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ABSTRACT.—The fountain darter *Etheostoma fonticola* is a federally endangered species that is associated with primarily clear, spring-fed systems, suggesting even minor changes in turbidity have the potential to affect behavior. We examined the effects of turbidity [control: <1 Nephelometric Turbidity Unit (NTU), minimal turbidity: mean = 8.7 NTU, moderate turbidity: mean = 23.2 NTU, and high turbidity: mean = 74.6 NTU] on the total number of prey items consumed, time to initiate foraging, total prey consumed out of the time left to forage, and number of strikes made per prey items (prey capture success). Our results indicate elevated turbidity significantly affects the number of prey consumed, time to initiate foraging, and total prey consumed out of the time left to forage. Turbidity does not appear to affect prey capture success. These data suggest even a slight elevation in turbidity (≥8.7 NTU) can significantly impair foraging behavior in *E. fonticola*.

INTRODUCTION

Elevated turbidity levels in freshwater systems resulting from major anthropogenic stressors such as pollution, climate change, and modification of flow pose a significant threat to the conservation of biodiversity (Dudgeon *et al.*, 2005; Xenopoulos *et al.*, 2005; Vörösmarty *et al.*, 2010; Collins *et al.,* 2011). Turbidity can modify community structure through benthic smothering and altered rates of photosynthesis (Davies-Colley and Smith, 2001; Evans-White *et al.,* 2009) but in addition to these well-studied habitat level effects; turbidity can affect individual survival and reproduction by altering behavior (Vogel and Beauchamp, 1999). Turbidity impairs the quality of visual information by reducing the intensity of light and narrowing the light spectrum (Seehausen *et al.*, 1997; Collins *et al.*, 2011), which can compromise an animal's ability to forage (Vogel and Beauchamp, 1999), select a mate (Seehausen *et al.*, 1997), and respond to a predator (Gregory, 1993). These behaviors are essential for long-term population viability and are especially concerning for threatened or endangered species. Examining the effects of turbidity on animal behavior is important as such studies provide a noninvasive means of assessing the biological effects of anthropogenic environmental change (Caro, 1999; Angeloni *et al.*, 2008).

Turbidity has been demonstrated to affect foraging behavior primarily through reactive distances and prey-capture success (Sweka and Hartman, 2001; Zamor and Grossman, 2007; Wellington *et al.*, 2010). However, turbidity can also affect additional aspects of foraging behavior such as prey-searching activity (Meager and Batty, 2007), foraging rate (Webster *et al.*, 2007), prey consumption (Bonner and Wilde, 2002; Salonen and Engström-Öst, 2010),

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environmental refuge (Pekcan-Hekim *et al.*, 2010), and prey selectivity (Rowe *et al.*, 2003; Carter *et al.*, 2009; Shoup and Wahl, 2009). In addition to reduction of caloric intake due to decreased prey consumption, turbidity can result in additional energetic cost to predators, such as increased time spent searching for prey and decreased foraging accuracy (Huene-mann *et al.*, 2012). Increases in the amount of energy and time devoted to foraging can result in time allocation tradeoffs with other beneficial behaviors such as mating and avoiding pre-dation, potentially affecting individual fitness (Sih, 1992; Ljunggren and Sandström, 2007).

The fountain darter, *Etheostoma fonticola,* is a federally endangered species endemic to the San Marcos and Comal Rivers of central Texas. *Etheostoma fonticola* is most commonly found in the less turbid reaches (0.26 to 5.76 nephelometric turbidity units -NTU) of these spring-fed systems with relatively constant water temperature and moderate flow and is particularly sensitive to environmental conditions, with reproductive behavior being temperature and flow dependent (Schenck and Whiteside, 1977; Saunders *et al.*, 2001). In both systems large portions of the riverbanks front public parks and are utilized for community events, festivals, and social gatherings. The physical impact of litter and erosion is evident in the public parks and the rivers (Jenkins *et al.*, 1986; TWDB, 2010). In these systems normal turbidity ranges are 0.26–5.76 NTU (Groeger *et al.*, 1997; Saunders *et al.*, 2001; Araujo, 2012) but are elevated up to 13 NTU (Araujo, 2012) or even 47 NTU (T. Hardy, pers. obs.) during drought or flood events and heavy recreational use. Although turbidity levels do not typically remain elevated in these systems and exposure to turbid conditions is typically not prolonged, the effects of rapid influxes of turbidity on behavior are also of interest and importance.

