The Role of Metalimnetic Hypoxia in Striped Bass Summer Kills: Consequences and Management Implications

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Abstract.—Historically, striped bass *Morone saxatilis* summer kills have been attributed to two mechanisms: stressors associated with crowding when striped bass are confined in isolated, cool refuges; and thermal stress or energetic deficit when hypolimnetic hypoxia (dissolved oxygen less than 2 mg/L) forces them into high-temperature surface waters. Here, we present observations suggesting that a third mechanism may account for some of these striped bass mortality events. During summer stratification, many relatively deep southeastern reservoirs develop hypoxia in the metalimnion, as well as near the bottom, isolating a layer of oxygenated hypolimnetic water between them. As these hypoxic zones expand in thickness and severity of oxygen depletion, the oxygenated layer between them shrinks both horizontally and vertically, and its oxygen content declines. Evidence suggests that striped bass summer kills can occur when fish are trapped in this isolated layer and its oxygen concentration declines below 2 mg/L or disappears altogether. The presence of coolwater forage fish such as alewife *Alosa pseudoharengus* or blueback herring *A. aestivalis* may increase the risk of striped bass kills by attracting them into the hypolimnetic oxygenated layer where they may become trapped. We draw upon examples from two southeastern reservoirs to illustrate this phenomenon, and discuss its implications for reservoir fisheries management, as well as possible approaches to minimize or avoid impacts.

Introduction

Over the past 50 years striped bass *Morone saxatilis* fisheries have been established in hundreds of reservoirs throughout much of the United States (Van Horn 2013; Gustaveson and Blommer 2013; both this volume). However, the success of these fisheries has not been uniform; high variability in growth among sys-
tems (Wilson et al. 2013, this volume) and the occurrence of summer mortality events in many reservoirs (Matthews 1985) have posed vexing problems for fishery managers. These puzzling observations led Coutant (1985) to develop and publish the “temperature–oxygen squeeze” hypothesis, suggesting that many otherwise paradoxical observations concerning growth and survival of striped bass in different systems could be explained by interactions between habitat conditions and striped bass physiological requirements. Coutant (1985) defined suitable summer habitat for striped bass as having water temperatures of 18–25°C and dissolved oxygen (DO) concentrations greater than 2–3 mg/L, and suggested that when this habitat becomes limited or unavailable it can result in stress, reduced growth, and mortality.

In many reservoirs, striped bass avoid unsuitable habitat that develops due to warming of surface waters and deoxygenation of hypolimnetic waters as summer progresses by crowding into confined refuge areas such as springs, cool stream inflows, or uplake tailraces. If these refuges persist throughout the summer, are large enough, and contain sufficient food, they can benefit striped bass by providing suitable habitat for growth and survival (e.g., Watts Bar Reservoir, Tennessee, Cheek et al. 1985; Lake Seminole, Georgia–Florida, Van Den Avyle and Evans 1990; Robert S. Kerr Reservoir, Oklahoma, Wilkerson and Fisher 1997; Lake Murray, South Carolina, Schaffler et al. 2002). However, Coutant (1978, 1985) pointed out that even with the existence of a persistent refuge, striped bass mortality could still occur due to depletion of or segregation from food resources, increased harvest vulnerability, disease, and other stressors related to crowding. He documented examples of such stress and mortality in Cherokee Reservoir, Tennessee (Coutant 1978, 1985). Thus, issues associated with confinement in refuge habitats represent one mechanism known to account for some striped bass summer mortality events.

Coutant formulated his hypothesis based on telemetry observations of striped bass behavior in systems where suitable habitat, at least in refuges, was available throughout the summer (Coutant 1985 and 2013, this volume). However, striped bass populations have been established in many reservoirs where such habitat does not exist for extended periods during the summer. Coutant (1985) inferred from his observations that under these circumstances, striped bass would choose to occupy warmer water to avoid DO less than 2 mg/L, a prediction amply supported by subsequent studies (Matthews et al. 1985; Farquhar and Gutreuter 1989; Thompson et al. 2010; Coutant 2013). He suggested that prolonged exposure to warmer water would likely cause mortality of adult striped bass, either directly due to thermal or respiratory stress or indirectly by causing them to stop feeding and die of starvation.

Over the past 25 years, however, studies in reservoirs where habitat traditionally considered suitable is not present for part of the summer have revealed a wider range of responses in growth, condition, and survival of striped bass than predicted by Coutant’s (1985) original hypothesis. Thompson et al. (2010) demonstrated that when hypoxia (DO less than 2 mg/L) forced striped bass into warmer water, they consistently moved to the top of the oxycline, sometimes occupying relatively high temperatures (27–30°C) for several weeks to several months. Yet fish in many of these reservoirs continue to survive, feed, and grow, although maximum sizes attained are limited (Matthews et al. 1985; Farquhar and Gutreuter 1989; Davias 2006; Thompson et al. 2010; Thompson and Rice 2013, this volume). However, significant striped bass mortality events are occasional or even common occurrences in other reservoirs with similar summer conditions (Matthews 1985).

Recent evidence suggests that these inconsistent growth and mortality patterns among reservoirs lacking summer thermal refuges are related to differences in food availability (Davias 2006; Thompson 2006; Thompson and Rice 2013). Striped bass forced into warm water overlap spatially with warmwater prey
such as threadfin shad *Dorosoma petenense* and gizzard shad *D. cepedianum*, which commonly dominate the forage base in such systems (Schael et al. 1995; Thompson et al. 2010). Although exposure to high summer temperatures will increase metabolic costs (Hartman and Brandt 1995), the net effect of metabolic costs and food consumption rates can span a wide continuum depending on food availability, ranging from good growth if consumption rates are sufficient to compensate for high costs to poor growth and condition or even mortality if low food consumption results in an energy deficit.

Some striped bass summer mortality events do appear to be due to starvation or bioenergetic deficit. For example, Zale et al. (1990) found that common summer mortality events in Keystone Reservoir, Oklahoma occurred when hypoxia forced prolonged exposure of striped bass to 28–29°C; based on a sharp decline in angling success once temperatures reached 27°C, they inferred that mortality was caused by cessation of feeding and subsequent malnutrition. Dead striped bass from summer mortality events are rarely collected or necropsied, but in several cases, examinations have revealed enlarged and darkened gallbladders, indicating that the fish had not been feeding recently (Matthews 1985). Thus, in reservoirs without any thermal refuge, a severe energetic deficit resulting from the combined effects of limited food availability and elevated metabolic demands constitutes a second mechanism accounting for some summer mortality events.

However, we have observed some striped bass summer mortality events that cannot be adequately explained by complications of crowding in persistent thermal refuges or energetic deficit. The fish that die do not exhibit unusually poor condition or other signs of malnutrition or disease. These kills typically include the full size range of adult striped bass in the population, whereas many other die-offs are dominated by large (5–9+ kg) individuals (Matthews 1985), which are more likely to experience energetic constraints (Kitchell 1983; Hartman and Brandt 1995). Though many mortality events tend to occur later in the summer (mid-August through September; Matthews 1985; Zale et al. 1990), these kills generally occur earlier in the summer before temperature and DO conditions throughout the reservoir are at their worst. They do not continue, even though habitat conditions remain poor for the rest of the summer, and they also tend to occur in a restricted area of the reservoir, usually in the deepest area near the dam.

