EFFECTS OF TURBIDITY ON ANTI-PREDATOR RESPONSE AND FORAGING

BEHAVIOR IN THE FOUNTAIN DARTER,

ETHEOSTOMA FONTICOLA

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ABSTRACT

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Turbidity resulting from anthropogenic stressors poses a significant threat to freshwater systems and is occurring on a global scale. The pervasive impacts of turbidity include degraded visual ability resulting in altered animal behavior. Anti-predator response and successful foraging ability, both essential elements of ecological communities, are two aspects of behavior that can be affected by turbidity. The federally endangered fountain darter (*Etheostoma fonticola*) is an important species for investigating the impacts of turbidity on behavior. *Etheostoma fonticola* is endemic to

the clear, spring-fed waters of the San Marcos and Comal Rivers. These rivers are currently subject to a number of anthropogenic threats that may affect turbidity such as pollution, climate change, and increased recreational use. I tested the affects of clear water and low (~30 NTU) turbidity on anti-predator response and foraging behavior in *E. fonticola* and found that *E. fonticola* requires a combination of visual and chemical cues to respond to a native fish predator. However, low turbidity did not significantly affect anti-predator response. Given that turbidity degrades vision, these results imply that higher turbidity levels than included in my study may impact anti-predator response. I also found that prey consumption and time spent searching for prey were significantly altered across three levels of low to medium turbidity compared to clear water. Prey-capture success was not affected by increased turbidity. Thus, foraging behavior is significantly compromised even at relatively low levels of turbidity. These results suggest that the affects of turbidity on foraging and anti-predator behavior may be of considerable concern in *E. fonticola* habitat.

CHAPTER I

TURBIDITY AND BEHAVIOR

Animal Communication

Animal communication involves often-complex interactions between signalers, modes of signals and signal components (reviewed in Johnstone 1997). At the most basic level, communication involves a direct interaction between a signaler and receiver, although in many cases multiple signalers and receivers with divergent interests can be involved. In the case of predator-prey interactions, an unintended recipient can intercept signals. For example, fringe-lipped bats (*Trachops cirrhosus*) eavesdrop on acoustic mating calls of edible frogs to locate and capture prey (Tuttle & Ryan 1981). Although not a form of direct communication per-se, a receiver (prey) may engage in spying by detecting and responding adaptively to cues originating from another animal (predator) (Wisenden & Stacey 2004).

Signals can be transmitted through a variety of modalities (e.g. visual, chemical, acoustic, tactile), sometimes of differing effectiveness for the receiver (Rowe 1999). Signals of different modalities can be transmitted alone or in combination. Multi-modal cues can provide greater accuracy when detecting and responding to the risk of predation. The back-up signal hypothesis predicts that multi-modal signals presented simultaneously

can improve accuracy of interpretation (Johnstone 1996). For example, mosquitofish (*Gambusia holbrooki*) were more successful at avoiding predation when presented with visual and chemical cues simultaneously (Ward & Mehner 2010). However, the specific modality used and the use of single versus multi-modal cues can vary based on the situation and environment.

Environmental noise can cloud signals, making interpretation difficult and thus affecting signal usage (Endler 1993). In addition to improving interpretation accuracy, back-up signals can also function as a means to compensate for primary signals impaired due to environmental conditions. In aquatic environments, low-light conditions or turbidity can greatly influence the accuracy of signal transmission, resulting in reliance on back-up signals. For example, female preference for larger males in a cave-dwelling population of Atlantic mollies (*Poecilia mexicana*) was maintained through chemical detection in the absence of accurate visual information (Plath et al. 2004). Thus, environmental conditions can directly influence signal modality and the use of multi-modal signals.

<u>Predator Avoidance Behavior</u>

Prey animals must endure a constant struggle against predation in the wild. Defenses against detection and capture by predators are therefore essential for survival and can result in trade-offs between time allocated for other behaviors such as foraging and mating (Sih 1992). These ecological trade-offs are explained by the threat sensitivity hypothesis (Helfman 1989), which predicts an increased anti-predator response in prey

when threats are perceived as more severe. For example, a predator that is larger or closer would be expected to elicit a stronger anti-predator response from its prey than a smaller predator or one that is further away. Such threat sensitive behavioral responses have been widely documented in aquatic organisms (Sih 1982; Brown 2003; Ferrari et al. 2008).

In general, prey animals respond to the threat of predation through behavior (Petranka 1983; Kesavaraju et al. 2007), morphology (Brönmark & Miner 1992; Tollrian 1995; Swaddle & Lockwood 1998; Relyea 2001), and life history (Skelly & Werner 1990; Sih & Moore 1993; Werner & Anholt 1996). A single species may rely on multiple anti-predator strategies. Behavioral responses are the most widely studied of the three and can vary tremendously across taxa. Fleeing, mobbing, and freezing are a few of many anti-predator behaviors common in the animal kindgom. Reduced activity (freezing) is one behavioral response that has been shown to be particularly common among aquatic prey in response to predators such as birds and fish (Skelly 1994; Vilhunen & Hirvonen 2003).

Anti-predator response can be innate, learned or can exist on a continuum between the two types. Innate response occurs when a prey animal without prior experience is able to detect and identify a predator and is expected in environments with high predation pressure and low variation in potential predators, or most typically when there is an evolutionary relationship between predator and prey species (Brown & Chivers 2005). Innate response has been documented in a number of fishes (Berejikian et al. 2003; Vilhunen & Hirvonen 2003; Hawkins et al. 2004), and in some cases a baseline innate response in predator-naïve fish has been heightened in the laboratory through

conditioning with conspecific chemical alarm cues presented simultaneously with visual

or chemical predator stimuli (Berejikian et al. 2003). Such examples of a learned

increase in anti-predator response occurring in fish with some innate ability for predator

recognition provide evidence of the continuum possible between innate and learned

response. Conditioning through simultaneous alarm cues and predator stimuli is

generally required for species depending on learned predator recognition. Learned

predator recognition has been documented in a wide variety of aquatic prey species

(reviewed in Brown 2003) and is expected in fluctuating environments with high

diversity of potential predators (Brown & Chivers 2005). In general, innate anti-predator

response in common in amphibian prey while fish prey trend toward learned predator

recognition. However, this generalization is not true for all species studied and the

predator recognition ability of many species is yet unknown. In *Etheostoma*, innate

versus learned anti-predator response had not been determined prior to this research.

