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[Article]

The Fundamental Thermal Niche of Adult Landlocked Striped Bass

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Abstract.—Researchers have described the temperatures selected by landlocked striped bass *Morone saxatilis* in different locales throughout the USA. However, seasonally low concentrations of dissolved oxygen (DO) in many systems prevented striped bass from using the cool waters (<22°C) they may have preferred. In Melton Hill Reservoir, a 92-km-long impoundment on the Clinch River in east Tennessee, 15 adult striped bass were tagged with temperature-sensing radio tags and tracked for an average of 418 d in 1999–2000. Cold, hypolimnetic discharges from an upstream dam and heated discharge from a steam-generating electric facility near the midpoint of this run-of-the-river reservoir provided a broad range of temperatures in most seasons, and hypoxic habitats were uncommon even during stratification. The mean temperature occupied by striped bass varied seasonally (repeated-measures analysis of variance, $P < 0.0001$) and was highest in summer (17.5°C), intermediate in spring and fall (15.4–16.9°C), and lowest in winter (13.0°C). The mean and modal temperatures occupied during the growing season (May–October 1999) were 17.5°C and 19.0°C, respectively; 30% of the observations were between 9°C and 15°C. These data indicate that the fundamental thermal niche of adult landlocked striped bass may be lower than literature estimates. These results also represent the first unbiased field estimates of the influence of season on the thermal ecology of adult striped bass. The thermal characteristics of habitats considered optimal in habitat suitability index models for adult landlocked striped bass (i.e., 18–24°C) should be revised to include cooler waters.

The establishment of landlocked populations of striped bass *Morone saxatilis* in reservoirs across the USA was a significant success story for fisheries managers in the 20th century. Landlocked striped bass fisheries were created in many locales to provide recreational opportunities with concomitant economic impacts (e.g., Schorr et al. 1995), which prompted subsequent studies on the ecology of this species. In particular, the thermal ecology of striped bass in freshwater has been widely studied. One reason for this is that reservoirs and rivers do not always provide combinations of temperature and dissolved oxygen that are suitable to support healthy populations of striped bass, particularly large adults (e.g., Coutant and Carroll 1980). Adult striped bass usually occupy waters with temperatures cooler than 25°C and dissolved oxygen concentrations greater than 3–4 mg/L (Coutant 1985), but they can tolerate higher temperatures for brief periods if dissolved oxygen concentrations remain above 2 mg/L (Farquhar and Gutreuter 1989; Zale et al. 1990). In the Albermarle Sound, North Carolina, striped bass tolerated temperatures as high as 27–29°C in midsummer, but dissolved oxygen concentrations were always 4 mg/L or higher (Haeseker et al. 1996). In Lake Norman, North Carolina, striped bass occupied 20–26°C waters in midsummer, but they could not choose cooler temperatures due to low (<3 mg/L) dissolved oxygen concentrations in the hypolimnion (Lewis 1985).

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Moss (1980) was one of the first to note that striped bass occupied cool (22–26°C), spring-fed tributaries or ‘‘refuges’’ when Alabama reservoirs warmed to 27°C. Striped bass in a Tennessee reservoir sought thermal refuges (~20°C) in summer and fall and avoided waters warmer than 25°C (Cheek et al. 1985). In the Flint River portion of the Apalachicola River system, striped bass moved into spring-fed refuges when the ambient river temperature exceeded 24°C, and temperatures selected by fish in the refuges averaged about 22°C (Van Den Avyle and Evans 1990). In the Combahee River, South Carolina, striped bass moved into the headwaters, where the temperatures (25–27°C) were as much as 5°C cooler than in the lower river (Bjorgo et al. 2000). Bjorgo et al. (2000) noted that temperatures in the upper river during summer were closer to the preferred temperature

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of striped bass than available downriver temperatures were.

Coutant and Carroll (1980) studied temperature selection by striped bass in systems with suitable dissolved oxygen at all depths, but the fish (n = 9) were small (43–63 cm total length), as were the two study lakes (each ~2 ha). In that study, the thermal niche of subadult striped bass during the growing season (April–October) was considered to be 20–24°C and centered near 22°C. Based on a review of the literature, Coutant (1985) concluded that the thermal niche for large adult striped bass was in the range of 18–25°C and centered around 20°C. However, such a niche would be a realized niche (Coutant 1990) rather than the fundamental niche because temperature selection by large striped bass in that study (and all other prior studies) was constrained by a lack of alternative temperatures or by hypoxia. In this study, I estimated the fundamental thermal niche of adult landlocked striped bass in a reservoir with a wide range of temperatures and suitable dissolved oxygen concentrations year-round. The study area and its water quality were also amenable to describing the effect of season on temperature selection by adult striped bass. Seasonal differences in acute temperature preference have been described for several species (e.g., Sullivan and Fischer 1953; Hesthagen 1979); however, such findings are almost ?1 always derived from laboratory studies, and the effect of season on preferred temperatures has not been adequately described for free-ranging adult striped bass.