It follows that *E. fonticola* may be especially vulnerable to rapid influxes in turbidity as are other fishes adapted to clear conditions in contrast to species well adapted to turbid condi-tions (Bonner and Wilde, 2002; Grosse *et al.*, 2010; Allen-Ankins *et al.*, 2012). *Etheostoma* are benthic feeders (Vogt and Coon, 1990; Greenberg, 1991) and *E. fonticola* held in aquaria pre-ferentially feed on moving invertebrates while ignoring static ones (USFWS, 1996), suggesting they rely on visual cues to forage. *Etheostoma fonticola* also require the combination of visual and chemical information to respond to the threat of predation, implying vision is likely important in antipredator responses as well (Swanbrow Becker and Gabor, 2012). Given tur-bidity degrades the quality of visual information, animals relying on visual more heavily than olfactory signals while foraging may be disproportionally affected by turbidity (Allen-Ankins *et al.*, 2012). We investigated the effects of turbidity on *E. fonticola* foraging behavior by testing the predictions increasing turbidity reduces the total number of prey items consumed, time it takes to initiate foraging, total prey consumed out of the time left to forage, and number of strikes made per prey items (prey capture success).

METHODS

Experimental trials (n = 80) were conducted at the San Marcos Aquatic Resources Center (ARC) in San Marcos, Texas (29°52′46″N 97°56′20″W) from December 2011 to February 2012. All trials were conducted from 0900–1400h. Fish were hatchery-reared, first generation adult *E. fonticola* and were housed and maintained at the ARC in fiberglass tanks with well water (23 C). The tanks contained three to four pieces of polyvinyl chloride pipe and native vegetation to provide fish with cover. Lighting was timed to mimic natural conditions. All fish were maintained with a diet of live black worms (*Lumbriculus variegatus*), amphipods, and zoo-plankton fed ad lib. daily.

We tested the effects of turbidity on prey consumption in *E. fonticola* across four treatments: clear water control: <1 NTU (N = 20), low turbidity: mean = 8.7 NTU (N = 20), moderate turbidity: mean = 23.2 NTU (N = 20), and higher turbidity: mean = 74.6 NTU (N = 20).

These turbidity levels were chosen in order to maintain consistency with the relatively low levels naturally occurring in *E. fonticola* habitat (0.26 to 13 NTU; Saunders *et al.,* 2001) along with the higher levels of turbidity (20 to 75 NTU) consistent with temporary events such as heavy recreational use and rainfall (USEPA, 1999). The effects of turbidity on time to initiate foraging and prey-capture success were tested across only three treatments, clear, low, and moderate as higher turbidity levels (74.6 NTU) did not allow us to accurately observe fish during trials. We used live black worms (*Lumbriculus variegatus*) as prey because they were consistently fed to the test fish, that reduced any potential effects of learning a new type of prey, and they are large enough to easily quantify.

