

The Effects of Turbidity on Prey Selection by Piscivorous Largemouth Bass

DANIEL E. SHOUP*¹ AND DAVID H. WAHL

*Kaskaskia Biological Station, Illinois Natural History Survey,
Rural Route 1, Box 157, Sullivan, Illinois 61951, USA*

Abstract.—Turbidity in aquatic systems can change rapidly, affecting the visual ability of predators. Increased turbidity is known to reduce the reactive distance and foraging success of some planktivores and insectivores, leading to decreased growth rates. However, little is known about the effects of turbidity on prey selection by piscivores. We examined the interactions between largemouth bass *Micropterus salmoides* and their prey in 1.8-m-diameter tanks (58 cm deep) at four turbidity levels (0, 5, 10, and 40 nephelometric turbidity units [NTU]). Prey selectivity was significantly affected by turbidity. At lower turbidity levels (0 and 5 NTU), largemouth bass consumed mostly gizzard shad *Dorosoma cepedianum* and bluegills *Lepomis macrochirus* and had negative selectivity for northern crayfish *Orconectes virilis*. At 10 NTU, all three prey types had similar selectivity, presumably because the largemouth bass had more difficulty in capturing rapidly moving fish prey as their reactive distances decreased. At 40 NTU, the overall foraging rate was much lower and bluegills were selected significantly more often than the other prey types. Low light levels at the bottom of the tanks combined with reductions in visual clarity from clay sediments probably made it difficult for largemouth bass to feed effectively on virile crayfish at higher turbidities. Our results suggest that trophic interactions may be altered as turbidity levels change.

Turbidity often varies on a seasonal basis in aquatic systems (Nellis et al. 1998; Dimberger and Weinberger 2005) and can fluctuate rapidly owing to changes in phytoplankton density, sediment additions, or sediment resuspension (Chow-Fraser 1999; Anthony and Downing 2003; Parkos et al. 2003; Cozar et al. 2005). Because turbidity affects the ability of aquatic organisms to find prey (Vinyard and O'Brien 1976; Gregory and Northcote 1993), it has the potential to affect predator–prey interactions. Contrast degradation theory predicts that organisms that feed on large prey types (such as piscivores) should be more affected by increases in turbidity than organisms that feed on small prey types (such as planktivores) (Utne-Palm 2002; De Robertis et al. 2003). Despite this, most turbidity research has focused on planktivorous and insectivorous fishes, relatively little being done on piscivorous species. In particular, how prey selection by piscivores is affected by changes in turbidity is not known.

The effects of turbidity on the foraging success of planktivorous and insectivorous fishes vary by species (Bonner and Wilde 2002). For many species, increased turbidity leads to reduced foraging return (Gardner 1981; Johnston and Wildish 1982; Barrett et al. 1992;

Gregory and Northcote 1993; Benfield and Minello 1996), presumably because of decreased reactive distance (Vinyard and O'Brien 1976; Gregory and Northcote 1993). However, foraging return appears to be unaffected in some species (Sweka and Hartman 2001; Rowe et al. 2003; Granqvist and Mattila 2004) and may even increase with moderate increases in turbidity in other species (Boehlert and Morgan 1985; Rowe and Dean 1998). Species that experience reduced foraging return at higher turbidity levels often exhibit lower growth and survival (Buck 1956; Sigler et al. 1984; Sweka and Hartman 2001). Other fish compensate for reduced foraging return by increasing their activity levels, thereby increasing their encounter rates with prey so that foraging return is unchanged at higher turbidity levels (Gradall and Swenson 1982; Sweka and Hartman 2001).

Turbidity can also affect antipredator behavior in ways that vary by prey species. Prey may switch habitats (Swenson 1978; Matthews 1984; Miner and Stein 1996), reduce their use of cover (Gradall and Swenson 1982; Johnson et al. 1988; Gregory 1993; Snickars et al. 2004), or reduce school cohesiveness (Vandenbyllaardt et al. 1991) as turbidity increases—presumably because turbidity reduces the risk of predation. Because not all prey species in a given system respond to changes in turbidity in the same way (Matthews 1984; Miner 1990), some prey species may be more vulnerable to a predator at different turbidity levels.

Little information is available as to whether

* Corresponding author: dshoup@okstate.edu

¹ Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Ag Hall, Stillwater, Oklahoma 74078, USA.

Received January 27, 2009; accepted April 27, 2009

Published online July 27, 2009

turbidity-related changes in prey behavior affect prey selection by piscivores. Several studies found that piscivores had less foraging success at higher turbidities (Reid et al. 1999; De Robertis et al. 2003; Stuart-Smith et al. 2004; Radke and Gaupisch 2005), and feeding behavior may also be affected. Miner and Stein (1996) found that largemouth bass *Micropterus salmoides* became less active at turbidities of 27–54 nephelometric turbidity units (NTU) than at turbidities of 10–19 NTU. Similarly, Crowl (1989) observed that largemouth bass became less discriminating, were quicker to strike at prey, and had shorter reactive distances with respect to white river crawfish *Procambarus acutus* when turbidity increased to 17–19 NTU. Studies have also found that piscivores were less likely to eat small prey as turbidity increased (Abrahams and Kattenfeld 1997; Reid et al. 1999). Because prey species respond differently to changes in turbidity and piscivores change their behavior, it is likely that the resulting interaction could cause piscivores to consume different prey types under different turbidity conditions. Understanding how prey selection is affected by turbidity is important in understanding how food web dynamics might change at different turbidity levels. The purpose of this study was to determine whether largemouth bass, an important sport fish, select different prey types (with disparate antipredator strategies) at different turbidity levels.

