

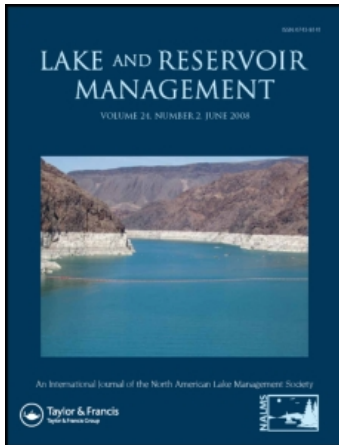
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Temperature and oxygen in Missouri reservoirs

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Abstract

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Vertical profiles of water temperature ($n = 7193$) and dissolved oxygen ($n = 6516$) were collected from 235 Missouri reservoirs during 1989–2007; most data were collected during May–August and provide a regional summary of summer conditions. Collectively, surface water temperature ranged from a mean of ~ 22 C in May to ~ 28 C in July, and individual summer maxima typically were 28–32 C. Most ($\sim 95\%$) reservoirs stably stratify by mid-May, but few are deep enough to have hypolimnia with near-uniform temperatures. Among stratified reservoirs, maximum effective length and maximum depth accounted for 75% of the variation in mixed depth and thermocline depth. Ephemeral, near-surface thermoclines occurred in $\sim 39\%$ of summer profiles and were most frequent in small, turbid reservoirs. Isotherms below the mixed layer deepen during stratification, and the water column is >20 C by August in all but the deepest reservoirs. Most reservoirs showed incipient dissolved oxygen (DO) depletion by mid-May, and by August, 80% of profiles had DO minima of <1 mg/L. Surface area and chlorophyll (Chl) explained 37% of variation in the earliest date of anoxia, and Chl explained $>50\%$ of variation in DO below the mixed layer during summer. Warm summer temperatures and widespread low DO often limit available fish habitat in Missouri reservoirs and compress warm-water fish communities into subsurface layers that exceed their thermal preferences. This study provides a regional baseline of reservoir temperature and oxygen conditions useful for future evaluations of eutrophication and the effects of a warming climate.

Key words: dissolved oxygen, fish habitat, Missouri, oxygen depletion, reservoir, temperature

Water temperature and dissolved oxygen (DO) are 2 water quality variables routinely measured in aquatic systems. In lakes and reservoirs, temperature regulates water movement and seasonal stratification patterns that establish thermal classification schemes (Lewis 1983). Local air temperature, wind fetch, morphology (size and depth), and water clarity collectively influence lake temperature and stratification (Hanna 1990, Demers and Kalff 1993, Fee et al. 1996, Xenopoulos and Schindler 2001). In turn, temperature influences the productivity, biodiversity, and metabolism of aquatic organisms (Brylinsky and Mann 1973, Morin et al. 1999, Allen et al. 2002).

Dissolved oxygen dynamics are affected by stratification and lake trophic state (Nürnberg 1996) and, with water temperature, determine biochemical reactions, nutrient cycling,

and distribution of biota in the water column. These topics have long been the focus of limnological studies worldwide, and a warming climate will affect water quality and biota (Schindler 1997). Despite the profound effect water temperature and DO have on the physical, chemical, and biological characteristics of lakes and reservoirs, few studies have quantified regional patterns.

In this paper we summarize patterns in archived water temperature and DO profiles from a long-term summer inventory of Missouri reservoirs, along with available annual measurements, to document processes and baseline conditions (Jones et al. 2008).

Datasets and analyses

Vertical profiles of water temperature ($n = 7193$) and dissolved oxygen ($n = 6516$) were collected from 226 Missouri

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reservoirs and 9 oxbow lakes during 1989–2007 as part of a statewide monitoring effort (location map given in Jones et al. 2008). For parsimony, we refer to these lentic systems as reservoirs while recognizing that few oxbows are impoundments. During the study, profiles typically were collected from individual water bodies 1 to 141 times (average = 31) near the dam or at the deepest part of oxbow lakes. Most profiles (~80%) were measured in summer (mid-May to mid-August) and represent daylight conditions. Winter data (December–February) comprise less than 3% of the dataset, and most (89%) are from 25 statewide reservoirs sampled on 10 to 18 occasions between February and December 1994 and 15 northwestern Missouri reservoirs sampled for 49 weeks in 2004.

Measurements from 2004 are the most temporally comprehensive dataset available for Missouri reservoirs and illustrate annual patterns in temperature, stratification, and DO. Weather in 2004 was near typical; annual mean temperature and total precipitation were about 1 C and 11 cm, respectively, above the long-term (1895–2009) average (Missouri Climate Center 2011).

Water temperature (C) and DO (mg/L) were measured using calibrated Yellow Springs Instrument meters. Measurements were typically at 1 m intervals from the surface to ~0.5 m above the sediment; additional readings were from the Secchi depth and at 0.5 m intervals within the metalimnion. From 1989 to 1995 and in 2002, measurements were limited to 15 m; otherwise readings extended to 30 m. These limitations precluded collections from the deepest water columns, which are under-represented in the dataset. Water temperature and DO data from Table Rock Lake collected by the US Geological Survey and the University of Missouri Table Rock Lake Long-term Monitoring

Program (Obrecht et al. 2005) show deep-water conditions.

Prior to analysis, water temperature and DO at 0.5 m intervals from the surface to the maximum collection depth were estimated by interpolation. Because many profiles (~39%) lacked a homothermal surface layer, the depth where temperature was 1 C lower than that at 1 m was identified, and a depth 0.5 m deeper was used as an estimate of the epilimnion (mixed depth). This estimate of mixed depth closely agreed with visual location of the epilimnion–metalimnion transition (knee) in temperature–depth plots and was often slightly less than the depth of the maximum temperature gradient (thermocline). Thermocline depth was defined as the depth below which the greatest temperature gradient occurred, excluding the upper 1 m.