Predator Avoidance in Fishes

Many freshwater fish use a combination of visual and chemical cues to assess and

respond to the risk of predation (Chivers & Smith 1994; Wisenden et al. 2003; Holmes &

McCormick 2011). In general, visual cues are important to many prey fishes (Murphy &

Pitcher 1997; Smith & Belk 2001). For example, when a predator model was closer,

larger, or in a feeding position, damselfish (*Stegastes planifrons*) demonstrated a stronger

anti-predator response (Helfman 1989). However, aquatic amphibian prey often rely

primarily on chemical cues (Petranka et al. 1987; Mathis &Vincent 2000). This

distinction may be due to different sensory capabilities among aquatic prey types. For instance, freshwater fish tend to perceive visual signals faster than chemical signals but may rely on chemical signals for more species-specific information (Endler 1993).

Prey species can use many forms of chemical information with regard to predator detection. Chemical cues detected by prey can be in the form of kairomones, or chemicals emitted by a species that can be detected by another species (Kats & Dill 1998; Mathis et al. 2003) or diet cues based on recent foraging activity (Chivers & Mirza 2001). Kairomones alone can convey enough information for a prey animal to distinguish between a predator and a non-predator (Mathis 2003). Diet cues are often combinations of kairomones from a predator and alarm cues released by an injured conspecific upon consumption (reviewed in Chivers & Smith 1998). Chemical alarm cues are also important regarding recognition of a novel predator, especially in fishes lacking innate anti-predator response (Chivers & Smith 1994). Chemical alarm cues have been documented in numerous genera of freshwater fish including *Etheostoma* (Gibson & Mathis 2006; Crane et al. 2009). Disturbance pheromones, or cues released from conspecifics under threat of predation but in the absence of physical injury, have also been documented in *Etheostoma* (Wisenden et al. 1995).

Foraging Behavior of Carnivorous Fishes

Foraging is an essential element in the regulation of aquatic communities. Fish alter community structure by way of their prey populations (Murdoch et al. 1975) and can alter their foraging behavior in response to habitat characteristics (Werner et al. 1983).

Predatory fishes can feed primarily on benthic prey (e.g. cod, bass, sculpins, darters), drift prey (e.g. trout), or a combination of both prey types (e.g. salmonids) (Dahl & Greenberg 1996). Specific foraging strategies in addition to affects of biotic and abiotic factors are widely variable among different types of feeders. Biotic factors such as changes in prey density and abundance (Ringler 1979), prey size (Werner & Hall 1974), and predation risk (Schmitt & Holbrook 1985) can cause foraging behavior to flux, as can abiotic factors such as turbidity and reduced cover. For example, response to varying stream sediment resulted in divergent foraging mechanisms in two darter species with similar diets (Schlosser & Toth 1984). Turbidity in particular has been shown to affect various aspects of foraging behavior in fishes, including selectivity of benthic versus drift prey types (Shoup & Wahl 2009).

Turbidity and Anti-Predator Response

Elevated turbidity can have tremendous and often devastating impacts on aquatic ecosystems. Turbidity can drastically alter community structure through benthic smothering and altered rates of photosynthesis (Davies-Colley & Smith 2001). From a behavioral standpoint, turbidity degrades the quality and transmission of visual information, which can impair an animal's ability to forage (Vogel & Beauchamp 1999), select a mate (Seehausen & van Alphen 1997), and respond to a predator (Gregory 1993).

Turbidity has been documented to affect predator-prey interaction in a number of ways. Prior studies have shown that turbidity decreases the ability of fish to generalize predator recognition (Ferrari et al. 2010) and increases high-risk behavior (Miner & Stein

1996) thus increasing the risk of predation. Turbidity can also weaken the intensity of anti-predator response in fish. For example, juvenile chinook salmon (*Oncorhynchus tshawytscha*) displayed a weaker and shorter anti-predator response to both bird and fish predator models in turbid conditions (Gregory 1993). Conversely, turbidity has also been found to increase anti-predator response through heightened reliance on chemical cues due to sensory compensation (Hartman & Abrahams 2000). In habitats where both visual and chemical cues are important, prey may increase reliance on chemical cues when vision is impaired. For instance, when exposed to visual and chemical predator stimuli, spiny damselfish (*Acanthochromis polyacanthus*) reduced their foraging by approximately 40 percent in turbid conditions (Leahy et al. 2011).

Turbidity and Foraging

Turbidity affects foraging behavior primarily through reactive distances and prey-capture success (Vogel & Beauchamp 1999; Sweka & Hartman 2001; Quesenberry et al. 2007; Zamor & Grossman 2007; Wellington et al. 2010). However, additional aspects of foraging behavior such as prey-searching activity (Meager & Batty 2007), foraging rate (Webster et al. 2007) and prey consumption (Bonner & Wilde 2002) can also be affected by turbidity. While the majority of such studies have focused on game fishes, effects of turbidity on foraging have been documented in non-game fishes as well and a need for more work in this area remains. For example, rosyside dace (*Clinostromus fundoloides*) exposed to turbidity levels less than 56 nephelometric turbidity units (NTU) displayed significantly lower capture rates and reactive distances (Zamor & Grossman 2007). Also, elevated turbidity reduced prey consumption in stream fishes not adapted to highly

turbid environments (Bonner & Wilde 2002).

In general, turbidity has been shown to affect accuracy of foraging to a greater degree than searching behavior. As it decreases accuracy, turbidity can actually increase the number of unsuccessful foraging attempts, which can be energetically costly for predators. For example, perch (*Perca fluviatilis*) displayed reduced prey-capture success but a higher number of attacks (strikes against prey) in turbid conditions (Ljunggren & Sandström 2007). Turbidity has also been shown to affect prey selectivity in a number of game fishes (Rowe et al. 2003; Carter et al. 2009). For example, juvenile rainbow trout (*Oncorhynchus mykiss*) displayed decreased size-selection of both limnetic and benthic prey in turbid conditions (Rowe et al. 2003). Also, Shoup & Wahl (2009) found that largemouth bass (*Micropterus salmoides*) preferentially foraged on prey occurring higher in the water-column, ostensibly due to light-turbidity interactions impairing the ability of bass to capture prey near the bottom of experimental tanks. Thus, turbidity may result in a shift in preference for limnetic over benthic prey if foraging accurately for benthic prey becomes disproportionately difficult in turbid conditions. However, studies on the effects of turbidity on prey selectivity are currently few and largely limited to game fishes.

