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Effects of Turbidity on the Foraging Abilities of Brook Trout (*Salvelinus fontinalis*) and Smallmouth Bass (*Micropterus dolomieu*)

By

John A. Sweka

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Abstract

Effects of Turbidity on the Foraging Abilities of Brook Trout (*Salvelinus fontinalis*) and Smallmouth Bass (*Micropterus dolomieu*)

John A. Sweka

Sedimentation is the major pollutant of waters in North America. Most research on the effects of increased sedimentation has focussed on its effects on stream habitat and its ramification on the reproductive potential of fish. Although relatively large sediment loads may be necessary to alter stream habitat, only small loads are needed to raise mean stream turbidity levels. Turbidity may be an important, yet relatively unexamined factor in stream fish production. With this, I sought to determine the influence of elevated turbidity on the foraging abilities of two predatory species representing both cold and warmwater stream habitas, brook trout (*Salvelinus fontinalis*) and smallmouth bass *(Micropterus dolomieu*).

This research was conducted in an artificial stream at West Virginia University and consisted of determination of effects of turbidity on reactive distance and foraging success of both species and determination of the effects of turbidity on brook trout mean daily consumption and specific growth rates. During reactive distance and foraging success experiments, three fish were tested at a time creating a situation of competition. In trials the fish first recognizing a potential prey item was at an advantage over the other fish by striking at that prey item at the moment of recognition. Thus, a measure of maximum reactive distance was established. Increasing turbidity resulted in an exponential decrease in reactive distance for both species, but the rate of decrease was found to be greater for brook trout than for smallmouth bass. Also, brook trout reactive distance was found to be lower for dark colored prey items than it was for light colored prey items. Decreased reactive distance resulted in a lower portion of prey being recognized, but had little influence on foraging success after recognition.

When conducting growth and consumption experiments with brook trout, a single fish was tested at a time. Turbidity had no effect on mean daily consumption despite the previously found decrease in reactive distance. Brook trout were found to become more active in turbid water, which increased their chance of encountering prey. Although consumption did not decrease with increasing activity, specific growth rates decreased due to an increase in the activity necessary to locate each prey item.

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Introduction

Sedimentation is considered the major pollutant of streams in the United States. Naturally occurring inputs of sediment are considered to be small and nondestructive to stream habitat and biota. However, excessive sediment loading resulting from anthropogenic activities and can overwhelm a stream's natural processing capabilities and damage its biological components (Waters 1995).

Sources of excessive sediment input may include agriculture, mining, road construction, and timber harvest (Waters 1995). The major contributors of sediment to Appalachian streams are timber harvest and its associated road construction, which will be the focus of my discussion here. Burns (1972) suggested that increased flow due to logging operations was beneficial to fish populations by providing more living area and increasing the fish rearing capacity of the stream, especially during low flow periods of the summer. However, increased stream flow may be accompanied by increased sediment loads due to the erosion of streambanks and runoff from surrounding slopes and road surfaces (Hartman et al. 1996). Both logging and associated roads accelerate the delivery of sediment to the stream bed, but the greatest contribution to sediment delivery is from roads (Eaglin and Hubert 1993; Grayson et al. 1993; Davies and Nelson 1993). Grayson et al. (1993) found than a road of 4-m width and 100-m length produced more sediment than a logging operation of 30.5-ha. Even if logging roads do not cross runoff producing areas, mean stream turbidity values can still increase 20%. Grayson et al. (1993) considered this to be an unavoidable impact of logging even under strict enforcement of operation codes.

Increased sediment loading can be detrimental to stream fish production through habitat degradation and reduction of the reproductive potential of fish. Loss of microhabitats and increased competition for available niches increases the territorial competition between individual fish . This could force fish to live in poorer habitat with less cover and increase their vulnerability to predation (Alexander and Hansen 1986). In addition to competition for optimum foraging habitat, the prey base for many stream fishes can be reduced through reduction in macroinvertebrate production due to the filling of interstitial spaces by fine sediment (Hartman et al. 1996), or change benthic habitat from cobble and gravel to gravel and sand. This filling of interstitial spaces also reduces the permeability of streambed substrate. Substrate with less permeability results in reduced salmonid egg survival (Allexander and Hansen 1986) and emergence (Harshbarger and Porter 1982).

