



Turbidity Impairs Foraging Behavior in the Endangered Fountain Darter (*Etheostoma fonticola*)

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1 **Turbidity Impairs Foraging Behavior in the Endangered Fountain Darter (*Etheostoma***
2 ***fonticola*)**

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17 **RUNNING TITLE: TURBIDITY IMPAIRS FORAGING**

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20

21 *Abstract*

22 Turbidity can alter the foraging behavior and success of fish. We tested the effects
23 of turbidity on foraging behavior in the U.S. federally endangered fountain darter,
24 *Etheostoma fonticola*. *Etheostoma fonticola* is associated with clear, spring-fed systems,
25 suggesting that even minor changes in turbidity have the potential to affect behavior. We
26 examined the affects of elevated turbidity levels on prey consumption, time to initiate
27 foraging, and prey-capture success at four turbidity levels: (1) control: <1 Nephelometric
28 Turbidity Unit (NTU), (2) minimal turbidity: mean = 8.7 NTU, (3) moderate turbidity:
29 mean = 23.2 NTU, and (4) higher turbidity: mean = 74.6 NTU. Our results indicate that
30 elevated turbidity significantly affects prey consumption and time to initiate foraging but
31 not prey-capture success. Prey consumption was significantly reduced and time to initiate
32 foraging increased at all turbidity levels other than the clear water control. These data
33 suggest that even a slight elevation in turbidity (≥ 8.7 NTU) can significantly impair
34 foraging behavior in *E. fonticola*.

35

36 Elevated turbidity levels in freshwater systems resulting from major anthropogenic
37 stressors such as pollution, climate change, and modification of flow pose a significant
38 threat to the conservation of biodiversity (Dudgeon et al. 2005; Xenopoulos et al. 2005;
39 Vörösmarty et al. 2010). Turbidity can modify community structure through benthic
40 smothering and altered rates of photosynthesis (Davies-Colley and Smith 2001) but in
41 addition to these well-studied community level effects, turbidity can affect individual
42 survival and reproduction by altering behavior. Turbidity impairs the quality of visual
43 information by reducing the intensity of light and narrowing the light spectrum (Seehausen
44 and van Alphen 1997), which can compromise an animal's ability to forage (Vogel and
45 Beauchamp 1999), select a mate (Seehausen and van Alphen 1997), and respond to a
46 predator (Gregory 1993). These behaviors are essential for long-term population viability
47 and are especially concerning for threatened or endangered species. Furthermore, the
48 impact of anthropogenic factors on the behavior of individuals in populations has often
49 been neglected in conservation biology (Caro 1999; Angeloni et al. 2008). Examining the
50 effects of turbidity on animal behavior is important as such studies provide a non-invasive
51 means of assessing the biological effects of anthropogenic environmental change.

52 Turbidity has been demonstrated to affect foraging behavior primarily through
53 reactive distances and prey-capture success (Sweka and Hartman 2001; Zamor and
54 Grossman 2007; Wellington et al. 2010). However, turbidity can also affect additional
55 aspects of foraging behavior such as prey-searching activity (Meager and Batty 2007),
56 foraging rate (Webster et al. 2007), prey consumption (Bonner and Wilde 2002),
57 environmental refuge (Pekcan-Hekim, et al. 2010), and prey selectivity (Rowe et al. 2003;

58 Carter et al. 2009; Shoup and Wahl 2009). In addition to reduction of caloric intake due to
59 decreased prey consumption, turbidity can result in additional energetic cost to predators,
60 such as increased time spent searching for prey and decreased foraging accuracy
61 (Huenemann et al. 2012). Increases in the amount of energy and time devoted to foraging
62 can result in time allocation tradeoffs with other beneficial behaviors such as mating and
63 avoiding predation, potentially affecting individual fitness (Sih 1992; Ljunggren and
64 Sandström 2007).

