

## Effects of Turbidity on Prey Consumption by Prairie Stream Fishes

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**Abstract.**—Reduced suspended-sediment loads (i.e., turbidity) in many Midwestern prairie rivers have been hypothesized as contributing to the replacement of species that historically occupied highly turbid main-channel habitats by visually feeding species that are competitively superior in less-turbid waters. We examined the relationship between prey consumption and turbidity for six fish species from the Canadian River (New Mexico, Oklahoma, and Texas) and found experimental support for this hypothesis. Among species adapted to highly turbid main-channel habitats, we found that prey consumption by the peppered chub *Macrhybopsis tetranema* and flathead chub *Platygobio gracilis* was unaffected ( $P > 0.12$ ) by elevated turbidity, whereas prey consumption by the Arkansas River shiner *Notropis girardi* was reduced ( $P < 0.01$ ). Among species characteristic of less-turbid habitats, prey consumption by the emerald shiner *N. atherinoides*, red shiner *Cyprinella lutrensis*, and sand shiner *N. stramineus* was reduced ( $P < 0.01$ ) by elevated turbidity. Compared with prey consumption at 0 nephelometric turbidity units (NTU), prey consumption at 4,000 NTU decreased 21% among peppered chub, 26% among flathead chub, and 59% among Arkansas River shiners, which was less than that observed among emerald (73%), red (84%), and sand shiners (89%). In general, elevated turbidity had less effect on the prey consumption of species that are adapted to highly turbid habitats than on those characteristic of less-turbid habitats. The high suspended-sediment loads that historically were characteristic of many prairie streams may have excluded emerald, red, and sand shiners from main-channel habitats.

Groundwater pumping, water diversion, and reservoir construction have dramatically altered aquatic habitats throughout the Missouri and Arkansas river basins (Williams and Wolman 1984; Cross and Moss 1987; Pflieger and Grace 1987; Stinnett et al. 1988; Limbird 1993; Friedman et al. 1998). Streams and rivers have been reduced in size and volume, channel morphology has changed so that many streams no longer meander or form multiple channels, frequency and intensity of flood events has decreased, and suspended-solid loads generally have decreased. These changes are associated with changes in stream fish assemblages: many species that historically inhabited the larger streams and rivers of the Arkansas and Missouri river drainages now are reduced in distribution and abundance (Cross and Moss 1987; Pflieger and Grace 1987; Limbird 1993; Bonner and Wilde 2000). In general, there has been a replacement of species that historically inhabited the main channels of these fluctuating, turbid rivers by species that were low in relative abundance or restricted

to river margins and tributary streams (Cross and Moss 1987; Pflieger and Grace 1987). For example, Bonner and Wilde (2000) found that the Arkansas River shiner *Notropis girardi*, flathead chub *Platygobio gracilis*, peppered chub *Macrhybopsis tetranema* (Eisenhour 1999), and plains minnow *Hybognathus placitus*, which historically composed 98% of the fish assemblage, have decreased in abundance or been extirpated from the Canadian River (an Arkansas River tributary) downstream from Lake Meredith, Texas, where discharge has been reduced 76% since the river was impounded in 1966. Conversely, the red shiner *Cyprinella lutrensis*, sand shiner *N. stramineus*, and emerald shiner *N. atherinoides* have increased in abundance, presently composing more than 90% of the fish assemblage in the affected area.

Species replacements such as that described by Bonner and Wilde (2000) were hypothesized by Cross and Moss (1987) and Pflieger and Grace (1987) to be due, in part, to decreases in suspended-sediment loads (turbidity) that allow fishes characteristic of less-turbid waters to displace (presumably via competition for food) species that are adapted to more-turbid conditions (Moore 1950; Davis and Miller 1967; Branson 1979; Huber and Rylander 1992). If this hypothesis is correct, we would predict a differential response in prey

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consumption to elevated turbidity between species that are adapted to very turbid waters (i.e., the Arkansas River shiner, flathead chub, and peppered chub) and those characteristic of less-turbid waters (i.e., the emerald, red, and sand shiners). Herein, we provide a test of this prediction. First, we test the null hypothesis that turbidity has no effect on the prey consumption of each species considered separately. Second, we test the null hypothesis that the effects of turbidity on feeding efficiency do not differ among species.

