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Thermal ecology of subadult and adult muskellunge in a thermally enriched reservoir

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Abstract The movement of adult muskellunge, *Esox masquinongy* Mitchill, has been investigated in a variety of systems, but temperature selection by muskellunge has not been examined where well-oxygenated waters were available over a range of temperatures for much of the year. Thirty subadult and adult muskellunge tagged internally with temperature-sensing radio tags were tracked from March 2010 to March 2011 in a Tennessee reservoir. Mean tag temperatures were 18.9 °C in spring (March to May), 22.1 °C in summer (June to August), 16.5 °C in autumn and 9.8 °C in winter (December to February). When the greatest range in water temperatures was available (7.1–33.3 °C; May to early August 2010), their realised thermal niche (mean ± 1 SD) was 22.3 °C ± 1.8; the realised thermal niche was affected by fish size (smaller fish selected slightly warmer temperatures) but not sex. An electric generating steam plant discharging warm water resumed operation in January 2011, and most (86%) tagged fish occupied the plume where temperatures were ≈10 °C warmer than ambient water temperatures. No mortalities were observed 15 days later when plant operations ceased. Their affinity for the heated plume prompted concerns that muskellunge will be too easily exploited when the plant operates during winter.

KEYWORDS: *Esox masquinongy*, temperature selection, thermal ecology, thermal niche.

Introduction

The native distribution of muskellunge, *Esox masquinongy* Mitchill is restricted to the upper Mississippi River, Ohio River and St. Lawrence River drainages of North America (Crossman 1978). In Tennessee, USA, muskellunge is native to large rivers and streams in both the Tennessee River and Cumberland River drainages (Etnier & Starnes 1993). However, dam construction and habitat loss resulted in the extirpation of muskellunge from most Tennessee watersheds. Since 1998, the Tennessee Wildlife Resources Agency (TWRA) has stocked muskellunge fingerlings into Melton Hill Lake, an impoundment on the Clinch River within the historical range of muskellunge in east Tennessee, at an average annual rate of 1.3 fish ha^{-1}, creating a sport fishery in this reservoir on the southern edge of this species' native range. Melton Hill Lake anglers are especially successful during winter and early spring when muskellunge and prey fishes appear to congregate in the vicinity of the warm-water discharge plume from the Tennessee Valley Authority's (TVA) coal-fired Bull Run Steam Plant (hereafter referred to as the steam plant) electric generating station.

Although several factors can affect the survival of muskellunge, water temperature is an important factor affecting their movements in natural (Minor & Crossman 1978; Dombeck 1979) and thermally-altered systems (Younk 1982). Many researchers have studied muskellunge habitat use and temperature selection in northern rivers and lakes using biotelemetry (e.g. Miller & Menzel 1986a; Strand 1986; Younk *et al.* 1996); however, little is known about muskellunge in southern U.S. systems. Melton Hill Lake, with its thermally heterogeneous environment throughout much of each year (see Study Area), provides an excellent opportunity to study the thermal ecology of muskellunge. Previous biotelemetry studies of muskellunge thermal preference occurred in

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lakes where the movements of muskellunge were constrained by low concentrations of dissolved oxygen (e.g. Miller & Menzel 1986b; Wagner & Wahl 2007). The waters of Melton Hill Lake, even during summer stratification, are rarely hypoxic or anoxic (Bettoli 2005); thus, Melton Hill Lake presents an opportunity to describe the thermal niche of adult muskellunge in a system where the influence of a common limiting factor, dissolved oxygen, was greatly reduced or absent.

Temperatures selected by fish in a stable environment with suitable prey and dissolved oxygen concentrations should represent the temperatures that optimise growth, survival, reproduction and fitness (Jobling 1981; Coutant 1987; Kelsch 1996). Although difficult (if not impossible) to estimate in a field study, the width of the fundamental thermal niche of fish in a laboratory gradient is about 4 °C when measured as the mean ± 1 SD (Magnuson *et al.* 1979). The first objective was to describe seasonal variation in temperatures selected by large subadult and adult muskellunge in Melton Hill Lake. The second objective was to estimate the fundamental thermal niche of large muskellunge during the growing season by describing their realised thermal niche (Magnuson *et al.* 1979; Magnuson & Destasio 1996).

Study area

Melton Hill Lake is a 2303 ha main-stem reservoir on the Clinch River in eastern Tennessee, USA (Fig. 1). Melton Hill Dam (35°53′07.22″ N, 84°18′00.28″ W) was built in 1963 by the TVA for hydropower and navigation and is located at Clinch River kilometre 37 (CRkm, measured from its confluence with the Tennessee River). The reservoir is narrow, with much of the lake less than 0.5-km wide and has a mean depth of 6.4 m and a maximum depth of 18.3 m. It is mesotrophic (Scholten *et al.* 2008), and the water level fluctuates ≈1.5 m annually (Peterson & Negus 2000). Melton Hill Lake extends 92 km upstream to Norris Dam at CRkm 129. Hypolimnetic water is discharged through two hydroelectric turbines at Norris Dam, creating a cold free-flowing tailwater that extends approximately 23 km below the dam. Melton Hill Lake becomes more lacustrine downstream of CRkm 106 in Clinton, TN. Upstream of CRkm 106, the Clinch River is riverine and comprised of extensive riffles and shoals.