Methods

Largemouth bass and fish prey were collected by electrofishing at lakes in central Illinois that experience a wide range of turbidity levels (Secchi depth, 0.15–4.75 m). We chose three prey species that are prevalent in the diet of largemouth bass and vary in a number of attributes. Two fish prey, bluegill *Lepomis macrochirus* and gizzard shad *Dorosoma cepedianum*, vary in morphology and antipredator behavior (Wahl and Stein 1988; Einfalt and Wahl 1997). Bluegills are highly maneuverable and have dorsal spines to deter predators, whereas gizzard shad rely on speed and schooling to avoid predation. A third common prey of largemouth bass, northern crayfish *Orconectes virilis*, is associated with bottom substrate and has chelae that are used for predatory defense. Northern crayfish were collected by seining ponds at the Sam Parr Biological Station, Kinmundy, Illinois. These three prey items are the most common ones found in the stomachs of largemouth bass in lakes throughout Illinois (Santucci and Wahl 1991; D. Wahl, unpublished data) and other parts of the USA (Aggus 1973; Van Den Avyle and Roussel 1980). All of the prey came from environments with predators. The prey were acclimated to laboratory tanks for at least 7 d before being used in

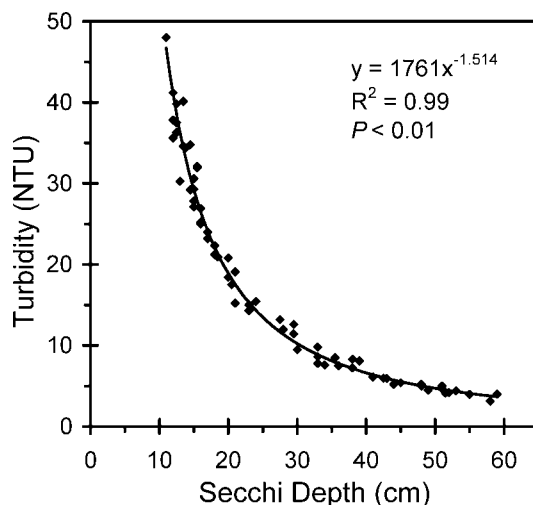


FIGURE 1.—Estimated relationship between turbidity and Secchi depth for various suspensions of bentonite clay. Turbidities less than 3.1 NTU were not measured because the Secchi depths were greater than that of the experimental tanks.

experiments. The experiments were conducted outdoors in a shaded area at the Kaskaskia Biological Station, Sullivan, Illinois. Trials were run when appropriate-size gizzard shad were available (six replicates were conducted from September 10 to October 22, 2003, and eight from July 21 to August 10, 2004).

Bentonite clay was added to produce the appropriate turbidity in round (1.8-m-diameter; total volume, 1.5 m³) aluminum tanks filled to a depth of 58 cm at least 24 h before the trials. Turbidity was measured with a tungsten lamp nephelometric turbidity meter (Cole-Parmer Model 8391–40) calibrated with a 10-NTU styrene polymer standard. Because of the variation in nephelometry readings among machines when the turbidity-generating particle has different physical characteristics (Duchrow and Everhart 1971; Austin 1973; Davies-Colley and Smith 2001), we also developed a relationship between Secchi depth and turbidity reading (Figure 1). A 15-cm air stone was placed in the center of each tank to keep the clay suspended and maintain turbidity levels within 10% of the desired level. No other cover was available to the prey during the trials. The turbidity levels tested were 0 NTU (actual turbidity range, 0.39–0.60 NTU; Secchi depth, >58 cm), 5 NTU (48 cm), 10 NTU (30 cm), and 40 NTU (12 cm). Turbidity levels in this range are typical of lakes and reservoirs throughout the USA. To further characterize tank conditions, we also measured light levels in the tanks on several dates. Light levels

were highly variable, depending on cloud cover; they ranged from 70 to 500 ft-candles (753–5,382 lumens/m²) at the surface but dropped to 20–60 ft-candles (215–646 lumens/m²) at the bottom of the tank in the 0-NTU treatment and to 0.5–6 ft-candles (5.4–64.6 lumens/m²) in the 40-NTU treatment.

Translucent plastic boxes (59 × 45 × 40 cm) with plastic hardware cloth panels (0.6-cm mesh) on two sides were used to hold the largemouth bass (205–250 mm total length [TL]) in the experimental tanks for 24 h before the start of a trial so that they could get acclimated to the turbidity. Prey were selected to match the optimal size for individual largemouth bass; bluegills were 25–32% of predator TL (Hoyle and Keast 1987), gizzard shad 30–35% (L. Einfalt and D. H. Wahl, Kaskaskia Biological Station, unpublished data), and northern crayfish 21–27% (Hoyle and Keast 1987). Five of each prey type were added to the tank and given 1 h to get acclimated before the largemouth bass was released from the translucent box. All largemouth bass were trained so that they would readily pursue prey after being released. During the training period, largemouth bass were fed all three prey types as well as fathead minnow *Pimephales promelas*. In the 0-NTU treatment, the trials were ended once the largemouth bass had consumed one or two prey items (typically 0.20–0.75 h, but up to 20 h in some trials). In other treatments, turbidity prevented direct observation, so the largemouth bass were allowed to forage for a predetermined amount of time (based on preliminary trials) that typically allowed them to eat one or two prey items (mean, 19 h [range, 15–22 h] at 5 NTU; 26 h [range, 19–49 h] at 10 NTU; and 55 h [range, 42–77 h] at 40 NTU). The trials in these treatments were deleted and repeated if no prey were consumed. Similarly, in trials in which multiple prey types were consumed the treatments were deleted and repeated if more than two of any given prey type had been eaten (to minimize the changes in encounter rates). The range of the mean number of prey eaten across treatments was 1.4–2.2. Largemouth bass were removed at the end of a trial by seining; the remaining prey were recovered and counted by draining the tank. Dead or injured prey were not counted as consumed.