Study Area

The upstream boundary of Melton Hill Reservoir is Norris Dam, which is located at Clinch ?2 River kilometer (CRkm) 129 in eastern Tennessee (Figure 1). Norris Dam was constructed in 1936 for the purposes of flood control and hydroelectric power generation. The tailwater extends 22 km below the dam, and the Tennessee Wildlife Resources Agency (TWRA) intensively manages it as a put-and-take and put-grow-and-take trout fishery. Striped bass do not reproduce in Melton Hill Reservoir; the population is maintained by emigration from upstream and downstream reservoirs that the TWRA stocks annually with fingerlings. Average width of the tailwater is 132 m during power generation and 95 m at base flow. Hypolimnetic discharges through two turbines maintain coldwater habitat throughout the tailwater. Maximum two-turbine discharge is about 241 m^3/s, and water level fluctuates by approximately 1.8 m between base flow and maximum discharge. Daily fluctuations in water temperature in the tailwater often exceed 8°C during summer. Dissolved oxygen concentrations are maintained by an autoventing turbine system designed to keep dissolved oxygen concentrations above 6 mg/L (Yeager et al. 1987). A weir dam located 3.2 km below Norris Dam provides a minimum flow of 5.7 m^3/s when the turbines are idle and provides additional aeration of hydroelectric releases.

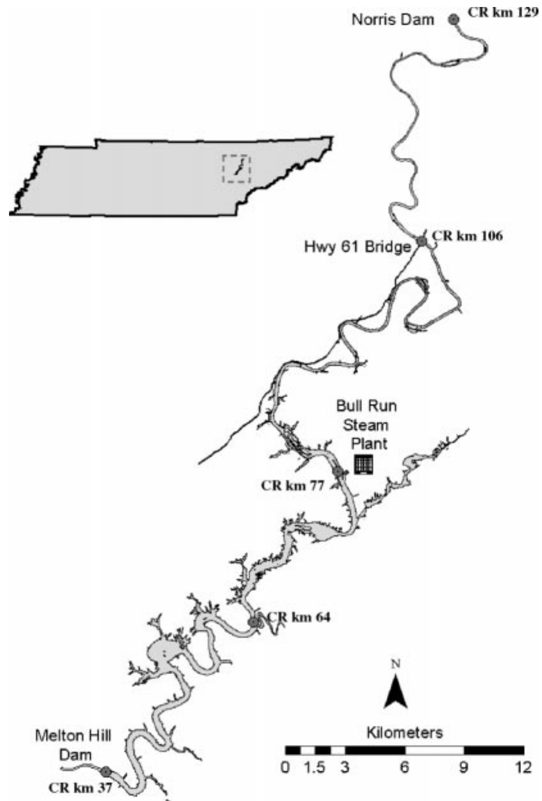

FIGURE 1.—Map of Melton Hill Reservoir on the Clinch River (CR), Tennessee.

The habitat in the Clinch River changes abruptly at the Highway 61 bridge (CRkm 106). An extensive series of bedrock shoals and riffles exists upstream of the bridge. Below the bridge, the river assumes a more lacustrine character, although Melton Hill Reservoir resembles a slow-moving river downstream to CRkm 80. The average hydraulic retention time of this main-stem reservoir is only 12 d. At Melton Hill Dam (CRkm 37), the impounded Clinch River is less than 0.5 km wide and no more than 22 m deep.

No major tributaries join the Clinch River in Melton Hill Reservoir. Given its narrow width, the

Clinch River between Norris and Melton Hill dams can be thought of as a 90-km-long thermal gradient tank in which fish can select a temperature from a wide range of choices. Of course, it is not a perfect thermal gradient system because on any given date, the possible thermal habitats are not all present at every reach and depth of the reservoir; thus, feral fish cannot change their thermal environment instantly or nearly so, as fish can do in an experimental laboratory tank. This caveat would be more applicable to a sedentary species (e.g., largemouth bass *Micropterus salmoides*) than a highly mobile predator such as striped bass, which are capable of movement rates as high as 5 km/d (Young and Isely 2002). Also, because of the inflow of heated effluent by the Tennessee Valley Authority's Bull Run Steam Plant (located about halfway down the reservoir at CRkm 77), the thermal gradient is not linear (Figure 1). The effect of this thermal plume is particularly apparent during the winter months, as evidenced by surface water temperatures recorded on 18 January 2000: 8°C at CRkm 106, 20°C at CRkm 77, 13°C at CRkm 71, and 8°C at CRkm 53.

