

Turbidity Affects Foraging Success of Drift-Feeding Rosyside Dace

RICHARD M. ZAMOR AND GARY D. GROSSMAN*

*D. B. Warnell School of Forestry and Natural Resources,
University of Georgia, Athens, Georgia 30602, USA*

Abstract.—The effects of suspended sediment on nongame fishes are not well understood. We examined the effects of suspended sediment (i.e., turbidity) on reactive distance and prey capture success at spring–autumn (12°C) and summer (18°C) temperatures for rosyside dace *Clinostomus funduloides* in an artificial stream. Experimental turbidities ranged from 0 to 56 nephelometric turbidity units (NTUs) at the two temperatures, and sample sizes for each turbidity–temperature combination ranged from 5 to 10 fish. All fish were tested at a single, randomly selected turbidity. Nonlinear regression (dosage–response curves) detected a negative relationship between turbidity and reactive distance at both spring–autumn ($R^2 = 0.96$) and summer ($R^2 = 0.90$) temperatures. Turbidity also had a strong negative effect on capture success at both spring–autumn ($R^2 = 0.88$) and summer ($R^2 = 0.70$) temperatures. Two-way analysis of variance showed that turbidity and temperature were significant in all models ($P < 0.0001$) and that there were no significant interactions. The median effective concentrations (EC50s, i.e., the concentrations required to elicit a response equal to 50% of the maximum response observed) for reactive distance regressions were 9.9 NTUs in spring and autumn and 9.2 NTUs in summer. Data from moderately impacted streams in the region indicate that these streams possess turbidities that exceed the EC50s approximately 50% of the time. These results suggest that turbidity negatively affects the foraging behavior of rosyside dace at even low to intermediate levels (>9 NTUs) and that these effects may vary seasonally.

Increased suspended sediment loads in North American streams pose an important management concern for fisheries biologists (Barrett et al. 1992; Walsh et al. 1995; Waters 1995; Sutherland et al. 2002). In general, these increases can be attributed to increased land disturbances from agriculture, urbanization, and home construction (Tebo 1955; Waters 1995; Sutherland et al. 2002; Roy et al. 2003). Increased stream sediment loads negatively affect both fish and macroinvertebrate assemblages (Tebo 1955; Murphy and Hall 1981; Culp et al. 1986; Jones et al. 1999; Shaw and Richardson 2001; Richardson and Jowett 2002; Sutherland et al. 2002) and may be linked to the threatened or endangered status of approximately 21% of the almost 300 percid or cyprinid species found in the southeastern United States (Walsh et al. 1995; Sutherland et al. 2002).

Turbidity, the amount of light scattered or absorbed by a sample of water, is the most common metric for quantifying suspended sediment in streams (Duchrow and Everhart 1971). Turbidity may be a useful index of the potential effects of sediment on stream fishes because even small changes in suspended sediment may change turbidity levels whereas larger quantities generally are necessary to produce changes in substra-

um composition (Waters 1995). However, the effects of turbidity on nongame fishes (i.e., the majority of fishes in North America) are not well understood. Nonetheless, studies of game and commercial species and one cyprinid show that turbidity negatively affects foraging success (salmonids: Berg and Northcote 1985; Redding et al. 1987; Barrett et al. 1992; Gregory and Northcote 1993; Sweka and Hartman 2001a), reproductive success, (cyprinid: Burkhead and Jelks 2001), and microhabitat selection (coregonid: Swenson and Matson 1976) in fishes.

Most researchers have quantified the effects of turbidity on fish foraging by measuring reactive distances and prey capture success (Berg and Northcote 1985; Barrett et al. 1992; Sweka and Hartman 2001a). Reactive distance is the distance between the fish's snout and a given prey item when the fish first orients toward the prey (Confer and Blades 1975; Vinyard and O'Brien 1975). Many fishes exhibit stereotypical orientation behavior when prey is sighted, the fish immediately aligning its head with the prey item (Confer and Blades 1975; Vinyard and O'Brien 1975). This behavior improves visual accuracy and capture success (Confer and Blades 1975; Vinyard and O'Brien 1975). After orientation, fish typically move to intercept the prey (Confer and Blades 1975).

The specifics of the relationship between increased turbidity and prey capture success are not well understood because investigators have used varying

* Corresponding author: grossman@uga.edu

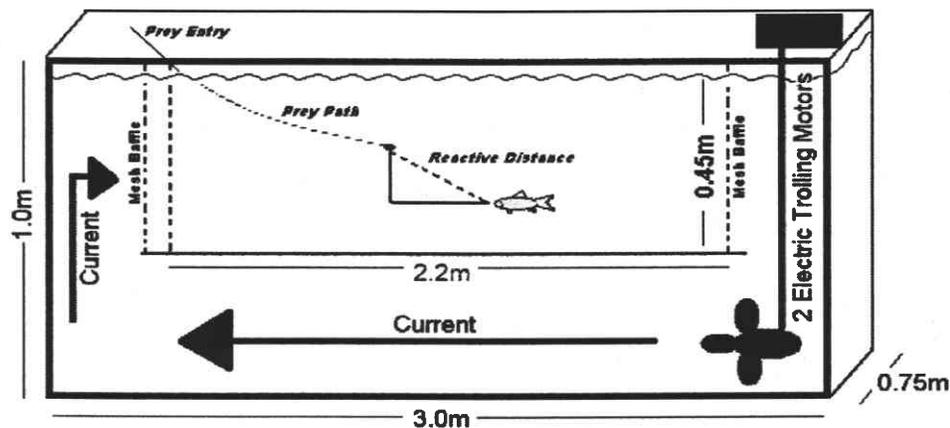


FIGURE 1.—Diagram of the artificial stream used in experiments assessing the effect of turbidity on the reactive distance and capture success of rosyside dace. Prey release and the measurement of reactive distance are also illustrated (figure by Peter Hazelton).

