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ARTICLE

Effects of Turbidity on Prey Selection and Foraging Return of Adult Largemouth Bass in Reservoirs

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Abstract

Previous laboratory studies have demonstrated that turbidity alters prey selection by Largemouth Bass *Micropterus salmoides*, but this has not been tested in the field. Laboratory studies have also suggested that daily rates of consumption by Largemouth Bass may decline as turbidity increases and that the rate of decline may differ among prey types, possibly providing a mechanism that drives the observed prey selection patterns. We conducted laboratory trials to measure daily consumption rates for Largemouth Bass when foraging on Bluegills *Lepomis macrochirus* and Gizzard Shad *Dorosoma cepedianum*; we also collected field data in three reservoir systems (Boomer, Sooner, and Guthrie lakes, Oklahoma) during 2 years to evaluate Largemouth Bass prey selection and consumption rates over a range of turbidity levels. In the laboratory trials, Largemouth Bass daily consumption rates declined with increased turbidity, but the decline was similar between the two prey types. We detected no correlations between turbidity and consumption rate (percentage of empty stomachs or mean weight of prey in stomach contents) in the field. Field-measured prey selection was highly variable among reservoirs and between sampling years, yet all but one reservoir × year combination had significant correlations between prey selection and turbidity, which generally followed the predictions of previous laboratory results (greater use of fish prey [especially centrarchids] and reduced use of crayfish at high levels of turbidity). However, the use of crayfish prey under low-turbidity conditions was higher than that expected based on previous laboratory trials. Further research is needed to determine which factors regulate the effects of increased turbidity on predator foraging return and to evaluate the food web implications of turbidity-related changes in the diets of top predators.

Turbidity is highly variable and often reaches high levels in many aquatic systems, leading to reduced visibility for visually oriented predators. Turbidity can vary daily due to wind (Chung et al. 2009) or rain events (Mallin et al. 2009), seasonally through changes in weather patterns or changes in the phytoplankton community (Nellis et al. 1998), and over larger time scales via eutrophication or anthropogenic disturbance (Bilotta and Brazier 2008). Changes in turbidity may strongly affect visual predators, including most sport fishes, leading to changes in the types and amounts of prey consumed; such changes could ultimately alter trophic dynamics in lakes and

reservoirs (Ranaker et al. 2012; Jönsson et al. 2013). Therefore, it is important to understand these turbidity-related dynamics when managing aquatic systems.

Turbidity likely reduces piscivores' foraging return (net energy gained from the foraging process) by decreasing the reactive distance between the piscivores and their prey (Crowl 1989; Miner and Stein 1996; Vogel and Beauchamp 1999), ultimately reducing the predators' ability to locate prey (Huenemann et al. 2012; Ranaker et al. 2012; Jönsson et al. 2013). This change in predator foraging efficiency could lead to reductions in the growth potential of piscivorous sport fishes.

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However, studies addressing this topic have produced conflicting results. Increased turbidity did not affect the rates of consumption by Yellow Perch *Perca flavescens* (Abrahams and Kattenfeld 1997) or Muskellunge *Esox masquinongy* (VanLandeghem et al. 2011) but did cause a decrease in consumption rates for Eurasian Perch *Perca fluviatilis* (Pekcan-Hekim and Lappalainen 2006). Even among studies that have investigated the same piscivore species (i.e., Largemouth Bass *Micropterus salmoides*), conflicting results have been reported. Reid et al. (1999) found that juvenile Largemouth Bass (FL range = 83–130 mm) had lower consumption rates during higher turbidity trials in a laboratory environment. However, those authors found no turbidity-related effects on the rates of consumption by adult Largemouth Bass (FL range = 192–245 mm). Similarly, VanLandeghem et al. (2011) found no effect of turbidity on the consumption rate of Largemouth Bass (mean TL = 170 mm) when turbidity reduced the Secchi depth to moderate levels (300 mm) in laboratory experiments. In contrast, during laboratory trials with Largemouth Bass, Shoup and Wahl (2009; predator TL range = 205–250 mm) and Huenemann et al. (2012; mean predator TL = 170 mm) found that the predators took longer to consume prey at higher turbidity levels. Although the two studies did not specifically quantify daily consumption rates, the results of both suggest that Largemouth Bass are unable to consume sufficient prey to meet daily energy requirements at high turbidity levels. Because of the conflicting results of previous studies, further research is needed to determine how turbidity affects piscivores' foraging return.

Turbidity can alter prey selection by piscivores in addition to affecting their foraging return. In laboratory trials, Largemouth Bass switched from eating fish prey (Gizzard Shad *Dorosoma cepedianum* or Bluegills *Lepomis macrochirus*) at low turbidity levels to a broader diet that included slower benthic prey (Northern Crayfish *Orconectes virilis*) at moderate levels of turbidity (Shoup and Wahl 2009). Largemouth Bass consumed few prey at high turbidity levels, but the prey that were consumed were almost exclusively Bluegills. Field tests are needed to determine whether these laboratory-observed prey selection patterns occur in natural systems. Furthermore, Shoup and Wahl (2009) reported that the capture efficiency of predators when feeding on different prey types declined at different rates as turbidity increased, thus providing a potential mechanism to explain the changes in prey selection at higher turbidity levels. However, this hypothesis remains untested.

Knowledge of turbidity effects on Largemouth Bass foraging return and prey selection will allow for a better understanding of food web changes that may occur as turbidity changes and will indicate which prey types are most suitable for Largemouth Bass at different turbidity levels. For example, if Largemouth Bass are not able to efficiently feed on Gizzard Shad at high turbidity levels (as was suggested by Shoup and Wahl 2009), then they could be food limited—even in lakes with high prey abundance—if Gizzard Shad are the

predominant prey. Further, if Largemouth Bass capture fewer prey at high levels of turbidity, this could result in weaker top-down trophic effects (Ranaker et al. 2012; Jönsson et al. 2013) and would suggest that management strategies requiring high growth rates (e.g., management for a trophy fishery) should be avoided in turbid systems. Therefore, to better understand the effects of turbidity on Largemouth Bass, we conducted a study with two objectives. The first objective was to quantify the daily rates of consumption by Largemouth Bass held at different turbidity levels in the laboratory, which would allow us to (1) assess the ability of Largemouth Bass to obtain sufficient food under turbid conditions and (2) test for prey-species-specific differences in the rate at which daily consumption declines in response to increasing turbidity (i.e., to determine whether this is a possible mechanism driving turbidity-specific changes in prey selection). The second objective was to use field data to determine whether the laboratory-derived patterns of foraging return and prey selection also occur in natural systems.

METHODS

Laboratory quantification of daily consumption at different turbidity levels.—Largemouth Bass (TL range = 230–350 mm) and prey fish (Bluegills and Gizzard Shad) were collected from reservoirs (near Stillwater, Oklahoma) where all three species co-occur. Bluegills and Gizzard Shad were chosen as prey types because they are common in the diets of Largemouth Bass that inhabit lakes and reservoirs (Van Den Avyle and Roussel 1980; Olson 1996) and because anecdotal observations suggest that Largemouth Bass consumption of these two prey types declines at different rates as turbidity increases (Shoup and Wahl 2009). Prey size was matched to each predator based on the optimal size (i.e., the prey size that minimizes the handling time : prey biomass ratio for a given predator size; Hoyle and Keast 1987). Bluegill lengths were 28% of predator TL (Hoyle and Keast 1987), and Gizzard Shad lengths were 33–35% of predator TL (L. M. Einfalt and D. H. Wahl, Illinois Natural History Survey, unpublished data). These prey lengths are well within the range commonly observed in the diets of field-collected Largemouth Bass (Timmons and Pawaputanon 1982; Hoyle and Keast 1987). Predators and prey were allowed to acclimate to laboratory conditions for at least 2 weeks. During this time, Largemouth Bass were fed equal amounts of both prey types. Trials were conducted when appropriate-sized Gizzard Shad were available (80–110 mm TL; August–October). Both predators and prey fish were held in clear water (i.e., tap water; <1 NTU) prior to the experiments.