Our experimental set-up consisted of eight, 9.5-liter glass aquaria (33 × 15.2 × 20.3 cm, L × D × H) with gravel substrate. We used a modified technique employed by Swanbrow Becker and Gabor (2012) and wrapped tanks in black plastic with the exception of the front-facing side to minimize disturbance to the fish from other tanks nearby. The front-facing side was covered with one-way tinting so the observer could not be seen and to standardize light penetration on all tanks sides. Testing aquaria were lit with fluorescent 32-watt bulbs. We used 3% hydrogen peroxide and water to clean aquaria between trials. We created turbidity during trials by adding bentonite (Sturgis Rock Solid Solutions) to well water and stirring vigorously while using an aerator to maintain suspension throughout the duration of trials. Turbidity levels for each of the replicate trials ranged from either clear control: <1 NTU, low: 5 to 10 NTU (mean = 8.7), moderate: 20 to 30 NTU (mean = 23.2), or higher: 60 to 80 NTU (mean = 74.6). Turbidity levels were measured at the end of each trial using a Hach ® Model 2100 N Laboratory Turbidity Meter.

To initiate testing we randomly assigned a turbidity treatment and placed two haphazardly selected subject fish of the same sex into an aquarium. Individual fish were only used once in our experiment. We randomly selected one fish of each pair as the focal individual for each trial. Each fish pair included one large and one small fish (with the large fish chosen as the focal individual half of the time) to aid identification of the focal individual during feeding trials. We defined large fish as individuals longer than or equal to 23.4 mm standard length (mean size of sample of 25 individuals from experimental population) while small fish were individuals shorter than that length. We used two fish in each trial as *E. fonticola* foraging typically occurs in proximity to other individuals and isolated fish do not acclimate well to testing aquaria. We did not see evidence of aggression in these fish during trials. After a 48 h acclimation period without food, we added the appropriate amount of bentonite depending on the turbidity treatment to simulate a change in turbidity as would occur during a flood pulse or recreational disturbance to substrates in situ. We determined the amount of bentonite needed for each treatment before beginning trials by first testing the amount of bentonite needed in 9.5 L aquaria to consistently achieve our target turbidity levels. We used a 48 h acclimation period because these fish were well fed and we found in a pilot study that they needed more than 24 h to become hungry enough to forage in a reasonable amount of time in an experimental trial. The fish were then acclimated for an additional 10 min habituation period before a feeding trial was initiated. We began each 10 min focal trial by adding 10 live prey items precut to a standard length to the same location in the testing tank with a syringe. We cut prey items to a standard length to avoid any confounding effects from using prey of different sizes and found in a pilot study that this did not affect prey movement during the short duration of the trial. The trial was initiated immediately after food was added to the tank. During the trial we observed and recorded the time to initiate foraging (first strike at prey) and the number of strikes made at prey by the focal individual per prey items consumed by that individual. We terminated the trials at the end of the 10 min interval to reduce confounding factors associated with keeping the bentonite suspended in the water column.

TABLE 1.—Water turbidity levels (NTU) used as treatments to examine *Etheostoma fonticola* prey consumption and time to initiate foraging. Significant (alpha = 0.05) differences are based on Tukey's HSD. Asterisks denote contrasts not compared before. Turbidity levels were too high to quantify visual observations

Tukey's HSD (turbidity, NTU)	Total prey items consumed P-value	Time to initiate foraging P-value	Total prey consumed out of the time left to forage P-value
<1 vs. 8.7	**<0.001**	0.414	**<0.001**
<1 vs. 23.2	**<0.001**	**0.022**	**<0.001**
<1 vs. 74.6	**<0.001**	*	*
8.7 vs. 23.2	0.457	0.363	0.246
8.7 vs. 74.6	0.333	*	*
23.2 vs. 74.6	0.997	*	*

