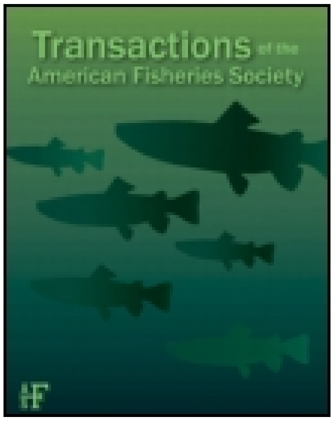

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Responses of Coastal Largemouth Bass to Episodic Hypoxia

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ARTICLE

Responses of Coastal Largemouth Bass to Episodic Hypoxia

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Abstract
The river systems inhabited by coastal populations of Largemouth Bass *Micropterus salmoides* in North Carolina and along the Atlantic and Gulf coast regions exhibit episodic (i.e., several times per year) fluctuations in environmental conditions (e.g., dissolved oxygen [DO]). Laboratory studies have documented the effects of low DO (hypoxia) on Largemouth Bass, yet few field studies have examined these effects in open systems. The objective of this study was to determine the effects of episodic hypoxia on Largemouth Bass distribution, survival, and feeding success in an open coastal system. We collected 45 Largemouth Bass from four tributaries of the Chowan River and tagged them with acoustic transmitters. Fish movements were monitored using active tracking and passive receivers, and these data were compared with DO levels recorded in the tributaries and main-stem Chowan River. We found that tagged Largemouth Bass exhibited avoidance behavior at DO concentrations below 1.8 mg/L, with some seeking higher DO in the main stem or near tributary mouths during hypoxic events in the tributaries. The natural mortality rate of Largemouth Bass was low compared with rates reported in other studies, indicating that Largemouth Bass in coastal systems are able to survive hypoxic events. Analysis of stomach contents collected during hypoxic and non-hypoxic periods indicated that Largemouth Bass had less food in their stomachs under hypoxic conditions; however, the CPUE (fish/h of pedal time) of potential prey fishes was not lower during hypoxic periods relative to non-hypoxic periods, and thus a change in foraging opportunities did not appear to drive Largemouth Bass movement.

The Largemouth Bass *Micropterus salmoides* is often the most sought-after sport fish in coastal rivers of North Carolina (Dockendorf et al. 2004; McCargo et al. 2007; Ricks and McCargo 2013). Coastal populations of Largemouth Bass typically exhibit higher abundance and condition than inland populations but have slower growth, smaller maximum size, and higher annual mortality (Colle et al. 1978; Guier et al. 1978; Meador and Kelso 1990; Glover 2010; Norris et al. 2010). Several authors (e.g., Meador and Kelso 1990; Glover 2010; Norris et al. 2010) have suggested that these characteristics may represent an alternative life history and energy allocation strategy reflecting coastal populations' adaptation to spatial and temporal variability in environmental conditions, such as dissolved oxygen (DO) concentration and salinity.

In coastal river systems, a host of factors (e.g., water temperature, salinity, flow patterns, eutrophication, and organic pollution) can influence variation in DO (Goldberg 1995; Sabo et al. 1999a, 1999b; Pollock et al. 2007; Franklin 2014). Additionally, river systems along the coast of North Carolina drain extensive wetlands or low-lying floodplains. Discharge of water entrained in these areas can lead to an influx of hypoxic water and dissolved solids into tributary creeks, resulting in periods of hypoxia (DO < 2.0 mg/L; Pinckney 2001) or anoxia (no detectable DO; Pinckney 2001) in both tributary and main-stem waters (Fontenot et al. 2001; Bales and Walters 2004; Thomas and Dockendorf 2009). Although tributary creeks have a higher susceptibility to hypoxia than the main stem, CPUE data indicate that tributary creek habitats support a high abundance of Largemouth Bass

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(McCargo and Dockendorf 2010). The combination of high Largemouth Bass abundances and rapid decreases in DO within tributary creeks after rain events (e.g., hurricanes and tropical storms) can lead to major die-offs of Largemouth Bass and other fish species (Thomas and Dockendorf 2009; Ricks and McCargo 2013). However, some individuals survive these events, and their offspring account for the recovery of Largemouth Bass populations within just a few years (Thomas and Dockendorf 2009; McCargo and Dockendorf 2010).

Avoidance of low DO concentrations has been well documented for many fishes (Davis 1975; Pihl et al. 1991; Wannamaker and Rice 2000), including Largemouth Bass (Burleson et al. 2001), yet field studies on the influence of DO on Largemouth Bass movement are relatively few and focus almost exclusively on freshwater environments. Hasler et al. (2009) found that Largemouth Bass that were exposed to hypoxia exhibited altered behavioral patterns and avoided hypoxic areas in an ice-covered lake. Conversely, Gaulke (2012) observed that hypoxic events (mean daily DO of 0.96–1.82 mg/L for 4 d or more) in the Chicago Area Waterway System did not significantly influence Largemouth Bass movement. These conflicting results appear to indicate that factors in combination with DO may influence Largemouth Bass movement. Previous work has shown that hypoxia is not an absolute barrier to fish movement and that fish will use hypoxic zones for opportunistic feeding (e.g., Pihl et al. 1992; Rahel and Nutzman 1994).

Centrarchids are among the fishes most frequently observed in chronically hypoxic habitats, and it is thought that they can adapt to prolonged hypoxia exposure in the field (Sabo et al. 1998). However, laboratory studies of Largemouth Bass have found that prolonged exposure to sublethal DO concentrations can reduce maximum sustainable swimming speed (Dahlberg et al. 1968), impede feeding success (Yamanaka et al. 2007), and decrease growth (Stewart et al. 1967). Periods of low DO often coincide with high metabolic demand due to warm water temperatures from late spring through early fall (North Carolina Division of Marine Fisheries, unpublished data), which can exacerbate these sublethal effects. In addition, prey and predators may have different responses to hypoxia, leading to differences in habitat selection during hypoxic events (Yamanaka et al. 2007); such differences may separate Largemouth Bass from potential foraging opportunities and effectively encourage the utilization of suboptimal habitats.

The present study encompassed two objectives. The first objective was to assess the effects of episodic hypoxia on the distribution and mortality of Largemouth Bass in an open coastal river system. To achieve this, we used acoustic telemetry to track the movements of Largemouth Bass in a section of the Chowan River, North Carolina, and four associated tributaries that are known to exhibit frequent hypoxia events. Largemouth Bass responses to variations in DO were assessed by examining the movements of tagged individuals relative to changes in DO concentration within the study area. Our second objective was to examine the fish assemblage, the relative abundances of potential prey fishes and Largemouth Bass, and the feeding success of Largemouth Bass during hypoxic and non-hypoxic conditions in the main-stem Chowan River and tributaries to determine how foraging opportunities change with DO concentration.