In this paper we make the case for a third mechanism, associated with the formation of a hypoxic or anoxic zone in the metalimnion, which may account for these striped bass summer mortality events. We draw upon observations from two reservoirs to illustrate this phenomenon, and discuss its implications for managing striped bass populations as well as possible approaches to minimize or avoid its impacts.

**Metalimnetic Oxygen Minimum Formation and Implications for Fish**

During summer stratification, many reservoirs not only develop a hypoxic zone at the bottom of the hypolimnion that expands upward, but also form a metalimnetic oxygen minimum, or hypoxic zone in the metalimnion, that expands and becomes more severe over time (Figure 1). This phenomenon is a common occurrence in relatively deep reservoirs (Cole and Hannon 1990; Wetzel 2001). It is caused by a variety of mechanisms (often in combination), such as biological oxygen demand from decaying organic material accumulating in the density gradient of the metalimnion, inflow of water with high oxygen demand, timing of hydrologic events in relation to the onset of thermal stratification, or dynamics of midlevel water withdrawals (Cole and Hannon 1990; Ruane et al. 2013, this volume). This hypoxic zone in the metalimnion overlays a hypolimnetic oxygen maximum, or isolated layer of higher oxygen concentrations in the upper hypolimnion (Figure 1). As the hypoxic zones on the bottom and in the met-
alimnion expand in thickness and become more severe over time, the hypolimnetic oxygenated layer between them shrinks both horizontally and vertically as its oxygen content declines. The rate of decline in oxygen concentration will depend on system-specific conditions, but we have observed rates of 0.06–0.1 mg/L/d in some southeastern U.S. reservoirs.

The impact on striped bass of the development of hypoxia in the metalimnion will depend on whether their preferred temperatures occur within the metalimnion or in the oxygenated layer below it. If their preferred temperatures are in the hypolimnetic oxygenated layer but the forage community consists only of species such as threadfin or gizzard shad that prefer warm temperatures, then striped bass must choose between occupying preferred temperatures with no food below the hypoxic metalimnion or warmer-than-preferred temperatures, with food, above the hypoxic metalimnion. Telemetry studies of striped bass indicate that when habitat with preferred temperatures and adequate DO is available, this combination apparently takes precedence over food availability (Coutant 1985). Thus, faced with this choice, striped bass are likely to occupy the oxygenated layer, even if it isolates them from their prey. However, if coolwater prey such as alewife *Alosa pseudoharengus* or blueback herring *A. aestivalis* are present in sufficient numbers along with preferred temperatures and adequate DO (as they are in some reservoirs), the hypolimnetic layer constitutes ideal habitat as described by Coutant’s (1985) original hypothesis. Its long-term value will depend on whether or not these conditions persist until destratification occurs, or if fish can escape through the hypoxic metalimnion if DO in the hypolimnion drops below 2 mg/L.

In many reservoirs, formation of hypoxia in the metalimnion directly overlaps the range of temperatures preferred by adult striped bass. When DO in this zone declines below 2 mg/L,
the role of metalimnetic hypoxia in striped bass summer kills

striped bass will be forced to move into water that is warmer or colder than preferred to remain at sufficient oxygen levels. The distribution of forage fish may influence that decision. In systems with only warmwater forage species, warmer epilimnetic water with available food may be more attractive than colder water with no food. If coolwater forage species like alewife or blueback herring are present in the oxygenated hypolimnetic layer, their presence may entice some striped bass to occupy this layer as well, even though it is cooler than they prefer.

Regardless of why fish choose to occupy the oxygenated layer below the hypoxic zone in the metalimnion, this behavior can be risky given the ephemeral nature of this habitat in many reservoirs. If the severity or thickness of metalimnetic hypoxia poses a sufficient barrier to movement, fish could become trapped in this isolated zone, resulting in striped bass summer kills when DO in this zone declines below critical levels. Below, we present evidence from two southeastern U.S reservoirs to support the premise that formation of a metalimnetic oxygen minimum constitutes an important, but previously overlooked, factor contributing to some striped bass mortality events not adequately explained by other mechanisms.

Lake Norman

Lake Norman, North Carolina is a 12,634-ha reservoir on the Catawba River (Figure 2). Impounded by Cowans Ford Dam in 1963, it has a mean depth of 10.2 m, has a maximum depth of 36.6 m, and has been classified as oligotrophic since the late 1970s (NCDENR 2008). It is operated by Duke Energy and is used to provide cooling water for two steam electric power generation plants, as well as for hydroelectric power generation. Striped bass have been stocked into Lake Norman by the North Carolina Wildlife Resources Commission (NCWRC) since the late 1960s; the annual stocking rate averaged about 7.8 fingerlings/ha until 1988, when it was increased to about 12.4 fish/ha (Waters and McRae 2008). Historically, the forage base and diets of striped bass have been dominated by threadfin shad, with a small contribution from gizzard shad (Lewis 1985; Thompson 2006). Striped bass in Lake Norman grow fairly well through age 3, reaching an average size of about 490 mm total length (TL) and 1.25 kg, but older fish exhibit slow growth and relatively poor condition due to habitat and forage availability limitations (Van Horn et al. 2001; Thompson 2006; Thompson and Rice 2013). Only 6% of the population is age 6 or older (Thompson et al. 2005), likely due to high angling mortality rates of striped bass in southeastern reservoirs (Hightower et al. 2001; Young and Isely 2004; Thompson et al. 2007).

Extensive long-term limnological and fisheries monitoring has been conducted on Lake Norman. From 1997 to 2010, Duke Energy personnel monitored water quality about once a month from September to June and about once a week from July to August at 15 stations (11 along the main channel) throughout Lake Norman (Figure 2), with additional sampling during striped bass mortality events. Some water quality monitoring was conducted in years prior to 1997, but the frequency of data collection varied substantially among years. Temperature, DO, and several other variables are measured with a Hydrolab data sonde at each location, starting at the surface (0.3 m) and continuing at 1-m intervals to 1 m above the bottom.

Long-term data have also been collected on the number of summer striped bass mortalities in Lake Norman. From 1983 to 2010, Duke Energy personnel conducted weekly roving boat surveys to search for floating, dead striped bass. Observers searched all open water and main shoreline areas throughout the main body and major tributary arms of the reservoir from the dam to station 15.0 (Figure 2). All dead striped bass encountered were collected, counted, and their location noted. Surveys were conducted more frequently (typically daily) during striped bass mortality events.

Each September from 1993 to 2010, Duke Energy personnel sampled pelagic forage fish in Lake Norman using a purse seine (9 m deep,
Figure 2. Map of Lake Norman, North Carolina, showing locations of water quality monitoring stations (numbered dots) and primary area of striped bass kills.
118 m long, 4.8 mm mesh), typically set in three main regions of the lake. These samples provided data on the species and size composition of the pelagic prey community in the epilimnion over time.

