

## Turbidity-Induced Changes in Reactive Distance of Rainbow Trout

JEFFREY C. BARRETT<sup>1</sup>

*School of Forest Resources and Institute of Ecology  
University of Georgia, Athens, Georgia 30602, USA*

GARY D. GROSSMAN<sup>2</sup> AND J. ROSENFELD

*School of Forest Resources, University of Georgia*

**Abstract.**—We used artificial stream channels to conduct feeding trials with wild rainbow trout *Oncorhynchus mykiss* at three levels of suspended sediment. To examine the effects of turbidity on reactive distance and pursuit speed, we fed rainbow trout (87–185 mm standard length) pieces of mealworms *Tenebrio* sp. as test prey. A video camera system was used to record the pursuit speed and reactive distance of fish during foraging bouts. Turbidity had a consistent and negative effect on reactive distance (analysis of variance,  $P < 0.05$ ). On average, reactive distances in the 15- and 30-NTU (nephelometric turbidity units) treatments were only 80% and 45%, respectively, of those observed at ambient turbidities (4–6 NTUs). By contrast, turbidity did not significantly affect pursuit speed. Pursuit speed varied greatly among individuals but was similar for each fish across turbidity levels. These results indicate that sediment-producing activities, such as logging and road building, could reduce foraging success within trout populations.

Fisheries managers in the southeastern USA are hampered by incomplete knowledge of the variables that determine the structure of stream fish assemblages. In particular, uncertainty over the relative importance of biotic and abiotic factors to the organization of assemblages makes the development of management strategies difficult. One poorly studied but potentially important abiotic variable is suspended sediment. Suspended sediment is of special concern because many watersheds are subject to anthropogenic disturbances (e.g., timber harvesting) that can produce substantial inputs of sediments to stream ecosystems (e.g., Tebo 1955; Brown and Krygier 1971; Murphy and Hall 1981; Everest et al. 1987; Yount and Niemi 1990). The coarser fractions of these sediments are suspended during high flows but more typically are part of the stream bed load (Everest et al. 1987). Nonsuspended sediments can affect fish and invertebrate populations by altering substrate characteristics or subsurface flows in stream reaches (Tebo 1955; Hynes 1970; Everest et al. 1987). Suspended sediments, by contrast, typically exert their effects on organisms by reducing illumination and visual clarity (Noggle 1978). Ac-

ordingly, an optical measurement, turbidity, is typically used by biologists who examine effects of suspended sediment on fishes.

Turbidity is a measure of the quantity of light absorbed or scattered by a sample of water (Duchrow and Everhart 1971; McCluney 1975). Although relatively large sediment inputs may be required to affect stream bed loads, even small quantities of suspended sediment may markedly affect turbidity (Duchrow and Everhart 1971). Consequently, in many systems, turbidity may be a more important influence on fishes than other sediment-related effects.

The existing literature on effects of turbidity is contradictory and limited in scope. Some studies have shown that increases of turbidity can reduce feeding rates and growth of fishes (Sykora et al. 1972; Gardner 1981; Sigler et al. 1984; Redding et al. 1987), but other workers have reached different conclusions (Swenson and Matson 1976; Boehlert and Morgan 1985; Breitburg 1988). Other turbidity-related effects on fishes include increased emigration rates (Bisson and Bilby 1982; Sigler et al. 1984), changes in foraging behavior (Vinyard and O'Brien 1976; Noggle 1978; Berg and Northcote 1985) and increased activity (Graddall and Swenson 1982). Documented negative effects often have been associated with turbidity much higher than is encountered in all but the most disturbed streams (e.g., Redding et al. 1987).

We undertook the following study to assess the

<sup>1</sup> Present address: EA Engineering, Science and Technology, 8520 154th Avenue NE, Redmond, Washington 98052, USA.

<sup>2</sup> To whom correspondence should be addressed.