Experiments were conducted indoors in round, polypropylene tanks (total volume = 2.46 m³; diameter = 2 m; depth = 860 mm); water temperature was between 18°C and 19°C, and natural light was provided by skylights. We tested 16 Largemouth Bass during the Bluegill trials and 12 Largemouth Bass during the Gizzard Shad trials. Each predator was tested

once at each of six turbidity ranges (0–3, 3–7, 7–11, 11–15, 15–25, and 25–57 NTU), which were administered in randomized order. Turbidity ranges were narrower at lower turbidity levels because the effects per unit of change (1 NTU) are typically greatest at low turbidity. The specific turbidity level within each range was measured for each trial by using a tungsten-bulb nephelometric turbidity meter (Hach Model 18900 ratio turbidimeter) that was calibrated with a 10-NTU formazin standard. This range of turbidity is typical of lakes and reservoirs in the United States (Bigham Stephens et al. 2015; USEPA and NALMS 2015). To produce the appropriate turbidity level for each trial, a bentonite clay slurry was added to the tanks at least 24 h before the trial began. A 15-cm air stone in the middle of each tank was used to keep clay suspended, maintaining turbidity at the desired level ($\pm 10\%$).

Because a single type of clay was used in the laboratory experiment, turbidimetric measurements were preferable to Secchi depth measurements, as the former are more precise under these conditions. However, different turbidimeters can vary substantially (e.g., by more than an order of magnitude) in their turbidity readings on the same sample (Davies-Colley and Smith 2001), thus hindering comparison among studies. Furthermore, turbidimeter readings are also heavily influenced by particle size and shape even when the same meter is used (Davies-Colley and Smith 2001). Given the variety of particle shapes generating in-lake turbidity over time, nephelometric turbidity readings could vary independently of visibility (the environmental condition that is hypothesized to affect Largemouth Bass consumption rates) in field studies. Therefore, Secchi depths are preferable to turbidimetric measurements for field sampling because they avoid this issue and have more immediate environmental relevance (Duchrow and Everhart 1971; Davies-Colley and Smith 2001). To facilitate direct comparison of our laboratory results with those of other studies and with our field objective, we developed a regression equation to describe the relationship between Secchi depth and the turbidity measured by our turbidimeter.

To standardize hunger among Largemouth Bass, the predators were fed to satiation 72 h prior to the start of each trial and were not fed again until the trial began. Each Largemouth Bass was placed in a translucent plastic box within the experimental tank 24 h prior to the start of the trial to allow acclimation to the given turbidity level. Holes were drilled in the sides of the box, allowing the turbid tank water to flow through the container. Ten individuals of a single prey type (Bluegill or Gizzard Shad, tested in separate trials) were also added to each tank 24 h prior to the trial, producing a prey density of approximately 6 fish/m² (or 10 fish/m³), which is similar to that used in previous predator–prey studies (Savino and Stein 1989; Reid et al. 1999; Shoup and Wahl 2009) and is within the range of natural prey densities encountered in the field (Hackney 1978; Degan and Wilson 1995). After the 24-h acclimation period, the hinged top of the predator cage was opened to release the Largemouth Bass, and the predator was

given 24 h to forage. At the end of the trial, the Largemouth Bass was removed by seining the tank. The tank was then drained to recover and count the remaining prey.

Generalized linear mixed regression models (GLIMMIX procedure in the Statistical Analysis System [SAS], with Poisson distribution specified in the model statement; SAS Institute 2011) with repeated measurements (i.e., random intercept, with Largemouth Bass specified as subjects in the GLIMMIX random statement) were used to evaluate relationships between turbidity (NTU; treated as a fixed factor in the model) and the number of prey consumed in a 24-h period. Separate regression models were used to test data from Bluegill trials and Gizzard Shad trials. A *t*-test was used to compare the slopes of the models for the Bluegill and Gizzard Shad trials. Measured daily consumption rates were compared to literature values for Largemouth Bass daily rations to determine whether turbidity reduced consumption to a degree that would be likely to limit growth.

Field study.—Largemouth Bass were sampled by electrofishing in Boomer Lake (105 ha), Sooner Lake (2,185 ha), and Guthrie Lake (274 ha), Oklahoma. These reservoirs have average to moderately high electrofishing catch rates for Largemouth Bass and have variable turbidity levels (OWRB 2004, 2005; Oklahoma Department of Wildlife Conservation, unpublished data). Reservoirs were electrofished from a 4.9-m boat (Smith-Root Model SR-16EB) equipped with a Smith-Root 5.0 generator-powered pulsator and two boom-mounted Smith-Root SAA-6 anode arrays using pulsed-DC electricity (50–500-V setting, 60 pulses/s; percent of range was adjusted for conductivity to apply approximately 60 $\mu\text{W}/\text{cm}^3$ to the fish). Electrofishing transects (10 min/transect) at fixed locations (11 sites for Boomer Lake, 14 sites for Sooner Lake, and 9 sites for Guthrie Lake) were sampled approximately once per week for 4–7 weeks during spring 2008 and spring 2009 (Guthrie Lake was only sampled in 2009). Transects were selected with a stratified random design to incorporate all available habitat types (e.g., rip-rap, brush, and standing timber). Spring sampling was selected because it produced relatively high electrofishing catch rates and because prey abundances were stable during this time.

We were unable to obtain comparable data on prey abundance because we would have needed several different gears to sample all prey types (e.g., crayfish traps for burrowing crayfish; gill nets or hydroacoustics for Gizzard Shad; electrofishing or seining for centrarchids; etc.); the various gears would have had incomparable units of effort and differing biases. For cases in which the variety of consumed prey types requires multiple sampling methods, comparisons of prey availability at best have numerous theoretical problems and at worst have no meaningful relationship with actual availability to the predator (Wallace 1981). Therefore, instead of attempting to quantify prey abundance in a situation where gear bias would confound the results, we chose a study design that allowed us to assume that prey availability and size structure

within the lake were relatively stable during the study. We did this by (1) confining the annual sampling in each lake to a short period (i.e., spring) that occurred before young-of-the-year fish were large enough to be consumed by adult piscivores; and then (2) confining the analysis to samples within each lake \times year combination.

Stomach contents were removed from sampled Largemouth Bass (≥ 230 mm TL) by inserting an acrylic tube through the esophagus and into the stomach (Van Den Avyle and Roussel 1980). Stomach contents were identified to the lowest possible taxonomic level, and intact prey were measured for length (TL, SL, or backbone length). A Secchi disk was used to measure visual clarity at each transect on each sampling date. Secchi disk measurements were always taken by the same person (without wearing sunglasses), and the disk was deployed on the shaded side of the boat.

Prey items sampled from Largemouth Bass stomachs were assigned to one of five taxonomic groups: centrarchids, Gizzard Shad, crayfish, other fish (primarily Inland Silversides *Menidia beryllina*, juvenile Largemouth Bass, and cyprinids), and other non-fish items (primarily amphibians, reptiles, and insects). Prey selection was quantified in terms of percentages based on predigested weight to reflect the relative importance of each prey type to the energy budget of the predator (Bowen 1996). Predigested weights were estimated from prey length measurements (TL, SL, or backbone length) by using regression equations (Knights et al. 1984; Wahl and Stein 1991; Brown and Konoval 1993; Raborn et al. 2002; D. E. Shoup, unpublished data for crayfish). In a few cases, advanced digestion prevented the accurate measurement of prey lengths, so mean prey weight for the taxon was used instead (prey weight was not significantly correlated with predator length, so no attempt was made to scale this to predator size). To estimate the effects of turbidity on the total quantity of food consumed, we also quantified diet data based on (1) the percentage of fish with empty stomachs and (2) the mean predigested weight of all prey types (combined) divided by the predator weight.