A repeated-measures design was used whereby each of 14 individual largemouth bass were tested once at each turbidity level. Each fish was tested in the same tank at the same location in all four turbidity trials (treatment orders were assigned randomly). Prey selectivity was calculated using Chesson's electivity value, which is appropriate when multiple prey are eaten and there is no replacement of consumed items during the experiment (Chesson 1983). Chesson's electivity value is calculated by first calculating the

relative selectivity for each prey item as

$$\hat{\alpha}_i = \frac{\log_e \left(\frac{n_{i0} - r_i}{n_{i0}} \right)}{\sum_{j=1}^m \log_e \left(\frac{n_{j0} - r_j}{n_{j0}} \right)},$$

where n_{i0} is the number of prey type i at the beginning of the experiment, r_i is the number of prey type i consumed by the predator, and m is the number of different prey types. The estimated values of α_i are then centered on zero by means of the equation

$$\varepsilon_i = \frac{m\hat{\alpha}_i - 1}{(m - 2)\hat{\alpha}_i + 1}.$$

Chesson's electivity value can range from -1 (indicating complete avoidance of that prey type) to +1 (indicating that that prey type was the only one selected). Values near 0 indicate no preference. The electivity values were arcsine-transformed to normalize the data and analyzed via a repeated-measurements multivariate analysis of variance (MANOVA) using SAS Proc Mixed (Wright 1998; SAS 2004; individual largemouth bass were treated as subjects). This allowed us to test for differences in selectivity among the three prey types and turbidity levels simultaneously. To further examine the relationships with turbidity, we developed regression models for Chesson's electivity for each species. The best models were determined through lack-of-fit tests and residual analysis (Neter et al. 1996). The coefficients of multiple determination (R^2) were calculated as the ratios of the variance explained by the model to the total amount of variance in a reduced model with no predicting variables (i.e., only an intercept; Kreft and De Leeuw 1998). Although the experiment was not designed to directly test foraging return (the durations of the trials were adjusted to minimize the differences in the number of prey consumed among treatments), we used the mean number of prey consumed per hour as an approximation. Foraging returns with respect to each prey species and all prey species combined were also analyzed by analysis of variance (ANOVA) and regression models, as described above. The data for all analyses were transformed as necessary (arcsine for Chesson's electivity, \log_{10} or square root for the foraging return data) to normalize them. Significant results ($P < 0.05$) were subsequently analyzed by means of Tukey's test.

Results

The prey type with the highest electivity varied with turbidity (MANOVA: $F_{6, 53} = 4.42, P < 0.01$; Figure 2). At 0 NTU, gizzard shad had higher electivity than northern crayfish (Tukey's test; $P = 0.05$) and bluegills

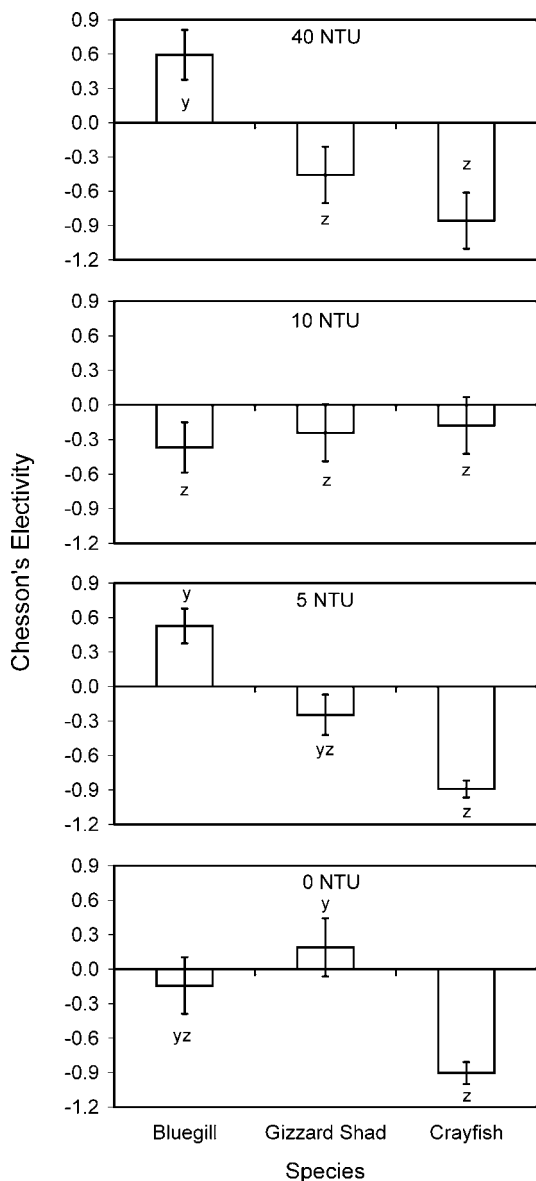


FIGURE 2.—Chesson electivity values for largemouth bass foraging on bluegills, gizzard shad, and northern crayfish at different turbidities, arranged by turbidity level. An electivity value of +1 indicates that that prey type was the only one consumed, a value of -1 that that prey type was avoided altogether, and a value of 0 that there was no selection for or against that prey type. The bars represent means and the thin vertical lines SEs; means with different letters within the same panel are significantly different ($P \leq 0.05$).

