (km)	sill	nugget
Region 1	18%	0.2461	0.2077	0.0837
Region 2	33%	0.5663	0.2469	0.0725
Region 3	17%	0.3058	0.1723	0.1065
Region 4	66%	0.1804	0.2937	0.0609
Region 5	30%	0.1501	0.2792	0.0450

Table 4.6. Results of partial Mantel tests examining correlation between the spatial distribution of striped bass abundance and the distributions of forage fish density, temperature, and growth rate potential in late October 2002. Spatial scales and tests are as described for Table 4.2. An additional test was conducted to test for correlation between striped bass abundance and growth rate potential while controlling for the effect of temperature.

	60 bins	30 bins	20 bins	15 bins	12 bins
forage fish density	$r = 0.167$ $p = 0.082$	$r = 0.309$ $p = 0.070$	$r = 0.427$ $p = 0.052$	--	--
temperature	$r = 0.697$ $p = 0.005$	$r = 0.804$ $p = 0.007$	$r = 0.871$ $p = 0.001$	$r = 0.793$ $p = 0.009$	$r = 0.836$ $p = 0.003$
growth rate potential	--	--	--	--	--
growth rate potential temperature	$r = 0.143$ $p = 0.095$	$r = 0.230$ $p = 0.083$	$r = 0.265$ $p = 0.097$	--	--

Table 4.7. Percent of variability in forage fish density explained by GAM trend and spherical variogram parameters fit to GAM residuals for forage fish densities measured by hydroacoustics in early October 2003. Results are provided for the five regions of Badin Lake identified in Figure 4.1.

	% of variability explained by GAM	spherical variogram model parameters		
		range (km)	sill	nugget
Region 1	23%	0.1096	0.2727	0.1958
Region 2	46%	0.4216	0.6789	0.0815
Region 3	18%	0.4661	0.6451	0.3069
Region 4	64%	0.5671	1.0844	0.3390
Region 5	62%	0.2599	0.6235	0.1560

Table 4.8. Results of partial Mantel tests examining correlation between the spatial distribution of striped bass abundance and the distributions of forage fish density, temperature, and growth rate potential in early October 2003. Spatial scales and tests are as described for Table 4.2. An additional test was conducted to test for correlation between striped bass abundance and growth rate potential while controlling for the effect of temperature.

	60 bins	30 bins	20 bins	15 bins	12 bins
forage fish density	--	--	--	--	--
temperature	$r = 0.285$ $p = 0.060$	$r = 0.448$ $p = 0.046$	$r = 0.668$ $p = 0.035$	$r = 0.851$ $p = 0.031$	$r = 0.906$ $p = 0.048$
growth rate potential	--	--	--	--	--
growth rate potential temperature	--	--	--	--	--

Figures

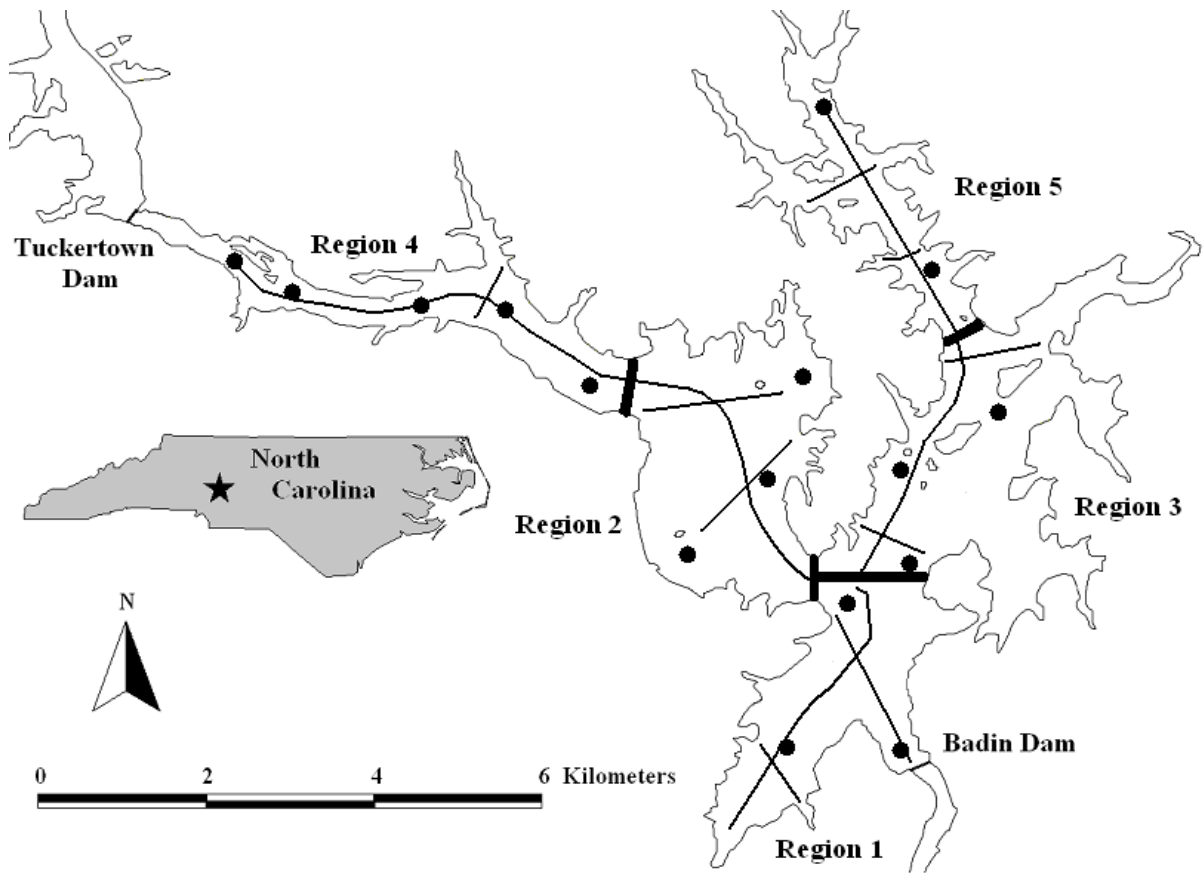


Figure 4.1. Map of Badin Lake, North Carolina, showing sites of temperature and dissolved oxygen profiles (dots), hydroacoustic survey transects (thin lines), and regions 1 through 5 used in spatial analysis of hydroacoustic data (delineated by thick lines).

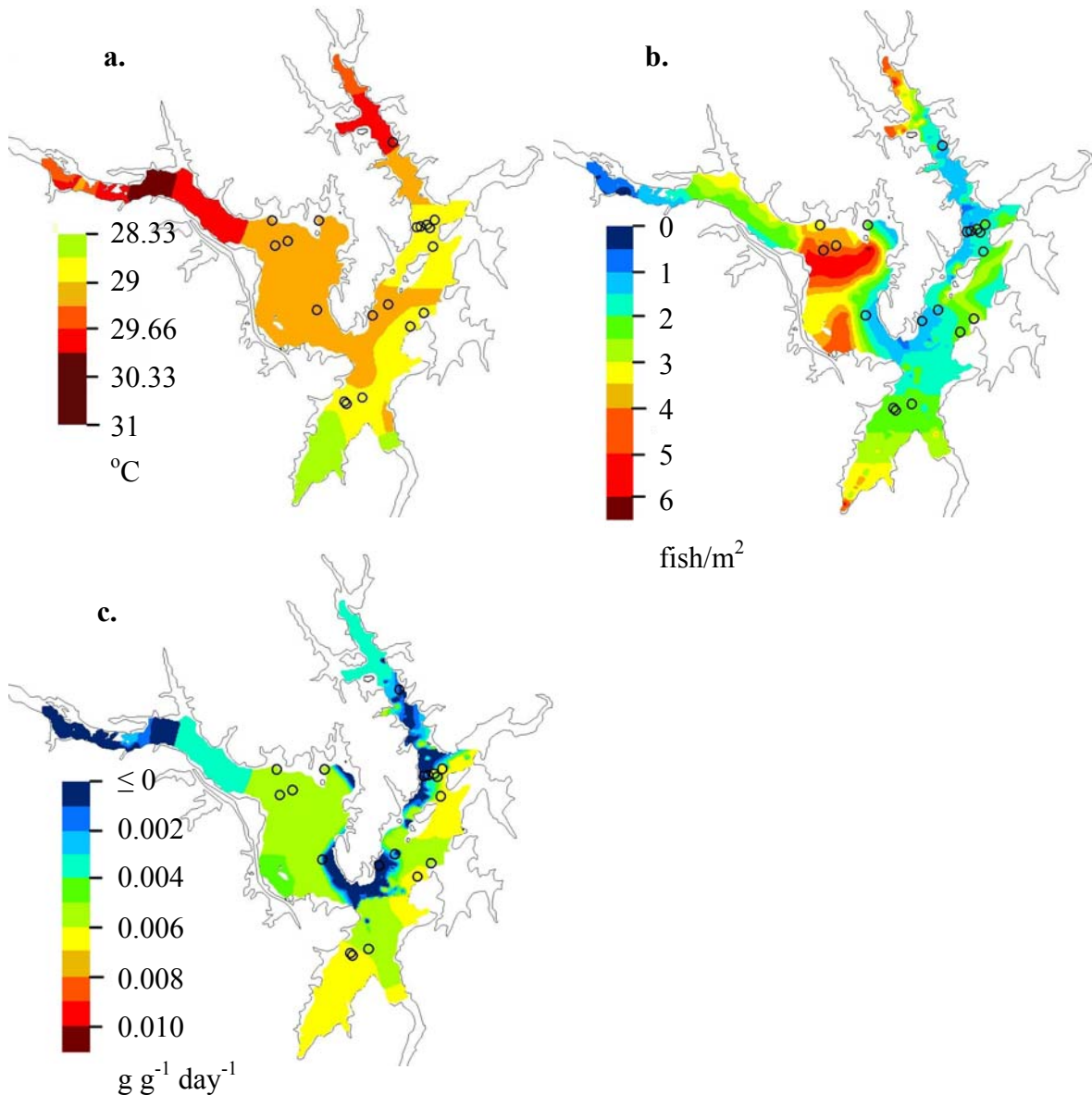


Figure 4.2. Map of Badin Lake, NC, in early August 2002 showing (a) temperatures ($^{\circ}\text{C}$) available to striped bass based on application of thermal selection rules to spline-interpolated temperature and dissolved oxygen profiles, (b) forage fish density (fish/m^2) based on geostatistical analysis of hydroacoustic data, and (c) growth rate potential ($\text{g g}^{-1} \text{day}^{-1}$) of striped bass based on forage fish densities and temperatures input to foraging and bioenergetics models as described in the text. Black circles represent locations of tagged striped bass. Temperature color legend is consistent with Figure 4.4a; forage fish density and growth rate potential legends are consistent between figures displaying those variables.

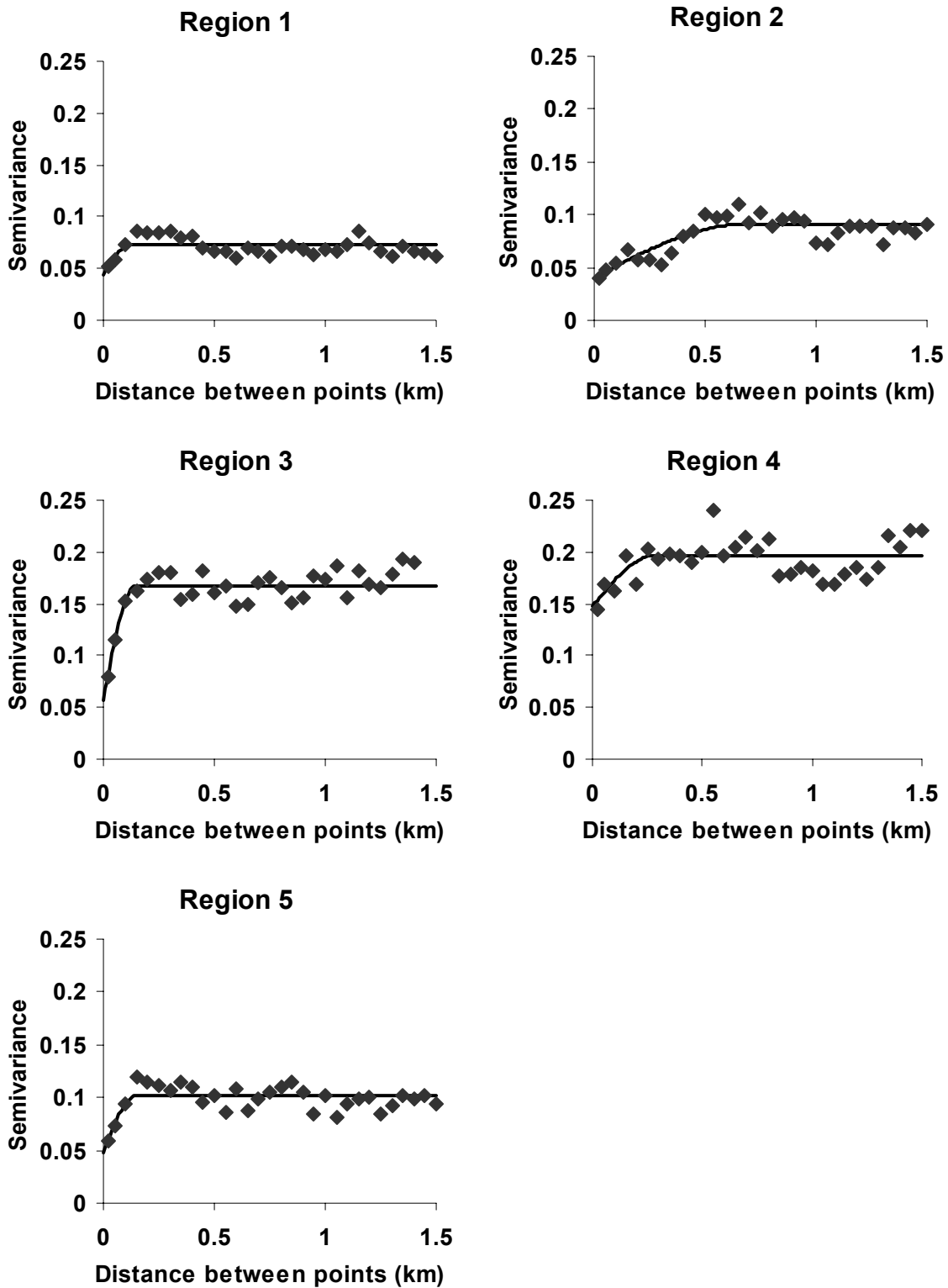


Figure 4.3. Empirical variograms (dots) and spherical variogram models (lines) fit to GAM residuals of hydroacoustic data collected in early August 2002 for five regions used in spatial analysis, indicated in Figure 4.1. Variogram parameters provided in Table 4.1.

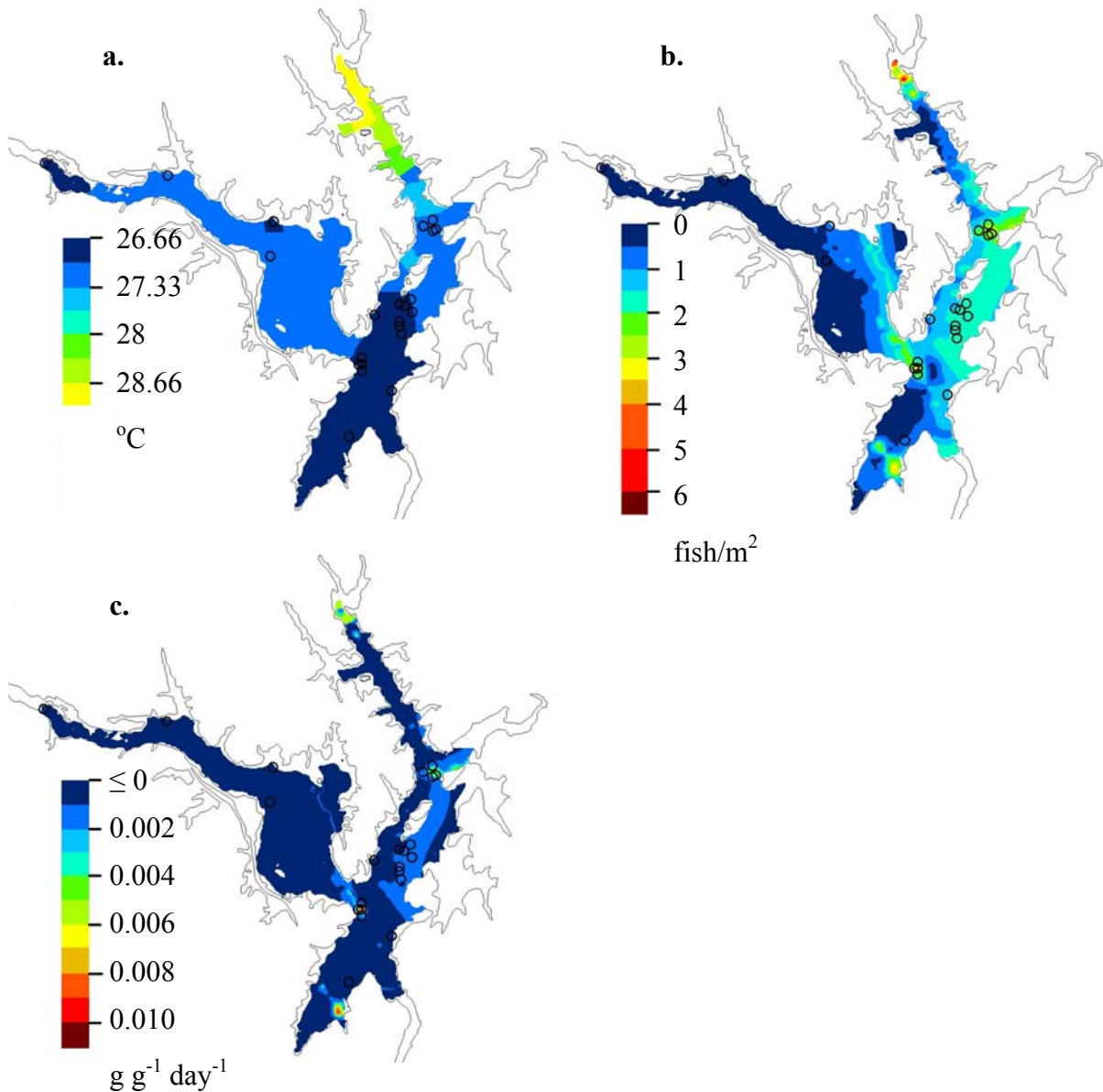


Figure 4.4. Map of Badin Lake, NC, in late July 2003 showing (a) temperatures (°C) available to striped bass based on application of thermal selection rules to spline-interpolated temperature and dissolved oxygen profiles, (b) forage fish density (fish/m²) based on geostatistical analysis of hydroacoustic data, and (c) growth rate potential (g g⁻¹ day⁻¹) of striped bass based on forage fish densities and temperatures input to foraging and bioenergetics models as described in the text. Black circles represent locations of tagged striped bass. Temperature color legend is consistent with Figure 4.2a; forage fish density and growth rate potential legends are consistent between figures displaying those variables.

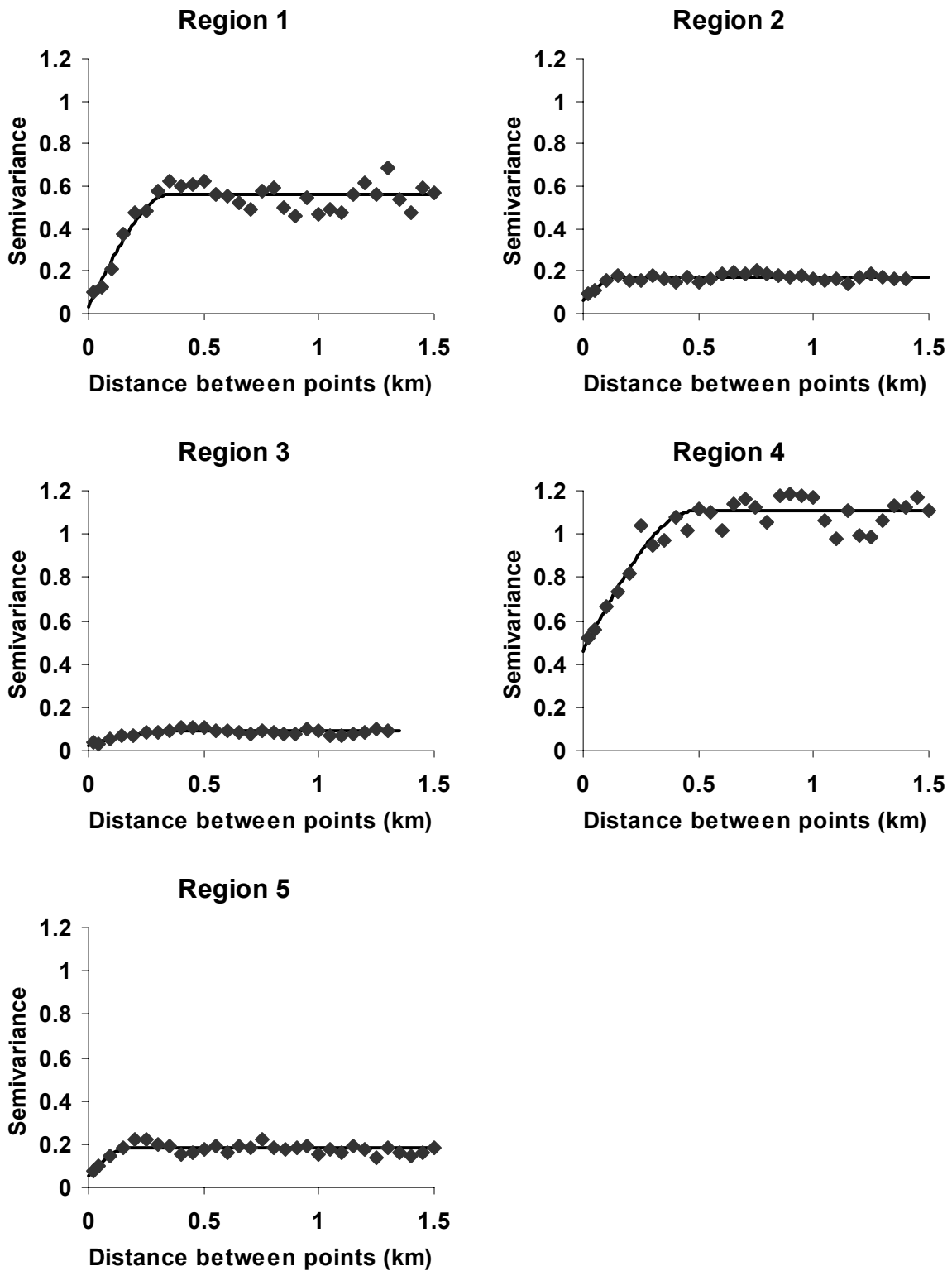


Figure 4.5. Empirical variograms (dots) and spherical variogram models (lines) fit to GAM residuals of hydroacoustic data collected in late July 2003 for five regions used in spatial analysis, indicated in Figure 4.1. Variogram parameters provided in Table 4.3.

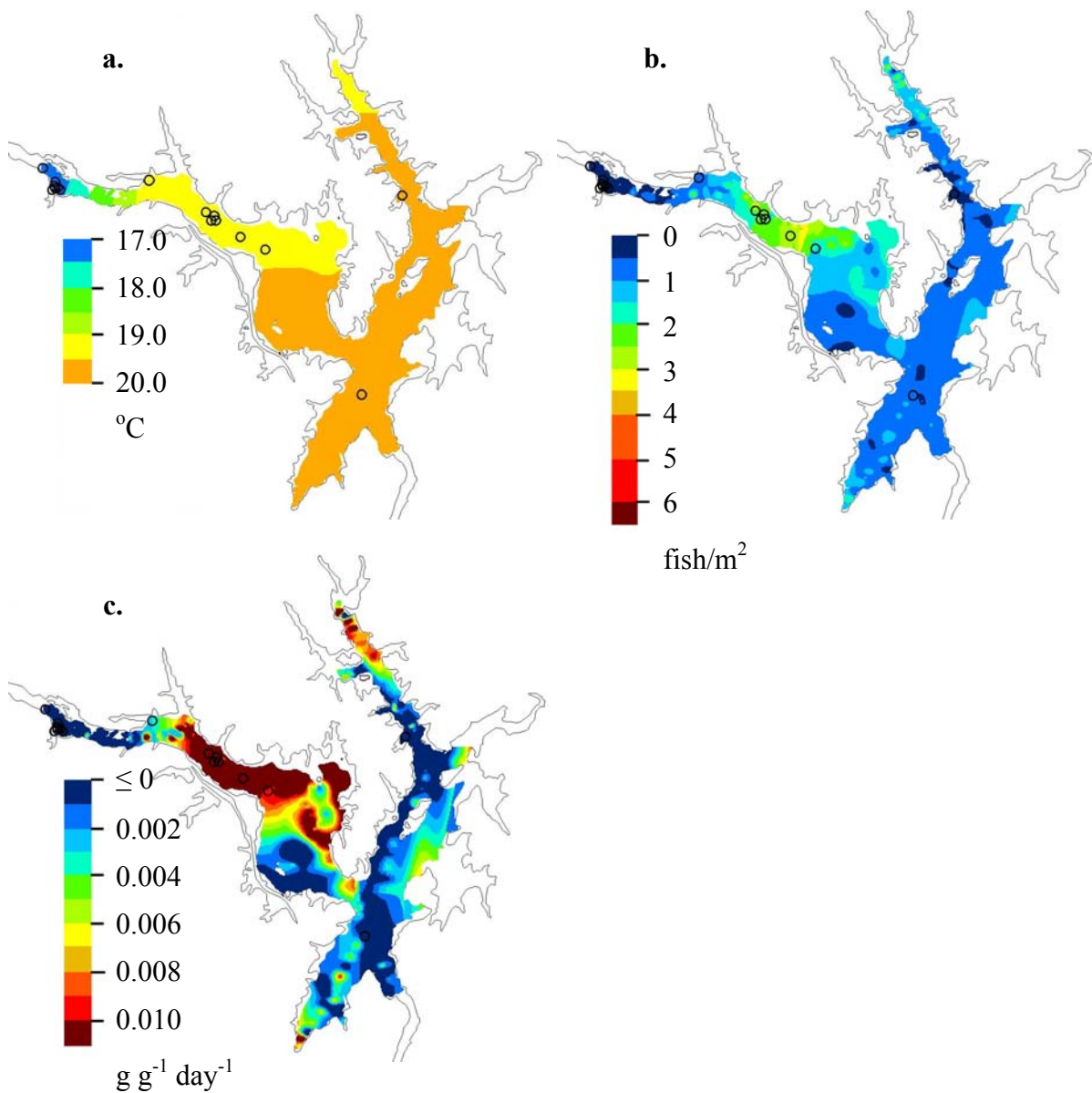


Figure 4.6. Map of Badin Lake, NC, in late October 2002 showing (a) spline-interpolated temperatures ($^{\circ}\text{C}$) at a depth of 2 m, (b) forage fish density (fish/m^2) based on geostatistical analysis of hydroacoustic data, and (c) growth rate potential ($\text{g g}^{-1} \text{day}^{-1}$) of striped bass based on forage fish densities and temperatures input to foraging and bioenergetics models as described in the text. Black circles represent locations of tagged striped bass. Temperature color legend differs from Figure 4.8a; forage fish density and growth rate potential legends are consistent between figures displaying those variables.

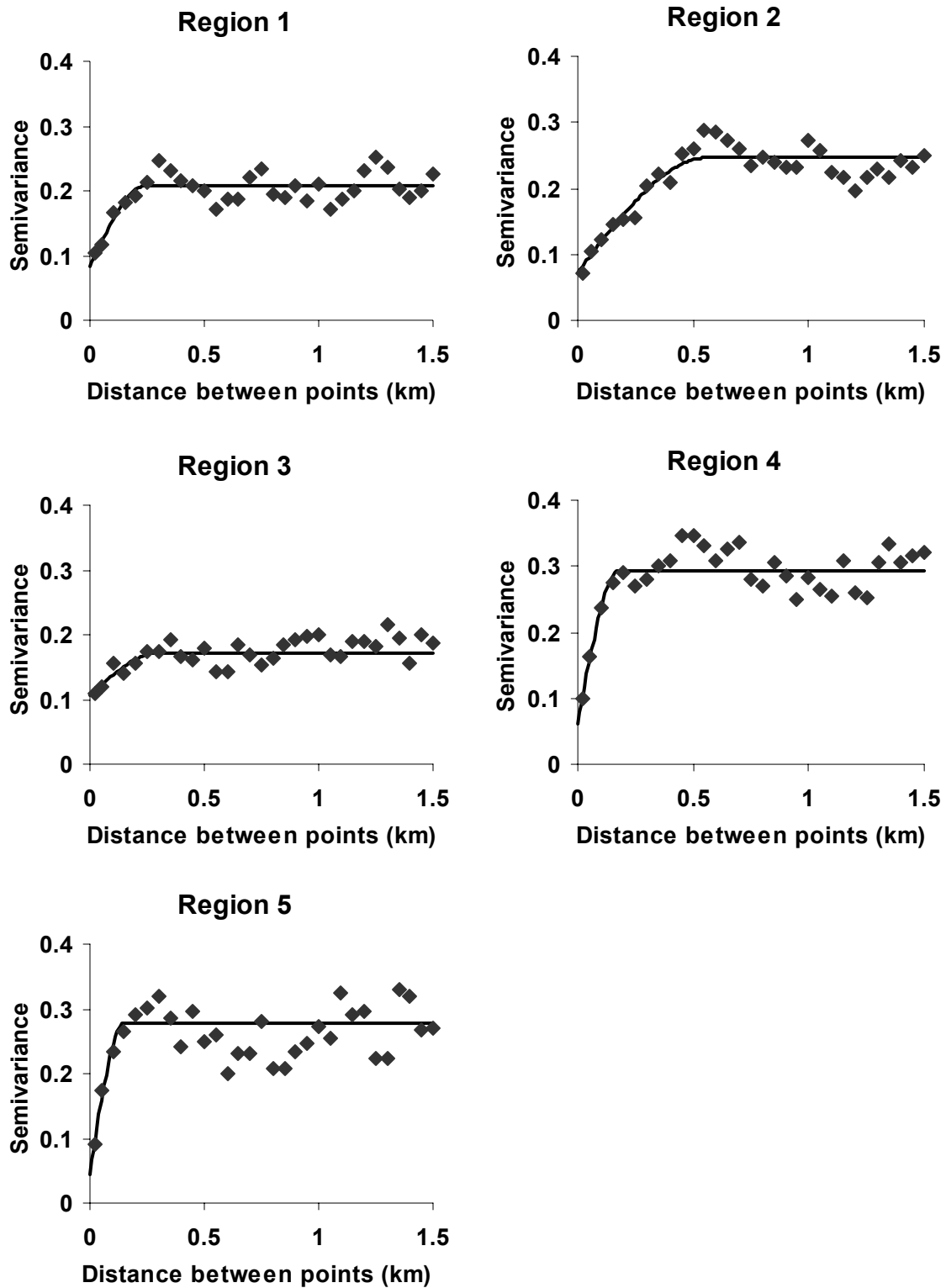


Figure 4.7. Empirical variograms (dots) and spherical variogram models (lines) fit to GAM residuals of hydroacoustic data collected in late October 2002 for five regions used in spatial analysis, indicated in Figure 4.1. Variogram parameters provided in Table 4.5.