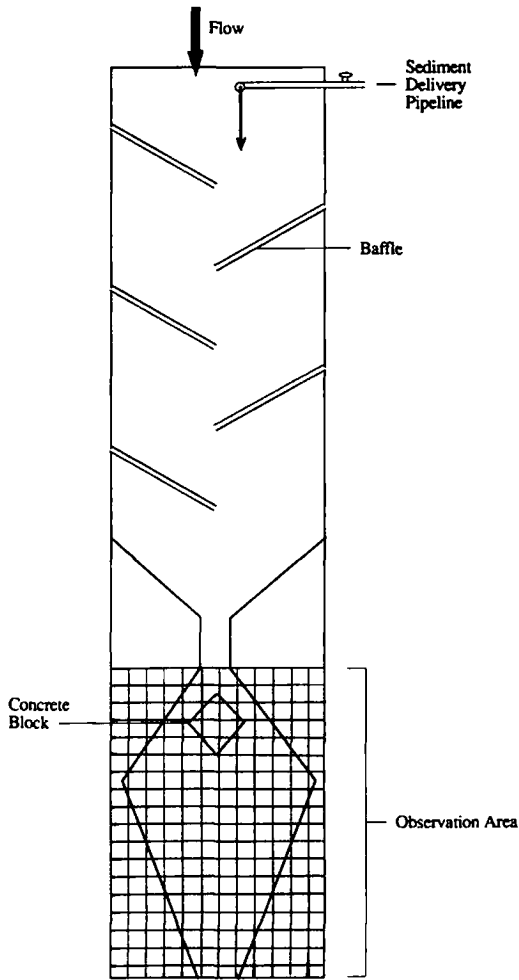


FIGURE 1.—Overhead view of one of the experimental streams showing the observation area and the sediment delivery system. The observation area is 2 m long and covered by a wire grid.

effects of turbidity on foraging by wild rainbow trout *Oncorhynchus mykiss* in a southern Appalachian stream. Specifically, we investigated the relationships between turbidity, reactive distance, and prey pursuit speed during active foraging by rainbow trout. In addition, we assessed whether water temperature and fish size influence reactive distance at particular turbidities.

#### Study Site

All studies were conducted in artificial stream channels within an abandoned weir on Henson Creek, at the Coweeta Hydrologic Laboratory of the U.S. Forest Service, Otto, North Carolina. Henson Creek is a third-order stream in the south-

ern Appalachian Mountains. It drains a forested watershed of approximately 203 hectares. The watershed contains a mixed hardwood forest including tulip poplar *Liriodendron tulipifera* and various species of oaks *Quercus* spp., hickories *Carya* spp., and rhododendron *Rhododendron* spp. Water in Henson Creek is generally clear with ambient turbidities of 4–6 nephelometric turbidity units (NTUs). Water temperatures range from 2 to 18°C annually (mean, 12°C), and the stream is completely shaded by overstory.

#### Methods

Three artificial stream channels (approximately 5 m long  $\times$  1.3 m wide  $\times$  0.6 m high  $\times$  0.25 m deep) were installed in Henson Creek for a previous study (Barrett 1989). We modified these channels to allow the observation and measurement of rainbow trout foraging behavior at various turbidities. Water flowing into the upstream end of each channel was constricted by gravel bars lining the sides of the channel and by baffles extending into the flow (Figure 1). The resulting turbulent flow assured the complete mixing of any sediment added to the system. Downstream, a series of plexiglass walls guided the flow into a diamond-shaped observation area approximately 2 m long  $\times$  0.75 m wide. This observation area was covered by a grid of wire mesh that divided the observation area into 5-cm<sup>2</sup> rectangles that allowed accurate measurement of fish movements by either an observer or a video camera perched in an overhead blind. A concrete block at the head of the observation area obstructed flows, creating an eddy of slower water in which trout could feed. This obstruction did not visually affect turbidity in the stream. Upstream and downstream screens prevented fish from leaving the observation area.

Turbidity was manipulated by adding controlled quantities of sediment to the water flowing into each channel. The sediment was collected from an abandoned weir within the Coweeta Hydrologic Laboratory, approximately 8 km from Henson Creek. The weir collected sand, silt, and fine organic material derived from natural erosional processes within the watershed. Consequently, these sediments were representative of the material typically contributing to stream turbidity within geologically similar areas of the Blue Ridge Province of the Appalachian Mountains. After some of the coarsest material (sands) was removed, sediments were suspended in water with an electric trolling motor and piped to a 208-L drum adjacent to the artificial stream channels.