research methodologies. For example, capture success has been measured in four different ways: (1) prey consumption rate (Gregory and Northcote 1993; Rowe et al. 2003), (2) percent fewer prey consumed (Breitburg 1988), (3) probability of detection (Sweka and Hartman 2001a, 2003), and (4) capture and consumption of individual prey (Berg and Northcote 1985; De Robertis et al. 2003). In addition, some investigators have used nonflowing experimental systems for fishes that normally feed on drift (Gregory and Northcote 1993; Rowe et al. 2003) as well as non-naturally occurring substances (bentonite, kaolin) for turbidity agents (De Robertis et al. 2003). Finally, several researchers have used turbidity levels in experiments that may not be applicable to many streams (810 nephelometric turbidity units [NTUs]: Gregory and Northcote 1993; 320 NTUs: Rowe et al. 2003). Nevertheless, high turbidities have been shown to decrease either prey capture success or feeding rate in the following drift-feeding species: coho salmon *Oncorhynchus kisutch* (Berg and Northcote 1985; Redding et al. 1987), Chinook salmon *O. tshawytscha* (Gregory and Northcote 1993), steelhead (anadromous rainbow trout) *O. mykiss* (Redding et al. 1987), and brook trout *Salvelinus fontinalis* (Sweka and Hartman 2001a).

Given the lack of information on the effects of turbidity on the foraging behavior of nongame fishes and the prevalence of those fishes in North American streams, we assessed the effects of turbidity on the reactive distance and prey capture success of rosyside dace *Clinostomus funduloides*, a drift-feeding minnow of special concern in North Carolina (North Carolina Wildlife Resources Commission 2004). We also determined whether temperature and fish size affected

reactive distance and capture success at different turbidities. To our knowledge, there is little or no information on how seasonal temperature change or fish size affect turbidity–foraging behavior relationships.

Methods

Study species.—The rosyside dace is widely distributed across Atlantic Slope streams from Delaware to the Savannah River (DeHaven et al. 1992). In western North Carolina, rosyside dace are members of the mid-water column habitat guild (Grossman et al. 1998) and occupy deeper microhabitats with higher focal point velocities and varying substrata far from both shelter and the substratum. Rosyside dace typically breed between May and August, and gonadal recrudescence is positively correlated with photoperiod (DeHaven et al. 1992). Rosyside dace are opportunistic drift feeders, primarily consuming aquatic macroinvertebrates and terrestrial insects (Stouder 1990). In Coweeta Creek, North Carolina, rosyside dace occupy focal point velocities (i.e., microhabitats) that maximize their rate of net energy gain, which presumably increases individual fitness (Hill and Grossman 1993; Grossman et al. 2002). Given their biology, local distribution, and abundance (Jones et al. 1999; Scott and Helfman 2001) and the changes in land use patterns in the region, it is likely that changing turbidity levels affect both the distribution and ecology of rosyside dace in western North Carolina.

Experimental stream.—We conducted experiments in a 3.0-m \times 0.75-m \times 1.0-m Plexiglas artificial stream (Figure 1). Flows within the stream were generated with electric trolling motors, and water was recirculated via a false bottom. A collimator composed of baffles covered with net mesh maintained semilaminar flow

within the flume and bounded the upstream and downstream ends of the test chamber. The dimensions of the test chamber were $2.2 \times 0.75 \times 0.5$ m. We used a 4-cm layer of pebbles (maximum diameter, ~ 1 –50 mm) as substratum. The flume was marked with a grid (2-cm \times 3-cm rectangles) on the back wall and a scale (1-cm intervals) on the bottom of the front wall. We surrounded the stream flume with a black plastic blind to prevent disturbance of the fish during observation. Experimental conditions simulated the habitats in which fish are found in the natural environment (i.e., depth, 45 cm; pH, ~ 7 ; and flow, 12 cm/s; Grossman and Freeman 1987; Grossman and Ratajczak 1998; Grossman et al. 1998). We have previously shown that rosyside dace preferentially occupy this velocity to maximize their rate of net energy gain in Coweeta Creek (Grossman et al. 2002). We conducted experiments at two seasonal temperatures (12°C for spring and autumn and 18°C for summer) and photoperiods (12 h light : 12 h dark for spring–autumn and 14 h light : 10 h dark for summer). The stream had a constant-reading thermometer that was checked regularly throughout our experiments. We never saw temperature deviate from the test temperatures; hence there was no variance in stream temperature measurements.

Experimental procedures.—We collected adult rosyside dace for experiments via electrofishing and seining from Coweeta Creek, a fifth-order tributary stream of the Little Tennessee River in the Blue Ridge Mountains of North Carolina. Fish for summer trials were collected from July 2004 to February 2005, whereas fish for spring–autumn trials were collected from February 2005 to May 2005. We only used fish that behaved naturally and displayed no physical or behavioral evidence of collecting stress ($\sim 95\%$ of the fish collected) in trials. We also did not use fish that displayed breeding coloration or behavior, because some collections in early summer and late spring overlapped with the potential breeding season. Because rosyside dace continue to feed and occupy optimal foraging positions during winter (Hill and Grossman 1993), we were able to use fish collected from various seasons in both temperature trials (e.g., fish collected in February in summer temperature trials). As a prophylactic, we treated fish with a general antibiotic, Kanamycin, upon introduction to a holding tank that simulated the conditions in the experimental flume. We acclimated fish for at least 4 d prior to experimental trials, which, based on pilot studies, produced no observable inhibitory effects on foraging behavior. During both the holding period and trials, we fed fish miniature mealworms *Tenebrio molitor* (length, 8–10 mm; mass, ~ 0.02 g). We used mealworms for a variety of reasons, including (1) their resemblance to natural prey and rapid consumption by rosyside dace, (2)

their high visibility during experiments, and (3) their previous use in similar research (Barrett et al. 1992). After the test fish were acclimated to the holding system, we removed them to a similar holding tank for a 48-h nonfeeding period to ensure that all test individuals were in similar condition and would feed readily during trials.