Suspended sediments exert forces on organisms by reducing light and visual clarity (Barret et al. 1992). Turbidity is a measure of the light absorbing properties of a sample of water (Duchrow and Everhart 1971) and is directly related to the amount of suspended sediment. Turbidity rarely reaches lethal levels in natural systems, suggesting that its effects on fish production are the product of behavioral responses (Gradall and Swenson 1982). Large sediment loads may be required to alter steam substrate, but small loads can significantly increase mean stream turbidity (Barret et al. 1992). Turbidity may thus be an important, yet relatively unexamined factor in stream-fish production.

Effects of turbidity on fish behavior include avoidance and redistribuation, changes in activity, and decreased foraging ability (Sigler et al. 1984, Gradall and Swenson 1982; Barret et al. 1992). In laboratory experiments, Sigler et al. (1984) found steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) showed a net emigration from sections of raceway channels with elevated turbidity to those of clear water. Bisson and Bilby (1982) found similar results. Coho salmon acclimated to clear water showed significant avoidance of water of greater than 70 nephelometric turbidity units (NTU). These authors believed that the fish were avoiding turbid waters in an effort to maintain view of potential prey. Larimore (1975) found that turbidity caused young smallmouth bass (*Micropterus dolomieu*) to be displaced downstream due to the loss of visual orientation. Such avoidance behavior among fish species could leave long stream reaches devoid of fish (Waters 1995). Larval shad (*Dorosoma* spp.) were found to be distributed nearer the surface of the water under trubid conditions where light intensities would be expected to be greatest (Mathews 1984). Zooplankton migrate downward during the day, and migration of fish larvae near the surface where light intensities are suitable for predation may result in larval fish occupying a zone in which optimal prey concentrations are not available. Vertical segregation of larval fish and their prey during turbid episodes could increase the possibility of nutritional stress (Mathews 1984).

Using a turbidity gradient chamber, Gradall and Swenson (1982) studied the influence of turbidity on behavior and distribution of brook trout (*Salvelinus fontinalis*) and creek chubs (*Semotilus atromaculatus*). They found that creek chubs concentrated in turbid water while brook trout showed no preference. Both species were more active in turbid water and used overhead cover less. This would suggest that similar responses in natural stream systems should promote increased activity during periods of high invertebrate drift (Gradall and Swenson 1982). The question then arises as to whether increased activity can compensate for decreased visual acuity under turbid conditions and what this would mean for the accuracy of predictions from bioenergetics models for stream fishes.

Several studies have shown either decreased consumption rates or decreased growth rates of fish under turbid conditions. Gardner (1981) found feeding rates of bluegill (*Lepomis macrochirus*) on *Daphnia pulex* to decrease linearly with increasing turbidity from 0 to approximately 200 NTU's. Similar results were found by Benfield and Minello (1996) with gulf killifish (*Fundulus grandis*) preying on grass shrimp (*Palaemonetes pugio*) in 100 NTU's water compared to clear water. An exception to this trend is walleye (*Stitzostedion vitreum*). Vandenbyllaardt et al. (1991) found feeding rates for juvenile walleye (<85 mm) to increase in waters greater than 7 NTU and remain higher than in clear water up to 160 NTU. Walleye possess unique visual adaptations for feeding under turbid conditions which other species may not (Vinyard and Yuan 1996). Reduced growth rates of fish under turbid conditions have been demonstrated for steelhead and coho salmon (Sigler et al. 1984) which was attributed to a decrease in visual acuity and reduced prey consumption. Contrary to these findings, Swenson and Matson (1976) found normal ranges of turbidity seen in nature to have no influence on the growth rates of larval lake herring (*Coregonus artedii*). They did find, however, that the fish tended to congregate closer to the water surface where light intensities would be greatest. A problem with the above studies is that they either showed decreased feeding rates or decreased growth rates. None of them were designed to show both in the same experiment.

The reactive distance of a fish is the distance between a fish's holding position or focal point and the point at which potential prey is recognized (Barret et al. 1992).

Researchers agree that as turbidity increases, a fish's reactive distance decreases. Vinyard and O'Brien (1976) and Miner and Stien (1996) both showed bluegill reactive distance to decrease as a curvilinear function with the greatest decrease in reactive distance at low turbidity levels. Barret et al. (1992) found rainbow trout reactive distance to decrease as a linear function with increasing turbidity. Decreases in reactive distance under turbid conditions would be expected to decrease encounter rates between predators and prey (Gerritsen and Strickler 1977) which would thus be expected to result in decreased prey consumption and reduced growth rates.