METHODS

Study area.—Our study area included a 16-km section of the lower Chowan River and its tributaries (Bennett's Creek, Catherine's Creek, Wiccacon River, and Sarem Creek) above Albemarle Sound in eastern North Carolina (Figure 1). All of these systems are surrounded by cypress swamps and agricultural lands, and the resulting inputs of organic material, particularly during storm events, often produce widespread hypoxia that can persist for extended periods due to low stream gradients and low rates of flushing. In addition, Catherine's Creek drains an extensive swamp system, and Bennett's Creek receives runoff from the town of Gatesville, North Carolina.

Fish tagging.—We captured 11–12 Largemouth Bass in each of the four tributaries ($n = 45$ total fish) via daytime boat electrofishing in April 2012. We recorded TL and weight to determine each individual's suitability for tagging. Fish that did not meet weight requirements for tagging were released. Weight (nearest g) was recorded for calculation of relative weight (W_r) to assess fish condition (Anderson and Neumann 1996). We then placed individual fish into a 40-L tank containing a 100-mg/L solution of tricaine methanesulfonate (MS-222) for approximately 5 min to induce anesthesia for tag implantation. Once stage-3 sedation (partial loss of equilibrium; Summerfelt and Smith 1990) was attained, the fish was transferred to a surgical table, where its gills were continuously irrigated with a 50-mg/L solution of MS-222 for the duration of the surgery. A small (~15-mm) incision was made along the linea alba posterior to the pelvic girdle. An individually coded Vemco V13-1L acoustic transmitter (13×36 mm, 11 g in air; Vemco, Halifax, Nova Scotia) was inserted through the incision into the body cavity. The Vemco tags emitted a signal every 60–180 s for 10 d, followed by a 5-d period during which they emitted a signal every 15–45 s (necessary for active tracking). The incision was closed using three to four sutures (polydioxanone absorbable synthetic monofilament 3-0 FS-1; Ethicon, Cornelia, Georgia), and a small amount of povidone-iodine gel was applied to the incision; the fish was then placed into a 150-L tank of aerated river water treated with Stress Coat (Aquarium Pharmaceuticals, Franklin, Tennessee). When the tagged fish regained equilibrium and resumed normal opercular movement, we released it back into the tributary of capture. Release points were located near receivers (see below) to monitor Largemouth Bass dispersal and identify any mortality associated with the tagging procedure.

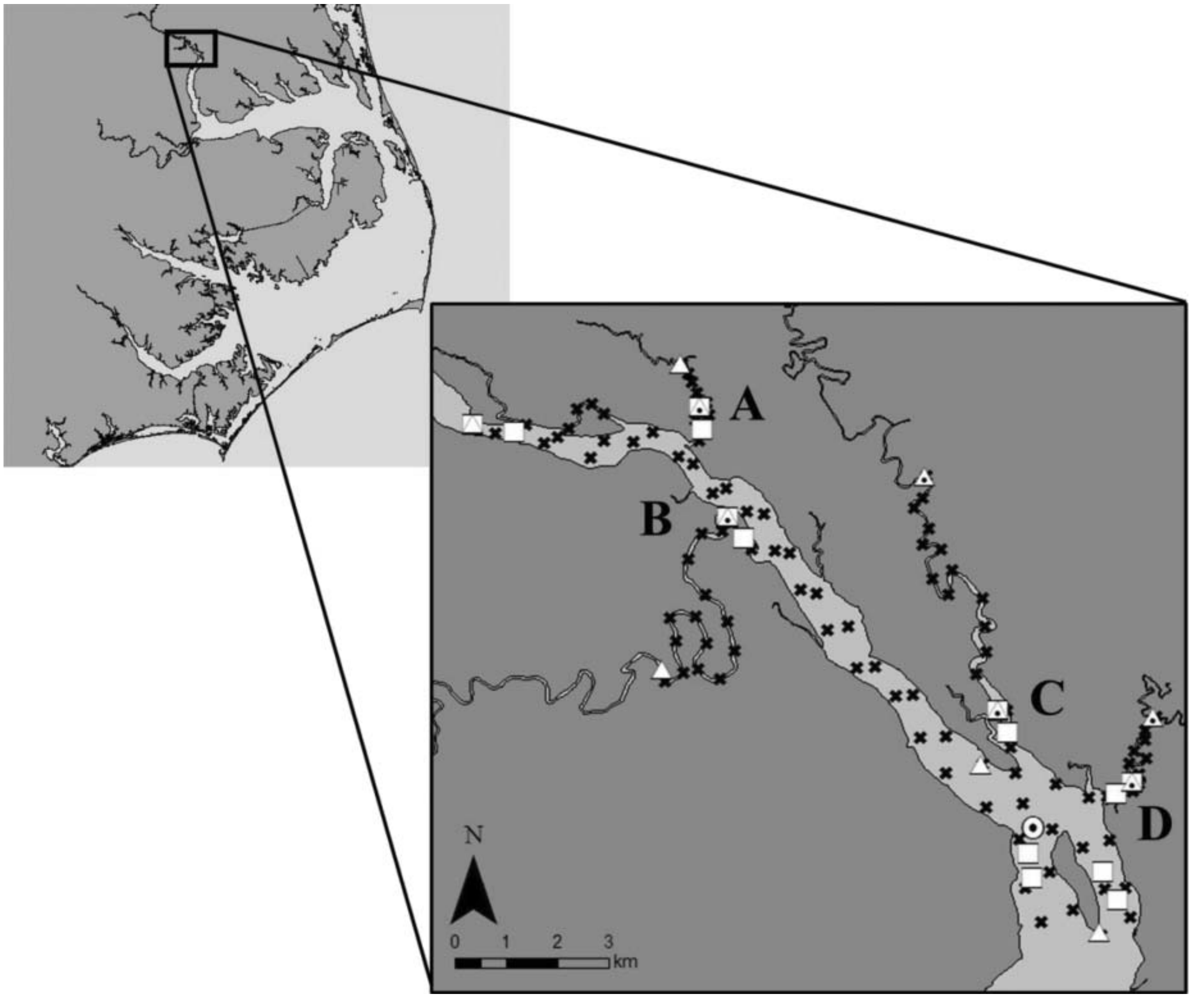

FIGURE 1. Map of the study area in the Chowan River system, North Carolina, showing tributary creeks (A = Sarem Creek; B = Wiccacon River; C = Bennett's Creek; D = Catherine's Creek) and the locations of Vemco VR2W receivers (white squares), vertical water quality profiles (white triangles), water quality sondes deployed in the present study (black dots), a water quality sonde deployed by the North Carolina Department of Environment and Natural Resources (white circle with black dot), and fixed listening points used during active tracking (×-symbols).