**2004 striped bass mortality event**

A major striped bass die-off occurred on Lake Norman during the summer of 2004. From July 22 through August 13, Duke Energy and NCWRC personnel collected nearly 2,500 dead striped bass (Figure 3). In contrast, over the previous 20 years, the total number of dead striped bass found in July and August during weekly surveys of the lake averaged 8.75 fish/year (range 0–43). All but about 40 of the fish collected during the 2004 die-off were found within 6 km of the dam (Figure 2).

In 2004, DO began to decline in the metalimnion by early June and metalimnetic hypoxia was well established throughout the main body of the lake by late June, overlaying an oxygenated layer in the hypolimnion in the lower 15 km of the lake (Figure 4). Throughout July, the metalimnion became increasingly hypoxic while the oxygenated area in the hypolimnion declined in thickness, receded down-lake toward the dam, and steadily declined in maximum DO concentration. When the kill began in earnest in late July, only a small, cold (13–14°C) vestige of oxygenated hypolimnion remained with DO slightly above 2 mg/L, separated from the warm (28–30°C), oxygenated epilimnion by a hypoxic layer in the metalimnion 14 m thick, with 7 m less than 0.5 mg/L and 4 m at 0.1 mg/L (Figure 5). Daily collections of dead striped bass increased substantially at the beginning of August as maximum hypolimnetic DO dropped below 2 mg/L, and ended as DO dropped below 0.9 mg/L (Figures 3 and 5). The timing of the mortality event in relation to the decline in hypolimnetic DO concentration immediately behind the dam (Figure 5) suggests that the kill was precipitated by loss of this oxygenated refuge.

Several other lines of evidence also support this hypothesis. Nearly all the dead striped bass were found in a restricted area near the dam, coinciding with the location of the shrinking

**Figure 3.** Number of dead striped bass collected on Lake Norman during the 2004 summer kill. No surveys were conducted on dates without a histogram bar. A total of 17 additional fish were collected prior to the period shown in surveys on 1, 6, 9 and 15 July, and 11 fish were collected in late August.
FigurE 4. Vertical distribution of dissolved oxygen concentrations (contour lines, mg/L) and temperature (shading) along the main channel of Lake Norman from Cowans Ford Dam upstream 25 km on six dates from 28 June to 16 August 2004. Dissolved oxygen and temperature isopleths were estimated in SigmaPlot 12.0 (Systat Software, San Jose, California) using a running average with 0.1 sampling proportion and nearest neighbors bandwidth method.

oxygenated habitat in the hypolimnion. Anglers were catching striped bass in this area at depths just above and below the layer of metalimnetic hypoxia prior to and during the die-off event (B. K. Baker, Duke Energy, personal communication), indicating that at least some striped bass were occupying the oxygenated zone in the hypolimnion. Many of the dead striped bass
were already in an advanced state of decomposition when they appeared at the surface (fish were removed as they were found), consistent with fish dying deep in the water column and floating to the surface after several days.

Had this mortality event been due to starvation or malnutrition, we would have expected disproportionate mortality of the largest individuals in the population because total maintenance costs increase with body size (Kitchell 1983; Hartman and Brandt 1995). However, the size distribution of fish that died did not differ greatly from that of striped bass collected during annual gill-net monitoring (equal lengths of 38-, 51-, 64-, and 76-mm bar mesh) conducted the previous December by Duke Energy and NCWRC biologists (Figure 6) or from similar samples collected 2000–2002 (Thompson et al. 2005). Based on selectivity of the mesh sizes used, fish smaller and larger than 600 mm would have been underrepresented in these samples (McRae et al. 2013, this volume). Yet the fish that died included proportionally fewer smaller and larger fish than in the gill-net sample (Figure 6). Given the higher preferred temperatures of small striped bass (Coutant 1985), these fish may have been more likely to occupy the epilimnion, but if larger fish were more vulnerable to the cause of mortality, they should have constituted a higher percentage of the dead fish.

**2009 striped bass mortality event**

Another striped bass die-off occurred on Lake Norman during the summer of 2009 that was
smaller but otherwise quite similar to the event in 2004. From 3 through 8 August, 358 dead striped bass were collected close to the dam in the same region of the lake as the 2004 kill. Water quality conditions were comparable to 2004, with a pronounced metalimnetic hypoxic zone above an oxygenated hypolimnetic zone that decreased in size and DO concentration through time (Figure 7). Dead striped bass were first observed on Monday, 3 August, during the normal weekly survey, when maximum DO in the hypolimnion was just below 1.0 mg/L (Figure 7); more than half of the dead striped bass in this mortality event were collected on 3 August, so mortality may have started several days earlier. The physical condition and size distribution of fish that died in 2009 were nearly identical to those collected in 2004.
**2010 striped bass mortality event**

During 2010, another major striped bass summer kill occurred on Lake Norman; from 14 July through 9 August, 6,996 dead striped bass were collected in the same region of the lake as during previous die-offs. Hypoxia had already begun to develop in the metalimnion by late May–early June, and by June 28 extended more than halfway up the main channel of the reservoir with at least 4 m of water below 2.0 mg/L DO. By the time the first nine dead striped bass were collected on 14 July, hypoxia in the metalimnion was 9 m thick with 4 m below 0.5 mg/L (Figure 8). However, unlike previous kills, mortality began while maximum DO in the hypolimnion was still 3.0–3.2 mg/L in the lower few kilometers of the reservoir. Four percent of all mortalities were collected in the first 11 d, before maximum DO in the hypolimnion declined to 2.0 mg/L. Biologists monitoring the kill suspected that these early mortalities resulted from catch-and-release mortality due to high angling pressure in the area near the dam where striped bass were concentrated. The kill accelerated on 25 July as DO in the hypolimnion dropped below 2.0 mg/L, overlain by metalimnetic hypoxia 13 m thick with 7 m at or below 0.5 mg/L and 4 m at 0.1 mg/L. Over the next 12 d, daily mortality collections ranged from 148 to 884 fish as DO in the hypolimnion declined to less than 0.6 mg/L.
In order to comply with permitted maximum temperature discharge requirements, Duke Energy withdrew cold water through the lower level intake (LLI) for the McGuire Nuclear Station for 7 d in July 2010 (14 July and 19–24 July). Unlike previous years, this use of the LLI occurred while there was still oxygenated habitat in the hypolimnion. Depth of the LLI (26–30 m) overlaps the depths of maximum DO concentration in the hypolimnion. To determine what impact, if any, water withdrawal through the LLI had on the loss of oxygenated habitat in the hypolimnion, we compared the rate of decline in maximum hypolimnetic DO from mid-June through mid-August in 2010 with the rate of decline over the same period in 2004 and 2009, both years with striped bass die-offs, and 2008, a year with no die-off. In 2004, 2008, and 2009, the average rate of decline in maximum hypolimnetic DO was 0.07 mg/L/d. In 2010, the average rate of decline was also 0.07 mg/L/d, except during the 6-d period of LLI use (19–24 July) when maximum DO in the hypolimnion declined from 3.0 to 2.0 mg/L (0.17 mg/L/d), 0.6 mg/L more than it would have at the average rate. Thus, the effect of withdrawing water through the LLI in 2010 was to cause maximum hypolimnetic DO to become hypoxic (and subsequently nearly anoxic) about 8 d earlier than it otherwise would have. However, because DO levels would have become too low to sustain striped bass anyway, use of the LLI only had a modest effect on when the die-off occurred, not if it would occur.
**Differences in conditions among years with and without striped bass kills**