It was anticipated that striped bass in Melton Hill Reservoir would rarely encounter the environmental constraints present in other systems where the thermal ecology of large adults has been studied. The temperature–oxygen squeeze during summer described by Coutant (1985) and others was not present in Melton Hill Reservoir over the 10-year period preceding this study (Peterson and Negus 2000). Peterson and Negus (2000) concluded that suitable dissolved oxygen concentrations were available over a wide range of water temperatures in Melton Hill Reservoir each summer. The collection of dissolved oxygen and temperature profile data by TWRA biologists was subsequently discontinued in 1999.

Methods

Twenty-two striped bass were collected by use of DC electrofishing gear between December 1998 and May 1999. Mean total length was 862 mm (range, 530–1,350 mm). Although most fish were not weighed, tagged fish averaged 8.2 kg based on length–weight relationships for other striped bass populations in Tennessee. Most of the fish collected in the reservoir were captured at or near the Bull Run Steam Plant. Most fish were collected, tagged, and released quickly; however, four fish were collected and transported to a fish hatchery, where they were held overnight before tagging and release. To increase sample size, seven striped bass were collected in the tailwater below Melton Hill Dam in late May 1999, transported in a hatchery truck to a ramp located 0.5 km above the dam, tagged, and released immediately.

Striped bass were anesthetized by use of an electric cradle that supplied a weak electrical current to the fish (Jennings and Looney 1998). Once a fish was immobilized, several scales were removed from an area adjacent to the ventral midline and anterior to the pelvic girdle. A small incision was made and the radio tag was inserted; the antenna emerged externally through the incision. A surgical stapler was used to close the incisions of the first two tagged fish, but nonabsorbable nylon sutures were used on all other fish. Before the incision was closed, antibiotic powder was placed in the wound. After the sutures were tied off, antibiotic ointment was applied to the wound to form a temporary water barrier. When the electrical field was turned off, fish recovered almost immediately from galvanonarcosis and were released without further delay.

Radio transmitters were manufactured by Advanced Telemetry Systems (Isanti, Minnesota), weighed 30 g, were fitted with a 20-cm whip antenna, and possessed a battery life of at least 400 d. Each tag broadcasted a unique frequency between 30.000 and 31.999 MHz and was equipped with a mortality switch that would activate (and double the pulse rate) if the fish remained immobile for 8 h. The tags also telemetered the temperature of the tag by varying the pulse rate with changes in temperature. Each tag came with a calibration curve, which was checked at one temperature in the laboratory before implantation. It was assumed that the temperature of the tag was a good approximation of the ambient temperature a fish was in at the time it was located. Each tag was labeled with the word ''reward'' and a phone number to call about returning the tag.

The Clinch River between Norris and Melton Hill dams was traversed by motorboat or canoe at irregular intervals 17 times between April 1999 and May 2000. The average traverse took 1.9 d (range, 1–7 d) and was considered a single sample date. On each sample date, fish locations were recorded only once (i.e., if a fish was located twice or more on a sample date, only the first location would be considered in subsequent analyses). When a fish was located, the pulse interval was determined by measuring the amount of time elapsed during 10 pulses, and dividing that time by 10. This process was repeated, and the average pulse interval was then calculated and subsequently used to determine the temperature of the tag. Temperature and movement data collected within 10 d of tagging were ignored in subsequent analyses. The approximate location of the fish was recorded manually by use of navigation maps. The range of movements for tagged fish was defined as the distance between the extreme upstream and extreme downstream locations for individual fish over the duration of the study.

Seasonal differences in temperature selected by striped bass were assessed by use of a split-plot repeated-measures analysis of variance (ANOVA; Maceina et al. 1994; Paine 1996), where season was the between-replicates variable and day was the within-replicates variable. The seasons were winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Tukey's minimum significant difference was calculated by hand and used to compare the four seasonal means at a significance level of 0.05. A repeated-measures ANOVA model was also used to test whether fish size influenced temperature selection; size was the between-replicates variable, and day was the within-replicates variable. Ontogenetic shifts in the thermal requirements of striped bass are well documented (reviewed by Coutant 1985), although the contrast is greatest for age-0 fish and age-2 and older fish. I tested the mean temperatures selected by the five smallest (3.1–5.1 kg) and five largest (6.5–13.3 kg) fish with two or more observations during summer 1999 (June–August).