No major tributaries enter the Clinch River in Melton Hill Lake. The cold hypolimnetic release from Norris Dam coupled with the short average hydraulic retention time of 12 days maintains cool water temperatures and suitable (>4.0 mg L^{-1}) dissolved oxygen concentrations over a wide range of water temperatures in Melton Hill Lake each summer (Peterson & Negus 2000). A density underflow occurs in the spring and summer beginning near CRkm 80 when the cold inflowing water from Norris Dam reaches the main basin of Melton Hill Lake and plunges below the warm surface waters (Bettoli 2005).

Melton Hill Lake exhibits a distinct longitudinal temperature gradient. However, this thermal gradient is not uniform due to the influence of the steam plant, located approximately mid-reservoir at CRkm 77. The steam plant uses lake water to cool the facility and releases heated water into Melton Hill Lake, creating a thermal plume. The longitudinal temperature gradient in Melton Hill Lake is dynamic and varies with discharges at Norris Dam and Melton Hill Dam, steam plant operations and ambient air temperature. Dissolved oxygen concentrations below 4 mg L^{-1} were rarely observed anywhere at any depth in Melton Hill Lake by Bettoli (2005). Unlike natural lakes or other reservoirs where the thermal ecology of muskellunge and other esocids has been studied, fish in Melton Hill Lake can move vertically or longitudinally to seek cooler or warmer temperatures, especially during summer months.

Methods

Fish collection and tag implantation

Muskellunge were collected between CRkm 66 and 77 from January to March 2010 using boat-mounted DC electrofishing gear. Temperature-sensing radio tags from Advanced Telemetry Systems (Isanti, MN, USA) were surgically implanted into 30 subadult and adult muskellunge averaging 968 mm total length (TL) (SE = 27) and varying in length from 720 to 1240 mm TL. Most of the fish (n = 19) were females, and the seven largest fish tagged (≥1100 mm TL) were all females. Most (9 of 11) of the males were of intermediate length (899–1049 mm TL). Each tag broadcast a unique frequency within the bandwidth range of 30.000 and 31.999 MHz. Tags were 55 × 15 mm, weighed 21 g out of water, had a 30-cm whip antenna and a guaranteed battery life that exceeded 3 years. Based on estimated weights of tagged fish, the tag burden ranged from 0.1 to 0.8% of each fish's weight. Tags telemetered the temperature within ±0.5 °C by varying the pulse rate as a function of temperature. Each tag had an associated second-order regression equation relating the pulse rate to its temperature.

Immediately following capture, fish were placed in a livewell containing a solution of lake water and 80 mg L^{-1} tricaine methanesulfonate (MS-222; Strand 1986). After 5–6 min, fish lost equilibrium and were adequately sedated for tag implantation surgery. All fish