Relationships between Secchi depth and each prey consumption metric (total mass consumed, percentage of stomachs that were empty, and prey percentage by weight; total mass was $\log[x + 1]$ transformed and percent variables were arcsine-square root transformed to normalize the residuals) were tested with several regression model types (linear, exponential, power, second-order polynomial, and third-order polynomial) by following the methods of Shoup and Wahl (2009) to account for differing curvatures in the data from different lake \times year combinations. All models accounted for repeated measurements (transects repeatedly sampled on different dates; transects were treated as subjects, and date was treated as a random factor) by using the MIXED procedure in SAS (SAS Institute 2011). The most appropriate model for each metric was determined through lack-of-fit tests and residual analyses (Kutner et al. 2005) and was then tested for the significance of slope functions to determine whether the

predator's prey selection varied with changes in turbidity. Data from each lake \times year combination were analyzed separately because the prey assemblages could have differed among lakes or between years, and we only wanted to test for turbidity patterns within similar prey assemblages. Preliminary analyses indicated that the regression model with the best fit to the data differed among prey types (i.e., multivariate responses). Because a MANOVA model would have required all multivariate responses to have the same model shape, we did not use an initial multivariate test to control type I error. Instead, we tested each univariate response (i.e., prey type) separately, and type I error was controlled by using a Holm-Bonferroni adjustment to constrain the familywise α to 0.05. Significant best-fit models were then compared with the trends reported by Shoup and Wahl (2009) to determine whether our field observations were consistent with the predictions from that laboratory study (i.e., a positive or negative relationship with turbidity).

RESULTS

Laboratory Study

A decaying exponential function best described the relationship between Secchi depth (mm) and turbidity (NTU; Figure 1). Secchi depths used in the experiment ranged from over 760 mm (760 mm was the water depth during trials; a Secchi depth of 760 mm = a turbidity of 1.7 NTU) to 109 mm (57 NTU).

For both Bluegills and Gizzard Shad, daily consumption (number of prey consumed/24 h) by Largemouth Bass decreased significantly as turbidity increased (Figure 2). When foraging on Bluegills, Largemouth Bass consumption rates were highest (averaging ~ 3 fish/24 h; range = 1–7 fish/24 h)

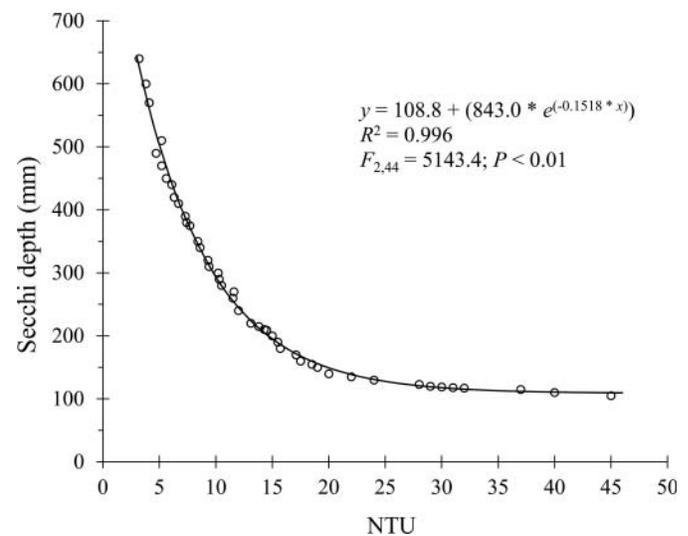


FIGURE 1. Relationship between Secchi depth (mm) and turbidimetric measurements (NTU) for bentonite clay turbidity levels used in laboratory trials examining Largemouth Bass foraging rates.

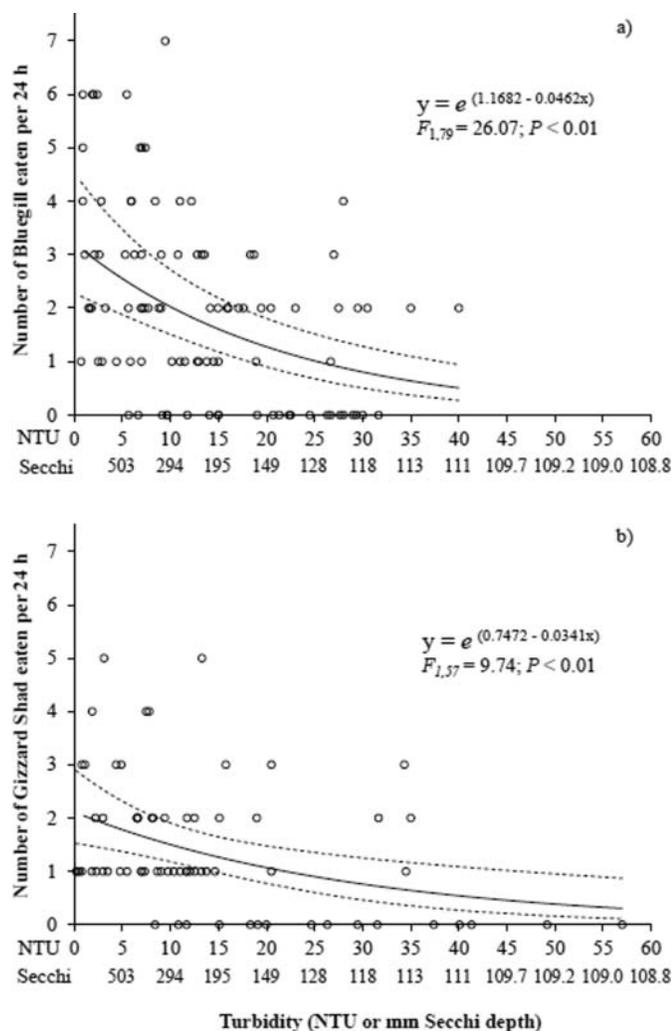


FIGURE 2. Consumption rates (number of Bluegills or Gizzard Shad consumed per 24 h) for Largemouth Bass held at different turbidity levels (NTU; with corresponding Secchi depths, mm) in the laboratory (solid line = trend line; dashed lines = 95% confidence interval).

at turbidity levels between 0 and 3 NTU (Secchi depth > 643 mm) and declined rapidly as turbidity increased, leading to an average consumption rate of 0.5 fish/24 h (range = 0–4 fish/24 h) at turbidity levels greater than 25 NTU (Secchi depth < 128 mm; Figure 2a). Each Largemouth Bass ate at least one Bluegill when turbidity was less than 6 NTU (Secchi depth > 448 mm). Over half of the Largemouth Bass did not eat any prey when tested at turbidity levels exceeding 25 NTU (Secchi depth < 128 mm).

When foraging on Gizzard Shad, Largemouth Bass also exhibited their highest consumption rates at turbidity levels between 0 and 3 NTU (Secchi depth > 643 mm), averaging about 2 fish/24 h (range = 1–5 fish/24 h; Figure 2b). Consumption rates declined as turbidity increased, resulting in an average of 0.6 fish/24 h (range = 0–3 fish/24 h) at turbidity levels greater than 25 NTU (Secchi depth < 128 mm). Each

Largemouth Bass ate at least one Gizzard Shad when tested at turbidities less than 8 NTU (Secchi depth > 359 mm). Only 25% of the predators consumed at least one Gizzard Shad at turbidity levels exceeding 25 NTU (Secchi depth < 128 mm); no Gizzard Shad were consumed by any predator when turbidity was greater than 36 NTU (Secchi depth < 112 mm). The regression slopes were not significantly different ($P = 0.39$) between the Bluegill trials and the Gizzard Shad trials, indicating that the rate at which consumption decreased in response to turbidity was not species specific.