This was enough time for fish to respond to the treatment. At the end of the feeding trial, we removed the test fish and counted remaining prey items to measure total prey consumption by both fish and divided this value by two. This measurement of total prey consumption was necessary in order to include the highest turbidity level treatment in which we were not able to observe the focal individual consuming prey. We measured total prey consumed out of the time left to forage (600 s − time to initiate foraging) to control for total amount of time spent foraging. Ten prey items were added to the tank so that numerous prey items always remained at the end of the trial. Fish were only used for a single experimental trial and not used for any subsequent trial or treatment. Those fish that did not exhibit foraging behaviors were excluded from analyses for number of strikes made per prey items consumed. Data were analyzed using Analysis of Variance (ANOVA) to look at the effects of treatment and size and their interaction on total number of prey items consumed, time to initiate foraging, total prey consumed out of time left to forage, and the number of strikes made per prey items consumed. Two trials were excluded from statistical analyses because of abnormal fish behavior, we presume due to the short habituation period used for these experiments. All the data met the assumptions of parametric data. Significant ANOVAs (alpha = 0.05) were followed by Tukey's Honest Significant Difference tests to assess differences among turbidity levels. All analyses were performed using JMP 11 software (SAS, 2012).

RESULTS

Sudden changes in turbidity levels appeared to negatively affect foraging behavior. All fish subjected to the lowest turbidity level (*i.e.*, clear control) consumed prey. Conversely, those subject to 8.7, 23.2, and 74.6 NTU had similar percentages of individuals [25% (N = 5), 20% (N = 4), and 30% (N = 6), respectively] that never consumed prey during their respective 10 min trial.

The total number of prey items consumed for one fish was negatively affected by turbidity level ($F_{3,71} = 16.31$, P < 0.001; Table 1). There was no effect of focal fish size and no interaction between treatment and focal fish size. All three turbidity treatments resulted in significantly less prey consumption when compared to the clear control. The total prey consumption was not significantly different among the higher turbidity (*i.e.*, 8.7, 23.2, and 74.6 NTU) treatments.

Time to initiate foraging was negatively affected by turbidity level ($F_{2,38} = 5.11$, P = 0.01; Table 1). There was no effect of focal fish size and no interaction between treatment and focal fish size. Darters took longer to initiate foraging at 23.2 NTU compared to controls. Time to

initiate foraging did significantly differ between the control and 8.7 NTU and 8.7 and 23.2 NTU. We could not observe time to forage for the 74 NTU treatment, so this treatment was excluded from the analysis.

The total prey consumed out of the time left to forage was negatively affected by turbidity level ($F_{2,38}$ = 16.24, P < 0.001; Table 1). There was no effect of focal fish size and no interaction between treatment and focal fish size. The control group consumed significantly more prey during the time left to forage than the 8.7 NTU and the 23.2 NTU treatments. The prey items consumed in the time left to forage did not differ between the 8.7 and 23.2 NTU treatments.

There was not a significant difference in the number of strikes made per prey items consumed (prey-capture success) among any turbidity or control treatments ($F_{2,42}$ = 0.65, P = 0.53; Table 1). There was no effect of focal fish size and no interaction between treatment and focal fish size.

DISCUSSION

This study demonstrates a relatively minimal rise in turbidity can significantly decrease the total number of prey items consumed by *E. fonticola* and increase the time to initiate foraging. However, once a prey item was located, turbidity did not reduce their ability to capture prey successfully. More specifically, prey consumption decreased significantly at the lowest turbidity (8.7 NTU) level we tested. This suggests even a slight increase in turbidity may reduce foraging in *E. fonticola*. Similar findings of low levels of turbidity affecting foraging behavior in fishes have been documented previously (8 to 10 NTU: Zamor and Grossman, 2007), although much of the literature reports effects at far higher turbidity levels (*e.g.,* 810 NTU: Gregory and Northcote, 1993; 320 NTU: Rowe *et al.*, 2003). Nevertheless, the turbidity levels tested in this study are consistent with those found in the native range of *E. fonticola*, with 7.2 NTU being typical of daily turbidity readings during high recreation summer months (Araujo, 2012). In our study foraging declined sharply at the lowest level of turbidity rather than gradually decreasing across the three turbidity levels tested. As such it appears that *E. fonticola* has a low-threshold for turbidity with regards to foraging and once crossed, prey consumption is reduced. It is possible that *E. fonticola* would respond differently to long-term exposure to turbidity, perhaps acclimating to a higher turbidity level over time and regaining some ability to forage successfully in moderately turbid waters. However, short-term influxes in turbidity, as measured in our study, are common in *E. fonticola* habitat so these findings appear to be relative to the ecology of this species.