Temperature profiles were measured on 10 dates between April 1999 and May 2000 at five or more stations between Melton Hill Dam and the Highway 61 bridge (a distance of 69 km). The five stations where profiles were always measured on each date were located at CRkm 37, 53, 69, 85, and 101 (i.e., every 16 km [10 miles]). Dissolved oxygen concentration profiles at five or more stations were measured on only six dates because summer dissolved oxygen concentrations less than 4 mg/L were rarely observed in the preceding 10 years (Peterson and Negus 2000). An automatic temperature logger was placed in the Clinch River 19 km downstream of Norris Dam, and it recorded the water temperature every 30 min between 15 April and 25 September 1999. Surface water temperature was recorded on one date in midwinter (18 January 2000) at eight stations along the length of the reservoir in lieu of taking profile measurements. These temperature data provided conservative estimates of the minimum and maximum temperatures available to striped bass on 11 dates

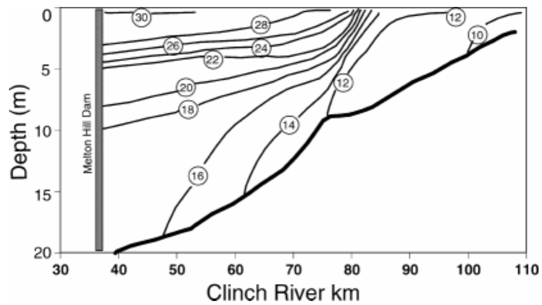

FIGURE 2.—Temperature isopleths (°C) based on eight vertical profiles at Melton Hill Reservoir, Tennessee, on 11 June 1999. Heated effluent from the Bull Run Steam Plant enters the reservoir at Clinch River km 77.

in the Clinch River between Norris and Melton Hill dams.

Results

Temperature and Dissolved Oxygen Conditions

Temperature profiles in Melton Hill Reservoir were dynamic and varied according to the discharges from Norris and Melton Hill dams, steam plant operations, and air temperature. A distinct density underflow occurred during the spring and summer months when cold, hypolimnetic water released from Norris Dam reached the warm surface waters downlake (Figure 2). The plunge point was ?5
usually observed near CRkm 80, upstream of the steam plant. The main basin of Melton Hill Reservoir (between CRkm 37 and 64) was usually weakly stratified in late spring and summer; however, hypoxic water was rarely observed (Table 1). Dissolved oxygen concentrations below 4 mg/L were only observed at the conclusion of this study (May 2000), and severely hypoxic conditions (≤2 mg/L) were limited to the deep waters of the forebay of Melton Hill Dam. With that exception, dissolved oxygen concentrations suitable for adult striped bass were available year-round over a wide range of water temperatures, although not necessarily in every reach or depth of the reservoir on any given date.

Fate and Movements of Tagged Fish

The entire 92-km reach of Melton Hill Reservoir was traversed on 10 dates. The entire reservoir except the tailwater reach (i.e., between Norris Dam and the Highway 61 bridge) was traversed on three more dates, but the absence of any tagged fish in the tailwater could be inferred with certainty (i.e., all fish at large were accounted for downlake). On three of the remaining four sample dates when

TABLE 1.—Temperature (°C) and dissolved oxygen (DO [mg/L]) profiles measured in the forebay of Melton Hill Reservoir, Tennessee, on six dates. Hypoxic (<4 mg/L DO) water was never observed at any uplake station during this study. Well-oxygenated (>6 mg/L DO) water over a range of temperatures (12.2–25.4°C) was present at uplake stations on the last sample date.