Given that a metalimnetic oxygen minimum forms in Lake Norman every year but striped bass kills do not occur every year, it appears that fish occupying the hypolimnetic oxygen maximum are able to escape as it becomes hypoxic in some years, but not in others. We examined water quality data from 2000 to 2010 to see if there were any particular characteristics that consistently differentiated the 3 years with summer striped bass die-offs during that period from those without. We focused on conditions at station 1.0 (nearest the dam) on the last sample date when DO in the hypolimnion was still at least 2.0 mg/L, and the first sample date (~1 week later) when maximum DO in the hypolimnion was less than 2.0 mg/L. We quantified a variety of metrics to characterize habitat conditions, including the thickness (m) of hypoxia in the metalimnion at various levels of severity (DO <2.0, <1.5, <1.0, <0.5, and ≤0.1 mg/L), the maximum DO concentration in the hypolimnion, and the thickness (m) of the hypolimnetic oxygen maximum with DO exceeding various concentrations (Table 1). We conducted t-tests to determine if the thickness of metalimnetic hypoxia at each of the five levels of severity listed above differed significantly between years with and without striped bass kills in the period from 2000 to 2010. We used Bonferroni’s adjusted alpha for multiple comparisons (Miller 1981) to constrain the overall alpha to 0.05 across the resulting 10 t-tests.

The extent of severe hypoxia in the metalimnion clearly differentiated conditions during summers with and without striped bass kills in the 11 years we analyzed. On the last sample date when DO in the hypolimnion still exceeded 2.0 mg/L, years with mortality events had significantly thicker zones of DO less than 0.5 mg/L (5–8 m) and at or below 0.1 mg/L (3–5 m) than in years without such events (P < 0.05; Table 1). None of the 8 years without a striped bass die-off had any water in the metalimnion with DO of 0.1 mg/L or less, and only one had any water (3 m) below 0.5 mg/L. In 2004, 2009, and 2010, portions of the metalimnion (3, 1, and 1 m, respectively) were actually below 0.5 mg/L DO for 2 weeks before DO in the hypolimnion declined below 2.0 mg/L. In contrast to the sharp differences in severe metalimnetic hypoxia between years with and without striped bass mortality, total thickness of metalimnetic hypoxia was not a factor. In all the years we analyzed, DO less than 2.0 mg/L formed a thick zone (7–18 m) in the metalimnion before maximum DO in the hypolimnion dropped below 2.0 mg/L (Table 1), but its thickness was not related to striped bass mortality.

These same two metrics also distinguished years with and without striped bass mortality on the first sample date after maximum hypolimnetic DO had declined below 2.0 mg/L. Metalimnetic hypoxia below 0.5 mg/L was present in five of eight nonkill years, but it was significantly thicker (7 m) in years with mortality events than in years without (0–6 m, mean = 2.6 m) (P < 0.05; Table 1). The metalimnetic zone at or below 0.1 mg/L was much thicker in years with mortality (6–7 m) than in nonkill years (0–3 m) (P < 0.05; Table 1). A week later, metalimnetic DO conditions were no longer markedly different between kill and nonkill years, as hypoxia became more severe in both the metalimnion and hypolimnion.

**Potential role of forage fish in Lake Norman mortality events**

A change in the Lake Norman forage fish community may have increased the likelihood of striped bass mortality events in recent years. Historically, the catch in annual epilimnetic September purse-seine samples of the pelagic prey community by Duke Energy personnel (Table 2), as well as the diets of Lake Norman striped bass (Lewis 1985; Thompson 2006), have consisted almost entirely of threadfin shad, with a few gizzard shad. These warmwater species occupy the epilimnion and upper metalimnion almost exclusively while the lake is stratified (Shael et al. 1995; Thompson et al. 2010). In the late 1990s, members of a striped bass angling group intentionally stocked alewives
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<td>7/27</td>
<td>7/26</td>
</tr>
<tr>
<td>Coolest $T$ above $M_{\text{min}}$ with $\geq 2 \text{ mg/L DO}$ (ºC)</td>
<td>24.7</td>
<td>25.8</td>
<td>26.4</td>
<td>25.2</td>
<td>28.2</td>
<td>26.0</td>
<td>25.5</td>
<td>27.0</td>
<td>26.7</td>
<td>26.3</td>
<td>28.7</td>
</tr>
<tr>
<td>$M_{\text{min}} &lt; 2.0 \text{ mg/L DO}$</td>
<td>9</td>
<td>11</td>
<td>13</td>
<td>17</td>
<td>14</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>11</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td>$M_{\text{min}} &lt; 1.5 \text{ mg/L DO}$</td>
<td>9</td>
<td>11</td>
<td>12</td>
<td>15</td>
<td>12</td>
<td>13</td>
<td>8</td>
<td>7</td>
<td>10</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>$M_{\text{min}} &lt; 1.0 \text{ mg/L DO}$</td>
<td>7</td>
<td>8</td>
<td>4</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>$M_{\text{min}} &lt; 0.5 \text{ mg/L DO}$</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>5</td>
<td>7</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>$M_{\text{min}} &lt; 0.1 \text{ mg/L DO}$</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Max DO in $H_{\text{max}}$ (mg/L)</td>
<td>1.4</td>
<td>1.2</td>
<td>1.5</td>
<td>1.6</td>
<td>1.7</td>
<td>1.7</td>
<td>1.9</td>
<td>1.8</td>
<td>1.5</td>
<td>1.7</td>
<td>1.8</td>
</tr>
<tr>
<td>$H_{\text{max}} \geq 1.5 \text{ mg/L DO}$</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>3</td>
<td>9</td>
<td>11</td>
<td>3</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>$H_{\text{max}} \geq 1.0 \text{ mg/L DO}$</td>
<td>4</td>
<td>8</td>
<td>13</td>
<td>10</td>
<td>10</td>
<td>11</td>
<td>15</td>
<td>14</td>
<td>9</td>
<td>12</td>
<td>9</td>
</tr>
</tbody>
</table>
and blueback herring based on the notion that diversifying the prey species community would increase the forage base for striped bass. Alewives were first detected in annual purse-seine samples in 1999 and rapidly became established as a modest component of the forage fish community (Table 2) and of striped bass diets (Thompson 2006).

Hydroacoustic observations in mid-July 2004 showed fish beginning to concentrate in the upper meters of the oxygenated zone in the hypolimnion. To determine their identity, variable mesh gill nets were set (10-, 13-, 19-, 25-, 32-, and 38-mm bar mesh) overnight on 20 and 21 July (just prior to the start of striped bass mortality) in this depth zone (18.3–21.0 m deep) at station 1.0 (Figure 2). The catch confirmed the presence of both alewives (n = 44, mean TL = 119 mm) and blueback herring (n = 4, mean TL = 120 mm), as well as striped bass (n = 2, 545 and 564 mm TL). Other fish collected included 14 juvenile and adult blue catfish Ictalurus furcatus (101–464 mm TL), one white perch Morone americana (224 mm TL), and one gizzard shad (127 mm TL).