We used commercially purchased red clay to vary turbidity levels within the flume because it is a naturally occurring suspended sediment in the southeastern United States (M. Riedel, Coweeta Hydrologic Laboratory, Otto, North Carolina, personal communication). A paint mixer powered by an electric drill mixed water from the artificial flume with red clay in a 18.9-L bucket to create a clay–water suspension. We allowed this mixture to settle for 15 min before adding the suspension to the flume. In the trials, we measured turbidity with a Hach Model 2100P turbidity meter and took three measurements immediately before and after each trial to ensure that the test turbidity was maintained throughout the trial. Because many hydrologists and resource managers measure turbidity as total suspended solids (TSS; Price and Leigh 2006), during one trial we also took a 1-L sample (four 250-mL subsamples) from different positions of the tank at each turbidity level to derive a relationship between turbidity and TSS for both spring–autumn and summer trials using nonlinear regression.

For trials, we first randomly selected a turbidity level and then placed an arbitrarily selected fish in the test chamber. For summer trials, we measured reactive distances and prey capture success for a total of 85 fish at 0, 5, 10, 15, 20, 25, 30, 35, 45, and 55 NTUs (5 fish at 0, 5, 10, and 15 NTUs and 10 fish at turbidity levels greater than 10 NTUs). Fish for summer trials had a mean length (SD) of 60.1 mm (8.3 mm) and a mean (SD) wet weight of 4.97 g (1.8 g). We chose the particular turbidity levels that we did because they encompass the range that commonly occurs in streams occupied by rosyside dace in the region (Bolstad and Swank 1997; Sutherland et al. 2002; Price and Leigh 2006; M. Riedel, unpublished data). Lightly impacted and reference streams in the region (100% forested with no recent disturbance, i.e., Coweeta Creek) typically experience base flow turbidities of 2.1–3.9 NTUs, while moderately impacted or disturbed streams (73–87% forested, low-density agricultural and residential developments) experience 9.3–15 NTUs (Bolstad and Swank 1997; Sutherland et al. 2002; Price and Leigh, 2006).

For spring–autumn trials, we measured reactive distance and capture success for a total of 80 fish at 0, 8, 16, 24, 32, 40, 48, and 56 NTUs (10 fish at each turbidity level). Fish for spring–autumn trials had a mean length (SD) of 54.5 mm (10.5 mm) and a mean

wet weight (SD) of 4.56 g (3.6 g). We conducted summer trials prior to spring–autumn trials, and based on logistical constraints and the patterns in the data, we determined that eight treatment levels were sufficient to depict the patterns present in the data. Hence, spring–autumn trials were run with 8 rather than 10 treatments. Each test fish was allowed to acclimate to the trial chamber for a period of at least 2 h after the test turbidity had been attained and was tested at only one turbidity level.

We began each trial by releasing prey at approximately 2-min intervals from a known, constant submerged position at the front of the experimental chamber. This position was approximately 10–15 cm from the front wall of the tank to facilitate observation. Forceps were used to release prey, which traveled the length of the stream as submerged drift. We began measuring reactive distance and prey capture success after a test fish captured its first prey, because even at low turbidities fish did not always react to the first few prey. Once the first prey was captured, a fish typically would hold position at the point at which it first observed the first prey. At low turbidities (0–16 NTUs), if a fish did not feed on the first five prey presented it was not used in a trial and was not included in data analysis. At high turbidities (20–56 NTUs) if fish did not react we began to record observations after five prey items had been placed in the tank. We used this criterion for high turbidities because we could not distinguish nonfeeders from fish that would feed but did not observe prey because of the turbidity. Although this could have biased trials if a large number of “inefficient feeders” were removed from the low-turbidity trials, only 5 of the 65 fish (~8%) used in such trials were removed for lack of feeding (spring–autumn: 1 at 0 NTUs; summer: 2 at 0 NTUs and 2 at 5 NTUs). Consequently, it is unlikely that the different criteria used at different turbidity levels for nonfeeders significantly biased our results.

We measured reactive distance and prey capture using videography. As noted above, reactive distance was measured as the distance from the prey to the tip of the fish’s snout upon first orientation (Barrett et al. 1992). We achieved this measurement during video playback by marking the positions of both the prey (which was released from a known position) and the fish’s snout after it oriented to the prey. With these positions marked, we used a grid to determine both the vertical (above the fish) and horizontal (in front of the fish) distances of the prey from the fish’s snout. We then constructed a right triangle with these data, which allowed us to calculate reactive distance as the hypotenuse (Figure 1). Nonetheless, our estimates may have been slightly biased because we reduced a

three-dimensional process to two dimensions (although observations indicated that the lateral movement of prey was not extensive during a trial). The use of a high-resolution video camera greatly enhanced our ability to determine the locations of both prey and fish in treatments above 20 NTUs because we could examine fish and prey positions on a frame-by-frame basis. Most fish occupied a relatively stable position for the length of a trial and hence were fairly easy to locate on the tape. However, a few fish occasionally exhibited increased search behavior during high-turbidity trials. Use of frame-by-frame video also enabled us to backtrack the position of these fish from the point of capture. The lack of a positive correlation between the standard deviations and NTU values for reactive distance measurements suggests that the measurements at higher turbidities did not suffer from substantial measurement error (see Results). We calculated prey capture success as the percentage of prey captured in a given trial. Our null hypotheses were that turbidity would have no effect on either the reactive distance or the prey capture success of rosyside dace.