Study System and Species

The San Marcos and Comal Rivers are part of the largest spring system in Texas, and are unique aquatic ecosystems to the southwestern United States (USFWS 1996). These waters are constant in temperature and flow, and are home to many endemic flora and fauna including seven threatened and endangered species (USFWS 1996). The San Marcos River is also home to a large community of native fish predators. Centrarchid

fishes are particularly voracious and opportunistic in foraging (Hodgson & Kitchell 1987). However, these ecosystems are currently facing many threats and are at risk of losing biodiversity. These threats are largely anthropogenic in nature and include habitat loss due to increased riverside urbanization, pollution, increased groundwater withdrawal, recreational use, and introduced species. Global climate change is also predicted to affect freshwater systems by causing decreases in suitable habitat yielding altered distribution of some specialized fishes (Chu et al. 2005; Xenopoulos et al. 2005). Specifically, climate change is predicted to exacerbate water shortages in the Edwards Aquifer system (Loaiciga et al. 2000). Additionally, general warming trends are predicted to affect central Texas by causing more extreme flooding and periods of drought, all of which may affect turbidity levels in the associated spring systems. Currently, turbidity in the San Marcos River ranges from 0.26-5.76 NTUs at the headwaters and up to 18 NTU downriver from the headwaters (Saunders et al. 2001), where 20 NTU is considered a threshold for low turbidity streams (USEPA 1999). Turbidity likely increases far beyond these levels during heavy recreational use and storm events.

The fountain darter (*Etheostoma fonticola)* is endemic to the San Marcos and Comal rivers (Guadalupe River drainage) of central Texas. Fountain darters are associated with vegetated stream-floor habitats with relatively constant water temperature and moderate flow. *Etheostoma fonticola* is threatened by reduction of spring flow resulting from drought and water withdrawals from the Edwards Aquifer (Bonner & McDonald 2005), thus maintenance of adequate stream flow is important for their survival. In response to this threat, *E. fonticola* is maintained at the San Marcos National

Fish Hatchery and Technology Center (USFWS) in San Marcos, Texas (SMNFHTC) in

the event that reintroduction becomes necessary.

     Etheostoma is a member of the benthic invertebrate feeding guild and is generally

diurnally active (Vogt & Coon 1990; Greenberg 1991). Fountain darters held in aquaria

preferentially feed on moving invertebrates while ignoring static ones, which suggests

that they use visual cues to forage (USFWS 1996). However, the use of visual versus

chemical cues had not been tested in *E. fonticola* prior to this study, thus better

understanding of cue use is an important result of this research.

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CHAPTER II

EFFECTS OF TURBIDITY AND VISUAL VERSUS CHEMICAL CUES ON ANTI-

PREDATOR RESPONSE IN THE FOUNTAIN DARTER

(*ETHEOSTOMA FONTICOLA*)[1]

Abstract

Altered turbidity resulting from anthropogenic stressors is a global problem.
Currently threatened by climate change, pollution, and increased recreational usage, the
streams and rivers of central Texas are no exception. The impacts of turbidity include
behavioral effects as turbidity degrades visual information, which can impair an animal's
ability to accurately detect and respond to a predator. Here, we tested the impact of
simulated turbidity on anti-predator response in the fountain darter, *Etheostoma fonticola.*
We examined the response of *E. fonticola* to four predator cue treatments (chemical,
visual, chemical and visual, and no cues) using a native predator, the green sunfish
(*Lepomis cyanellus*). All cue treatments were tested across two vision levels: clear and
impaired, to simulate the visual effects of low turbidity (~30 NTU). Our results indicate
that *E. fonticola* requires a combination of visual and chemical stimuli to respond to fish
predator. In the absence of one or the other sensory modality, *E. fonticola* did not show
an anti-predator response. However, vision impaired due to simulated turbidity had no

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significant effect on anti-predator response. These results indicate that although *E. fonticola* may be able to accurately detect and respond to a predator at low levels of turbidity, the absence of vision hampers anti-predator response. This implies that more significant visual impairment (higher turbidity) than tested within the scope of our study is likely to degrade anti-predator response in *E. fonticola*.

Introduction

Turbidity affects behavior primarily through clouding visual signals, which can make accurate signal interpretation difficult (Endler 1993). Aquatic prey animals can use a number of signal modalities for predator detection, with visual and chemical being two of the most common and well studied (Kats & Dill 1998; Collin & Whitehead 2004; Preisser et al. 2005). Visual and chemical signals can be used alone or in combination to distinguish a predator from a non-predator and to gauge an appropriate response (Ferrari et al. 2010). Although not a direct form of communication between a signaler and receiver, "spying" by detecting and responding adaptively to signals originating from a predator may aid a prey animal in avoiding capture (Wisenden & Stacey 2004). Although the specific modality used and the efficacy of single versus multi-modal cues can vary based on the situation and environment, multi-modal cues such as the combination of visual and chemical often provide greater interpretation accuracy (Johnstone 1996; Ward & Mehner 2010).

In addition to improving interpretation accuracy, multi-modal cues can also function as back-up signals, compensating for primary signals impaired due to environmental conditions such as turbidity (Endler 1993). If vision is impaired, chemical back-up signals used for sensory compensation often become increasingly important

(Hartman & Abrahams 2000; Leahy et al. 2011). Yet turbidity can affect anti-predator behavior in sometimes contrasting ways. Turbidity decreases the ability of fish to generalize predator recognition (Ferrari et al. 2010), increases high-risk behavior (Miner & Stein 1996) and weakens the intensity of anti-predator response, thus increasing the risk of predation (Gregory 1993). Conversely, turbidity also increases anti-predator response through sensory compensation in the form of heightened reliance on chemical signals (Hartman & Abrahams 2000; Leahy et al. 2011). Though increased anti-predator response in turbid conditions may decrease the risk of capture and consumption, it also results in trade-offs between time allocated for other beneficial behaviors such as foraging and mating (Sih 1992), which may also be compromised in turbid conditions.

Many freshwater fish use a combination of visual and chemical signals in predator avoidance (Chivers & Smith 1994; Wisenden et al. 2003; Holmes & McCormick 2011). Aquatic prey species can use many forms of chemical information with regard to predator detection including kairomones, or chemicals emitted by a species that can be detected by another species (Kats & Dill 1998; Mathis et al. 2003), diet cues based on recent foraging activity (Chivers & Mirza 2001), or alarm cues released from an injured conspecific (Gibson & Mathis 2006; Crane et al. 2009). Kairomones alone can convey enough information for a prey animal to distinguish between a predator and a non-predator (Mathis 2003). An important organism for examining the sensory modality being used for predator recognition and the impact of turbidity is the U.S. federally endangered fountain darter, *Etheostoma fonticola* (USFWS 1996).