65 The fountain darter, *Etheostoma fonticola*, is a federally endangered species found
66 in the San Marcos and Comal Rivers of central Texas where turbidity values can be as low
67 as 0.26 NTU near spring orifices to 13 NTU in the furthest downstream reaches (Saunders
68 et al. 2001). Many endemic flora and fauna including at least seven threatened and
69 endangered species coexist in these waters, which are currently subject to numerous
70 anthropogenic threats that affect turbidity levels including pollution, climate change and
71 alterations in flow, and recreational use. Pollutants such as sediment and nutrient loads
72 from urban areas may directly or indirectly increase turbidity levels (Nisbet 2001), while
73 climate change is predicted to exacerbate the intensity and frequency of extreme weather
74 events in central Texas in the near future (Loaiciga et al. 2000). Such weather events may
75 directly increase turbidity during and after extreme flooding or indirectly affect it by
76 promoting eutrophication during low flow or drought conditions. Recreational use may be
77 an especially significant source of fluctuating turbidity levels in *E. fonticola* habitat.
78 Turbidity levels in 2010 were found to be significantly elevated in the Comal River (10.3
79 to 13 NTU) during periods of heavy recreational use compared to periods of light

80 recreational use (0.26 to 1.0 NTU) (Saunders et al. 2001; Araujo 2012). *Etheostoma*
81 *fonticola* is most commonly found in the less turbid reaches (0.26 to 5.76 NTU) of spring-
82 fed systems with relatively constant water temperature and moderate flow and has been
83 found to be particularly sensitive to environmental conditions, with reproductive behavior
84 being temperature and flow dependent (Schenck and Whiteside 1977; Saunders et al.
85 2001). *Etheostoma fonticola* may be especially vulnerable to increases in turbidity as are
86 other fishes traditionally adapted to clear conditions in contrast to species well adapted to
87 turbid conditions (Bonner and Wilde 2002; Grosse et al. 2010; Allen-Ankins et al. 2012).
88 *Etheostoma* are benthic feeders (Vogt and Coon 1990; Greenberg 1991) and *E. fonticola*
89 held in aquaria preferentially feed on moving invertebrates while ignoring static ones
90 (USFWS 1996), which suggests that they rely on visual cues to forage. *Etheostoma*
91 *fonticola* also require the combination of visual and chemical information to respond to the
92 threat of predation, implying that vision is likely important in foraging as well (Swanbrow
93 Becker and Gabor 2012). Given that turbidity degrades the quality of visual information,
94 animals relying on visual as opposed to olfactory signals for foraging may be
95 disproportionately affected by turbidity (Allen-Ankins et al. 2012). Thus, a visual predator
96 adapted to clear headwaters such as *E. fonticola* is an ideal model to test the possible
97 effects of turbidity on foraging and the results of this study have significant conservation
98 implications for this endangered species as well as other aquatic predators from similar
99 systems. We investigated the effects of turbidity on prey consumption, time to initiate
100 foraging, and prey-capture success in *E. fonticola* by testing the predictions that increasing
101 turbidity reduces total prey consumption, increases the time to initiate foraging, and

102 reduces the accuracy of prey-capture, thus increasing the number of attempts made at
103 capturing prey.

104

105 **METHODS**

106 Experimental trials were conducted at the San Marcos Aquatic Resources Center
107 (ARC) in San Marcos, Texas from December 2011 through February 2012. All trials were
108 conducted between the hours of 0900 and 1400. Fish were hatchery-reared, first
109 generation adult *E. fonticola* and were housed and maintained at the ARC in fiberglass
110 tanks with well water (23 °C). The tanks contained 3 to 4 pieces of polyvinyl chloride pipe
111 and native vegetation to provide the fish with cover. Lighting was timed to mimic natural
112 conditions. All fish were maintained with a diet of black worms (*Lumbriculus variegatus*),
113 amphipods, and zooplankton fed ad libitum daily.

114 We tested the effects of turbidity on prey consumption in *E. fonticola* across four
115 treatments: (1) clear water control: <1 Nephelometric Turbidity Unit (NTU) ($n=20$), (2)
116 minimal turbidity: mean = 8.7 NTU ($n=20$), (3) moderate turbidity: mean = 23.2 NTU
117 ($n=20$), and (4) higher turbidity: mean = 74.6 NTU ($n=20$). Herein, treatments will be
118 referred to as (1) <1, (2) 8.7, (3) 23.2 and (4) 74.6 NTU. The effects of turbidity on time to
119 initiate foraging and prey-capture success were tested across only three treatments, <1
120 NTU, 8.7 NTU, and 23.2 NTU as higher turbidity levels (74.6 NTU) did not allow us to
121 accurately observe fish during trials. These turbidity levels were chosen in order to
122 maintain consistency with the relatively low levels naturally occurring in *E. fonticola*
123 habitat (0.26 to 13 NTU; Saunders et al. 2001) along with the higher levels of turbidity (20

124 to 75 NTU) consistent with temporary events such as heavy recreational use and rainfall
125 (USEPA 1999). We used black worms (*Lumbriculus variegatus*) as prey because they
126 were consistently fed to the test fish, which eliminated any potential effects of learning and
127 they are large enough to easily quantify.