Our measured daily consumption rates were well below the reported daily ration levels for Largemouth Bass—typically 2.2% to 5.0% of wet weight (Hunt 1960; Cochran and Adelman 1982). Given the average sizes of prey used in our experiment (433 g for Bluegills; 353 g for Gizzard Shad), Largemouth Bass would have had to consume 0.9–1.6 Bluegills/d or 1.0–2.2 Gizzard Shad/d to match the 2.2–5.0% daily ration. Largemouth Bass ate fewer prey on average than the lower reported daily ration of 2.2% when turbidity levels were above 22–26 NTU (Secchi depth < 139 mm to 125 mm; Figure 2).

Field Study

Overall, 714 Largemouth Bass (>230 mm TL) were sampled from the three lakes during the 2-year study (125–205 individuals per lake × year combination) and were analyzed for diet composition. Secchi depth in the field ranged from 860 mm to 150 mm, corresponding to approximately 0.75–20.0 NTU in the present laboratory experiments and to 2.1–29.2 NTU in the prey selection laboratory experiments of Shoup and Wahl (2009). Across all samples, the most commonly eaten prey types were centrarchids, Gizzard Shad, and crayfish, although the prey type that was most frequently eaten varied among systems and between years (Figure 3). In Sooner Lake during 2009, Largemouth Bass diets were very consistent and were almost entirely composed of crayfish. Other lake × year combinations had several prey types that were commonly consumed.

The effect of turbidity on the total (combined) prey mass per unit of predator weight was best described by an exponential model, but none of the lake × year combinations had a significant slope for this metric ($P > 0.14$ for all lake × year combinations). The mean prey mass ranged from 0.9% to 2.7% of predator weight across lakes and years. Similarly, no significant correlation was found between turbidity and the percentage of empty stomachs observed (a power function was the best model for all lake × year combinations, but $P > 0.22$ for the slope in all cases). The mean percentage of fish with empty stomachs ranged from 39% to 68% across lakes and years.

Significant relationships between Secchi depth and the prey percentage by weight were found for at least one prey type in all lake × year combinations (Table 1; Figure 4) except Sooner

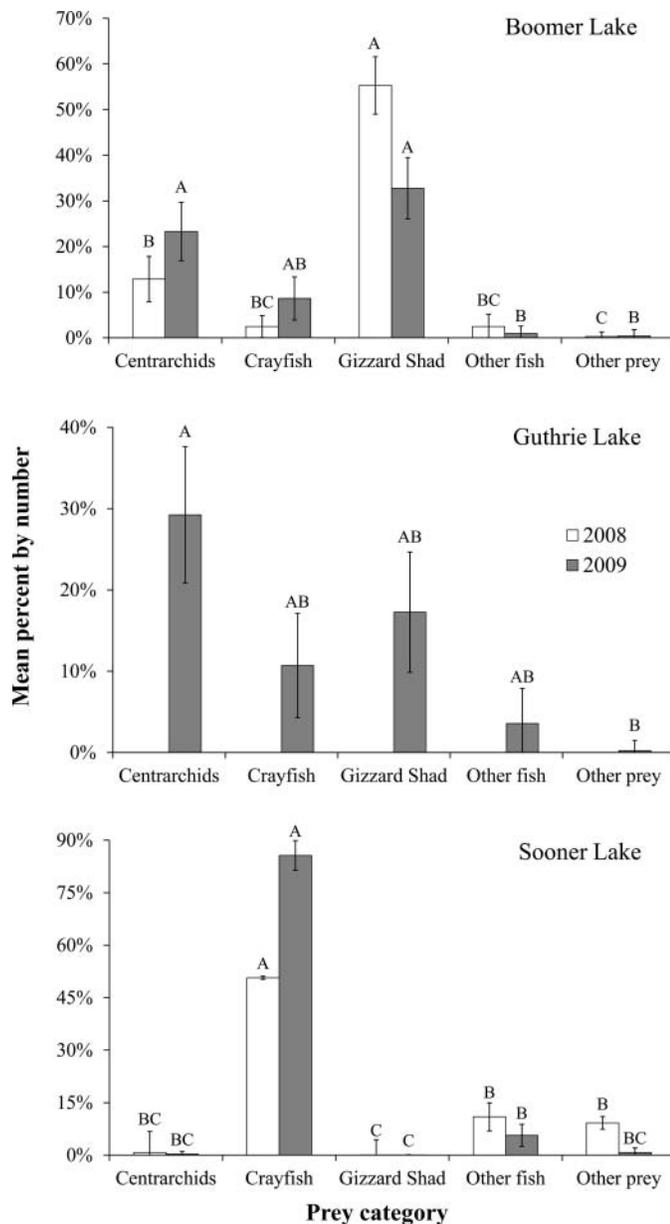


FIGURE 3. Mean (\pm SE) percent composition (by number) of prey types in the stomach contents of Largemouth Bass sampled from Boomer, Sooner, and Guthrie lakes, Oklahoma, during 2008 and 2009. Letters indicate significant differences ($P \leq 0.05$) among prey types. Note that the y-axis scaling differs among the three panels.

Lake in 2009, where almost all Largemouth Bass had consumed crayfish during all sample dates (Secchi depth range = 190–1,260 mm). Much variability among lakes existed with respect to the best-fitting model, specific regression parameter values, and even which prey types were correlated with turbidity, suggesting that lake-specific conditions were important. However, the broad patterns (i.e., positive or negative slopes) were generally similar for each prey type when significant correlations existed (Figure 4). Proportional consumption of

centrarchids typically increased exponentially as turbidity increased (i.e., as Secchi depth decreased). The one exception was for Sooner Lake in 2008: the centrarchid percentage by weight initially increased as Secchi depth decreased from 740 to 500 mm, but then the metric leveled off and subtly decreased as Secchi depth further declined from 500 to 390 mm. The crayfish percentage by weight typically decreased linearly or as an exponential decay function in response to a decrease in Secchi depth (Figure 4). Correlations between turbidity (Secchi depth) and the centrarchid and crayfish percentages by weight were significant for three of the five lake \times year combinations tested (Table 1). For the other prey types examined, significant correlations with turbidity were not as consistent among lakes and years. The “other fish” category was positively correlated with turbidity at Boomer Lake in 2009 and at Guthrie Lake in 2009. The Gizzard Shad percentage by weight exhibited a positive correlation with turbidity at Boomer Lake in 2009. The “other prey” category was positively correlated with turbidity at Sooner Lake in 2008. Overall, few significant relationships between prey percentages by weight and turbidity level were found for Guthrie Lake in 2009 or Sooner Lake in 2009 relative to the other lake \times year combinations (Table 1).