Study System

Headwater streams contribute significant biodiversity to river networks, often supporting a large number of endemic or endangered species and thus are particularly vulnerable to anthropogenic impacts (Meyer et al. 2007). The waters of the San Marcos and Comal Rivers of central Texas, Hays and Comal CO, are no exception. These rivers are home to many endemic flora and fauna including seven threatened and endangered species including *E. fonticola* (USFWS 1996). They are also part of the Edwards Aquifer system, the source of water for over two million users and one of the most prolific artesian aquifers in the world. Current anthropogenic threats affecting these waters include pollution, run-off, recreational use, introduced species, and climate change, which are predicted to exacerbate water shortages in central Texas (Loaiciga et al. 2000). Water shortages due to increased withdrawal are expected to especially impact Texas rivers and streams in the near future. The Edwards Aquifer is the primary source of drinking water for the city of San Antonio, Texas, the seventh largest city in the United States. Increasing water consumption coupled with a rapidly growing population and predicted water shortages due to drought events seriously threatens the maintenance of adequate water levels and flow in rivers sourcing from the Edwards Aquifer. Although occupying broad habitat types within their limited range, *E. fonticola* occurs primarily at the spring-fed headwaters of these rivers and is associated with vegetated stream-floor habitats with relatively constant water temperature and moderate flow. As such, this species is particularly threatened by reduction of spring flow (Bonner & McDonald 2005). Such reduction of flow is associated with increased turbidity levels as are other threats to this system including recreation and run-off. Increased recreation in the form

of swimming, kayaking, and tubing may be a major source of increased turbidity in the

shallow waters of the San Marcos and Comal Rivers during the summer months.

Turbidity levels in 2010 were found to be significantly elevated in the Comal River

during periods of heavy recreational use compared to periods of light recreational use

(Araujo, *in prep.*). We are not aware of any previous behavioral studies of *E. fonticola*

and as many endemic fauna are exposed to similar threats, this organism may be an

important model for understanding predator avoidance behavior and the effects of

turbidity in this and similar freshwater systems.

Here, we investigated the effects of turbidity simulated by decreased visibility on

predator avoidance in *E. fonticola.* Specifically, we tested the importance of visual cues

versus predator kairomones in the laboratory, while also examining the effects of reduced

visibility on predator avoidance behavior. We tested the hypothesis that *E. fonticola* uses

visual cues to detect and respond to fish predators and that simulated turbidity would

decrease anti-predator response. An alternative hypothesis predicts that simulated

turbidity would increase anti-predator response in *E. fonticola* when exposed to chemical

cues due to sensory compensation.

Methods

Trials were conducted at the San Marcos National Fish Hatchery and Technology

Center (USFWS) in San Marcos, Texas from January - May 2011. Predator naïve first

generation, hatchery-reared adult *Etheostoma fonticola* were used for all trials. Prior to

testing, individuals were housed in holding tanks with recirculating well water ($23\,^{\circ}$C).

Test fish were fed a diet of black worms (*Lumbriculus variegatus*), amphipods, and zooplankton once daily.

We examined the response of adult *E. fonticola* in four predator cue treatments across two vision level treatments ((a) clear and (b) impaired to simulate the visual effects of turbidity). We tested the following predator cue treatments: (1) chemical cues only (n=15 x 2 vision levels), (2) visual cues only (n=15 x 2 vision levels), and (3) visual and chemical cues (n=15 x 2 vision levels), and (4) no predator cues (water control) (n=15 x 2 vision levels). We used a native predator, the green sunfish (*Lepomis cyanellus*) for all predator cue treatments. Green sunfish are opportunistic foragers (Hodgson & Kitchell 1987) that occur sympatrically with fountain darters. We acquired six adult green sunfish of similar size from hatchery stock ponds.

Our experimental set-up consisted of four sets of adjacent, 9.5 litre drip-flow tanks (Figure 1). The adjacent tank design allowed for separate or combined exposure to visual and chemical stimuli. We affixed Glass-tinting allowing 70 % visible light transmission (WindowTint.com film) to two of the testing tanks on the side allowing exposure to the adjacent tank to simulate turbidity following methods of Sundin et al. (2010). Testing tanks included a fine gravel substrate and were wrapped in black plastic with the exception of the front-facing side and the side allowing visual exposure to the adjacent tank, in order to minimize disturbance to the fish. We covered the front-facing side with one-way tinting in order to further minimize disturbance while still allowing for visibility during trials. We randomized the location of specific tanks and used hydrogen peroxide and water to clean tanks between trials. We conducted all trials between 1000h – 1500h dates from start to end.

To initiate testing, we habituated the subject fish in the test tank for $\geq$24 h. Subsequent to habituation, we measured fish movement for 10 min (pre-stimulus). We quantified movement in terms of the number of movements (darts). We then subjected the test fish to a randomly selected predator cue treatment and measured movement for another 10 min (post-stimulus). We calculated the response variable as the difference in the number post-stimulus and pre-stimulus movements so that a negative final movement score indicated reduced movement (freezing) while a positive score indicated increased movement. Reduced activity is a very common anti-predator response in aquatic prey (Skelly 1994; Vilhunen & Hirvonen 2003). After testing, we removed each fish and recorded the standard length (SL) and sex.

To test the response to chemical cues only (treatment 1), we placed an opaque divider between the two adjacent tanks and then removed it for the second 10 min stimulus exposure period, exposing the test fish to an empty predator tank in order to replicate the procedure followed for exposing test fish to visual cues. We next injected 50 ml of chemical cues with a 60-ml syringe attached to airline tubing. The tubing was attached to the back of the tank using a suction cup and we injected water approximately 10 cm below the surface of the water at a rate of roughly 2 ml per second. We flushed the tubing with an additional 50 ml of well water introduced at the same rate, following the methods of Epp & Gabor (2008). To test the response to visual cues only (treatment 2), we placed an individual green sunfish in the adjacent 9.5 liter tank. We then removed an opaque divider prior to the post-stimulus exposure period, allowing the test fish visual access to the adjacent tank containing the predator. We randomly selected the green sunfish from the six available before each trial. We injected blank well water rather than

chemical stimulus material. To test the response to visual and chemical cues (treatment 3), during the post-stimulus exposure period we allowed visual access to an adjacent tank containing a green sunfish and injected 50 ml of chemical cues flushed with 50 ml of well water following cue injection. Finally, to test the response to no predator cues (control) (treatment 4), we allowed visual access to an empty adjacent tank for the second 10 min stimulus exposure period and injected blank well water into the testing tank.