had intermediate electivity ($P > 0.99$ with respect to gizzard shad, $P = 0.09$ with respect to crayfish). At 5 NTU, bluegills had higher electivity than crayfish ($P < 0.01$) and gizzard shad had intermediate electivity ($P =$

0.55 with respect to bluegills, $P = 0.08$ with respect to crayfish). At 10 NTU, the electivity of all three prey types was similar (all $P > 0.99$). At 40 NTU, bluegills had significantly higher electivity than either gizzard shad ($P = 0.05$) or crayfish ($P < 0.01$). The mean electivity of crayfish was negative and significantly lower those of other prey types at all turbidities except 10 NTU. Electivity was highest for at least one of the fish prey types at all turbidity levels except 10 NTU. The mean electivity was positive for gizzard shad at 0 NTU and for bluegills at 5 and 40 NTU.

The pattern of electivity within each species also varied with turbidity (Figure 3). Bluegill electivity was significantly higher at 40 NTU than at 10 NTU (Tukey's test; $P = 0.02$) but not different from those at 0 and 5 NTU (all $P > 0.36$). A linear model of bluegill electivity was significant with a positive slope, indicating greater electivity at higher turbidities, but this model explained only a small amount of the measured variability ($P = 0.04$, $R^2 = 0.08$; Table 1). The electivity of gizzard shad and northern crayfish did not differ significantly at any turbidity level in the MANOVA analysis (all $P > 0.68$ for gizzard shad; $P > 0.24$ for crayfish; Figure 3). A power function model significantly fit the gizzard shad data ($P = 0.03$), indicating that electivity declined with increasing turbidity, although the model only explained a small amount of the measured variability ($R^2 = 0.11$; Table 1). A second-order polynomial model significantly fit the crayfish electivity data ($P < 0.01$), indicating that electivity was highest at intermediate turbidity levels (the inflection point occurred at about 21 NTU) and lower at both lower or higher values (Table 1). Again, however, this model only explained a small amount of the measured variability ($R^2 = 0.17$).

The foraging rate (number of prey captured/h) for largemouth bass decreased dramatically with increased turbidity (Figure 4). For all prey species combined, the foraging rate at each turbidity level was significantly different from those at all other levels, declining as turbidity increased (ANOVA: $F_{4, 14} = 230.56$, $P < 0.01$; Tukey's test: all $P < 0.01$). This was best described by a power function with a negative slope ($P < 0.01$, $R^2 = 0.47$; Table 1). The rates of foraging on bluegills and gizzard shad also declined as turbidity increased. For bluegills, the foraging rate was highest at 0 and 5 NTU and lowest at 10 and 40 NTU ($F_{4, 14} = 242.16$, $P < 0.01$; Figure 4), with a significant negative slope in a power function regression ($P = 0.01$, $R^2 = 0.11$; Table 1). For gizzard shad, the foraging rate was higher at 0 NTU than at any other turbidity level ($F_{4, 14} = 239.29$, $P < 0.01$; Figure 4), with a significant negative slope in a power function regression ($P < 0.01$, $R^2 = 0.29$; Table 1). For northern crayfish, the

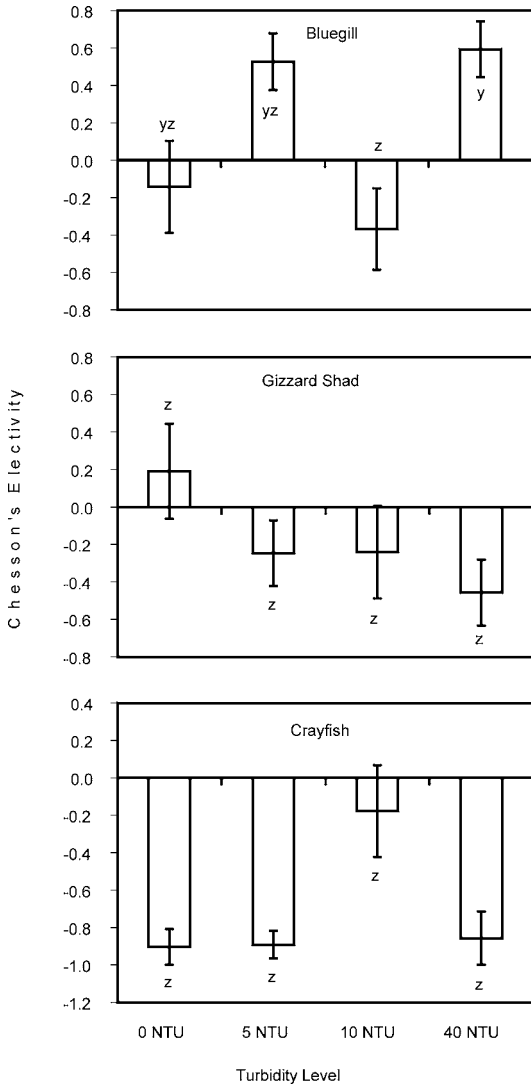


FIGURE 3.—Chesson electivity values for largemouth bass foraging on bluegills, gizzard shad, and northern crayfish at different turbidities, arranged by prey species. See Figure 2 for additional details.

foraging rate was higher at 10 NTU than at any other turbidity level ($F_{4, 14} = 4,239.63, P < 0.01$; Figure 4). None of the tested model types adequately fit the response of crayfish electivity to changes in turbidity.