128 Our experimental set-up consisted of eight, 9.5-liter glass aquaria with gravel
129 substrate. We wrapped tanks in black plastic with the exception of the front-facing side to
130 minimize disturbance to the fish and block light penetration. The front-facing side was
131 covered with one-way tinting to minimize disturbance and light penetration while still
132 allowing observations. Testing aquaria were lit with fluorescent 32-watt bulbs. We
133 randomized the location of specific aquaria and used 3% hydrogen peroxide and water to
134 clean aquaria between trials. We created turbidity during trials by adding bentonite
135 (Sturgis Rock Solid Solutions) to well water and stirring vigorously while using an aerator
136 to maintain suspension throughout the duration of trials. Turbidity levels for each of the
137 replicate trials ranged from either control: < 1 NTU, minimal: 5 to 10 NTU (mean = 8.7),
138 moderate: 20 to 30 NTU (mean = 23.2), or higher: 60 to 80 NTU (mean = 74.6). Turbidity
139 levels were measured at the end of each trial using a Hach ® Model 2100 N Laboratory
140 Turbidity Meter.

141 To initiate testing we randomly assigned a turbidity treatment and placed two
142 haphazardly selected subject fish of the same sex into an aquarium. We randomly selected
143 one fish as the focal individual for each trial. Each fish pair included one large and one
144 small fish (with the large fish chosen as the focal individual half of the time) of the same
145 sex to aid identification of the focal individual during feeding trials. We used two fish in

146 each trial as *E. fonticola* foraging typically occurs in proximity to other individuals and
147 isolated fish do not acclimate well to testing aquaria. After a 48-h habituation period
148 without food, we added the appropriate amount of bentonite depending on turbidity
149 treatment. The fish were then acclimated for an additional 10-min habituation period
150 before a feeding trial was initiated. We began each 10-min focal trial by adding ten live
151 prey items cut to standard length to the same location in the testing tank. The trial was
152 initiated immediately after food was added to the tank. During the trial, we observed and
153 recorded the time to initiate foraging and prey-capture success as the number of strikes
154 made at prey by the focal individual per prey items consumed by that individual. At the
155 end of the feeding trial, we counted remaining prey items to quantify total prey
156 consumption. Ample food was added to the tank so that numerous prey items always
157 remained at the end of the trial. All three response variables analyzed met the assumptions
158 required for parametric tests after being transformed. We added one constant to the
159 original value in order to eliminate zeros and then took the log for prey consumption and
160 prey-capture success. The log of the original value was used for time to initiate foraging.
161 Data were analyzed using Analysis of Variance (ANOVA). Significant ANOVAs ($\alpha =$
162 0.05) were followed by Tukey's Honest Significant Difference tests to assess differences
163 among turbidity levels. All analyses were carried out using JMP 9 software (SAS 2012).

164

165 **RESULTS**

166 The number of prey items consumed was negatively affected by turbidity level
167 ($F_{3,76} = 14.34$, $P < 0.01$; Figure 1a; Table 1). All three turbidity treatments resulted in

168 significantly less prey consumption when compared to the control (P 's < 0.05).
169 Conversely, total prey consumption was similar among the higher turbidity (i.e. 8.7, 23.2,
170 and 74.6 NTU) treatments.

171 Time to initiate foraging was negatively affected by turbidity level ($F_{2,43} = 4.44$, P
172 = 0.02; Figure 1b; Table 1). Darters initiated foraging in a significantly shorter amount of
173 time in the control treatment than at 23.2 NTU. Time to initiate foraging did not
174 significantly differ between the control and 8.7 NTU. Likewise, time to initiate foraging
175 did not differ between fish subjected to 8.7 and 23.2 NTU.

176 There was not a significant difference in the number of strikes made per prey items
177 consumed (prey-capture success) among any turbidity treatment or control ($F_{2,45} = 0.25$, P
178 = 0.77; Figure 1c).