We used individual pipes to distribute the sediment mixture to each channel. Valves on the distribution pipelines allowed control of the flow running to each channel. Turbidity was measured every 5–10 min with an electronic turbidometer that reported values to the nearest NTU.

Rainbow trout were captured as needed from streams at the Coweeta Laboratory with DC electrofishing equipment. Rainbow trout populations in these streams are self-sustaining and are not subject to additions of hatchery fish. After fish were weighed and measured (range, 87–185 mm standard length, SL), one was introduced into each channel. Supplemental fish from each collection, if any, were stored in a streamside holding tank until needed. The holding tank received fresh water, approximately 8 L/min, from the adjacent stream. Fish introduced into the channels were allowed a minimum of 12 h to acclimate before feeding trials began.

Feeding trials were conducted three times per day: in the morning (0700–0900 hours Eastern Standard Time), around noon (1200–1300 hours), and in the evening (1700–1900 hours). Initially, three to eight mealworm pieces (each 4–7 mm long) were offered to rainbow trout under ambient conditions to determine whether individual fish would feed. Frequently fish did not feed. These individuals were subsequently ignored until the next feeding period. Fish that did feed were further examined in a feeding trial. We sequentially tested these individuals at three turbidity levels: ambient (4–6 NTUs), low (14–16 NTUs), and high (29–31 NTUs). Approximately 1 h was required to conduct a feeding trial. Initially the sequence of turbidity levels used for each fish was randomly determined. Subsequent analyses indicated that the order of treatment presentation did not affect foraging response (analysis of variance [ANOVA]:  $F = 1.65$ ;  $df = 3, 5$ ;  $P > 0.29$ ). Behavioral observations also indicated that satiation was not affecting foraging measurements. Thereafter, treatments were presented in ascending order (ambient first, 15 NTUs second, and 30 NTUs last) to ease sampling logistics. At each turbidity level, mealworm pieces (4–7 mm) were introduced into the upstream end of the observation chamber. Because most (>85%) of the mealworms floated, it was possible to accurately follow a prey item once it was introduced into a channel.

Rainbow trout used in our experiments generally did not alter their behavior during turbidity changes. The total time necessary to change turbidity levels was typically about 5 min. During

these changes, fish generally remained in their holding positions. Distinct fright responses (e.g., high-speed swimming, high ventilation rates) were rare.

Foraging behavior was documented in two ways. We made visual observations by looking down onto the observation area from an overhead blind. For each foraging event, the observer recorded the number of grid squares between the original holding position of the fish and the location where the prey was taken. We also installed a Panasonic video camera (model AG 1900) in the overhead observation area to record feeding trials. Tapes from the video recorder were later analyzed to determine the distance moved in the pursuit and capture of individual prey items. The camera, however, frequently lacked sufficient contrast to display the fish clearly, particularly during the highest turbidity treatment. Accordingly, visual observations, either alone or in tandem with video recordings, made up the majority of the data collected.

We defined reactive distance as the distance moved by the fish from its holding position to the point where it took the prey. Water depth was kept constant (approximately 0.25 m) throughout the observation area and across all turbidity levels of a given trial. In addition, fish did not change their location in the water column as turbidity levels were varied. Consequently, we ignored depth-related changes in position in our analyses of reactive distance.

On occasion, the prey moved between the first movement by the fish and the time the prey was actually consumed, which may have biased our measurements. Prey movement was typically small, however, because fish pursued prey rapidly, typically catching it within 1 s, water velocities below the concrete block obstruction were not rapid, and eddying currents tended to move the prey in small circles rather than unidirectionally. Our experimental design also minimized the possibility of bias because multiple measurements (4–10) were made of each individual at each turbidity level.

The swimming speed of trout pursuing prey, referred to in our analyses as pursuit speed, was measured by advancing through foraging video tapes frame by frame and recording the distance moved by the fish per unit time, as indicated by an on-screen timer. The on-screen timer was accurate to 0.1 s, which allowed precise measurement of elapsed time during each prey pursuit.

Measures of turbidity vary among studies (Jack-

son turbidity units, mg/L, etc.) and they are not readily interconvertible (McCluney 1975). Because many results are reported gravimetrically, we calculated a conversion factor for the relationship between turbidity (NTUs) and sediment concentration (mg/L). One of the experimental channels was set up for a regular observation. At each of the three turbidities, we collected four 2-L water samples from the overflow at the end of the channel. These samples were later filtered through oven-dried, preweighed, 5- $\mu$ m-pore filter papers. We then oven-dried and weighed these filters and their associated sediment. Linear regression analysis was used to relate turbidity to sediment concentration.