Discussion

Previous studies examining the effects of turbidity on piscivores are limited. Largemouth bass become less active (Miner and Stein 1996), have lower foraging return, and may select larger prey as turbidity increases (Reid et al. 1999). Our study demonstrates that changes

in turbidity can also affect the type of prey selected by piscivorous fish. At lower turbidity levels (0–5 NTU), largemouth bass selected fish prey (i.e., showed neutral or positive electivity with respect to them) and avoided northern crayfish, which is consistent with the results of previous clear-water research (Lewis et al. 1961). As turbidity increased to moderate levels (10 NTU), selection declined for gizzard shad and increased for crayfish, so that there was no difference in electivity among the three prey types at such levels. At the highest turbidity level tested (40 NTU), one fish species (bluegills) was again selected, as electivity declined for both of the other prey types. The overall foraging return was much lower at this turbidity (almost two orders of magnitude less than that at 0 NTU). The higher electivity for bluegills probably did not represent an ideal foraging situation for the largemouth bass, as it is unlikely that they were able to capture sufficient amounts of prey. Daily rations for largemouth bass are typically 2.2–3.9% of wet weight (Markus 1932; Hunt 1960). Therefore, the largemouth bass in our experiment would be expected to consume 0.96–2.6 prey/d (depending on the size of the bass and the prey type being consumed), yet in our trials it typically took more than 2 d for predators to ingest prey.

Changes in electivity between 0 and 10 NTU probably reflect the greater difficulty of capturing rapidly moving prey (such as gizzard shad and bluegills) when the reactive distance of the predator decreases, as it typically does at moderate and high turbidities (Crowl 1989; Miner and Stein 1996). Turbidity does not affect the capture efficiency (number of captures/number of pursuits) of largemouth bass preying on northern crayfish (Crowl 1984), even though it decreases the reactive distance and therefore lowers the encounter rate. The effect of turbidity on the capture efficiency of largemouth bass feeding on fish prey is unknown, but our foraging rate information provides some insight into this issue. Foraging rates on highly mobile fish prey decreased at higher turbidity levels but were unaffected by turbidity for the more sedentary crayfish prey at all turbidity levels except 10 NTU (where foraging return actually increased). Fish prey often move rapidly, and the time from the moment a largemouth bass first detects the prey until the prey has left its field of view would be greatly reduced at higher turbidities owing to the decreased reactive distance (Miner and Stein 1996). Largemouth bass may have had time to orient themselves for an optimal approach and strike at sedentary crayfish at higher turbidity levels (there was no decrease in the foraging rate on this species as turbidity increased); encounters with fish prey, however, required a much more rapid response and there may not have been enough time for

TABLE 1.—Results of regression analyses of the effect of turbidity on Chesson's electivity for three prey types and predator foraging return in prey preference experiments with largemouth bass. Lack-of-fit tests and residual analysis were used to select between linear ($Y = b_1X + a$), power function ($Y = aX^{b_1}$), and 2nd-order polynomial ($Y = b_1X^2 + b_2X + a$) models. P -values are for tests examining whether the slopes (b) or intercepts (a) are different from zero. The electivity values were arcsine transformed.

Response variable	Model type	Slope(s)				Intercept		R^2
		b_1	P	b_2	P	a	P	
All prey species combined								
Electivity	Not applicable							
Foraging return	Power function	-0.542	<0.01			0.607	0.25	0.47
Bluegills								
Electivity	Linear	0.022	0.04			-0.132	0.38	0.08
Foraging return	Power function	-0.126	0.01			0.024	<0.01	0.11
Gizzard shad								
Electivity	Power function	-0.095	0.03			11.233	0.00	0.11
Foraging return	Power function	-0.451	<0.01			0.145	<0.01	0.29
Northern crayfish								
Electivity	2nd-order polynomial	0.141	<0.01	-0.003	<0.01	-1.601	<0.01	0.17
Foraging return	No significant models found							

the bass to position themselves for an optimal strike. These mechanisms have been suggested to explain the reduced capture rates of planktivores as turbidity increases (Vinyard and O'Brien 1976). Reduced

capture efficiency has also been observed among largemouth bass foraging on fish prey at low light levels (McMahon and Holanov 1995), which would be the case with increased turbidity. While the encounter