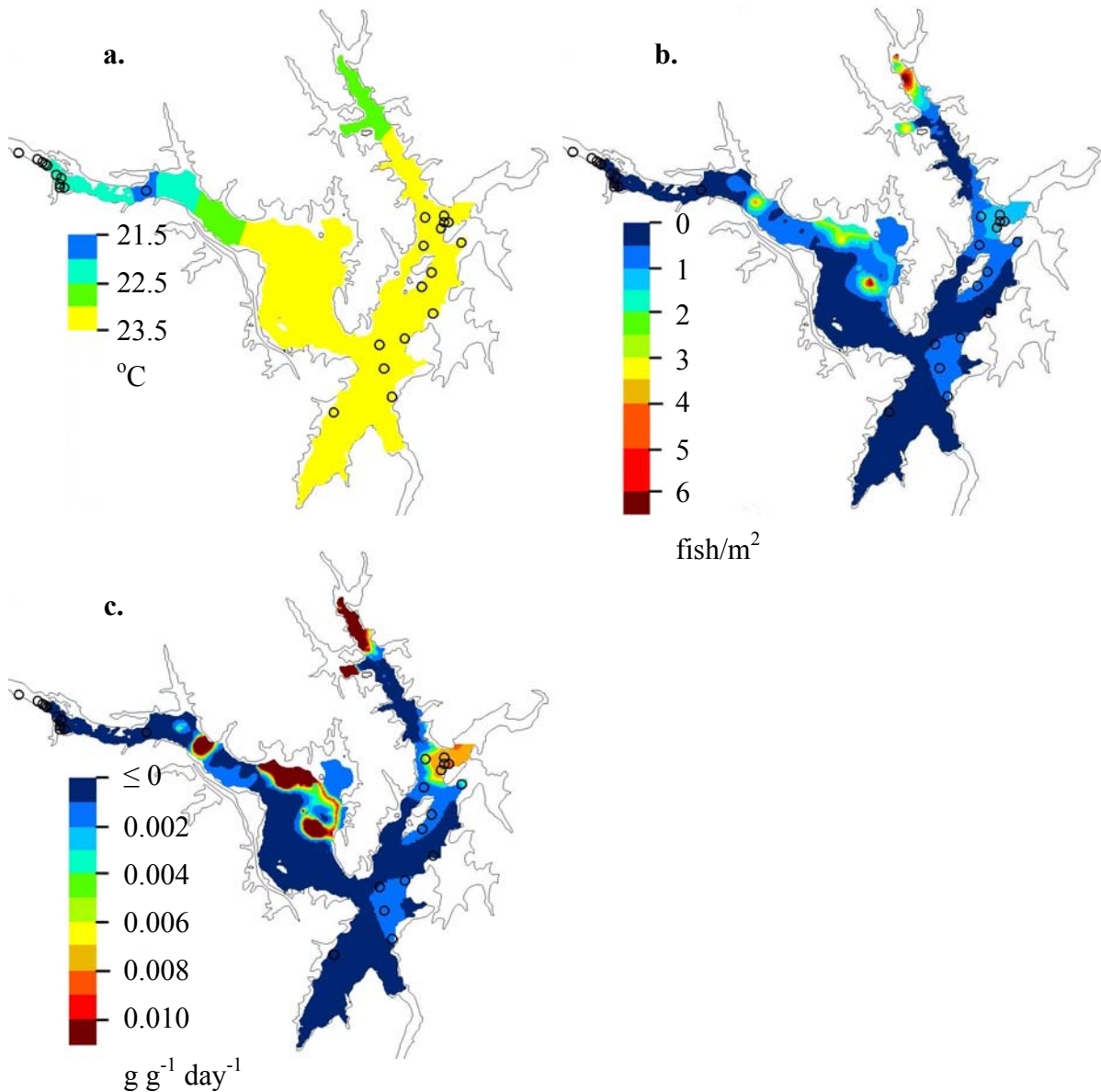


Figure 4.8. Map of Badin Lake, NC, in early October 2003 showing (a) spline-interpolated temperatures ($^{\circ}\text{C}$) at a depth of 2 m, (b) forage fish density (fish/m^2) based on geostatistical analysis of hydroacoustic data, and (c) growth rate potential ($\text{g g}^{-1} \text{day}^{-1}$) of striped bass based on forage fish densities and temperatures input to foraging and bioenergetics models as described in the text. Black circles represent locations of tagged striped bass. Temperature color legend differs from Figure 4.6a; forage fish density and growth rate potential legends are consistent between figures displaying those variables.

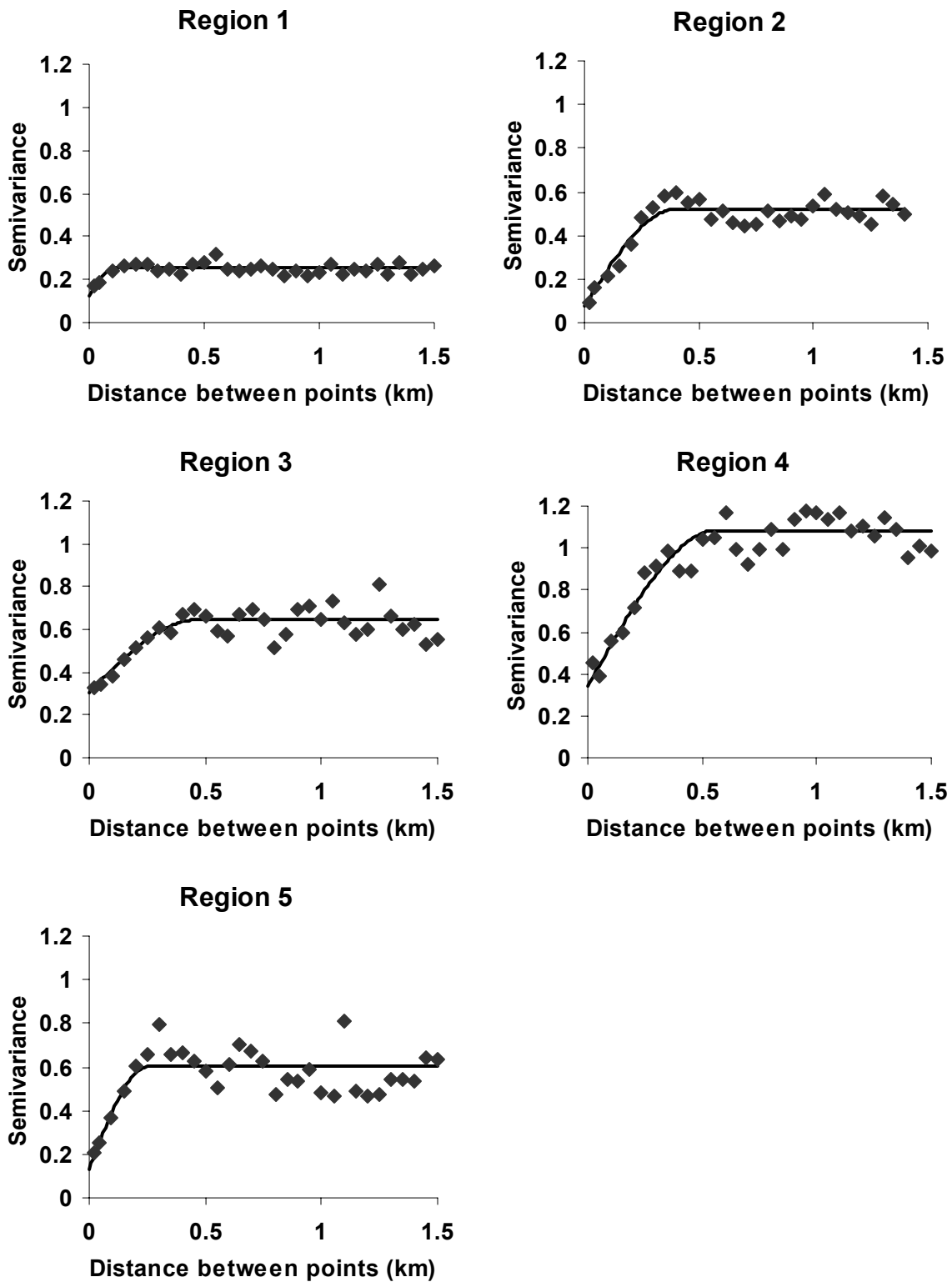


Figure 4.9. Empirical variograms (dots) and spherical variogram models (lines) fit to GAM residuals of hydroacoustic data collected in early October 2003 for five regions used in spatial analysis, indicated in Figure 4.1. Variogram parameters provided in Table 4.7.

Chapter 5

Conclusion

Striped bass in southern reservoirs

The traditional paradigm used to understand the biology and ecology of striped bass stocked into southern reservoirs has focused solely on the effects of unsuitable physical habitat during periods of summer stratification (Coutant 1985). This study upholds some of the relationships between striped bass and abiotic conditions described by Coutant (1985) but also illustrates that these relationships cannot be viewed in isolation. The biotic conditions in a particular reservoir can strongly modify the effects of physical factors on growth and habitat selection of striped bass, indicating that our understanding and management of reservoir striped bass will be improved by characterizing these systems more holistically.

The telemetry data from Badin Lake striped bass confirm that low dissolved oxygen is the primary habitat constraint determining the vertical position of striped bass when the reservoir is stratified. Even in a system where avoiding low dissolved oxygen resulted in the occupation of temperatures of 28 to 30°C, striped bass were not found at dissolved oxygen levels below 2 mg/l, a result that supports Coutant's (1985) view of low dissolved oxygen forcing striped bass into unsuitable thermal conditions. However, Badin Lake striped bass did not simply occupy the depth with the coolest temperatures available at a dissolved oxygen level of 2 mg/l. Instead, fish chose to occupy temperatures just above the oxycline with higher dissolved oxygen levels of 4 to 8 mg/l (Chapter 2), a range of occupied dissolved oxygen levels that has also been identified in other studies of reservoir striped bass

(Matthews et al. 1985; Farquhar and Gutreuter 1989). This pattern may result from striped bass being unable to occupy low dissolved oxygen levels for an extended period of time, particularly at very warm temperatures, or there may be insufficient energetic advantage to micromanaging depth to occupy the coolest temperatures with the minimum dissolved oxygen level required. The summer thermal selection pattern of Badin Lake striped bass demonstrates, however, that once striped bass are forced into warm epilimnetic water, they have greater thermal plasticity than suggested by Coutant's (1985) original hypothesis.

Thermal conditions also influenced the spatial distribution of striped bass across Badin Lake during the summer, but as with the vertical distribution of these fish, Badin Lake striped bass displayed greater thermal tolerance than was expected in this highly unsuitable thermal environment. From late-June through late-July, most tagged striped bass in Badin Lake were located in the east arm of the reservoir in both years of the telemetry study (Chapter 2). The slightly deeper oxycline in this region allowed striped bass to access water 1 to 2°C cooler than elsewhere in the reservoir, indicating that striped bass were responding to differences in the thermal constraints across the system despite the lack of a true thermal refuge in this system. This spatial pattern in temperature disappeared by late-July, and striped bass began to occupy a greater range of locations across the reservoir. While striped bass continued to avoid the warmest temperatures in the system, they did not occupy the coolest temperatures just above the oxycline that were available. Instead, striped bass appeared to be integrating information on the spatial distributions of both temperature and forage fish density, occupying regions of high growth rate potential within the lower range of temperatures available (Chapter 4). This habitat selection pattern was particularly evident in the first summer of the telemetry study, when temperatures across the system were higher

than in the second summer. This result was contrary to my original expectations because I expected striped bass to thermoregulate more stringently as temperatures increased. However, the energetic advantage gained by tracking growth rate potential (based on both temperature and forage fish density) may be greater than the advantage gained by minimizing occupied temperatures within a degree or two, and this may be particularly true as temperatures increase. Unfortunately, I do not have information on forage fish density for the earlier part of the summer when striped bass were more frequently found in the east arm, where temperatures were just a degree or two cooler at that time. Such information would be useful to provide a more comprehensive view of the temporal relationship between striped bass habitat selection and habitat characteristics as it is certainly possible that the importance of one habitat characteristic or another may change with the duration of thermal or energetic stress.

Interestingly, Badin Lake striped bass continued to respond to both biotic and abiotic habitat characteristics in the fall, when thermal conditions were suitable for striped bass across the reservoir and I expected habitat selection to be primarily dependent on biotic conditions. While many striped bass were found in regions of high forage fish density and high growth rate potential, at least in the fall of 2002, a fairly high proportion of tagged fish on both fall sampling dates were found in cool, flowing water in the Tuckertown Dam tailrace despite the lack of forage fish in this area (Chapter 4). The temporal nature of this habitat selection pattern is unknown, and we may expect that striped bass would move out of this habitat into the remainder of the reservoir to feed. This hypothesis is supported by the high consumption rates and rapid growth of Badin Lake striped bass in the fall (Chapter 3) and the fact that individual tagged fish were seldom found in the tailrace on successive

biweekly tracking dates (J. S. Thompson, unpublished data). Whatever the temporal nature of this pattern, these results indicate that, just as understanding the spatial distribution of striped bass during the summer requires consideration of the distribution of forage fish density in addition to temperature, understanding the spatial distribution of striped bass during the remainder of the year requires consideration of physical habitat conditions such as temperature and flow in addition to the distribution of prey resources.

As with habitat selection, the results of this study show that the pattern of striped bass growth in southern reservoirs will be determined both by the temperatures available within the limitations imposed by low dissolved oxygen and by forage fish density. Bioenergetics model simulations in which habitat conditions were exchanged between Badin Lake and Lake Norman indicate that differences in forage availability between the systems have a greater relative effect on growth of striped bass than differences in thermal regime (Chapter 3). High forage availability over the summer, as indicated by high consumption rates, allows Badin Lake striped bass to maintain their body weight through this thermally stressful period, and the continuation of fairly high consumption into the fall when temperatures begin to cool provides these fish with the ideal conditions for rapid growth. On the other hand, the consumption rates of Lake Norman striped bass in the summer are not sufficient to completely meet metabolic costs, particularly for older fish. Consumption also declines more substantially through the fall, likely due to the depletion of young-of-year shad, preventing Lake Norman fish from experiencing conditions conducive to rapid growth. The relative effect of temperature on striped bass growth may increase when comparing reservoirs with more widely divergent thermal regimes, but the system comparison conducted in this study clearly indicates that the relationship between striped bass growth and habitat conditions

cannot be understood solely by considering variation along the single axis of temperature. It is important to note that striped bass growth will also be dependent on conditions over the entire year, rather than just over the summer. Variation in striped bass growth between systems will, therefore, depend on the intersection of seasonal thermal and forage fish dynamics and the resulting presence or lack of conditions (i.e., cool temperatures and abundant prey) suitable for rapid growth.

Overall, this study suggests we rethink our criteria for judging the suitability of southern reservoirs for striped bass. The most rapid growth would certainly be expected in systems that provide reasonably cool temperatures and abundant forage throughout a large portion of the year. However, highly productive systems with unsuitable summer thermal conditions can also produce striped bass with fairly good growth and condition. Positive growth is possible if striped bass can attain a high proportion of their physiological maximum consumption rate even up to 28 to 29°C (Chapter 2). Bioenergetics modeling results for the Badin Lake population demonstrate that such high proportions of maximum consumption can be attained in a productive system, and these consumption rates result in maintenance of body weight among larger fish and an increase in body weight among smaller fish over the summer and rapid growth for all fish over the fall as temperatures decline (Chapter 3). While thermal conditions do appear to prevent Badin Lake striped bass from accessing some regions of high prey density during the summer, tagged fish were still able to track regions of high growth rate potential fairly closely over this season (Chapter 4). In contrast, forage limited systems, particularly those such as Lake Norman where striped bass are still exposed to high temperatures over some portion of the summer, will be more susceptible to poor growth and condition. The quality of striped bass growth in Lake Norman and similar

systems will be very sensitive to management decisions that affect the balance between predator demand and prey supply. In addition, striped bass in systems with thermal refuge habitats that differ substantially from ambient temperatures, drawing these fish into those regions, may also experience poor growth and condition if that habitat selection pattern segregates them from prey resources. The lack of a thermal refuge in Badin Lake may, ironically, actually improve growth rates by promoting the mobility that allows these fish to track prey resources.

Reservoir striped bass as a model system for understanding fish growth and habitat selection

The results of this study provide evidence that even in habitats with one highly unsuitable characteristic, such as warm temperatures imposed by hypolimnetic hypoxia in the case of striped bass in southern reservoirs, fish still respond to multiple environmental factors when resolving energetic constraints and the effect of each factor will not necessarily be proportional to its degree of unsuitability. In order to understand the influence of habitat conditions on fish growth and habitat selection, it is necessary to evaluate the effects of multiple environmental variables simultaneously. In the case of fish growth, habitat exchange simulations conducted in the context of bioenergetics modeling provide a useful method of quantifying the relative effect of multiple habitat characteristics that may affect a fish's energy budget. The effects of differences in thermal regime, forage availability, the energetic quality of food resources, the cost of spawning, and activity costs could all be assessed with this technique. Quantifying these effects could be done in the context of a system comparison, such as the comparison between Badin Lake and Lake Norman in this study (Chapter 3), but this approach could also be used to compare an actual system with a

range of hypothetical systems with widely divergent conditions. Such comparisons may be helpful in assessing the validity of potential explanations for observed growth patterns by identifying which habitat characteristics have a sufficient effect on growth to produce the observed patterns over a reasonable range of values.

In the case of habitat selection of fishes, growth rate potential appears to be a useful approach to integrating information on both temperature and forage fish density in a way that has relevance to patch choice behavior. While the distribution of striped bass in Badin Lake was not explained entirely by the distribution of growth rate potential, this factor provided a better explanation for striped bass distribution across sampling dates than did temperature or forage fish density alone (Chapter 4). Based on these results, I suggest that further field testing of the correlation between fish distribution and the distribution of growth rate potential is warranted, but I also caution that we should not simply assume that fish will consistently optimize patch choice with respect to growth rate potential. Improving the parameterization of foraging models used to estimate predator consumption, conducting temporally synoptic sampling of all habitat characteristics, and comparing the distribution of fish and growth rate potential over a larger number of seasonal samples will improve our ability to test growth rate potential as a predictor of the spatial distribution of fishes.

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Appendix A

Growth, condition, and diet of striped bass in Badin Lake and Lake Norman, NC

This appendix details the methods used in sampling striped bass *Morone saxatilis* in Badin Lake and Lake Norman and analysis of their growth, condition, energy density, gonadosomatic index, and diet. Data are provided that are relevant to bioenergetics models of the Badin Lake and Lake Norman striped bass populations in 2001 and 2002 (Chapter 3). Data are also given for 2000; simulations were not conducted for that year, but these data allowed for the development of model inputs for the early portion of 2001 and provided an additional source of data for estimating general trends when data were lacking for specific time periods or particular sizes of striped bass. Energy density and diet composition data are also provided for Badin Lake for summer and fall dates in 2003, as these data were required for the estimation of growth rate potential using bioenergetics models (Chapter 4).

Methods

Fish collection

Striped bass were collected in Lake Norman from summer 2000 through winter 2002 and in Badin Lake from spring 2000 through winter 2002 and the summer and fall of 2003. Large samples (>20 fish) were collected at three times during the year: June or July, September, and December. These intervals were chosen because they bracket major periods in the life history of reservoir populations. Spring (bracketed by the December and June samples) is characterized by cold temperatures and, in some fish, gonad development.

Summer (bracketed by the June and September samples) is characterized by limited habitat suitability and potential energetic stress due to stratification and high epilimnetic temperatures. Fall (bracketed by the September and December samples) is a period of good conditions for growth due to more moderate temperatures and high forage fish availability.

These large samples were collected using gill nets set opportunistically at locations throughout each reservoir with the help of NC Wildlife Resources Commission personnel. A mixture of 25 mm (1 inch), 51 mm (2 inch) and 76 mm (3 inch) bar mesh nets were originally used, but the 25 mm mesh nets never produced striped bass and were plagued by an abundance of by-catch. Therefore, 51 mm and 76 mm mesh nets were used for the majority of sampling, and most fish were collected in the 51 mm mesh nets. Nets were typically set during dusk and nighttime, with sets lasting from overnight in cool weather to only a couple of hours in warm months in order to keep captured striped bass fresh. Total length and wet weight were taken in the field for all fish, and fish were then packed in ice for transport back to the lab. Smaller samples (5-10 fish) were also collected in both reservoirs at about 6-week intervals between the larger samples with the particular goal of obtaining additional information on seasonal changes in energy density. These samples came from a variety of sources, including anglers assisting the study, gill net sets, and electroshocking in the spring. Gill net and electroshocking samples were weighed in the field, while angler samples were typically frozen whole and length and weight measurements taken in the lab.

Age and growth

Striped bass growth patterns were based on ageing of sagittal otoliths for all fish collected and backcalculation of length-at-age for a subsample of fish. Heidinger and

Clodfelter (1987) found that ages estimated from otoliths of known-age striped bass agreed 100% of the time with actual age, and back-calculated mean total lengths agreed with corresponding empirical mean total lengths. One otolith from each fish was cleaned, sectioned with a Buehler low-speed isomet saw, and mounted on a glass slide using Permunt. Otoliths were allowed 10 days to dry and were then read under a compound microscope (100X) independently by two readers naïve of the fish's total length or weight. When readers disagreed on a fish's age, a third read was conducted by an additional reader and the age common to two of the three readers was assigned to that fish. A January 1st birthday was assumed for all fish. Because annulus formation typically occurred during February and March, fish collected between June and December were assigned an age equal to the total number of visible annuli. Fish collected between January and May were assigned an age equal to the total number of annuli plus one additional year for the otolith edge when a recent annulus was not observed. However, when a recent annulus was present, age was assigned as the total number of annuli observed.

When available, a subsample of five otoliths from each year class was randomly selected for back-calculation using the Fraser-Lee direct proportion method (Carlander 1982). Otolith radius was measured using Image Pro (Media Cybernetics 2000) with the total radius equaling the distance between the center of the nucleus and the edge of the otolith. Annual measurements were made from the anterior edge of one annulus to the anterior edge of the next successive annulus. Backcalculated lengths represent the length at annulus formation, which was assumed to occur on March 15th of each year.

The length-at-age relationship for each cohort of fish collected from each reservoir was modeled using the von Bertalanffy growth curve:

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

where L_t is length at time t , L_{inf} is maximum length, k is the Brody growth coefficient (or the rate at which L_{inf} is achieved), and t_0 is the theoretical age at which the fish would have zero length (Quinn and Deriso 1999). In fitting the growth curve, data on observed length-at-age and backcalculation of length at the age of annulus production were weighted equally. In both cases, fractional ages were used to incorporate the day of the year on which the fish were collected or on which annulus production was assumed to occur, in the case of backcalculated lengths. Model fitting was conducted assuming a multiplicative error structure (Quinn and Deriso 1999), which seemed appropriate considering the increase in variation in length at older ages, particularly in Lake Norman. Two older fish from Lake Norman were excluded from the growth curve analysis because the inner section of their otoliths were obscured. Back-calculated lengths for these two fish were consistently above all other lengths for the same age fish, suggesting that the first annulus was not correctly identified for these fish.

The length-weight relationship for striped bass in each reservoir was also determined using data from all fish collected. Analysis of variance (ANOVA) of log-transformed data was used to test if the relationships were significantly different for the two reservoirs. In addition, multiple regression analysis was used to test if year, day of year, or powers of these variables had a significant effect on each system's length-weight relationship.

Relative weight and somatic energy density

Relative weight (W_r) was calculated using established parameters for striped bass standard weight (W_s ; Brown and Murphy 1991; Anderson and Neumann 1996):

$$\log_{10}(W_s) = -4.924 + 3.007 \cdot \log_{10}(L)$$

$$W_r = 100 \cdot (W/W_s)$$

where L is observed total length (mm) and W is observed weight (g). Wet weight measured in the field was used in all instances when such data had been collected; otherwise, the weights of fish thawed in the lab were used. The minimum length of fish collected in this study (143 mm) was approximately equal to the minimum length for which the standard weight equation was developed (150 mm; Brown and Murphy 1991).

The seasonal, size-specific energy density of striped bass somatic tissue from both reservoirs was also determined for comparison with relative weight, as both are potential measures of fish condition, and for use in bioenergetics modeling. Whole striped bass (with the gonads, stomach contents, and otoliths removed) were homogenized using a commercial blender. Two random 20- to 30-g subsamples of each homogenized fish were then placed in individual aluminum trays and dried to a constant weight at a temperature of 70°C; two samples were dried to prevent the loss of the entire fish if one tray was damaged, but both samples were combined for calorimetry analysis. About thirty of these combined, dried specimens from each reservoir were individually ground to a powder for analysis in a Parr 1425 Semimicro Bomb Calorimeter. These specimens were chosen to represent the full range of season, fish size, sex, and relative weight. Two replicates from each fish specimen were processed using standard techniques (Parr Instrument Company 1991), and the dry weight caloric density obtained by the calorimeter was converted to a wet weight energy density using the ratio of dry weight to wet weight for a given sample and a calorie to Joule conversion. If the difference between the energy density of the two replicates was less than 100 J/g wet wt, the energy density of that fish specimen was determined by the average of the

values of the two replicates. If the difference was greater than 100 J/g wet wt, a third replicate was also processed, and the values of all three replicates were averaged to determine the specimen's energy density.

The calorimetry analysis was used to calculate regression equations relating the energy density of a fish sample to the sample's percent dry weight ($100 \times \text{dry weight} / \text{wet weight}$). The relationship between energy density and percent dry weight is well established for fish somatic tissue (Hartman and Brandt 1995). We modeled energy density as dependent on percent dry weight (producing a linear fit) and as dependent on the log of percent dry weight (producing a slightly curvilinear fit). The model with the lowest residual sum of squares was chosen. Analysis of variance was used to determine if the regression models were significantly different for Badin Lake and Lake Norman.

After the regression relationships were determined, subsamples from all additional fish collected in the study were dried to a constant weight, as described above, and each percent dry weight was input to the appropriate equation to estimate energy density. Energy density was compared to relative weight for fish from each reservoir, and patterns in energy density through time and with fish size were evaluated using polynomial regressions fit to the data in Splus 6.1 (Insightful Corp.). In the absence of significant models to capture these patterns, the energy densities for categories of fish size and season were estimated based on the average energy densities observed within those categories.

Gonadosomatic index and gonad energy density

Gonads were removed from all striped bass collected during the study. In some fish less than 400 mm total length, gonad development was insufficient for sex to be determined,

and these fish were considered immature. For mature fish, sex was determined by visual inspection, using indicators such as the degree of veination, texture, and to a lesser degree, color (S. Van Horn, personal communication). Gonads were weighed, and gonadosomatic index (GSI) was then calculated and expressed as a percentage: (gonad weight/body weight) x 100 (Strange 1996).

The season- and size-specific energy density of male and female gonadal tissue was also determined for comparison with individual GSI and to assess the energetic cost of gonad development for potential inclusion in the striped bass bioenergetics model. Gonads were dried to a constant weight as described above for somatic tissue. Twenty to twenty-five specimens of each sex from each reservoir were analyzed using the calorimetry techniques described above. These specimens were chosen to represent the full range of season, fish size, and gonad ripeness. Linear and logarithmic models were fit to energy density-dry weight data for each sex and each reservoir. The models with the lowest residual sum of squares were chosen, and ANOVA was used to test for an effect of sex and reservoir. These equations were then used to estimate the energy density of additional gonad samples based on their percent dry weight.

Diet composition

Stomachs of all striped bass caught during the study were removed, and stomach contents were carefully extracted and preserved in 70% ethanol. Fish found in the stomachs were identified to the lowest possible taxon. In some cases, only the backbone was present, making any definitive identification impossible. Other specimens could be identified as clupeids, based on shape and size and distinguishing characteristics such as silvery skin. For

some clupeid specimens, the presence of a gizzard allowed them to be identified as genus *Dorosoma*, which includes both threadfin shad (*D. petenense*) and gizzard shad (*D. cepedianum*). These species were rarely distinguishable because their primary difference lies in their jaw structure (Jenkins and Burkhead 1993), which was typically obscured due to partial digestion. In cases where the degree of digestion suggested a gizzard should remain if it had been present, its absence allowed the specimen to be identified as genus *Alosa*, which includes both alewife (*A. pseudoharengus*) and blueback herring (*A. aestivalis*). These species can be distinguished based on the color of the peritoneum, as blueback herring typically have a dark peritoneum while alewife have a light peritoneum (Jenkins and Burkhead 1993). Fish other than clupeids were identified to the lowest possible taxon, typically species, using standard keys (Jenkins and Burkhead 1993). These fish included centrarchids and moronids, and the number of dorsal and anal spines was the most commonly used meristic in identification. Invertebrates were also identified to the lowest possible taxon (in all cases, Order) using standard keys (Voshell 2002).

Depending of the degree of digestion, total length or backbone length was recorded for each fish found in the stomachs. For most clupeids, only backbone length was determined. To convert backbone length to total length, the relationship between these measurements was determined for a subsample of threadfin shad, gizzard shad, alewife, and blueback herring captured in purse seine samples (Appendix B). Species-specific relationships were used in cases in which diet items were identified to species. A general *Dorosoma* relationship (which included equal numbers of threadfin shad and gizzard shad) was applied to specimens identified only as *Dorosoma*. A general clupeid relationship was also determined for each reservoir to capture the typical forage fish community; the Badin

Lake equation included equal numbers of threadfin shad, gizzard shad, and blueback herring, while the Lake Norman equation included equal numbers of threadfin shad, gizzard shad, and alewife. These general clupeid equations were applied to specimens identified only as clupeids, as well as to unidentified backbones that did not have any characteristics suggesting they were not clupeid.

The total length of each clupeid prey item was then used to estimate its undigested wet weight. In cases where the prey species was determined, a species-specific length-weight relationship was applied (Appendix B). In cases where the prey species was not determined, each prey item was assigned an assumed species based on the proportion of each forage species observed in the same 10-mm length category in the purse seine sample (Appendix B) closest to the date when the striped bass was collected. The appropriate species-specific length-weight relationship was then applied. For fish other than clupeids, length-weight relationships based on data from Lake Tillery and Blewett Falls, reservoirs downstream of Badin Lake along the Yadkin River, were used to estimate the wet weight of each specimen (Progress Energy, unpublished data). For each Order of insect found in the stomachs, a length-weight relationship fit to data on the most common species of aquatic insect larvae in the southeastern U.S. was used to estimate dry weight from total length (Benke et al. 1999). Dry weight was then converted to wet weight based on Order-specific dry to wet weight ratios utilized in the Fish Bioenergetics 3.0 software (Hanson et al. 1997 and references therein).

All prey items, including ones for which only a partial length could be determined, were included in the analysis of prey item frequency. Only those for which a total length and associated wet weight could be estimated, as described above, were included in the analysis

of percent composition by number and percent composition by weight. The relationship between striped bass length and prey fish length was also analyzed by testing for the significance of a linear regression model relating the two variables for data from all sampling dates combined.

Results

The size distribution of fish collected differed between the systems (Figure A.1). In Badin Lake, similar proportions of fish were collected in each 50-mm size class between 400 and 550 mm total length, with each size class accounting for 17% to 20% of the fish caught (Figure A.1a). Slightly fewer fish were collected in the size classes between 550 and 650 mm, and few fish were captured that were less than 400 mm or greater than 650 mm (Figure A.1a). In contrast, almost 35% of the striped bass collected in Lake Norman were between 500 and 550 mm total length, and fish in the two 50-mm size classes between 400 and 500 mm accounted for the next largest proportions (Figure A.1b). Striped bass less than 400 mm accounted for a slightly larger proportion of the catch in Lake Norman than in Badin Lake, while fish larger than 600 mm total length made up a much smaller proportion of the catch in Lake Norman than in Badin Lake (Figure A.1).

Age and growth

Striped bass collected from Badin Lake in 2000 through 2002 ranged from age 0 to age 7, while those collected from Lake Norman ranged from age 0 to age 10. In both reservoirs, the age structure was strongly shifted toward young fish less than age 5 (Figure A.2). Fish were fully recruited to the gillnets by age 2, and this age class represented the

largest proportion of the catch in all years in both systems (Figure A.2), with the exception of 2000 in Lake Norman, when age-3 fish represented a slightly larger proportion (Figure A.2b). Fish age 0 through age 3 composed 89% of the catch across years in Badin Lake, and adding age-4 fish increases that percentage to 99% (Figure A.2a). These values were slightly lower in Lake Norman, with fish age 0 through age 3 composing 77% of the catch across years and fish age 4 composing an additional 11% for a total of 88% of the catch age 0 through age 4 (Figure A.2b). While most striped bass were collected in the 51-mm mesh gillnets, 76-mm mesh nets were set on each sampling occasion to attempt to capture larger, potentially older fish, so the absence of older age classes in these catches is likely a fair representation of the population age structure, rather than a result of gear selectivity.