DISCUSSION

Predation is an important force shaping freshwater communities (Shurin et al. 2002; Vander Zanden et al. 2005; Jonsson et al. 2007), but its effects vary depending on abiotic conditions (Hunter 1968; Jackson et al. 2001). When considering potential competitive interactions and prey availability, it is important for fisheries managers to understand how changes in habitat characteristics, such as turbidity, affect predator behavior. For example, Evans et al. (2014) provided a tool for use in evaluating predator demand and prey sufficiency for Gizzard Shad. However, our present results demonstrate that at some turbidity levels, Largemouth Bass may not consume as many Gizzard Shad relative to other prey types, even when Gizzard Shad abundance is unchanged. Therefore, managing for increased abundance of Gizzard Shad may not benefit Largemouth Bass to the same extent predicted by Evans et al. (2014) if turbidity reduces their use of Gizzard Shad. Most turbidity research with piscivores has been conducted in a laboratory environment; our study is the first to investigate the effects of turbidity on prey selection by piscivores in the field. We found that in most of the systems examined, Largemouth Bass changed their prey selection in relation to turbidity. However, it is important to remember that the observed turbidity-related changes in the diet were due to short-term changes, whereas fish in chronically clear or chronically turbid systems might not maintain such prey selection patterns over longer periods of time. Nevertheless, our results suggest that fisheries managers should be mindful that not all prey types are equally accessible to Largemouth Bass populations at different turbidity levels. Piscivores can alter the biomass at each trophic level

TABLE 1. Results of regressions correlating Secchi depth (mm) with prey percentages by weight in the stomach contents of Largemouth Bass sampled from Boomer, Guthrie, and Sooner lakes, Oklahoma, during 2008 and 2009. Significant models (Holm–Bonferroni-adjusted familywise $\alpha = 0.05$) are presented in bold italics. Constants were derived from the linearized forms of the curves as defined below the table.

Prey type	Model type ^a	Slope(s)				Intercept		<i>R</i> ²	<i>N</i>		
		<i>b</i> ₁	<i>P</i>	<i>b</i> ₂	<i>P</i>	<i>a</i>	<i>P</i>				
Boomer Lake, 2008											
<i>Centrarchids</i>	<i>Power</i>	<i>−4.34</i>	<i><0.01</i>					<i>9.45</i>	<i>0.04</i>	<i>0.39</i>	<i>21</i>
<i>Crayfish</i>	<i>Linear</i>	<i>3.5 × 10^{−3}</i>	<i>0.03</i>					<i>−0.54</i>	<i>0.17</i>	<i>0.57</i>	<i>21</i>
Gizzard Shad	Power	1.55	0.34					−3.86	0.36	0.43	21
Other fish	Power	0.39	0.72					−1.72	0.54	<0.01	21
Other prey	Power	−0.04	0.97					−0.81	0.72	<0.01	21
Boomer Lake, 2009											
<i>Centrarchids</i>	<i>Exponential</i>	<i>−1.5 × 10^{−3}</i>	<i>0.01</i>					<i>0.28</i>	<i>0.25</i>	<i>0.65</i>	<i>17</i>
<i>Crayfish</i>	<i>Exponential</i>	<i>2.0 × 10^{−3}</i>	<i><0.01</i>					<i>−1.36</i>	<i><0.01</i>	<i>0.46</i>	<i>17</i>
<i>Gizzard Shad</i>	<i>Power</i>	<i>−1.80</i>	<i>0.01</i>					<i>4.16</i>	<i>0.04</i>	<i>0.68</i>	<i>17</i>
<i>Other fish</i>	<i>Linear</i>	<i>−7.7 × 10^{−4}</i>	<i>0.02</i>					<i>0.41</i>	<i>0.02</i>	<i>0.58</i>	<i>17</i>
Other prey	Linear	4.5 × 10 ^{−4}	0.10					−0.10	0.37	0.51	17
Guthrie Lake, 2009											
Centrarchids	Exponential	1.8 × 10 ^{−3}	0.12					−1.56	0.10	0.42	12
Crayfish	Exponential	−1.0 × 10 ^{−3}	0.44					0.23	0.78	<0.01	12
Gizzard Shad	Linear	6.0 × 10 ^{−4}	0.48					−0.18	0.75	0.57	12
<i>Other fish</i>	<i>Linear</i>	<i>−3.4 × 10^{−3}</i>	<i>0.01</i>					<i>2.43</i>	<i>0.04</i>	<i>0.50</i>	<i>12</i>
Other prey	Linear	8.2 × 10 ^{−6}	0.98					0.03	0.87	0.80	12
Sooner Lake, 2008											
<i>Centrarchids</i>	<i>Third-order polynomial</i>	<i>0.02</i>	<i>0.01</i>	<i>−2.8 × 10^{−5}</i>	<i><0.01</i>	<i>1.3 × 10^{−8}</i>	<i><0.01</i>	<i>−3.24</i>	<i>0.05</i>	<i>0.95</i>	<i>17</i>
<i>Crayfish</i>	<i>Exponential</i>	<i>2.9 × 10^{−4}</i>	<i>0.04</i>					<i>−0.20</i>	<i>0.10</i>	<i>0.95</i>	<i>17</i>
Gizzard Shad	Linear	−5.5 × 10 ^{−5}	0.68					0.08	0.49	<0.01	17
Other fish	Second-order polynomial	3.4 × 10 ^{−3}	0.13	−2.4 × 10 ^{−6}	0.09			−0.71	0.41	0.54	17
<i>Other prey</i>	<i>Linear</i>	<i>−7.1 × 10^{−4}</i>	<i>0.01</i>					<i>0.63</i>	<i>0.03</i>	<i>0.80</i>	<i>17</i>
Sooner Lake, 2009											
Centrarchids	Linear	3.4 × 10 ^{−5}	0.80					0.05	0.62	0.47	23
Crayfish	Power	−0.05	0.86					0.19	0.83	0.73	23
Gizzard Shad	Linear	−3.9 × 10 ^{−5}	0.55					0.04	0.41	0.44	23
Other fish	Linear	−3.7 × 10 ^{−4}	0.26					0.55	0.08	0.15	23
Other prey	Second-order polynomial	−2.5 × 10 ^{−4}	0.71	3.9 × 10 ^{−7}	<0.01			0.06	0.81	0.73	23

^aLinear model: $y = bx + a$; exponential model: $y = a' \times 10^{(bx)}$; linear form of the exponential model: $\log(y) = bx + a$; power model: $y = a' \times x^b$; linear form of the power model: $\log(y) = b \cdot \log(x) + a$; second-order polynomial model: $y = b_1x + b_2x^2 + a$; third-order polynomial model: $y = b_1x + b_2x^2 + b_3x^3 + a$. In all equations $a' = 10^a$.

through prey consumption, the effects of which can lead to top-down cascades (Hairston et al. 1960; Carpenter et al. 1985). Changes in turbidity could alter these trophic cascades either by weakening the original piscivore–prey link or by changing piscivore diets from zooplanktivorous prey (e.g., Gizzard Shad or other fish that strongly influence zooplankton assemblages) to more insectivorous or omnivorous prey (e.g., Bluegills) or even herbivorous prey types (e.g., crayfish). These changes in piscivore–prey linkages could ultimately

change community structure and therefore warrant further investigation.

Prey Selection

Largemouth Bass diets in Oklahoma reservoirs were variable; however, when relationships between Largemouth Bass diets and turbidity were identified, they were generally consistent across systems and years and were similar to the results of