We used several methods to analyze our results. For fish providing measurements at all three turbidities (i.e., complete observations), a repeated-measures ANOVA was used to test whether reactive distance or pursuit speed was significantly reduced by increases of turbidity. If a significant result was found, we examined pairwise differences with Scheffe's *F*-test. A level of  $P \leq 0.05$  was used to determine significance of these and all subsequent statistical tests.

Regression analysis was used on all observations (including those for which measurements were not available at all three turbidity levels) to determine the relationship between turbidity and reactive distance or pursuit speed at each turbidity level. We also quantified reductions in reactive distance as percentages of the distance observed at ambient turbidity. For this analysis, the reactive distance measured at ambient turbidity was assumed to be 100% of the maximum for each fish, and the reactive distances at 15 and 30 NTUs were expressed as a percentage of this maximum. This approach had two advantages: it standardized observations for the effects of variables such as temperature and fish size, and it enabled us to quantitatively assess the level of feeding impairment induced by increasing turbidities. Finally, we regressed average reactive distance at each turbidity against fish size and water temperature to determine whether these variables significantly affected reactive distance.

### Results

We examined the behavior of over 150 rainbow trout during the study. Approximately half of all fish failed to take prey within 3–4 d of introduction into the channels and were released. We obtained measurements on reactive distance at all three turbidity levels for 28 fish. In other cases, either individuals did not feed at all turbidities or

the number of feeding observations at one or more turbidity levels was too low for inclusion into statistical analyses.

Turbidity had a strong effect on reactive distance (ANOVA:  $F = 159.0$ ;  $df = 2, 54$ ;  $P < 0.0001$ ). Comparisons of reactive distance among individuals, however, were not significant ( $F = 0.38$ ;  $df = 27, 56$ ;  $P = 0.99$ ). Hence, increasing turbidity levels significantly reduced reactive distance of individual fish, but individuals did not differ significantly from one another in their reactive distances across treatments.

Multiple comparisons with Scheffe's *F*-test were significant in all cases, indicating that reactive distance at each turbidity was statistically different from that at the other two turbidities. Hence, even a 9–11-NTU increase in turbidity (from ambient to 15 NTUs) was sufficient to significantly reduce reactive distance of rainbow trout. Reactive distance differed more between 15 and 30 NTUs than between ambient and 15 NTUs, suggesting a non-linear effect of turbidity on reactive distance. Nevertheless, the linear regression of reactive distance versus turbidity was highly significant ( $P < 0.001$ ) and fit the data well despite scatter ( $r^2 = 0.71$ ; Figure 2). These results were obtained even though the centroids for reactive distance at each turbidity overlapped (Figure 2). Hence, the significant results obtained here and with the repeated-measures ANOVA are due to a consistent reduction in reactive distance as turbidity increased.

The regression of percent ambient reactive distance versus turbidity was also highly significant ( $P < 0.001$ ). The regression fit the percentage data better than the raw data ( $r^2 = 0.83$ ; Figure 3). Although the percent reduction varied among fish, in general an increase in turbidity from ambient to 15 NTUs (a 10-NTU increase) reduced reactive distance approximately 20%, or about a 2% reduction for each 1 NTU increase in turbidity. Similarly, reactive distances at 30 NTUs were reduced approximately 55% from values at ambient turbidity, or a 2.2% reduction per unit increase in turbidity. From 15 to 30 NTUs, reactive distance declined approximately 35% or 2.33% per NTU. Hence, per-unit decreases in reactive distance increased slightly as turbidity increased.