Von Bertalanffy growth model parameters were fit to each cohort of striped bass collected in Badin Lake and Lake Norman (Table A.1). The pattern of striped bass growth in both reservoirs, with all observed and backcalculated data combined across cohorts, was similar for fish up to age-3 (Table A.2, Figure A.3). However, after age 3, the growth rates diverge and Badin Lake fish continued to increase in length through the ages observed in the study (Figure A.3a). Growth in most Lake Norman striped bass greatly diminished after age 4 (Figure A.3b), although the variability in length at these older ages was high and some fish appeared to achieve growth rates more similar to those seen in Badin Lake. At the time of this study, fish in Lake Norman reached harvestable size (20 inches, 508 mm) between age 3 and age 4, so the observed declining growth rates of older fish may have been influenced by preferential harvesting of the fastest-growing, largest fish in the population. Length-at-age estimates based only on backcalculation data (Table A.2) were slightly smaller than those based just on observed data, showing that the growth may be somewhat slower for the

majority of fish surviving to older ages. However, fishing pressure on the Badin Lake population is also high (Thompson et al. In press) and fish may be harvested at a smaller size (16 inches, 406 mm), yet growth appeared to continue at a higher rate among the small number of fish surviving to older ages (Figure A.3a). In Badin Lake, predicted lengths-at-age based only on backcalculated data were actually higher than values estimated based only on observed data (Table A.2), but this result was likely due to the influence on model fit of two older, faster-growing fish included in the backcalculation data.

The relationships between length and weight were significantly different for the two reservoirs (p-value <0.01), with the two curves beginning to diverge at 400 mm (Figure A.4). For lengths above 400 mm, Badin Lake striped bass had a higher weight than a similar length fish in Lake Norman, and this difference in weight increased with increasing length (Figure A.4). Year did not have a significant effect on the relationship in either reservoir, but day of the year and day of the year squared were both significant covariates in each reservoir ($\alpha = 0.05$):

$$\text{Badin Lake: } \log W = -4.69 + 2.94 \log L - (1.28 \times 10^{-3})D + (3.18 \times 10^{-6})D^2, R^2 = 0.97$$

$$\text{Lake Norman: } \log W = -4.57 + 2.87 \log L - (7.35 \times 10^{-4})D + (1.46 \times 10^{-6})D^2, R^2 = 0.98$$

where W is weight (g), L is length (mm), and D is day of the year. For a given length fish, estimated weight declined in the mid- through late-summer in relation to the spring and fall, and this decline was greater for larger fish.

Relative weight and somatic energy density

In Badin Lake, striped bass relative weight ranged from 64.5 to 119.0, with a mean value of 88.7 (standard deviation = 11.0) across 2000 through 2002. Relative weight of

striped bass in Lake Norman over the course of the study ranged from 59.2 to 105.1, with a mean value of 80.6 (standard deviation = 8.3). This mean value was significantly lower than the mean for Badin Lake (t-test, p-value <0.01). A relatively consistent seasonal pattern in relative weight that was independent of fish sex was seen in both reservoirs (Figure A.5). Relative weight was generally higher in winter and early spring, declined through late spring and summer, and rebounded in the late fall (Figure A.5). In 2001, relative weights of fish in Lake Norman continued to decline through the fall and did not increase until spring 2002 (Figure A.5b). In Badin Lake, significant differences in mean relative weight were observed among fish of differing total length (t-tests, $\alpha = 0.05$), but the relationship between relative weight and fish length was highly variable with no consistent pattern across years (Figure A.6). In Lake Norman, a more consistent pattern of declining relative weight with increasing fish length was apparent, with relative weight declining between fish less than 450 mm and those larger than 450 mm in all three years of the study (Figure A.7).

In addition to relative weight, somatic energy density was determined for each striped bass collected in the study using a regression model relating percent dry weight of a homogeneous sample from each fish to somatic energy density. A curvilinear relationship using the natural log of percent dry weight as a predictor of energy density provided the best fit to the data (Table A.3). Hartman and Brandt (1995) used a linear relationship to relate percent dry weight and energy density of striped bass, but their analysis only included data in the middle range of our percent dry weight values. Our data also appear linear through this range but the curvilinear model was necessary to fit data at either end of the percent dry weight values, which tended to have lower energy densities than would have been predicted by a linear relationship. No significant effect of lake in the curvilinear model was found

(ANOVA, p-value 0.09), so a single equation was used for fish from both Badin Lake and Lake Norman (Table A.3). While energy density was initially determined separately for somatic and gonad tissue, these values were combined into a total energy density, based on the proportionate weights of each component, for the analysis presented below and for inclusion in bioenergetics models. The decision to combine these values was based on the inconsistency of gonad development exhibited by individuals in both populations and the low energy density of the gonads (described below). No significant differences in total energy density were found between males, females, and immature fish in Badin Lake (ANOVA, p-value 0.16; Figure A.8a) or Lake Norman (ANOVA, p-value 0.18; Figure A.8b) so all sexes were analyzed together.

In Badin Lake, striped bass total energy density ranged from 5,201.5 to 9,525.7 J/g wet wt, with a mean value of 7,299.1 J/g wet wt (standard deviation = 790.5) between 2000 and 2002. The mean total energy density of Lake Norman striped bass (mean \pm standard deviation = 6,937.0 \pm 857.0 J/g wet wt) was significantly lower than that of fish from Badin Lake (t-test, p-value <0.01), with total energy densities ranging from 4,597.7 to 8,685.6 J/g wet wt between 2000 and 2002. Variation in energy density was high among individuals in both systems (Figure A.8), even when accounting for differences due to year, season, and fish size. In Badin Lake, a seasonal pattern in total energy density similar to that seen in relative weight was seen in 2000 and 2001, but no seasonal pattern was evident in 2002 (Figure A.8a). Only a weak seasonal pattern in energy density was seen in Lake Norman, with values slightly higher in the spring and lower in the summer and fall (Figure A.8b). As with relative weight, the annual relationship between energy density and fish length was highly variable in Badin Lake (Figure A.9). Significant differences in energy density with

total fish length (t-tests, $\alpha = 0.05$) were observed in 2000 and 2001 (Figure A.9a, b), but not in 2002 (Figure A.9c). In Lake Norman, significant differences in mean total energy density with increasing fish length were found in all years (Figure A.10). In 2000, total energy density increased from the smallest fish through fish 449 mm total length, before declining through all remaining size categories (Figure A.10a). In 2001, energy density remained fairly constant up to 499 mm, before declining through all remaining size categories (Figure A.10b), and in 2002, energy density declined steadily with increasing fish length (Figure A.10c). These patterns in energy density are similar to the generally negative relationship observed between relative weight and fish size.

Due to the high variability in energy density in both reservoirs, particularly in Badin Lake, no single regression model for either system sufficiently captured changes in total energy density with increasing fish size or through time, such as is required for input to the bioenergetics model. This lack of fit occurred even when the model included potential covariates such as fish sex, gonadosomatic index, and relative weight. Therefore, a value was estimated for each size category in each season that captured the general trend in energy density through time and across fish length (Table A.4). These values are not as idealized as those generated from a smooth function, but they provide a more realistic representation of the observed data. Energy density for each size category of Badin Lake striped bass was also determined for late July and early October 2003 (Table A.4) based on the general relationship between energy density and fish size for striped bass sampled on those dates. These data were used in modeling growth rate potential on those dates; this approach required only a point estimate for each date, rather than seasonal estimates for the entire year.

Given that sampling was more limited in this year, these data were not included in analysis of the seasonal or size-based trends in energy density described for 2000 through 2002.

Gonadosomatic index and gonad energy density

Gonadosomatic index (GSI) values were generally low for both males and females in Badin Lake and Lake Norman in all seasons. Some individuals caught between mid-March and mid-June in both reservoirs exhibited higher GSI values, but this increase was not consistent across the populations as some individuals still exhibited low GSI during that period (Figure A.11). Mean GSI for males from 2000 through 2002 in Badin Lake was 0.28% (standard deviation = 0.31%) during non-spring months, while this value increased only slightly to 1.79% (SD = 2.47%) during the spring months. For females in Badin Lake across these years, mean GSI was 0.81% (SD = 0.54%) in non-spring months and 1.09% (SD = 1.79%) during the spring months. In Lake Norman, mean male GSI was 0.43% (SD = 0.43%) in non-spring months, increasing somewhat more to 3.49% (SD = 3.22%) during the spring. Lake Norman female GSI followed a similar pattern of slight increase and high variation, increasing from 0.98% (SD = 0.55%) in the summer through winter to 2.35% (SD = 2.68%) in the spring. In the spring months, there was a generally positive relationship between GSI and total length among males with maturing gonads in both populations (Figure A.12). However, even at larger sizes, not all males had high GSI in the spring, indicating that gonad development was not consistent among all male fish. Among females, high spring GSI appeared to be an even more variable condition, with no discernable relationship to fish length (Figure A.12).

In addition to GSI, gonad energy density was determined for each mature fish collected during the study. Linear regression equations relating percent dry weight and energy density were used to allow energy density to be estimated from dried gonad samples (Table A.3). A significant effect of sex (p -value <0.01) on linear regression parameters was found for samples from both lakes, so males and females were investigated separately. For males, no significant effect of lake was found (p -value 0.69) so a single regression equation was estimated for male gonads from both Badin Lake and Lake Norman (Table A.3). For females, a significant effect of lake did exist (p -value <0.01) so separate equations were used for females from the two reservoirs (Table A.3).

Gonad energy density was similar for both males and females in both reservoirs, although these values were highly variable (Figure A.13). In Badin Lake, the mean energy density of male gonads collected over the course of the study was 4,705.7 J/g wt weight (standard deviation = 935.8 J/g wet wt). This value was similar to the mean for female gonads of 4,666.9 J/g wet wt (SD = 1185.5). In Lake Norman, males gonads had a mean energy density of 4,333.5 J/g wet wt (SD = 802.8) and female gonads had a mean energy density of 5,151.4 J/g wet wt (SD = 1761.8). Gonad energy density of both sexes was fairly constant through time in both reservoirs; several fish had relatively high gonad energy density (Figure A.13), but these high values did not always occur in the spring as they did with GSI. Interestingly, the highest energy density for a female in Badin Lake did occur in the spring (Figure A.13a) and several of the highest female gonad energy densities in Lake Norman also occurred in the spring (Figure A.13b). This pattern reflects a positive relationship between gonad energy density and GSI that was seen among females in both

reservoirs. A positive relationship was not apparent among males, likely reflecting the differential provisioning of gametes between the sexes.

Gonad energy density was generally lower than somatic energy density for any individual fish (Figure A.14). This pattern combined with the highly variable GSI values during the spring spawning months indicates that, as a population, striped bass in neither Badin Lake nor Lake Norman expend a large quantity of energy in gonad development. There is also little evidence of active spawning by striped bass in either reservoir, which suggests that fish may not actually release gametes during the spring. Reabsorption of these materials, especially by females, may help offset any costs experienced by individual fish that do expend resources to provision gametes. For these reasons, gonad development was not explicitly modeled as an energetic cost in the striped bass bioenergetics model, and total energy density (combining somatic and gonad energy density in proportion to their weights) was used as the appropriate model input to capture season- and size-specific striped bass energy density.

Diet composition

In Lake Norman, 72.4% of striped bass stomachs analyzed contained identifiable contents. The percentage was slightly lower (58.9%) in Badin Lake. The proportion of stomachs with contents varied by sampling date in both reservoirs, with dates in the spring often having a larger number of empty stomachs, particularly in Badin Lake (Figure A.15). This seasonal pattern could be the result of depressed feeding due to cold temperatures or due to the relative lack of forage available before recruitment of young-of-year shad.

The relationship between striped bass length and fish prey length was evaluated in each reservoir. This analysis was possible because backbone length and total length were highly correlated for all clupeid species in the study systems (Table A.5), allowing prey total length to be estimated even when it could not be measured directly. Significant positive linear regression models (p-value <0.01) related prey length to predator length in both Badin Lake and Lake Norman (Figure A.16). In both cases, the slope of the regression relationship was very shallow and the proportion of variability explained by the model was minimal (Badin Lake: $R^2 = 0.05$; Lake Norman: $R^2 = 0.02$), suggesting that the significance of the regression models was mainly a result of the large sample size. However, visual inspection of the data did reveal three categories of predator length with differing relationships to prey length. The first length category included striped bass less than 425 mm in Badin Lake and fish less than 475 mm in Lake Norman. These fish consumed almost entirely small clupeid prey (40 to 80 mm total length) and prey length appeared to be independent of predator length (Figure A.16). In the second length category, small clupeid prey still composed the largest component of the diet, but larger clupeids (>100 mm) and large non-clupeids also appeared in the diet. This category included fish 425 to 600 mm in Badin Lake and fish 475 to 575 mm in Lake Norman (Figure A.16). In the final length category, larger clupeids and non-clupeids still appeared sporadically in the diet, but the length of the majority of clupeid prey also increased (60 to 100 mm total length). This category included fish greater than 600 mm in Badin Lake and fish greater than 575 mm in Lake Norman (Figure A.16). These length categories were used to adjust the diet proportions input to the striped bass bioenergetics model; however, there were insufficient data in each length category for the

majority of sampling dates to allow for detailed analysis of the diet by striped bass length so the following discussion combines data across predator length.

Clupeids were the most frequent prey item in both reservoirs (Table A.6). In Badin Lake, 92.4% of stomachs with some contents collected in 2000 through 2002 contained clupeid prey. In both 2000 and 2001, clupeids occurred with a frequency of 89.1%, and clupeids accounted for almost all prey in 2002 (Table A.6). Sampling was much more limited in 2003 as it was directed specifically at the late July and early October dates included in growth rate potential models, but clupeids dominated the stomachs of striped bass collected in this year as well (Table A.6). In Lake Norman, 97.0% of non-empty stomachs from striped bass contained clupeids, and this value was basically constant across years (Table A.6). Invertebrates represented the next most frequent component of the diet. In Badin Lake, invertebrates were found in 8.1% of stomachs with contents from 2000 through 2002; this value was influenced by a particularly high percentage in 2000, while the frequencies of invertebrates in 2001 and 2002 were lower (Table A.6). No invertebrates were found in striped bass stomachs in 2003 (Table A.6). In Lake Norman, invertebrates were found in 4.5% of stomachs, and this value varied only slightly by year (Table A.6). The invertebrates identified in striped bass stomachs were predominantly mayfly nymphs (Order Ephemeroptera). In addition, fly larvae (Order Diptera), alderfly larvae (Order Megaloptera), and a single crayfish (Order Decapoda) were found in one stomach each. Fish other than clupeids comprised the final component of striped bass prey items, but these fish were infrequent. Non-clupeids occurred in 3.8% of Badin Lake stomachs and 1.0% of Lake Norman stomachs from 2000 through 2002 (Table A.6). This frequency varied from a low of zero in Lake Norman in 2000 and 2002 to a high of 8.7% in Badin Lake in 2001 (Table A.6).

Non-clupeid prey were found in a higher percentage (15.8%) of striped bass collected in Badin Lake in 2003 (Table A.6). Non-clupeid species identified included white perch *M. americana*, bluegill *Lepomis macrochirus*, and black crappie *Pomoxis nigromaculatus*.

Striped bass diet was also analyzed in terms of percent composition by number and percent composition by weight for Badin Lake (Figures A.17 through A.20) and Lake Norman (Figures A.21 through A.23). The significant relationship between backbone length and total length for each clupeid species found in the two reservoirs (Table A.5) allowed the analysis of striped bass diet composition to be conducted based on categories of prey total length. In Badin Lake, clupeids were the dominant prey item by number and by weight for most dates, and threadfin shad were the most common clupeid by both measures (Figures A.17 through A.20). The greatest proportions of threadfin shad by item were generally between 40 and 70 mm total length. On dates when larger clupeid prey were found in the diet, these prey often contributed a large percentage of the diet by weight (Figures A.17b, A.18d, A.19b, d). In August 2000 and June 2001, invertebrates represented a large proportion of the diet of Badin Lake striped bass by number (Figures A.17c, A.18a), but these prey composed a small percentage of the diet by weight due to their small size (Figures A.17d, A.18b). In both cases, the high percent composition by number was due to a small number of stomachs, each of which contained a large number of invertebrates. On dates when non-clupeid fish were found in the diet, only a very small number of these prey items were found but they were large (>100 mm total length), contributing a large percentage to the diet by weight (Figures A.17b, A.18 b, f, A.20d).

The pattern of prey composition in Lake Norman was similar in composition to that observed in Badin Lake. In June 2001, invertebrates composed a fairly large proportion of

the diet by number (Figure A.22a) and non-clupeid prey composed almost the entire diet by weight (Figure A.22b). On all other dates sampled, clupeids dominated the diet by number and by weight (Figures A.21 through A.23). Alewives were a higher percentage of the diet in 2001 and 2002 (Figures A.22, A.23) than in 2000 (Figure A.21) and a higher percentage than bluebacks were in Badin Lake striped bass diets in any year (Figures A.17 through A.20). However, threadfin shad were still the most common clupeid prey by number and by weight in Lake Norman (Figures A.21 through A.23). The length range of threadfin shad consumed was more variable between dates in Lake Norman than observed in Badin Lake.

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Tables

Table A.1. Von Bertalanffy growth model parameters fit to striped bass data from Badin Lake (top) and Lake Norman (bottom). Parameters are shown for each cohort observed during the study, as well as for all cohorts combined. Observed length-at-age and backcalculation of length-at-annulus formation were weighted equally in model fit. L_{inf} = maximum length, k = Brody growth coefficient (or the rate at which L_{inf} is achieved), t_0 = the theoretical age at which the fish would have zero length (Quinn and Deriso 1999), n_{OBS} = the number of length-at-age observations used in fitting the model, and n_{BC} = the number of backcalculated length-at-annulus formation estimates used in fitting the model.

Badin Lake, NC:

	All cohorts	1995*	1996*	1997	1998	1999	2000	2001**
L_{inf}	797.55	934.60	788.05	652.10	784.68	654.74	1069.15	--
k	0.32	0.26	0.35	0.68	0.31	0.54	0.18	--
t_0	-0.25	-0.60	-0.38	0.03	-0.52	0.24	-0.58	--
n_{OBS}	347	1	1	20	139	105	66	15
n_{BC}	79	7	6	16	20	15	10	5

Lake Norman, NC:

	All cohorts	1993*	1994	1995	1996	1997	1998	1999	2000	2001
L_{inf}	563.70	910.64	587.56	586.21	623.91	573.04	563.19	599.45	792.43	567.77
k	0.69	0.15	0.43	0.49	0.41	0.54	0.72	0.58	0.32	0.86
t_0	0.07	-1.07	0.02	-0.42	-0.46	0.04	0.21	-0.10	-0.39	0.29
n_{OBS}	223	1	2	4	21	44	45	50	37	20
n_{BC}	141	7	12	24	39	20	20	13	9	4

* Parameters for the 1995 and 1996 cohorts in Badin Lake and the 1993 cohort in Lake Norman are based on observation and backcalculation for a single fish.

** Parameters could not be estimated for the 2001 cohort in Badin Lake due to insufficient range of lengths collected.

Table A.2. Estimated length-at-age (mm) for striped bass in Badin Lake and Lake Norman, NC, based on von Bertalanffy growth models fit to all growth data, to just backcalculated length-at-annulus formation, and to just observed length-at-age data. All ages assume a January 1st birthday, such that length-at-age is the length of a fish on January 1st of the calendar year. Growth models were fit to data combined for all cohorts of fish collected during the study, with the exception of the 1990, 1992, and 1993 cohorts in Lake Norman.

	Badin Lake			Lake Norman		
	All data	Backcalculated	Observed	All data	Backcalculated	Observed
age-1	263	281	205	266	274	269
age-2	410	432	401	414	392	424
age-3	516	540	519	488	464	499
age-4	593	616	590	526	507	535
age-5	649	669	633	545	532	553
age-6	690	708	658	554	548	561
age-7	719	735	674	559	557	566
age-8	741	754	683	561	563	568

Table A.3. Equations, R² values, and sample sizes for regression models relating percent dry weight (*DW*) to energy density (J/g wet wt; *ED*) estimated for striped bass somatic tissue, male gonads, and female gonads. Separate equations are presented if a significant effect of reservoir was found; otherwise, a single equation is presented for both Badin Lake and Lake Norman.

	Equation	R ²	Sample size
Somatic tissue	$ED = -22742 + 8720.70 \cdot \ln(DW)$	0.92	62
Male gonads	$ED = -1504.22 + 295.35 \cdot DW$	0.94	46
Female gonads:			
Badin Lake	$ED = -1893.22 + 302.35 \cdot DW$	0.81	20
Lake Norman	$ED = -2128.12 + 324.51 \cdot DW$	0.99	26

Table A.4. Total energy density (J/g wet wt) of Badin Lake (top) and Lake Norman (bottom) striped bass through time and across total length categories in 2000, 2001, and 2002. Values were estimated based on the general trend of energy density across season and fish size. Additional values are provided for Badin Lake striped bass in late July and early October 2003 based on sampling conducted to provide data necessary for modeling growth rate potential on those dates.

Badin Lake:						
	<400 mm	400-449 mm	450-499 mm	500-549 mm	550-599 mm	≥600 mm
1-Jan-00	7,900	8,200	8,200	7,900	7,900	8,000
1-Apr-00	8,000	8,500	8,500	8,000	8,000	8,100
1-Jul-00	6,700	7,400	7,400	6,700	6,600	6,900
1-Oct-00	7,000	7,800	7,800	7,300	7,200	7,300
1-Jan-01	8,100	8,200	8,200	8,100	8,000	7,800
1-Apr-01	8,100	8,600	8,600	8,200	8,100	7,900
1-Jul-01	7,000	7,500	7,500	7,100	7,000	6,900
1-Oct-01	6,100	7,000	7,000	6,600	6,600	6,100
1-Jan-02	7,500	7,500	7,500	7,500	7,500	7,500
1-Apr-02	7,800	7,800	7,800	7,800	7,800	7,800
1-Jul-02	7,100	7,100	7,100	7,100	7,100	7,100
1-Oct-02	7,400	7,400	7,400	7,400	7,400	7,400
31-Dec-02	7,500	7,500	7,500	7,500	7,500	7,500
31-Jul-03	7,000	7,200	7,300	7,100	6,900	6,900
1-Oct-03	7,600	7,700	7,700	7,600	7,600	7,500

Lake Norman:						
	<400 mm	400-449 mm	450-499 mm	500-549 mm	550-599 mm	≥600 mm
1-Jan-00	7,400	7,500	7,300	7,000	6,800	6,600
1-Apr-00	7,800	8,000	7,600	7,400	7,200	7,000
1-Jul-00	7,000	7,200	6,900	6,600	6,400	6,200
1-Oct-00	7,400	7,600	7,300	7,000	6,800	6,600
1-Jan-01	7,700	7,700	7,700	7,400	7,100	6,800
1-Apr-01	7,900	7,900	7,900	7,600	7,400	7,200
1-Jul-01	7,200	7,200	7,200	6,800	6,500	6,200
1-Oct-01	7,500	7,500	7,500	7,200	6,900	6,600
1-Jan-02	7,200	7,100	7,100	7,100	6,700	6,500
1-Apr-02	7,500	7,300	7,300	7,300	7,100	7,000
1-Jul-02	7,100	6,900	6,900	6,900	6,500	6,100
1-Oct-02	7,200	7,000	7,000	7,000	6,700	6,500
31-Dec-02	6,700	6,500	6,500	6,500	6,200	6,000

Table A.5. Backbone length (mm; *BL*) to total length (mm; *TL*) regression equations, R^2 values, and samples sizes for forage fish in Badin Lake and Lake Norman, NC. Equations are shown for species, as well as combined equations for *Dorosoma* and for clupeids. Species- and genus-specific equations combine data from both reservoirs, while clupeid equations are lake-specific to account for differences in the forage fish communities.

	Equation	R^2	Sample size
Threadfin shad	$TL = -0.67 + 1.70BL$	0.98	320
Gizzard shad	$TL = 1.83 + 1.55BL$	0.99	103
Blueback herring	$TL = 0.92 + 1.61BL$	1.00	49
Alewife	$TL = 1.81 + 1.64BL$	0.99	168
<i>Dorosoma</i> spp.	$TL = 0.29 + 1.63BL$	0.98	206
Badin Lake clupeids	$TL = 0.43 + 1.63BL$	0.99	147
Lake Norman clupeids	$TL = 0.81 + 1.63BL$	0.98	309

Table A.6. Frequency of occurrence of broad categories of diet items found in striped bass stomachs from Badin Lake and Lake Norman. Empty stomachs were excluded from the analysis; values represent the proportion of stomachs with contents that contained the particular items. Data are presented for both reservoirs for 2000 through 2002 combined, as well as by year. Additional data are provided for 2003 for Badin Lake; these data were not used in calculating the percentages for all years combined.

	Badin Lake	Lake Norman
All years		
Clupeids	0.924	0.970
Invertebrates	0.081	0.045
Non-clupeid fish	0.038	0.010
2000		
Clupeids	0.891	0.986
Invertebrates	0.145	0.014
Non-clupeid fish	0.036	0
2001		
Clupeids	0.891	0.952
Invertebrates	0.065	0.072
Non-clupeid fish	0.087	0.024
2002		
Clupeids	0.988	0.977
Invertebrates	0	0.045
Non-clupeid fish	0.013	0
2003		
Clupeids	0.895	--
Invertebrates	0	--
Non-clupeid fish	0.158	--

Figures

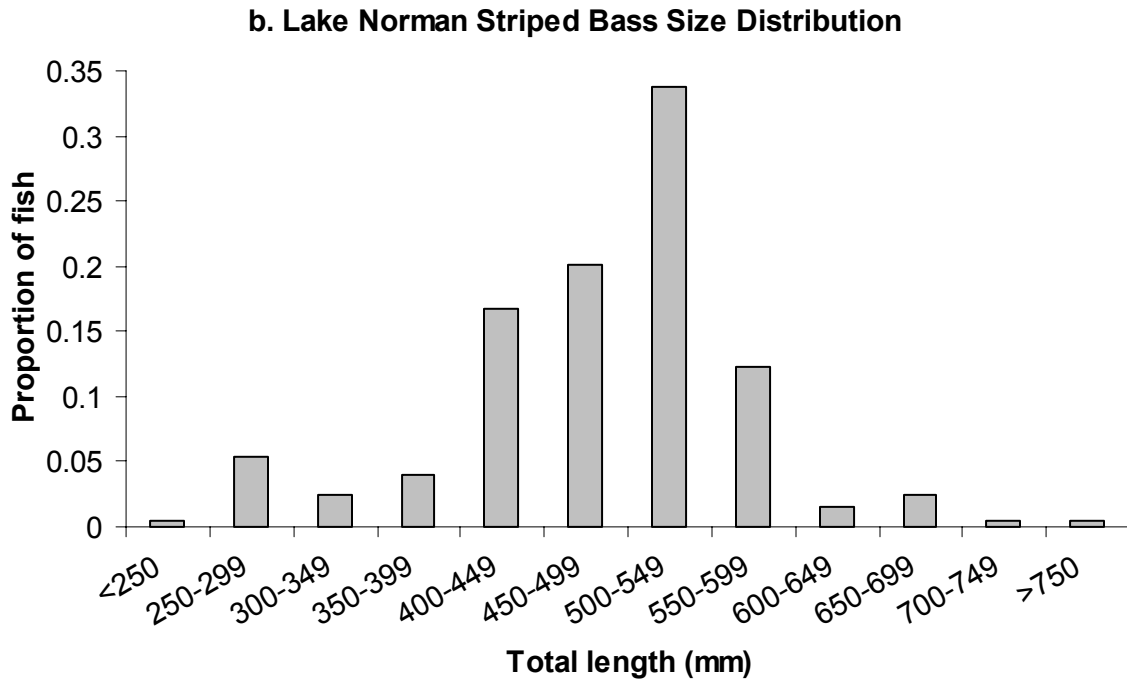
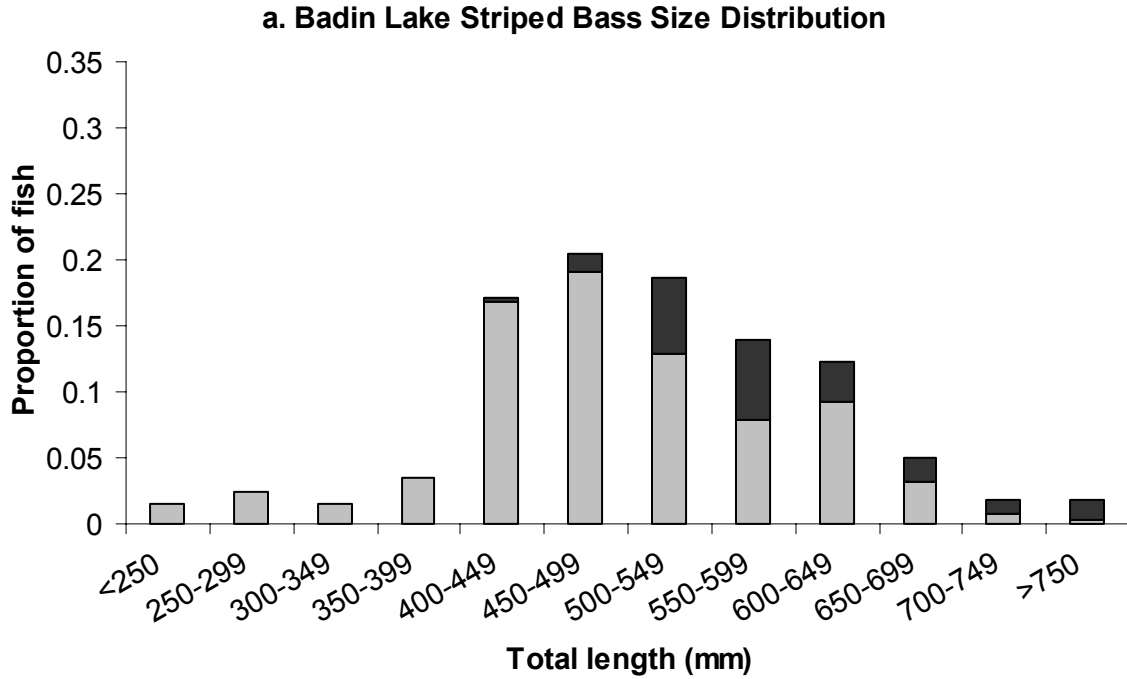
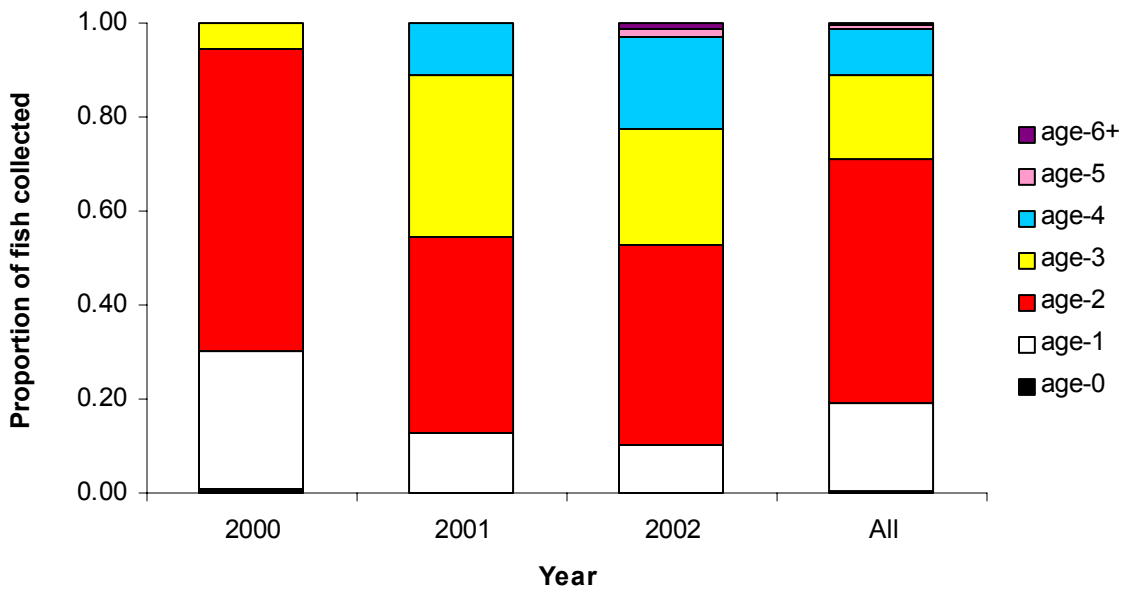


Figure A.1. Size distribution of all striped bass caught in (a) Badin Lake and (b) Lake Norman from 2000 through 2002. Badin Lake fish include those collected by gill net and intermittent angler sampling (light bars) and those collected by electroshocking (dark bars). All Lake Norman fish were collected by gill net or angler.

a. Badin Lake Striped Bass Age Structure



b. Lake Norman Striped Bass Age Structure

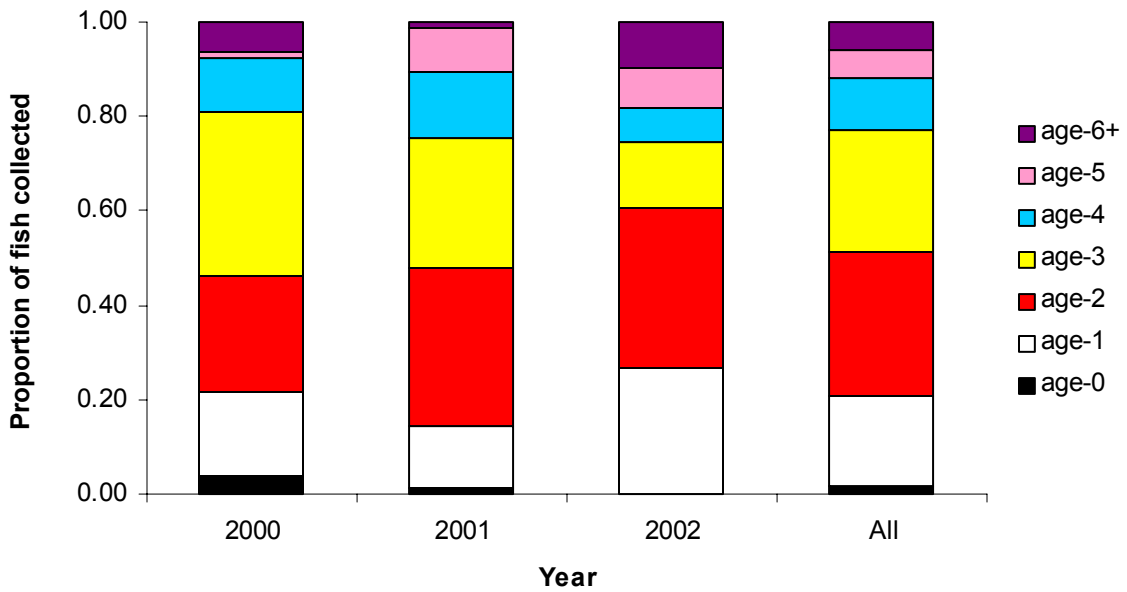


Figure A.2. Age structure of striped bass collected from (a) Badin Lake and (b) Lake Norman in 2000 through 2002. Ages are based on examination of sagittal otoliths.