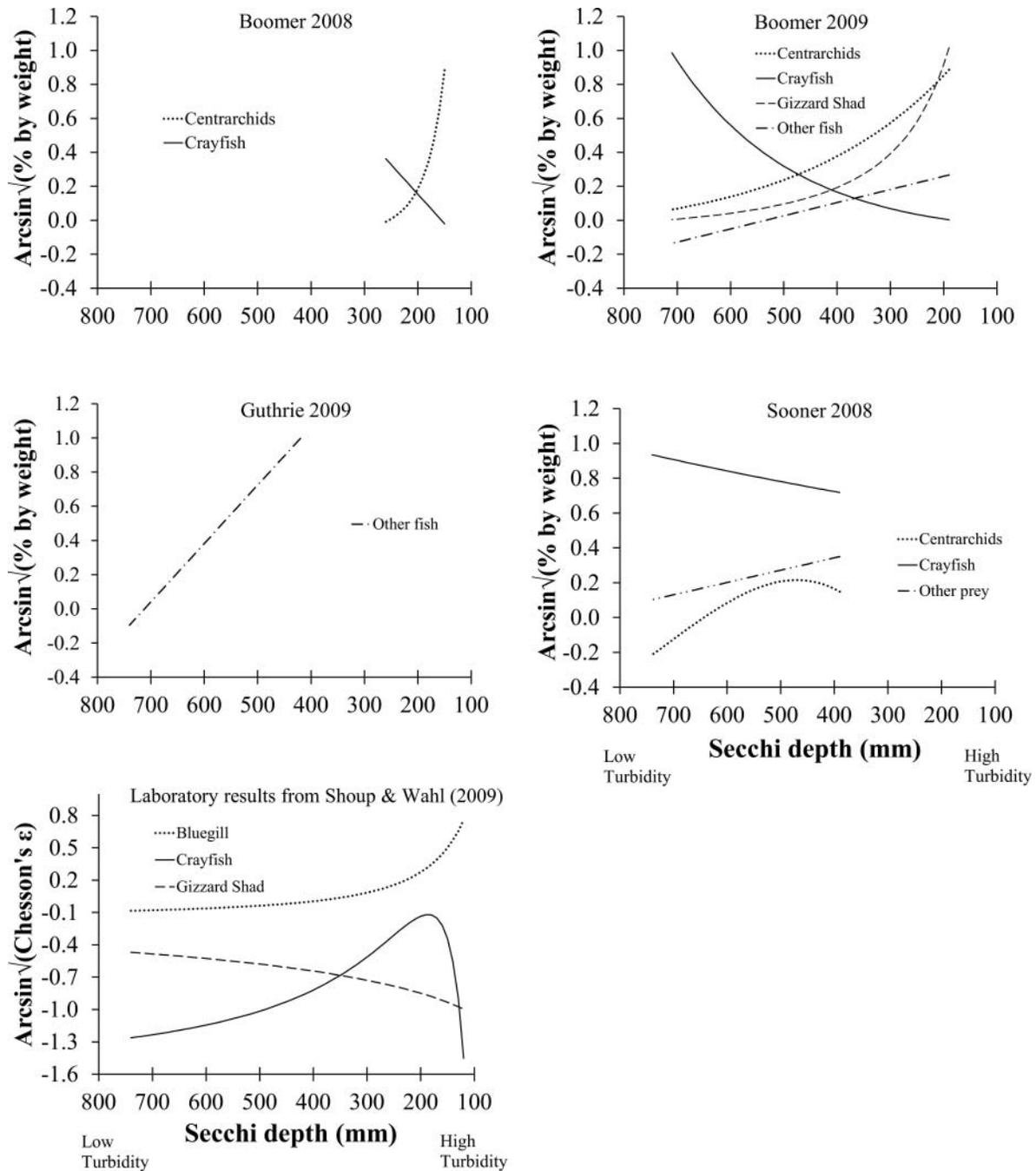


FIGURE 4. Trend lines from regression models relating mean prey percentages by weight (predigested weight of consumed prey, as estimated from prey length via regression) and Secchi depth (turbidity level) for Largemouth Bass sampled from Boomer, Sooner, and Guthrie lakes during 2008 and 2009. Regression lines are only shown for significant ($P < 0.05$) correlations. Regression statistics are provided in Table 1. Data were arcsine-square root transformed to normalize the residuals. These data were designed as a field test of the laboratory patterns observed by Shoup and Wahl (2009); therefore, regression lines from Shoup and Wahl (2009) are provided for comparison.

previous laboratory studies (Shoup and Wahl 2009). Specifically, Largemouth Bass ate mostly crayfish at lower turbidity levels and shifted to a more piscivorous diet (primarily by increasing the use of centrarchid prey) as turbidity increased. Shoup and Wahl (2009) also found increased proportional

consumption of centrarchids and decreased proportional consumption of crayfish at high turbidity levels, but they found that the proportional use of crayfish was highest at intermediate turbidity (i.e., 10 NTU; equivalent to a Secchi depth of 304 mm), whereas in the current study the proportional

crayfish consumption was highest at the lowest turbidity level encountered (i.e., Secchi depth = 700 mm). Shoup and Wahl (2009) speculated that their observed crayfish selection pattern was a function of the interaction between turbidity and light attenuation at the bottom of the tank (i.e., a fixed depth in their experiment). It is possible that the crayfish selection pattern we observed in the field resulted from the ability of Largemouth Bass to forage on crayfish at different depths (i.e., perhaps being able to find a depth where the light level was optimal). Alternatively, Largemouth Bass or their prey may have sought other habitats as turbidity changed in the reservoirs (Gradall and Swenson 1982; Johnson et al. 1988; Gregory 1993; Snickars et al. 2004), thereby altering prey encounter rates in a way that differed from laboratory trials. Regardless of why crayfish selection patterns differed between the present study and the Shoup and Wahl (2009) study, both studies indicate that increases in turbidity often were accompanied by an increase in Largemouth Bass use of piscine prey and a decrease in the use of crayfish once high turbidities (Secchi depth < 304 mm) were reached.

The proportional consumption of rare prey types (the “other fish” and “other prey” categories) was positively correlated with turbidity in several lake × year combinations, suggesting that Largemouth Bass diets became more diverse at higher levels of turbidity. This pattern is consistent with previous laboratory trials showing that Largemouth Bass display reduced diet specificity in turbid water (Crowl 1989; Miner and Stein 1996). A reduction in diet specificity under turbid conditions is likely an adaptation that helps to maintain foraging return even though the encounter rates of most prey types decline at higher turbidity (Crowl 1989; Huenemann et al. 2012). Similar reductions in diet specificity at higher turbidity levels have also been suggested for other top-level predators, such as the Northern Pike *Esox lucius* (Jönsson et al. 2013).

Foraging Return

We found that increases in turbidity greatly reduced the daily consumption rates for Largemouth Bass in laboratory trials, but the rate of decline was similar between predators foraging on Bluegills and those foraging on Gizzard Shad; therefore, it does not explain the previously identified changes in prey selection as turbidity increases (Shoup and Wahl 2009). Consumption rates in our trials declined enough to indicate that Largemouth Bass in turbid environments may obtain less food than required for their daily maintenance and growth. However, we saw no evidence of reduced consumption rates in the field (i.e., no difference in the percentage of empty stomachs or the total prey biomass in the stomach contents of predators captured at different turbidities) based on samples taken at Secchi depths as low as 150 mm (~20 NTU in the laboratory study). It is possible that consumption rates in the field would have been correlated with turbidity if we had sampled at higher turbidity levels, but the laboratory data indicated that

the reduced consumption rate should have been apparent even when turbidity was as low as 15 NTU (Secchi depth = 195 mm). Alternatively, holding the Largemouth Bass in clear water prior to the laboratory trials may have changed the predator response during trials conducted under more turbid conditions. Turbidity levels can change rapidly in the field (including rapid increases within relatively clear systems, such as the changes observed in Boomer Lake during 2009), and all of the Largemouth Bass used in our laboratory trials came from natural systems with dynamic turbidity (some fish were from the same lakes used in the field study). Therefore, it seems unlikely that the observed disagreement between the laboratory and field results is simply an artifact of acclimation conditions. Different forms of turbidity (e.g., types of clay; or clay versus algal turbidity) may affect Largemouth Bass to different extents. Turbidity can occur naturally through phytoplankton production or via the natural erosion and transport of sediments in geographic areas with a high clay content (Chow-Fraser 1999; Cozar et al. 2005). Turbidity can also be generated by anthropogenic activities, such as poor riparian management and storm sewers (Mallin et al. 2009). Each of these turbidity sources may have different particle shapes, sizes, and color. These attributes may differentially alter Largemouth Bass prey selection and consumption rates.