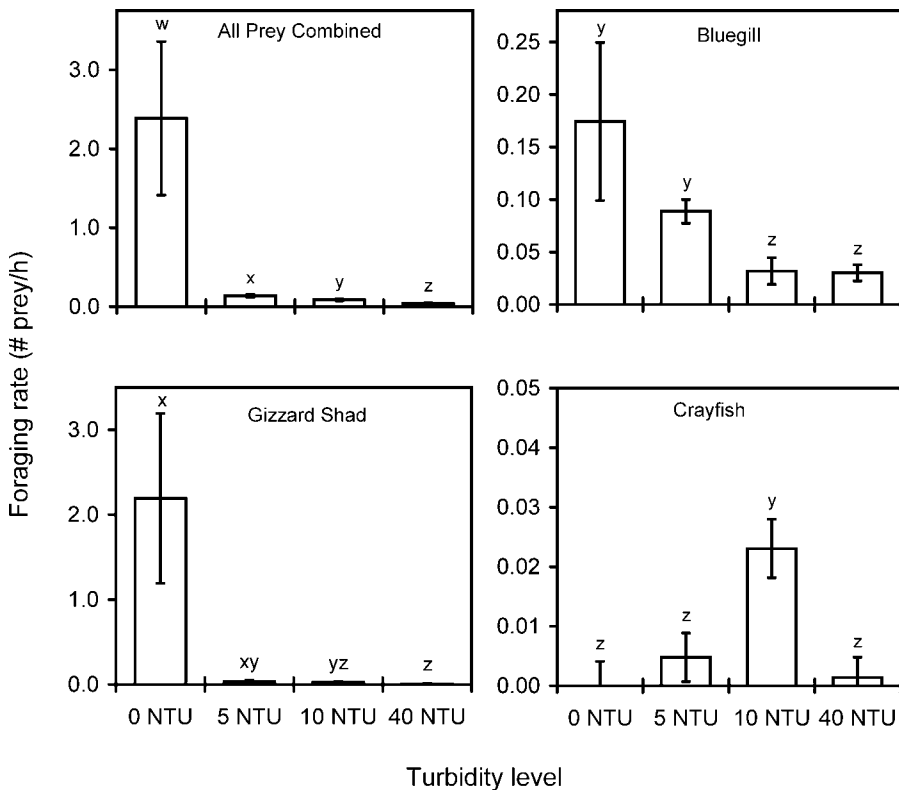


FIGURE 4.—Foraging rates of largemouth bass on bluegills, gizzard shad, and northern crayfish at different turbidities. The trials were conducted for different lengths of time to minimize the differences in the number of prey consumed (see text for details). The bars represent means and the thin vertical lines SEs; means with different letters within the same panel are significantly different ($P \leq 0.05$).

rates for all prey types were probably reduced as turbidity increased (Crowl 1984; Miner and Stein 1996), the crayfish that were encountered may have been more likely to be captured because of their sedentary behavior. While our experiment cannot address these hypotheses, a similar mechanism has been used to explain why skipjack *Elops machnata* (more commonly known as tenpounder) eat fish prey in clear habitats but more slowly moving crustaceans (mostly Mysidacea) in turbid environments (Hecht and van der Lingen 1992). Further research is needed to determine how turbidity affects the encounter rate and capture efficiency of piscivores feeding on fish prey.

Northern crayfish had higher electivity at intermediate turbidities (10 NTU) than they did at lower or higher ones. Differences in capture efficiency provide a possible reason why crayfish would be selected over fish as turbidity increases to intermediate levels but do not explain why crayfish electivity would decline at the highest turbidity (40 NTU). At 40 NTU, light attenuation was strong enough that the illumination at the bottom of the tanks was low relative to that in other turbidity treatments. Largemouth bass probably had difficulty locating crayfish on the bottom at the highest turbidities (i.e., the encounter rate dropped precipitously). It took about 55 h for largemouth bass to capture prey at 40 NTU (compared with ≤ 1 h for most largemouth bass in the 0-NTU treatment), indicating that foraging efficiency on all three prey types was dramatically lower at these turbidity levels. A decline of nearly two orders of magnitude also occurred in the foraging rate (from 2.4 prey/h at 0 NTU to 0.04 prey/h at 40 NTU). Visibility at the bottom would be lower than at other depths owing to the interaction of turbidity with light intensity (Vinyard and O'Brien 1976; Miner and Stein 1993; Benfield and Minello 1996). Although the light levels at the bottom were above the minimum needed for largemouth bass to forage in clear water (McMahon and Holanov 1995), the interaction of light and turbidity may have made it difficult for them to forage at higher turbidities. Fish prey located higher in the water column, where there was more light (Einfalt and Wahl 1997; Wahl and Stein 1988), may have been easier to detect and capture than benthic prey. It is also possible that the longer duration of the higher-turbidity trials (which were run overnight) allowed for an interaction of light and turbidity that influenced prey selection throughout the water column. Additional research is needed to determine the interactive effect of light and turbidity on piscivores and its potential to alter prey selection.

Selectivity was higher for bluegills than for gizzard shad at the highest turbidity. Previous studies at lower turbidities have found that bluegills often move to the

air-water interface or tank wall and remain motionless with their spines erect when they are under the threat of predation (Howick and O'Brien 1983; Wahl and Stein 1988; Einfalt and Wahl 1997). However, these behaviors have not been observed at higher turbidities (Miner and Stein 1996). We observed similar behaviors; bluegills were frequently found at the air-water interface when turbidity was 10 NTU or less but rarely when it was 40 NTU. Increased turbidity could reduce encounter rates enough that bluegills do not perceive a significant predation risk under these conditions. Similar changes in behavior have also been observed with other species, which reduced their use of protective cover at increased turbidities (Gradall and Swenson 1982; Johnson et al. 1988; Gregory 1993; Snickars et al. 2004). If changes in bluegill behavior lead to increased electivity at higher turbidities, they would appear to be maladaptive. However, the predator foraging rate was much lower at higher turbidities, so the increase in selectivity relative to the other prey types may not result in increased predation risk. Indeed, the number of prey consumed per hour declined as turbidity increased despite the fact that electivity increased. Further, antipredator behavior by bluegills reduces growth rates (Mittelbach 1981; Werner et al. 1983; Pothoven et al. 1999), so growth and survival trade-offs should lead to the cessation of these behaviors even if some moderate risk of predation is still perceived (Gilliam and Fraser 1988).