179

180 **DISCUSSION**

181 This study demonstrates that a relatively minimal rise in turbidity significantly
182 decreases the total number of prey items consumed by *E. fonticola* and increases their time
183 to initiate foraging; however, once a prey item was located turbidity did not reduce their
184 ability to capture prey successfully. More specifically, prey consumption decreased
185 significantly at the lowest turbidity (8.7 NTU) level we tested. This suggests that even a
186 slight increase in turbidity may reduce foraging in *E. fonticola*. Similar findings of low
187 levels of turbidity affecting foraging behavior in fishes have been documented previously
188 (8 to 10 NTU: Zamor and Grossman 2007) although much of the literature reports effects at
189 far higher turbidity levels (e.g. 810 NTU: Gregory and Northcote 1993; 320 NTU: Rowe et

190 al. 2003). Nevertheless, the turbidity levels tested in this study are consistent with those
191 found in the native range of *E. fonticola*, with 7.2 NTU being typical of daily turbidity
192 readings during high recreation summer months (Araujo 2012). In our study, foraging
193 declined sharply at the lowest level of turbidity rather than gradually decreasing across the
194 three turbidity levels tested. As such, it appears that *E. fonticola* has a low-threshold for
195 turbidity with regards to foraging and once crossed, prey consumption is greatly reduced.

196 In our study the time it took *E. fonticola* to initiate foraging increased as turbidity
197 increased. Although time to initiate foraging was slowed at the lowest turbidity level, this
198 difference was not significant relative to controls. However, time to initiate foraging at
199 moderate turbidity (23.2 NTU) was significantly slower than the control treatment.
200 Although time to initiate foraging was not recorded at the highest turbidity level (74.6
201 NTU) because fish could not be observed we presume that it was also slower than controls;
202 however, additional testing will be needed to confirm this hypothesis. Thus, it appears that
203 *E. fonticola* only significantly delays initiating foraging at slightly higher turbidity levels
204 (23.2 NTU) in contrast to prey consumption, which dropped sharply in the lowest turbidity
205 level (8.7 NTU) included in our study. We speculate that this increase in time to initiate
206 foraging at relatively moderate turbidity levels may be related to a reduced visual acuity
207 because the spectrum of information available for foraging decisions is reduced for *E.*
208 *fonticola* at turbidity levels greater than 8.7 NTU. Regardless, a lengthened time to initiate
209 foraging in turbid conditions implies additional time spent searching for prey. This result
210 is important as additional time devoted to foraging is energetically costly and inevitably
211 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.

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 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 and 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 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

233 made per prey items consumed, but it is possible that another method of quantifying prey
234 capture success would have yielded different results.

235 Interestingly, increased turbidity also resulted in a significant drop in the number of
236 fish foraging. In the control treatment, 100% of fish tested initiated foraging and
237 consumed at least one prey item. In the following two turbidity levels tested (8.7 and 23.2
238 NTU), only 80% of fish tested engaged in foraging during the 10-min trial, with only 70%
239 foraging at the highest turbidity level (74.6 NTU). This pattern of a steep initial decline at
240 the lowest turbidity level tested (8.7 NTU) remaining constant through the highest turbidity
241 level tested (74.6 NTU) is similar to the pattern observed for prey consumption. There are
242 multiple hypotheses for these results. First, given the exceptionally low turbidity levels
243 typical of *E. fonticola* habitat and the effects of low turbidity levels detected in previous
244 studies (Zamor and Grossman 2007), it is possible that this species is highly intolerant of
245 turbidity and thus foraging behavior is affected at extremely low levels. However, it is
246 also possible that these effects are a result of the non-visual impacts of turbidity (i.e.
247 adding suspended sediment to the water). Suspended solids can alter chemical properties
248 in the water in ways that either enhance (Reddy 1981) or degrade (Engström-Öst and
249 Candolin 2007) chemical signals and can cause a physiological response in the form of gill
250 trauma (Berg 1982). Given that turbidity is in fact caused by suspended sediment, non-
251 visual effects at such low levels of turbidity are still an important finding. Alternatively,
252 the effects documented at such low turbidity levels in this study could be a result of using
253 hatchery-reared fish as compared to wild caught fish, which have different learning
254 experiences (Fenderson et al. 1968; Swain and Riddell 1990) and have never been

255 subjected to turbid water. Fish in general are able to learn and foraging is a well-
256 documented area in which learning occurs (Warburton 2003). Wild fish, even those
257 occurring in such naturally clear waters as *E. fonticola*, are naturally subjected to
258 fluctuating turbidity levels to at least some extent. The fish used in our study, however,
259 had never been exposed to any form of turbidity. Therefore, if learning plays a role in how
260 wild *E. fonticola* responds to turbidity while foraging, then the effects detected in our study
261 may be greater than those predicted for wild fish. However, further study will be required
262 to test this hypothesis.