Along with a Secchi depth (m) reading, total phosphorus (TP, $\mu\text{g/L}$) and chlorophyll (Chl, $\mu\text{g/L}$) were measured in all surface samples, while dissolved organic carbon (DOC, mg/L) was measured in most samples after 1996. Methods are detailed in Knowlton and Jones (1995) and Watanabe et al. (2009). Reservoir morphology was determined from geographic information system (GIS) analysis (Jones et al. 2004, 2009) or the Dam Safety Data Base (Missouri Department of Natural Resources 2011). Morphological metrics included surface area, maximum basin length, maximum effective length (MEL, greatest uninterrupted straight line distance along the reservoir main stem), and maximum effective width (MEW, greatest uninterrupted straight line distance from shore to shore perpendicular to the MEL axis). Maximum depth was estimated from profile data for basins <30 m and from maps for deeper reservoirs. One-half of the 235 water bodies in this study have surface areas <23 ha and maximum depths <7 m (Table 1). Only

Table 1.—Means and percentiles of morphological reservoir characteristics and May–Aug Secchi depth, mixed depth, thermocline depth (averaged by reservoir) and summer maximum temperatures for 235 waterbodies and 1755 summer datasets. Five reservoirs lacked Secchi data and 2 never stratified.

	Percentiles							
	Mean	Min	10	25	50	75	90	Max
Surface area (ha)	443.0	2.0	5.7	8.9	22.0	69.0	195.0	21,787.0
Maximum length (km)	3.3	0.2	0.4	0.5	1.0	2.0	3.5	145.0
Maximum effective length (km)	1.4	0.2	0.4	0.6	0.9	1.7	2.7	12.9
Maximum effective width (km)	0.6	0.1	0.2	0.2	0.4	0.6	1.1	5.4
Maximum depth (m)	8.5	1.0	3.0	5.0	7.0	9.5	15.0	66.0
Secchi (m)	1.3	0.1	0.4	0.7	1.0	1.6	2.6	4.7
Mixed depth (m)	2.4	1.0	1.4	1.7	2.2	2.8	3.7	6.5
Thermocline depth (m)	3.5	1.3	1.8	2.5	3.4	4.1	5.2	10.9
Summer maximum temperatures								
Surface	29.0	10.3	26.3	27.8	29.2	30.5	31.5	37.7
1 m	28.5	10.4	25.9	27.5	28.8	30.0	31.0	35.0
2 m	27.8	9.9	24.8	26.7	28.2	29.4	30.3	34.8

20% of reservoirs had maximum depths >10 m, and 20% had maximum depths of ≤ 4 m.

Four reservoirs with annual water temperature and DO data were used to illustrate seasonal patterns in stratification. Three (Sterling Price, Forest, Nehai Tonkayla) were sampled in 2004. Annual data for the fourth reservoir (Table Rock) were collected approximately bimonthly during 1996. These reservoirs were selected because they span the range of maximum depths (Sterling Price: 2.5 m; Forest: 11 m; Nehai Tonkayla: 19 m; Table Rock: 66 m) and surface area (Sterling Price: 10 ha; Forest: 572 ha; Nehai Tonkayla: 240 ha; Table Rock 21,787 ha) found in Missouri reservoirs (Table 1).

Individual measurements from profiles collected over the period of record were used for certain analyses and comparisons. For other analyses, surface water temperatures and DO were averaged across reservoirs sampled in a given week or month and are presented as weekly or monthly mean values. Regression models were developed using reservoir means for each of the 235 waterbodies in the dataset. Reservoir means were calculated as the average of summer (May–Aug) geometric means. Data analyses, including correlation and regression (simple, multiple, and stepwise) were performed using \log_{10} transformed data; all DO data were adjusted by adding 1 mg/L to allow zero values in the dataset. Correlation coefficients (r), coefficients of determination (r^2), and root mean squared error (RMSE) are presented as measurements of goodness of fit. Statistical analyses were conducted using SAS (v.9.1).

Results

Water temperature

During 2004, surface water temperature (average of the upper 2 m) in 15 northwestern Missouri reservoirs ranged from 2 C in February to >28 C in July and closely tracked air temperature with little apparent lag, except during subfreezing weather when water remained warmer than air (Fig. 1a). The data show a strong correlation between surface water and air temperature (weekly mean values, $r = 0.95$, $n = 48$; Fig. 1b); during summer, surface water averaged 2.6 C less than maximum air temperature.

Summer surface water temperatures for statewide data ranged from a monthly mean temperature of ~ 22 C in May to ~ 28 C in July and declined to ~ 27 C in August. Maximum surface temperatures were typically >28 C, but rarely >32 C (Table 1). There was a weak negative correlation between maximum water temperature and latitude ($r = -0.14$, $n = 1730$ summer means), amounting to an average difference of ~ 1 C between peak values in northern and southern reservoirs (separated by ~ 4 degrees latitude). Minimum surface