Telemetry.—We continuously monitored the distribution and movement of tagged Largemouth Bass within our study area by using an array of 14 Vemco VR2W passive receivers (69 kHz). We established gates at the upper and lower bounds of the study area as well as near the mouth of each tributary (Figure 1). Each gate consisted of a pair of receivers, one upstream of the other; the gates allowed us to detect any movement of tagged Largemouth Bass into or out of a tributary and to detect any emigration from the study area. An effective detection range of approximately 500 m was determined by following the Vemco range test protocol. Detection ranges can vary due to environmental conditions (Topping and Szedlmayer 2011); thus, to ensure the highest probability of detection, we deployed receivers 800 m apart and within 400 m of shore in the Chowan River main stem. Receivers in the tributaries were deployed 400–500 m apart and were separated (where possible) by a bend in the creek to avoid simultaneous detections by both receivers.

In addition to passive tracking by the receiver array, we used a Vemco VR100 manual receiver and VH180 omnidirectional hydrophone to conduct 1-d active tracking surveys on an approximately monthly basis. Relocation efforts occurred at 150 fixed listening points throughout the main stem and tributaries (Figure 1). We used a directional hydrophone to locate any tagged Largemouth Bass that were detected at fixed listening points. During a preliminary field test, we determined that under calm conditions, operators were able to locate a stationary transmitter to within approximately 4 m of the actual location. We recorded GPS coordinates after successful transmitter relocations to aid in determining natural mortality rates and to evaluate movement patterns that were not detected on the passive receivers. The combination of movement data from the passive receivers and active tracking surveys was used to determine the number of trips made by each fish from the tributaries into the main stem. We used one-way ANOVA (general linear model [GLM] procedure in SAS version 9.3; SAS Institute, Cary, North Carolina) to test for differences in the mean number of trips into the main stem by fish tagged in each tributary.

Water quality monitoring.—To monitor variation in water quality throughout the water column, we collected vertical profiles at two fixed sites per tributary and at three fixed sites in the main-stem Chowan River (n = 11 total fixed sites; Figure 1) during each active tracking survey. We recorded temperature, DO, and salinity at 1-m intervals from the surface to the bottom by using a manually deployed sonde (YSI 600 XLM; YSI, Yellow Springs, Ohio). We deployed six water quality sondes (YSI Model 6600 EDS or 600 XLM) that recorded near-surface water temperature, DO, and salinity values every 15 min from April 2012 through September 2013. Depth of the sondes varied between 0.6 and 1.5 m depending on the water level. One sonde was placed 800 m upstream of the mouth in each tributary, and two additional sondes were deployed at the upstream-most manual detection fixed sites in Bennett's and Catherine's creeks to record any potential differences between upstream and downstream water quality (Figure 1). We also received hourly water quality data throughout the study from a sonde in the main-stem Chowan River (maintained by the North Carolina Department of Environment and Natural Resources; Figure 1).

Sondes were downloaded, cleaned, and recalibrated approximately monthly. The first four to six readings taken after recalibration were discarded to ensure that the sondes had equilibrated to the instream conditions. To determine whether any adjustments were necessary due to instrument drift or biofouling, we compared the last four DO readings prior to sonde servicing with (1) the first four readings after the sonde had equilibrated and (2) readings taken near the sonde with a calibrated hand-held YSI 600QS unit just before or after the sonde was serviced (Campbell and Rice 2014). If the absolute difference between the hand-held reading and either the pre-service or postservice readings was greater than 0.3 mg/L (Wagner et al. 2006), we adjusted the data using Aquarius version 2.0 (Aquatic Informatics, Vancouver). We reconciled differences between hand-held and postservice readings by adjusting the data for the entire deployment period up or down to meet the hand-held reading. To correct any differences between the hand-held reading and the pre-service sonde readings, we used a function within Aquarius software that generated a linear drift correction over time for the entire deployment period. We applied postservice corrections first if corrections were required at both ends of the same deployment period. Corrections were applied to the entire length of deployment between servicing events because calibration drift is assumed to occur at a constant rate throughout the correction period, and sensor fouling commonly begins as soon as the sonde is deployed in an aquatic environment (Wagner et al. 2006). If the absolute difference between the hand-held reading and either the pre-service or postservice readings was greater than 2.0 mg/L, the data were deemed unusable and were not included in the analysis (29.4% of readings).

Fish assemblage, relative abundances, and Largemouth Bass feeding success.—To evaluate potential changes in prey fish assemblages and relative abundance of Largemouth Bass in relation to DO levels, we collected fish from three transects in each tributary and two transects in the lower, middle, and upper portions of the main stem via daytime boat electrofishing. Transect length covered approximately 150–200 m of shoreline, with an average pedal time of 969 s (range = 523–1,443 s). We sampled the fish assemblage during the spring (n = 17 transects) and fall (n = 12 transects) of 2013 to account for potential seasonal differences. Spring assemblage transects were located near the midpoint and at the upstream and downstream extent of our study area in each of the tributaries and the main stem. One transect from each tributary (the upper transect in Bennett's and Catherine's creeks and the middle transect in the Wiccacon River and Sarem Creek) and two transects in the main stem (one lower and one middle) were dropped from fall sampling due to time constraints. We recorded surface DO at the beginning of each transect, and we measured all fish (i.e., other than Largemouth Bass) to the nearest millimeter TL before releasing them back into the stream. Captured Largemouth Bass were retained for diet sampling as described below. All fish other than Largemouth Bass were placed into size categories (<40, 40–100, 101–250, and >250 mm TL) for analysis, and we calculated a CPUE (fish/h of pedal time) for all Largemouth Bass and for each size category of non-Largemouth Bass. To quantify potential differences in fish assemblage CPUE and Largemouth Bass CPUE associated with differences in DO concentration among the tributaries and main stem, we used one-way ANOVA (GLM procedure in SAS). If the main effect was significant, we used Tukey's honestly significant difference post hoc test to determine which samples differed from each other. We also used linear regression to assess the relationship between Largemouth Bass CPUE and DO concentration (REG procedure in SAS).

To determine the effect of DO on Largemouth Bass feeding success and diet composition, we collected stomach contents from individuals captured during the fish assemblage sampling transects as well as supplemental transects (n = 77 transects total). Supplemental transects were conducted, if necessary, to attain 25 stomach samples containing at least one prey item in each of the tributaries and the main stem. Data from these transects also were included in the analysis of Largemouth Bass CPUE in relation to DO described above. We used the proportion of captured Largemouth Bass with at least one prey item in their stomachs as an indicator of feeding success at various DO concentrations. Stomach contents of Largemouth Bass greater than 200 mm TL were removed via acrylic tubes and gastric lavage (Van Den Avyle and Roussel 1980; Cailteux et al. 1992), and prey lodged in the esophagus were removed with forceps. All prey items were weighed (g), placed in individually labeled jars, and preserved in 70% ethanol. Largemouth Bass smaller than 200 mm TL were placed on ice, and their stomach contents were removed in the laboratory. Diet items were assigned to five general categories: aquatic invertebrates (e.g., chironomids, odonate nymphs, Ephemeroptera, etc.), crayfish, fish, terrestrial invertebrates (e.g., odonate adults), or other items (i.e., amphibians and mollusks). We used the chi-square test (FREQ procedure in SAS) to identify differences in feeding success and diet composition under different DO conditions. We also used a logistic regression (LOGISTIC procedure in SAS) to determine the odds of a Largemouth Bass having food in its stomach over a range of DO concentrations.