### Methods

We collected emerald shiners (62–72 mm total length), flathead chub (72–110 mm), peppered chub (50–65 mm), red shiners (56–64 mm), and sand shiners (65–75 mm) from the Canadian River in Texas and Oklahoma in June 1999. We collected Arkansas River shiners (56–71 mm) from an introduced population in the Pecos River, New Mexico (Bestgen et al. 1989) in June 1999. All fish were age 1 or older. Fish were transported to Texas Tech University in insulated containers and maintained in the laboratory for approximately 3 weeks in flow-through systems at a photoperiod of 14 h light : 10 h dark. Fish were fed commercial flake food ad libitum twice a day and dead bloodworms (Chironomidae) ad libitum for 2 weeks before the feeding trials. Bloodworms were selected as prey for the feeding trials because all study species feed on dipteran larvae in the field, including those of Chironomidae (Miller and Robison 1973; Mendelson 1975; Cross and Collins 1995; Wilde et al. 2001). Food was withheld from fish for 48 h before the feeding trials.

Experimental aquaria for the feeding trials consisted of four 75-L glass aquaria. The bottom and sides of each aquarium were covered with black plastic to prevent light penetration. Each aquarium was divided into three 25-L compartments using sheets of opaque Plexiglas. Each compartment was equipped with an aeration stone to keep the water oxygenated and to keep sediments suspended during feeding trials (we measured <1% change in turbidity during trials). Three replicates of each of four treatments (0, 1,000, 2,000, and 4,000 nephelometric turbidity units [NTU]) were randomly assigned to the compartments. Turbidity levels were selected to span much of the range observed in the Canadian River, Texas, where mean turbidity ranged from 22 to 264 NTU during winter (December–February) and from 1,359 to 4,770 NTU during summer (June–August) under typical flow conditions (Bonner 2000). We added sodium ben-

tonite to the dechlorinated water in sufficient amounts to achieve target turbidity levels. We used sodium bentonite rather than sand and silt from the Canadian River to ensure consistency in turbidity across feeding trials. Turbidity was measured with a LaMotte turbidimeter.

Feeding trials were conducted separately for each species. Three randomly selected individuals of each species were placed in a compartment, except that only one peppered chub was placed in each compartment because of their low abundance in the Canadian River. Fish were allowed to adjust to conditions in the experimental aquaria for 45 min, after which 50 bloodworms were introduced into each compartment. Fish were allowed to feed for 10 min. After this period, the fish were removed, the aquaria drained, and the remaining prey items collected and counted. Ten-minute trials were conducted because preliminary trials showed that fish neither fed to satiation nor consumed all prey during this period.

We used linear and polynomial least-squares regression (Neter et al. 1996) to model prey consumption by each species as a function of turbidity, that is,

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \varepsilon_i,$$

where  $Y_i$  is the  $\log_{10}(n + 1)$  transformed number of prey consumed in the  $i$ th trial,  $X_i$  is turbidity in the  $i$ th trial,  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$  are regression coefficients, and  $\varepsilon_i$  is the error term. The equality of first-order linear slopes was assessed with multiple regression using species as a class variable followed by Fisher's least-significant-difference test to identify differences ( $\alpha = 0.05$ ) among regression slopes (Graybill 1976).

### Results

All species consumed prey at all experimental turbidity levels (Figure 1), although sand shiners consumed no prey in one replicate trial at 4,000 NTU. Generally, prey consumption was greatest at 0 NTU and decreased with increased turbidity. There was no significant relationship between prey consumption and turbidity among flathead chub ( $P = 0.45$ ) and peppered chub ( $P = 0.12$ ) (Table 1). For these two species, prey consumption decreased by only 21% (peppered chub) and 26% (flathead chub) over the range of turbidity studied. The relationship between prey consumption and turbidity was significant for Arkansas River ( $P = 0.0098$ ), emerald ( $P = 0.013$ ), red ( $P = 0.0002$ ), and sand shiners ( $P = 0.0036$ ), leading us to reject