We simulated turbid water in the testing tank via glass tinting following Sundin et al. (2010). Turbidity has traditionally been experimentally manipulated using some type of bentonite. However, such materials may produce odors that interfere with chemical cues or toxins that impact behavior and the use of simulated turbidity controls for these effects. The semi-transparent tinting between tanks allowed 70 % of visible light to be transmitted (70% VLT). The semi-transparent tinting was approximated to NTU by comparing light absorbency with that of known NTU standards using a spectrometer. Across the visible light spectrum (400–790 THz), the tinting corresponded with a turbidity range of 15 – 45 NTU. The clear vision tanks with no tinting affixed permitted for close to 100 % VLT, approximately equivalent to zero NTU.

We acquired the chemical stimulus material of two *L. cyanellus* individuals that were maintained in aquaria and fed a neutral diet of earthworms for six days to eliminate the potential effects of diet cues. We then determined the volume of each stimulus animal by displacement and placed each individual in a separate 75.7 liter tank with an amount of aerated well water equal to approximately 230 ml per 1 ml of stimulus animal. After 24 h, we removed animals from the aquaria and combined and stirred equal

proportions of water from each tank. We froze the stimulus material in quantities of 75

ml to be thawed immediately prior to testing following Epp & Gabor (2008).

We analyzed anti-predator response measured by the number of movements using

a two-factor ANOVA. We conducted post-hoc comparisons between treatments groups

using Tukey's Honest Significant Difference (HSD) test. All analyses were carried out

using JMP 9 software (SAS Institute Inc., SAS Campus Drive, Building S, Cary, NC,

27513, USA).

Figure 1. Experimental set-up. The tank housing the test fish (*E. fonticola*) is shown with
syringes and airline tubing for chemical stimulus introduction (right) and the tank
housing the predator species for treatments involving visual cues (left).

Results

Using a two-factor ANOVA we found a significant difference across predator cue treatment ($F_{7,109}$= 3.39, $P = 0.02$) but not vision level ($F_{7,109}$= 1.82, $P = 0.18$) or an interaction between cue treatment and vision level ($F_{7,109}$= 1.55, $P = 0.20$). Post-hoc comparisons between all treatments revealed only one significant difference between the control and the visual plus chemical combination cue treatment (Tukey's HSD, $P = 0.02$). When separated by vision level, this difference was only present at the clear vision level (Figures 2 a,b). When included as a factor in the model, there was no affect of sex on movement score.
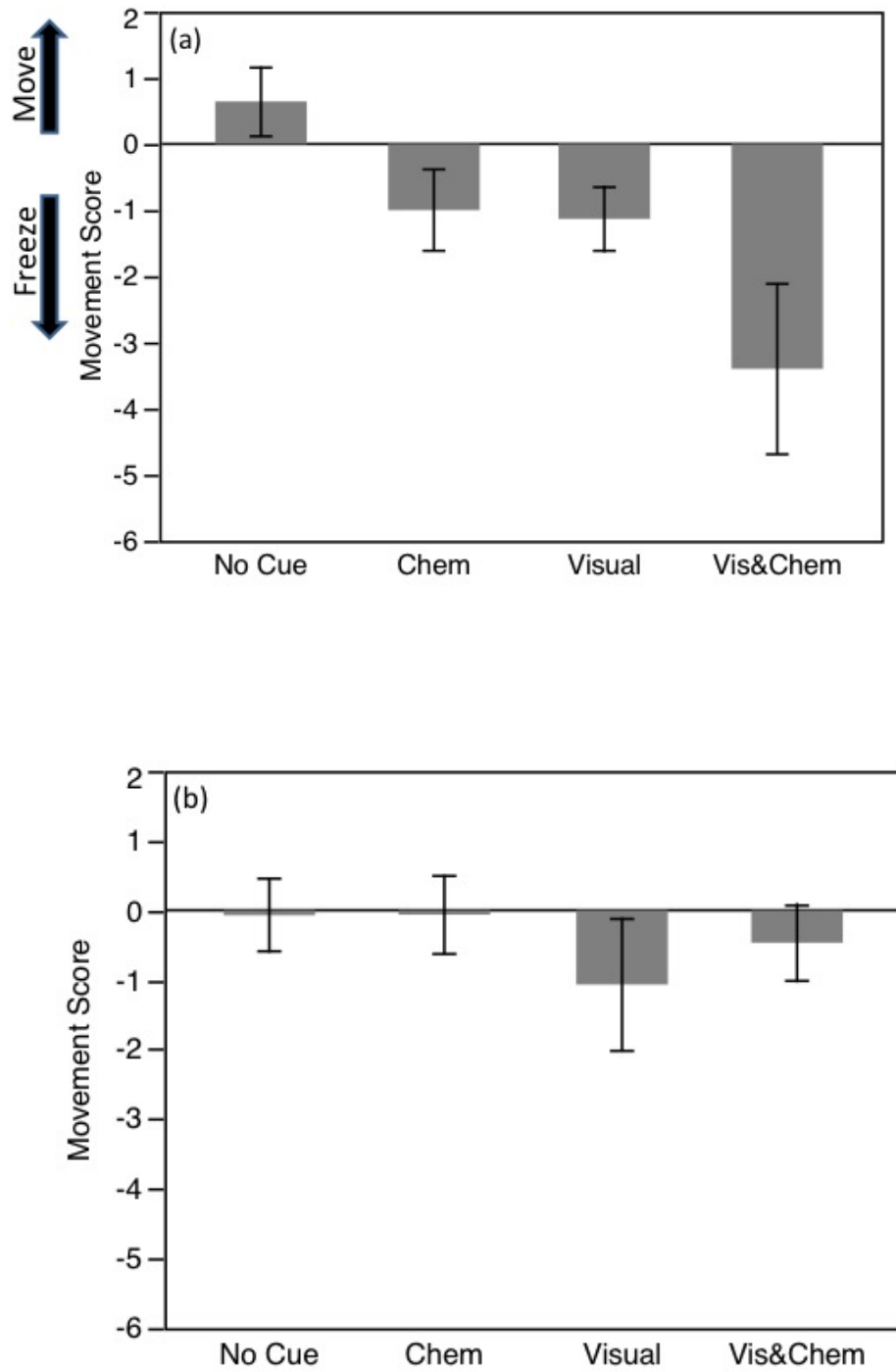
Figure 2. Mean ± 1 SE movement score for (a) clear vision, and (b) impaired vision (~30 NTU).