Depth (m)	14 Jul 1999		26 Aug 1999		30 Sep 1999		21 Nov 1999		25 Apr 2000		26 May 2000	
	°C	DO	°C	DO	°C	DO	°C	DO	°C	DO	°C	DO
Surface	26.4	8.5	24.7	16.3	20.8	13.1	16.6	10.8	16.2	11.9	23.9	9.0
1	25.7	8.3	24.4	16.5	20.8	12.8	15.7	10.9	16.2	11.6	24.2	8.4
2	25.4	7.3	22.8	16.8	20.8	12.8	15.1	10.5	16.1	11.5	24.1	8.9
3	24.9	5.7	20.4	15.9	20.5	12.3	15.0	10.2	16.1	11.1	24.1	8.2
4	23.4	4.3	18.3	11.5	19.8	12.3	14.9	9.6	16.0	11.0	23.8	7.2
5	21.8	4.4	17.7	10.3	19.1	11.9	14.8	9.5	16.0	10.9	23.6	6.3
6	20.5	4.5	17.1	10.0	18.6	10.9	14.8	9.3	16.0	10.9	22.8	4.9
7	19.2	5.2	16.5	8.9	18.0	10.3	14.7	9.2	16.0	10.8	21.7	3.0
8	17.6	5.9	15.5	9.0	17.6	9.7	14.7	9.2	15.9	10.6	19.9	1.7
9	16.9	6.4	15.5	9.0	17.3	9.3	14.7	9.1	15.8	10.5	18.9	1.1
10	16.5	6.6	15.4	9.0	16.9	9.0	14.6	8.8	15.5	9.8	18.2	0.9
11	16.4	6.7	15.3	9.1	16.6	8.7	14.5	8.8	15.4	9.4	17.9	0.9
12	16.4	6.7	15.3	9.1	16.3	8.6	14.4	8.7	15.0	8.2	17.6	0.9
13	16.3	6.7	15.2	9.2	16.2	8.5	14.3	8.7	14.9	7.8	17.4	0.8
14	16.3	6.7	15.2	9.0	15.9	8.4	14.3	8.7	14.7	7.5	17.1	0.7
15	16.3	6.7	15.2	8.8	15.7	8.3	14.3	8.6	14.6	7.0	17.0	0.8
16	16.3	6.7	15.1	8.1	15.5	8.2	14.2	8.5	14.6	6.5	16.8	0.6
17	16.3	6.7			15.3	8.0	14.2	8.4	14.4	5.8	16.7	0.6
18	16.3	6.6			15.2	7.8	14.2	8.3	14.3	5.3	16.5	0.3
19	16.3	6.5			15.2	7.8	14.2	8.2	14.2	4.5		
20	16.3	6.5			15.2	7.8			14.2	4.3		

the tailwater could not be traversed (21 April, 1 June, and 21 November 1999), the next tailwater surveys revealed the absence of tagged fish. On the last sample date (26 May 2000), the tailwater was not traversed, but the four tagged fish that were still at large but not located were probably not in the tailwater because (1) no fish were observed in the tailwater during the previous year until late July, (2) all four fish were last seen 30–70 km below the tailwater, and (3) only one of the four fish was ever observed within 10 km of the tailwater.

Collecting and holding four striped bass overnight in the hatchery prior to tag implantation was ill advised. After surgery and release, two of the four fish were never located and were presumed dead. The other two fish died at 90–134 d postimplantation, although the interval of time between surgery and death (or tag loss) suggests that they survived the surgery. In contrast, only two of the seven striped bass collected below Melton Hill Dam and tagged and released in Melton Hill Reservoir subsequently died or were lost, despite the presence of water temperatures close to 25°C. An angler harvested one striped bass 35 d after tagging. Thus, 15 striped bass were known to have survived surgery and were successfully tracked for 278–530 d. On 1 August 2003, or 1,632 d after tagging, an angler subsequently harvested one of those 15 fish. Tagged fish were located an average of 13.8 times (range, 9–17 times)

Striped bass displayed their pelagic nature over the course of this study. The average range of tagged fish was 56 km (compared to a maximum possible range of 92 km between Norris and Melton Hill dams). The shoals above the Highway 61 bridge (at CRkm 107) appeared to impede further upstream movement by some striped bass. Five striped bass were often located in the upper reaches of Melton Hill Reservoir, including the reach just downriver of the Highway 61 bridge, yet they were never observed upriver of the bridge (Figure 3). The shoals also affected the movements of three other striped bass that were located at least once above the Highway 61 bridge; those three fish were more likely to be found just below the shoals than above the shoals when they moved into the headwaters of Melton Hill Reservoir. The shallowness of the shoals was probably the factor limiting striped bass movements into the reach of the river immediately below Norris Dam. Only four tagged striped bass moved into the reach above the Highway 61 bridge; only two fish moved upstream of the bridge by more than 1 km. Both of those fish moved upstream as far as CRkm 122 and inhabited the tailwater between late July and September 1999. By November 1999, all fish had left the Nor-

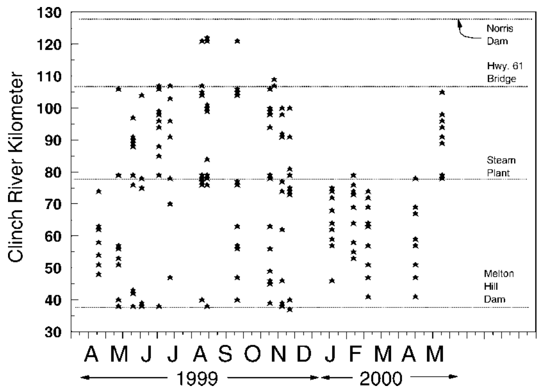

FIGURE 3.—Locations of 15 radio-tagged striped bass in Melton Hill Reservoir, Tennessee, during April 1999–May 2000.