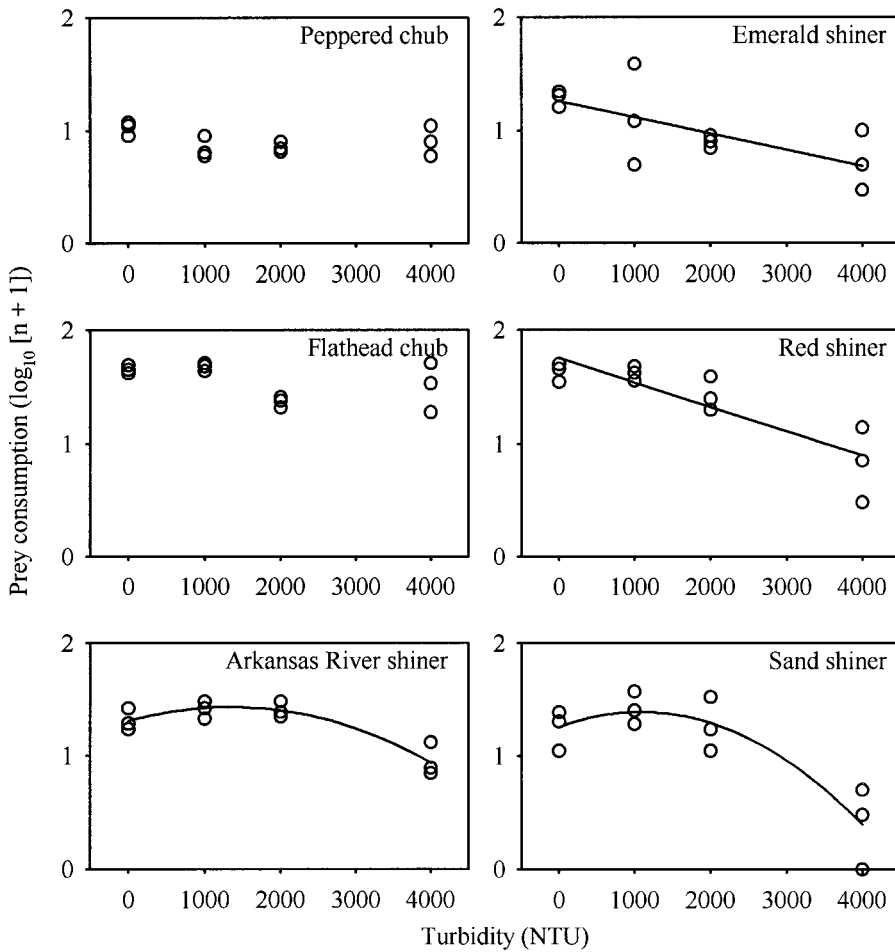


FIGURE 1.—Relationships between prey consumption and turbidity for six species of fish from the Canadian River (New Mexico, Oklahoma, and Texas). Circles represent the  $\log_{10}(n + 1)$  transformed number of prey consumed in replicate feeding trials. Regression statistics are presented in Table 1.

the null hypothesis that turbidity has no effect on prey consumption for these species. Compared with prey consumption at 0 NTU, consumption at 4,000 NTU decreased by 59% among Arkansas

River shiners, 73% among emerald shiners, 84% among red shiners, and 89% among sand shiners. There was significant ( $F = 4.64$ ;  $df = 5, 60$ ;  $P = 0.0012$ ) heterogeneity in linear regression

TABLE 1.—Linear regression models describing  $\log_{10}(n + 1)$  prey consumption as a function of turbidity (nephelometric turbidity units) in six Canadian River fishes. For pairwise contrasts, different lowercase letters indicate significant ( $P < 0.05$ ) differences among regression models.

Species group	Species	Coefficients				MSE	$r^2$	P	Pairwise contrasts
		$\beta_0$	SE	$\beta_1$	SE				
Turbid, main-channel species	Pepered chub	0.934	0.0468	-0.00002	0.000020	0.01093	0.06	0.45	w
	Flathead chub	1.645	0.0678	-0.00005	0.000030	0.03958	0.23	0.12	wx
	Arkansas River shiner	1.442	0.0731	-0.00010	0.000039	0.02673	0.50	0.0098	xy
Large-eyed, sight-feeding species	Emerald shiner	1.258	0.1076	-0.00014	0.000047	0.02673	0.48	0.013	xyz
	Red shiner	1.756	0.0890	-0.00022	0.000039	0.05786	0.75	0.0002	yz
	Sand shiner	1.480	0.1407	-0.00023	0.000061	0.09912	0.58	0.0036	z

slopes ( $\beta_1$ ) among species (Table 1); therefore, we reject the null hypothesis that the effects of turbidity on prey consumption did not differ among species. In general, the slopes for emerald, red, and sand shiners were steeper than those for peppered chub, flathead chub, and Arkansas River shiners.

Prey consumption by two species, Arkansas River and sand shiners, was best modeled as a quadratic function of turbidity. Therefore, the nature as well as the magnitude of the change in prey consumption as a function of turbidity varied among species. The estimated relationship between  $\log_{10}(n + 1)$  prey consumption ( $Y$ ) and turbidity ( $X$ ) was  $Y = 1.303 + 0.00019X - 6.8 \times 10^{-8} \cdot X^2$  ( $r^2 = 0.84$ ,  $P = 0.0003$ ) for Arkansas River shiners and  $Y = 1.252 + 0.00025X - 1.2 \times 10^{-7} \cdot X^2$  ( $r^2 = 0.80$ ,  $P = 0.0007$ ) for sand shiners.