Estimation of fishing mortality and natural mortality.—A Bayesian multistate model approach adapted from Kéry and Schaub (2012) in OpenBUGS software was used to calculate instantaneous and discrete estimates of Largemouth Bass fishing mortality and natural mortality. The model allowed for four possible fates of each individual tagged Largemouth Bass on day *i*: (1) alive, (2) dead due to natural causes, (3) emigrated from the study area, or (4) harvested. We assumed that any tag detected in the same location during three or more consecutive sampling trips represented natural mortality. Estimates of natural mortality included any catch-and-release mortality that may have occurred, as these could not be differentiated (Hightower et al. 2001). We assumed that a fish emigrated from the study area if it was detected passing both receivers at one of the main-stem gates and had no subsequent detections. We assumed that a fish had been harvested if it was not detected in the study area during at least three consecutive sampling trips and was not detected again for the duration of the study. Any tagged Largemouth Bass that were transported out of the study area by anglers and subsequently released (e.g., as part of a fishing tournament) were included in estimates of fishing mortality, as we could not differentiate their disappearance from actual harvest. Estimates of mortality and emigration were calculated for the period through July 2013. Tracking occurred until September 2013, but mortality and emigration rates were not estimated for August or September 2013 because we could not confirm possible natural mortality or fishing mortality in these months based on the criteria described above. The first month after release was considered a "probationary period." Data collected during that time were excluded from our mortality estimates so that any mortality or behavioral response associated with tagging would not bias the emigration or mortality estimates upward (Thompson et al. 2007).

In our mortality analysis, we used a $\log_e$ scaled uniform prior distribution to calculate the likelihood of each fate. We included the assumptions described by Friedl et al. (2013) in our model: (1) all tagged Largemouth Bass within the study area at time i had the same survival rate to time $i + 1$ unless they were confirmed as a natural death or had emigrated, (2) marked and unmarked fish had the same survival rates, (3) the probability of tag expulsion or tag failure was negligible, (4) movement patterns could be used to determine whether a tagged fish remained alive or had died due to natural causes, and (5) emigrating fish could be detected and therefore censored from the analysis. We calculated the median value and the 2.5th and 97.5th percentiles from the posterior distribution as the monthly estimates and credible intervals of mortality and emigration. The timing of this study prevented us from calculating a classic (January–December) estimate of annual mortality. As an alternative, we followed the method of Brown (2014) to calculate discrete annual mortality estimates, in which instantaneous monthly estimates were averaged and rescaled to a 12-month period before conversion to discrete values.

RESULTS

Spatial and Temporal Patterns in Water Quality Conditions

Readings from the sondes indicated that salinity was typically between 0.0‰ and 0.1‰ throughout the study area; peak salinities in the tributaries (0.5–0.8‰) and the main stem (1.5‰) were observed during a prolonged but modest salinity increase in summer 2012. The vertical profiles showed the same pattern of low salinity at tributary and main-stem sites and indicated that salinity was typically consistent from surface to bottom throughout the study area. Sonde data indicated that temperature variation was consistent throughout our study area; summer highs of about 29–30°C (maximum = 32°C) were recorded during mid- to late July, and winter lows of typically 5–7°C (minimum = ~0–2°C) were observed in January and February 2013. Daily maximum and minimum temperatures usually differed by less than 2°C, and the largest differences were close to 4°C. Temperature was often homogeneous throughout the water column during the winter and summer seasons.

The DO concentration in near-surface waters ranged from 0.0 to 21.9 mg/L throughout the study, with periods of hypoxia being observed in each of the tributaries during May–October 2012 and May–September 2013 (Figure 2). Hypoxic periods ranged from 1 h (in all tributaries) to over 35 h (in Catherine's and Sarem creeks). More than 24% of the DO readings recorded by the sondes in Catherine's Creek, Sarem Creek, and the Wiccacon River were below 2.0 mg/L, whereas only 8% of the DO readings in Bennett's Creek were below 2.0 mg/L. The DO concentration in the main-stem Chowan River declined below 2.0 mg/L for part of three consecutive days during July 2012. These brief decreases in DO typically lasted less than 4 h (range = 1–9 h) and constituted less than 1% of the recorded data. Dissolved oxygen