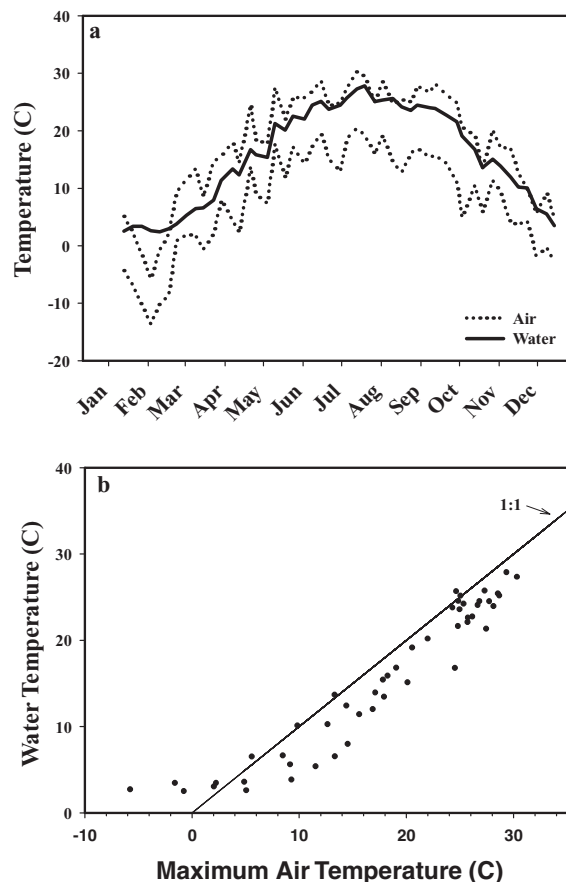


Figure 1.—Relations between air and surface water temperatures (average of the upper 2 m) in 15 northwestern Missouri reservoirs sampled weekly during 2004. (a) Weekly mean surface water temperatures and weekly mean minimum and maximum air temperatures from local climate stations. (b) Relation between weekly mean surface water temperatures and maximum air temperature ($n = 48$).

water temperature in summer averaged ~ 23 C ($n = 1755$) and values were <20 C in $\sim 17\%$ of the dataset.

Most Missouri reservoirs ($\sim 95\%$) thermally stratify during summer. In the shallowest basins (<3 m), however, stratification was rare or ephemeral; 13 (including 7 oxbows) had homothermal profiles in $>75\%$ of the collections. Morphology varied among reservoirs, and a combination of maximum depth and maximum effective length (MEL) explained 52% of variation in the frequency of homothermal conditions (Fig. 2a). These, and other standard dimensions (surface area, maximum length, maximum effective width), are strongly intercorrelated, and alternate combinations explained similar variation in mixing frequency. Interestingly, while most Missouri reservoirs stably stratify, the analysis by Gorham and Boyce (1989) shows that natural lakes with similar depth and length would not stratify (reference line in Fig. 2a).

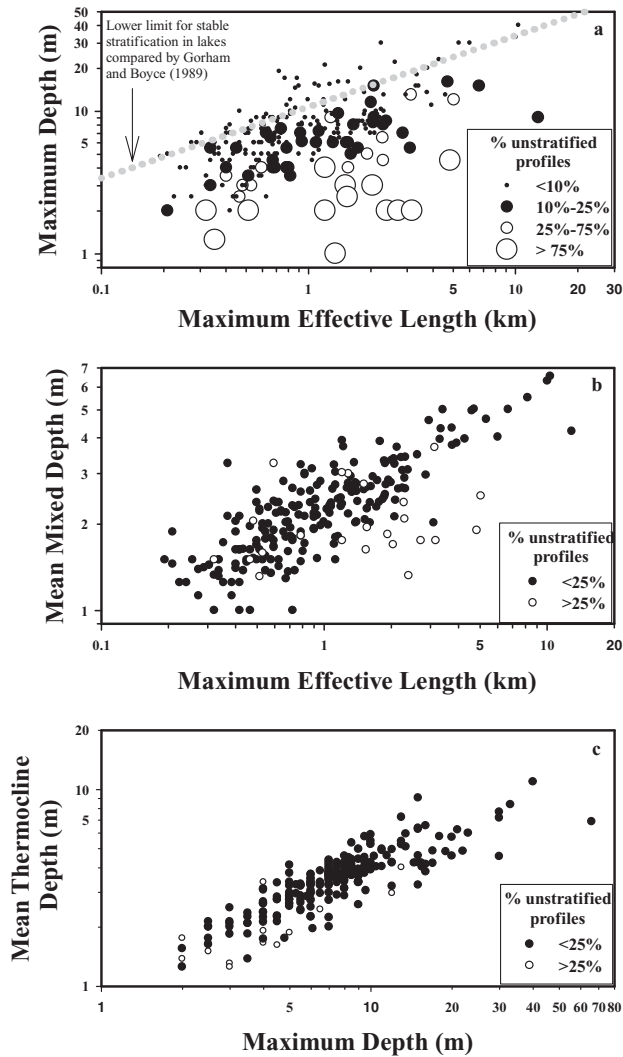


Figure 2.—Relations between maximum depth, maximum effective length, and proportion of unstratified profiles during May–Aug. (a) Maximum depth versus maximum effective length ($n = 231$). The reference line was found by Gorham and Boyce (1989) to separate north-temperate natural lakes with and without stable stratification. (b) Mean mixed depth vs. maximum effective length ($n = 229$). (c) Mean thermocline depth vs. maximum depth ($n = 229$).

About 39% of all summer profiles ($n = 5755$) had temperature gradients >0.2 C/m between the surface and 1 m, conditions indicative of ephemeral near-surface thermoclines. About 15% of profiles had surface gradients >1 C/m. Similar to Canadian lakes (Xenopoulos and Schindler 2001), the incidence of near-surface gradients decreased with increasing reservoir dimensions and increasing water clarity. For reservoirs with ≥ 10 summer profiles ($n = 159$), frequency of gradients >0.2 C/m was negatively correlated with log-transformed values of maximum depth ($r = -0.34$), MEL ($r = -0.29$), MEW ($r = -0.33$), surface area ($r = -0.24$), and Secchi depth ($r = -0.22$).