Fish size and water temperature were not significantly correlated with reactive distance at any turbidity level (all  $P$ s  $> 0.05$ ). However, the total variation in size we investigated was less than 100 mm SL. Although we conducted feeding trials at water temperatures ranging from 8 to 18°C, most observations were made at temperatures above

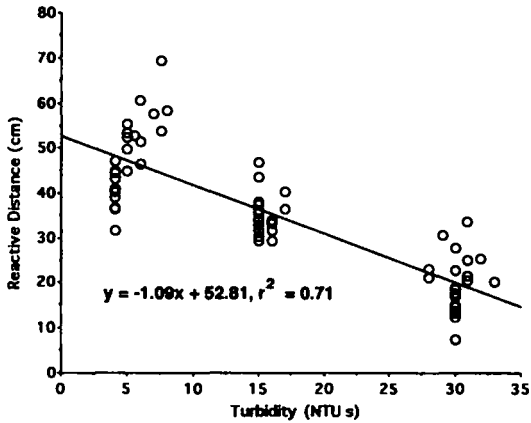


FIGURE 2.—Regression of average reactive distance ( $y$ ) of rainbow trout versus turbidity ( $x$ , nephelometric turbidity units, NTUs). Each point represents the mean reactive distance of an individual trout in a single feeding trial.

12°C, perhaps limiting our ability to detect temperature-induced changes in reactive distance.

Turbidity did not have a significant effect on pursuit speed (ANOVA:  $F = 1.24$ ;  $df = 2, 14$ ;  $P = 0.32$ ). At each turbidity, pursuit speed varied significantly among individuals ( $F = 2.75$ ;  $df = 7, 16$ ;  $P = 0.04$ ), but the regression of pursuit speed on turbidity was not significantly different from zero ( $P = 0.13$ ). Mean (SD) pursuit speeds were 32.2 (12.2) cm/s at ambient turbidity, 30.1 (12.1) cm/s at 15 NTUs, and 28.8 (11.0) cm/s at 30 NTUs.

The regression of sediment concentration ( $y$ , mg/L) versus turbidity ( $x$ , NTU) was highly significant ( $P < 0.001$ ) and yielded good fit ( $r^2 = 0.944$ ). The equation  $y = 3.399x - 5.603$  can therefore be used to convert our optical measurements of turbidity to sediment concentrations.

### Discussion

Increased turbidity significantly reduced the reactive distance of rainbow trout. There was substantial variation, however, in both the reactive distance of individual fish and in the amount of reduction produced by turbidity treatments. We believe that this variation reflected individual abilities to see prey under turbid conditions and was not due to differences in hunger or motivation. Upon viewing prey, most rainbow trout rapidly accelerated toward the item and then immediately consumed it. The intensity and speed of this behavior suggested that these foraging bouts represented maximal efforts by the fish. If this type

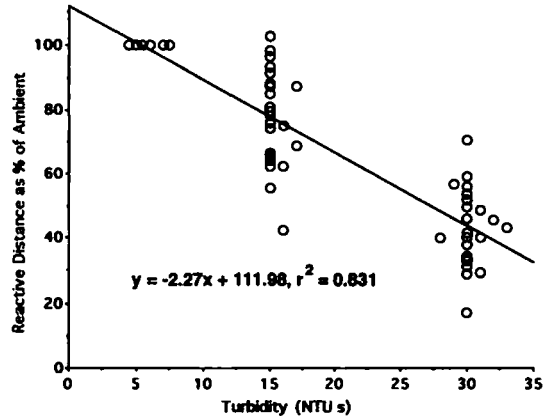


FIGURE 3.—Regression of percent reactive distance ( $y$ ) of rainbow trout, relative to the distance at ambient turbidity, versus turbidity ( $x$ , nephelometric turbidity units, NTUs). Each point represents the mean percentage for an individual trout in a single feeding trial.

of response was not evident during a feeding trial, we excluded the results for that effort from all analyses.

We observed reductions in reactive distance over a relatively narrow range of turbidities, which suggests that rainbow trout in the Coweeta drainage may be especially sensitive to increases in suspended sediment concentrations. Differences in sediment types and turbidity measures make it difficult to compare our results to other studies. Berg and Northcote (1985) found that an increase in turbidity from 0 to 20 NTUs reduced reactive distance of coho salmon *Oncorhynchus kisutch* approximately 52%; an increase from 0 to 30 NTUs resulted in a 62% reduction. Although these reductions are greater than those we observed, Berg and Northcote used brine shrimp *Artemia* sp. as prey in their trials. The mealworm pieces we used were lighter in color than brine shrimp and floated, which could have increased the ability of our fish to detect these prey. Vinyard and O'Brien (1976) reported that an increase in turbidity from 6.25 to 30 JTUs (Jackson turbidity units) resulted in a 60–70% reduction in reactive distance of bluegills *Lepomis macrochirus*. Although JTUs and NTUs are similar units of measure, Vinyard and O'Brien's description indicates that their 30-JTU suspension was muddier than our 30-NTU treatment.