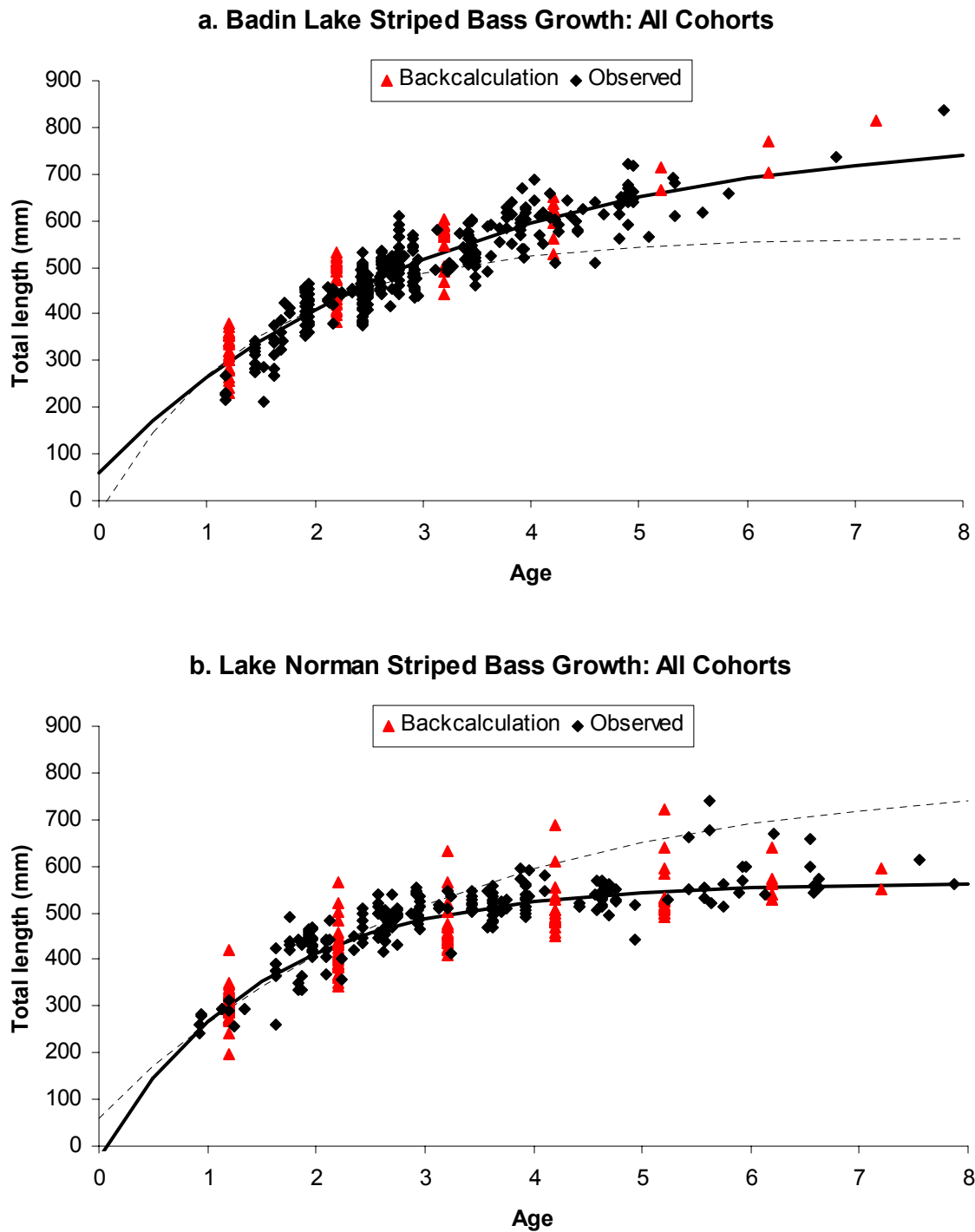
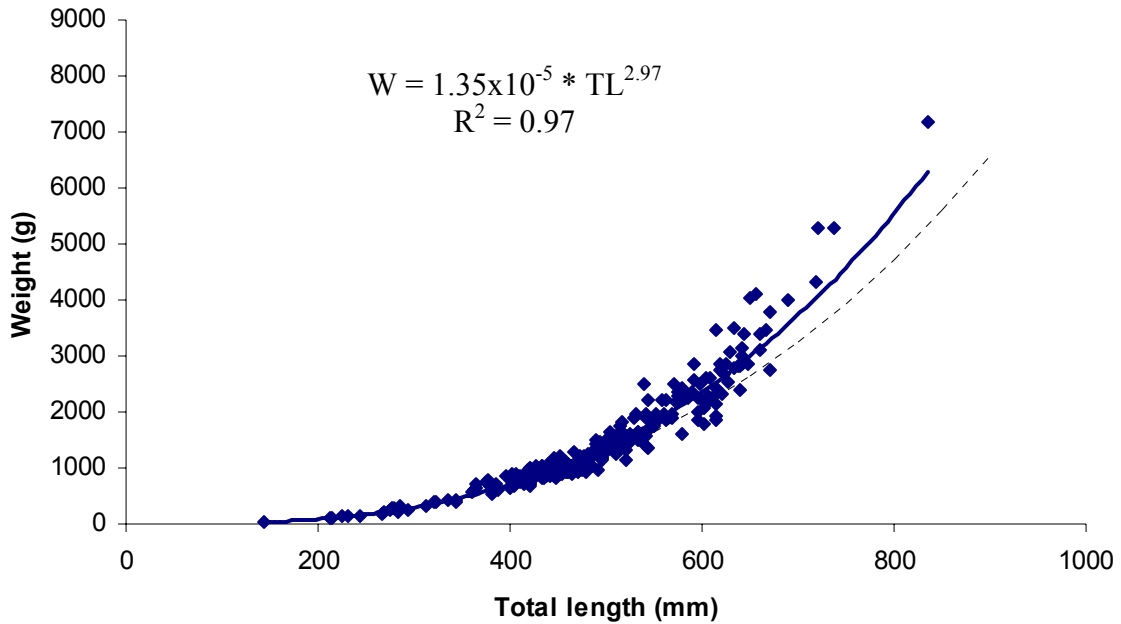


Figure A.3. Observed length-at-age and backcalculation of length at annulus formation for all striped bass collected in (a) Badin Lake and (b) Lake Norman. Each solid line indicates a von Bertalanffy growth curve fit to the data for that reservoir, weighting each observed and backcalculated data point equally, while each dashed line indicates the von Bertalanffy growth curve for the other reservoir for reference.

a. Badin Lake Striped Bass Length-Weight



b. Lake Norman Striped Bass Length-Weight

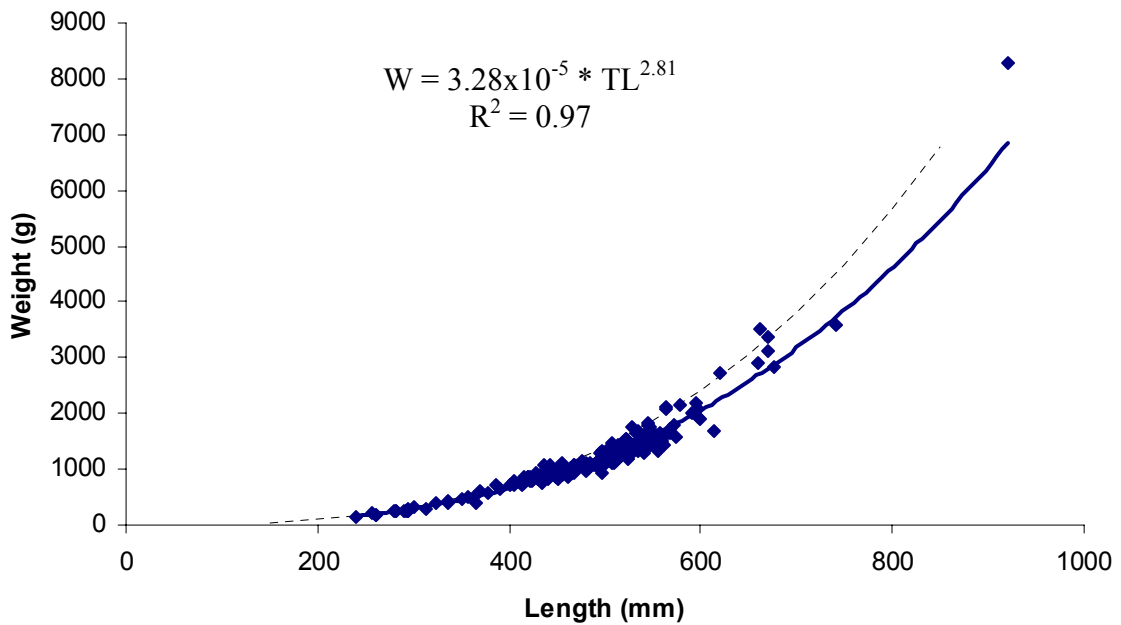
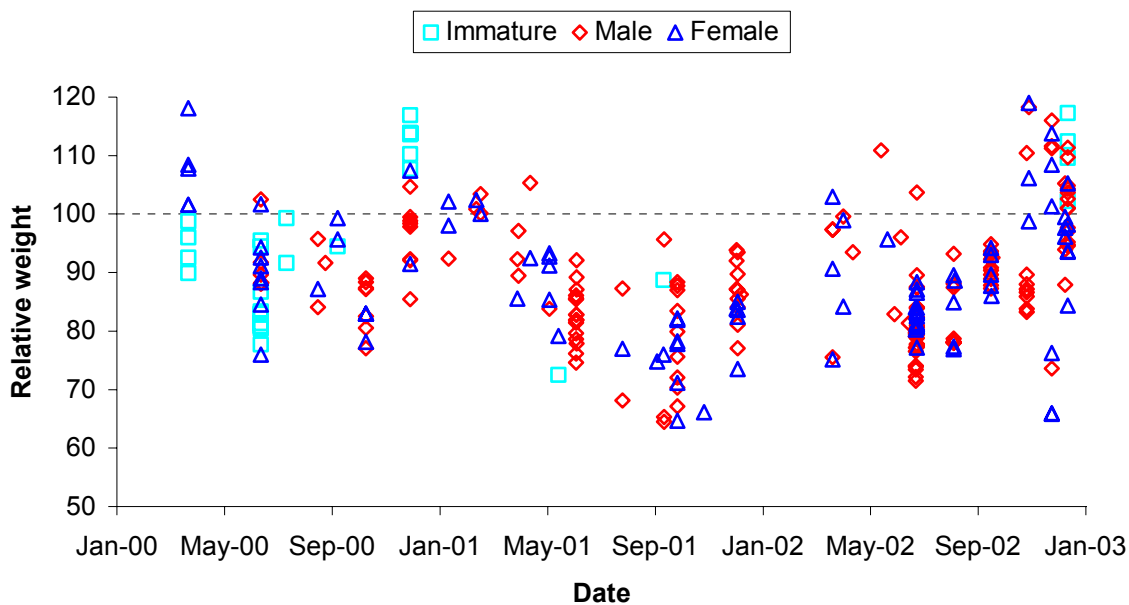


Figure A.4. Length-weight data for (a) Badin Lake and (b) Lake Norman striped bass. Each solid line shows the fitted relationship between the variables for that reservoir, with the equation and R^2 value shown, and each dotted line indicates the other reservoir's relationship for reference.

a. Badin Lake Striped Bass Relative Weight



b. Lake Norman Striped Bass Relative Weight

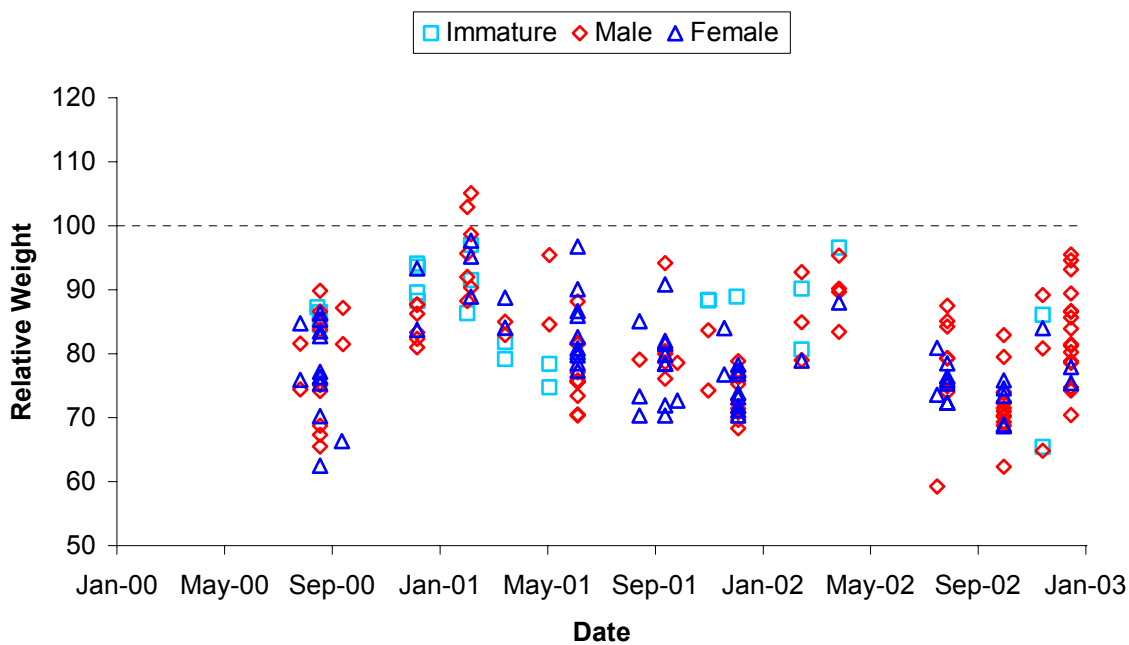


Figure A.5. Relative weight of (a) Badin Lake and (b) Lake Norman striped bass from 2000 through 2002. Data are presented by sex.

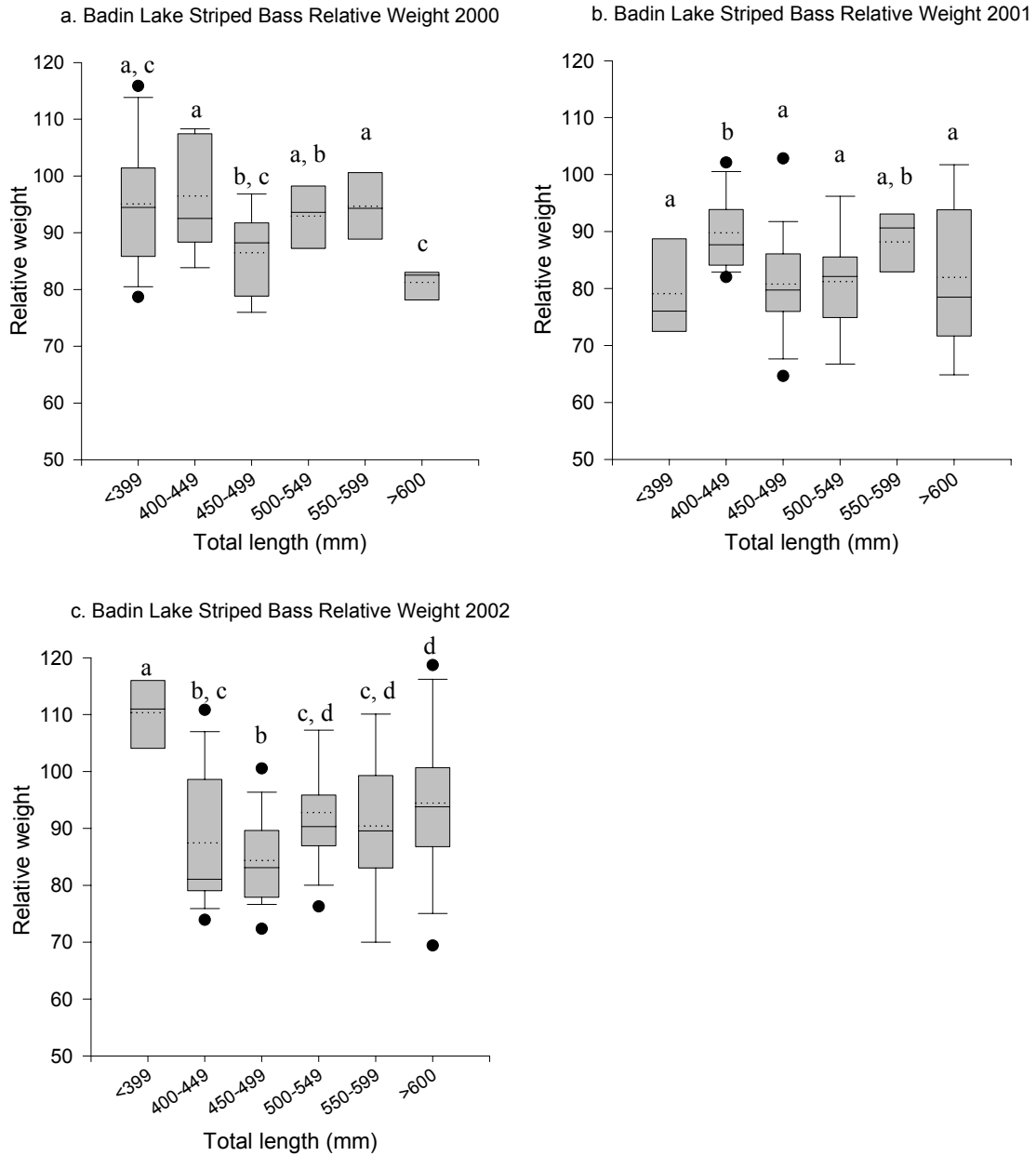


Figure A.6. Relative weight of Badin Lake striped bass by total length for (a) 2000, (b) 2001, and (c) 2002. The solid line in each box indicates the median and the dotted line indicates the mean. The bottom and top of each box indicate the 25th and 75th percentile, respectively. When sufficient data occur in a given length category, the bottom and top whisker indicate the 10th and 90th percentile, respectively, and the bottom and top point indicate the 5th and 95th percentile, respectively. The letters above each box indicate the results of t-tests between the means; means within the same letter category are not significantly different ($\alpha = 0.05$) while those in different letter categories are significantly different.

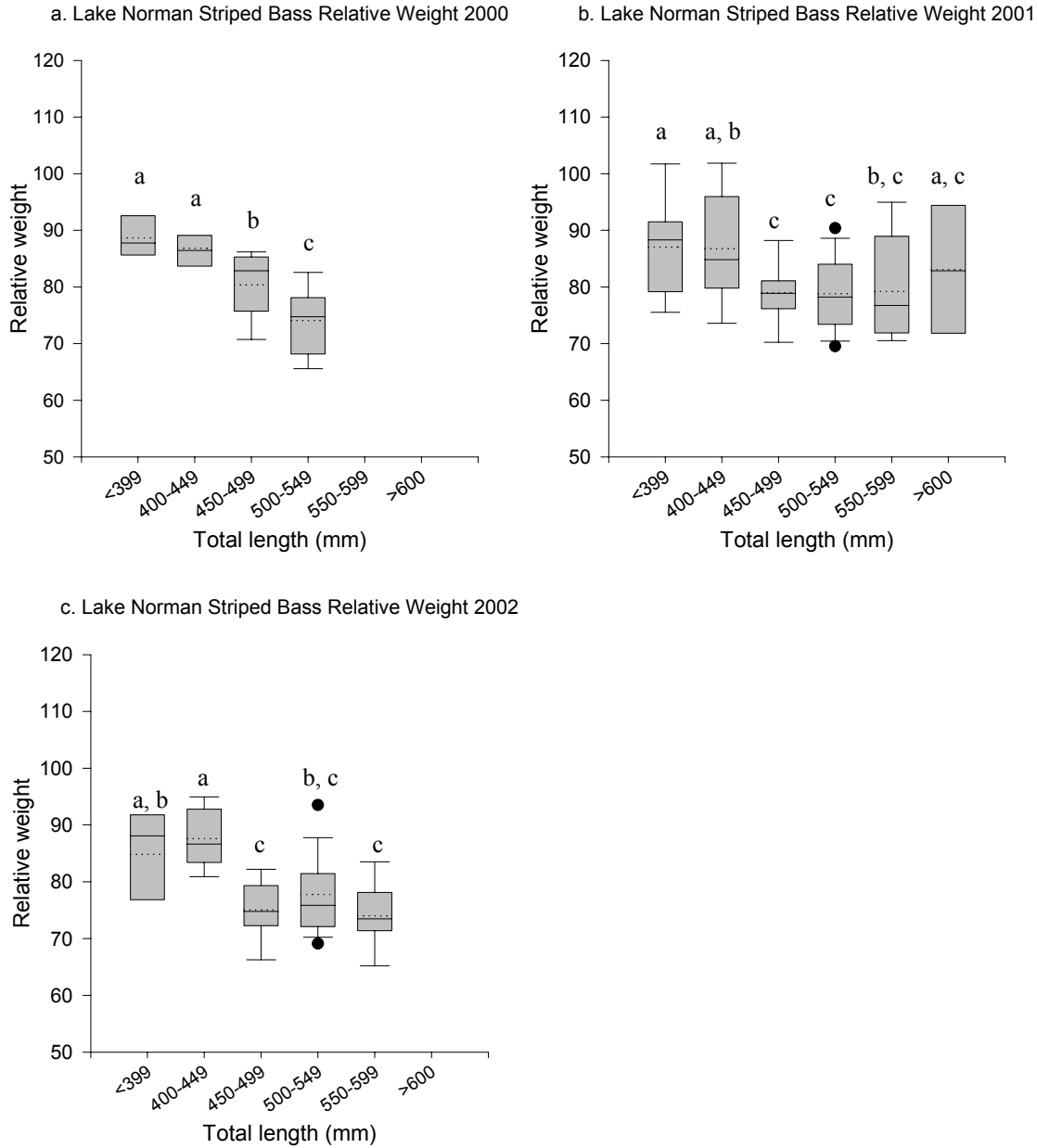


Figure A.7. Relative weight of Lake Norman striped bass by total length for (a) 2000, (b) 2001, and (c) 2002. Missing data indicate two fish or fewer collected in a given length category. The solid line in each box indicates the median and the dotted line indicates the mean. The bottom and top of each box indicate the 25th and 75th percentile, respectively. When sufficient data occur in a given length category, the bottom and top whisker indicate the 10th and 90th percentile, respectively, and the bottom and top point indicate the 5th and 95th percentile, respectively. The letters above each box indicate the results of t-tests between the means; means within the same letter category are not significantly different ($\alpha = 0.05$) while those in different letter categories are significantly different.

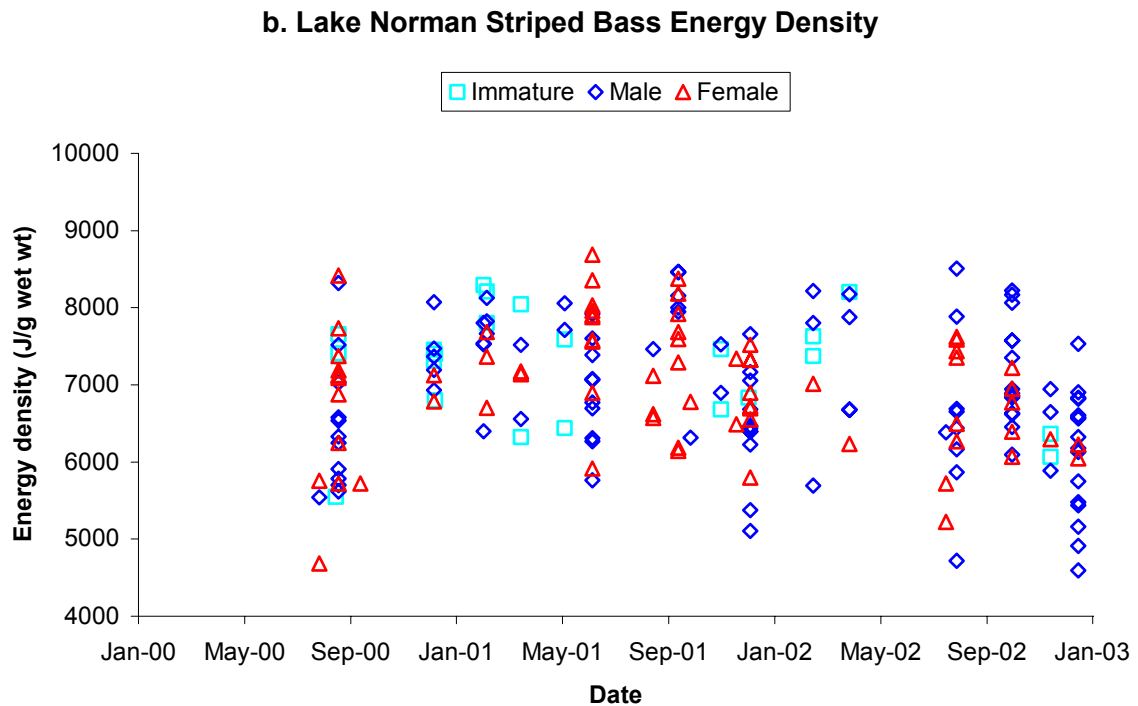
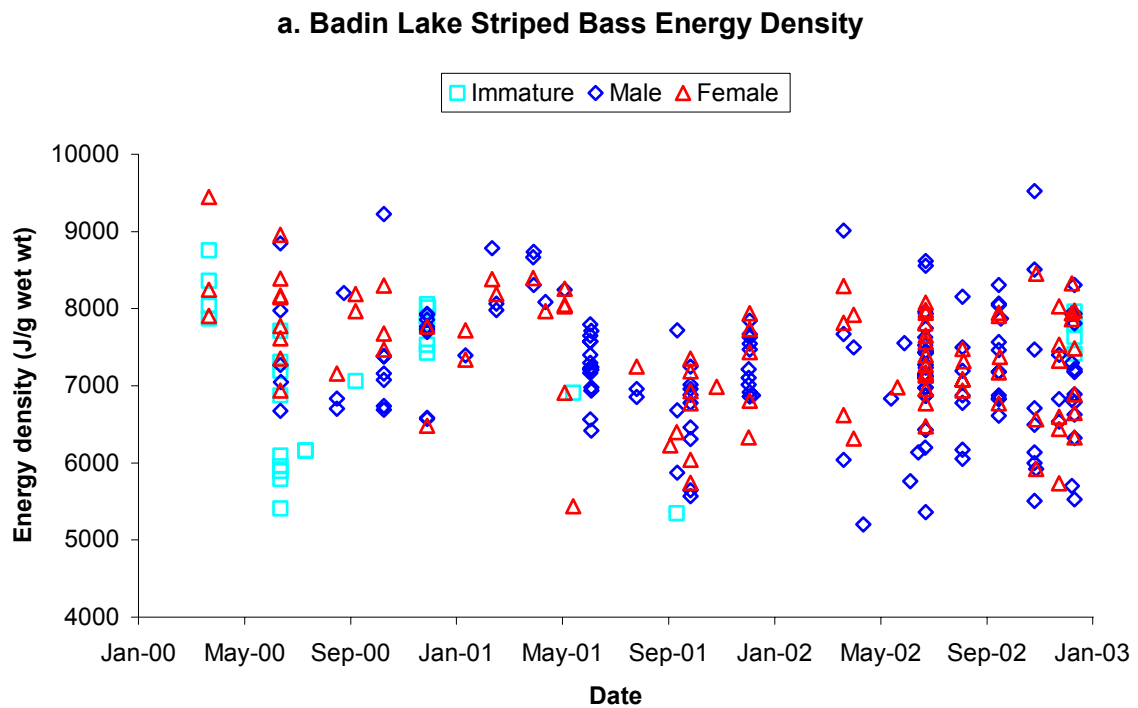


Figure A.8. Total energy density (somatic and gonad energy density combined in proportion to wet weight; J/g wet wt) of striped bass in (a) Badin Lake and (b) Lake Norman in 2000 through 2002. Data are presented by sex.