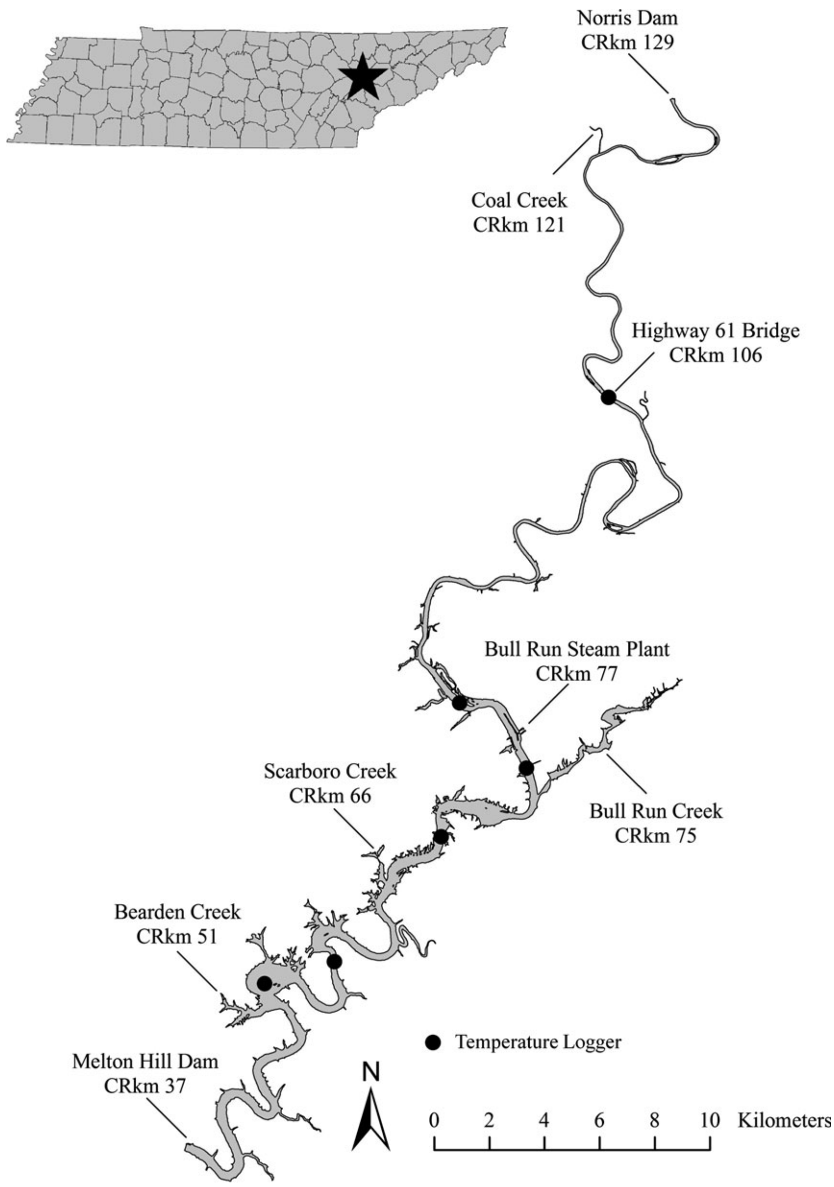

Figure 1. Melton Hill Lake on the Clinch River in east Tennessee, USA. Filled circles show locations of automated temperature loggers.

were sexed prior to surgery by inspecting the urogenital pore (Lebeau & Pageau 1989). Standard surgical practices (e.g. autoclaved instruments; no reuse of sutures) were followed to avoid compromising the health of the fish (Wagner & Cooke 2005), and the antenna was positioned through the body wall posterior to the incision using the shielded needle technique described by Ross and Kleiner (1982). Anaesthetised fish were positioned ventral side up on a V-shaped operating trough covered with a waterproof non-abrasive sterile drape. During surgery, water containing 40 mg L^{-1} of MS-222 was pumped over the fish's gills to maintain sedation and provide continuous irrigation. After surgery, fish were restrained alongside the boat by holding their caudal peduncle until equilibrium was regained. Fish regained equilibrium and exhibited swimming behavior after 1–5 minutes of recovery. Fish were released at their capture location and the position noted with a Global Positioning System (GPS).

Tracking

Tracking operations were conducted from a motorboat using an ATS 4500S digital scanning receiver, a boat-mounted directional loop antenna and an omni-directional antenna (i.e. coaxial cable with an exposed wire end). An analogue ATS R2000 scanning receiver was occasionally used to locate tagged fish; this receiver did not have temperature-sensing capabilities. Instead, tag temperature was determined from the pulse interval by measuring the amount of time (s) elapsed during 11 pulses with a stopwatch. This process was repeated, and the average pulse interval was then calculated and subsequently used to determine the temperature of the tag.

Fish were located from long range using the loop antenna. After a fish was located by triangulation with the loop antenna, the boat was moved to the expected position of the fish and the location was pinpointed with the omni-directional antenna; water depth (m) and GPS coordinates were determined with a Garmin® (Olathe, KS, USA) GPSmap 188 Sounder at this location. Water temperature (°C) and dissolved oxygen concentrations (mg L^{-1}) were measured at the surface, midwater and bottom at each fish location with a Eureka Environmental (Austin, TX, USA) Manta® submersible multiprobe.

Tracking began 2 weeks after implantation of the last tag (March 2010) to allow fish to recover and avoid potential changes in behavior due to capture and surgery (Paukert *et al.* 2001). Fish were located approximately fortnightly for 13 months (March 2010 to March 2011). The entire 69-km reach of Melton Hill Lake between CRkm 106 and Melton Hill Dam was traversed tracking event, and each tracking event spanned 2–3 days. The Clinch River from Norris Dam to the Bull Run Steam Plant was also searched in March 2011 and May 2011 to locate unaccounted tagged fish. For statistical analyses, the data were partitioned seasonally, with seasons defined as spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February).

Thermal environment

To monitor spatial and temporal variation in the thermal environment, six Onset HOBO® (Bourne, MA, USA) U22 Water Temp Pro v2 automatic temperature loggers were deployed longitudinally throughout the reservoir at a depth of 3 m, the approximate depth of the thermocline when it is present in the lower basin of Melton Hill Reservoir (CRkm 37–64; Peterson & Negus 2000). These devices recorded the water temperature at 1-h intervals and were affixed to navigation markers at CRkms 52, 59, 69, 76 and 80. The uplake temperature logger was anchored on the bottom in the headwaters of Melton Hill Lake (CRkm 106; Fig. 1) because the water was less than 3 m deep.