Weekly hydroacoustic surveys from the dam to about 3.2 km up the main channel confirmed that fish became increasingly concentrated in the layer of oxygenated hypolimnetic habitat as it declined in DO concentration and receded toward the dam. No fish were observed at these depths in hydroacoustic surveys once DO in the hypolimnion dropped below 0.5 mg/L. Dead alewives were not observed on the surface, but during the 2004 striped bass kill some were collected on water intake screens located just below the water surface at the McGuire Nuclear Station.

During summer 2009, weekly surveys documented a similar pattern of fish concentration in the receding oxygenated habitat in the hypolimnion. On 4 August, during the striped bass

Table 2. Species composition (percent by number) of clupeids collected in annual September purse-seine samples in Lake Norman, 1993–2010. The purse seine sampled the upper 9 m of the water column.

<table>
<thead>
<tr>
<th>Year</th>
<th>Threadfin shad</th>
<th>Gizzard shad</th>
<th>Alewife</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>1994</td>
<td>99.9</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>1995</td>
<td>99.9</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>1996</td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>1997</td>
<td>&gt;99.9</td>
<td>&lt;0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>1998</td>
<td>99.9</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>1999</td>
<td>99.3</td>
<td>0.3</td>
<td>0.5</td>
</tr>
<tr>
<td>2000</td>
<td>87.4</td>
<td>0.2</td>
<td>12.4</td>
</tr>
<tr>
<td>2001</td>
<td>76.5</td>
<td>0.0</td>
<td>23.5</td>
</tr>
<tr>
<td>2002</td>
<td>75.0</td>
<td>0.0</td>
<td>25.0</td>
</tr>
<tr>
<td>2003</td>
<td>82.6</td>
<td>0.1</td>
<td>17.3</td>
</tr>
<tr>
<td>2004</td>
<td>86.6</td>
<td>0.2</td>
<td>13.2</td>
</tr>
<tr>
<td>2005</td>
<td>98.1</td>
<td>0.0</td>
<td>1.9</td>
</tr>
<tr>
<td>2006</td>
<td>94.9</td>
<td>0.0</td>
<td>5.1</td>
</tr>
<tr>
<td>2007</td>
<td>98.3</td>
<td>0.0</td>
<td>1.7</td>
</tr>
<tr>
<td>2008</td>
<td>95.6</td>
<td>0.0</td>
<td>4.4</td>
</tr>
<tr>
<td>2009</td>
<td>91.7</td>
<td>0.0</td>
<td>8.3</td>
</tr>
<tr>
<td>2010</td>
<td>95.4</td>
<td>0.4</td>
<td>4.3</td>
</tr>
</tbody>
</table>
mortality event, we suspended two small-mesh gill nets (4.9 × 15.4 m panels of 6-, 10-, and 13-mm bar mesh) and three larger-mesh nets (25-, 51-, and 64-mm bar mesh, each 1.8 × 100 m) overnight in the remnant of the hypolimnetic oxygen maximum (0.6–0.8 mg/L DO, 21–26 m deep) near Cowans Ford Dam. The small-mesh nets caught 18 alewives (mean TL 155 mm), and 19 blue catfish (428–634 mm TL) were caught in the two largest-mesh nets. Two blue catfish had empty stomachs, but all the others contained alewives (mean 4.3/stomach). No striped bass were caught, but 71% of the documented striped bass mortalities had already been collected by the time these nets were set, so few, if any, striped bass may have remained in the hypolimnion. On 10 August, when maximum DO in the hypolimnion was 0.5 mg/L and 2 d after the last dead striped bass were collected on the surface, a hydroacoustic survey showed no fish in the hypolimnion. The same pattern was observed in 2010, with weekly hydroacoustic surveys documenting an increasing concentration of fish in the shrinking oxygenated hypolimnomic habitat that disappeared when DO levels dropped below about 0.5 mg/L (coinciding with the end of striped bass mortality in 2010). Since alewives became established in Lake Norman, hydroacoustic surveys in years without striped bass mortality have also shown the same pattern of hypolimnetic fish distribution in relation to DO dynamics (D. Coughlan, Duke Energy, personal communication).

During the middle of the 2010 die-off a number of dead striped bass that were collected were dissected and their stomach contents examined. Many of these contained multiple alewives about 150 mm TL (B. McRae, North Carolina Wildlife Resources Commission, unpublished data). No hypolimnetic gill netting was conducted in 2010, but the size and species of prey in these fish were consistent with the size and species of the dominant forage fish collected in the oxygenated portion of the hypolimnion during gill netting in 2004 and 2009. In contrast, summer diets of striped bass collected above the metalimnion are dominated by clupeids less than 90 mm TL (primarily threadfin shad with a small proportion of alewives; Thompson 2006).

Taken together, these observations indicate that introduction of alewives established a coolwater forage species in Lake Norman that consistently inhabited the oxygenated hypolimnetic habitat and provided a food source for striped bass also occupying that zone. Thus, it seems plausible that availability of coolwater prey may have increased the likelihood that some striped bass would choose to occupy this habitat when their preferred temperatures in the metalimnion became hypoxic.

Though the increased frequency of striped bass mortality events over the past decade is consistent with that hypothesis, it by no means confirms it; these events may still have occurred if striped bass would have occupied the hypolimnion even in the absence of coolwater forage fish. To further explore this issue, we examined all water quality data available from Lake Norman prior to 2000 to identify those years with sufficiently detailed data for us to characterize summer habitat conditions using the same metrics as for 2000–2010. Seven years met these criteria; three of them exhibited characteristics of severe metalimnetic hypoxia similar to those that typified years with striped bass mortality events during the 2000s (Table 3). In 1983, the thicknesses of metalimnetic DO less than 0.5 mg/L (7 m) and less than or equal to 0.1 mg/L (4 m) on the last sample date when DO in the hypolimnion was still at least 2.0 mg/L were in the same range as those observed in 2004, 2009, and 2010 (Table 1). In 1993, these metrics were even more extreme, with DO less than 0.5 mg/L 9 m thick, and 7 m at or below 0.1 mg/L DO. A week later, when DO in the hypolimnion had dropped below 2.0 mg/L, 12 m of the metalimnion contained less than 0.5 mg/L DO. In 1998, the extent of severe hypoxia in the hypolimnion was modest on the last date before the hypolimnion became hypoxic (2 m < 0.5 mg/L), but a week later, when DO in the hypolimnion had declined to 1.9 mg/L, this
Table 3. Characteristics of the metalimnetic oxygen minimum ($M_{\text{min}}$) and hypolimnetic oxygen maximum ($H_{\text{max}}$) at station 1.0 in Lake Norman on the last sample date (month/day) when dissolved oxygen (DO) in the $H_{\text{max}}$ was still at least 2.0 mg/L, and the first sample date (month/day) when DO in the $H_{\text{max}}$ was less than 2.0 mg/L, for years prior to 2000 with sufficient data. Values indicate thickness (m) of the $M_{\text{min}}$ and $H_{\text{max}}$ within given DO ranges, maximum temperature and maximum DO values in the $H_{\text{max}}$, and coolest temperature in water above the $M_{\text{min}}$ with at least 2.0 mg/L DO. Shading indicates that a striped bass mortality event occurred. Values in bold indicate thickness of metalimnetic hypoxia consistent with those that differentiated years with striped bass mortality events from those without during 2000–2010 (see Table 2).