Not all fish prey exhibit changes in behavior with increased turbidity; for example, habitat use by gizzard shad is unaffected by turbidity up to 100 NTU (Miner and Stein 1996). Gizzard shad often reach very high densities in eutrophic, turbid Midwestern impoundments. Several mechanisms have been proposed to account for the abundance of gizzard shad in these systems (Stein et al. 1995). We found reduced electivity and foraging rates on gizzard shad by largemouth bass at higher turbidities. High turbidity may provide an additional mechanism reducing the predatory control of young-of-year gizzard shad by largemouth bass. The abundance of gizzard shad is often positively related to turbidity (Schaus and Vanni 2000; Aday et al. 2003, 2005), suggesting that there may be a feedback loop that reinforces the abundance of gizzard shad by suppressing predator efficiency.

Our findings with respect to the effects of turbidity on piscivorous fish need to be examined in the field and for other piscivore-prey combinations. Reid et al. (1999) found that the number of fish in the stomachs of juvenile largemouth bass (43–132 mm TL) was not related to the turbidity level in Canadian lakes and concluded that prey fish abundance was more important than turbidity in determining diet. Changes in diet

have been associated with turbidity in field studies with piscivorous tenpounders (Hecht and van der Lingen 1992) and brown trout *Salmo trutta* (Stuart-Smith et al. 2004), but these studies cannot separate the effects of changes in prey abundance from predator foraging ability and selection. No other studies have investigated the effect of turbidity on prey selection in the field. Further research in complex natural systems is needed.

The effects of turbidity on prey selection by piscivores may have important implications for food web dynamics. For example, largemouth bass have been used as a biological control for planktivores, leading to greater zooplankton densities and ultimately to increased water clarity as a result of lower algal turbidity (Carpenter et al. 1995; Mittelbach et al. 1995). However, our results suggest that foraging by largemouth bass on fish prey is highest under clearwater conditions and that these bass select alternative prey at moderate turbidity levels. At high turbidity levels, the largemouth bass in our experiment switched back to fish but the foraging return was greatly reduced (nearly two orders of magnitude smaller), suggesting that largemouth bass are not able to control fish prey populations under highly turbid conditions. Therefore, a positive feedback mechanism could stabilize lakes in either a clearwater or turbid-water condition. We hypothesize that the predatory control of planktivores will be strongest in clearwater systems because electivities for and foraging rates on planktivores were highest in such systems. However, our results suggest that in moderately turbid systems largemouth bass will pursue other prey types such as northern crayfish and will have a lower foraging return. The piscivore-planktivore link would therefore be weakened, allowing planktivores to reduce zooplankton densities, in turn increasing algal turbidity. While our results suggest that largemouth bass will switch back to planktivorous fish prey at very high turbidities, their foraging return may be diminished to the point that they do not exert significant predatory control on any prey species, especially if increased turbidity affects piscivore foraging return to a greater extent than it affects planktivores (De Robertis et al. 2003). The outcome would be further complicated if planktivores, such as bluegills, alter their behavior or habitat use (as suggested by Miner and Stein 1996) with changes in turbidity. There is clearly a need for further studies on the food-web-level effects of turbidity in aquatic ecosystems to determine whether these types of feedbacks and cascades occur.

Acknowledgments

We thank J. G. Miner for his helpful suggestions during the design of the experiments. We also thank the

staff of the Kaskaskia Biological Station (KBS) for their help in collecting largemouth bass and prey organisms. L. Einfalt facilitated use of the wet laboratory at KBS. C. L. Goad provided useful statistical advice.