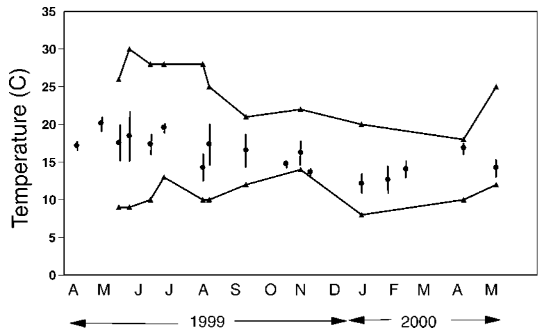

FIGURE 4.—Maximum and minimum temperatures observed in Melton Hill Reservoir, Tennessee, between Clinch River km 129 (Norris Dam) and km 37 (Melton Hill Dam), and mean temperatures (with 95% confidence intervals) occupied by radio-tagged striped bass on 18 dates between April 1999 and May 2000.

ris Dam tailwater and moved below the Highway 61 bridge.

Rapid upstream movements in excess of 40 km were undertaken by 5 of 15 tagged striped bass in April and May 1999. The timing and extent of these movements resembled those of a spawning run. However, most of the tagged fish did not display this behavior, suggesting that attempts to spawn did not override other factors that might influence habitat (and temperature) selection.

Thermal Ecology

The mean temperatures occupied by individual striped bass over the entire survey period (14.1–16.8°C) did not differ statistically (ANOVA: $F = 0.8$; df = 14, 191; $P = 0.72$). Striped bass occupied a wide range of temperatures (7.1–24.0°C), but none of the fish were ever located in the warmest (25–28°C) waters, which were observed in late June and July 1999 in the forebay of the reservoir (Figure 3). Striped bass temperature selection differed among seasons (repeated-measures ANOVA: $F = 26.04$; df = 3, 132; $P < 0.0001$). Mean (SE) selected temperatures were as follows (means sharing the same letter were statistically similar according to Tukey's test; $P \geq 0.05$): 13.0°C^{A} (0.43°C) in winter, 16.9°C^{BC} (0.39°C) in spring, 17.5°C^{C} (0.46°C) in summer, and 15.4°C^{B} (0.36°C) in fall. Selected temperatures declined steadily between June 1999 and January 2000. Striped bass occupied significantly cooler waters in winter despite the fact that warmer waters (~20°C) were usually available (Figure 4), albeit in a small reach of river downstream of the Bull Run Steam Plant. Striped bass rarely ($n = 2$ observations) occupied the thermal plume at the steam plant (17–20°C) during the winter months; most of the temperatures occupied during winter ($n = 28$ observations) were between 7°C and 15°C.

When Melton Hill Reservoir was stratified (May–October 1999), the average temperature selected by striped bass was 17.5°C (SE = 0.4; $n = 92$); the modal temperature was 19.0°C. The frequency distribution of temperatures selected during stratification was skewed toward cooler temperatures (Figure 5). Temperatures below 13°C were associated with fish located in or near the Norris Dam tailwater (i.e., above CRkm 98). Temperatures between 13°C and 17°C were recorded for fish located between CRkm 76 and 105.

I detected no difference in the mean temperatures selected by the five smallest and five largest

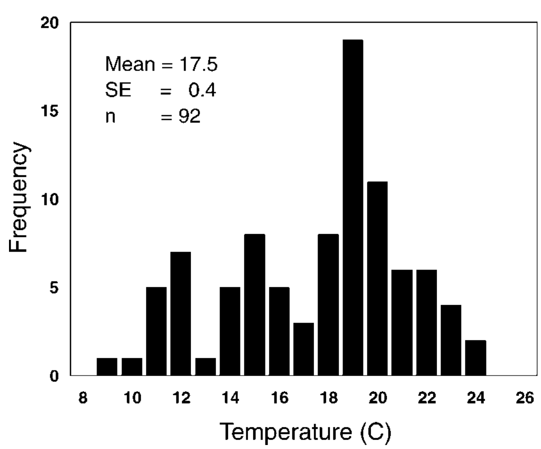

FIGURE 5.—Frequency distribution of temperatures selected by radio-tagged striped bass in Melton Hill Reservoir, Tennessee, during May–October 1999.