We quantified the relationships among turbidity, reactive distance, and prey capture success using a four-parameter nonlinear dose–response regression with a variable slope parameter, namely,

$$y = \text{minimum} + (\text{maximum} - \text{minimum}) \\ \div (1 + 10^{(\log \text{EC}_{50} - x) \text{ hill slope}})$$

(Sigmaplot 2002). The parameters were as follows: (1) the minimum (bottom of the curve), (2) the maximum (top of the curve), (3) the median effective concentration (EC₅₀, i.e., the concentration required to elicit a response equal to 50% of the maximum response observed), and (4) the hill slope (the slope of the curve at its midpoint). We also analyzed the data using two-way analysis of variance (ANOVA) with season and turbidity as main effects (SAS 1999). We considered seasonal turbidities that were within 3 NTUs of each other to be identical treatments (see previous section). Therefore, only comparable turbidities from the two seasonal trials were used in the ANOVA, the remaining four treatments (summer: 5, 20, and 35 NTUs; spring–autumn: 40 NTUs) being excluded from analyses. We also used analysis of covariance (ANCOVA) to determine whether size affected the relationship between either reactive distance or capture success and turbidity (SAS Institute, Inc. 1999).

Results

Total Suspended Solids

Turbidity and TSS were strongly correlated during both spring–autumn ($y = -0.0052x^2 + 0.7832x -$

0.9229; $P < 0.0001$, $R^2 = 0.9985$) and summer ($y = -0.0031x^2 + 0.6158x - 1.4658$; $P < 0.0001$, $R^2 = 0.9873$) trials and for both temperatures combined ($y = -0.0037x^2 + 0.6797x - 1.2819$; $P < 0.0001$, $R^2 = 0.9547$; Figure 2). The TSS values were slightly higher at a given NTU for particular spring–autumn temperatures than for the same summer temperatures. Unfortunately, owing to a lack of replication it was impossible to test for temperature effects in the TSS–turbidity relationship.

Reactive Distance

We detected a strong, negative curvilinear relationship between increasing turbidity and reactive distance for rosyside dace in both spring–autumn ($P < 0.0001$, $R^2 = 0.96$) and summer ($P < 0.0001$, $R^2 = 0.90$) trials (Figure 2A). These curves displayed an exponentially declining phase followed by a phase with a lower negative slope at turbidities above 20 NTUs. The median EC50 values were approximately 9 NTUs for both seasons (spring–autumn: 9.89; summer: 9.22), indicating that a 50% decrease in the observed maximum reactive distance occurred at relatively low turbidities. Two-way ANOVA detected highly significant turbidity ($F = 357.46$, $df = 6$, $P < 0.0001$) and seasonal temperature effects ($F = 137.79$, $df = 1, 6$, $P < 0.0001$; Table 1) with a nonsignificant interaction term ($F = 0.00$, $df = 6$, $P = 1.0$). Rosyside dace had significantly greater reactive distances at spring–autumn temperatures than they did at summer temperatures at all NTUs except 0 regardless of turbidity level (Figure 2A; Table 1). Despite the negative effects of turbidity on reactive distance, some rosyside dace reacted to prey even at the highest turbidities.

Within seasonal treatments, differences in mean reactive distances were most pronounced at low to intermediate turbidities (Tukey tests; Table 1). Comparisons of reactive distances at a given NTU between seasonal treatments also detected significant differences at intermediate to high turbidities (8–32 NTUs; a posteriori *t*-tests; Table 1). Finally, neither fish length nor mass significantly affected reactive distance in either spring–autumn trials (length: $F = 2.20$, $df = 1$, $P = 0.1432$; mass: $F = 1.89$, $df = 1$, $P = 0.1741$) or summer trials (length: $F = 0.02$, $df = 1$, $P = 0.9$; mass: $F = 0.1$, $df = 1$, $P = 0.7516$).

Prey Capture Success

We also obtained highly significant (all P -values < 0.0001) curvilinear negative relationships between turbidity and capture success for both spring–autumn ($R^2 = 0.88$) and summer ($R^2 = 0.70$) trials (Figure 2b). During both seasonal trials, the relationship had an asymptote at low turbidities followed by an exponential

decline and then a phase with a low slope at high turbidities. The EC50s for capture success in both seasonal trials occurred at approximately 30 NTUs (spring–autumn: 33.3398; summer: 29.011). Two-way ANOVA also showed that both turbidity ($F = 106.48$, $df = 1, 6$, $P < 0.0001$) and temperature ($F = 11.04$, $df = 1, 6$, $P = 0.0012$ (Table 2) significantly affected capture success, whereas the interaction term was nonsignificant ($F = 0.00$, $df = 6$, $P = 1.0$). Overall, rosyside dace caught more prey at spring–autumn temperatures than they did at summer temperatures.

Tukey a posteriori *t*-tests indicated that capture success within seasonal trials did not differ among low to intermediate (0–10 NTUs) turbidities, nor were differences detected at higher turbidity levels (>30 NTUs) (Figure 2B; Table 2). Between-season comparisons also indicated that differences in capture success were strongest at intermediate (15–16 and 24–25 NTUs) turbidities (Table 2). Finally, ANCOVA indicated that neither fish specimen length nor mass significantly affected the capture success of rosyside dace in either spring–autumn trials (length: $F = 0.74$, $df = 1$, $P = 0.3927$; mass: $F = 1.53$, $df = 1$, $P = 0.2213$) or summer trials (length: $F = 0.01$, $df = 1$, $P = 0.9340$; mass: $F = 0.20$, $df = 1$, $P = 0.6603$).