Temperature (°C) and dissolved oxygen (mg L^{-1}) profiles (1-m intervals) were measured each month at six main basin locations and in three embayments (Fig. 1). The embayments were Bull Run Creek (CRkm 75), Scarboro Creek (CRkm 66) and Bearden Creek (CRkm 51). Profiles were taken in the middle of the embayment. Main basin profiles were taken in the navigation channel at CRkm 94, above the steam plant (CRkm 80), opposite the mouths of Bull Run Creek, Scarboro Creek and Bearden Creek and in the dam's forebay (CRkm 38).

Data analysis

All radio telemetry locations were converted into shapefiles in ArcMap 9.3 (ESRI, Redlands, CA, USA). Fish locations were spatially joined to the nearest CRkm in ArcMap 9.3, and fish located in embayments were assigned to the CRkm nearest the mouth of the embayment. The minimum range of each fish over the course of the study was the distance between their most upstream and downstream locations. Seasonal differences amongst means for tag temperature were tested with a repeated-measures ANOVA (Penne & Pierce 2008) using the MIXED procedure with the spatial power covariance structure in the Statistical Analysis System version 9.2 (SAS Institute, Cary, NC, USA). Season was the fixed effect, and fish ID and the fish ID*×season interaction term were random effects. Bonferroni's multiple-comparisons procedure ($\alpha = 0.05$) was used to assess differences in tag temperature amongst seasons when the global model was statistically significant ($P \leq 0.05$). Data were tested for normality using the Shapiro–Wilke test statistic, W.

All temperatures measured in main channel profiles, embayment profiles, profiles where fish were located and by the temperature loggers were compiled to determine the distribution of temperatures available to tagged fish during each tracking event. Box and whisker plots were created from tag temperatures observed during each tracking event.

The realised thermal niche was estimated using tag temperature data when the greatest range of water temperature was available (May to early August 2010) and was defined as the mean ± 1 SD. Magnuson *et al.* (1979) discussed the subtle differences between niche breadths measured as the mean ± 1 SD and the median ±33% of the observations and suggested the latter approach when using laboratory-derived data because they are often skewed. Given that data were obtained in the field, the former approach was used. Tag temperature data were pooled from this period, and summary statistics (e.g. mean, median, SD) were determined. The influence of size and sex on the temperatures selected during that same period was tested by repeated-measures ANOVA models and the MIXED procedure. The three size groups were small ($\leq$889 mm TL; $n = 11$), intermediate

(905-1010 mm TL; n = 10) and large ($\geq$1049 mm TL; n = 8).

Results

Tracking summary and movements

Thirty radio-tagged muskellunge were located 604 times during 26 tracking events. At the conclusion of this study in March 2011, 22 of the 30 tagged fish were still alive and being tracked. One fish was located once 11 days post-tagging, but was never located during a tracking event. Therefore, it was either illegally harvested or the tag failed. Three fish likely died; two of those tags were recovered on shore and one was on the bottom. Those suspected mortalities occurred 132–337 days post-tagging, indicating mortality was unlikely to have resulted from the tagging process or that the tag was expelled. One fish was harvested downstream of Melton Hill Dam in September 2010, and the tag was returned for its reward; that fish was last located in Melton Hill Lake in mid-June 2010. Three tagged fish were lost for unknown reasons (i.e. illegal harvest, tag failure, downstream dam passage) after 225–305 days at large. Anglers reported catching and releasing 17 radio-tagged muskellunge during the study.

Tagged muskellunge rarely occupied the tailwater below Norris Dam or the riverine headwaters of Melton Hill Lake above the steam plant (Fig. 2). Although most (74%) locations of tagged fish over the entire study were in an 11-km reach extending downstream of the steam plant, long movements were the norm. The average minimum range of all tagged fish was 26.9 km (SE = 2.97; range 9–69 km). Two tagged fish were located 8 km below Norris Dam at CRkm 121 in late-March 2011 at the conclusion of formal tracking. Their occupancy of the tailwater was relatively short-lived, as neither fish was located in the Norris Dam tailwater when it was searched in May 2011.

Temperature selection

The thermal environment in Melton Hill Lake was extremely dynamic, and muskellunge were able to select from a wide range of temperatures throughout much of the year, especially in spring and summer (Fig. 3). Mean tag temperatures varied significantly amongst seasons (d.f. = 3, 74; F = 419.91; P < 0.0001) and were warmest in the summer (mean = 22.1 °C; SD = 2.2; n = 144), coolest in the winter (mean = 9.8 °C; SD = 3.8; n = 120) and intermediate (and statistically similar; P = 0.1397) during the spring (mean = 18.9 °C; SD = 4.3; n = 171) and autumn (mean = 16.5 °C;