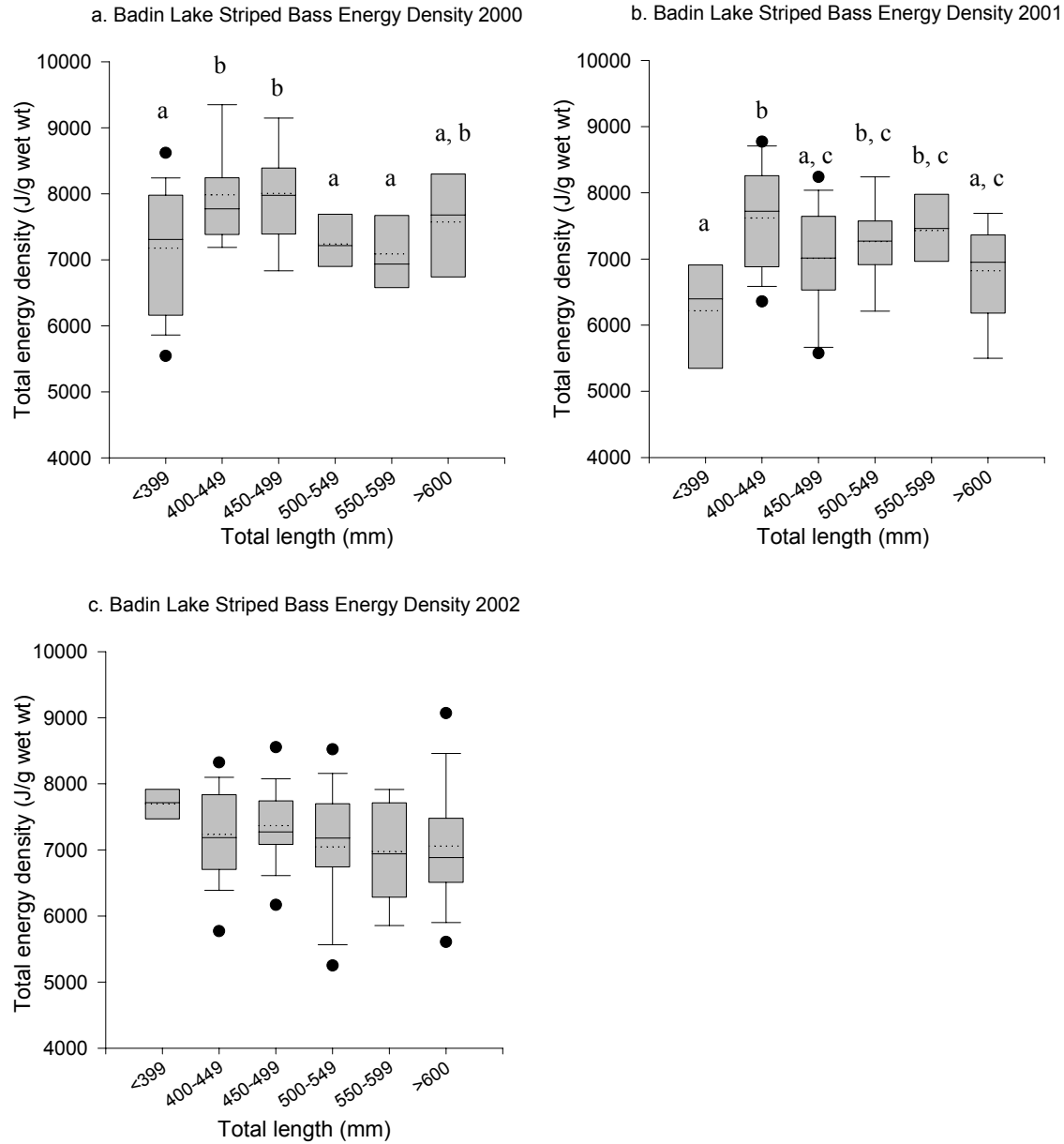


Figure A.9. Total energy density (J/g wet wt) versus total length for striped bass collected in Badin Lake in (a) 2000, (b) 2001, and (c) 2002. The solid line in each box indicates the median and the dotted line indicates the mean. The bottom and top of each box indicate the 25th and 75th percentile, respectively. When sufficient data occur in a given length category, the bottom and top whisker indicate the 10th and 90th percentile, respectively, and the bottom and top point indicate the 5th and 95th percentile, respectively. The letters above each box in graphs for 2000 and 2001 indicate the results of t-tests between the means; means within the same letter category are not significantly different ($\alpha = 0.05$) while those in different letter categories are significantly different. No significant differences between categories were found in 2002.

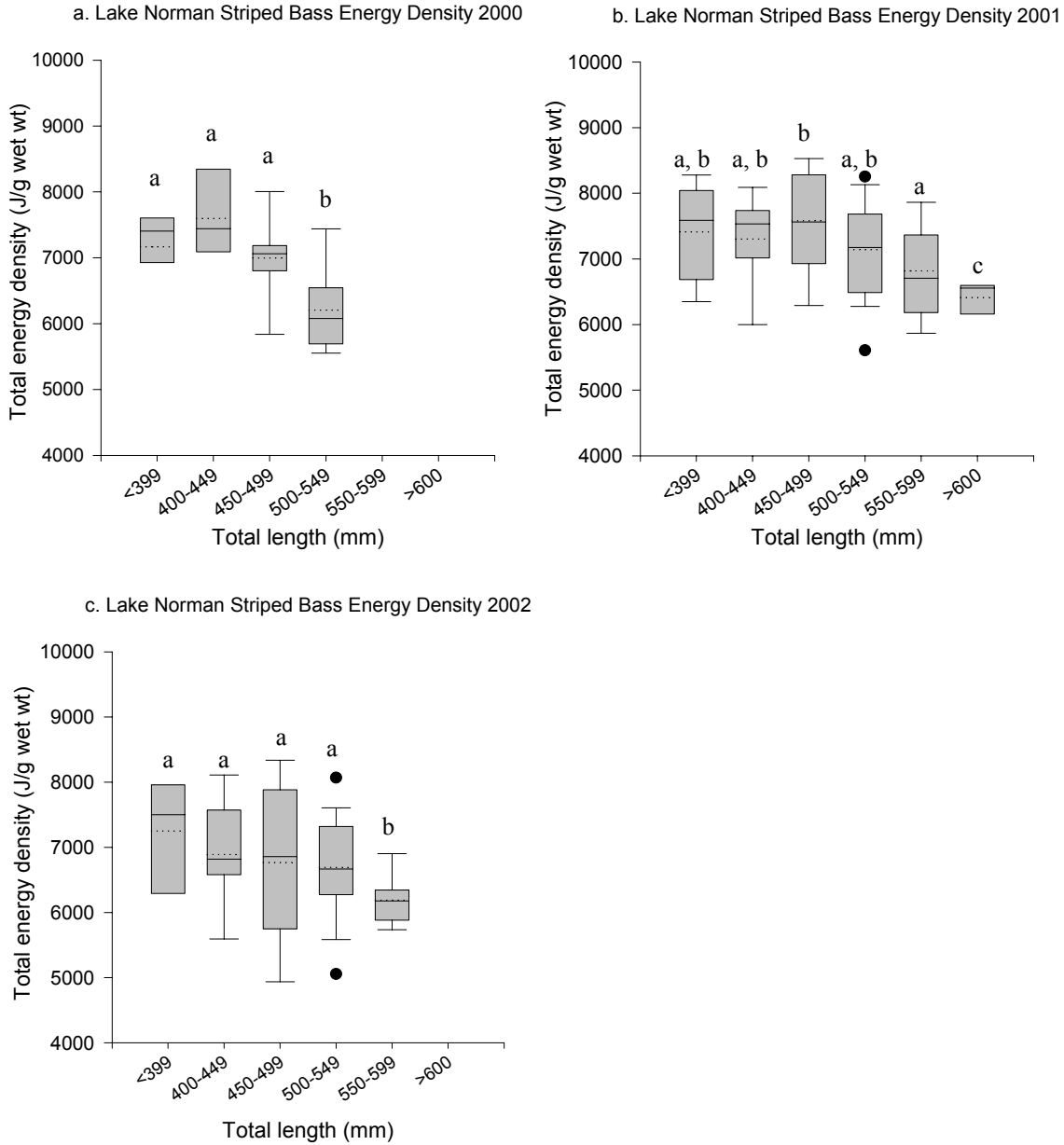
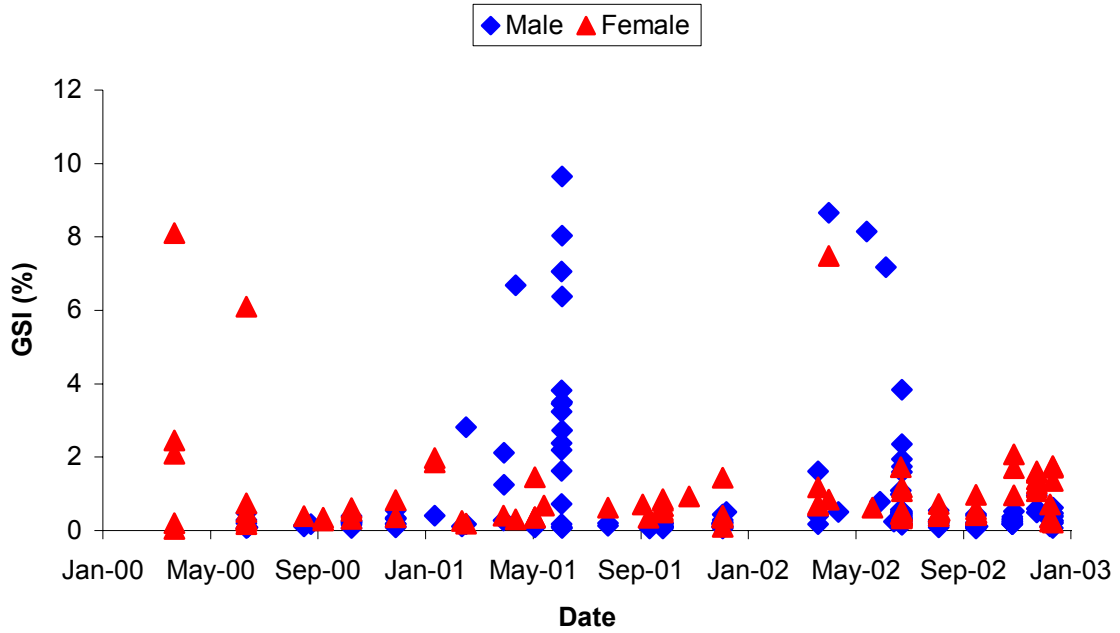


Figure A.10. Total energy density (J/g wet wt) versus total length for striped bass collected in Lake Norman in (a) 2000, (b) 2001, and (c) 2002. Missing data indicate two fish or fewer collected in a given length category. The solid line in each box indicates the median and the dotted line indicates the mean. The bottom and top of each box indicate the 25th and 75th percentile, respectively. When sufficient data occur in a given length category, the bottom and top whisker indicate the 10th and 90th percentile, respectively, and the bottom and top point indicate the 5th and 95th percentile, respectively. The letters above each box indicate the results of t-tests between the means; means within the same letter category are not significantly different ($\alpha = 0.05$) while those in different letter categories are significantly different.

a. Badin Lake Striped Bass Gonadosomatic Index



b. Lake Norman Striped Bass Gonadosomatic Index

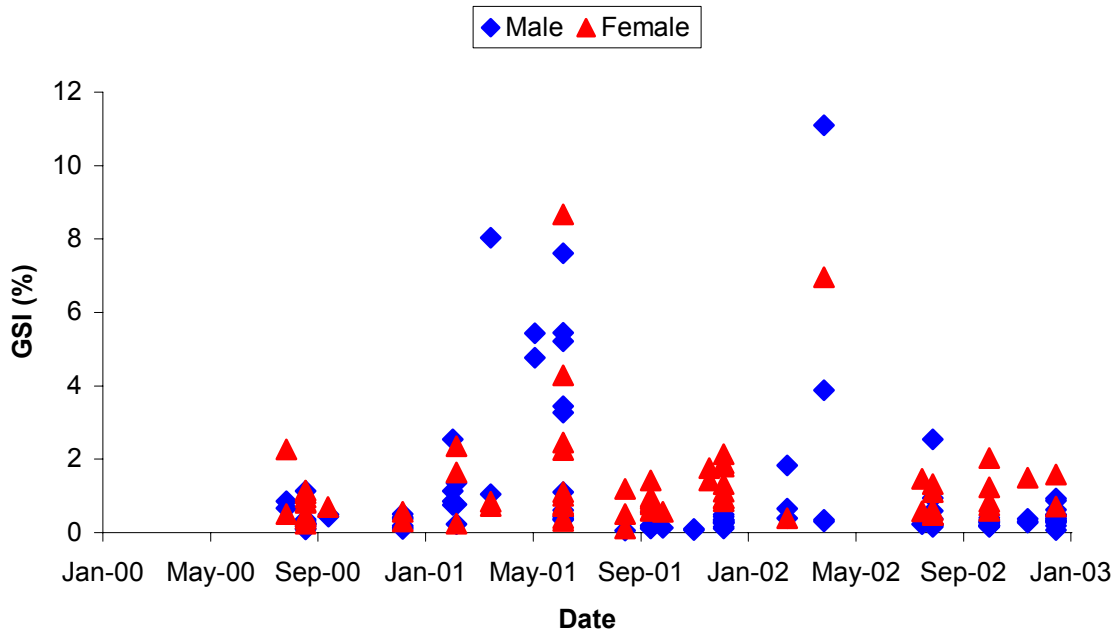
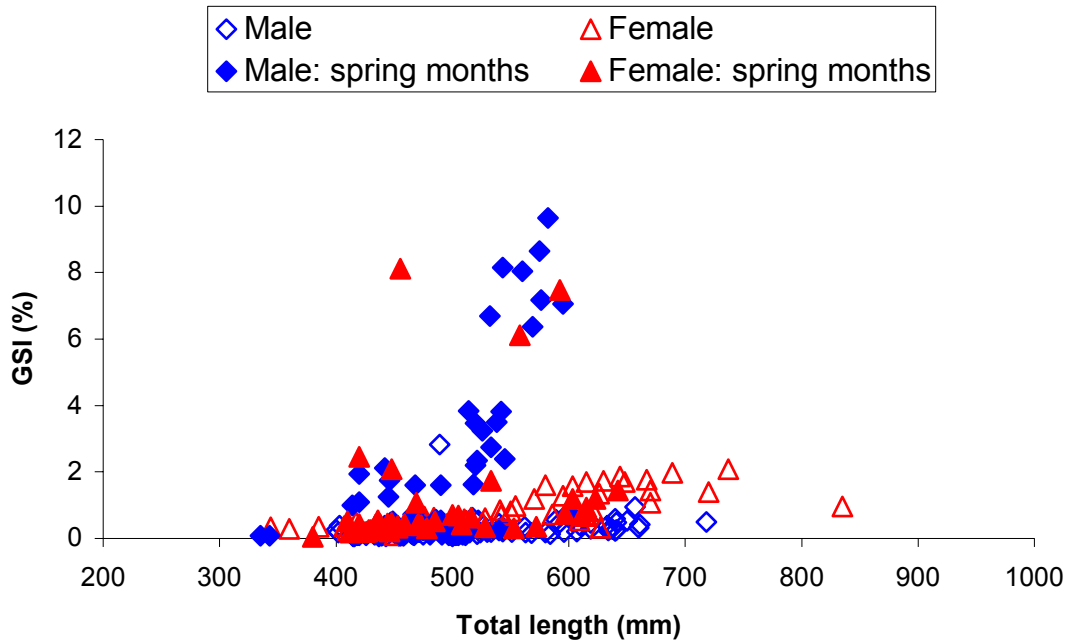


Figure A.11. Gonadosomatic index by date for males and females collected in (a) Badin Lake and (b) Lake Norman. Data shown are for 2000 through 2002.

a. Badin Lake Striped Bass Gonadosomatic Index



b. Lake Norman Striped Bass Gonadosomatic Index

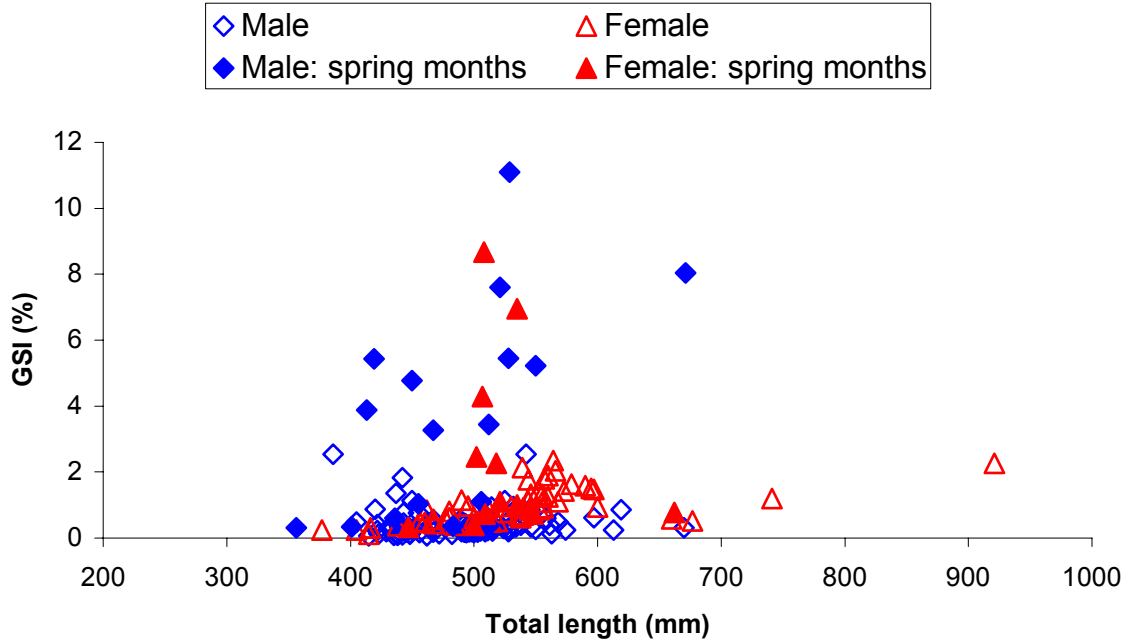
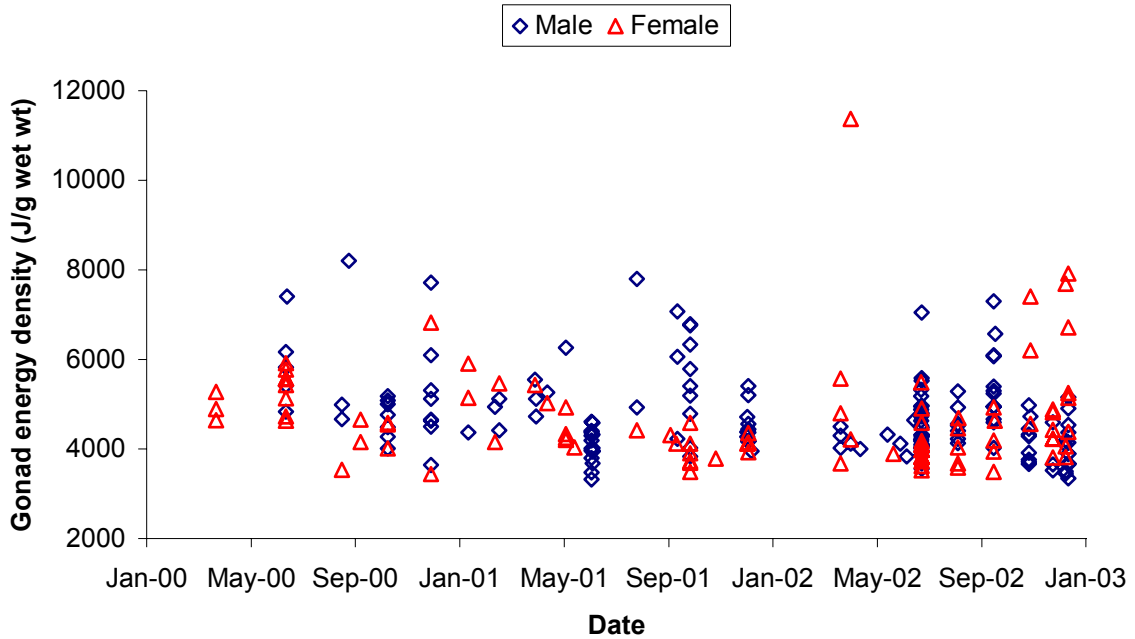


Figure A.12. Gonadosomatic index by length for males and females in (a) Badin Lake and (b) Lake Norman for 2000 through 2002. Solid symbols are spring data (March through mid-June), and open symbols are data from all other months.

a. Badin Lake Striped Bass Gonad Energy Density



b. Lake Norman Striped Bass Gonad Energy Density

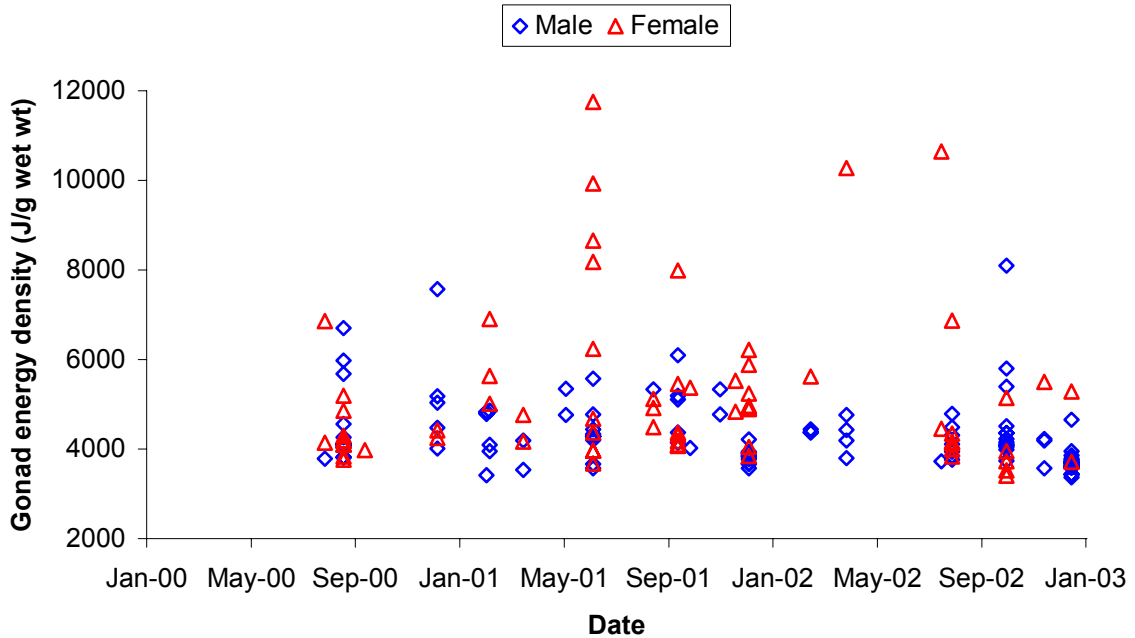
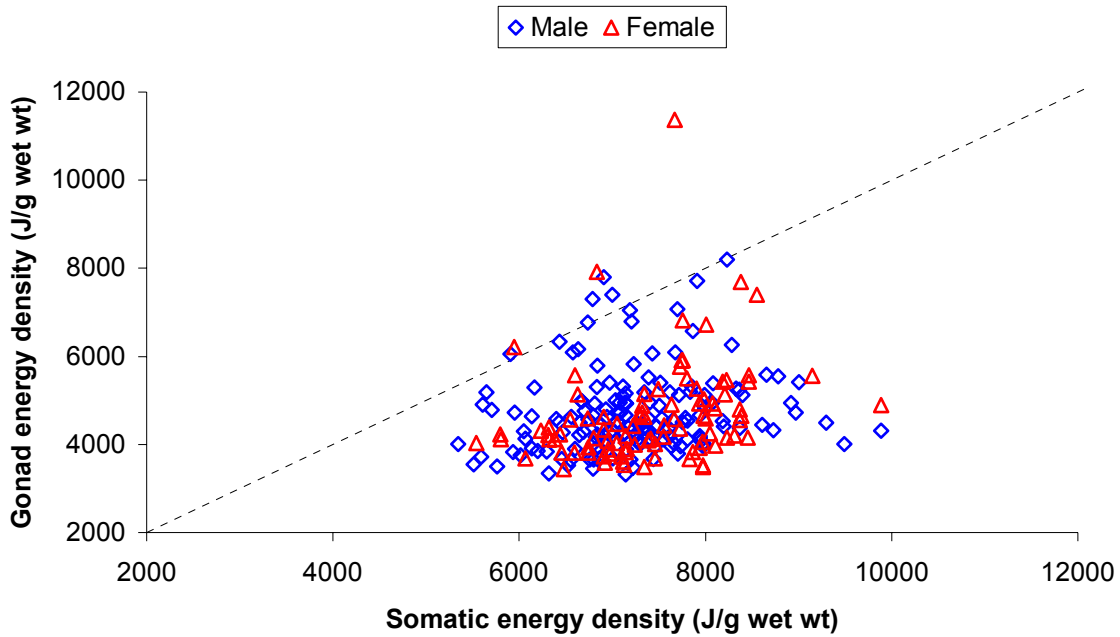


Figure A.13. Gonad energy density (J/g wet wt) of striped bass in (a) Badin Lake and (b) Lake Norman in 2000 through 2002. Data are presented for males and females

a. Badin Lake Striped Bass Gonad and Somatic Energy Density



b. Lake Norman Striped Bass Gonad and Somatic Energy Density

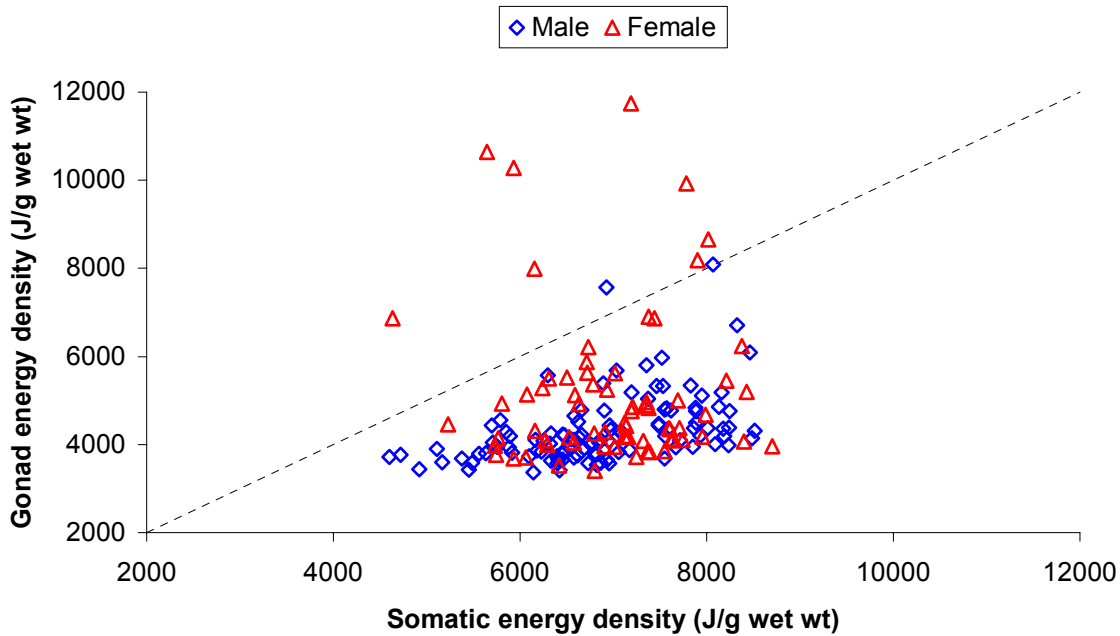


Figure A.14. Gonad energy density versus somatic energy density for males and females collected in 2000 through 2002 from (a) Badin Lake and (b) Lake Norman. Dotted line indicates 1:1 ratio.

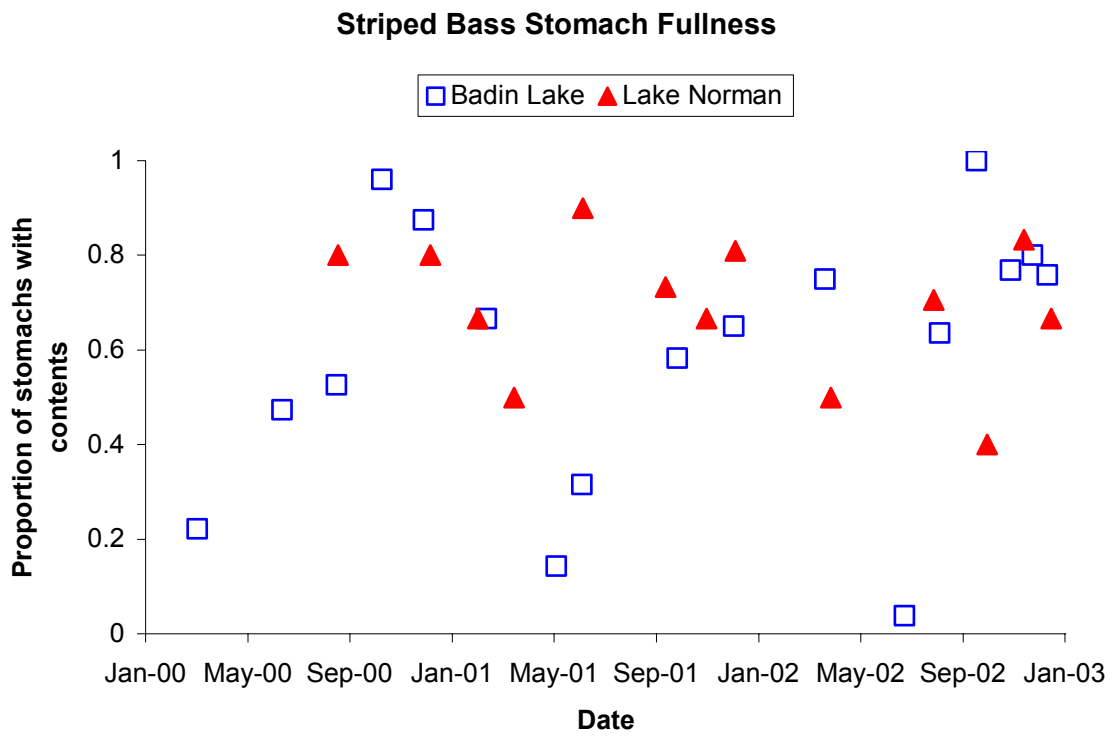


Figure A.15. Proportion of striped bass stomachs from fish collected in Badin Lake and Lake Norman, NC, that contained contents. Data are shown for 2000 through 2002.