Discussion

Our results demonstrate that increased turbidity significantly reduced reactive distance and capture success for rosyside dace at both spring–autumn and summer temperatures. We observed significant reductions in foraging success at turbidities as low as 8 NTUs, a turbidity that is frequently observed in moderately impacted streams such as Coweeta Creek (Bolstad and Swank 1997; Sutherland et al. 2002; Price and Leigh, 2006; M. Riedel, unpublished data) and other streams in the southern Appalachians (Walters et al. 2003). It is curious that rosyside dace had greater capture success and longer reactive distances in spring–autumn trials even though TSS values were higher for all turbidities at this temperature. Total suspended solids in Blue Ridge Mountain streams do change seasonally, typically decreasing in the winter (Riedel et al. 2003). However, because our TSS analysis was unreplicated, it is unclear whether the observed seasonal differences in the TSS–NTU relationship are real. But even so, the ability to convert NTU values to TSS values greatly increases the utility and interpretability of our data for both hydrologists and resource managers.

The range of turbidities used in our study encompassed the range found in the streams occupied by rosyside dace in the region ((Bolstad and Swank 1997; Sutherland et al. 2002; Walters et al. 2003; Price and

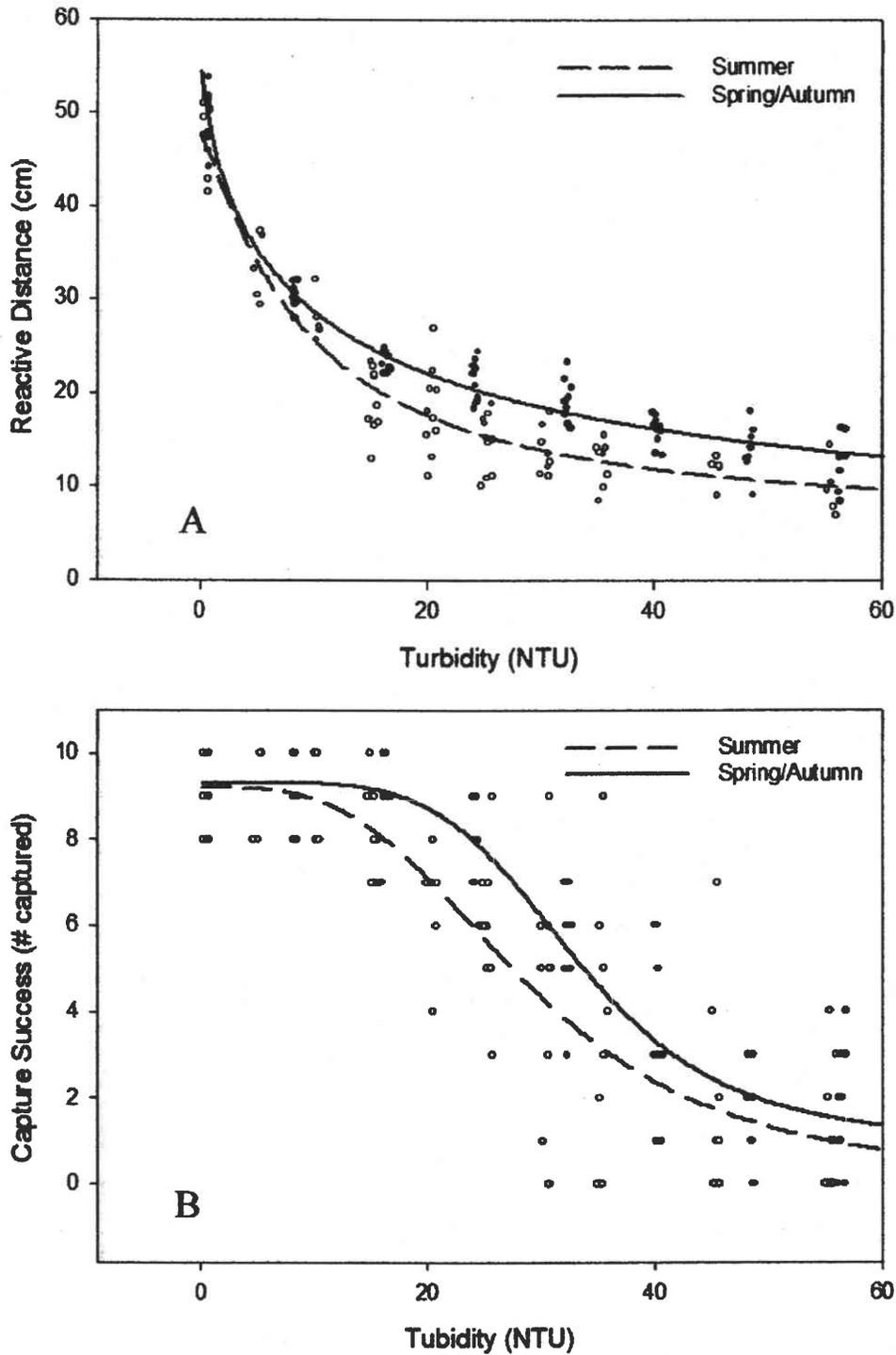


FIGURE 2.—Panel (A) shows the regressions of reactive distance on turbidity at spring and autumn (12°C) and summer temperatures (18°C). Filled circles represent data points for the spring–autumn regression, open circles those for the summer regression. The spring–autumn regression equation is $y = 57.7527/[1 + (x/9.892)^{0.6772}]$ ($R^2 = 0.96$), indicating that the $\text{EC}_{50} = 9.892$; the summer regression equation is $y = 5.5717 + 42.2936/[1 + (x/9.2245)^{1.1938}]$ ($R^2 = 0.90$; $\text{EC}_{50} = 9.2245$). Panel (B) shows analogous regressions of prey capture success (number captured out of a possible 10 prey) on turbidity. The spring–autumn regression equation is $y = 0.9419 + 8.3802/[1 + (x/33.3398)^{5.051}]$ ($R^2 = 0.88$; $\text{EC}_{50} = 33.3398$); the summer regression equation is $y = 9.2034/[1 + (x/29.011)^{3.2812}]$ ($R^2 = 0.70$; $\text{EC}_{50} = 29.011$).