Averaged by reservoir, summer mixed depth (epilimnion) ranged from 1 to 6.5 m (median 2.2 m; Table 1). Mixed depths may overestimate recent mixing because in 60% of July–August profiles ($n = 2207$) DO at the mixed depth was >0.5 mg/L less than at 1 m. Thermocline depth ranged from 1.3 to 10.9 m (median = 3.4 m) and averaged 1.5 m deeper than mixed depth (among profiles with maximum gradients >1 C/m, $n = 5451$). Both average mixed depths and thermocline depths (Table 1) were strongly correlated with reservoir dimensions, and the fit was improved by limiting data to reservoirs that were stratified in $>75\%$ of profiles (stably stratified dataset). Variation in mixed depth was explained by both MEL (57% in the full dataset, and 68% in the stably stratified dataset; Fig. 2b) and by maximum depth (Z_{\max} , $>72\%$ of variation in both datasets; Fig. 2c). In stepwise multiple regression, a combination of MEL and Z_{\max} accounted for 75% of variation in mixed depth and thermocline depth in the stably stratified dataset, so that:

$$\begin{aligned} \text{Mixed Depth}_{\log 10} = & 0.138 + 0.268 (\text{MEL}_{\log 10}) \\ & + 0.241 (Z_{\max} - \log 10), \end{aligned} \quad (1)$$

($r^2 = 0.75$, RMSE = 0.081, $p < 0.01$, $n = 202$), and

$$\begin{aligned} \text{Thermocline Depth}_{\log 10} = & 0.163 + 0.10 (\text{MEL}_{\log 10}) \\ & + 0.434 (Z_{\max} - \log 10), \end{aligned} \quad (2)$$

($r^2 = 0.75$, RMSE = 0.076, $p < 0.01$, $n = 202$). Secchi depth and DOC provided $<1\%$ improvement in these models. This finding contrasts with studies showing water clarity is a strong correlate of mixed depth (Fee et al. 1996).

In 2004, stratification began in early to mid-April (Fig. 3a–c) and, based on seasonal temperature gradients in the metalimnion (Fig. 4a), this period likely approximates the onset of annual stratification in many Missouri reservoirs. Summer data suggest nearly all reservoirs were stratified at the time of the first sample in mid-May, with maximum metalimnetic temperature gradients >3 C/m (Fig. 4a). Stability of stratification increased during mid-summer and declined during August–September (Fig. 4a). Few Missouri reservoirs are deep enough to have a hypolimnion with near-uniform temperature. In more than one-half of sampled reservoirs ($n = 126$), temperature gradients below the thermocline were always >1 C/m. Only 14% ($n = 32$) of the reservoirs, all with maximum depths >8 m, had homothermal hypolimnia in $\sim 50\%$ of summer profiles.

During summer, isotherms deepened (Fig. 3), and temperatures in the upper 2 m of the metalimnion increased by about 10 C, from ~ 14 to 24 C (Fig. 4b). Warming in the deep strata of large reservoirs with controlled discharge during summer varied with outlet design. In those where hypolimnetic discharge is replaced by warmer flow from shallower strata (e.g., Table Rock Lake and Lake of the Ozarks) there is

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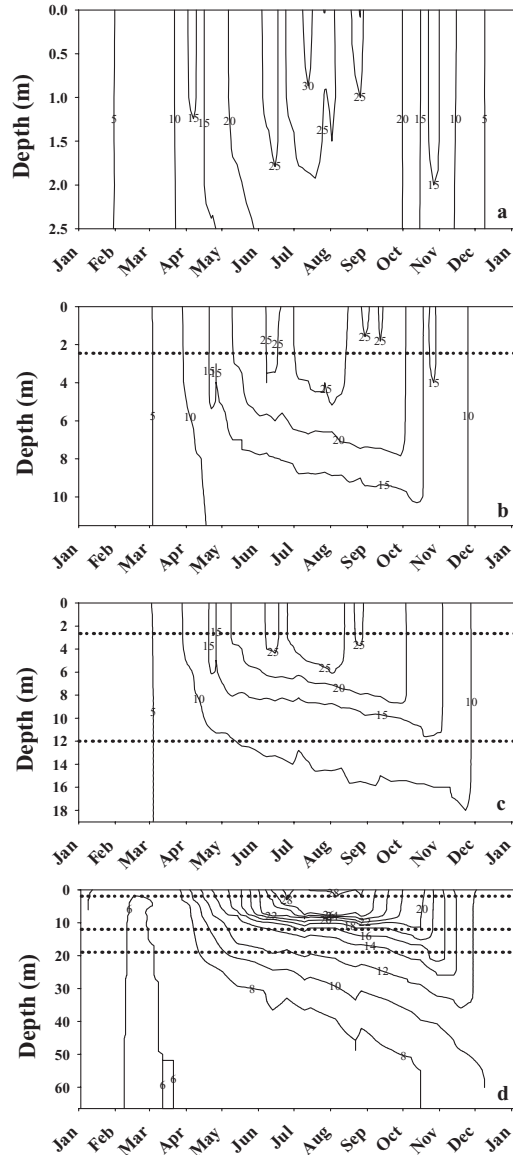


Figure 3.-Temperature (C) isopleths for select Missouri reservoirs: (a) Sterling Price in 2004; (b) Forest in 2004; (c) Nehai Tonkayla in 2004; and (d) Table Rock Lake in 1996. Dotted lines in panels b–d denote maximum depth of reservoirs in the preceding panels. Corresponding dissolved oxygen isopleths are shown in Figure 8.

a strong relation between warming and discharge. In Table Rock Lake (Fig. 5) temperatures at 20 m increase ~ 1 C/month during summer ($n = 31$), while in Lake of the Ozarks this increase was ~ 4 C/month ($n = 10$). In contrast, in deep reservoirs with surface outlets or diversion berms, temperatures at 20 m increased by <0.25 C (e.g., Mark Twain and Stockton) to ~ 0.7 C/month (e.g., Pomme de Terre).