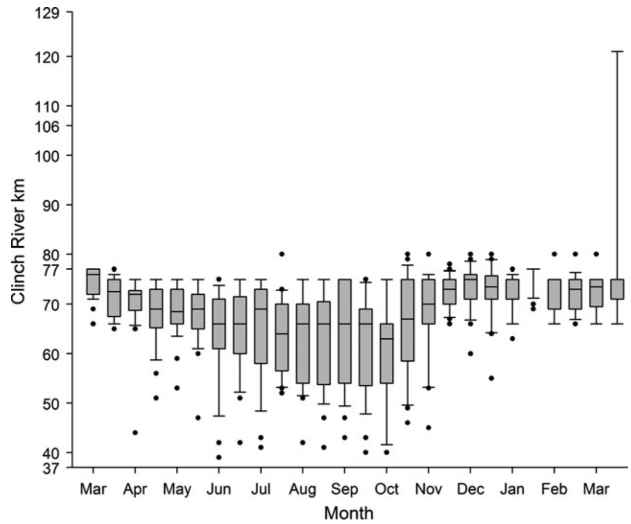

Figure 2. Longitudinal distribution of radio-tagged muskellunge in Melton Hill Lake, Tennessee by Clinch River km, March 2010 to March 2011. Each plot represents an individual tracking event. The lower and upper boundaries of each box indicate the 25th and 75th percentiles, respectively, the median is shown as a line within the box, the whiskers below and above each box represent the 10th and 90th percentiles, and individual points are detections beyond 10th and 90th percentiles. Key landmarks are Melton Hill Dam (CRkm 37), Bull Run Steam Plant (CRkm 77) and Norris Dam (CRkm 129).

SD = 3.8; n = 138). The decrease in maximum observed water temperatures in late August 2010, and subsequent decrease in tag temperatures, coincided with the influx of cool water when TVA began lowering Norris Lake to winter pool. Subsequently, a narrower range of temperatures was available to tagged fish between October 2010 and early January 2011.

The steam plant operated briefly during late January 2011, and most (86%) tagged fish moved into the discharge canal; tag temperatures of those fish (mean = 16.4 °C; SD = 2.9) were ≈10 °C warmer than they were only 15 days earlier (Fig. 3). No mortalities were observed 15 days later after plant operations ceased abruptly and tagged fish occupied more typical winter water temperatures (mean = 6.2 °C; SD = 0.7).

Realised thermal niche

The greatest range and most stable water temperatures available to tagged fish occurred between May and early August 2010. Over that same interval, the coldest (bottom) and warmest (surface) temperatures in the water column where fish were located ranged from 11 to 32 °C, and the mean tag temperature was 22.3 °C (SD = 1.8; Fig. 4). The median temperature selected was 22.5 °C, and the data were normally distributed (W = 0.9855; P = 0.0561). Fish rarely occupied water

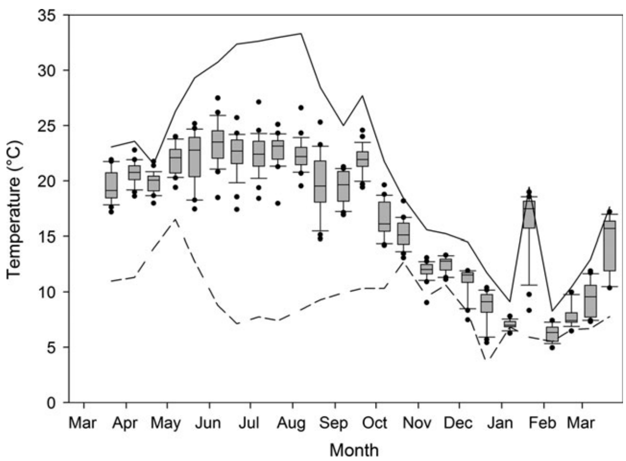

Figure 3. Tag temperatures of radio-tagged muskellunge in Melton Hill Lake, Tennessee, March 2010 to March 2011. The lines represent the maximum and minimum temperatures observed in the reservoir during tracking events. Each box plot represents an individual tracking event. The lower and upper boundaries of each box indicate the 25th and 75th percentiles, respectively, the median is shown as a line within the box, the whiskers below and above each box represent the 10th and 90th percentiles, and individual points are detections beyond 10th and 90th percentiles.

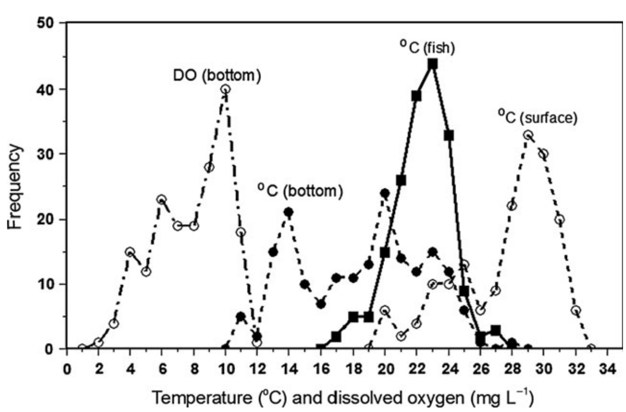

Figure 4. Frequency of temperatures occupied by radio-tagged muskellunge (°C fish), bottom (°C bottom) and surface (°C surface) water temperatures at each fish location, and the dissolved oxygen (DO) concentration measured at the bottom at each fish location (DO bottom), during May through early August 2010, the interval of time with the widest range of water temperatures available to tagged fish.