More attention has been given to how turbidity affects coldwater species, particularly salmonids, than to how it effects warmwater species (Waters 1995). This may be due to the perception that warmwater streams are generally more turbid than coldwater streams and that their species have evolved mechanisms to deal with chronically turbid conditions (Waters 1995). According to the river continuum concept, species assemblages shift from cold to warmwater species as stream temperature increases with increasing stream order. Also, large rivers may be permanently turbid (Vannote et al. 1980). A comparison of the foraging abilities of predatory species representing various habitats is needed to determine which species and habitats would be most affected by increased turbidity.

The objective of this research is to determine how turbidity influences the foraging abilities of predatory fish found in Appalachian streams. Brook trout and smallmouth bass are economically important gamefish and represent cold and warmwater stream habitats respectively. Both are predatory species which feed primarily by sight and their habitats are susceptible to increased sedimentation due to land-use activities such as timber harvest, road construction, and agriculture. The specific questions to be addressed in this study were: (1) how does turbidity influence the reactive distance and foraging success of both species? (2) what effect does turbidity have on the mean daily consumption and specific growth rates of brook trout?; (3) what implications does turbidity have for bioenergetics modeling of stream fishes?; and (4) how do predatory species adapted to different habitats compare in their responses to increasing turbidity?

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Chapter 1:

Influence of Turbidity on Brook Trout (Salvelinus fontinalis) Reactive Distance and Foraging Success

Abstract

Past research has focussed on the effects of sediment action on stream morphology and brook trout (*Salvelinus fontinalis*) habitat. However, there is little information on the effects of suspended sediment, on brook trout foraging behavior. The objectives of this study were to determine (1) the effects of turbidity on brook trout reactive distance, (2) how turbidity affects foraging success of brook trout, (3) if prey color influences reactive distance, and (4) how turbidity affects encounter rate between predator and prey. I used videographic techniques to study brook trout foraging behavior in an artificial stream. Larval and adult houseflies (*Musca domestica*) were used as prey, which allowed a comparison of reactive distance between light and dark colored prey. Three brook trout were tested during each sampling period, creating a competitive situation under which a measure of maximum reactive distance could be made. Treatment turbidity levels ranged from 0-43 NTU. Maximum brook trout reactive distance decreased exponentially with increasing turbidity. With decreasing reactive distance, the proportion of prey recognized also decreased significantly. However, turbidity had no influence on the proportion of recognized prey that were attacked, the proportion of attacked prey items that were captured, or the proportion of captured prey that were ingested. Furthermore, brook trout reactive distances for dark colored prey were significantly lower than for light colored prey. In natural streams, invertebrate drift densities typically increase with turbidity as

flows increase, but this increase may not be enough to compensate for decreased ability to detect prey.

Introduction

Increased fine sediment loading can have negative impacts on fish production due to reduced availability and permeability of spawning gravel (Davies and Nelson 1993, Hartman et al. 1996), reduction of invertebrate density (Hartman et al. 1996), and altered stream geomorphology (Alexander and Hansen 1986). Whereas bed sediments affect fishes by altering substrate composition, suspended sediments exert forces on organisms by reducing light penetration and visual clarity (Barret et al. 1992), increasing physiological stress, reducing tolerance to disease (Redding et al. 1987), and causing respiratory impairment (Berg and Northcote 1985). Turbidity seldom reaches lethal levels in natural systems, suggesting that its effects on community structure are the products of behavioral responses (Gradall and Swenson 1982). Relatively large sediment loads may be required to significantly alter stream morphometry, but small inputs can significantly raise the amount of suspended sediment and markedly increase turbidity (Duchrow and Everhart 1971). Consequently, Barret et al. (1992) suggested that turbidity may have more influence on fish production than any other sediment related effect.

Responses to turbidity vary among species. Steelhead (*Oncorhynchus mykiss*) and coho salmon (*Onocorhynchus kisutch*) avoid turbid water (Sigler et al. 1984 and Bisson and Bilby 1982). Avoidance of turbidity, in an effort to maintain view of potential prey, can result in the absence of salmonids from long stream reaches (Waters

1995). Elevated turbidity levels can reduce the feeding rates and growth rates of fishes (Gardner 1981; Sigler et al. 1984; Berg and Northcote 1985; Mcleay et al. 1987; Redding et al. 1987; Reynolds et al. 1989), but others have reached different conclusions (Swenson and Matson 1976; Breitburg 1988). Reduced visual acuity has been attributed to reduced consumption and growth of bluegill (*Lepomis macrochirus*), coho salmon, steelheads, and arctic grayling (*Thymallus articus*) (Gardner 1981; Berg and Northcote 1985; Sigler et al. 1984; and McLeay et al. 1987).