Shallow depths in many Missouri reservoirs and discharge of hypolimnetic water from deep reservoirs results in warm

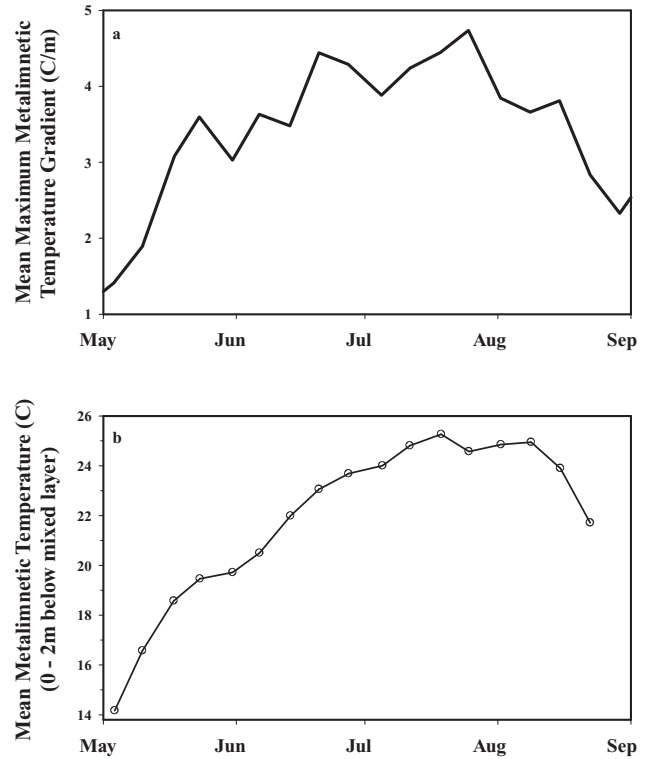


Figure 4.-Seasonal patterns in metalimnetic temperatures averaged by week through all years and all reservoirs: (a) mean maximum temperature gradient in the metalimnion; and (b) mean temperature in the metalimnion (0–2 m below the mixed layer).

bottom temperatures during summer. In August, nearly 60% of profiles from reservoirs with depths ≤ 7 m ($n = 788$ profiles) had no bottom water <20 C, and 86% of profiles had no bottom water <15 C (Fig. 6). Only 9% of all August profiles ($n = 1220$) had bottom water <10 C. Bottom temperatures in August were broadly related to depth of the profile

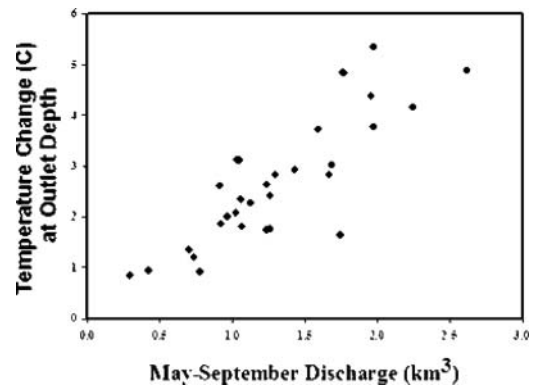


Figure 5.-Change in water temperature in Table Rock Lake at the outlet depth between May and Sep 1975–2005 in relation to reservoir discharge during the same period (insufficient data for 1990).

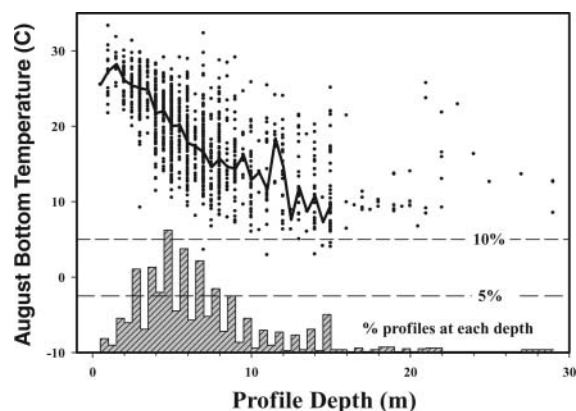


Figure 6.—August temperatures at the reservoir bottom (or at the deepest depth measured) versus profile depth and the percentage of all profiles in each depth increment ($n = 1220$ profiles). The solid line is the median temperature for a given depth.

(Fig. 6); however, the deepest water, in the thalweg near the dam, represents a small fraction of the total reservoir volume. In Table Rock Lake, for example, the deepest third of the water column accounts for <5% of the average volume. Simply put, not much impounded water in Missouri reservoirs is <20 C during August.

Most reservoirs sampled in 2004 were homothermal by late September (Fig. 3a–c), although reservoirs with deep basins (~19 m) did not fully destratify until late November. Table Rock, located on the southern border, is the deepest Missouri impoundment (66 m) and often remains stratified into December (Fig. 3d). Nearly all northern Missouri reservoirs have complete ice cover intermittently during most winters, while large reservoirs in southern Missouri seldom, if ever, freeze in the lower reaches near the dam.

Dissolved oxygen

Dissolved oxygen in the mixed layer of Missouri reservoirs inversely tracks seasonal water temperatures and typically more than doubles between summer minima and winter maxima. Data from 2004 indicate mean DO peaked at ~15 mg/L under the ice in February, and values were below 5 mg/L in August (Fig. 7). Surface DO was often undersaturated relative to temperature; more than one-half of surface measurements (56%, $n = 6350$) were <95% of saturation and 21% were <75% of saturation. Supersaturation, likely the result of photosynthesis, occurred in some 25% of surface measurements; in nearly all cases where DO was $\geq 150\%$ of saturation, Chl was $>10 \mu\text{g/L}$. There was no simple relation between DO and Chl because most undersaturated observations also occurred at high Chl.

Hypolimnetic oxygen depletion is common in Missouri reservoirs; all showed reduced DO during stratification. The

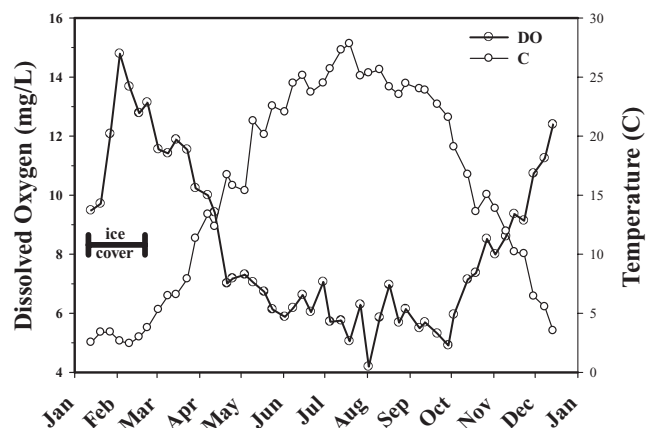


Figure 7.—Weekly mean temperature (C) and dissolved oxygen (DO) (upper 2 m) for 15 northwestern Missouri reservoirs in 2004.

timing, depth, and extent of hypolimnetic anoxia (<1 mg/L) varied among reservoirs; initial anoxia occurred anytime from May (Fig. 8a–b) to late summer (Fig. 8c–d), with minimum depth of anoxia ranging from <2 to >30 m (Fig. 8).