TABLE 1.—Mean reactive distances for turbidity treatments measured in nephelometric turbidity units (NTUs) in seasonal trials. Reactive distance data are also presented as the percent of the maximum observed value. We used Tukey tests to identify significant differences in reactive distance among turbidities within a season; values in seasonal columns without a letter in common are significantly different. *T*-tests (aposteriori) test for significant differences between seasonal treatments at a given turbidity.

Turbidity treatment (NTUs)	Reactive distance (cm)		Reactive distance (percent maximum)		<i>T</i> -test for seasonal differences <i>P</i> -value
	Spring–autumn	Summer	Spring–autumn	Summer	
0–0	49.4 ± 2.9 z	46.5 ± 2.9 z	100.0	100.0	0.1394
8–10	30.1 ± 1.4 y	27.9 ± 2.5 y	60.1	60.0	0.0459
16–15	23.5 ± 1.1 x	19.0 ± 3.4 x	47.6	40.9	0.0008
24–25	21.3 ± 2.2 xw	14.8 ± 3.1 xw	43.1	31.8	<0.0001
32–30	20.7 ± 2.2 w	13.8 ± 2.5 w	41.9	29.7	0.0002
48–45	13.9 ± 2.7 v	11.8 ± 1.6 w	28.1	25.4	0.1297
56–55	12.6 ± 3.0 v	9.9 ± 2.9 w	25.5	21.3	0.1478

Leigh, 2006; M. Riedel, unpublished data). Lightly impacted regional streams (i.e., those that are 100% forested with no recent disturbance) have turbidities that generally would not affect the foraging success of rosyside dace (i.e., ≤4 NTUs; (Bolstad and Swank 1997; Sutherland et al. 2002; Price and Leigh 2006; M. Riedel, unpublished data). Moderately impacted or disturbed streams have turbidity levels greater than the EC50s for reactive distance (>9 NTUs) for both seasons during base flow conditions (Sutherland et al. 2002; Price and Leigh, 2006) more than 50% of the time and have turbidity levels that exceed our highest levels slightly more than 10% of the time (M. Riedel, unpublished data). In addition, data from two other Blue Ridge Mountain rivers, the Chattooga (M. Riedel, unpublished data) and the Etowah (Walters et al 2003), indicate that turbidities capable of reducing foraging success in rosyside dace commonly occur in these streams and their tributaries. These findings suggest that the foraging success of some populations of rosyside dace in the region is negatively affected by turbidity and thus they may aid fishery biologists in developing management strategies for declining populations of rosyside dace.

Behavioral shifts may allow fish to forage effectively even with reduced reactive distances. For example, fish may increase searching behavior as turbidity increases (Sweka and Hartman 2001b). Observations of rosyside dace at high turbidities (>30 NTUs) revealed that a few fish adopted a mobile searching mode rather than holding a static position within the artificial stream (personal observation). Nonetheless, even in the highest turbidities, once a rosyside dace detected a prey item it nearly always captured it (R. M. Zamor, personal observation). Sweka and Hartman (2001a) observed similar phenomena with brook trout, which also displayed reduced reactive distances with increased turbidity but no change in either prey capture or consumption rates once a prey item was detected. Increased searching behavior, however, should result in higher net energy expenditure per prey and reduce overall energy intake, which would certainly would have a negative effect on individual fitness. Because we used optimal velocities for rosyside dace in our experiments, and because these velocities typically are occupied by rosyside dace in the field (Grossman et al. 2002), the reduced foraging efficiency observed at

TABLE 2.—Mean capture success for turbidity treatments measured in nephelometric turbidity units (NTUs) in seasonal trials. Capture success is also presented as the percent of the maximum observed value. Significant differences in capture success among turbidities within seasonal treatments were determined by Tukey tests; values in columns without a letter in common are significantly different. *T*-tests examine significant differences between capture success values for seasonal treatments at a given turbidity.

Turbidity treatment (NTUs)	Successful captures (number caught out of 10 possible)		Prey capture success (percent maximum)		<i>T</i> -test <i>P</i> -value
	Spring–autumn	Summer	Spring–autumn	Summer	
0–0	9.3 ± 0.8 z	9.4 ± 0.9 z	100.0	100.0	0.8324
8–10	9.3 ± 0.8 z	8.8 ± 1.1 zy	100.0	93.6	0.3370
16–15	9.2 ± 0.9 zy	8.1 ± 1.1 zy	98.9	86.2	0.0260
24–25	7.8 ± 1.0 y	6.1 ± 1.6 yx	83.9	64.9	0.0111
32–30	5.5 ± 1.2 x	4.0 ± 2.9 x	59.1	42.6	0.1520
48–45	1.7 ± 1.2 w	1.5 ± 2.3 xw	18.3	16.0	0.8102
56–55	1.7 ± 1.4 w	1.1 ± 1.4 w	18.3	11.7	0.3618

intermediate and high turbidities is probably applicable to field populations subjected to similar turbidities.

The reactive distance and capture success curves were curvilinear and followed a dosage-dependent relationship. A similar curvilinear response has been seen for reactive distance in other species (Vinyard and O'Brien 1976; Gregory and Northcote 1993; Benfield and Minello 1996; Sweka and Hartman 2001a, 2003), which suggests that this is a general relationship. If true, dosage-dependent curves may provide a useful statistical approach to the quantification of these relationships.

Although we expected prey capture success to be highest at 0 NTUs, there was little difference between prey capture success at 0 and 5 NTUs in either seasonal trial. At 0 NTUs rosyside dace appeared more unsettled than at 5 or 8 NTUs. Perhaps rosyside dace perceived a more secure feeding environment (i.e., greater visual isolation) in slightly turbid water. Even though the predation pressure in Coweeta Creek is for the most part very low (Grossman et al. 1998), fish may have perceived an increased vulnerability to predation in clear water owing to the lack of physical structure. Gregory and Northcote (1993) observed similar results for Chinook salmon, though their data are confounded by a prey visibility effect (De Robertis et al. 2003) and the fact that they used nonflowing systems to study a drift feeder.