Discussion

Our data indicate that a combination of visual and chemical stimuli is necessary to fountain darters for predator detection. Only the visual plus chemical treatment (treatment 3) differed from the control. The lack of anti-predator response (freezing) when only one signal (visual or chemical) was presented indicates that *E. fonticola* is unable to increase reliance on another modality when one signal is lost. This result is consistent with previous work documenting the importance of multi-modal cues in interpretation accuracy (Johnstone 1996; Ward & Mehner 2010). For instance, freshwater fish have been shown to perceive visual signals faster than chemical signals but rely on chemical signals for more detailed information (Endler 1993). Our finding is significant in that it suggests that *E. fonticola* may not be able to adjust signal usage to rely exclusively on chemical cues when vision is significantly impaired due to turbidity. This has significant conservation implications for an endangered species living in a habitat highly subject to varying turbidity levels due to recreation and flood or drought events.

However, we did not detect a significant effect of impaired vision due to turbidity in our study. Although fish at the clear vision level demonstrated a stronger anti-predator response when exposed to visual and chemical cues than fish at the impaired vision level, this difference was not statistically significant. These results are contradictory to our finding that *E. fonticola* requires both visual and chemical cues to respond to a fish predator. When vision was completely blocked, *E. fonticola* was not able to respond to a predator using chemical stimuli alone. As turbidity impairs vision, we would expect a significant effect of impaired vision as well. The primary explanation for this result is

that *E. fonticola* was able to interpret enough visual information at the impaired vision level to detect and respond to the predator when chemical information was also available. The tint used to simulate turbidity allowed for 70% VLT and was found to be comparable to a turbidity level of approximately 30 NTU. It is possible that using a darker film (i.e. greater NTU) would have impaired vision to a greater degree, which could have produced a significant effect. Our finding that visual information in addition to chemical stimuli is necessary for anti-predator response in *E. fonticola* implies that some level of impaired vision degrades anti-predator response. A follow up study examining the specific level of impairment required to produce a significant effect would be of interest in further research.

The use of chemical and visual cues in anti-predator response has not been tested previously in *E. fonticola*. However, both disturbance pheromones (Wisenden et al. 1995) and alarm cues (Commens-Carson & Mathis 2007) have been documented in other species of *Etheostoma*. We are not aware of any studies that document the use of predator kairomones in *Etheostoma* prior to this one. It is possible that using another form of chemical signal such as alarm cues would have produced a stronger anti-predator response, potentially allowing for sensory compensation when vision was blocked or impaired. Alternatively, manipulating turbidity with bentonite as opposed to simulating turbidity with tinting may have produced a stronger or weaker anti-predator response. Suspended solids can alter chemical properties in the water in ways that either enhance (Reddy 1981) or degrade (Engström-Öst & Candolin 2007) chemical signals. Specifically, we aimed to target the visual impacts of turbidity and chose to eliminate

these potential effects in addition to the possible confounding effects on behavior resulting from introduced suspended solids.

Although our results indicated that *E. fonticola* has an innate ability to respond to a native fish predator, innate versus learned response exists on a continuum in many species (Ferrari et al. 2010). Previous studies have shown that a baseline innate response in fishes can be heightened in the laboratory through conditioning with conspecific chemical alarm cues presented simultaneously with visual or chemical predator stimuli (Berejikian et al. 2003). Thus, using wild-caught *E. fonticola* may have resulted in a more dramatic anti-predator or reliance on one modality in the absence of another. However, using predator naïve fish eliminated the potential effects of differential predator experience levels present in wild populations and maternal affects.

In conclusion, we experimentally demonstrate that visual and chemical signals combined were required to produce an anti-predator response in *E. fonticola*. Blocked vision when only chemical signals were presented weakened anti-predator response so that it did not differ from the water control yet impaired vision due to turbidity did not produce a significant effect. Thus, we found no evidence of sensory compensation when one signal modality is removed or altered. These findings highlight the need for further study of the effects of turbidity on this endangered, endemic species as an indication of the impact on these darters and other similar endemics living in habitats currently threatened by fluctuating turbidity levels due to anthropogenic impacts.

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CHAPTER III

TURBIDITY IMPAIRS FORAGING BEHAVIOR IN THE ENDANGERED FOUNTAIN DARTER (*ETHEOSTOMA FONTICOLA)*[2]

Abstract

Turbidity can alter the foraging behavior and success of fish. Therefore, we tested the effects of turbidity on foraging behavior in the U.S. federally endangered fountain darter *Etheostoma fonticola.* Specifically, we examined the affect of elevated turbidity levels on prey consumption, time to initiate foraging, and prey-capture success at four turbidity levels: clear water (<1 Nephelometric Turbidity Units [NTU]), $\bar{x} = 8.7$ NTU, $\bar{x} = 23.2$ NTU, and $\bar{x} = 74.6$ NTU). Our results indicate that elevated turbidity significantly affects prey consumption and time to initiate foraging but not prey-capture success. Prey consumption was significantly reduced and time to initiate foraging lengthened at all turbidity levels other than the clear water control. These data suggest that even a slight elevation in turbidity ($\bar{x} = 8.7$ NTU) can significantly impair foraging behavior in *E. fonticola*.

<u>Introduction</u>

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). Turbidity can modify community structure through benthic smothering and altered rates of photosynthesis (Davies-Colley & Smith 2001), but in addition to these well-studied community level effects turbidity can affect individual survival and reproduction by altering behavior. Turbidity impairs the quality of visual information by reducing the intensity of light and narrowing the light spectrum (Seehausen & van Alphen 1997), which can compromise an animal's ability to forage (Vogel & Beauchamp 1999), select a mate (Seehausen & van Alphen 1997), and respond to a predator (Gregory 1993). These behaviors are essential for long-term population viability, especially for species of conservation concern. Examining the effects of turbidity on animal behavior is important as such studies provide a non-invasive means of assessing the biological effects of anthropogenic environmental change.

Turbidity has been demonstrated to affect foraging behavior primarily through reactive distances and prey-capture success (Sweka & Hartman 2001; Zamor & Grossman 2007; Wellington et al. 2010). However, turbidity can also affect additional aspects of foraging behavior such as prey-searching activity (Meager & Batty 2007), foraging rate (Webster et al. 2007), prey consumption (Bonner & Wilde 2002), environmental refuge (Pekcan-Hekim, et al. 2010), and prey selectivity (Rowe et al. 2003; Carter et al. 2009; Shoup & Wahl 2009). In addition to reduction of caloric intake due to decreased prey consumption, turbidity can result in additional energetically costly

effects on predators, such as increased time spent searching for prey and decreased foraging accuracy. 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 predation, potentially further impacting individual fitness (Sih 1992; Ljunggren & Sandström 2007).