Most reservoirs showed incipient oxygen depletion in the first summer profile (mid-May; e.g., Fig. 8a–b). Below the mixed layer, DO saturation averaged only 44% in late May ($n = 758$ profiles) and declined to 16% by mid-August ($n = 687$ profiles). About 65% of all May profiles had DO <4 mg/L and 42% had <1 mg/L; the same percentages for August profiles were 90% and 80%, respectively. Collectively, these data suggest oxygen depletion is common during summer stratification.

In reservoirs with ≥ 4 profiles in a given summer ($n = 137$), anoxia was first measured from late May to late summer. Onset of anoxia was a general function of basin dimensions, with depletion occurring earliest in small, shallow reservoirs. Surface area (\log_{10} transformed) explained 24% of variation in the mean first date of anoxia. On average, a reservoir of 10,000 ha would become anoxic about 4 weeks later than one of 10 ha. Trophic state variables (TP, Chl, and Secchi) also showed weak ($r < 0.4$, $p < 0.05$) correlations with anoxia, suggesting enrichment speeds the onset of anoxia. In multiple regression analysis, a combination of surface area ($\text{Area}_{\log_{10}}$) and Chl ($\text{Chl}_{\log_{10}}$) explained 37% of variation in the earliest date of anoxia:

First anoxia (week of the year)

$$= 23.8 + 1.25(\text{Area}_{\log_{10}}) - 1.86(\text{Chl}_{\log_{10}}), \quad (3)$$

($r^2 = 0.37$, RMSE = 1.57, $p < 0.01$, $n = 137$). This model shows a weak effect of trophic state; a 10-fold increase in Chl would accelerate the onset of anoxia by <2 weeks.

Nonetheless, trophic state had a large influence on DO below the mixed layer. Using averages for reservoirs with

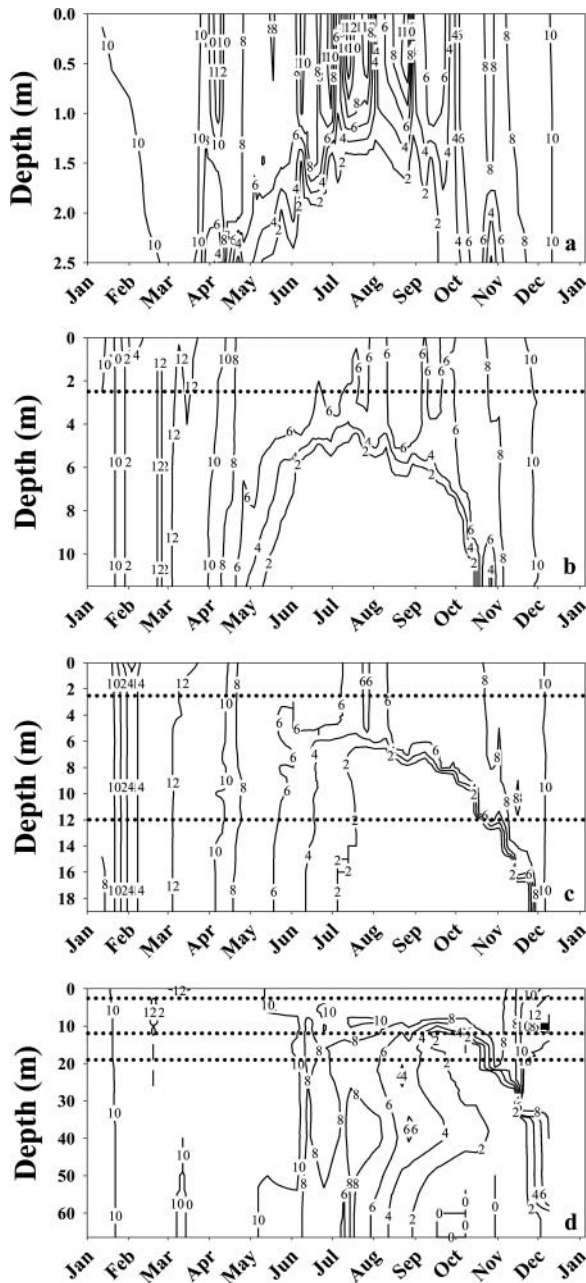


Figure 8.—Dissolved oxygen (mg/L) isopleths for select Missouri reservoirs: (a) Sterling Price in 2004; (b) Forest in 2004; (c) Nehai Tonkayla in 2004; and (d) Table Rock Lake in 1996. Dotted lines in panels b–d denote maximum depth of reservoirs presented in the preceding panels. Corresponding temperature isopleths are shown in Figure 3.