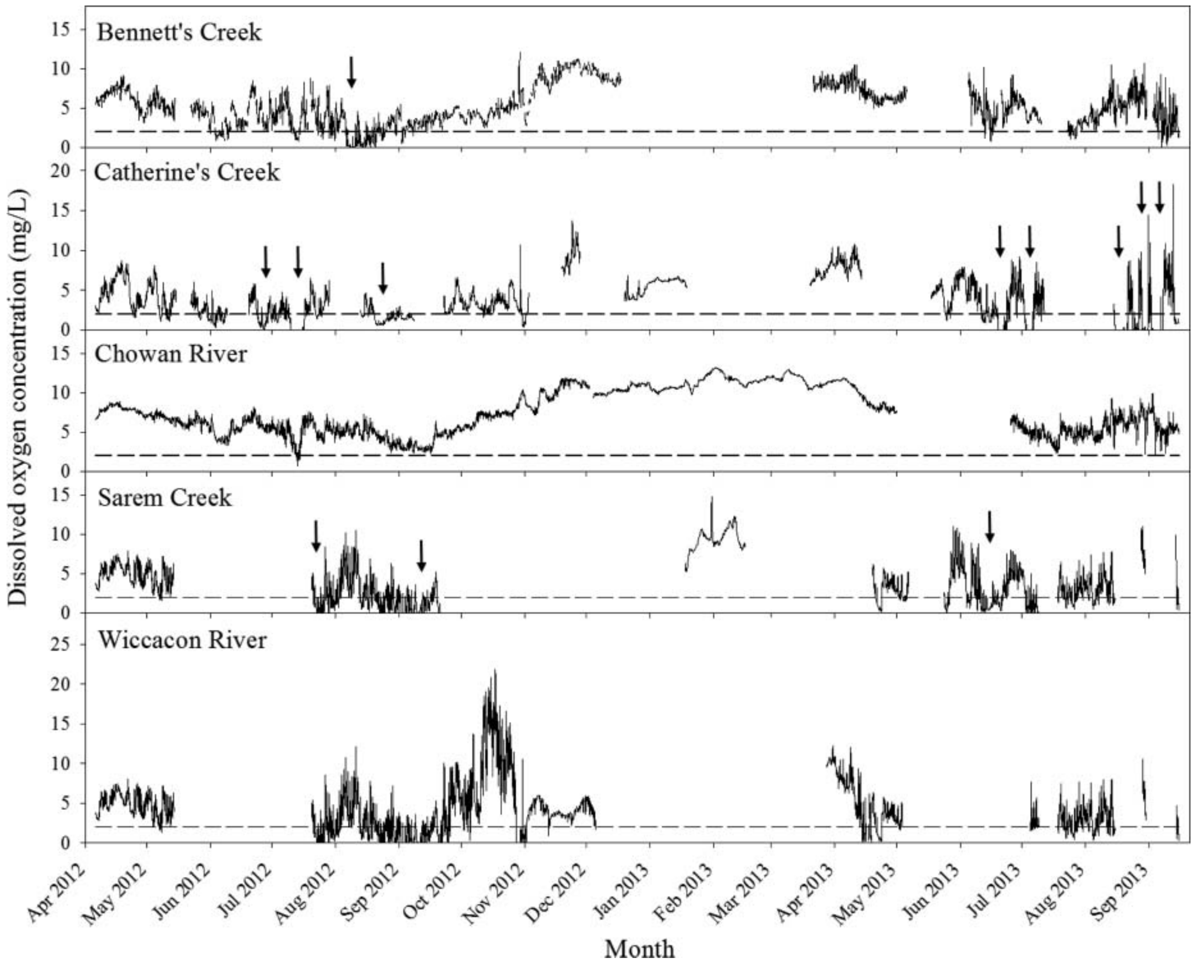

FIGURE 2. Comparison of hourly dissolved oxygen (DO) readings in the Chowan River and tributaries, April 2012–September 2013. Arrows indicate severe hypoxic events (see Results text); the dashed line indicates a DO concentration of 2.0 mg/L. Gaps in the data resulted from equipment malfunctions.

concentrations were generally lower at upstream sampling points in the tributaries than at points near the tributary mouths, which usually had lower DO concentrations than the main stem.

Distribution and Movement Patterns

The 45 Largemouth Bass that were retained for tagging averaged 367.7 mm TL (SD = 73.1; range = 240–586 mm TL) and 777.2 g (SD = 643.1; range = 186–3,371 g). There were no significant differences in mean TL (ANOVA: F = 0.21, df = 44, P = 0.89), weight (F = 0.34, df = 44, P = 0.80), or W_r (F = 1.07, df = 44, P = 0.37) among Largemouth Bass that were tagged in the four tributaries. The tag burden ranged from 0.3% to 5.9% of body weight and averaged 2.2% of body weight (SD = 1.29). Of the 45 individuals that were tracked, 12 were only detected in their tributary of capture. Of the 33 fish that were detected in both tributary and main-stem habitats, 30 individuals (66.7% of tagged fish) made fewer than 10 trips into the main stem during the study period, and 3 fish (6.7%) made 13–35 trips into the main stem. Thirteen of the fish with both tributary and main-stem detections (28.9% of tagged individuals) were detected in a tributary other than the tributary of capture. Although most of these fish remained in other tributaries for only a short time (range = 1–8% of total tag detections), two fish (4.4% of tagged individuals) were detected in a different tributary for substantial periods (46% and 95% of total detections) before returning to the tributary of capture. Eventually, 18 Largemouth Bass (40% of tagged fish) remained in the main stem and did not return to their tributaries of capture. Fish that were tagged in Catherine's Creek made significantly more trips into the main stem (mean = 8.9 trips, SE = 0.91; Figure 3) than fish that were tagged in Bennett's Creek (mean = 2.4 trips, SE = 0.26; ANOVA: F = 4.26, df = 21, P = 0.05). However, the number of trips into the main stem did not differ between fish tagged in Catherine's Creek and those tagged in Sarem Creek (mean = 3.0 trips, SE = 0.22; F = 3.93, df = 22, P = 0.06) or in the Wiccacon River (mean = 3.8 trips, SE = 0.26; F = 2.68, df = 21, P = 0.11).

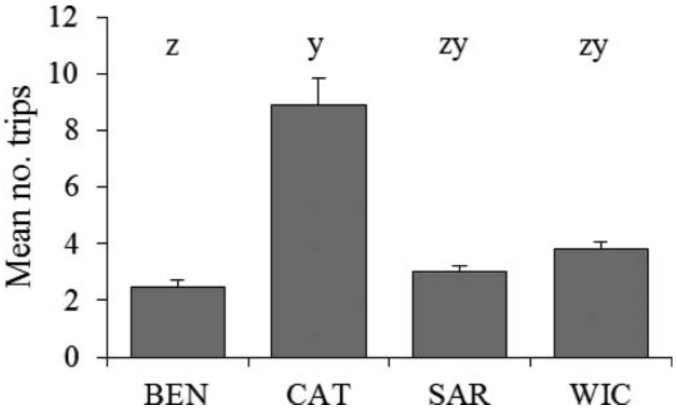

FIGURE 3. Mean (+SE) number of trips taken by Largemouth Bass from tributaries into the main-stem Chowan River between April 2012 and September 2013 for fish that were tagged in Bennett's Creek (BEN), Catherine's Creek (CAT), Sarem Creek (SAR), or the Wiccacon River (WIC). Means without a letter in common are significantly different.

Movement Relative to Water Quality Conditions

Coordinated movement of tagged Largemouth Bass (i.e., when more than one fish moved in a similar direction) out of an individual tributary occurred on eight occasions; seven (87%) of the eight coordinated movement events occurred when daily mean DO was below 1.8 mg/L (range = 0.0–2.9 mg/L). The single instance of coordinated movement that did not coincide with daily mean DO below 1.8 mg/L involved movement out of Catherine's Creek during August 2013, when DO was below 1.8 mg/L for 11 h yet daily mean DO was 2.9 mg/L (range = 0.1–9.8 mg/L). In contrast, there were 158 occasions when a single tagged Largemouth Bass moved out of a tributary, but only 37% of those movement events took place when daily mean DO was below 1.8 mg/L (range = 0.0–7.3 mg/L).

An active tracking effort during late August 2012 coincided with a period of low DO in Catherine's Creek, which allowed us to collect detailed information on Largemouth Bass movements in response to hypoxia. Analysis of water quality in Catherine's Creek during this period indicated that DO was below 1.2 mg/L for over 75% of the day on more than three consecutive days. Prior to the onset of these conditions, we detected six tagged Largemouth Bass in the creek. After the onset of these hypoxic conditions, three fish that were previously located near the tributary mouth remained near the mouth, two fish that were previously located upstream of the receivers moved downstream to the mouth, and one fish that was previously located near the receivers moved into the main stem (Brown 2014). One of the Largemouth Bass that moved downstream traveled over 2 km. Only after the hypoxic conditions abated did the tagged Largemouth Bass return to the creek or venture upstream of the mouth. Because Largemouth Bass appeared to be avoiding these conditions, we used them to define a "severe hypoxic event" as follows: DO less than or equal to 1.2 mg/L for more than 75% of the day on three or more consecutive days. Using this convention, we identified 12 severe hypoxic events in Bennett's, Catherine's, and Sarem creeks during the study (Table 1). The events did not occur synchronously among the tributaries (Figure 2), and DO in the main stem ranged from 1.8 to 8.0 mg/L during all of the recorded severe hypoxic events in the tributaries.