The fountain darter, *Etheostoma fonticola,* is a federally endangered species found in the San Marcos and Comal Rivers of central Texas. Many endemic flora and fauna including seven threatened and endangered species coexist in these waters, which are currently subject to numerous anthropogenic threats that affect turbidity levels including pollution, climate change, reduction of flow, and recreational use. Climate change is predicted to exacerbate water shortages in central Texas in the near future (Loaiciga et al. 2000). Recreational use may be an especially significant source of fluctuating turbidity levels in *E. fonticola* habitat. Turbidity levels in 2010 were found to be significantly elevated in the Comal River during periods of heavy recreational use compared to periods of light recreational use (Araujo *in prep*). *Etheostoma fonticola* is associated with clear, spring-fed systems with relatively constant water temperature and moderate flow and has been found to be particularly sensitive to environmental conditions, with reproductive behavior being temperature and flow dependent (Schenck & Whiteside 1977). *Etheostoma fonticola* may be especially vulnerable to the impacts of turbidity as are other fishes traditionally adapted to clear conditions versus species well adapted to turbid conditions (Bonner & Wilde 2002; Grosse et al. 2010; Allen-Ankins et al. 2012). *Etheostoma* are benthic feeders (Vogt & Coon 1990; Greenberg 1991) and *E. fonticola* held in aquaria preferentially feed on moving invertebrates while ignoring static ones

(USFWS 1996), which suggests that they rely on visual cues to forage. *Etheostoma fonticola* also requires the combination of visual and chemical information to respond to the threat of predation, implying that vision is likely important in foraging as well (Swanbrow Becker & Gabor, *in prep.*) Given that turbidity degrades the quality of visual information, animals relying on visual as opposed to olfactory signals for foraging may be disproportionally affected by turbidity (Allen-Ankins et al. 2012). Thus, a visual predator adapted to crystal clear headwaters such as *E. fonticola* is an ideal model to test the possible effects of turbidity on foraging and the results of this study have significant conservation implications for this endangered species as well as other aquatic predators.

We investigated the effects of turbidity on prey consumption, time to initiate foraging, and prey-capture success in *E. fonticola.* We tested the predictions that increasing turbidity reduces total prey consumption, lengthens the time to initiate foraging, and reduces the accuracy of prey-capture, thus increasing the number of attempts made at capturing prey.

Methods

Experimental trials were conducted at the San Marcos National Fish Hatchery and Technology Center (SMNFTC) in San Marcos, Texas. Fish were hatchery-reared, first generation adult *E. fonticola* and were housed and maintained at SMNFTC in holding tanks with well water (23 $^{\circ}$C). The tanks contained 3 to 4 pieces of polyvinyl chloride pipe and native vegetation to provide the fish with cover. All fish were maintained with a diet of black worms (*Lumbriculus variegatus*), amphipods, and zooplankton fed ad libitum daily.

We tested the effects of turbidity on prey consumption in *E. fonticola* across four treatments: (1) clear water control (<1 Nephelometric Turbidity Units [NTU]) (n=20), (2) $\bar{x}$ = 8.7 NTU (n=20), (3) $\bar{x}$ = 23.2 NTU (n=20), and (4) $\bar{x}$ = 74.6 NTU (n=20). Herein, treatments will be referred to as (1) <1, (2) 8.7, (3) 23.2 and (4) 74.6 NTU. The effects of turbidity on time to initiate foraging and prey-capture success were tested across only three treatments, <1 NTU, 8.7 NTU, and 23.2 NTU as elevated turbidity levels at 74.6 NTU seriously impaired the ability to accurately observe fish during trials. These turbidity levels were chosen in order to maintain consistency with the relatively low levels naturally occurring in *E. fonticola* habitat (0-20 NTU), along with the higher levels of turbidity consistent with temporary events such as heavy recreational use and rainfall (Saunders et al. 2001). We used black worms (*Lumbriculus variegatus*) as prey because they were consistently fed to the test fish, which eliminated any potential effects of learning and they are large enough to easily quantify.

Our experimental set-up consisted of eight, 9.5-liter glass aquaria with a fine gravel substrate. We wrapped tanks in black plastic with the exception of the front-facing side to minimize disturbance to the fish and block light penetration. The front-facing side was covered with one-way tinting to minimize disturbance and light penetration while still allowing observations. We randomized the location of specific aquaria and used hydrogen peroxide and water to clean aquaria between trials. We created turbidity during trials by adding commercially purchased 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 were measured at the end of each trial using a calibrated turbidity meter (Hach Model 2100 N Laboratory Turbidity

Meter). Precise turbidity levels at each trial fell into four ranges: < 1 NTU, 5 - 10 NTU

($\bar{x} = 8.7$), 20 - 30 NTU ($\bar{x} = 23.2$), and 60 - 80 NTU ($\bar{x} = 74.6$).

To initiate testing, we randomly assigned a turbidity treatment and placed two

haphazardly selected subject fish of the same sex into a drip-flow testing aquaria with

well water. We randomly selected one fish 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), of the same sex, to aid identification of the focal individual

during feeding trials. We used two fish in each trial as foraging in *E. fonticola* typically

occurs in proximity to other individuals and isolated fish do not acclimate well to testing

aquaria. After a 48-h habituation period without food, we added the appropriate amount

of bentonite depending on turbidity treatment. 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 ten live prey items cut to standard length to the same

location in the testing tank. The trial was initiated immediately after food was added to

the tank. During the trial, we observed and recorded the time to initiate foraging and

prey-capture success as the number of strikes made at prey by the focal individual per

prey items consumed by that individual. At the end of the feeding trial, we counted

remaining prey items to quantify total prey consumption. Ample food was added to the

tank so that numerous prey items always remained at the end of the trial. All three

response variables analyzed met the assumptions required for parametric tests after being

transformed. We added one constant to the original value in order to eliminate zeros and

then took the log for prey consumption and prey-capture success. The log of the original

value was used for time to initiate foraging. Data were analyzed using ANOVA and

Tukey's Honest Significant Difference (HSD) test to assess differences among turbidity

levels. All analyses were carried out using JMP 9 software (SAS Institute Inc., SAS

Campus Drive, Building S, Cary, NC, 27513, USA).

<div align="center">Results</div>

Total prey consumption was significantly affected by turbidity level (ANOVA:

$F_{3,76}$=14.34, $P < 0.0001$). All three turbidity treatments resulted in significantly less prey

consumption when compared to the control (Tukey's HSD: P's < 0.05). Prey

consumption was similar among all the turbidity treatments (Figure 1a; Table 1).

Time to initiate foraging was significantly affected by turbidity level (ANOVA:

$F_{2,43}$=4.44, $P = 0.02$). Darters initiated foraging in a significantly shorter amount of time

in the control treatment than at 23.2 NTU. Time to first feeding did not significantly

differ between the control and the lower turbidity level measured or between the two

turbidity treatments (Tukey's HSD; Figure 1b; Table 2).