≥ 4 profiles in a given month, variation in $\text{Chl}_{\log 10}$ explained 56% of variation in DO ($\text{DO} + 1_{\log 10}$) below the mixed layer in June, and 50–53% in May, July, and August (Fig. 9). A combination of Chl and day-of-the-year ($\text{DOY}_{\log 10}$) accounted for 68% of variation in monthly mean

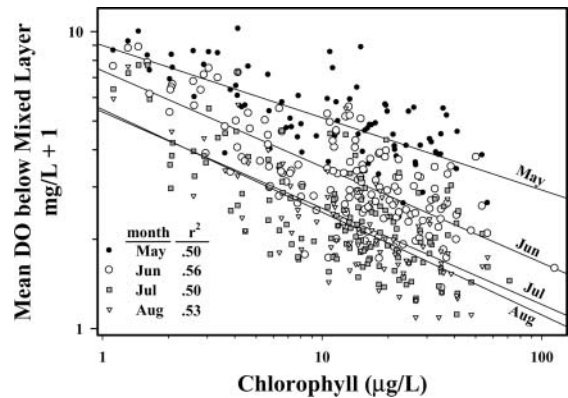


Figure 9.—Mean dissolved oxygen (DO) for all depths below the surface mixed layer versus chlorophyll concentration averaged by reservoir and month across all summers. Oxygen measurements were increased by 1 mg/L to permit \log_{10} transformation.

DO below the mixed layer:

$$\text{DO} + 1_{\log 10} = 4.64 - 0.31 (\text{Chl}_{\log 10}) - 1.70 (\text{DOY}_{\log 10}), \quad (4)$$

($r^2 = 0.68$, $\text{RMSE} = 0.12$, $p < 0.01$, $n = 449$). Surprisingly, morphological variables including surface area, depth, MEL, and thickness of the strata below the mixed layer had much less effect on DO than Chl. In stepwise regression, no variable added more than 3% to model 4.

Metalimnetic DO maxima with values > 1 mg/L greater than the surface layer were found in $\sim 6\%$ of profiles. Only 33 reservoirs showed metalimnetic DO peaks more than once, and occurrence was strongly correlated with mean Secchi depth ($r = 0.74$). In 2 Ozark reservoirs with mean Secchi depth > 4 m, metalimnetic peaks were common (72% of profiles). Light penetration did not always result in DO peaks; in May–August profiles where Secchi depth was below the mixed layer ($n = 733$), DO at the Secchi depth averaged 89% of saturation, and metalimnetic maxima were detected in 15% of profiles. It seems respiratory oxygen consumption usually exceeded photosynthetic evolution even in these lighted metalimnia.

Temperature/oxygen squeeze

High surface water temperatures and subsurface anoxia during summer limits optimal fish habitat in Missouri reservoirs. During summer, strata with relatively cool temperatures are sufficiently DO-deficient to stress intolerant species. In July–August, strata with temperatures cooler than 20 C had $\text{DO} < 1$ mg/L in 76% of all measurements, and DO was < 4 mg/L in 89%. In strata with temperatures cooler

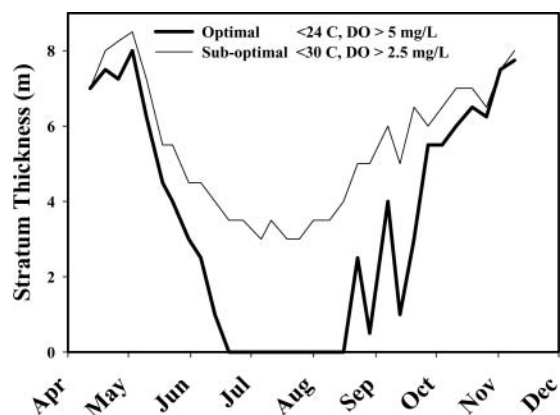


Figure 10.—Median thickness of strata with optimal and suboptimal conditions for fish calculated by week-of-the-year through all years and all reservoirs. Optimal: $<24\text{ C}$, $>5\text{ mg/L}$ dissolved oxygen (DO); suboptimal: $<30\text{ C}$, $>2.5\text{ mg/L}$ DO.

than 25 C , these proportions were 64 and 78%, respectively. In profiles with $>6\text{ mg/L}$ DO, water temperature averaged 26.5 C , with 40% of observations warmer than 28 C . Even the mixed layer showed DO depletion; among reservoirs with ≥ 10 profiles during June–August ($n = 141$), 87% had $<5\text{ mg/L}$ DO in the mixed layer at least once, and the minimum temperature was $>27\text{ C}$. On average, low DO in the mixed layer occurred in 13% of June–August profiles and was negatively correlated with latitude ($r = -0.66$).

For many warm-water fish species, optimal conditions broadly include temperatures cooler than 24 C with $\text{DO} > 5\text{ mg/L}$ (Ellis 1937, Matthews et al. 1985, Headrick and Carlisle 1993). In most Missouri reservoirs this temperature and DO combination is not present for several weeks during summer (Fig. 10), and fish are relegated to the suboptimal warmer mixed layer ($<30\text{ C}$ and $>2.5\text{ mg/L}$ DO). The average thickness of the mixed layer from mid-July through late August is between 30 and 50% of the maximum depth (mean = 41%) and accounts for more than one-half the volume of most reservoirs in this study. This summary suggests suboptimal conditions characterize available habitat in most reservoirs during summer stratification.

Discussion

Most Missouri reservoirs stably stratify during summer as a consequence of regimes that grade from dimictic in the north, with ice cover during part of winter, to warm monomictic circulation prevailing in the south. The pattern reflects the approximate 3 C difference in north–south mean annual air temperature (~ 10 vs. $\sim 13\text{ C}$) and is consistent with findings in other northern hemisphere lakes where dimictic and monomictic stratification regimes would occur

across this temperature gradient (Demers and Kalff 1993). Ice phenology records are incomplete but, as documented elsewhere, the timing, duration, and southerly extent of ice cover in Missouri reservoirs shifts with interannual differences in winter severity (Assel 2005). In most Missouri reservoirs, the onset of stratification in April and turnover in September is generally consistent with empirical models for temperate lakes based on air and hypolimnetic temperatures (Nürnberg 1988, Demers and Kalff 1993).