Studies of the effects of turbidity on the foraging behavior of stream fishes have been conducted in both flowing-water and static systems. We primarily compared our results with those of studies conducted with flowing-water systems because static tanks could easily produce artifacts when used with drift-feeding stream fishes. It is likely that some of the differences observed among studies (e.g., the occurrence of reduced foraging success only at extremely high turbidities—810 NTUs in Gregory and Northcote [1993] and 320 NTUs in Rowe et al. [2003]) stem from using static rather than more realistic flowing-water systems.

To our knowledge, there have been no studies on the effects of temperature on reactive distance in fishes. However, studies of the effects of temperature on capture success show that increased temperatures have a variety of effects on foraging behaviors, including (1) increased prey consumption or attack rate (Persson 1986; Bergman 1987; Johnston and Mathias 1994; Taniguchi et al. 1998), (2) decreased handling time (Persson 1986; Bergman 1987; Taniguchi et al. 1998), (3) increased capture success (Persson 1986; Magoulick and Wilzbach 1998; Taniguchi et al. 1998), and (4) decreased capture success or no effect on capture success (Schmidt and O'Brien 1982; Persson 1986;

Bergman 1987; Johnston and Mathias 1994; Taniguchi et al. 1998). Increased temperatures produced increases in capture success in roach *Rutilus rutilus* (12, 15, 18, and 21°C: Persson 1986), brook and rainbow trout (13°C and 18°C: Magoulick and Wilzbach 1998), and creek chub *Semotilus atromaculatus* (range of treatments from 3°C to 26°C; Taniguchi et al. 1998). Nonetheless, increased temperature had no effect on the capture success of European perch *Perca fluviatilis* (12, 15, 18, and 21°C: Persson 1986; range of treatments from 4°C to 20°C: Bergman 1987), ruffe *Gymnocephalus cernuus* (4–20°C: Bergman 1987), or walleye *Sander vitreus* (15, 18.5, and 22°C: Johnston and Mathias 1994) and was higher at cooler temperatures for stream-dwelling Arctic grayling *Thymallus arcticus* (5, 10, and 15°C: Schmidt and O'Brien 1982), brook trout, and brown trout *Salmo trutta* (3–26°C: Taniguchi et al. 1998). The higher capture success rate for Arctic grayling at lower temperatures are probably the result of slower prey escape responses at those temperatures (Schmidt and O'Brien 1982), whereas the lack of differences between brook and brown trout in Taniguchi et al. (1998) are probably attributable to exposure to experimental temperatures that were near the upper thermal limit for trout survival. By contrast, Hill and Grossman (1993) showed that the capture success of rosyside dace and rainbow trout from Coweeta Creek was much more strongly affected by velocity and the distance of the prey from the fish than by temperature. In our study, rosyside dace had consistently higher capture success at spring–autumn temperatures but the differences were only significant at intermediate turbidities. Consequently, interpretation of the general relationship between turbidity, temperature, and prey capture success is currently problematical.

Our results may provide a mechanism for the observation that rosyside dace and other highland endemic species are found at reduced densities in, or are absent from, streams with high turbidities and fine substrata in Blue Ridge Mountain and foothill streams in North Carolina (Jones et al. 1999; Scott and Helfman 2001) and Georgia (Walters et al. 2003). Because fine sediments may affect streams in many ways (e.g., smothering invertebrates, reducing habitat complexity, deoxygenating sediments), fish occupying these systems experience habitat degradation in a variety of forms besides reduced foraging efficiency (Berkman and Rabeni 1987; Waters 1995; Dilts 1999).

In conclusion, we have demonstrated that turbidity significantly reduced the reactive distance and capture success of rosyside dace at both spring–autumn and summer temperatures. Even relatively small amounts of naturally occurring sediments (i.e., red clay)

produced turbidities that reached the EC50 values for rosyside dace at both seasonal temperatures and probably would reduced foraging success or increase the energetic cost of foraging for rosyside dace in the field. At present, similar turbidities are not uncommon in southeastern streams, which suggests that increasing land disturbance within the range of rosyside dace could negatively affect the abundance and distribution of this species. Our data also should be useful in the determination of total maximum daily loads in the streams inhabited by this species. It is likely that experiments that examine the effects of turbidity on fitness-related parameters such as foraging success will be useful in establishing environmental standards and interpreting correlative relationships between suspended sediments and fish abundance and biodiversity.