The time it took *E. fonticola* to initiate foraging increased with turbidity. Although time to initiate foraging was slowed at the lowest turbidity level, this difference was not significant relative to controls. However, time to initiate foraging at moderate turbidity (23.2 NTU) was significantly slower than the control treatment. Although time to initiate foraging was not recorded at the highest turbidity level (74.6 NTU) because fish could not be easily observed, we presume that it was also slower than controls; however, additional testing will be needed to confirm this hypothesis. Therefore, it appears *E. fonticola* only significantly delays initiating foraging at moderate turbidity levels (23.2 NTU) in contrast to prey consumption, which dropped sharply in the lowest turbidity level (8.7 NTU) included in our study. We speculate this increase in time to initiate foraging at relatively moderate turbidity levels may be related to a reduced visual acuity. This is because the spectrum of information available for foraging decisions is reduced for *E. fonticola* at turbidity levels greater than 8.7 NTU. Regardless, a lengthened time to initiate foraging in turbid conditions implies additional time spent searching for prey. This result is important as additional time devoted to foraging is energetically

costly and inevitably results in a trade-off with time allocated for other beneficial behaviors such as mating (Sih, 1992). As a higher turbidity level was required to produce a delay in initiating foraging as opposed to prey consumption, it is possible that *E. fonticola* is able to maintain foraging efficiency at minimal levels of turbidity although consumption is reduced. However, slightly higher turbidity levels (*i.e.,* 23.2 NTU) may result in lower efficiency (additional time spent searching for prey), in turn resulting in greater energetic cost to the animal than reduced consumption alone. With this said, our result that consumption was lower even if we account for the time left to forage, due to the delay in initiating foraging, indicates that the time to initiate foraging is not driving the change in consumption across turbidity levels.

Turbidity did not affect prey-capture success in our study. The number of strikes made per total number of prey items consumed did not differ between the control and either turbidity level tested (data were not recorded at the 74.6 NTU due to poor visibility). We hypothesize *E. fonticola* was able to accurately forage once prey was detected. Therefore, elevated turbidity levels may have produced an all or nothing response by impairing foraging, resulting in lower prey consumption and slower time to initiate foraging, but if prey was detected, accuracy of foraging was not affected. For example Sweka and Hartman (2003) found elevated turbidity significantly reduced the probability of reacting to a prey item in smallmouth bass, *Micropterus dolomieu*, but did not affect prey-capture success following a reaction. Also, the precise mechanisms controlling prey-capture success are not well understood. This is partially due to the variation in methodologies used by researchers in measuring prey-capture success. For example prey consumption rate (Rowe *et al.,* 2003), probability of detection (Sweka and Hartman, 2001), and percentages of prey consumed (Zamor and Grossman, 2007) have all been used to quantify prey-capture success. We attempted to pinpoint accuracy by measuring strikes made per prey items consumed, but it is possible that another method of quantifying prey capture success would have yielded different results.