The distinguishing feature of the mostly shallow Missouri reservoirs is that they are quite warm during summer stratification. Surface waters are often warmer than 28 C , and incidence of ephemeral near-surface thermoclines closely matches that found in other temperate lakes (Xenopoulos and Schindler 2001). These reservoirs have strong thermal gradients that extend through the water column in summer, and few have a homothermal hypolimnion. The isotherms below the mixed layer characteristically deepen during stratification, resulting in most of the impounded water being $>20\text{ C}$ by late summer.

Several published studies have quantified relations between surface dimensions (MEL or area) and mixed depth and/or thermocline depth (Cruikshank 1984, Gorham and Boyce 1989, Hanna 1990, Fee et al. 1996). When compared with natural lakes characterized in these models, Missouri impoundments are shallow relative to their surface area, and most models overestimate observed mixing and maximum depth. For example, a global model of the relation between maximum depth and maximum surface length (Gorham and Boyce 1989) over-predicts depth in Missouri reservoirs 5.7-fold (32 m) on average. The model by Cruikshank (1984), based on maximum depth from the Experimental Lakes Area (ELA) in Canada (2.4–33 m), predicts mixed and thermocline depths in Missouri reservoirs with average differences (observed–predicted) of only 0.13 m and 0.0005 m, respectively. Models based on fetch and area from the ELA lakes, however, over-predicted mixing by ~ 2 m. Compared with ELA lakes of similar surface area or MEL (Cruikshank 1984), Missouri basins are about half as deep but have similar relations between both MEL and surface area, and between mean and maximum depth.

Many natural lakes that are shallow relative to their surface area and with similar dimensions to Missouri reservoirs would not stratify (Fig. 2a; Gorham and Boyce 1989). An explanation for this difference is that Missouri reservoirs are impounded in the valleys of erosional topography, and many are located in public lands with forested riparian zones; both features potentially reduce wind exposure and favor stratification of shallow water bodies (Demers and Kalff 1993, France 1997). Also, empirical models from the literature are largely based on lakes in cooler climates than Missouri. Warmer winters, modest ice cover, and earlier springs likely

contribute to earlier stratification and shallower mixed layers than in cool climates. Warm summers also contribute to shallow mixing and strong metalimnetic thermal gradients (Snucins and Gunn 2000).

Another factor contributing to stratification is that most Missouri reservoirs have limited water clarity; median Secchi depth is <1 m (Jones et al. 2008). Among Canadian lakes <500 ha, Fee et al. (1996) found mixed depth strongly related to water clarity; adjusted for surface area, mixed depth increased by ~4 m between the least and most transparent lakes. In the Missouri data, water clarity had virtually no effect on mixing depth once lake dimensions were considered (models 1 and 2 in this paper). Average light transmission in ~80% of Missouri reservoirs is between 5 and 35%/m, with more than one-half <21%/m (Watanabe et al. 2009). In contrast, the median value in the Canadian dataset was 55%/m. The Canadian model shows that the difference in light transmission between 21 and 55%/m would result in a 2 m difference in mixing depth. Nonalgal seston, chiefly clay minerals, accounts for much of this difference (Jones et al. 2008, Jones and Hubbart 2011) and likely contributes to shallow mixing in Missouri water bodies relative to their surface area.

Most Missouri reservoirs are mesotrophic or eutrophic (80%; Jones et al. 2008) with sharp clinograde oxygen distribution during much of summer stratification. Noteworthy in these survey data, DO saturation of <50% is common in May (Fig. 8), and by August ~80% of profiles show anoxia in the water column. Trophic state, measured as Chl, has a weak effect on the onset of anoxia during summer stratification (model 3 in this paper) but a stronger influence on DO below the mixed layer (model 4). These regional relations suggest that, despite allochthonous organic inputs to these impoundments (Jones and Knowlton 2005), the effect of autotrophic processes on DO below the mixed layer are strong enough to stand out among other sources of variation. The findings are consistent with empirical patterns from productive lakes located worldwide (Nürnberg 1996).

Warm summer temperatures and widespread low DO often limit available fish habitat in Missouri reservoirs and compress warm-water fish communities into subsurface layers that exceed their thermal preferences (Fig. 10). Suboptimal conditions are common in productive reservoirs throughout the Midwest and South (Coutant 1985, Matthews et al. 1985). Our analysis found unfavorable conditions in late summer in more than one-half of the volume of water impounded statewide. Physiology, prey abundance, and social interactions can be affected by this restriction, causing reduced fish growth and condition; in extreme cases, loss of optimal thermal–oxygen niche space results in summer mortality (Matthews 1985). The temperature–oxygen squeeze can also constrain diel vertical migration patterns of zooplankton to marginal habitats, resulting in feeding at

greater light intensities and increased predation (De Stasio et al. 1996). Summer thermal and DO conditions are known to constrain the growth of white crappies (*Pomoxis annularis*) in most Missouri reservoirs (Hayward and Arnold 1996, Bajer et al. 2007) with potential effect on other fish communities.

Extensive literature describes the effect of climatic warming on freshwater ecosystems and expected interactions with other anthropomorphic stresses such as eutrophication (e.g., Magnuson et al. 1997, Schindler 1997). Among the projected changes in lakes are less frequent ice cover, temperature increases in the mixed layer during summer, sharper thermoclines, and longer summer stratification, resulting in less oxygen deep in the water column and greater nutrient release from sediments. These changes in the physical and chemical characteristics of lakes will directly affect the composition and productivity of biota. Zoological boundaries also will shift in response to habitat change in the water column and longer growing seasons. Projections are that climate warming will be extreme in Missouri and result in loss of warm-water fish habitat in streams as thermal tolerances are exceeded (Eaton and Scheller 1996). The potential impact of climate warming would presumably also alter warm-water fish communities in reservoirs through modifications in temperature–oxygen squeeze within the water column.

This holistic analysis of archived temperature and oxygen profiles provides an overview of current conditions and further documents the status of Missouri reservoirs (Jones et al. 2008). Such information has value for assessing the response of these impoundments to potential changes from anthropomorphic alterations of watersheds and climate warming.

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