<table>
<thead>
<tr>
<th>Last sample date with DO in $H_{\text{max}}$ ≥2.0 mg/L</th>
<th>1983</th>
<th>1992</th>
<th>1993</th>
<th>1996</th>
<th>1997</th>
<th>1998</th>
<th>1999</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_{\text{min}}$ &lt; 2.0 mg/L DO</td>
<td>17</td>
<td>14</td>
<td>17</td>
<td>10</td>
<td>0</td>
<td>16</td>
<td>11</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 1.5 mg/L DO</td>
<td>13</td>
<td>3</td>
<td>13</td>
<td>6</td>
<td>0</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 1.0 mg/L DO</td>
<td>10</td>
<td>0</td>
<td>11</td>
<td>3</td>
<td>0</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 0.5 mg/L DO</td>
<td>7</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 0.1 mg/L DO</td>
<td>4</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Max $T$ in $H_{\text{max}}$ (ºC)</td>
<td>14.4</td>
<td>14.1</td>
<td>13.8</td>
<td>13.8</td>
<td>15.4</td>
<td>14.2</td>
<td>14.5</td>
</tr>
<tr>
<td>Max DO in $H_{\text{max}}$ (mg/L)</td>
<td>2.6</td>
<td>2.2</td>
<td>2.0</td>
<td>2.8</td>
<td>2.3</td>
<td>2.3</td>
<td>2.2</td>
</tr>
<tr>
<td>$H_{\text{max}}$ ≥ 2 mg/L DO</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>8</td>
<td>4</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>$H_{\text{max}}$ ≥ 1.5 mg/L DO</td>
<td>11</td>
<td>6</td>
<td>1</td>
<td>8</td>
<td>6</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>First sample date with DO in $H_{\text{max}}$ &lt; 2.0 mg/L</td>
<td>9/7a</td>
<td>7/30</td>
<td>8/04</td>
<td>7/29</td>
<td>7/17</td>
<td>7/21</td>
<td>8/16</td>
</tr>
<tr>
<td>Coolest $T$ above $M_{\text{min}}$ with $H_{\text{max}}$ ≥ 2 mg/L DO (ºC)</td>
<td>26.4</td>
<td>25.6</td>
<td>28.5</td>
<td>24.9</td>
<td>19.1</td>
<td>26.6</td>
<td>25.9</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 2.0 mg/L DO</td>
<td>–</td>
<td>16</td>
<td>17</td>
<td>11</td>
<td>8</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 1.5 mg/L DO</td>
<td>–</td>
<td>9</td>
<td>16</td>
<td>11</td>
<td>0</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 1.0 mg/L DO</td>
<td>–</td>
<td>3</td>
<td>14</td>
<td>7</td>
<td>0</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 0.5 mg/L DO</td>
<td>–</td>
<td>0</td>
<td>12</td>
<td>4</td>
<td>0</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>$M_{\text{min}}$ &lt; 0.1 mg/L DO</td>
<td>–</td>
<td>0</td>
<td>3b</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>max DO in $H_{\text{max}}$ (mg/L)</td>
<td>–</td>
<td>1.9</td>
<td>1.5</td>
<td>1.6</td>
<td>1.9</td>
<td>1.9</td>
<td>1.3</td>
</tr>
<tr>
<td>$H_{\text{max}}$ ≥ 1.5 mg/L DO</td>
<td>–</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>$H_{\text{max}}$ ≥ 1.0 mg/L DO</td>
<td>–</td>
<td>4</td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>6</td>
<td>2</td>
</tr>
</tbody>
</table>

a By this date, the metalimnion and hypolimnion were completely anoxic.
b 10 m ≤ 0.2 mg/L.

Layer of severe hypoxia had expanded to 7 m thick, as in years in the 2000s with striped bass mortality.

Of the 3 years in which some or all metrics of severe metalimnetic hypoxia were comparable to those associated with striped bass mortality in the 2000s, 1983 was the only year in which a mortality event occurred (the only striped bass kill of note in Lake Norman prior to 2004).

Between 15 and 23 August 1983, 163 dead fish were collected near the dam. Although alewives and blueback herring were not present, there was another coolwater forage fish in the reservoir at that time. In the late 1970s and early 1980s, Lake Norman had an abundant population of small yellow perch *Perca flavescens*, which were preyed upon by striped bass and were a preferred bait of striped bass anglers. A major die-
off of these small yellow perch (~5,000 fish) in the same area of the lake near the dam preceded the striped bass kill by about 7–10 d. Though these observations are anecdotal, the timing and location of these mortalities suggests that both the dead yellow perch and striped bass may have been trapped in the hypolimnion as it became hypoxic.

In contrast, metalimnetic hypoxia was more severe in 1993 than in every other year we were able to evaluate (Tables 1 and 3). Had striped bass been present in the hypolimnion, the patterns observed in other years suggest that a striped bass mortality event would have occurred. By 1993, yellow perch were no longer common in Lake Norman, and alewives and blueback herring had not yet been introduced. It is possible that in the absence of coolwater prey, striped bass may have chosen not to occupy this habitat when their preferred temperatures in the metalimnion became hypoxic, accounting for the lack of striped bass mortality when oxygenated habitat in the hypolimnion disappeared.

**Badin Lake**

Though not nearly as comprehensive as data available from Lake Norman, observations from Badin Lake, North Carolina provide relevant information regarding striped bass behavior and mortality events in relation to formation of a metalimnetic oxygen minimum. Badin Lake is a deep (mean depth 21 m, maximum depth 54 m), 2,165-ha, eutrophic reservoir (NCDENR 2002, 2007) on the Yadkin River, stocked annually with 29.6 striped bass fingerlings/ha. The forage base is composed primarily of threadfin shad, but also includes blueback herring and gizzard shad (Thompson 2006). Three years of temperature and DO data collected during 2001–2003 show annual formation of a hypoxic zone in the metalimnion beginning in late May–early June, with DO in the hypolimnion dropping below 2.0 mg/L around late June to mid-July and disappearing shortly thereafter (Thompson et al. 2005).

Occasional die-offs of otherwise healthy-looking striped bass have been documented in Badin Lake with mortality concentrated in the lower lake near the dam, in the same area and about the same time as DO in the hypolimnion dropped below 2.0 mg/L, as shown in 2001–2003 water-quality monitoring (~400–500 fish, 13–17 July 1997; ~400–500 fish, 2–5 July 2001; ~750 fish, 20–29 June 2004; M. Hale, North Carolina Department of Environment and Natural Resources, and L. Dorsey, North Carolina Wildlife Resources Commission, unpublished data). The 2001 kill is the only one for which any limnological data are available. Sampling was not frequent enough to characterize conditions immediately before DO in the hypolimnion dropped below 2.0 mg/L, but a limnological profile was conducted in the dam forebay on 3 July, shortly after the mortality event began. On that date, 7 m of the metalimnion had DO below 0.5 mg/L and 6 m were less than 0.3 mg/L, while DO in the limnetic oxygen maximum ranged from 0.9 to 1.9 mg/L. These conditions are consistent with those that differentiated years with striped bass mortality events in Lake Norman from those without such events during 2000–2010.