### Discussion

All species studied herein are commonly characterized as being tolerant to turbidity (Robison and Buchanan 1988; Huber and Rylander 1992; Cross and Collins 1995; Pflieger 1997). Nevertheless, we found differences between species that were abundant historically (flathead chub, peppered chub, and Arkansas River shiners) and those that had low abundance (emerald, red, and sand shiners) in the main channels of prairie streams. Prey consumption by flathead and peppered chub decreased slightly (by 26% and 21%, respectively) between 0 and 4,000 NTU. However, prey consumption by Arkansas River shiners was significantly affected by turbidity, decreasing 59% between 0 and 4,000 NTU. In contrast, prey consumption by emerald, red, and sand shiners decreased 73–89% between 0 and 4,000 NTU. The latter species are among those reported by Cross and Moss (1987) and Pflieger and Grace (1987) to have increased in abundance as turbidity decreased within the Arkansas and Missouri river drainages. Our results thus provide support for the hypothesis of Cross and Moss (1987) and Pflieger and Grace (1987) and suggest that although turbidity generally is viewed as having negative effects on aquatic organisms (e.g., Waters 1995), it may be important in maintaining the integrity of fish assemblages in systems, such as prairie streams, that naturally have high suspended-sediment loads. Further, these differences have the potential to affect the outcome of competition among species and thus species distribution and abundance in highly turbid waters.

Prey consumption by peppered chub, which pri-

marily feed at or near the substrate (Wilde et al. 2001), and flathead chub, which feed in the water column (Olund and Cross 1961), was little affected by turbidity. This suggests that observed differences among species in the effect of turbidity on prey consumption do not result from differences in feeding behavior. Both flathead and peppered chub possess a number of morphological adaptations for feeding in turbid waters, including barbels, large numbers of olfactory lamellae, and numerous cutaneous taste buds (Moore 1950; Olund and Cross 1961; Davis and Miller 1967; Branson 1979). We speculate that these species used a combination of visual cues (while prey were near the surface) and nonvisual cues (once prey sank into the water column or settled onto the substrate) to detect prey at 4,000 NTU; however, we were unable to observe the feeding behavior of fish at this turbidity.

The nature of the relationship between prey consumption and turbidity differed between emerald and red shiners (for which it was linear) and Arkansas River and sand shiners (for which it was quadratic). The linear decrease in prey consumption by emerald and red shiners suggests a simple attenuation of vision as a function of increased turbidity. Quadratic relationships, such as those we observed for Arkansas River and sand shiners, have been observed in other fishes (Boehlert and Morgan 1985; Miner and Stein 1993; Utne 1997), and two hypotheses have been advanced to explain them. First, turbidity may heighten the contrast between prey and their surroundings, thereby increasing prey detection at intermediate turbidity (Boehlert and Morgan 1985). Second, increased turbidity may increase feeding activity because the risk of predation is reduced (Boehlert and Morgan 1985). Our laboratory results provide no insight into the relative probabilities of these explanations; however, during extensive sampling from 1995 to 1999 we found predatory fish to be scarce in the Canadian River, which suggests that the physical-contrast hypothesis is the correct one.

Although our results provide support for the hypothesis that turbidity plays an important role in structuring prairie stream fish assemblages, they do not eliminate other possible explanations from consideration. The observed changes in species composition might have resulted from the differential susceptibility of some species to downstream displacement by flood events (Starrett 1951; Summerfelt and Minckley 1969; Cross and Moss 1987; Minckley and Meffe 1987; Kelsch 1994), which have been less common in the Ar-

kansas and Missouri River drainages in recent years (Cross and Moss 1987; Pflieger and Grace 1987). Periods of high discharge also are important for reproduction. Several prairie stream fishes, including Arkansas River shiners, flathead chub, peppered chub, and plains minnow, are members of a reproductive guild that broadcast-spawns semi-buoyant eggs (Platania and Altenbach 1998). Reproductive success among these species appears to depend on the frequency and magnitude of summer floods (Moore 1944; Bottrell et al. 1964; Bonner 2000; Bonner and Wilde 2000). The potential effects of these alternative mechanisms on prairie stream fish assemblages are as yet untested.

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