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

275 The conservation implications of this study are important as the San Marcos and
276 Comal Rivers periodically and seasonally experience increases in turbidity often as a result

277 of anthropogenic disturbance. Turbidity levels in this system are traditionally low, ranging
278 from 0.26 to 5.76 NTU at the headwaters up to 13 NTU downstream (Saunders et al.
279 2001), where 20 NTU is considered a threshold for low turbidity streams (USEPA 1999).
280 However, even low turbidity levels in our experiment (8.7 NTU) significantly reduced
281 prey consumption in our study. Also, heavy recreational use during the summer months
282 and severe storm events can cause these levels to far exceed such thresholds. Previous
283 studies have indicated that the behavioral effects of rising turbidity may be especially
284 significant for species not adapted to habitats traditionally associated with high turbidity
285 (Bonner and Wilde 2002; Grosse et al. 2010; Allen-Ankins et al. 2012) such as *E. fonticola*
286 and turbidity has been found to alter anti-predator response in *E. fonticola* in particular
287 (Swanbrow Becker and Gabor 2012). These implications are therefore important not only
288 in the San Marcos and Comal Rivers but may also have relevance for freshwater systems
289 worldwide, especially for species traditionally adapted to low turbidity conditions, as
290 major anthropogenic stressors associated with rising turbidity such as runoff and
291 modification of river flow are occurring on a global scale.

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300

301 REFERENCES

- 302 Allen-Ankins, S., R.J. Stoffels, P.A. Pridmore, and M.T. Vogel. 2012. The effects of
303 turbidity, prey density and environmental complexity on the feeding of juvenile
304 Murray cod, *Maccullochella peelii*. *Journal of Fish Biology* 80:195-206.
305
- 306 Angeloni, L., M.A. Schlaepfer, J. J. Lawler, and K.R. Crooks. 2008. A reassessment of the
307 interface between conservation and behaviour. *Animal Behaviour* 75:731-737
308
- 309 Araujo, D. 2012. Effect of drought and subsequent recovery of endangered fountain darter
310 habitat in Comal Springs Texas. Thesis Texas State University Pg. 92.
311
- 312 Berg, L. 1982. The effect of exposure to short-term pulses of suspended sediment on the
313 behavior of juvenile salmonids. pp. 177-196 in G.F. Hartman et al. [eds.] Proceedings
314 of the Carnation Creek workshop: a ten-year review. Department of Fisheries and
315 Oceans, Pacific Biological Station, Nanaimo, Canada.
316
- 317 Bonner, T.H. and G.R. Wilde. 2002. Effects of turbidity on prey consumption by prairie
318 stream fishes. *Transactions of the American Fisheries Society* 131:1203-1208.
319
- 320 Carter, M.W., D.E. Shoup, J.M. Dettmers, and D.H. Wahl. 2009. Effects of turbidity and
321 cover on prey selectivity of adult smallmouth bass. *Transactions of the American*
322 *Fisheries Society* 139:353-361.
323
- 324 Engström-Öst, J. and U. Candolin. 2007. Human-induced water turbidity alters selection
325 on sexual displays in sticklebacks. *Behavioral Ecology* 18:393-398.
326
- 327 Fenderson, O. C., W. H. Everhart, and K. M. Muth. 1968. Comparative agonistic and
328 feeding behavior of hatchery-reared and wild salmon in aquaria. *Journal of the*
329 *Fisheries Research Board of Canada* 25:1-14.
330
- 331 Greenberg, L.A. 1991. Habitat use and feeding behavior of thirteen species of benthic
332 stream fishes. *Environmental Biology of Fishes* 31:389-401.
333
- 334 Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile
335 chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and*
336 *Aquatic Sciences* 50:241-246.
337