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fish tagged during the summer months (repeated-measures ANOVA: $F = 0.71$; df = 1, 27; $P = 0.42$). In fact, the results were counterintuitive; the mean temperature occupied by the largest (≥6.5 kg) fish was about 1°C higher than the mean temperature (16.7°C) occupied by the smallest fish (3.1–5.1 kg).

Discussion

Several theories that might explain the behavior of striped bass in Melton Hill Reservoir include behavioral thermoregulation, optimal foraging, behavioral bioenergetics, and maximization of available power (Brandt 1993; Kelsch 1996; Young and Isely 2002). Testing the plausibility of each of these theories in the present context was beyond the scope of this study. However, several factors known to affect fish behavior and temperature selection require comment. First, prey availability affects the habitat choices of some species (e.g., smallmouth bass *M. dolomieu*; Bevelhimer 1996) and could have influenced the temperatures selected by striped bass in Melton Hill Reservoir. The types of prey available to striped bass varied in different reaches of the reservoir. Above CRkm 106 (Highway 61 bridge) and in the reach immediately downstream, the Clinch River supports a depauperate fish fauna due to the regulated flows and hypolimnetic releases from Norris Dam (Scott et al. 1996). Stocked rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* were the most abundant large prey in the upper reaches of the reservoir, and striped bass are known to prey readily on stocked trout in other tailwaters (Deppert and Mense 1980; Walters et al. 1997). Further downstream in the lacustrine reach of the reservoir, potential prey fish included gizzard shad *Dorosoma cepedianum* and threadfin shad *D. petenense* (Peterson and Negus 2000), two species that striped bass readily prey upon in other locales (e.g., Combs 1979; Persons and Bulkley 1982; Filipek and Tommey 1987). It is unknown whether striped bass selected particular habitats because of the temperature in those habitats or the types of forage available; however, striped bass had access to abundant prey in any habitat they occupied, and the influence of forage on temperature selection was probably minimal.

Secondly, landlocked striped bass populations in large reservoirs often display distinct spawning migrations to tributaries and upstream reaches of the reservoirs (Combs and Peltz 1982; Braschler et al. 1989; Jackson and Hightower 2001; Schaffler et al. 2002). Such migrations would dictate the temperatures occupied by striped bass, particularly in a system with a distinct longitudinal temperature gradient like that of Melton Hill Reservoir. Most of the tagged striped bass in Melton Hill Reservoir did not display this spring migration behavior; therefore, the biological imperative to reproduce probably exerted only minimal influence on temperatures occupied or selected by striped bass in the reservoir.

A third factor that influences habitat choice and temperature selection by striped bass in other southern U.S. reservoirs is site fidelity (e.g., Jackson and Hightower 2001; Young and Isely 2002), which is especially apparent when a reservoir experiences poor water quality in summer. Spring (April–May) was the only season in which striped bass in this study were observed in consecutive years, and only 2 of 12 fish located in spring 1999 were located in the same 10-km reach in spring 2000. Low site fidelity contrasted sharply with the behavior of striped bass in a South Carolina reservoir, where several fish returned to within 10 m of their original capture location the following year (Schaffler et al. 2002). Low site fidelity in Melton Hill Reservoir supports the premise that water quality was adequate for striped bass throughout the reservoir on nearly all sample dates.

Finally, the possibility exists that striped bass selected cooler temperatures in winter because of reduced rations. This phenomenon has been described for several species, including Atlantic cod *Gadus morhua* (Despatie et al. 2001) and lake trout *Salvelinus namaycush* (Mac 1985). Woiwode and Adelman (1991) demonstrated that the optimum temperature for growth, which usually coincides with the final temperature preferendum, decreased with decreasing ration for striped bass × white bass *Morone chrysops* hybrids. These and all other such studies were conducted in the laboratory, but the same trends would probably exist for feral fish. No food habits data for striped bass in Melton Hill Reservoir were available during the present study; however, there is no evidence that striped bass suffered from reduced rations. Melton Hill Reservoir harbored large, robust striped bass, a finding that is inconsistent with reduced forage availability in any season. More importantly, during electrofishing in the previous winter, large schools of gizzard shad were commonly observed in the vicinity of the Bull Run Steam Plant effluent, where striped bass were also observed and captured. The attraction of pelagic piscivores, their prey, and anglers to heated plumes in winter is a common phenom-

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enon in temperate lakes and reservoirs that receive heated effluent.