cooler than 20 °C (and never below 17 °C) even though water that cold was available at their locations. Likewise, fish rarely occupied water warmer than 25 °C (and never above 27.5 °C) even though water that warm was available to them. Hypoxic or anoxic conditions were uncommon. For instance, when the reservoir was stratified in August 2010 (when hypoxic conditions would be most likely to occur), dissolved oxygen concentrations at all depths in the main channel exceeded 8.0 mg L^{-1} (Table 1). Hypoxic conditions (<3 mg L^{-1}) in the hypolimnion were observed in May, June, July and September 2010 in one small embayment (Bearden Creek); the lowest concentration observed there was 0.4 mg L^{-1}. Over those same months, dissolved oxygen concentrations elsewhere in the reservoir at all depths were always above 3.0 mg L^{-1}. Where fish were located, dissolved oxygen concentrations at the bottom rarely were <4 mg L^{-1} and never less than 2 mg L^{-1} (Fig. 4). In the absence of any compelling evidence that low dissolved oxygen concentrations were commonplace or unduly influenced temperature selection, the realised thermal niche (mean ± 1 SD) of subadult and adult muskellunge in Melton Hill Lake was estimated to be 22.3 ± 1.8 °C (20.5–24.1 °C).

The preceding data and summary statistics on the width of the thermal niche between May and early August 2010 pertained to the pooled sample of tagged fish. Although differences between the sexes were not detected (d.f. = 1, 171; $F = 0.37$; $P = 0.5542$), mean temperatures selected by small (23.5 °C), intermediate (22.0 °C) and large muskellunge (21.5 °C) differed (d.f. = 2, 169; $F = 28.79$; $P < 0.001$). The mean temperatures for the two larger size groups did not differ ($P = 0.4026$), but both were less than the temperatures selected by the smallest fish ($P = 0.0001$).

Discussion

The survival and thermal preference of tagged muskellunge in this study should be representative of free-ranging muskellunge. Muskellunge implanted with telemetry tags in previous studies did not experience higher mortality (Miller & Menzel 1986a; Strand 1986; Younk *et al.* 1996; Eilers 2008) or slower growth (Minor & Crossman 1978; Miller & Menzel 1986a; Strand 1986; Eilers 2008) as a result of being tagged. The number of fish tracked in the present study ($n = 22$ at the end of the 13-month study) represents the largest sample size of any published study that described temperature selection and the thermal niche of subadult and adult muskellunge.

Melton Hill Lake is unlike any other system in North America where muskellunge have been studied with biotelemetry because of its range of thermal conditions with sufficient concentrations of dissolved oxygen, which allowed tagged muskellunge to select a wide range of temperatures throughout much of the year. Thus, it was a good 'field laboratory' to study temperature selection of large muskellunge. During the warmest months of the year, tagged fish seeking cooler temperatures could swim upstream or descend in the water column. Previous muskellunge biotelemetry studies have been conducted

Table 1. Temperature and dissolved oxygen profiles on 12–13 August 2010 at six locations (Clinch River km [CRkm]) along the main channel in Melton Hill Reservoir, Tennessee. A density underflow occurs between CRkm 75 and 80

Depth (m)	CRkm 94 °C	mg L^{-1}	CRkm 80 °C	mg L^{-1}	CRkm 75 °C	mg L^{-1}	CRkm 66 °C	mg L^{-1}	CRkm 51 °C	mg L^{-1}	CRkm 38 °C	mg L^{-1}
0	8.7	11.9	10.8	11.5	17.3	9.1	30.9	8.2	33.0	8.7	32.9	9.0
1	8.5	8.9	10.5	10.0	11.3	8.6	30.2	9.0	31.2	9.1	31.8	9.6
2	8.5	8.8	10.5	9.9	11.3	9.7	20.4	9.8	30.0	11.5	30.7	10.3
3	8.4	8.6	10.5	9.8	11.0	9.6	14.3	10.1	24.3	13.3	26.9	12.9
4	8.4	8.6	10.5	9.7	10.9	9.4	12.3	10.1	17.4	10.1	22.0	10.4
5	8.4	8.4	10.5	9.7	10.9	9.4	12.1	10.1	14.5	10.0	21.0	9.9
6	8.4	8.2	10.5	9.6	10.8	9.3	11.9	10.1	13.3	9.5	17.7	9.4
7			10.6	9.6	10.8	9.3	11.8	9.9	13.2	9.0	15.4	9.3
8			10.6	9.6	10.7	9.3	11.8	9.7	13.0	8.8	14.1	9.0
9							11.7	9.5	12.9	8.6	13.9	9.0
10							11.6	9.4	12.7	8.5	13.6	8.8
11							11.6	9.3	12.7	8.7	13.6	8.7
12							11.6	9.2	12.6	8.5	13.6	8.6
13							11.6	9.1	12.6	8.5	13.5	8.5
14									12.5	8.5	13.5	8.5
15									12.5	8.5	13.4	8.5