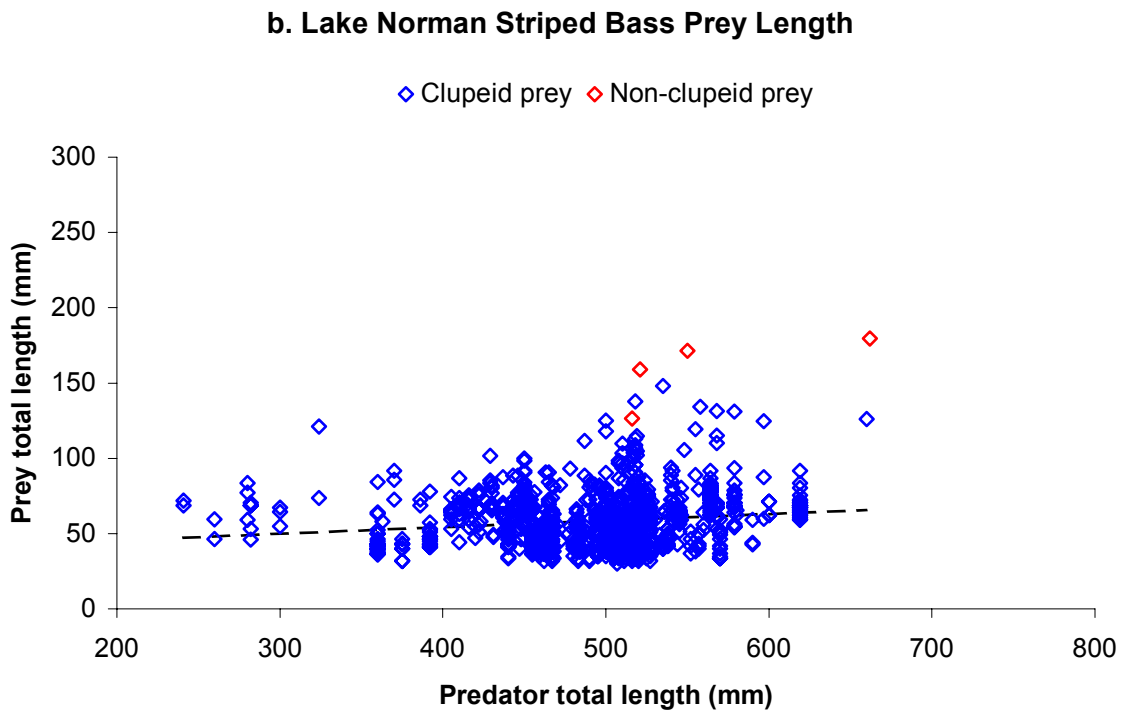
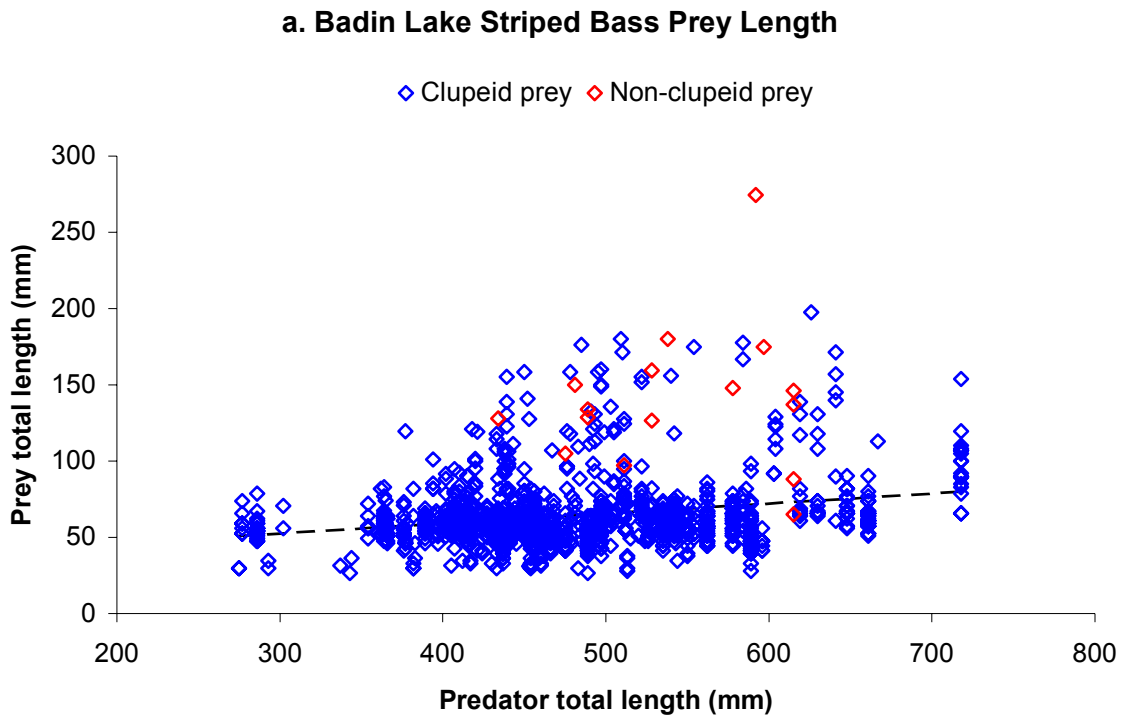


Figure A.16. Prey length of clupeid and non-clupeid prey from (a) Badin Lake and (b) Lake Norman striped bass stomachs as a function of predator length. Dashed lines indicate significant linear regression models fit to all prey data, both clupeid and non-clupeid.

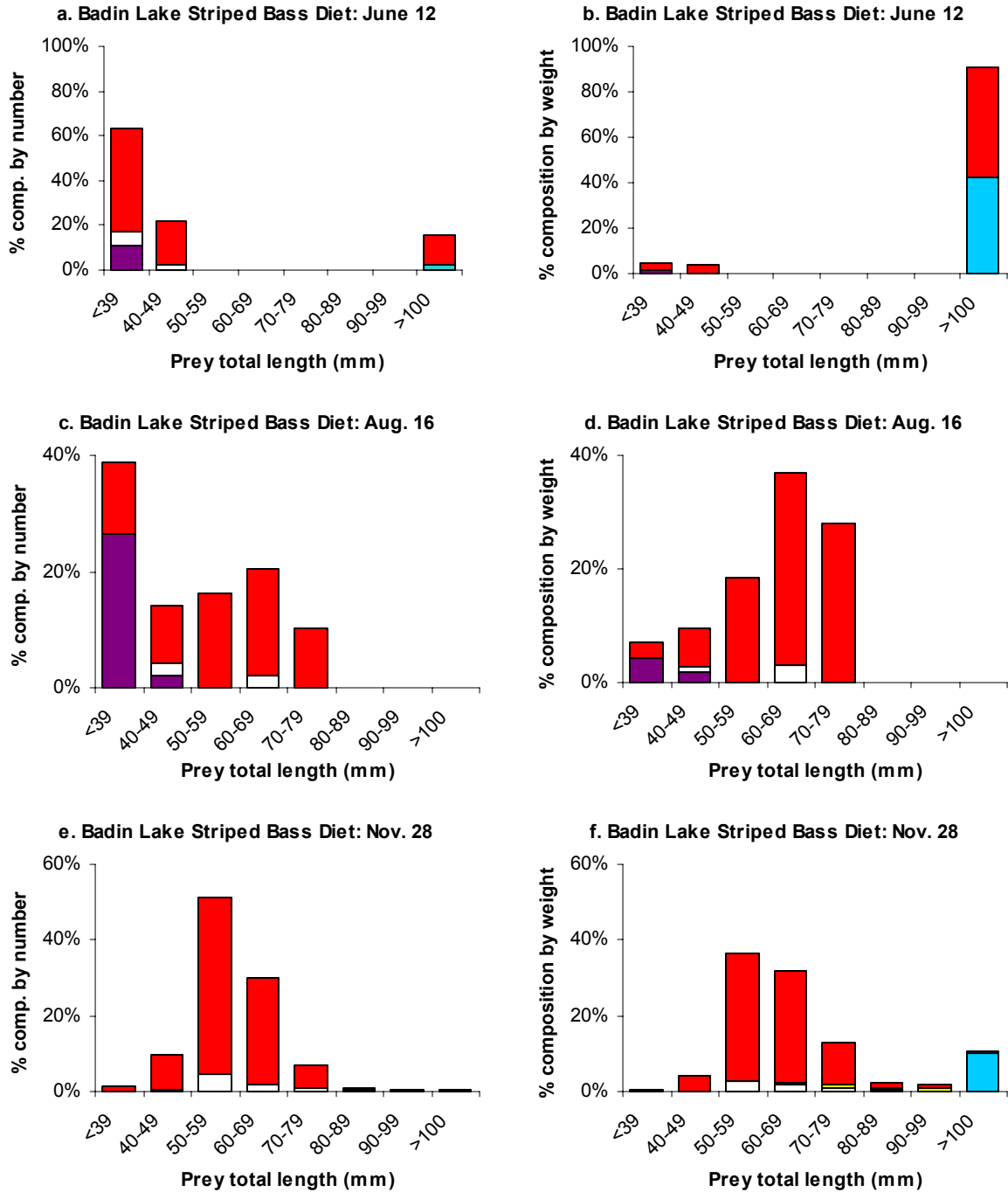


Figure A.17. Diet composition of striped bass collected from Badin Lake, NC, in 2000. Data are shown as (a, c, e) percent composition by number and (b, d, f) percent composition by weight for the (a, b) late spring, (c, d) summer, and (e, f) winter samples. Red bars indicate threadfin shad, yellow bars indicate gizzard shad, white bars indicate blueback herring, blue bars indicate non-clupeid fish, and purple bars indicate invertebrates. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

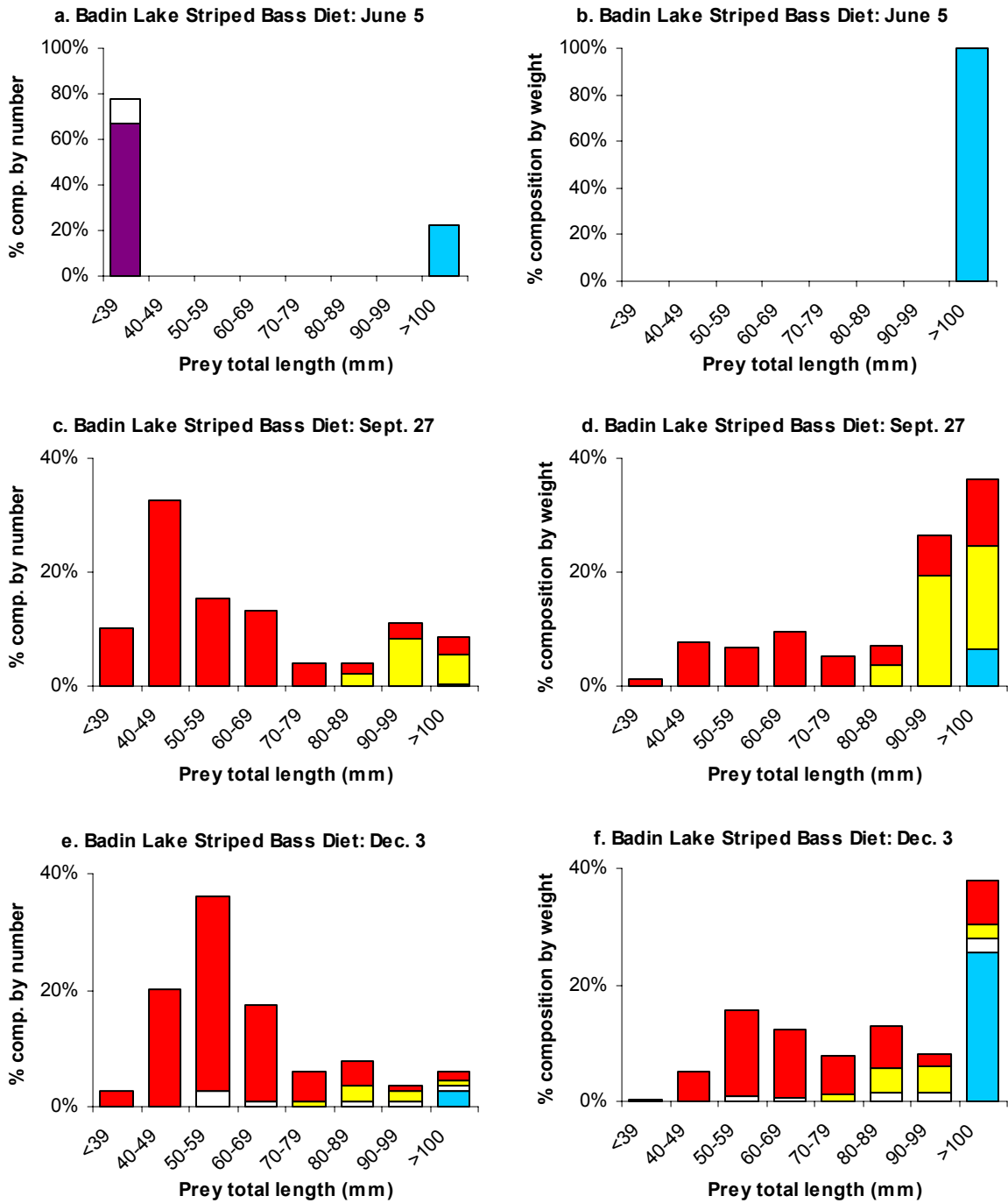


Figure A.18. Diet composition of striped bass collected from Badin Lake, NC, in 2001. Data are shown as (a, c, e) percent composition by number and (b, d, f) percent composition by weight for the (a, b) late spring, (c, d) late summer, and (e, f) winter samples. Red bars indicate threadfin shad, yellow bars indicate gizzard shad, white bars indicate blueback herring, blue bars indicate non-clupeid fish, and purple bars indicate invertebrates. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

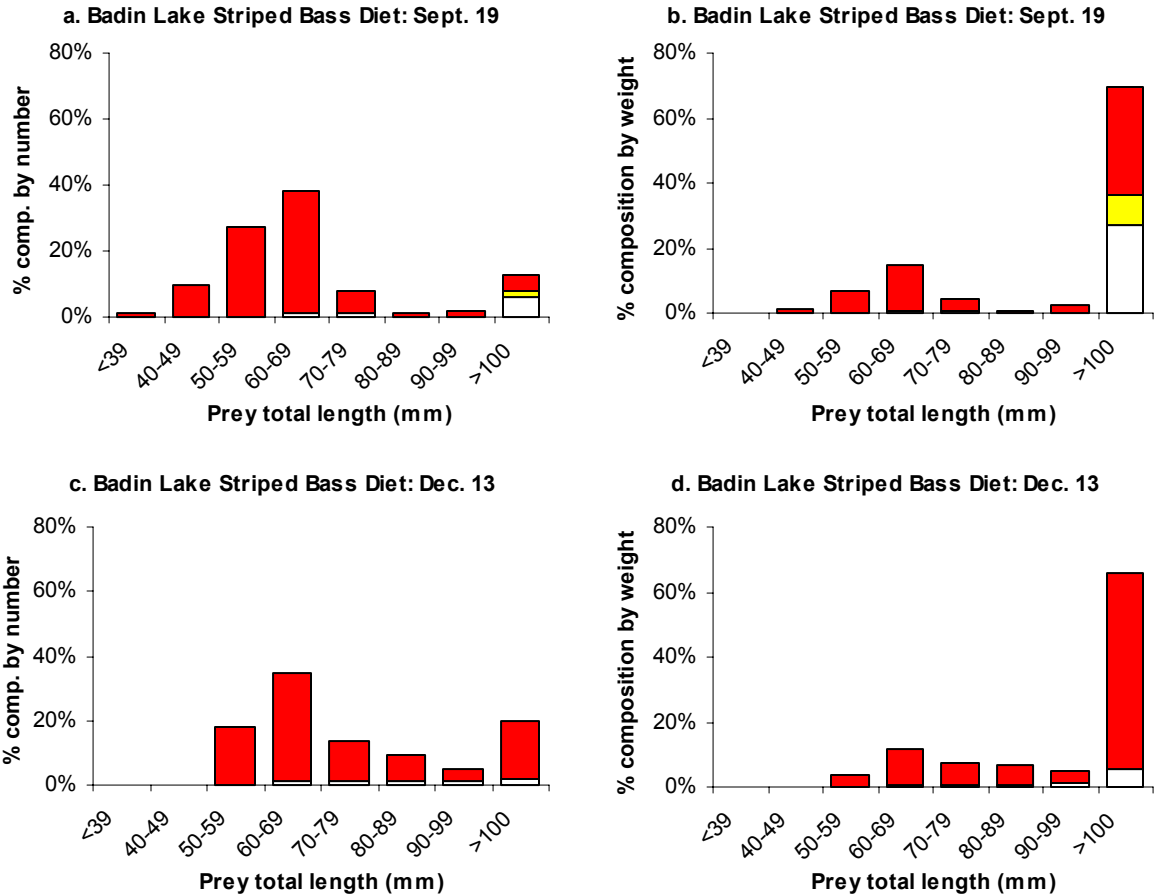


Figure A.19. Diet composition of striped bass collected from Badin Lake, NC, in 2002. Data are shown as (a, c) percent composition by number and (b, d) percent composition by weight for the (a, b) late summer and (c, d) winter samples. There were insufficient data in the late spring sample for analysis due to a high proportion of empty stomachs. Red bars indicate threadfin shad, yellow bars indicate gizzard shad, and white bars indicate blueback herring. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

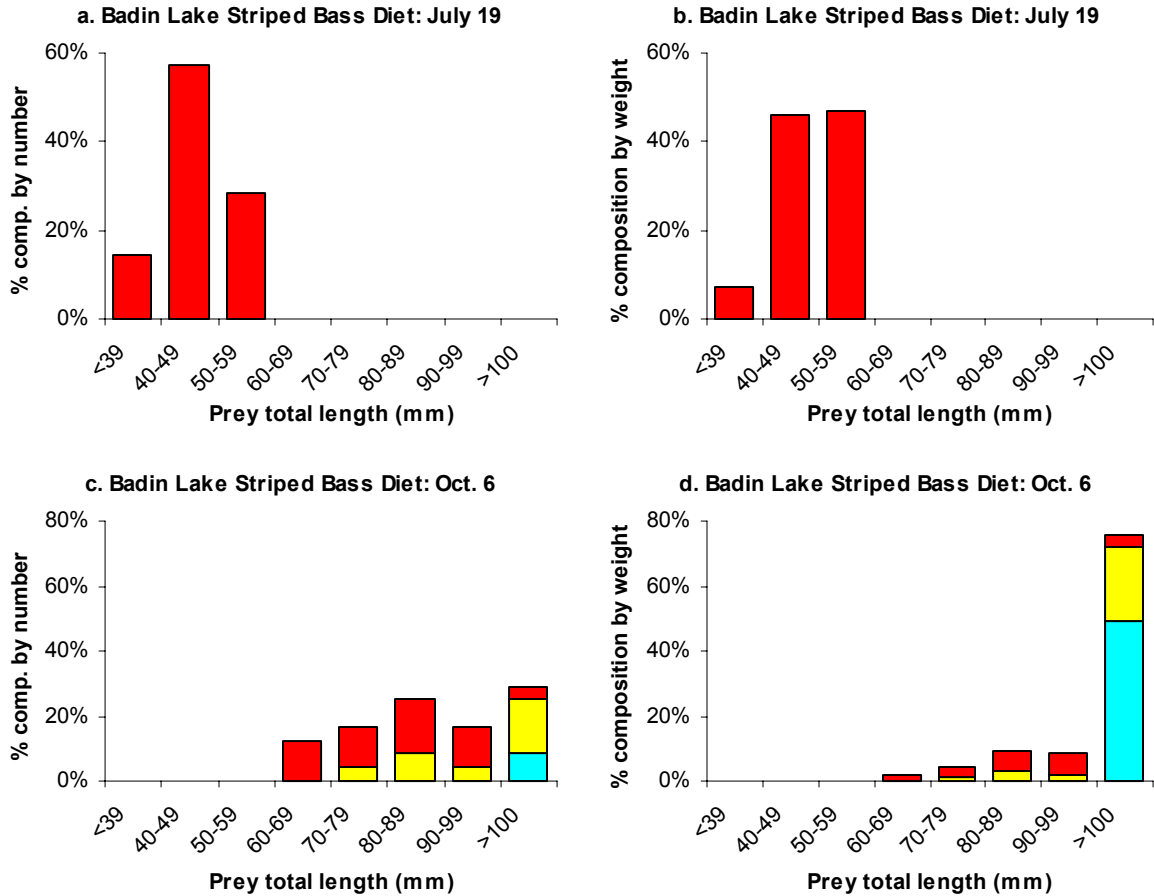


Figure A.20. Diet composition of striped bass collected from Badin Lake, NC, in 2003. Data are shown as (a, c) percent composition by number and (b, d) percent composition by weight for the (a, b) summer and (c, d) fall samples. Red bars indicate threadfin shad, yellow bars indicate gizzard shad, and blue bars indicate non-clupeid fish. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

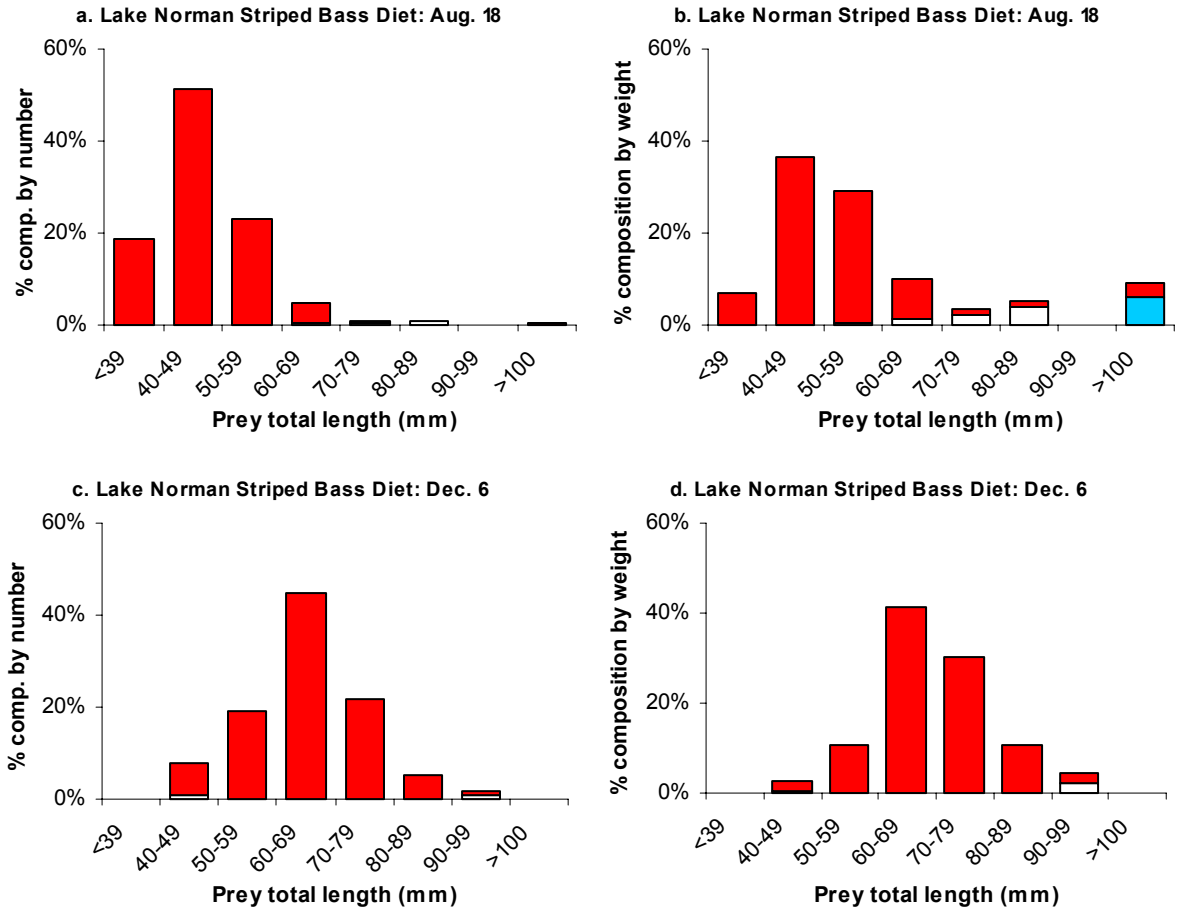


Figure A.21. Diet composition of striped bass collected from Lake Norman, NC, in 2000. Data are shown as (a, c) percent composition by number and (b, d) percent composition by weight for the (a, b) summer and (c, d) winter samples. Red bars indicate threadfin shad, white bars indicate alewife, and blue bars indicate non-clupeid fish. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

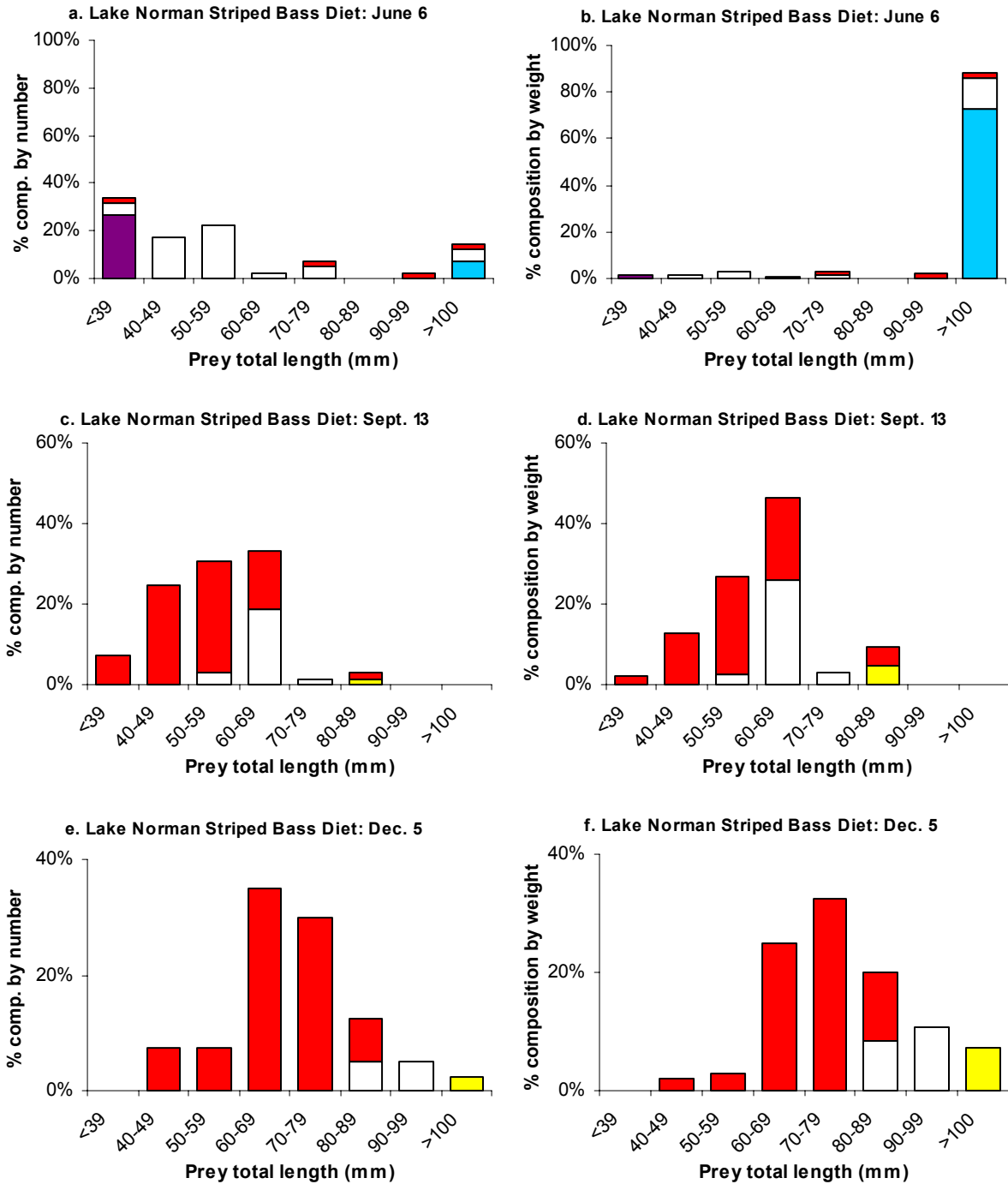


Figure A.22. Diet composition of striped bass collected from Lake Norman, NC, in 2001. Data are shown as (a, c, e) percent composition by number and (b, d, f) percent composition by weight for the (a, b) late spring, (c, d) late summer, and (e, f) winter samples. Red bars indicate threadfin shad, yellow bars indicate gizzard shad, white bars indicate alewife, blue bars indicate non-clupeid fish, and purple bars indicate invertebrates. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

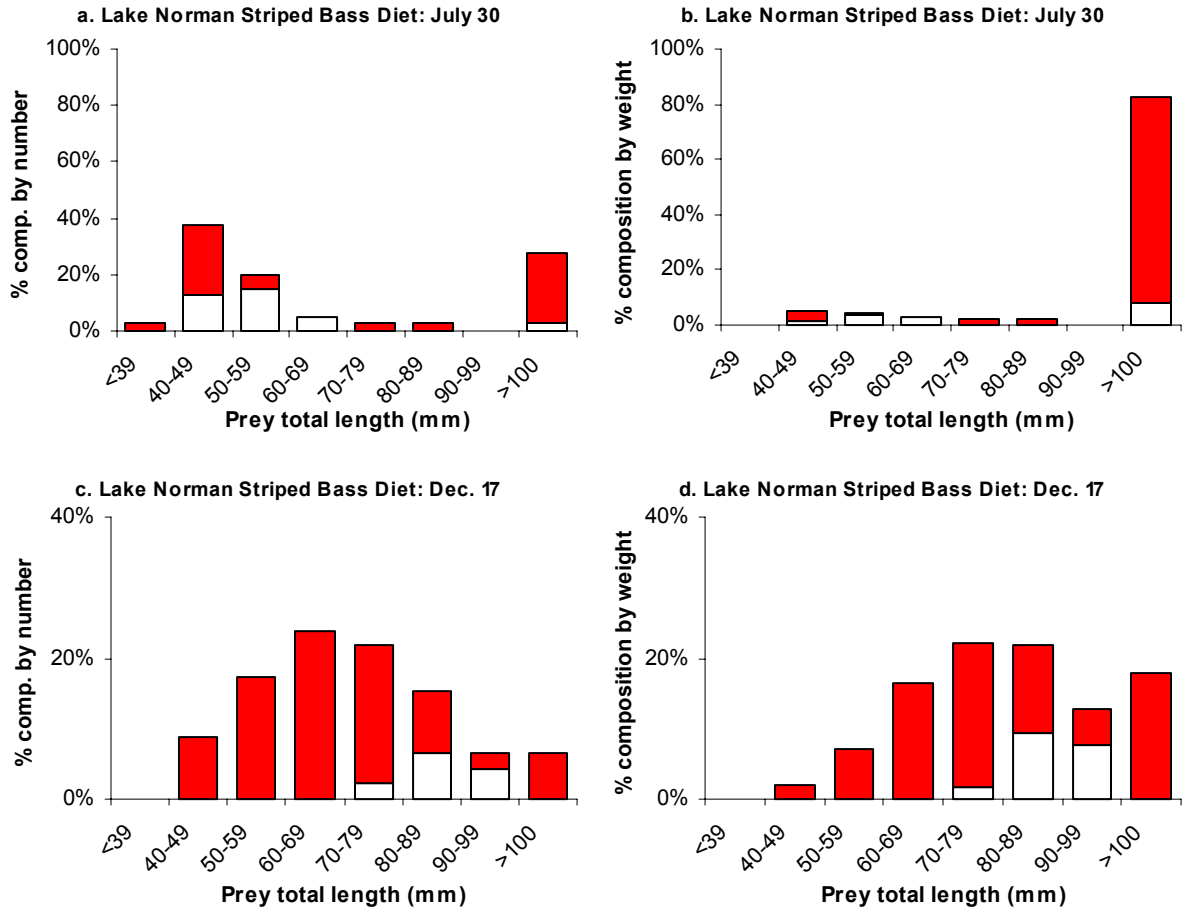


Figure A.23. Diet composition of striped bass collected from Lake Norman, NC, in 2002. Data are shown as (a, c) percent composition by number and (b, d) percent composition by weight for the (a, b) summer and (c, d) winter samples. Red bars indicate threadfin shad and white bars indicate alewife. Vertical axes are scaled the same within dates but differently between dates to allow all prey categories to be visualized.

Appendix B

Characterization of forage fish in Badin Lake and Lake Norman, NC

This appendix gives details of the methods used in sampling the forage fish communities in Badin Lake and Lake Norman and analysis of their species and size composition, as well as the length-weight relationship and energy density pattern of each forage fish species. Data are provided that are relevant to estimating the energy density of striped bass diet for inclusion in bioenergetics models of the Badin Lake and Lake Norman striped bass populations in 2001 and 2002 (Chapter 3). Data are also given for 2000; simulations were not conducted for that year, but these data allowed for the development of model inputs for the early portion of 2001 and provided an additional source of data for understanding the general trends in forage fish community dynamics. Species and size composition data are also provided for Badin Lake for summer and fall dates in 2003, as these data were used in developing the growth rate potential models for that year (Chapter 4).

Methods

Fish collection

Pelagic forage fish species were collected in both Badin Lake and Lake Norman from summer 2000 through winter 2002. Large samples were taken at three times during the year: June or July, September, and December. This sampling schedule corresponded with the sampling of striped bass (Appendix A). These forage fish samples were collected with a 9 m deep by 118 m long, 4.8 mm mesh purse seine operated by Duke Energy personnel. Purse

seine hauls were taken at three locations in Lake Norman throughout the study: in the lower lake near Norman Dam, in Davidson Creek, and in the upper portion of the lake. In Badin Lake, hauls were collected at three locations in July and September 2000: in the northwest portion of the west arm basin, just upstream of Badin Dam, and in the middle portion of the east arm. Thereafter, hauls were only taken in the west arm basin and upstream of Badin Dam. In situations where a very large number of fish were collected in a single haul, a subsample of fish was kept and the remainder were weighed and discarded. Bags of forage fish were packed in ice for transportation to the lab.

These large samples provided information on species and size composition of the forage fish community, as well as providing samples for analysis of forage fish energy density necessary for striped bass bioenergetics models. Additional information on seasonal patterns in forage fish energy density was gained through the collection of occasional smaller samples between large samples in both reservoirs in 2001 and 2002. These smaller samples were collected with a single purse seine haul or mid-water trawl (2.4 m by 1.2 m frame, 10 m long net, 5 mm minimum mesh size) in Lake Norman and with mid-water trawl or electrofishing in Badin Lake. Additional forage fish samples were collected in late July and early October, 2003, in Badin Lake using the mid-water trawl used in collecting small samples in the earlier years of the study.