In the absence of habitat constraints due to severely hypoxic conditions, and given a wide range of available temperatures throughout the year (although not necessarily in every reach or depth on any given date), striped bass in Melton Hill Reservoir selected different temperatures each season. Coutant and Benson (1990) concluded that adult striped bass in Chesapeake Bay chose temperatures within their preferred range (20–25°C) over several seasons (i.e., there was no seasonal effect), but their evidence was indirect and they only discussed the period from May to October of each year. The effect of season on temperature selection by fishes has long been recognized. It has been assumed that this behavior directs fishes to temperatures that are optimal for meeting specific physiological needs that vary with the seasons. For instance, the final preferred temperature of overwintering juvenile Atlantic salmon *Salmo salar* increased from winter to spring (Morgan and Metcalfe 2001), which would coincide with increased natural food abundance, appetite, and growth rate. Differences in thermal ecology among seasons have also been described for demersal marine species (sand goby *Pomatoschistus minutus*, Hesthagen 1979), subtropical snakeheads (Indian murrel *Channa punctatus*, Jain and Garg 1983), brook trout *Salvelinus fontinalis* (Sullivan and Fischer 1953), and four species in Lake Erie (Barans and
?3 Tubb 1973). However, these and nearly all other studies on seasonality relied on data collected in a laboratory. The selection of cooler temperatures in winter by striped bass in Melton Hill Reservoir even though those same temperatures were available in summer and fall indicates that striped bass were responding to environmental cues other than acclimation temperature (e.g., photoperiod). It is not known whether striped bass in Melton Hill Reservoir selected different temperatures in each season in anticipation of future metabolic requirements, as was suggested for juvenile Atlantic salmon (Morgan and Metcalfe 2001).

The preferred-temperature distribution of striped bass in Melton Hill Reservoir during the growing season was negatively skewed; the modal temperature (19°C) was much closer to the warmest temperature occupied (24°C) than the coolest temperature occupied (8°C). Such skewness is typical for freshwater fishes and suggests that the organism is thermoregulating more precisely at the upper thermal limit than the lower limit (Reynolds and Casterlin 1979).

Striped bass in Melton Hill Reservoir were never observed in waters warmer than 24°C. Cheek et al. (1985), Coutant and Benson (1990), and Young and Isely (2002) also concluded that the upper avoidance temperature for striped bass was 25°C; however, striped bass can tolerate water warmer than 25°C (e.g., Matthews et al. 1985; Farquhar and Gutreuter 1989). Coutant's (1985) assertion that the thermal niche of adult striped bass would be centered somewhere around 20°C was correct, albeit only during the growing season. Similarly, Coutant's (1990) assertion that the fundamental thermal niche of adult striped bass was around 19–23°C generally agrees with the data presented herein, but only for the growing season. My findings indicate that the range of the fundamental niche is wider than the consensus range of 18–25°C (Coutant 1985) or 19–23°C (Coutant 1990) and should include cooler temperatures.

The striped bass habitat suitability criteria proposed by Crance (1984) should be revisited based on the results reported herein. Based on Crance's (1984) work, Young and Isely (2002) defined optimal habitat as summer temperatures of 18–24°C and dissolved oxygen concentrations exceeding 5 mg/L. Suboptimal habitat was defined as summer temperatures between 12°C and 18°C (or greater than 24°C) and dissolved oxygen concentrations between 2.5 and 5.0 mg/L. Unsuitable habitat was defined as summer temperatures less than 12°C (or greater than 30°C) and dissolved oxygen concentrations less than 2.5 mg/L. In Melton Hill Reservoir, the mean (17.5°C) and modal (19.0°C) temperatures selected during stratification were in or near the range that Crance (1984) defined as suboptimal, yet warmer oxygenated waters were available to those fish. More importantly, 15% of striped bass locations in Melton Hill Reservoir during stratification were in waters at or below 12°C, which suggests that those cold habitats were in fact suitable, in contrast to the assertion by Crance (1984). Finally, the threshold of 5 mg/L or less for dissolved oxygen, which has defined suboptimal habitat for striped bass, should also be revisited. Although dissolved concentrations below 2.5 mg/L are avoided by striped bass (e.g., Schaffler et al. 2002; Young and Isely 2002), most research indirectly suggests that the zone of respiratory independence (i.e., when metabolic uptake of oxygen is independent of the partial pressure of oxygen) and therefore suitable habitat for adult striped bass are defined by dissolved oxygen concentrations at or exceeding levels as low as 4 mg/L (e.g., Farquhar and Gutreuter 1989; Haeseker et al. 1996).

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