largely in more northerly lakes (Crossman 1977; Miller & Menzel 1986b; Strand 1986; Eilers 2008), reservoirs (Wagner & Wahl 2007) and rivers (Younk *et al.* 1996; Gillis *et al.* 2010). Muskellunge have been infrequently monitored with biotelemetry in the southern USA (Brenden *et al.* 2006) or in altered thermal environments such as cooling reservoirs (Henley & Applegate 1982; Younk 1982).

The attraction of temperate fish to heated discharges in winter is well documented (e.g. Barkley & Perrin 1971; Benda & Proffitt 1973; Cooke *et al.* 2004), and muskellunge in Melton Hill Lake behaved similarly. Many researchers concluded that muskellunge were inactive and made only localised movements in winter (Minor & Crossman 1978; Dombeck 1979; Younk *et al.* 1996); however, in all of those studies water temperatures in winter were ≈4 °C or less. It is evident in the present study that adult muskellunge will select water as warm as 19 °C in winter if available. Henley and Applegate (1982) also documented the preference in winter of a single muskellunge for the thermal plume in a South Dakota power plant cooling reservoir.

Most previous studies on the thermal ecology of muskellunge have focused on juvenile fish. The mean temperatures selected by age-2 muskellunge in an Illinois reservoir were 21.7 °C in spring, 28.4 °C in summer and 14.8 °C in autumn (Wagner & Wahl 2007). The warm temperatures occupied during summer in that study were potentially influenced by the narrow temperature range (3 °C) with sufficient dissolved oxygen available. Preferred temperature and optimum temperature of juvenile muskellunge in laboratory settings ranged from 24.0 to 26.7 °C (Coutant 1977; Reynolds & Casterlin 1979; Jobling 1981; Bevelhimer *et al.* 1985; Clapp & Wahl 1996). Jobling (1981) and Wagner and Wahl (2007) proposed that the upper avoidance temperature for juvenile muskellunge was 32–34 °C; whereas the highest water temperature inhabited by subadult or adult muskellunge in the present study was only 27.5 °C, and few fish selected temperatures above 25 °C. The higher preferred and upper avoidance temperatures of juvenile muskellunge in previous studies compared with what larger fish in the present study selected and avoided may reflect an ontogenetic shift in their thermal ecology, which has been noted for other fish species (e.g. McCauley & Huggins 1979; Lafrance *et al.* 2005). Although juveniles were not studied *per se*, this study found that the smallest muskellunge (720–899 mm TL) in summer selected significantly warmer temperatures than the two larger size classes.

The width of the realised thermal niche of muskellunge in Melton Hill Lake (20.5–24.1 °C) agrees closely with the width that Magnuson *et al.* (1979) expressed as a rule-of-thumb (i.e. ≈4°C in a laboratory gradient when measured as the mean ± 1 SD). By definition, that thermal niche in Melton Hill Lake was a 'realised', not 'fundamental' thermal niche (cf. Magnuson & Destasio 1996), but it represents the only approximation in the literature to date of the fundamental thermal niche for adult muskellunge. Similar to what Bettoli (2005) reported for striped bass in Melton Hill Lake, the 'optimum temperatures' for adult muskellunge used in habitat suitability index models (23–24 °C; Cook & Solomon 1987) should be revisited and include cooler temperatures.

Although the influence of dissolved oxygen concentrations on temperatures selected by adult muskellunge in Melton Hill Lake is discounted, habitat use (and temperatures experienced by fish) is often mediated by other factors. For instance, the affinity of muskellunge for cover in the form of woody debris or vegetation is well documented in northern lakes and rivers (Scott & Crossman 1973; Miller & Menzel 1986b; Younk *et al.* 1996). Tagged muskellunge in Melton Hill Lake showed an affinity for nearshore habitats and large woody debris in winter, spring and autumn but moved offshore into deeper waters in June and July 2010 as shallow embayments warmed (Cole 2011). The offshore movements suggested that shallow-water cover had a minimal influence on the temperatures selected by muskellunge in Melton Hill Lake during summer.