Species and size composition

For each purse seine haul, total length and weight to 0.01 g were recorded for a subsample of fish from each species. Randomly chosen fish were processed until two hundred fish of the most common species were measured. This method maintained the same

proportion of each species in the subsample as was present in the overall sample while also assuring sufficient information on the most common fish species. These data were used to determine the species and size composition of the forage fish community on each sampling date.

Forage fish length-weight analysis

The relationship between total length and wet weight was determined for each species in each reservoir. Analysis of variance (ANOVA) of log-transformed data was used to test for significant differences ($\alpha = 0.05$) between species within a single reservoir, as well as to test for differences between reservoir populations for those species common to both systems.

Forage fish energy density

The season- and size-specific energy density of each species in each reservoir was determined for inclusion in striped bass bioenergetics models. Individual fish were placed in aluminum trays, dried to a constant weight at 70°C, and individually ground to a powder for analysis in a Parr 1425 Semimicro Bomb Calorimeter. Specimens were chosen to represent the full range of season and size, and in cases in which a single fish did not provide sufficient material for analysis, multiple fish of the same length were combined into a single sample. Two replicates of each sample were bombed using standard techniques (Parr Instrument Company 1991), and the dry weight caloric density obtained by the calorimeter was converted to a wet weight energy density using the ratio of dry weight to wet weight for a given sample and a calorie to Joule conversion. Results from the two subsamples were averaged to provide a single estimate. If the difference between the energy density of the

two replicates was greater than 100 Joules/gram wet weight, a third subsample was also bombed and the results from all three replicates were averaged. Fifteen to thirty samples were analyzed for each species.

The calorimetry analysis was used to calculate regression equations for each forage fish species relating the energy density of a fish sample to the sample's percent dry weight ($100 \times \text{dry weight} / \text{wet weight}$). The relationship between energy density and percent dry weight is well established for fish somatic tissue (Hartman and Brandt 1995). We modeled energy density as dependent on percent dry weight (producing a linear fit) and as dependent on the log of percent dry weight (producing a slightly curvilinear fit). The model with the lowest residual sum of squares was chosen. For each species occurring in both Badin Lake and Lake Norman, ANOVA was used to determine if the regression models were significantly different for the two systems.

After the regression relationships were determined, additional fish were dried to a constant weight as described above, and their percent dry weight was input to the appropriate equation to estimate energy density. For all species in each forage fish sample (i.e., a single date within a single reservoir), at least two fish from each 5-mm size-class collected were dried to determine energy density. These data were analyzed for trends in energy density with fish size and with season for each pelagic forage fish species.

Results

Species composition: Badin Lake and Lake Norman, 2000 to 2002

In Badin Lake, three pelagic forage fish species were collected during the course of the study: threadfin shad (*Dorosoma petenense*), gizzard shad (*D. cepedianum*), and blueback

herring (*Alosa aestivalis*). The forage fish community was dominated by threadfin shad (Figure B.1a, c, e). This pattern was particularly evident in 2000, when over 95% of all three seasonal samples were composed of this single species. In 2001, the first sample taken in mid-June was dominated by blueback herring. This sample was taken earlier in the season than either the early-summer sample in 2000 or 2002, and this timing may have affected the species composition of the sample. Blueback herring spawn earlier in the season than threadfin shad (Jenkins and Burkhead 1993), so the young-of-year fish would have already moved out of the inshore spawning areas into the pelagic region of the reservoir. Young-of-year threadfin shad likely had not yet moved into the pelagic zone and were, therefore, not available for capture by the purse seine gear. By September, threadfin shad had again become the dominant species, although the December 2001 sample had a larger proportion of blueback herring than the corresponding winter sample in 2000 (Figure B.1a, c), perhaps indicating a greater role of this species in the forage fish community in this year. In 2002, only the early-summer and winter samples were collected; the late-summer sample was not taken due to very low water levels during the summer of this year. Both of these samples were largely dominated by threadfin shad, with the proportion of blueback herring higher than in the corresponding 2000 samples and lower than in the corresponding 2001 samples (Figure B.1a, c, e). Gizzard shad were collected in almost every sample but were always a very low proportion of the catch.

In Lake Norman, three pelagic forage fish species were also collected: threadfin shad, gizzard shad, and alewife (*A. pseudoharengus*). The forage fish community was also dominated by threadfin shad in this reservoir (Figure B.1b, d, f), although alewife appeared to be more consistently abundant in this system than blueback herring were in Badin Lake.

In 2000, only the early-summer and early-fall samples were taken; the winter sample was not collected due to the unfortunate loss of the purse seine gear during the winter sample collection on Badin Lake. Threadfin shad composed over 85% of both samples, with alewife composing the remainder (Figure B.1b). The pattern of species composition in 2001 was very similar to that seen in Badin Lake in this year (Figure B.1c, d). The earlier timing of the early-summer sample resulted in dominance by alewife, which spawn even earlier than blueback herring (Jenkins and Burkhead 1993). By the later seasonal samples, threadfin shad had again become the most dominant species, but alewife made up a greater percentage than in the corresponding 2000 samples (Figure B.1b, d). In 2002, the early-summer sample had almost equal numbers of threadfin shad and alewife (Figure B.1f). Interestingly, the date of this sample was intermediate to the early-summer sample dates in 2000 and 2001, and the proportion of alewife was also intermediate to the proportions in those years, providing further evidence that the species composition of the early-summer sample is sensitive to the exact timing of that sample. The early-fall and winter samples were both composed of about 75% threadfin shad and 25% alewife (Figure B.1f).

Size composition: Badin Lake and Lake Norman, 2000 to 2002

In addition to analysis of species composition, purse seine samples provided data on the size composition of pelagic forage fish in both reservoirs. In July 2000, over 50% of forage fish collected in Badin Lake were 30 to 39 mm total length (Figure B.2a). This length category was also most common in Lake Norman on this date, but the proportions of fish 30 to 39 mm, 40 to 49 mm, and 50 to 59 mm were more similar than in Badin Lake (Figure B.2a). By September 2000, the size distributions of forage fish in both lakes were quite

similar. The largest proportion of fish were 50 to 59 mm, while fairly high proportions of fish were collected that were 40 to 49 mm and 60 to 69 mm (Figure B.2b). Only Badin Lake was sampled in November 2000. Over 60% of fish sampled on this date were 60 to 69 mm total length (Figure B.2c).

In June 2001, over 80% of forage fish collected in Badin Lake were 40 to 49 mm total length (Figure B.3a). In Lake Norman, this size category was also most common, but the proportions of fish 40 to 49 mm and 30 to 39 mm were more similar than in Badin Lake (Figure B.3a). In September 2001, the size distribution of forage fish in Badin Lake was bimodal, with the highest proportion of fish 50 to 59 mm and a smaller mode centered at 90 to 99 mm (Figure B.3b). Fish smaller than 80 mm were entirely threadfin shad, while those larger than 80 mm were predominantly blueback herring. In Lake Norman, similar proportions of fish 50 to 59 mm and 60 to 69 mm were collected (Figure B.3b). Fish smaller than 60 mm were predominantly threadfin shad, while fish larger than 60 mm were almost equally threadfin shad and alewife. In December 2001, the size distribution of forage fish in Badin Lake was again bimodal, with similar proportions of fish 60 to 69 mm and 70 to 79 mm as well as 100 to 109 mm and 110 to 119 mm (Figure B.3c). Fish smaller than 90 mm were entirely threadfin shad, while fish larger than 90 mm were mostly blueback herring. In Lake Norman, similar proportions of fish were collected that were 60 to 69 mm, 70 to 79 mm, and 80 to 89 mm (Figure B.3c). Fish smaller than 80 mm were entirely threadfin shad, while fish larger than 80 mm were predominantly alewife.

In June 2002, the size distribution of forage fish in Badin Lake and Lake Norman were almost identical for the smaller size categories, with the highest proportion of fish collected in the 40 to 49 mm size category (Figure B.4a). In Badin Lake, forage fish were

primarily threadfin shad on this date, while in Lake Norman, fish smaller than 50 mm were mostly threadfin shad while those larger than 50 mm were mostly alewife. In September 2002, only the Lake Norman sample was taken and the size distribution was quite similar to that of June 2002, with the largest proportion of fish 40 to 49 mm total length (Figure B.4b). This similarity was due largely to a shift in species composition. Fewer alewife were collected in September, reducing the proportions of larger fish, while the threadfin shad collected increased from primarily 30 to 50 mm total length to primarily 40 to 60 total length. In December 2002, similar proportions of fish 60 to 69 mm and 70 to 79 mm were collected in Badin Lake (Figure B.4c), and these fish were almost entirely threadfin shad. In Lake Norman, the highest proportions of fish were collected in the 50 to 59 mm and 60 to 69 mm size categories, while fairly high proportions were also found in the 70 to 79 mm and 80 to 89 mm categories (Figure B.4c). Fish smaller than 80 mm were entirely threadfin shad while larger fish were primarily alewife.

Species and size composition: Badin Lake, 2003

Trawl samples were conducted in late July and early October, 2003, in Badin Lake. Only threadfin shad were collected in the July sample, while the October sample was composed of 59% threadfin shad and 41% gizzard shad. In July 2003, most fish were 30 to 39 mm and 40 to 49 mm total length (Figure B.5a). In October 2003, the largest proportion of fish were 70 to 79 mm and 80 to 89 mm in length (Figure B.5b). While all fish smaller than 60 mm were threadfin shad on this date, the size distribution of larger threadfin shad and gizzard shad were similar.

Forage fish length-weight analysis

Data on total length and wet weight for each of the forage fish species collected during the study were used to determine the length-weight relationship for each species (Table B.1). Threadfin shad were found in both Badin Lake and Lake Norman, and the length-weight relationships for fish in the two systems were significantly different (Figure B.6). Threadfin shad in Badin Lake weighed more than fish of similar length in Lake Norman, particularly for fish longer than 80 mm. The relationship for threadfin shad in Badin Lake appears to underestimate the weight of fish longer than about 115 mm, but that does not affect our application of this relationship as striped bass diets were dominated by smaller fish (Appendix A). Gizzard shad were also found in both reservoirs, but no significant differences were detected between the length-weight relationship for fish from each system (Figure B.7). Blueback herring were found only in Badin Lake (Figure B.8), and alewife were found only in Lake Norman (Figure B.9).

The length-weight relationships for all pelagic forage fish species were similar for small fish less than 60 mm total length, although small gizzard shad were slightly heavier than fish of other species of similar length (Figure B.10). At longer lengths, threadfin shad had the greatest weight, followed by gizzard shad, alewife, and blueback herring. For example, at a length of 140 mm total length, threadfin shad in Badin Lake weighed almost 7 g (28%) more than blueback herring (Figure B.10). The length-weight relationships were significantly different between threadfin shad and gizzard shad in both Badin Lake and Lake Norman, despite these species being within the same genus, *Dorosoma*. Alewife and blueback herring are both within the genus *Alosa*, and the length-weight relationship for alewife from Lake Norman was not significantly different from that of blueback herring from

Badin Lake. The morphology of these two species is more similar than that of threadfin shad and gizzard shad, which differ in that threadfin shad have a terminal mouth and gizzard shad have an inferior mouth.

Forage fish energy density

Significant regression models relating energy density to percent dry weight were determined for each forage fish species in each reservoir (Table B.2). There was no effect of reservoir on the energy density-percent dry weight relationship for threadfin shad or gizzard shad, so data from both reservoirs were pooled for these species and a single equation was determined (Table B.2). These regression models were then used to determine the season- and size-specific energy density for each of these species for input to the striped bass bioenergetics model (Tables B.3, B.4). Insufficient data were obtained to determine yearly trends, so all energy density data collected during the three years of the study were combined. The data did not allow for estimation of a smooth function that related energy density to day of the year and fish size for each species; rather, trends in energy density with fish size and season were plotted and a mean value was chosen for each relevant size and date for striped bass bioenergetics modeling purposes. These values were also used in calculation of growth rate potential for Badin Lake striped bass in 2003.

Threadfin shad in both Badin Lake and Lake Norman had generally increasing energy density with increasing fish size, with threadfin shad in Badin Lake ranging from about 2,300 J/g wet wt to about 9,200 J/g wet wt and threadfin shad in Lake Norman ranging from about 2,400 J/g wet wt to about 6,100 J/g wet wt (Figure B.11). Small fish less than 50 mm total length in Lake Norman had greater energy density than small fish in Badin Lake. However,

the energy density of Lake Norman threadfin shad increased more slowly with increasing length, leading to fish greater than 75 mm in Badin Lake generally having higher energy density than in Lake Norman (Figure B.11). In Badin Lake, threadfin shad less than 100 mm total length had little seasonal pattern in energy density, while larger fish had generally higher energy density in late-spring and mid-summer (Figure B.12a). In Lake Norman, seasonal changes were less pronounced, although fish greater than 90 mm total length had higher energy density in the spring and summer than in the late fall and winter (Figure B.12b). These trends in energy density with fish size and season were used to determine the energy density for threadfin shad used in the Badin Lake and Lake Norman striped bass bioenergetics model simulations (Tables B.3, B.4).

Energy density of gizzard shad in both reservoirs increased with increasing length, although the slopes of the linear regression lines relating energy density and length for the two systems were shallower than those for threadfin shad (Figure B.11). Energy density of gizzard shad in Badin Lake ranged from about 1,700 J/g wet wt to about 6,800 J/g wet wt, while energy density of gizzard shad in Lake Norman ranged from about 2,600 J/g wet wt to about 6,500 J/g wet wt. There was no evidence of seasonal trends in energy density for gizzard shad in either reservoir, so energy density input to the striped bass bioenergetics model was based only on trends in energy density with fish length (Tables B.3, B.4).

Energy density of blueback herring in Badin Lake ranged from about 3,900 J/g wet wt to about 8,200 J/g wet wt. Energy density did not appear to increase with increasing fish length when data from all seasons were combined (Figure B.11). However, energy density of blueback herring varied strongly with season, and energy density did generally increase with increasing fish length when each sampling date was considered individually (Figure

B.13). Energy density was highest for fish collected in early summer and lowest through winter and early spring (Figure B.13). Both season- and size-specific trends in energy density were incorporated in the striped bass bioenergetics model input (Table B.3).

Alewife in Lake Norman displayed increasing energy density with increasing fish size, similar in pattern to the increase for threadfin shad in the same system, although alewife typically had a higher energy density than similarly sized threadfin shad (Figure B.11). Alewife energy density ranged from 3,300 J/g wet wt to 6,900 J/g wet wt. Alewife also appeared to have a somewhat higher energy density in summer than in winter and early spring (Figure B.14), but this pattern was less pronounced than the seasonal pattern for blueback herring in Badin Lake (Figure B.13). This result is similar to the energy density patterns of threadfin shad in the two systems, which showed a greater seasonal pattern in Badin Lake than in Lake Norman (Figure B.12). The overall trend in alewife energy density with size and season was used in the striped bass bioenergetics model input (Table B.4).

Acknowledgements

Numerous personnel assisted with collecting and processing forage fish samples. Scott Waters was instrumental in all components of field and laboratory activities associated with forage fish sampling. Duke Energy personnel operated the purse seine used in sampling on Badin Lake and Lake Norman; many thanks to Dave Coughlan, Kim Baker, Hugh Barwick, Mark Rash, Duane Harrell, Bob Doby, Brad Garner, Joe Grist, and Glenn Long. Lawrence Dorsey and Bob Barwick assisted with mid-water trawl sampling. Numerous undergraduate technicians provided laboratory assistance, including Paul Hubert, Jon Finch, Brandon Puckett, Chad Harris, Suzi Jones, Poem Turner, and Gabriela Gonzalez.

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Tables

Table B.1. Equations, R^2 values, and sample sizes for relationships between total length (mm; L) and weight (g; W) for threadfin shad and gizzard shad in Badin Lake and Lake Norman, blueback herring in Badin Lake, and alewife in Lake Norman. Equations were significantly different for threadfin shad in the two reservoirs but were not significantly different for gizzard shad.

Species	Reservoir	Equation	R^2	n
Threadfin shad	Badin Lake	$W = (3.76 \times 10^{-6}) L^{3.1761}$	0.99	4403
Threadfin shad	Lake Norman	$W = (4.79 \times 10^{-6}) L^{3.1007}$	0.98	5177
Gizzard shad	Both combined	$W = (2.01 \times 10^{-5}) L^{2.7872}$	0.99	1106
Blueback herring	Badin Lake	$W = (1.09 \times 10^{-5}) L^{2.8936}$	0.99	713
Alewife	Lake Norman	$W = (6.00 \times 10^{-6}) L^{3.0329}$	0.99	2708

Table B.2. Equations, R^2 values, and sample sizes for regression models relating percent dry weight (DW) to energy density (J/g wet wt; ED) estimated for threadfin shad, gizzard shad, blueback herring, and alewife. No significant effect of reservoir was found for either threadfin shad or gizzard shad, both of which occur in both Badin Lake and Lake Norman, so a single equation for each species was used for fish from both systems. The equation for blueback herring refers to fish collected from Badin Lake, while the equation for alewife refers to fish collected from Lake Norman.

Species	Equation	R^2	n
Threadfin shad	$ED = -1860.03 + 287.12 \cdot DW$	0.99	34
Gizzard shad	$ED = -2034.09 + 292.74 \cdot DW$	0.96	33
Blueback herring	$ED = -2144.06 + 313.44 \cdot DW$	0.97	21
Alewife	$ED = -1057.35 + 263.20 \cdot DW$	0.99	16

Table B.3. Energy density (J/g wet wt) of threadfin shad (top), gizzard shad (middle), and blueback herring (bottom) in Badin Lake by size and day of year. These energy densities reflect trends described in the text and were used as input to the striped bass bioenergetics model. Size categories reflect sizes of each species found during analysis of the striped bass stomach contents (Appendix A).

Threadfin shad:

Day	35 mm	45 mm	55 mm	65 mm	75 mm	85 mm	95 mm	110 mm
1	3,160	3,410	3,700	4,000	4,250	4,530	5,000	5,300
140	3,160	3,410	3,700	4,000	4,250	4,530	5,000	6,600
175	3,160	3,410	3,700	4,000	4,250	4,530	5,000	6,600
250	3,160	3,410	3,700	4,000	4,250	4,530	5,000	6,200
365	3,160	3,410	3,700	4,000	4,250	4,530	5,000	5,300

Gizzard shad:

Day	85 mm	95 mm	110 mm
1	3,600	3,700	3,900
140	3,600	3,700	3,900
175	3,600	3,700	3,900
250	3,600	3,700	3,900
365	3,600	3,700	3,900

Blueback herring:

Day	55 mm	65 mm	75 mm	85 mm	95 mm	110 mm
1	3,800	3,900	4,000	4,500	4,700	5,000
140	5,400	5,700	6,400	6,700	7,100	7,400
175	5,800	6,200	7,000	7,300	7,700	8,000
250	5,600	5,900	6,300	7,000	7,300	7,500
365	3,800	3,900	4,000	4,500	4,700	5,000

Table B.4. Energy density (J/g wet wt) of threadfin shad (top), gizzard shad (middle), and alewife (bottom) in Lake Norman by size and day of year. These energy densities reflect trends described in the text and were used as input to the striped bass bioenergetics model. Size categories reflect sizes of each species found during analysis of the striped bass stomach contents (Appendix A).

Threadfin shad:

Day	35 mm	45 mm	55 mm	65 mm	75 mm	85 mm	95 mm	110 mm
1	3,300	3,600	3,850	4,000	4,100	4,200	4,200	4,200
50	3,300	3,600	3,850	4,000	4,100	4,200	4,600	4,900
110	3,300	3,600	3,850	4,000	4,100	4,200	5,200	5,300
170	3,300	3,600	3,850	4,000	4,100	4,200	5,200	5,300
260	3,300	3,600	3,850	4,000	4,100	4,200	4,400	5,300
365	3,300	3,600	3,850	4,000	4,100	4,200	4,200	4,200

Gizzard shad:

Day	85 mm	95 mm	110 mm
1	4,400	4,450	4,500
50	4,400	4,450	4,500
110	4,400	4,450	4,500
170	4,400	4,450	4,500
260	4,400	4,450	4,500
365	4,400	4,450	4,500

Alewife:

Day	45 mm	55 mm	65 mm	75 mm	85 mm	95 mm	110 mm
1	4,000	4,100	4,200	4,300	4,650	4,850	5,000
50	4,100	4,300	4,350	4,600	4,800	5,000	5,150
110	4,150	4,400	4,500	4,800	5,050	5,300	5,700
170	4,300	4,800	5,200	5,800	6,100	6,300	6,800
260	4,300	4,800	5,200	5,800	6,100	6,300	6,800
365	4,000	4,100	4,200	4,300	4,650	4,850	5,000

Figures

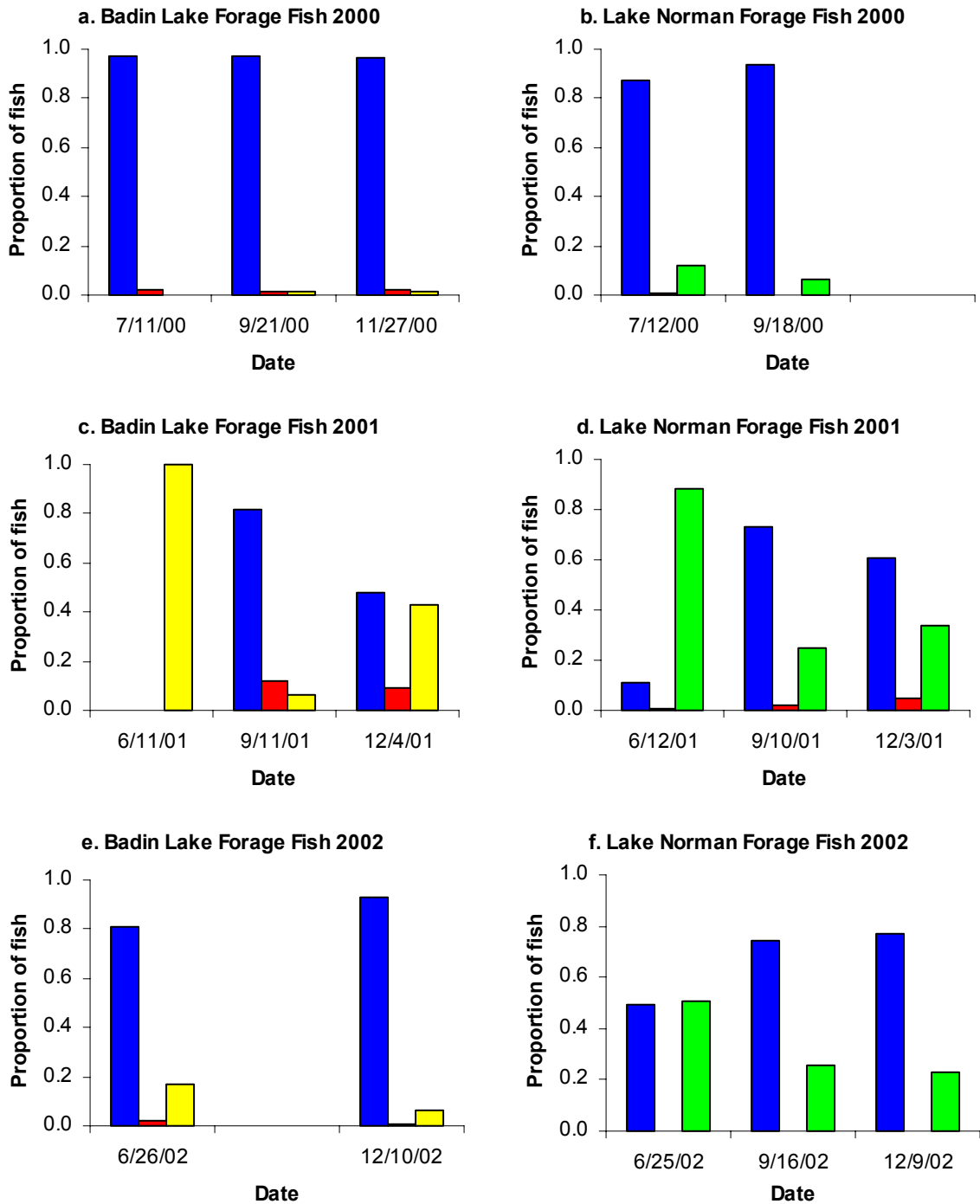


Figure B.1. Species composition of forage fish collected in seasonal purse seine samples in (a, c, e) Badin Lake and (b, d, f) Lake Norman in (a, b) 2000, (c, d) 2001, and (e, f) 2002. Values given are the proportion of each species by number collected on each sampling date. Blue bars indicate threadfin shad, red bars indicate gizzard shad, yellow bars indicate blueback herring, and green bars indicate alewife.

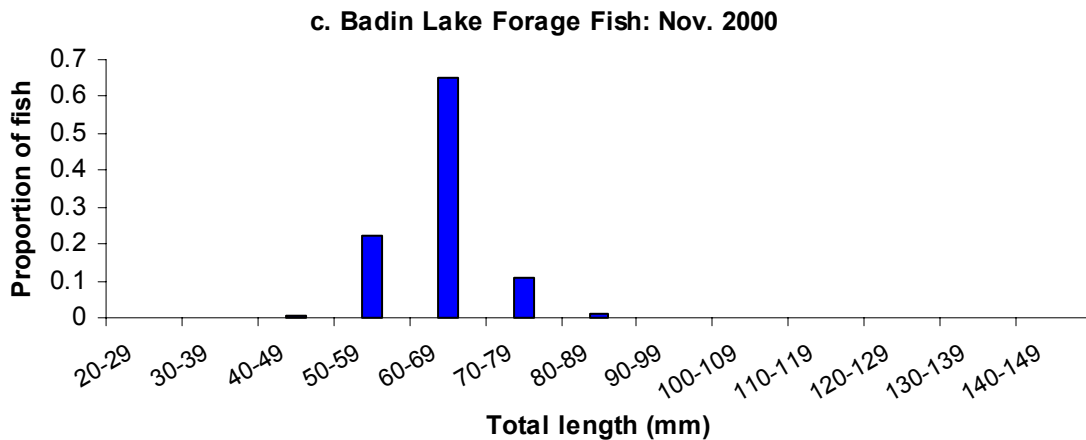
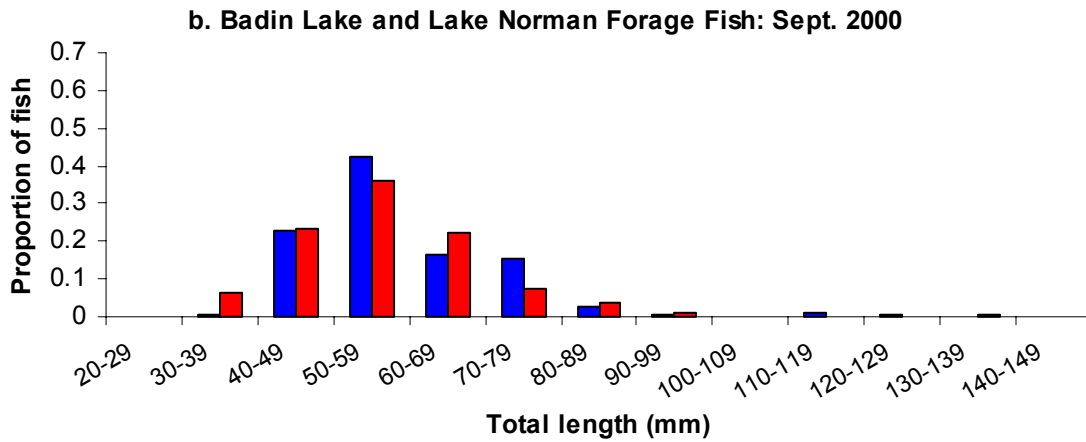
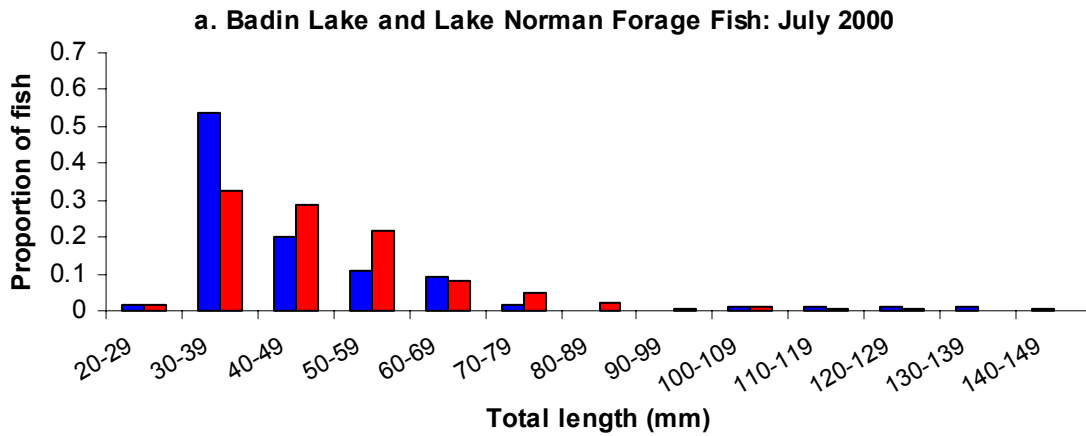


Figure B.2. Comparison of size composition of all forage fish collected at all sampling locations in Badin Lake and Lake Norman in (a) July 2000, (b) September 2000, and (c) November 2000. Only the Badin Lake sample was taken in November. Values given are proportion of fish collected in each size interval in each reservoir. Blue bars indicate Badin Lake data and red bars indicate Lake Norman data.