Although active tracking data were only available during one severe hypoxic event, detection data from the passive receivers indicated similar movement by tagged Largemouth Bass during other such events (Table 1). For example, during a severe hypoxic event in Catherine's Creek in July 2012, all

TABLE 1. Dates of hypoxic events in Chowan River tributaries, dissolved oxygen (DO) range during each event, percentage of time for which DO was below 1.2 mg/L, and the percentage and fraction of tagged Largemouth Bass present in the tributary that either moved toward the tributary mouth or into the main-stem Chowan River during the event, May 2012–September 2013. Asterisks indicate severe hypoxic events that corresponded with coordinated movement out of the tributary by two or more Largemouth Bass on the same day.

Tributary	Dates of hypoxic event	DO range (mg/L)	Percentage of time below 1.2 mg/L	Percentage (fraction) of fish avoiding low DO
Bennett's Creek	Aug 7–9, 2012	0.00–2.02	86	12 (1/8)
Catherine's Creek	Jun 25–27, 2012	0.00–2.85	86	87 (7/8)
	Jul 10–15, 2012*	0.00–0.47	100	100 (8/8)
	Aug 20–24, 2012	0.57–1.61	97	100 (6/6)
	Jun 20–22, 2013*	0.00–1.67	99	80 (4/5)
	Jul 3–5, 2013	0.00–0.79	100	100 (3/3)
	Aug 16–20, 2013*	0.00–0.26	100	100 (2/2)
	Aug 24–26, 2013	0.00–3.88	94	100 (3/3)
	Sep 2–7, 2013	0.00–4.09	93	(0/0)
Sarem Creek	Jul 22–25, 2012	0.00–3.33	87	66 (2/3)
	Sep 9–11, 2012	0.00–2.18	96	100 (2/2)
	Jun 11–15, 2013	0.00–2.18	86	0 (0/2)

eight tagged Largemouth Bass in the creek were detected leaving the creek, including three fish that were upstream of the receivers prior to the event. Some of the Largemouth Bass that left a tributary during a severe hypoxic event were sporadically detected on the downstream receiver in the tributary, but those fish only ventured far enough upstream to be detected on the upstream receiver during 3 of the 12 severe hypoxic events. Three of the eight coordinated movement events (i.e., when two or more Largemouth Bass moved out of a tributary on the same day) corresponded with severe hypoxic events as defined here (Table 1). Water quality profiles collected at the locations where tagged individuals were found during severe hypoxic events indicated that DO at those sites was not elevated relative to DO in adjacent areas.

Fish Assemblage, Relative Abundances, and Largemouth Bass Feeding Success

Electrofishing data were grouped based on whether transects were sampled at a DO concentration above 1.2 mg/L or at a concentration below 1.2 mg/L, the lower end of the range at which we detected avoidance behavior of Largemouth Bass. We sampled 19 transects in the main stem when DO was above 1.2 mg/L; 65 transects in tributaries when DO was above 1.2 mg/L; and 22 transects in tributaries when DO was below 1.2 mg/L. Dissolved oxygen concentrations below 1.2 mg/L were not observed in the main stem during any of the electrofishing transects. For these analyses, we combined data collected in the tributaries to allow for more statistical power.

We captured 27 fish species in transects conducted to determine the fish assemblage that was present in addition to Largemouth Bass. Bluegills *Lepomis macrochirus* made up the highest proportion of total fish (i.e., non-Largemouth Bass) that were caught under each of the three DO conditions (41% in the main stem at DO > 1.2 mg/L; 26% in tributaries at DO > 1.2 mg/L; and 45% in tributaries at DO < 1.2 mg/L); the next highest proportions consisted of Pumpkinseeds *L. gibbosus* (21, 13, and 18%, respectively) and Yellow Perch *Perca flavescens* (17, 6, and 8%, respectively). A majority of fish captured in these transects belonged to the 40–100 or 100–250 mm TL category; however, ANOVA performed with CPUE data from these transects indicated that CPUEs of the four size-classes did not significantly differ among the three DO conditions (Figure 4). We also found no significant differences in Largemouth Bass CPUE among the three DO conditions (main stem at DO > 1.2 mg/L: mean CPUE ± SE = 10.2 ± 0.4 fish/h; tributaries at DO > 1.2 mg/L: 11.4 ± 0.2 fish/h; tributaries at DO < 1.2 mg/L: 10.6 ± 0.6 fish/h; ANOVA: $F = 0.09$, df = 105, $P = 0.91$). However, linear regression indicated that Largemouth Bass CPUE increased with increasing DO concentration (slope $\beta = 1.8$, intercept $\alpha = 3.7$, $R^2 = 0.20$; $F = 2.7$, df = 57, $P = 0.003$).

We collected stomach content samples from 283 Largemouth Bass. The proportion of Largemouth Bass stomach samples containing at least one prey item (i.e., feeding success) was similar between the main stem (52%) and tributaries regardless of whether DO in the tributaries was above 1.2 mg/L (67%; $\chi^2 = 4.33$, df = 3, $P = 0.23$) or below 1.2 mg/L (34%; $\chi^2 = 3.98$, df = 3, $P = 0.26$). However, feeding success in the tributaries was significantly lower during severe hypoxic events (34%) than when DO was above 1.2 mg/L (67%; $\chi^2 = 21.03$, df = 3, $P < 0.0001$). Although the relationship was not significant, logistic regression of the proportion of Largemouth Bass feeding at observed DO concentrations provided some evidence that the odds of feeding success increased with increasing DO concentration (Figure 5; $\beta = 0.14$, $\alpha = -0.8$, $R^2 = 0.20$; Wald test statistic = 3.59, $P = 0.06$).

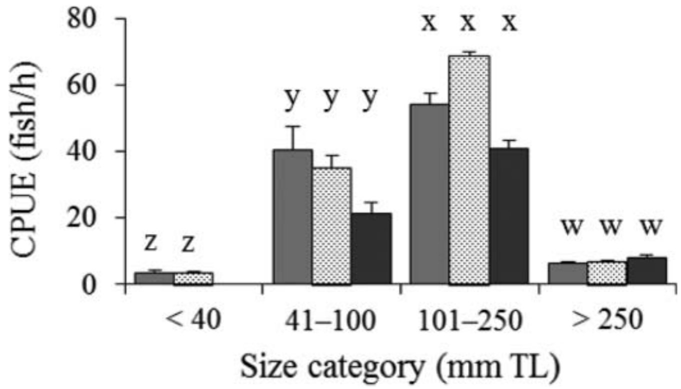

FIGURE 4. Comparison of the total fish species assemblage CPUE (mean + SE) for four size-classes (mm TL) at main-stem Chowan River sites (light gray bars), tributary sites during periods when dissolved oxygen (DO) was above 1.2 mg/L (stippled bars), and tributary sites during periods when DO was below 1.2 mg/L (dark gray bars). Letters indicate that within a given size-class, CPUE did not differ among DO conditions.