Anticipatory responses to changing environmental conditions such as day length have been documented for several fish species, including juvenile muskellunge (e.g. Evans 1984; Chipps *et al.* 2000; Morgan & Metcalfe 2001), and that phenomenon may explain the temperatures selected by muskellunge during periods of rapidly changing reservoir temperatures. Specifically, the temperatures selected by muskellunge in October and November 2010 decreased abruptly as the range of reservoir water temperatures narrowed and declined, even though warmer water closer in temperature to their fundamental thermal niche was available. After several months, the temperatures selected by muskellunge increased abruptly in March 2011 as the reservoir warmed rapidly and fish had the opportunity to select temperatures closer to their fundamental thermal niche. In a laboratory study, seasonal changes in metabolic rates of juvenile muskellunge were independent of temperature (Chipps *et al.* 2000). Such anticipatory responses have long been recognised in laboratory studies and may prepare a fish metabolically for predictable changes in environmental conditions (e.g. Evans 1984). Tagged fish in the present study were free-ranging and several orders of magnitude heavier than the age-0 muskellunge studied by Chipps *et al.* (2000); but the seasonal metabolic compensation observed in that study would help explain, in part, the temperatures selected by tagged muskellunge in Melton Hill Lake in the autumn and early spring.

Finally, the presence (or absence) of forage can influence habitat selection by fish (e.g. Bevelhimer 1996; Sims 2003). The diets of Melton Hill Lake muskellunge have not been examined, and the abundance and distribution of suitable forage system-wide have been described only generally (Cole 2011), thus the role of forage on the habitats and temperatures selected by muskellunge in Melton Hill Lake cannot be critically evaluated. However, forage was likely abundant based on these simple observations: muskellunge in Melton Hill Lake grow very quickly and achieve large sizes. For instance, within 10 years of starting the stocking programme in 1998, muskellunge were reaching lengths and weights of nearly 1200 mm TL and 14 kg (J. Negus, TWRA; unpublished data). Fast growth relative to populations at higher latitudes was also observed for microtagged age-0 muskellunge stocked in late 2009 that grew to 940-990 mm TL when recaptured in 2011 at age 3. Thirteen years after the stocking programme commenced, muskellunge as large as 1295 mm TL and 18.2 kg were captured during electrofishing surveys. These growth rates compare very favourably with the average total lengths achieved by muskellunge throughout North America at age 4 (814 mm), age 10 (1083 mm TL) and age 13 (1165 mm TL; Casselman & Crossman 1986). Although forage may have influenced habitat and temperature selection in some unknown fashion, it is doubtful that low forage availability played any role in the behavior of muskellunge in Melton Hill Lake. The role of forage availability may have influenced the short-term movement of muskellunge into the heated plume during steam plant operations in January 2010; gizzard shad, *Dorosoma cepedianum* (Lesueur) prefer temperatures between 20.5 and 23.0 °C (Dendy 1948; Reutter & Herdendorf 1976), and large shoals were observed in the vicinity of the steam plant when it was operating. However, any large effect of forage availability on the realised thermal niche of muskellunge during May through early August (when the realised thermal niche was estimated) is unlikely because muskellunge were widely dispersed at that time.

Although the work reported herein was conducted at the periphery of the native range of muskellunge, findings on seasonal temperature selection and the fundamental thermal niche of subadult and adult muskellunge should be relevant for muskellunge populations elsewhere in North America. Subspecies of muskellunge have not been designated despite earlier claims arguing for subspecies status (e.g. Trautman 1981) and latitudinal differences in seasonal *in situ* temperature selection by age-2 muskellunge were not evident (Wagner & Wahl 2007).

Managers and anglers in North America have recognised for several decades that high catch-and-release (CR) mortality is not compatible with the management of trophy muskellunge fisheries (Landsman *et al.* 2011). Concerns over CR mortality were evident at Melton Hill Lake before and during this study because it was widely known that muskellunge were attracted to the outfall of the steam plant if it was operating during winter. Those concerns prompted some anglers and managers to lobby (unsuccessfully) in 2010–2011 to place restrictions during winter on live-bait fishing (e.g. requiring the use of circle hooks or banning live-bait fishing entirely; J. Negus, TWRA, personal communication), which has been shown to cause high CR mortality (Margenau 2007). The findings of this movement study fuelled concerns regarding overharvest and CR mortality given that 19 of the 22 tagged muskellunge still at large were tracked to the thermal plume when the steam plant operated briefly in 2011, and most (9 of 17) reports of anglers capturing a tagged fish occurred during the winters of 2010 and 2011 when the steam plant was operating. However, findings from this study also suggested that CR mortality was perhaps not an immediate threat to the fishery in 2011 because only one mortality that could be attributed to CR fishing was observed. That one fish was located in the discharge canal and its lack of movement coincident with intense angling effort during brief steam plant operations in 2011 suggested that it suffered CR mortality. That potential CR mortality represented only 5% of the tagged fish in and around the thermal plume that winter, but a low rate of CR mortality does not always equate to minimal population effects (e.g. Kerns *et al.* 2012). Obviously, the possibly deleterious effects of high CR mortality during winter will be greatly influenced by frequency and duration of steam plant operations. Concerns over unsustainable exploitation or CR mortality due to fish being crowded into a small area are restricted to the winter months because tagged fish were more widely distributed throughout the reservoir in other seasons.

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