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References

- Barrett, J. D., G. D. Grossman, and J. Rosenfeld. 1992. Turbidity-induced changes in reactive distance in rainbow trout. *Transactions of the American Fisheries Society* 121:437-443.
- Benfield, M. C., and T. J. Minello. 1996. Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environmental Biology of Fishes* 46:211-216.
- Berg, L., and T. G. Northcote. 1985. Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1410-1417.
- Bergman, E. 1987. Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. *Environmental Biology of Fishes* 19:45-53.
- Berkman, H. E., and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285-294.
- Bolstad, P. V., and W. T. Swank. 1997. Cumulative impacts of landuse on water in a southern Appalachian watershed. *Journal of the American Water Resources Association* 33:519-533.
- Breitburg, D. L. 1988. Effects of turbidity on prey consumption by striped bass larvae. *Transactions of the American Fisheries Society* 117:72-77.
- Burkhead, N. M., and H. L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. *Transactions of the American Fisheries Society* 130:959-968.
- Confer, J. L., and P. L. Blades. 1975. Omnivorous zooplankton and planktivorous fish. *Limnology and Oceanography* 20:571-579.
- Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64:1345-1351.
- DeHaven, J. E., D. J. Stouder, R. Ratajczak, T. J. Welch, and G. D. Grossman. 1992. Reproductive timing in three southern Appalachian stream fishes. *Ecology of Freshwater Fish* 1:104-111.
- DeRobertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1517-1526.
- Dilts, E. W. 1999. Effects of fine sediments and gravel quality on survival to emergence of larval robust redbhorse *Moxostoma robustum*. Master's thesis. University of Georgia, Athens.
- Duchrow, R. M., and W. H. Everhart. 1971. Turbidity measurement. *Transactions of the American Fisheries Society* 100:682-690.
- Gregory, R. S., and T. G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 50:233-240.
- Grossman, G. D., and M. C. Freeman. 1987. Microhabitat use in a stream fish assemblage. *Journal of Zoology (London)* 212:151-176.
- Grossman, G. D., and R. E. Ratajczak, Jr. 1998. Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season, and fish length. *Ecology of Freshwater Fish* 7:108-131.
- Grossman, G. D., R. E. Ratajczak, Jr., M. Crawford, and M. C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs* 68:395-420.
- Grossman, G. D., P. A. Rincon, M. D. Farr, and R. E. Ratajczak, Jr. 2002. A new optimal foraging model predicts habitat use by drift-feeding stream minnows. *Ecology of Freshwater Fish* 11:2-10.
- Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74:685-698.
- Johnston, T. A., and J. A. Mathias. 1994. The effects of temperature on feeding in zooplanktivorous walleye, *Stizostedion vitreum*, larvae. *Environmental Biology of Fishes* 40:189-198.
- Jones, E. B. D., III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish

- assemblages in southern Appalachian streams. *Conservation Biology* 13:1454–1465.
- Magoulick, D. D., and M. A. Wilzbach. 1998. Effect of temperature and macrohabitat on interspecific aggression, foraging success, and growth of brook trout and rainbow trout pairs in laboratory streams. *Transactions of the American Fisheries Society* 127:708–717.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:137–145.
- North Carolina Wildlife Resources Commission. 2004. List of threatened and endangered species. North Carolina Wildlife Resources Commission, Raleigh.
- Persson, L. 1986. Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. *Journal of Animal Ecology* 55:829–839.
- Price, K., and D. S. Leigh. 2006. Comparative water quality of lightly and moderately impacted streams in the southern Blue Ridge Mountains, USA. *Environmental Monitoring and Assessment* 120:269–300.
- Redding, J. M., C. B. Schreck, and G. H. Everest. 1987. Physiological effects on coho salmon and steelhead of exposure to suspended solids. *Transactions of the American Fisheries Society* 116:737–744.
- Richardson, J., and I. G. Jowett. 2002. Effects of sediment on fish communities in East Cape streams, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 36:431–442.
- Riedel, M. S., J. M. Vose, and D. S. Leigh. 2003. The road to TMDL is paved with good intentions: total maximum daily loads for a wild and scenic river in the southern Appalachians. Pages 356–366 in A. Saleh, editor. Total maximum daily load (TMDL) environmental regulations—II. American Society of Agricultural and Biological Engineers, ASAE Publication 701P1503, St. Joseph, Michigan.
- Rowe, D. K., T. L. Dean, E. Williams, and J. P. Smith. 2003. Effects of turbidity on the ability of juvenile rainbow trout, *Oncorhynchus mykiss*, to feed on limnetic and benthic prey in laboratory tanks. *New Zealand Journal of Marine and Freshwater Research* 37:45–52.
- Roy, A. H., A. D. Rosemond, M. J. Paul, D. S. Leigh, and J. B. Wallace. 2003. Stream macroinvertebrate response to catchment urbanization (Georgia, U.S.A.). *Freshwater Biology* 48:329–346.
- SAS Institute, Inc. 1999. SAS/STAT user's guide, version 8. SAS Institute, Inc., Cary, North Carolina.
- Schmidt, D., and W. J. O'Brien. 1982. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). *Canadian Journal of Fisheries and Aquatic Sciences* 39:475–482.
- Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26(11):6–15.
- Shaw, A. L., and J. S. Richardson. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2213–2221.
- Sigmaplot. 2002. Sigmaplot, version 8.0. Sigmaplot, Chicago.
- Stouder, D. J. 1990. Dietary fluctuations in stream fishes and the effects of benthic species interactions. Doctoral dissertation. University of Georgia, Athens.
- Sutherland, A. B., J. L. Meyer, and E. P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47:1791–1805.
- Sweka, J. A., and K. J. Hartman. 2001a. Influence of turbidity on brook trout reactive distance and foraging success. *Transactions of the American Fisheries Society* 130:138–146.
- Sweka, J. A., and K. J. Hartman. 2001b. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 58:386–393.
- Sweka, J. A., and K. J. Hartman. 2003. Reduction of reaction distance and foraging success in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. *Environmental Biology of Fishes* 67:341–347.
- Swenson, W. A., and M. L. Matson. 1976. Influence of turbidity on survival, growth, and distribution of larval lake herring (*Coregonus artedii*). *Transactions of the American Fisheries Society* 105:541–545.
- Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1894–1901.
- Tebo, L. B. 1955. Effects of siltation resulting from improper logging on the bottom fauna of a small trout stream in the southern Appalachians. *Progressive Fish-Culturist* 17:64–70.
- Vinyard, G. L., and W. J. O'Brien. 1975. Dorsal light response as an index of prey preference in bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 32:1860–1863.
- Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on reactive distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33:2845–2849.
- Walsh, S. L., N. M. Burkhead, and J. D. Williams. 1995. Southeastern freshwater fishes. Pages 144–147 in E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, Washington D.C.
- Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River basin, USA. *Hydrobiologia* 494:5–10.
- Waters, T. F. 1995. Sediment in streams: source, biological effects, and control. American Fisheries Society, Bethesda, Maryland.