There was not a significant difference in the number of strikes made per prey

items consumed (prey-capture success) among any turbidity treatment or control

(ANOVA: $F_{2,45}$=0.259, $P = 0.772$; Figure 1c).

Table 1. Water turbidity levels used to examine fountain darter prey consumption (Tukey's HSD). Bold values indicate a significant difference ($P < 0.05$) between contrasts.

Turbidity (NTUs) Contrasts	P-value
<1 & 8.7	**0.0011**
<1 & 23.2	**<0.0001**
<1 & 74.6	**<0.0001**
8.7 & 23.2	0.116
8.7 & 74.6	0.061
23.2 & 74.6	0.611

Table 2. Treatment comparisons for time to initiate foraging (Tukey's HSD). Bold values indicate a significant difference ($P < 0.05$).

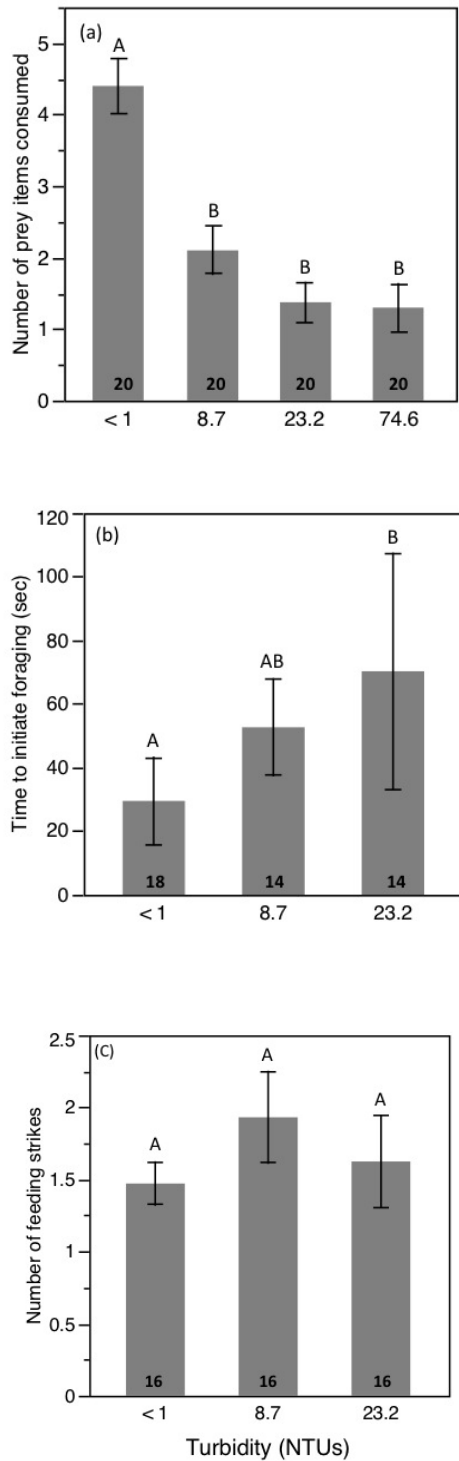| Turbidity Treatment Comparison (NTUs)	P-value
<1 & 8.7	0.059
<1 & 23.2	**0.028**
8.7 & 23.2	0.949

Figure 3. Mean ± 1 SE for: (a) number of prey items consumed, (b) time to initiate foraging, and (c) number of strikes made per prey items consumed at each turbidity level (NTU). Bold numbers on bars are the number of fish tested at each turbidity level, different letters represent significant differences among treatment groups ($P < 0.05$).

<div align="center">Discussion</div>

This study demonstrates that rising turbidity significantly affects total prey consumption and time to initiate foraging, but not prey-capture success. *Etheostoma fonticola* consumed significantly more prey items in clear water than when subjected to increased turbidity levels (Figure 1a). Prey consumption dropped significantly even at the lowest turbidity level, 8.7 NTU. This suggests that even a slight increase in turbidity reduces foraging in *E. fonticola*. Similar findings of low levels of turbidity affecting foraging behavior in fishes have been documented previously (8-10 NTUs: Zamor & Grossman 2007) although much of the literature reports effects at far higher turbidity levels (e.g. 810 NTUs: Gregory & Northcote 1993; 320 NTUs: Rowe et al. 2003). The turbidity levels tested in this study are consistent with those found in *E. fonticola*'s natural range, with 7.5 NTUs being typical of daily turbidity readings during high recreation summer months (Araujo, *in prep*). 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 tolerance and once crossed, prey consumption is greatly reduced.

Time to initiate foraging increased as turbidity increased. Although time to initiate foraging was slowed by the lowest turbidity level treatment, this difference was not significant. However, time to initiate foraging at the higher turbidity level recorded (23.2 NTUs) differed significantly from the control, with no differences between turbidity treatments detected. Time to initiate foraging was not recorded at the highest turbidity level included in our study, 74.6 NTUs as poor visibility in the testing tank

impaired our ability to observe fish. Thus, it appears that *E. fonticola* only significantly delays initiating foraging at slightly higher turbidity levels in contrast to prey consumption, which dropped sharply in the lowest turbidity level included in our study. 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 very low levels of turbidity although consumption is reduced. However, slightly higher turbidity levels (i.e. 23.2 NTUs) 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.

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 highest level due to poor visibility). We hypothesize that *E. fonticola* was able to accurately forage once prey was detected. Thus, 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 & Hartman (2003) found that 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 &

Hartman 2001), and percentages of prey consumed (Zamor & Grossman 2007) have all

been used to quantify prey-capture success. We attempted to pinpoint accuracy by

measuring strikes made per prey 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 possible 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 & Grossman 2007), it is possible that

this species is highly intolerant of turbidity and thus foraging behavior is affected at

extremely low levels. However, it is also possible that these effects are a result of the

non-visual 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 & Candolin 2007) chemical signals and can

cause a physiological response in the form of gill trauma (Berg 1982). Given that

turbidity is in fact caused by suspended sediment however, non-visual 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. 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* respond to turbidity while foraging, then the effects detected in our study may be greater than those predicted for wild fish.

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, thus 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 mating (Seehausen & van Alphen 1997) 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 are currently facing a number of anthropogenic threats that are linked to rising turbidity levels. Turbidity levels in this system are traditionally low, ranging from 0.26 to 5.76 NTU at the headwaters up to 18 NTU downriver (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 increasingly severe storm events due to climate change 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 & Wilde 2002; Grosse et al. 2010; Allen-Ankins et al. 2012) such as the fountain darter. 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.

Acknowledgements

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