Previous studies have also produced conflicting results regarding the relationship between piscivore consumption rates and turbidity. Several studies have found no effects (Shoup et al. 2007; VanLandeghem et al. 2011; our present field data) or only limited effects at extreme turbidity levels (Reid et al. 1999), whereas others have shown a strong decline in consumption rates with increasing turbidity (Radke and Gaupisch 2005; Shoup and Wahl 2009; Carter et al. 2010; Ferrari et al. 2014; our present laboratory data). The differing conclusions among these studies might be explained in some cases by differences in the predator or prey species used or differences in the turbidity range tested. However, many of the studies used Largemouth Bass as the predator species (Reid et al. 1999; Shoup et al. 2007; Shoup and Wahl 2009; VanLandeghem et al. 2011; present study), and several studies were similar enough that consistent results would be expected.

The disagreement among studies addressing the effects of turbidity on consumption rates suggests that other environmental factors are interacting with turbidity in a way that alters the behavior of Largemouth Bass or their prey. If true, this indicates that turbidity will have varying effects on foraging return for Largemouth Bass under different combinations of other environmental variables. For example, we demonstrated that Largemouth Bass include a wider variety of prey types in their diets as turbidity increases, which could be a mechanism for adapting to reduced foraging return in habitats where numerous prey types are available (i.e., not possible to evaluate by using the single-prey design of many laboratory studies, including ours). Alternatively, the way in which Largemouth Bass alter their predation strategy in response to turbidity may

differ among environments. Largemouth Bass change from a roaming strategy to an ambush strategy as structural complexity increases (Savino and Stein 1982), and this behavior no doubt has energetic consequences (both in terms of encounter rates and energy expenditures). Turbidity may induce similar behavioral changes (Crowl 1989), but such changes probably interact with the structural complexity of the system. Yet another mechanism that could account for the variable effects of turbidity on Largemouth Bass consumption rates is the alteration of habitat use (Gradall and Swenson 1982; Johnson et al. 1988; Gregory 1993; Snickars et al. 2004) or antipredator behavior (Shoup and Wahl 2009) of prey as turbidity changes. Prey may even seek out specific turbidity levels in order to improve their own foraging return (Boehlert and Morgan 1985; Rowe and Dean 1998) or to avoid predators. Changes in prey habitat use may be affected by the availability of different habitat types or by the perceived foraging profitability or predation risk of the current habitat relative to alternative habitats (Dill 1987; Gotceitas 1990; Shoup et al. 2003, 2014) such that the effects of turbidity on habitat use vary among systems with different habitat options. Thus, the interaction among all of these mechanisms will ultimately determine how a predator's foraging return changes in response to increasing turbidity. Despite the complex interaction of factors that can influence foraging return, the literature review above and the results of the current study clearly show that under some conditions, Largemouth Bass occupying higher turbidity levels experience a decrease in consumption rates (and presumably foraging return) that is large enough to potentially influence growth. However, there are also conditions under which Largemouth Bass are able to maintain a similar consumption rate over a wide range of turbidity levels. Further research is needed to determine the mechanisms influencing the ability of Largemouth Bass to successfully adapt to increased turbidity and avoid reductions in foraging return.

Conclusions

Relatively few studies have examined the effects of abiotic factors, such as turbidity, on the feeding behavior of piscivores; the few studies that do exist have largely been confined to laboratory trials (but note the field objective of Reid et al. 1999). For most piscivores, increases in turbidity lead to decreases in reactive distance (Barrett et al. 1992; Miner and Stein 1996; Quesenberry et al. 2007), thereby resulting in reduced encounter rates (Huenemann et al. 2012; Jönsson et al. 2013; Pekcan-Hekim et al. 2013) and capture rates (Shoup and Wahl 2009; Carter et al. 2010) in the laboratory and suggesting a reduction in predator foraging return. Turbidity changes can also lead to changes in the prey types selected in the laboratory (Shoup and Wahl 2009; Carter et al. 2010). We demonstrated that turbidity-related diet changes also occur for Largemouth Bass in the field, but field-measured consumption rates did not always decline at higher turbidity levels.

Therefore, fisheries managers who are concerned about prey sufficiency for Largemouth Bass populations should consider collecting diet information to ensure that they are managing the prey species actually utilized by this predator, as prey selection may change with turbidity. For example, if Largemouth Bass are primarily consuming crayfish at low turbidity levels, managing for increased abundance of Gizzard Shad may not improve the foraging return for Largemouth Bass at those turbidity levels. Only when equipped with diet data will a manager know which prey species are influencing the growth of Largemouth Bass. Additional research is needed to determine (1) whether turbidity-induced changes in piscivore diets (e.g., switching among herbivorous [crayfish], invertivorous [centrarchids], and zooplanktivorous [Gizzard Shad] prey) can lead to trophic cascades that affect community structure in aquatic ecosystems; and (2) the conditions under which turbidity causes foraging returns to decline to an extent that might influence the growth potential of Largemouth Bass.

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REFERENCES

- Abrahams, M., and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* 40:169-174.
- Barrett, J. C., G. D. Grossman, and J. Rosenfield. 1992. Turbidity-induced changes in reactive distance of Rainbow Trout. *Transactions of the American Fisheries Society* 121:437-443.
- Bigham Stephens, D. L., R. E. Carlson, C. A. Horsburgh, M. V. Hoyer, R. W. Bachmann, and D. E. Canfield Jr. 2015. Regional distribution of Secchi disk transparency in waters of the United States. *Lake and Reservoir Management* 31:55-63.
- Bilotta, G. S., and R. E. Brazier. 2008. Understanding the influence of suspended solids on water quality and aquatic biota. *Water Research* 42:2849-2861.
- Boehlert, G. W., and J. B. Morgan. 1985. Turbidity enhances feeding abilities of larval Pacific Herring, *Clupea harengus pallasii*. *Hydrobiologia* 123:161-170.
- Bowen, S. H. 1996. Quantitative description of the diet. Pages 513-532 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Brown, P. B., and G. Konoval. 1993. Length, weight and width relationships of form 1 *Orconectes virilis*. *Journal of the World Aquaculture Society* 24:112-115.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-639.
- Carter, M. W., D. E. Shoup, J. M. Dettmers, and D. H. Wahl. 2010. Effects of turbidity and cover on prey selectivity of adult Smallmouth Bass. *Transactions of the American Fisheries Society* 139:353-361.
- Chow-Fraser, P. 1999. Seasonal, interannual, and spatial variability in the concentrations of total suspended solids in a degraded coastal wetland of Lake Ontario. *Journal of Great Lakes Research* 25:799-813.