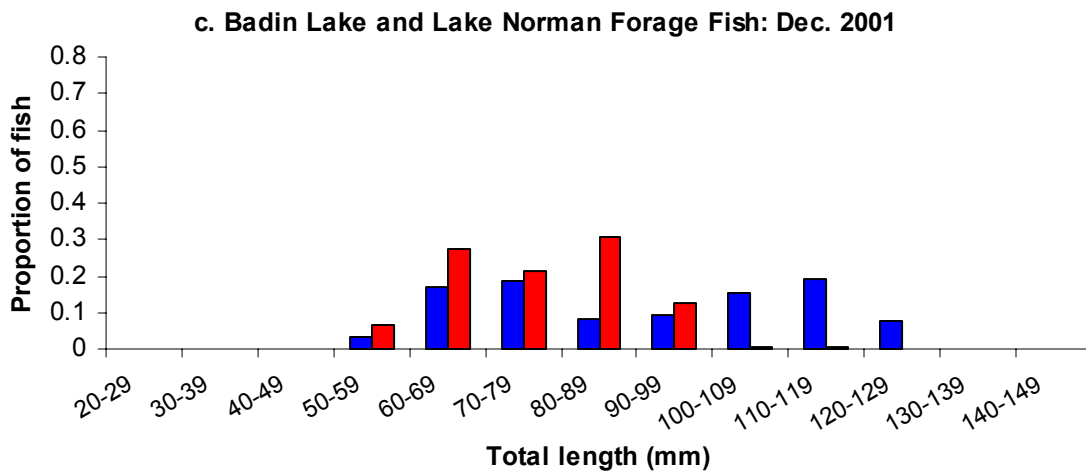
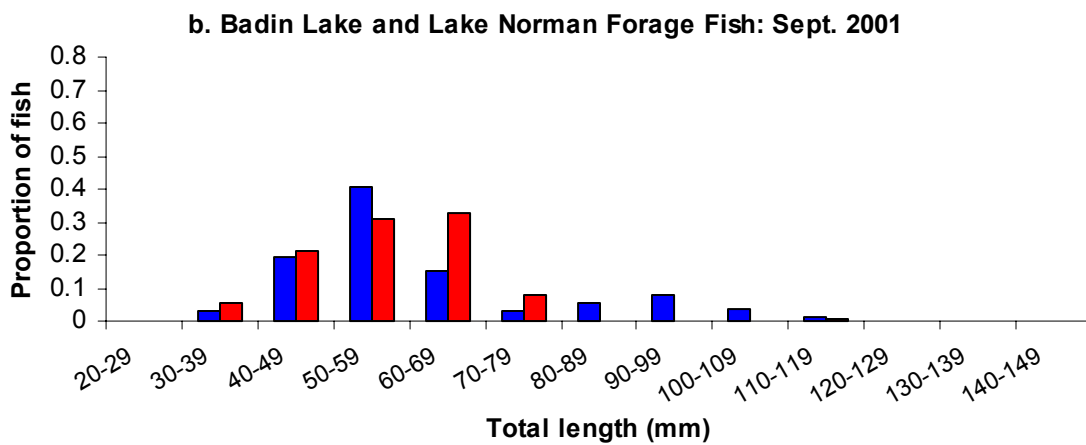
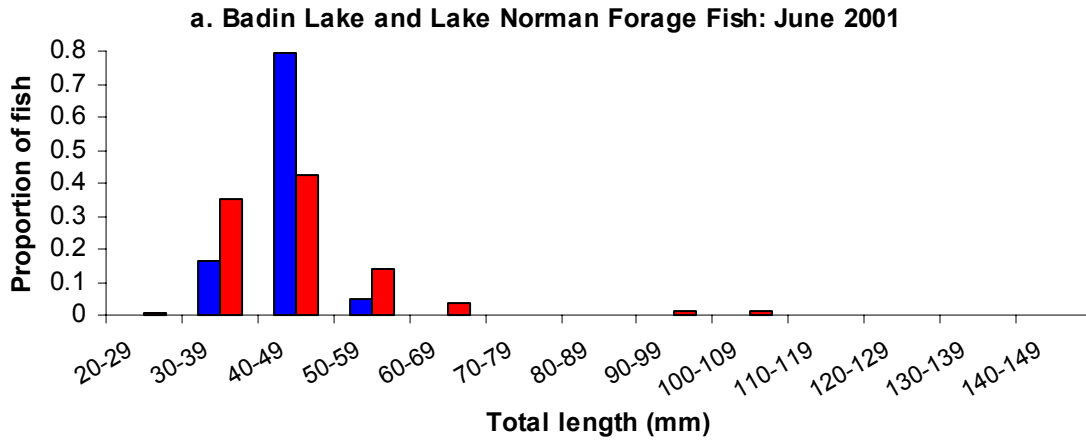


Figure B.3. Comparison of size composition of all forage fish collected at all sampling locations in Badin Lake and Lake Norman in (a) June 2001, (b) September 2001, and (c) December 2001. Values given are proportion of fish collected in each size interval in each reservoir. Blue bars indicate Badin Lake data and red bars indicate Lake Norman data.

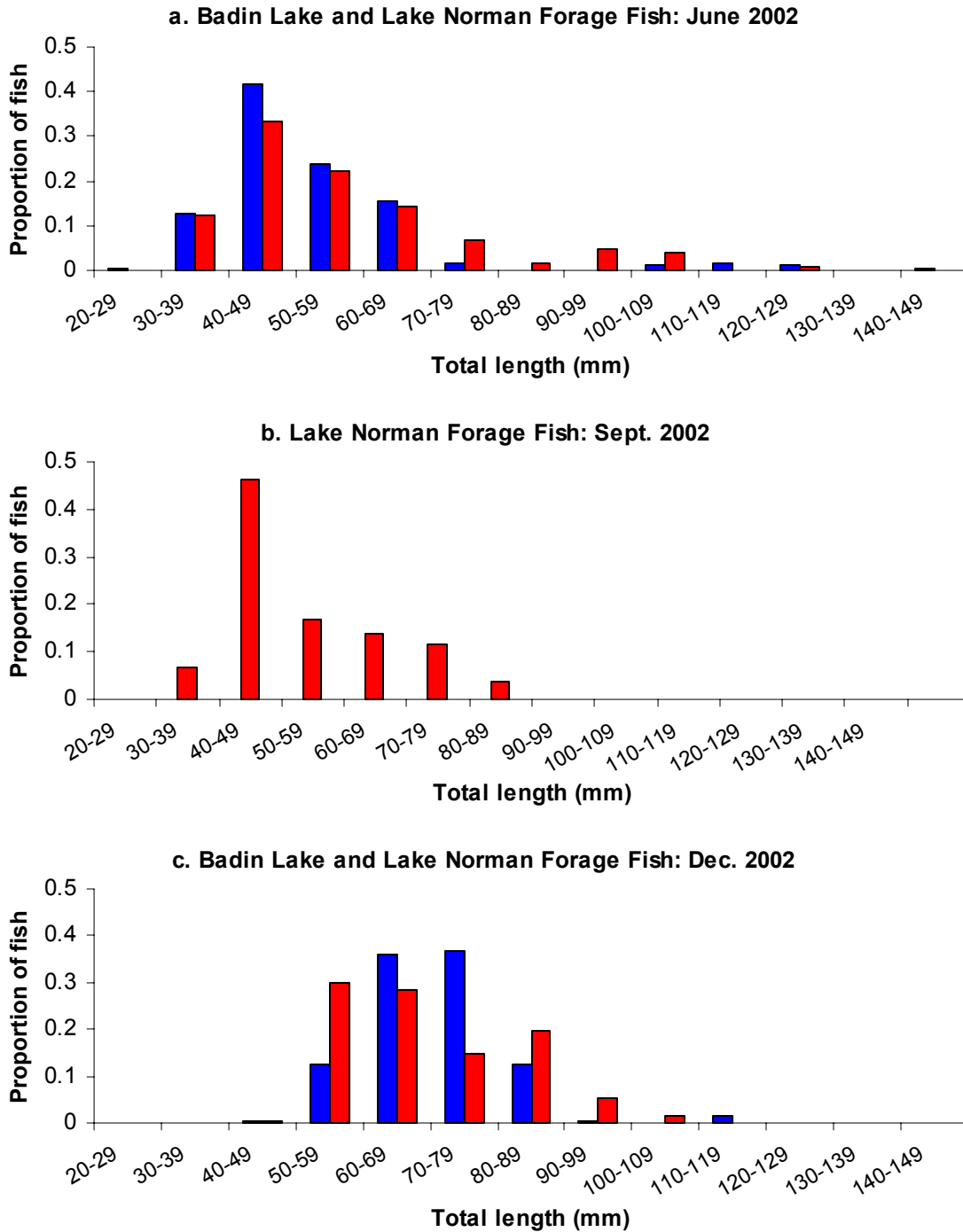


Figure B.4. Comparison of size composition of all forage fish collected at all sampling locations in Badin Lake and Lake Norman in (a) June 2002, (b) September 2002, and (c) December 2002. Only the Lake Norman sample was taken in September. Values given are proportion of fish collected in each size interval in each reservoir. Blue bars indicate Badin Lake data and red bars indicate Lake Norman data.

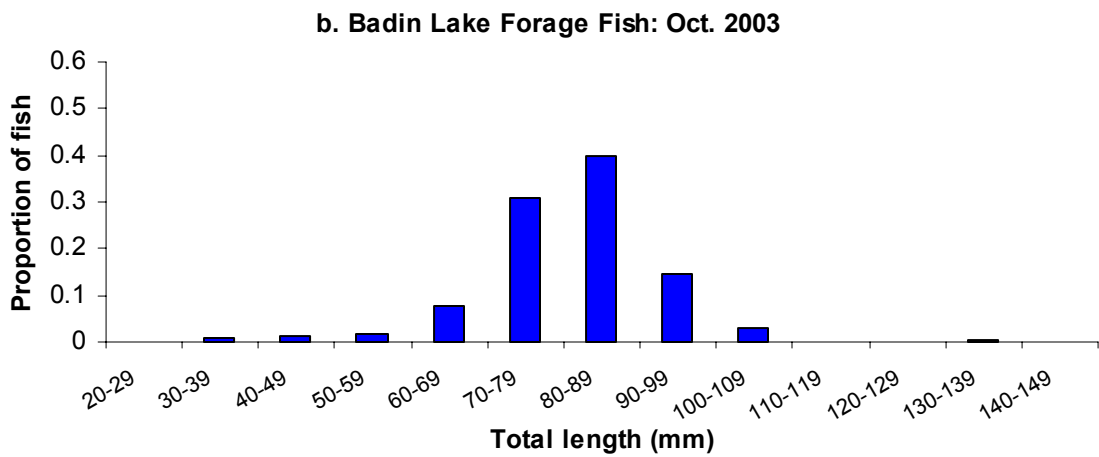
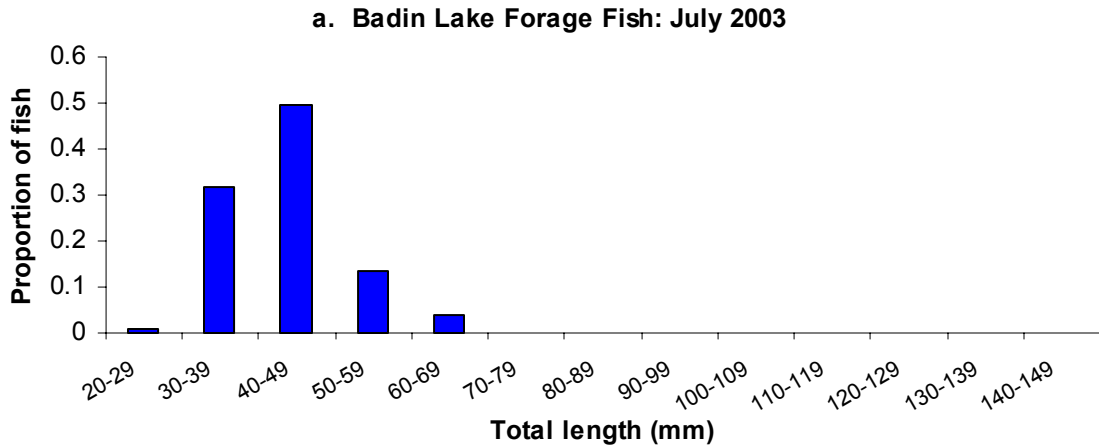


Figure B.5. Size composition of all forage fish collected by mid-water trawl in Badin Lake in (a) July 2003 and (b) October 2003. Values given are proportion of fish collected in each size interval on each date.

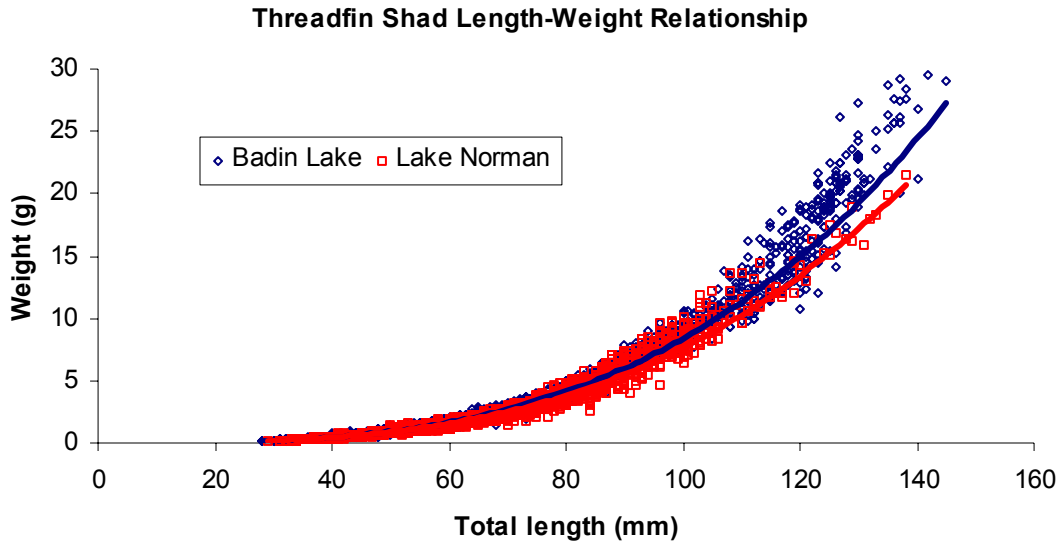


Figure B.6. Length-weight relationship for threadfin shad in Badin Lake (blue) and Lake Norman (red) for all fish collected from 2000 through 2002. The solid lines indicate significantly different best-fit lines for each data set; equations provided in Table B.1.

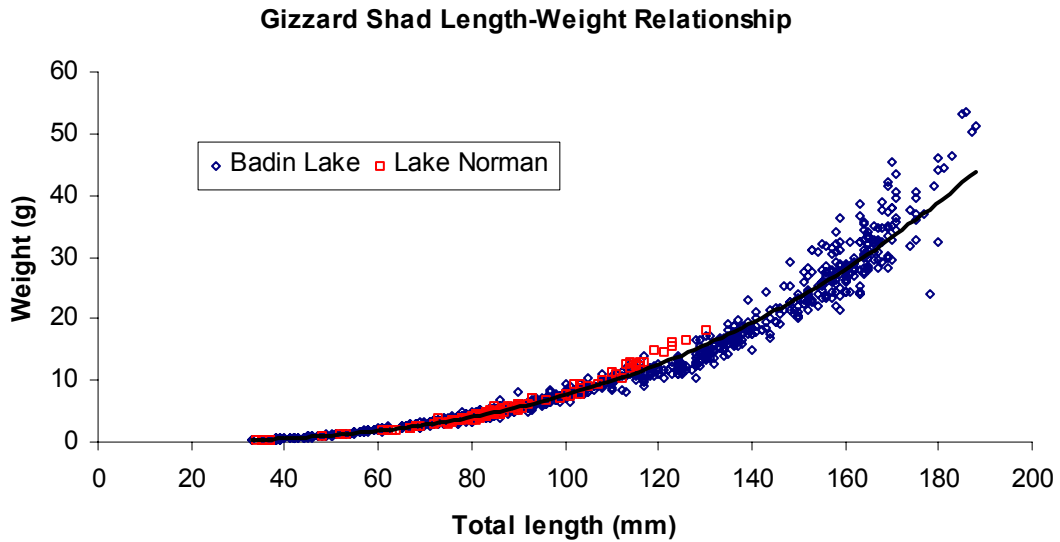


Figure B.7. Length-weight relationship for gizzard shad in Badin Lake (blue) and Lake Norman (red) for all fish collected from 2000 through 2002. The relationships were not significantly difference, and the solid lines indicates the best-fit line for the combined data from both lakes; equation provided in Table B.1.

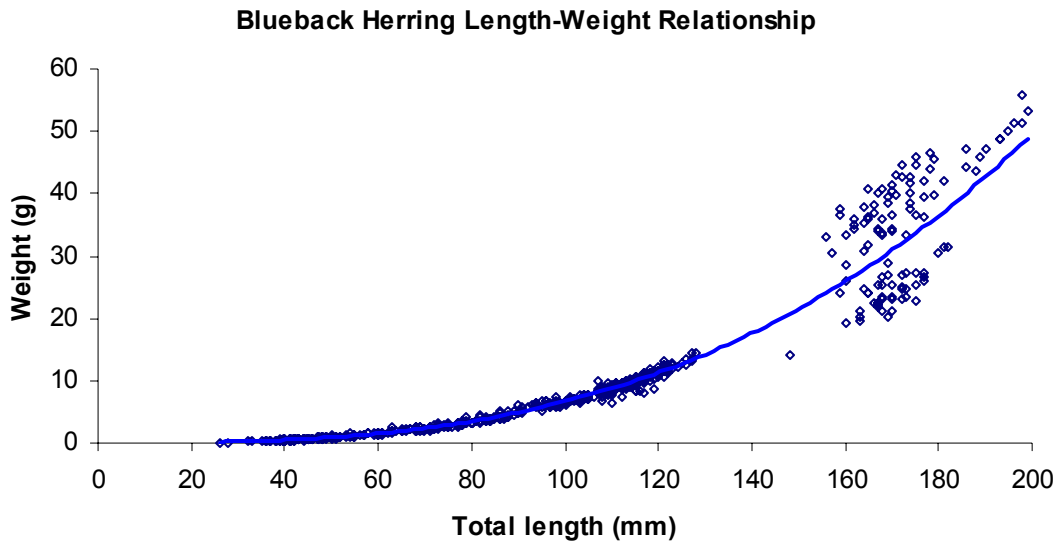


Figure B.8. Length-weight relationship for blueback herring in Badin Lake for all fish collected from 2000 through 2002. The solid line indicates the best-fit line for the data set; equation provided in Table B.1.

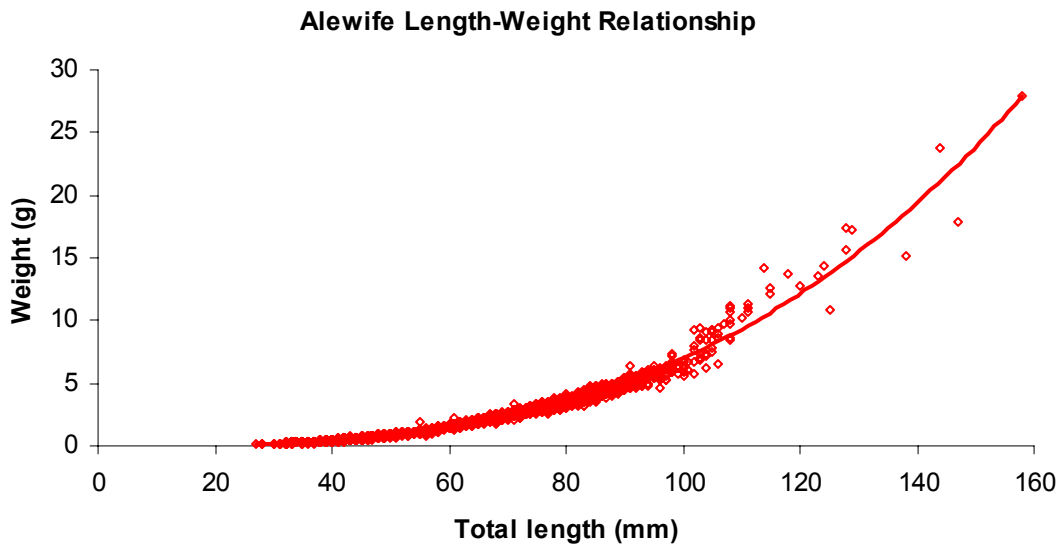


Figure B.9. Length-weight relationship for alewife in Lake Norman for all fish collected from 2000 through 2002. The solid line indicates the best-fit line for the data set; equation provided in Table B.1.

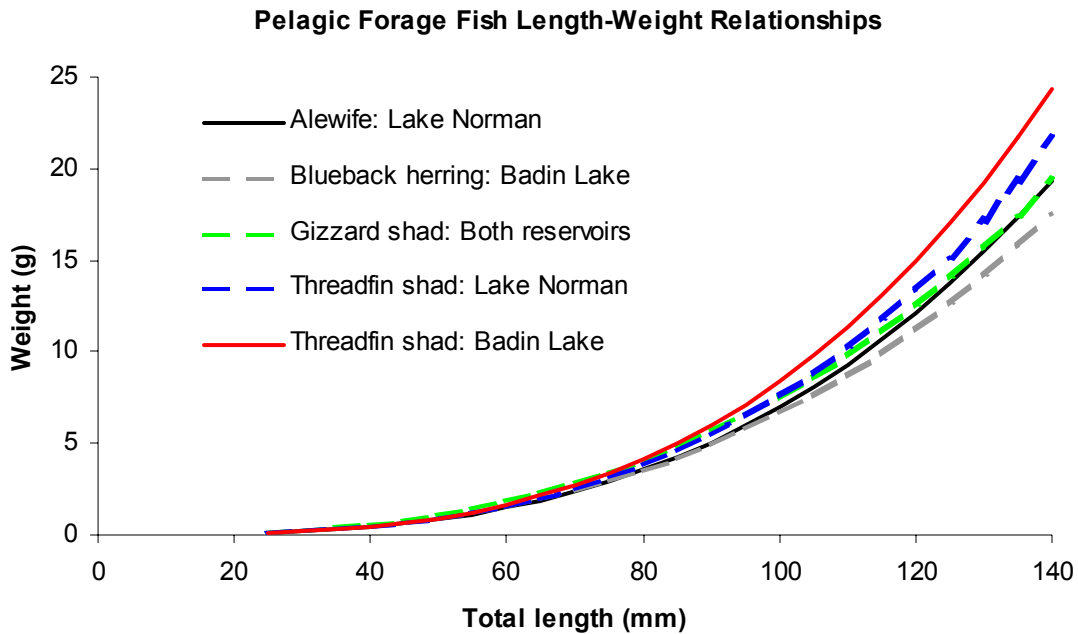


Figure B.10. Comparison between length-weight relationships for pelagic forage fish species in Badin Lake and Lake Norman. Equations provided in Table B.1.

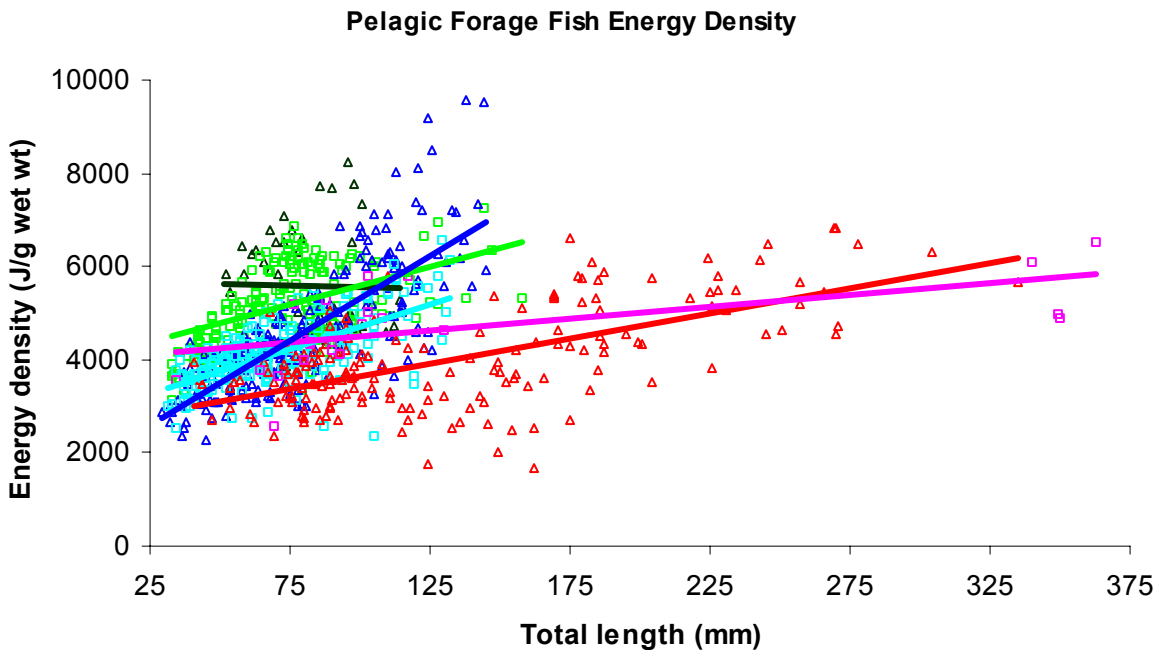


Figure B.11. Relationship between energy density (J/g wet wt) and total length (mm) for pelagic forage fish species: threadfin shad in Badin Lake (dark blue) and Lake Norman (light blue), gizzard shad in Badin Lake (red) and Lake Norman (pink), blueback herring in Badin Lake (dark green), and alewife in Lake Norman (light green). Solid lines are linear regression models fit to data for each species in each reservoir.

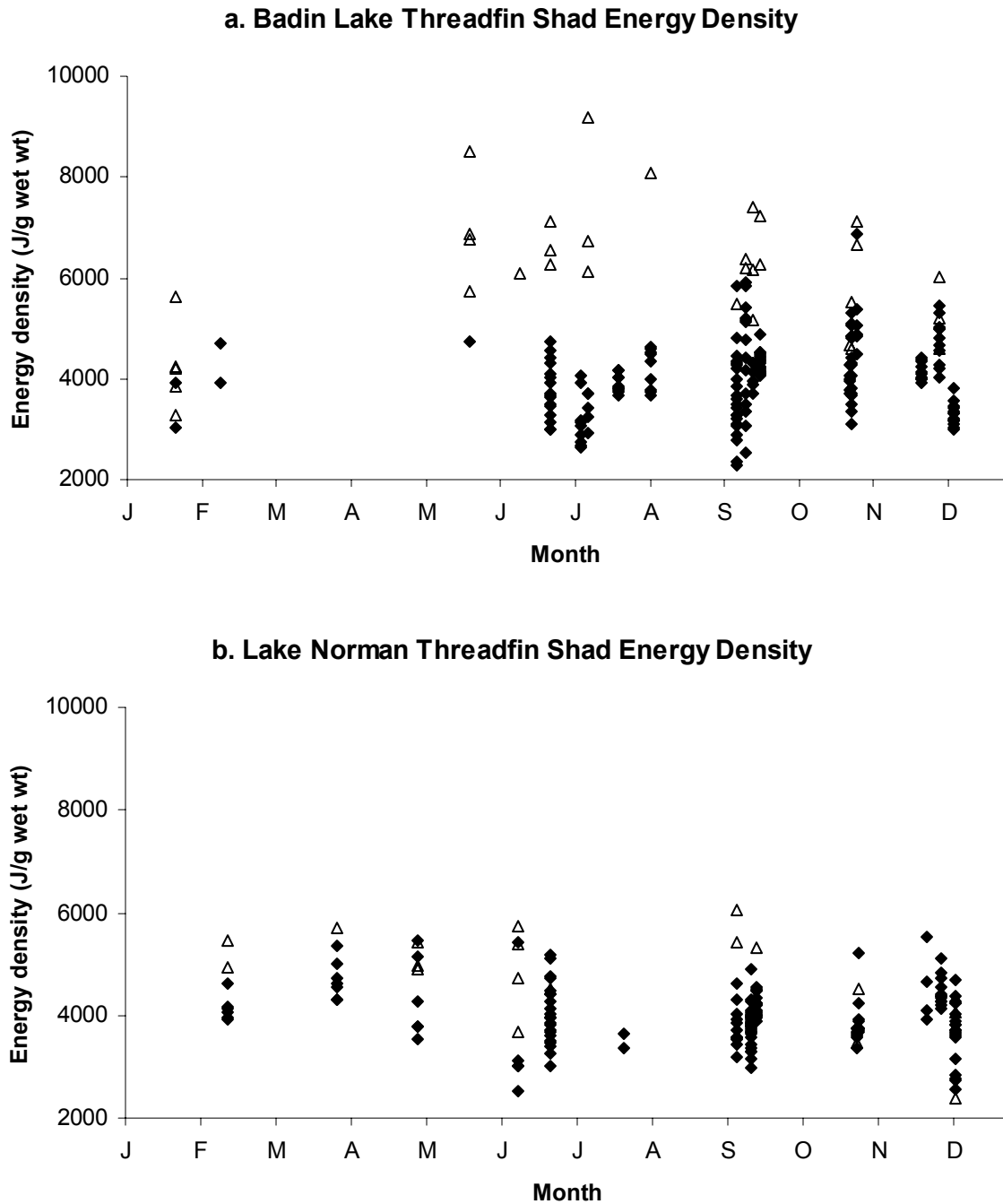


Figure B.12. Energy density (J/g wet wt) by date for threadfin shad in (a) Badin Lake and (b) Lake Norman collected in 2000 through 2002. Open symbols indicate fish greater than 100 mm total length in Badin Lake and fish greater than 90 mm total length in Lake Norman.

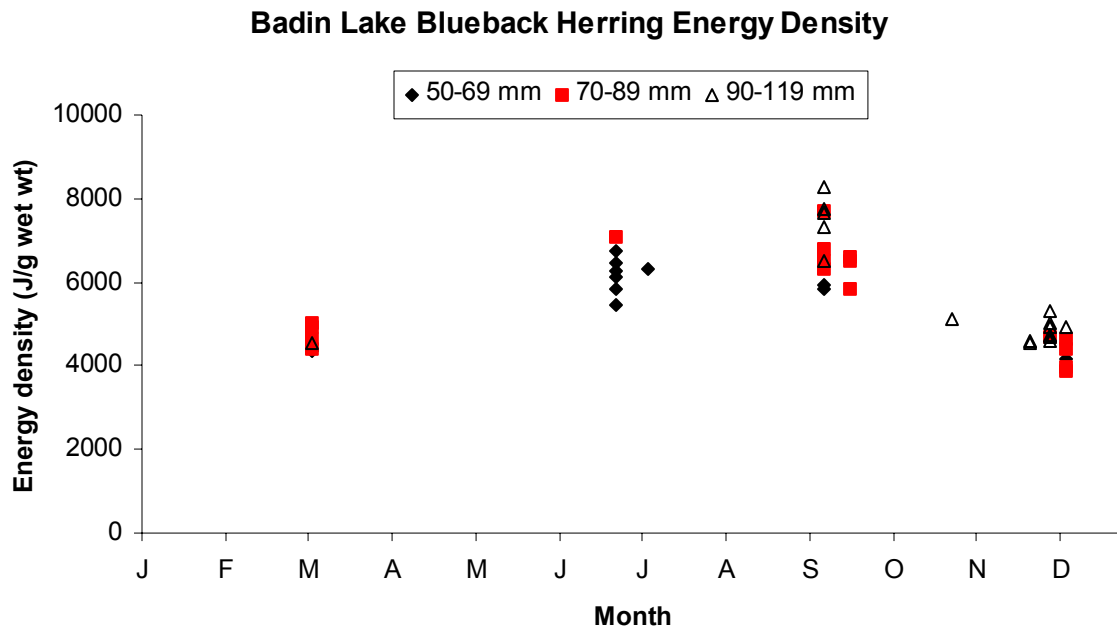


Figure B.13. Energy density (J/g wet wt) of blueback herring collected in Badin Lake in 2000 through 2002 by month and size class.

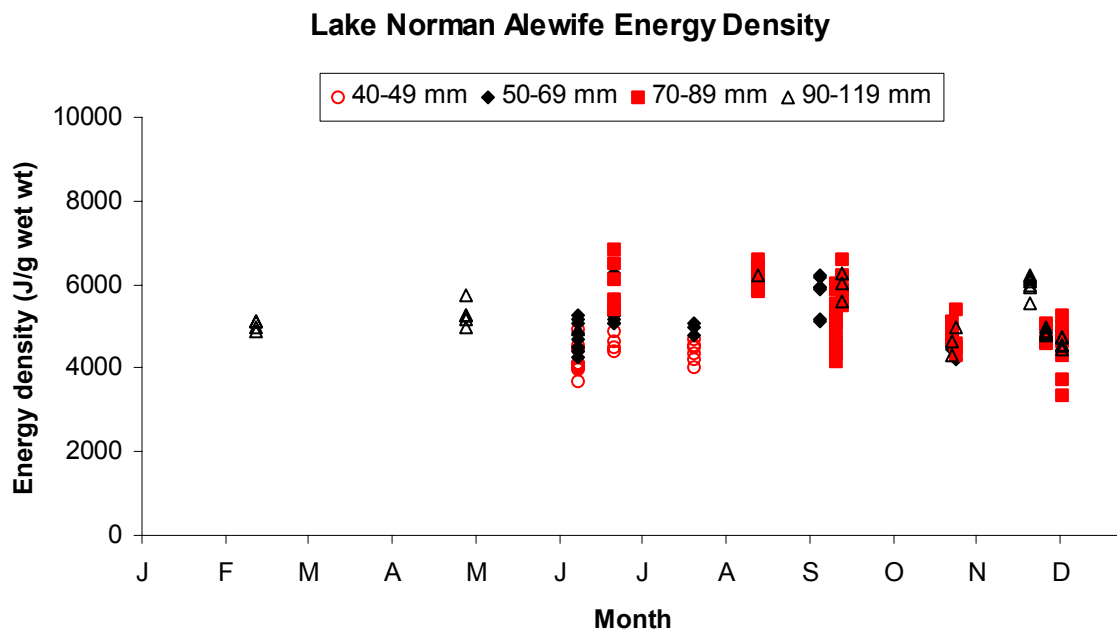


Figure B.14. Energy density (J/g wet wt) of alewife collected in Lake Norman in 2000 through 2002 by month and size class.