Increases in turbidity in our trials appeared to affect more than just reactive distance; we noted a decline in foraging strikes and in feeding behavior in general at the highest turbidity level. This

reduction was apparently independent of reactive distance, because even prey within the visual field were often ignored by rainbow trout that showed active feeding at lower turbidities. At 30 NTUs, many fish remained relatively stationary, swimming to maintain position against the current but otherwise showing no movement. Although the possibility that fish were affected by the suddenness of the turbidity changes cannot be discounted, we did not observe fright reactions such as those of coho salmon recorded by Berg and Northcote (1985) upon introduction of sediments to their system. In addition, at least three other studies with salmonids showed that moderate turbidity levels enhanced, or at least did not depress, feeding activities (Noggle 1978; Bisson and Bilby 1982; Gradall and Swenson 1982).

We also observed few fright reactions by fish that never fed during any observation. Typically, nonfeeders maintained position in the water column but did leave their holding location. Stress related to capture in general, and to electrofishing in particular, could have caused this reaction. However, nonfeeding trout left to acclimate in the channels for a week or more often did not begin feeding. Eventually, we retained new captives for only 3–4 d before replacing them if feeding had not begun. This rapid replacement of fish, some of which might have eventually fed, probably accounts in part for the large number of nonfeeders in our experiment.

Turbidity did not affect the swimming speed of fish in pursuit of prey. We had hypothesized that under low turbidity conditions, a greater likelihood of not losing sight of a prey item would lower pursuit speeds. Instead, we found that individual fish tended to show similar pursuit speeds at all turbidities, although pursuit speeds varied widely among fish. We were unable to attribute individual differences in pursuit speed to any one variable such as light level, fish size, or water temperature. Neither did we note any consistent decrease in pursuit speed as foraging bouts progressed, as might be expected if hunger level were the primary determinant of this variable.

Fish size and water temperature showed no relationship to reactive distance of our fish and apparently did not affect the ability of fish to see and identify prey. The limited range of fish sizes (87–185 mm SL) and temperatures (8–18°C) investigated may have limited our ability to detect the effects of these variables, however.

A significant, linear relationship was established between optical and gravimetric measurements of

turbidity. The sediments in our work were grey-brown silty muds with some fine organic material. Relatively little of this material was required to increase turbidity levels. The ambient, 15-NTU, and 30-NTU treatments had average sediment concentrations of 8.3, 44.8, and 96.6 mg/L, respectively. Duchrow and Everhart (1971) found that regressions of turbidity on suspended sediment varied among sediment types. This suggests that the level of visual impairment, if any, from a given quantity of suspended sediment is likely to vary from system to system.

The reductions in reactive distance and feeding behavior that we observed as turbidity increased may be biologically relevant. Rainbow trout are primarily visual feeders that search some volume of water to locate prey. If turbidity limits the volume of water that trout can effectively scan for prey, it will reduce food consumption rates (Noggle 1978). Several authors have noted decreases (19–42%) in capture success and prey consumption rates at turbidities of 30–60 NTUs (Noggle 1978; Gardner 1981; Berg and Northcote 1985). Their studies indicate that reductions in reactive distance can affect foraging success. We often noted that more prey passed through our channels without apparent detection at 15 and (especially) 30 NTUs than at ambient turbidity. Some of these prey may have been detected but ignored by the fish. Our inability to distinguish between unseen and ignored prey makes our data inappropriate for a statistical analysis of foraging success.

Our results indicate that wild rainbow trout exposed to increasing levels of suspended sediments experienced significant reductions in their ability to detect prey (i.e., in their reactive distances). In stream environments, such reductions would likely reduce prey capture rates and thus lower growth and fitness of the fish. This may be particularly likely in systems where few prey are available for rainbow trout, such as in the southern Appalachians (Hill 1989). These factors should be taken into consideration when plans for logging, road building, and other projects likely to increase suspended sediment loads in streams are evaluated.

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