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.
- Aday, D. D., J. H. Hoxmeier, and D. H. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill population size structure. *Transactions of the American Fisheries Society* 132:47-56.
- Aday, D. D., D. E. Shoup, J. A. Neviackas, J. L. Kline, and D. H. Wahl. 2005. Prey community responses to bluegill and gizzard shad foraging: implications for growth of juvenile largemouth bass. *Transactions of the American Fisheries Society* 134:1091-1102.
- Aggus, L. R. 1973. Food of angler harvested largemouth, spotted, and smallmouth bass in Bull Shoals Reservoir. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 26(1972):519-529.
- Anthony, J. L., and J. A. Downing. 2003. Physical impacts of wind and boat traffic on Clear Lake, Iowa, USA. *Lake and Reservoir Management* 19:1-14.
- Austin, R.W. 1973. Problems in measuring turbidity as a water quality parameter.
- 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.
- Benfield, M. C., and T. J. Minello. 1996. Relative effects of turbidity and light intensity on reactive distance and feeding rate of an estuarine fish. *Environmental Biology of Fishes* 46:211-216.
- Boehlert, G. W., and J. B. Morgan. 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasii*. *Hydrobiologia* 123:161-170.
- Bonner, T. H., and G. R. Wilde. 2002. Effects of turbidity on prey consumption by prairie stream fishes. *Transactions of the American Fisheries Society* 131:1203-1208.
- Buck, D. H. 1956. Effects of turbidity on fish and fishing. *Transactions of the North American Wildlife Conference* 21:249-261.
- Carpenter, S. R., D. L. Christensen, J. J. Cole, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, S. E. Knoght, M. L. Pace, D. M. Post, D. E. Schindler, and N. Voichick. 1995. Biological control of eutrophication in lakes. *Environmental Science and Technology* 29:784-786.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297-1304.
- 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.
- 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 Iberá (Argentina): a model based on turbidity. *Ecological Modeling* 186:63–76.
- Crowl, T. A. 1984. The feeding ecology of largemouth bass preying on crayfish in clear and turbid water. Master's thesis. University of Oklahoma, Norman.
- 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.
- De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1517–1526.
- Dimberger, J. M., and J. Weinberger. 2005. Influences of lake level changes on reservoir water clarity. *Lake and Reservoir Management* 21:24–29.
- Duchrow, R. M., and W. H. Everhart. 1971. Turbidity measurement. *Transactions of the American Fisheries Society* 100:682–690.
- Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2618–2626.
- Gilliam, J. F., and D. F. Fraser. 1988. Resource depletion and habitat segregation by competitors under predation hazard. Pages 173–184 in B. Ebenman and L. Persson, editors. *Size-structured populations: ecology and evolution*. Springer-Verlag, New York.
- Gardner, M. B. 1981. Effects of turbidity on feeding rates and selectivity of bluegills. *Transactions of the American Fisheries Society* 110:446–450.
- 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.
- Granqvist, M., and J. Mattila. 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia* 514:93–101.
- 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.
- Gregory, R. S., and T. G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 50:233–240.
- Hecht, T., and C. D. van der Lingen. 1992. Turbidity-induced changes in feeding strategies of fish in estuaries. *South African Journal of Zoology* 27:95–107.
- Howick, G. L., and W. J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. *Transactions of the American Fisheries Society* 112:508–516.
- 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.
- 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.
- 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.
- Johnston, D. D., and D. J. Wildish. 1982. Effect of suspended sediment on feeding by larval herring (*Clupea harengus harengus* L.). *Bulletin of Environmental Contamination and Toxicology* 29:261–267.
- Kreft, I., and J. De Leeuw. 1998. *Introducing multilevel modeling*. Sage Publications, London.
- Lewis, W. M., G. E. Gunning, E. Lyles, and W. L. Bridges. 1961. Food choice of largemouth bass as a function of availability and vulnerability of food items. *Transactions of the American Fisheries Society* 90:277–280.
- Markus, H. C. 1932. The extent to which temperature changes influence food consumption in largemouth bass. *Transactions of the American Fisheries Society* 62:202–210.
- Matthews, W. J. 1984. Influences of turbid inflows on vertical distribution of larval shad and freshwater drum. *Transactions of the American Fisheries Society* 113:192–198.
- McMahon, T. E., and S. H. Holanov. 1995. Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding. *Journal of Fish Biology* 46:759–767.
- Miner, J. G. 1990. Turbidity-mediated predator-prey interactions among piscivores, prey fishes, and zooplankton. Doctoral dissertation. Ohio State University, Columbus.
- Miner, J. G., and R. A. Stein. 1993. Interactive influence of turbidity and light on larval bluegill (*Lepomis macrochirus*) foraging. *Canadian Journal of Fisheries and Aquatic Sciences* 50:781–788.
- 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.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenburg. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–2360.
- Nellis, M. D., J. A. Harrington, Jr., and J. 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.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear regression models*, 3rd edition. Irwin, Chicago.
- Parkos, J. J., III, V. J. Santucci, Jr., and D. H. Wahl. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries and Aquatic Sciences* 60:182–192.
- Pothoven, S. A., B. Vondracek, and D. L. Pereira. 1999. Effects of vegetation removal on bluegill and largemouth

- bass in two Minnesota lakes. *North American Journal of Fisheries Management* 19:784–757.
- 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.
- 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.
- Rowe, D. K., T. L. Dean, E. Williams, and J. P. Smith. 2003. Effects of turbidity on the ability of juvenile rainbow trout, *Oncorhynchus mykiss*, to feed on limnetic and benthic prey in laboratory tanks. *New Zealand Journal of Marine and Freshwater Research* 37:45–52.
- Santucci, V. J., Jr., and D. H. Wahl. 1991. Use of a creel census and electrofishing to assess centrarchid populations. Pages 481–491 in D. Guthrie, J. M. Hoenig, M. Holliday, C. M. Jones, M. J. Mills, S. A. Moberly, K. H. Pollock, and D. R. Talhelm, editors. *Creel and angler surveys in fisheries management*. American Fisheries Society, Symposium 12, Bethesda, Maryland.
- SAS. 2004. *SAS/STAT user's guide*, version 9.1. SAS Institute, Cary, North Carolina.
- Schaus, M. H., and M. J. Vanni. 2000. Effects of gizzard shad on phytoplankton and nutrient dynamics: role of sediment feeding and fish size. *Ecology* 81:1701–1719.
- Sigler, J. W., T. C. Bjornn, and F. H. Everest. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. *Transactions of the American Fisheries Society* 113:142–150.
- 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.
- Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2518–2526.
- Stuart-Smith, R. D., A. M. M. Richardson, and R. W. G. White. 2004. Increasing turbidity significantly alters the diet of brown trout: a multiyear longitudinal study. *Journal of Fish Biology* 65:376–388.
- Sweka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 58:386–393.
- Swenson, W. A. 1978. Influence of turbidity on fish abundance in western Lake Superior. U.S. Environmental Protection Agency, Report 600/3-78-067, Duluth, Minnesota.
- Utne-Palm, A. C. 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. *Marine and Freshwater Behaviour and Physiology* 35:111–128.
- 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.
- Vandenbyllaardt, L., F. J. Ward, C. R. Braekveelt, and D. B. McIntyre. 1991. Relationships between turbidity, piscivory, and development of the retina in juvenile walleyes. *Transactions of the American Fisheries Society* 120:382–390.
- Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33:2845–2849.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117:142–151.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Wright, S. P. 1998. Multivariate analysis using the Mixed procedure. *Proceedings of the 23rd International SAS Users Group International, Statistics, Data Analysis, and Modeling Section*. Available: <http://www2.sas.com/proceedings/sugi23/Stats/p229.pdf>. (June 2009).