- Chung, E. G., F. A. Bombardelli, and S. G. Schladow. 2009. Sediment resuspension in a shallow lake. *Water Resources Research* [online serial] 45(5):W05422.
- Cochran, P. A., and I. R. Adelman. 1982. Seasonal aspects of daily ration and diet of Largemouth Bass, *Micropterus salmoides*, with an evaluation of gastric evacuation rates. *Environmental Biology of Fishes* 7:265–275.
- Cozar, A., J. A. Galvez, V. Hull, C. M. Garcia, and S. A. Loiselle. 2005. Sediment resuspension by wind in a shallow lake of Esteros del Ibera (Argentina): a model based on turbidimetry. *Ecological Modelling* 186:63–76.
- Crowl, T. A. 1989. Effects of crayfish size, orientation, and movement on the reactive distance of Largemouth Bass foraging in clear and turbid water. *Hydrobiologia* 183:133–140.
- Davies-Colley, R. J., and D. G. Smith. 2001. Turbidity, suspended sediment, and water clarity: a review. *Journal of the American Water Resources Association* 37:1085–1101.
- Degan, D. J., and W. Wilson. 1995. Comparison of four hydroacoustics frequencies for sampling pelagic fish populations in Lake Texoma. *North American Journal of Fisheries Management* 15:924–932.
- Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Canadian Journal of Zoology* 65:803–811.
- Duchrow, R. M., and W. H. Everhart. 1971. Turbidity measurement. *Transactions of the American Fisheries Society* 100:682–690.
- Evans, N. T., D. E. Shoup, and D. C. Glover. 2014. A simplified approach for estimating age-0 Gizzard Shad prey supply and predator demand. *Fisheries Management and Ecology* 21:140–154.
- Ferrari, M. C. O., L. Ranaker, K. L. Weinersmith, M. J. Young, A. Sih, and J. L. Conrad. 2014. Effects of turbidity and an invasive waterweed on predation by introduced Largemouth Bass. *Environmental Biology of Fishes* 97:79–90.
- Gotceitas, V. 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile Bluegill sunfish. *Oecologia* 83:346–351.
- Gradall, K. S., and W. A. Swenson. 1982. Responses of Brook Trout and Creek Chubs to turbidity. *Transactions of the American Fisheries Society* 111:392–395.
- Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:241–246.
- Hackney, P. A. 1978. Fish community biomass relationships. Pages 25–36 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hoyle, J. A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the Largemouth Bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65:1972–1977.
- Huenemann, T. W., E. D. Dibble, and J. P. Fleming. 2012. Influence of turbidity on the foraging of Largemouth Bass. *Transactions of the American Fisheries Society* 141:107–111.
- Hunt, B. P. 1960. Digestion rate and food consumption of Florida Gar, Warmouth, and Largemouth Bass. *Transactions of the American Fisheries Society* 89:206–211.
- Hunter, J. R. 1968. Effects of light on schooling and feeding of Jack Mackerel, *Trachurus symmetricus*. *Journal of the Biological Board of Canada* 25:393–407.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Johnson, D. L., R. A. Beaumier, and W. E. Lynch Jr. 1988. Selection of habitat structure interstice size by Bluegills and Largemouth Bass in ponds. *Transactions of the American Fisheries Society* 117:171–179.
- Jonsson, M., F. Johansson, C. Karlsson, and T. Brodin. 2007. Intermediate predator impact on consumers weakens with increasing predator diversity in the presence of a top predator. *Acta Oecologia* 31:79–85.
- Jönsson, M., L. Ranaker, P. A. Nilsson, and C. Brönmark. 2013. Foraging efficiency and prey selectivity in a visual predator: differential effects of turbid and humic water. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1685–1690.
- Knights, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by Walleyes and Yellow Perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677–693.
- Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2005. *Applied linear statistical models*, 5th edition. McGraw-Hill/Irwin, New York.
- Mallin, M. A., V. L. Johnson, and S. H. Ensign. 2009. Comparative impacts of stormwater runoff on water quality of an urban, a suburban, and a rural stream. *Environmental Monitoring and Assessment* 159:475–491.
- Miner, J. G., and R. A. Stein. 1996. Detection of predators and habitat choice by small Bluegills: effects of turbidity and alternative prey. *Transactions of the American Fisheries Society* 125:97–103.
- Nellis, M. D., J. A. Harrington, and J. P. Wu. 1998. Remote sensing of temporal and spatial variations in pool size, suspended sediment, turbidity, and Secchi depth in Tuttle Creek Reservoir, Kansas, 1993. *Geomorphology* 21:281–293.
- Olson, M. H. 1996. Ontogenetic niche shifts in Largemouth Bass: variability and consequences for first-year growth. *Ecology* 77:179–190.
- OWRB (Oklahoma Water Resources Board). 2004. 2004 Report of the Oklahoma beneficial use monitoring program. OWRB, Oklahoma City.
- OWRB (Oklahoma Water Resources Board). 2005. 2005 Report of the Oklahoma beneficial use monitoring program. OWRB, Oklahoma City.
- Pekcan-Hekim, Z., L. Joensuu, and J. Horppila. 2013. Predation by a visual planktivore perch (*Perca fluviatilis*) in a turbulent and turbid environment. *Canadian Journal of Fisheries and Aquatic Sciences* 70:854–859.
- Pekcan-Hekim, Z., and J. Lappalainen. 2006. Effects of clay turbidity and density of Pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). *Naturwissenschaften* 93:356–359.
- Quesenberry, N. J., P. J. Allen, and J. J. Cech Jr. 2007. The influence of turbidity on Three-spined Stickleback foraging. *Journal of Fish Biology* 70:965–972.
- Raborn, S. W., L. E. Miranda, and M. T. Driscoll. 2002. Effects of simulated removal of Striped Bass from a southeastern reservoir. *North American Journal of Fisheries Management* 22:406–417.
- Radke, R. J., and A. Gaupisch. 2005. Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian Perch (*Perca fluviatilis*): possible implications for fish community structure in lakes. *Naturwissenschaften* 92:91–94.
- Ranaker, L., M. Jonsson, P. A. Nilsson, and C. Bronmark. 2012. Effects of brown and turbid water on piscivore–prey fish interactions along a visibility gradient. *Freshwater Biology* 57:1761–1768.
- Reid, S. M., M. G. Fox, and T. H. Whillans. 1999. Influence of turbidity on piscivory in Largemouth Bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:1362–1369.
- Rowe, D. K., and T. L. Dean. 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research* 32:21–29.
- SAS Institute. 2011. *SAS/STAT 9.3 user's guide*. SAS Institute, Cary, North Carolina.
- Savino, J. F., and R. A. Stein. 1982. Predator–prey interaction between Largemouth Bass and Bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111:255–266.
- Savino, J. F., and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* 37:311–321.

- Shoup, D. E., K. M. Boswell, and D. H. Wahl. 2014. Diel littoral–pelagic movements by juvenile Bluegills in a small lake. *Transactions of the American Fisheries Society* 143:796–801.
- Shoup, D. E., S. P. Callahan, D. H. Wahl, and C. L. Pierce. 2007. Size-specific growth of Bluegill, Largemouth Bass and Channel Catfish in relation to prey availability and limnological variables. *Journal of Fish Biology* 70: 21–34.
- Shoup, D. E., R. E. Carlson, and R. T. Heath. 2003. Effects of predation risk and foraging return on the diel use of vegetated habitat by two size-classes of Bluegills. *Transactions of the American Fisheries Society* 132:590–597.
- Shoup, D. E., and D. H. Wahl. 2009. The effects of turbidity on prey selection by piscivorous Largemouth Bass. *Transactions of the American Fisheries Society* 138:1018–1027.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785–791.
- Snickars, M., A. Sandstrom, and J. Mattila. 2004. Antipredator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. *Journal of Fish Biology* 65:1604–1613.
- Timmons, T. J., and O. Pawaputanon. 1982. Relative size relationship in prey selection by Largemouth Bass in West Point Lake, Alabama–Georgia. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 34(1980):248–252.
- USEPA (U.S. Environmental Protection Agency) and NALMS (North American Lake Management Society). 2015. The Secchi dip-in. Available: <http://www.secchidipin.org/>. (August 2015).
- Van Den Avyle, M. J., and J. E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. *Progressive Fish-Culturist* 42:222–223.
- Vander Zanden, M. J., T. E. Essington, and Y. Vadeboncoeur. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? *Canadian Journal of Fisheries and Aquatic Sciences* 62:1422–1431.
- VanLandeghem, M. M., M. P. Carey, and D. H. Wahl. 2011. Turbidity-induced changes in emergent effects of multiple predators with different foraging strategies. *Ecology of Freshwater Fish* 20:279–286.
- Vogel, J. L., and D. A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distance of Lake Trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1293–1297.
- Wahl, D. H., and R. A. Stein. 1991. Food consumption and growth of three esocids: field tests of a bioenergetic model. *Transactions of the American Fisheries Society* 120:230–246.
- Wallace, R. K. Jr. 1981. An assessment of diet overlap indexes. *Transactions of the American Fisheries Society* 110:72–76.