- 338 Gregory, R.S. and T.G. Northcote. 1993. Surface, planktonic, and benthic foraging by
339 juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions.
340 Canadian Journal of Fisheries and Aquatic Sciences 50:233-240.
341
- 342 Grosse, A.M., S.C. Sterrett, and J.C. Maerz. 2010. Effects of turbidity on the foraging
343 success of the eastern painted turtle. Copeia 3:463-467.
344
- 345 Huenemann, T.W., E.D. Dibble, and J.P. Fleming. 2012. Influence of turbidity on the
346 foraging of largemouth bass. Transactions of the American Fisheries Society 141:107-
347 111.
348
- 349 Loaiciga, H.A., D. R. Maidment, and J. B. Valdes. 2000. Climate-change impacts in a
350 regional karst aquifer, Texas. Journal of Hydrology 227:173-194.
351
- 352 Ljunggren, L. and A. Sandström. 2007. Influence of visual conditions on foraging and
353 growth of juvenile fishes with dissimilar sensory physiology. Journal of Fish Biology
354 70:1319-1334.
355
- 356 Meager, J.J. and R.S. Batty. 2007. Effects of turbidity on the spontaneous and prey-
357 searching activity of juvenile Atlantic cod (*Gadus morhua*). Philosophical Transactions
358 of the Royal Society B-Biological Sciences 362:2123-2130.
359
- 360 Nisbet, T.R. 2001. The role of forest management in controlling diffuse pollution in UK
361 forestry. Forest Ecology and Management 143:215-226.
362
- 363 Pekcan-Hekim, Z., L. Nurminen, T. Ojala, M. Olin, J. Ruuhijarvi, and J. Horpilla. 2010.
364 Reversed diel horizontal migration of fish: turbidity versus plant structural complexity
365 as refuge. Journal of Freshwater Ecology 25:649-656.
366
- 367 Reddy, K.R. 1981. Diel variations of certain physico- chemical parameters of water in
368 selected aquatic systems I. Hydrobiologia 85:201-207.
369
- 370 Rowe, D.K., T.L. Dean, E. Williams, and J.P. Smith. 2003. Effects of turbidity of the
371 ability of juvenile rainbow trout (*Oncorhynchus mykiss*), to feed on limnetic and benthic
372 prey in laboratory tanks. New Zealand Journal of Marine and Freshwater Research
373 37:45-52.
374
- 375 SAS. 2012. Institute Inc., SAS Campus Drive, Building S, Cary, NC, 27513, USA.
376
- 377 Schenck, J.R. and B.G. Whiteside. 1977. Reproduction, fecundity, sexual dimorphism and
378 sex ratio of *Etheostoma fonticola* (Osteichthyes:Percidae). The American Midland
379 Naturalist 98:365-375.
380

- 381 Seehausen, O. and J.J. van Alphen. 1997. Cichlid fish diversity threatened by
382 eutrophication that curbs sexual selection. *Science* 277:1808-1811.
383
- 384 Shoup, D.E. and D.H. Wahl. 2009. The effects of turbidity on prey selection by
385 piscivorous largemouth bass. *Transactions of the American Fisheries Society*
386 138:1018-1027.
387
- 388 Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs.
389 *American Naturalist* 139:1052-1069.
390
- 391 Swain, D. P., and B. E. Riddell. 1990. Variation in agonistic behavior between newly
392 emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus*
393 *kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:566-571.
394
- 395 Swanbrow Becker, L.J. and C.R. Gabor. 2012. Effects of turbidity and visual vs. chemical
396 cues on anti-predator response in the endangered fountain darter (*Etheostoma*
397 *fonticola*). *Ethology* 118: 1-7.
398
- 399 Sweka, J.A. and K.J. Hartman. 2001. Influence of turbidity on brook trout reactive
400 distances and foraging success. *Transactions of the American Fisheries Society*
401 130:138-146.
402
- 403 Sweka, J.A. and K.J. Hartman. 2003. Reduction of reaction distance and foraging success
404 in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels.
405 *Environmental Biology of Fishes* 67:341-347.
406
- 407 U.S. Environmental Protection Agency. 1999. Guidance manual for the compliance with
408 interim enhanced surface water treatment rule: turbidity provisions. EPA-815-R-010.
409 Office of Water.
410
- 411 U.S. Fish and Wildlife Service. 1996. San Marcos/Comal (Revised) recovery plan. U.S.
412 Fish and Wildlife Service, Austin, Texas.
413
- 414 Vogel, J.L. and D.A. Beauchamp. 1999. Effects of light, prey size, and turbidity on
415 reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian*
416 *Journal of Fisheries and Aquatic Sciences* 56:1293-1297.
417
- 418 Vogt, G.F. and T.G. Coon. 1990. A comparison of the foraging behavior of two darter
419 (*Etheostoma*) species. *Copeia* 1990:41-49.
420
- 421 Warburton, K. 2003. Learning of foraging skills by fish. *Fish and Fisheries* 4:203-215.
422