A striped bass telemetry study initiated in Badin Lake in 2002 provided further insight regarding striped bass behavioral responses to changing temperature and DO conditions (Thompson et al. 2010). As the reservoir warmed, striped bass moved deeper to remain in oxygenated water with temperatures of 20–21°C; by mid-June, tagged fish were concentrated in the lower portion of the lake (where previous kills had occurred) in the hypolimnetic oxygen maximum, which contained about 4 m of water with 2.0–2.5 mg/L DO at 20–21°C (Thompson et al. 2010). Thickness and severity of hypoxic conditions in the metalimnion were mild compared to 2001, never exceeding 6 m of water with DO less than 2.0 mg/L and 2 m below 0.5 mg/L. When maximum DO concentration in the hypolimnion dropped below 2.0 mg/L in late June, the tagged fish immediately moved through the metalimnetic hypoxia into surface waters with
temperatures above 26°C and 4–6 mg/L DO and dispersed throughout the lake with no mortality (Thompson et al. 2010).

Discussion and Management Implications

Formation of a metalimnetic oxygen minimum overlaying a hypolimnetic oxygen maximum is a common phenomenon in many relatively deep reservoirs. The examples we have given indicate that changing habitat conditions caused by this limnological phenomenon may be more important in explaining some striped bass summer kills than previously recognized. Understanding the interactions between behavioral responses of fish and the spatial and temporal dynamics of DO and temperature in these systems may help us modify management strategies to alleviate, avoid, or minimize negative impacts on fish populations and better address concerns raised by the public about such events.

Striped bass mortality

Fortunately the extensive limnological record from Lake Norman allowed us to identify patterns in metalimnetic and hypolimnetic DO that appear to differentiate conditions likely to result in striped bass mortality from those that do not. The first prerequisite is isolation of oxygenated habitat in the hypolimnion (occupied by striped bass) that does not persist with adequate DO until fall turnover. If this habitat persists the whole summer, then the mechanism we have proposed obviously will not cause mortality (though other mechanisms could potentially cause stress, loss of condition, or mortality in such refuges (Coutant 1985, 2013). The second apparent prerequisite is formation of a thick layer of severe hypoxia in the metalimnion before DO in the hypolimnion falls below critical levels for striped bass survival. In Lake Norman, development of extensive moderate hypoxia (<2.0 mg/L) in the metalimnion was the norm (typically >10 m thick) and bore no relation to the occurrence of striped bass mortality. In contrast, years with striped bass mortality events were all characterized by 5–8 m of severe metalimnetic hypoxia (<0.5 mg/L) before the hypolimnion became hypoxic.

The patterns we observed in Lake Norman suggest that striped bass are able to leave the hypolimnion when DO declines to intolerable levels, if hypoxia in the metalimnion is relatively mild. Telemetry observations in Badin Lake confirmed that striped bass will move up through mild metalimnetic hypoxia to escape low DO when the hypolimnion becomes hypoxic (Thompson et al. 2010). Although we do not yet have definitive confirmation that thick, severe metalimnetic hypoxia will “trap” striped bass in the hypolimnion resulting in mortality as DO declines, as might be obtained from telemetry of striped bass during such a mortality event, we believe the circumstantial evidence is strong, and the timing and location of numerous die-offs are consistent with this explanation.

Temperature preference is likely to influence habitat selection by striped bass as hypoxia begins to exclude them from the metalimnion. When a wide range of temperatures with oxygenated water is available, adult striped bass in the size ranges found in Lake Norman and Badin Lake usually select temperatures in the 20–24°C range, most often about 20–22°C (Coutant and Carroll 1980; Thompson et al. 2010; Coutant 2013). As metalimnetic hypoxia first begins to form in Lake Norman, these temperatures almost always occur in the developing metalimnetic hypoxic zone and in the water just above it. In contrast, the warmest oxygenated water below this hypoxic zone is typically 15–16.5°C, well below the temperatures typically selected by the size ranges of adult striped bass in the reservoirs we studied and even lower than the fundamental thermal niche of adult striped bass reported by Bettoli (2005). Thus, if habitat selection by striped bass avoiding the metalimnetic hypoxic zone was based solely on available oxygenated temperatures, it seems more likely that they would move above the hypoxic layer where preferred temperatures were still available, rather than into colder than preferred temperatures below it.
Collectively, these observations support the notion that the presence of coolwater forage fish may increase the likelihood of striped bass mortality events associated with severe metalimnetic hypoxia. Coolwater forage fish were present in the hypolimnetic habitat of Lake Norman in each year that striped bass die-offs occurred. Yet no mortality event occurred in 1993, when coolwater forage fish likely to inhabit the hypolimnion were absent or rare, even though the thickness of severe metalimnetic hypoxia was substantially greater in that year than any other.

Until concrete evidence is available to show that during these mortality events striped bass remain in the hypolimnion and succumb as DO declines to lethal levels, we cannot rule out the possibility that some striped bass may move through even a severely hypoxic metalimnion to escape. Hydroacoustic observations made near the dam in Lake Norman have documented some large targets moving up and down through severely hypoxic conditions in the metalimnion. These fish may be hypoxia-tolerant blue catfish, but if future work documents that at least some of them are striped bass, it would beg the question, why don’t they all leave the hypolimnion when it becomes intolerable, even if hypoxia in the metalimnion is severe? If the fish were moving up to the lower epilimnion, mortality could possibly be due to thermal shock. However, the thermal change they would experience in years with severe hypoxia in the metalimnion would be the same as in years with mild hypoxia. In addition, if mortality occurred after fish reached the epilimnion we would expect most floating striped bass to initially look relatively fresh, whereas most looked like they had already been dead for several days when first collected during daily mortality surveys.

**Potential impacts on other coolwater or coldwater species**

The limnological dynamics we have described involving metalimnetic hypoxia and subsequent depletion of hypolimnetic oxygen may have important implications for other coolwater or coldwater species. Conditions of severe metalimnetic hypoxia similar to those that coincided with striped bass mortality events in Lake Norman and Badin Lake have also resulted in rainbow trout *Oncorhynchus mykiss* mortality in Bull Shoals Reservoir, Arkansas–Missouri (Love 1980). Such conditions may also contribute to entrainment or mortality of coolwater forage fish in some reservoir systems. As we observed for alewives in Lake Norman, blueback herring in J. Strom Thurmond (JST) Reservoir, Georgia–South Carolina can become concentrated in oxygenated hypolimnetic habitat isolated by extensive metalimnetic hypoxia. Hydroacoustic surveys have shown that as this oxygenated habitat shrinks the fish are crowded deeper and closer to the JST Dam penstock. In 2004, 2006, 2007, and 2008, major blueback herring entrainment events occurred at JST dam as hypolimnetic DO in the dam forebay declined below about 1.3–2.4 mg/L, and ended as it dropped to 0.7–0.8 mg/L. Visual observations indicated that in addition to entrainment through the dam, these dynamics can also result in mortality within the reservoir. Observations reported by a scuba diver following the 2004 entrainment event and photographic or video evidence obtained following the 2007 and 2008 events documented many dead blueback herring on the bottom in the dam forebay.