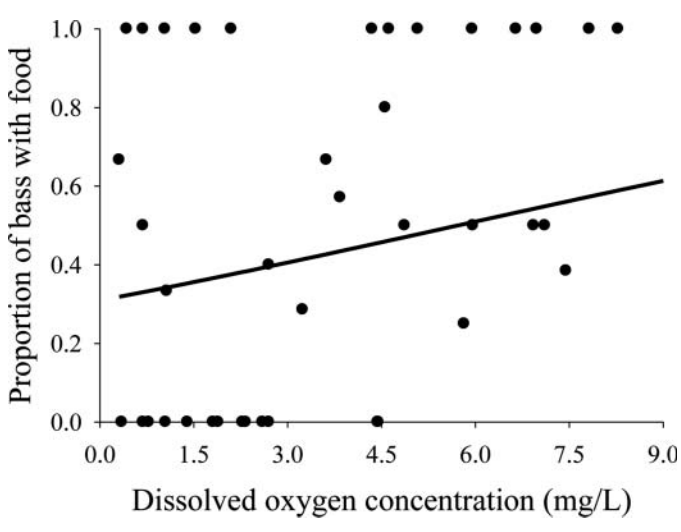

FIGURE 5. Observed proportion of Largemouth Bass that had food in their stomachs over a range of dissolved oxygen concentrations. The solid line indicates the predicted probability of a Largemouth Bass having food in its stomach, as calculated by logistic regression analysis.

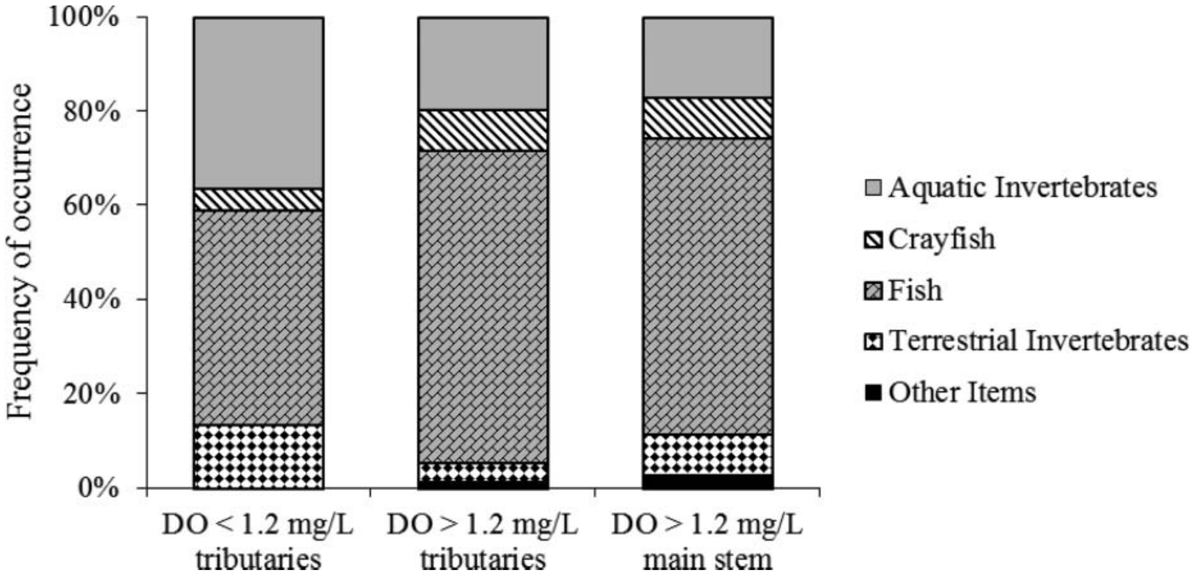

FIGURE 6. Frequency of occurrence for various prey types in the stomach contents of Largemouth Bass that were captured when the dissolved oxygen (DO) concentration was less than 1.2 mg/L (in tributaries only) or greater than 1.2 mg/L (in the main-stem Chowan River or tributaries).

We found a large proportion of fish—mainly small centrarchids—in the stomach contents of Largemouth Bass captured during the three DO conditions (Figure 6). There was little evidence that fish occurred less often in the stomach content samples of Largemouth Bass when captured at DO concentrations below 1.2 mg/L than when captured at DO above 1.2 mg/L ($\chi^2 = 7.86$, df = 3, $P = 0.49$); comparisons between the other conditions indicated no significant differences in the occurrence of fish prey. Furthermore, the occurrence of aquatic invertebrates in stomach contents did not differ between Largemouth Bass captured at DO less than 1.2 mg/L compared with fish captured at DO above 1.2 mg/L in the tributaries or main stem ($\chi^2 = 2.57$, df = 5, $P = 0.76$). We did not run statistical tests on the remaining prey types in the diet because sample sizes were too small.

Mortality Estimation

Monthly estimates of fishing mortality were below 5% for the first 10 months of our study. The highest estimate during that period occurred in January 2013 (2.2%); thereafter, estimates of fishing mortality fluctuated from near 0% to as high as 21% in April 2013 (Figure 7). We confirmed that six tagged fish died of natural causes during our study period; in accordance with this, our model estimated low natural mortality rates throughout the study period (Figure 7). Slight increases in the natural mortality estimates coincided with confirmed natural deaths in May 2012 ($n = 1$), September 2012 ($n = 2$), and April 2013 ($n = 1$). The highest monthly estimate of natural mortality occurred in July 2013, when we confirmed two deaths due to natural causes. Despite the same number of observed natural deaths, the natural mortality estimate for July 2013 was over twice the estimate for September 2012 due to the lower number of fish "at risk" within our study area at the time of estimation. Four Largemouth Bass were detected

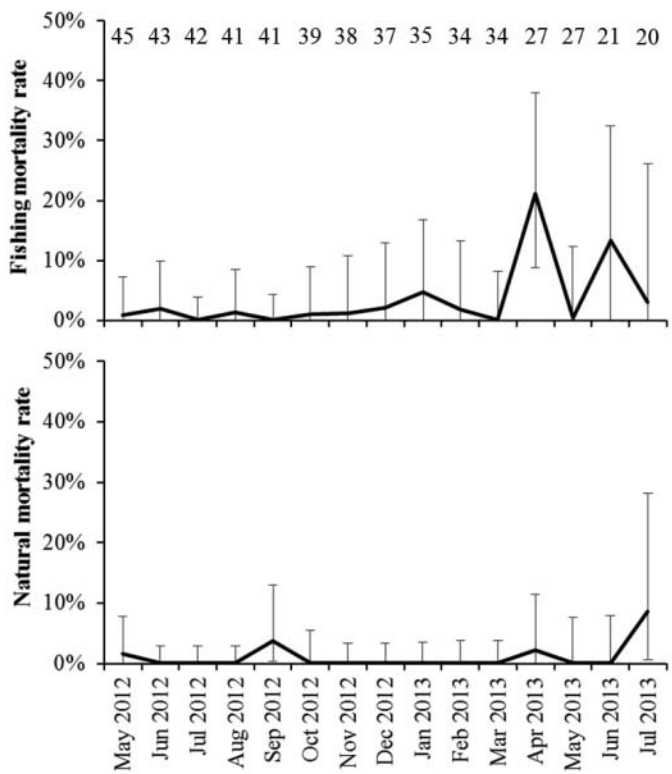

FIGURE 7. Median (±95% credible interval) monthly discrete rates of fishing mortality (upper panel) and natural mortality (lower panel) for Largemouth Bass in the Chowan River system, May 2012–September 2013. Numbers across the top of the upper panel indicate monthly sample sizes.

emigrating from our study area and were censored from the analysis after emigration.