Interestingly, increased turbidity also resulted in a significant drop in the number of fish foraging. In the control treatment, 100% of fish tested initiated foraging and consumed at least one prey item. In the following two turbidity levels tested (8.7 and 23.2 NTU), only 80% of fish tested engaged in foraging during the 10 min trial, with only 70% foraging at the highest turbidity level (74.6 NTU). This pattern of a steep initial decline at the lowest turbidity level tested (8.7 NTU) remaining constant through the highest turbidity level tested (74.6 NTU) is similar to the pattern observed for prey consumption. There are multiple hypotheses for these results. First, given the exceptionally low turbidity levels typical of *E. fonticola* habitat and the effects of low turbidity levels detected in previous studies (Zamor and Grossman, 2007), it is possible that this species is highly intolerant of turbidity and therefore foraging behavior is affected at extremely low levels. However, it is also possible that these effects are a result of the nonvisual impacts of turbidity (*i.e.,* adding suspended sediment to the water). Suspended solids can alter chemical properties in the water in ways that either enhance (Reddy, 1981) or degrade (Engström-Öst and Candolin, 2007) chemical signals and can cause a physiological response in the form of gill trauma (Berg, 1982). Given turbidity is in fact caused by particulates, nonvisual effects at such low levels of turbidity are still an important finding. Alternatively, the effects documented at such low turbidity levels in this study could be a result of using hatchery-reared fish as compared to wild caught fish, which have different learning experiences (Fenderson *et al.,* 1968; Swain and Riddell, 1990) and have never been subjected to turbid water. Additionally, our trials lasted only 10 min and it reasons that fish may acclimate to turbid conditions and become more proficient through time. Fish in general are able to learn and foraging is a well-documented area in which learning occurs (Warburton, 2003). Wild fish, even those occurring in such naturally clear waters as *E. fonticola*, are naturally subjected to fluctuating turbidity levels to at least some extent. The

fish used in our study, however, had never been exposed to any form of turbidity. Therefore, if learning plays a role in how wild *E. fonticola* responds to turbidity while foraging, then the effects detected in our study may be greater than those predicted for wild fish. However, further study will be required to test this hypothesis. Additionally, the hypothesis greater habituation or acclimation to turbidity might reduce some of the effects observed in our study does not preclude biological significance. *Etheostoma fonticola* lives in extremely clear waters where turbidity can increase dramatically and suddenly due to isolated events and then dissipate quickly as well. Therefore, a negative effect on foraging due to sudden changes in turbidity would still be significant for this species.

The decrease in prey consumption and increase in time to initiate foraging in turbid conditions detected in our study indicates that *E. fonticola* loses some ability to detect prey even at very low turbidity levels. The biological implications of decreased prey consumption, increased time spent searching for prey, and fewer individuals engaging in foraging are concerning as it is likely that *E. fonticola* is devoting greater amounts of energy to foraging, therefore reducing energy available for other behaviors essential for fitness (Sih, 1992). As turbidity has been demonstrated to affect other behaviors such as predator avoidance (Gregory, 1993) and reproduction (Seehausen *et al.*, 1997; Sutherland, 2007) as well, the biological implications for *E. fonticola* are not necessarily confined to foraging alone. If increased turbidity is also increasing the energy necessary for successful reproduction or predator avoidance, the effects on fitness could be far more significant than if only foraging is considered. Additional studies exploring these hypotheses would be of interest.

The conservation implications of this study are important as the San Marcos and Comal Rivers periodically and seasonally experience increases in turbidity often as a result of anthropogenic disturbance. Turbidity levels in this system are traditionally low, ranging from 0.26 to 5.76 NTU at the headwaters up to 13 NTU downstream (Saunders *et al.*, 2001), where 20 NTU is considered a threshold for low turbidity streams (USEPA, 1999). However, even low turbidity levels in our experiment (8.7 NTU) significantly reduced prey consumption in our study. Also, heavy recreational use during the summer months and severe storm events can cause these levels to far exceed such thresholds. Previous studies have indicated that the behavioral effects of rising turbidity may be especially significant for species not adapted to habitats traditionally associated with high turbidity (Bonner and Wilde, 2002; Grosse *et al.*, 2010; Allen-Ankins *et al.*, 2012) such as *E. fonticola* and turbidity has been found to alter anti-predator response in *E. fonticola* in particular (Swanbrow Becker and Gabor, 2012). These implications are therefore important not only in the San Marcos and Comal Rivers but may also have relevance for freshwater systems worldwide, especially for species traditionally adapted to low turbidity conditions, as major anthropogenic stressors associated with rising turbidity such as runoff and modification of river flow are occurring on a global scale.

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