Limnological dynamics similar to those resulting in blueback herring entrainment through JST Dam have also caused blueback herring entrainment events at Hartwell Dam, Georgia–South Carolina in about one-third of the years since blueback herring became abundant in the mid-1980s. Using temperature and DO data, as well as fish distribution data from vertical gill netting and hydroacoustic surveys, Alexander et al. (1991) showed that entrainment occurred in years when hypolimnetic hypoxia developed after severe metalimnetic hypoxia was already in place. Entrainment events did not occur in years without this combination of limnological conditions. The potential effects of metalimnetic hypoxia and subsequent loss of oxygenated hypolimnetic habitat on entrain-
ment and mortality of coolwater forage fishes warrant further detailed evaluation.

**Management implications**

The spatial and temporal dynamics of temperature and oxygen we have described are driven by interactions among multiple physical, chemical, and environmental factors (e.g., bathymetry, nutrient loading, residence time, hydrological and meteorological conditions, and reservoir operations; Cole and Wells 2002; Ruane et al. 2013). Here, we have focused on the consequences of these dynamics rather than their causes, but hydrodynamic and water quality models such as CE_QUAL-W2 (Cole and Wells 2002) have been developed that are very effective in characterizing the spatial and temporal distribution of DO and temperature throughout reservoir systems based on physical, chemical, and meteorological data that are often monitored by various public or private organizations. These models can be powerful tools for simulating water quality under various environmental conditions or management scenarios (e.g., Ruane et al. 2013; Taylor et al. 2013; this volume). Even routine empirical monitoring of water quality parameters, especially when coupled with hydroacoustic surveys of fish distributions, can help identify risks, predict impending periods of entrainment or mortality, and evaluate management options such as whether or not to stock striped bass or coolwater prey species in a particular system.

In some systems, these problems may be manageable despite the constraints of logistical limitations and competing priorities for dam operations. In reservoirs where the oxygenated hypolimnetic refuge is not going to persist all summer, hypolimnetic water withdrawals can sometimes be used to prevent its formation or remove it before fish are trapped. For example, in Lake Hartwell where blueback herring entrainment is a recurring problem, U.S. Army Corps of Engineers personnel who operate the dam have found that they can prevent herring aggregations near the penstocks by withdrawing water early in the season to eliminate oxygenated habitat in the hypolimnion before hypoxia in the metalimnion is well established. However, this management strategy can only be implemented in years with sufficient water availability. This approach may be a realistic option in some reservoirs operated primarily for hydroelectric power generation. However, in systems like Lake Norman where providing cooling water for steam electric power stations is the top priority, it is unlikely to be feasible. In Lake Norman, withdrawal of cold water from the hypolimnion is often necessary later in the summer to keep the temperature of cooling water discharged from McGuire nuclear power station below maximum permitted levels; withdrawal of hypolimnetic water early in the season might not leave sufficient cold water to meet this need.

Alternatively, in some systems particular patterns of water withdrawal may actually create problems by eliminating oxygenated hypolimnetic habitat that would otherwise persist all summer long. For example, in Lake Murray, good habitat below the hypoxic zone in the metalimnion usually persists during the summer if withdrawal from that depth is minimized. In 2005, one intake located at the same depth as the oxygenated hypolimnetic habitat was used extensively in June and July in response to high inflows, reducing this habitat, and a large striped bass kill started the last week of July when hypolimnetic DO fell below 2 mg/L (Ruane et al. 2013). Based on the results of model simulations, timing and relative use of metalimnetic and hypolimnetic water intakes in Lake Murray have since been altered to increase suitable summer habitat for striped bass (Ruane et al. 2013). Other habitat manipulations may allow good hypolimnetic habitat to persist when it otherwise would not. Oxygen diffuser systems have been installed in more than 20 reservoirs and lakes across the United States (Mobley et al. 2013, this volume). While the primary purpose for many of these systems is to improve downstream water quality, some are specifically intended to create and maintain usable coolwa-
ter habitat for striped bass and other species. For example, in 2011, installation of a DO injection system was completed in JST Reservoir. Located 8 km upstream from the JST Dam, this system is creating a large area of well-oxygenated, cool summer habitat for striped bass (and blueback herring) to mitigate the loss of cool, oxygenated habitat in the tailrace of Richard B. Russell Dam when its reversible turbines are used to operate the dam as a pumped-storage hydropower facility (Mobley et al. 2013).

In some systems, perhaps small-scale oxygenation could be used to create refuges of adequate size to enhance oversummer survival of striped bass in reservoirs with persistent water quality issues. However, if the oxygenated area is relatively small, special regulations may be required to protect striped bass that aggregate there during the summer. For example, oxygen diffusers installed in Cherokee Reservoir to improve DO conditions downstream of the dam created a relatively small zone of ideal striped bass habitat. Anglers heavily targeted striped bass aggregated in this area, leading the Tennessee Wildlife Resources Agency to close the area to fishing 15 July–15 September to halt substantial catch and release mortality that was occurring (Mobley et al. 2013).

Decisions regarding whether or not oxygen injection or other water management changes should be implemented will depend on operational priorities, economic considerations, and other factors unique to each system. Even if a striped bass fishery’s economic and recreational value alone is not sufficient to justify such changes, the fishery may benefit if installation of an oxygen injection system or other modification is the most cost-effective method to meet other priorities, such as satisfying regulatory requirements for minimum DO concentrations in tailwater releases or providing mitigation for other habitat loss or fish mortality. Modeling analyses can be useful in determining if striped bass habitat enhancement can be incorporated into such operational changes without compromising primary objectives (Ruane et al. 2013). However, both fisheries managers and anglers should recognize that in some systems with marginal habitat and recurring summer mortalities, discontinuation of striped bass stocking is a management option that may warrant consideration.

The observations we have reported here identify a significant issue affecting striped bass management in many reservoirs. We need detailed information from more systems and a wider range of conditions to determine whether or not the patterns we observed are general, and to elucidate exactly how striped bass occupying the hypolimnion below a hypoxic metalimnion are responding behaviorally to progressive loss of oxygenated habitat. Likewise, additional information is needed to clarify the fate of coolwater forage fish occupying this habitat and to assess the impacts on both striped bass and coolwater forage fish populations. Awareness of these dynamics can help us understand the constraints they impose on fisheries management and identify possible approaches to minimize or avoid their impact.

Even when management actions to alleviate striped bass summer mortalities are not possible, a clear understanding of the processes responsible for these events can still be a valuable tool for addressing questions and dispelling misinformation about their causes. Fish kills, especially of sport fish, can generate great concern among anglers and the public. When fish kills are associated with formation of metalmimetic hypoxia and the subsequent dynamics of the oxygenated layer below it, managers may be better able to address public concerns and misconceptions by conveying how limnological dynamics inherent to the reservoir system interact with habitat preferences of affected species (and with dam operations, if they are a factor) to cause such kills.

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