We estimated that annual survival within the study area was 36% (95% credible interval [CI] = 24–49%) during this study. This estimate does not include the four individuals that were detected emigrating from the study area (and might have still been alive outside of the study area). The emigration of the four fish resulted in an estimated annual emigration rate of 10% (95% CI = 4–20%). The discrete annual fishing mortality rate was estimated at 38% (95% CI = 26–52%; instantaneous fishing mortality = 0.61) for all Largemouth Bass used in the study; however, this estimate included 22 Largemouth Bass below 355 mm TL (14 in), which is the North Carolina Wildlife Resources Commission's minimum size limit for harvest. When we calculated separate estimates for legal and sublegal sizes of Largemouth Bass, the annual fishing mortality rate for legal-sized fish was 45% (95% CI = 27–64%), whereas the rate for sublegal-sized fish was 33% (95% CI = 18–51%). Our discrete estimate of annual natural mortality was 14% (95% CI = 6–26%; instantaneous natural mortality = 0.22) and was not affected by size regulations.

DISCUSSION

Dissolved oxygen concentrations below 2.0 mg/L are commonly defined as hypoxic conditions (Pinckney 2001; Eby and Crowder 2002); however, relative tolerance to hypoxia is dependent upon the species and its habitat and life history (Davis 1975; Domenici et al. 2013; Franklin 2014). Largemouth Bass in this study tolerated DO concentrations that were well below the commonly accepted threshold for hypoxia, and they initiated avoidance behavior at DO concentrations below 1.8 mg/L. However, some Largemouth Bass remained in the tributaries even under these conditions and did not seek higher DO levels near the tributary mouths or in the main stem. Conversely, Hasler et al. (2009) found that Largemouth Bass in a Canadian lake avoided areas with slightly higher DO concentrations (<2.0 mg/L). Although latitudinal differences in DO tolerance could explain the differences between studies (Smale and Rabeni 1995), Largemouth Bass in coastal systems are regularly exposed to seasonal and episodic hypoxia and are thought to adapt to prolonged exposure (Sabo et al. 1998). Such adaptation may better explain differences in tolerance of low DO by Largemouth Bass in the present study and previous studies. Furthermore, Hurricane Irene, which made landfall in North Carolina during August 2011 and triggered a major fish kill in the Chowan River, may have acted as a selection event, leaving behind the individuals that were already better adapted to hypoxia.

Our results indicate that although Largemouth Bass may be able to tolerate low DO concentrations, remaining in areas of severe hypoxia can negatively affect their feeding success. We found that the odds of a Largemouth Bass having food in its stomach decreased with decreasing DO concentration. Although other studies have not calculated an odds ratio, decreasing food consumption rates in hypoxic waters have been observed for Striped Bass *Morone saxatilis* (Brandt et al. 2009), Summer Flounder *Paralichthys dentatus*, and Winter Flounder *Pseudopleuronectes americanus* (Stierhoff et al. 2006). In the present study, Largemouth Bass CPUE was negatively correlated with DO concentration, whereas the CPUE of potential prey fishes was not affected by DO concentration. This finding is supported by a number of studies that have reported decreases in Largemouth Bass feeding rates under hypoxic conditions; these prior studies have suggested decreases in swimming speed (Stewart et al. 1967), increases in metabolic cost (reviewed by Domenici et al. 2013), and separation from prey (Yamanaka et al. 2007) as possible causes of depressed feeding rates. Although we observed a reduction in the feeding success of Largemouth Bass under hypoxic conditions in the tributaries, it did not appear to drive their movement into the main stem, as feeding success was not significantly higher under the non-hypoxic conditions present in the main stem.

In the Chowan River, a coastal North Carolina river system, the natural mortality of Largemouth Bass during a period without a prolonged extreme hypoxic event was similar to or lower than natural mortality rates in other systems. The overall mean instantaneous natural mortality rate of 0.22 in the present study was considerably lower than the rate of 0.46 reported by Beamesderfer and North (1995). However, their rate was calculated using data from 40 Largemouth Bass populations across North America and included individuals from all life stages starting at age 1. Similarly, for Largemouth Bass in a Puerto Rican reservoir, Waters et al. (2005) estimated an instantaneous natural mortality rate of 0.31, which was higher than the rate observed in our study. Waters et al. (2005) determined that a prolonged spawning season due to elevated water temperatures and catch-and-release mortality heavily influenced natural mortality in that system. We were unable to distinguish catch-and-release mortality from natural mortality in our study, but given the low observed natural mortality rate, catch-and-release mortality did not appear to substantially influence the natural mortality estimate.

Discrete annual fishing mortality in our study may have overestimated the actual fishing mortality during the study period. Our fishing mortality estimate potentially included fish that were transported from our study area during tournament or recreational angling activities. We confirmed one such event in May 2013, when we detected a tagged Largemouth Bass at a boat launch downstream of the Chowan River study reach after an angling tournament. That individual returned to our study area and was included in our analysis; however, this situation highlighted the potential for angler transport to affect mortality estimates. In addition, Largemouth Bass use of habitats upstream of fixed listening points in the tributaries or in forested shallows may have resulted in missed detections. Any natural mortality of fish utilizing these habitats would have been included in our estimates of fishing mortality, which may help to explain the high annual fishing mortality rates estimated for legal- and sublegal-sized Largemouth Bass.

The results presented here indicate that Largemouth Bass on the coast of North Carolina are well adapted to cope with episodic hypoxia during years without major storm activity. Our findings suggest that some Largemouth Bass exhibit avoidance behavior in association with a range of hypoxic conditions in the tributaries and that this movement is a direct response to hypoxia itself rather than to hypoxia-mediated reductions in foraging opportunity. An understanding of the effects of hypoxic events and the impact of fish kills on Largemouth Bass populations is imperative for successful management because supplemental stocking along the coast of North Carolina appears to be ineffectual (Thomas and Dockendorf 2009). Our low estimate of annual natural mortality suggests that years without major storm activity allow time for the Largemouth Bass population to recover from these detrimental events. An examination of the effects of hypoxia on juvenile Largemouth Bass was beyond the scope of this study but could provide valuable information on the population's ability to recover after major storm events.

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