- 423 Webster, M.M., N. Atton, A.J. Ward, and P.J. Hart. 2007. Turbidity and foraging rate in
424 threespine sticklebacks: the importance of visual and chemical prey cues. *Behaviour*
425 144:1347-1360.
- 426
427 Wellington, C.G., C.M. Mayer, J.M. Bossenbroek, and N.A. Stroh. 2010. Effects of
428 turbidity and prey density on the foraging success of age 0 year yellow perch (*Perca*
429 *flavescens*). *Journal of Fish Biology* 76:1729-1741.
- 430
431 Xenopoulos, M.A., D.M. Lodge, J. Alcamo, M. Marker, K. Schulze, and D.P. Van
432 Vuurens. 2005. Scenarios of freshwater fish extinctions from climate change and water
433 withdrawal. *Global Change Biology* 11:1557-1564.
- 434
435 Zamor, R.M. and G.D. Grossman. 2007. Turbidity affects foraging success of drift-feeding
436 rosyside dace. *Transactions of the American Fisheries Society* 136:167-176.
- 437

438 TABLE 1. Water turbidity levels (NTU) used as treatments to examine *Etheostoma*
 439 *fonticola* prey consumption and time to initiate foraging. Bold values indicate significant
 440 (alpha = 0.05) differences between contrasts. Asterisks denote contrasts not compared
 441 because turbidity levels were too high to quantify visual observations.

Contrasts (Turbidity, NTU)	<i>Prey</i>	<i>Time to Initiate</i>
	<i>Consumption</i>	<i>Foraging</i>
	<i>P-value</i>	<i>P-value</i>
<1 vs. 8.7	0.001	0.059
<1 vs. 23.2	<0.001	0.028
<1 vs. 74.6	<0.001	*
8.7 vs. 23.2	0.116	0.949
8.7 vs. 74.6	0.061	*
23.2 vs. 74.6	0.611	*

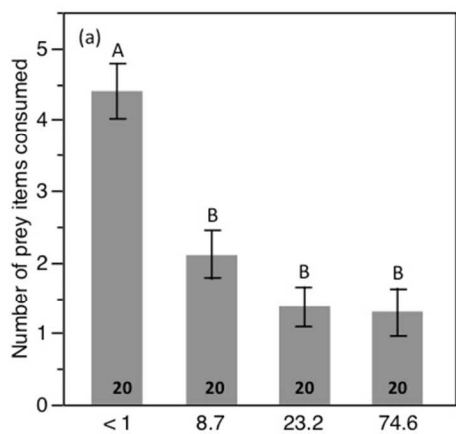
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443 **Figure Legends**

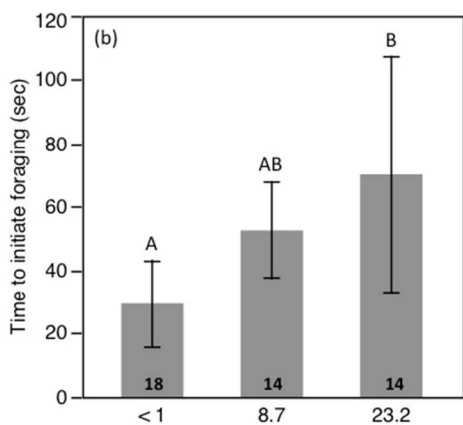
444 FIGURE 1. Mean \pm 1 SE for: (a) number of prey items consumed, (b) time to initiate
445 foraging, and (c) number of strikes made per prey items consumed at each turbidity level
446 (NTU). Bold numbers on bars are the number of fish tested at each turbidity level, different
447 letters represent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

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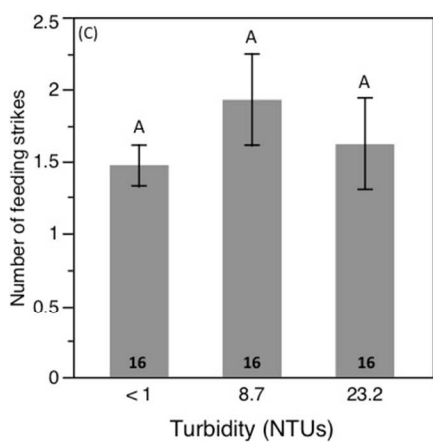
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451

452 Figure 1.

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