Reduced growth under turbid conditions may result from reduced reactive distance and reduced prey encounter rate. The reactive distance of a fish is the distance from a fish's holding position or focal point to the position of a prey item or predator when it is recognized (Barret et al. 1992, Miner and Stein 1996). As turbidity increases, a fish's reactive distance will decrease due to inhibited visual clarity (Sigler et al. 1984, Barret et al. 1992, Gardner 1981, Miner and Stein 1996). Reactive distance of juvenile bluegills was reduced to less than 3 cm at turbidities greater than 60 NTU (Gardner 1981) and bluegill reactive distance, in detecting largemouth bass, decreased with increasing turbidity as a negative power function (Miner and Stein 1996). Further, Barret et al. (1992) found a linear relationship between the reactive distance of rainbow trout and increasing turbidity with a 55% reduction in reactive distance at 30 NTU's. Mobile prey could escape these limited fields of vision thereby reducing consumption and growth rates. Turbidity could also alter the feeding selectivity of fish, causing fish to only capture slow moving and slow reacting prey types (Gardner 1981).

Relative to other fishes, there has been considerable research on effects of turbidity on salmonid foraging (Sigler et al. 1984, Barret et al. 1992, Bison and Bilby

1982), yet studies with brook trout are lacking. Brook trout are an important component of fish communities in Appalachian streams. Their habitat is easily influenced by land-use practices such as timber harvest and road construction. Turbidity may be an important, yet relatively unexamined, aspect affecting brook trout production. Consequently, I conducted an experiments to determine foraging behavioral responses of brook trout to turbidity. I addressed the following questions: (1) how turbidity affects the reactive distance of brook trout, (2) how turbidity affects the foraging success of brook trout, (3) if prey color has an influence on reactive distance, and (4) how turbidity effects the encounter rate between predator and prey?

Materials and Methods

Experiments to determine the effects of turbidity on brook trout reactive distance and foraging success were conducted in an artificial stream at West Virginia University. All feeding trials were videotaped and later analyzed to determine reactive distance. Foraging success was determined by observing the brook trout on a computer monitor while trials were being videotaped.

Artificial Stream Design. - The artificial stream used to measure reactive distance was a 1.2 x 2.4 m galvanized steel tank (Fig. 1). The tank had two removable 1.8 m baffles which separated the tank into one large longitudinal and two smaller sections. The largest section was used to observe the fish. Fish were contained by fences of 1 cm^2-square galvanized wire fencing material positioned upstream and downstream of the viewing portion of the tank. The artificial stream was surrounded by a curtain to minimize outside disturbance. Current ($0.06\ m\cdot s^{-1}$) within the artificial stream was created with the use of three powerhead pumps placed in front of the viewing area.

Water temperatures were maintained at 12.0 ± 0.5°C (mean ± 95% C.I.) within the artificial stream. Water was chilled in a head tank with a 16 amp Frigid Units® chiller and a 6 amp submersible pump was used to deliver chilled water to the artificial stream.

Fish.- Brook trout were obtained from Bowden Fish Hatchery, Bowden, WV. Mean total length of the fish was 136 ± 2.5 (± 95% C.I.) mm and mean weights were 25.3 ± 5.2 g (± 95% C.I.). I chose hatchery-raised fish because wild fish were difficult to acclimate to a laboratory environment. Fish were treated in accordance to the guidelines of the West Virginia University Animal Care and Use Committee (protocol #9801-12).

My experimental protocol for reactive distance measurement differed slightly from others reported in the literature. Here, three brook trout were tested at a time. Other studies have measured reactive distance using only a single fish (Vinyard and O'Brien 1976; Barret et al. 1992). Single fish may not react to a prey item when it is first seen, but may wait until the prey drifts closer to react. This could give an underestimate of maximum reactive distance. By testing three fish at once, a competitive situation was established. The fish first recognizing a potential prey item was at an advantage over the other two by striking at that prey item before it was recognized by the other fish. The result would be a measure of maximum reactive distance.

To begin each experiment, brook trout were anesthetized with MS-222, weighed, measured, and placed into the viewing portion of the artificial stream. Each set of three fish was given twelve hours to acclimate to the artificial stream before testing began.

Videotaping of Foraging Behavior. - Recording of reactive distance and foraging behavior was done with a Sharp E550 view cam. The camera was mounted on the ceiling of the lab, 2 m above the viewing area of the artificial stream. The camera was connected to a computer and the image of the tank and fish could be viewed on the monitor using Media Studio Pro software® while videotaping foraging trials.

Treatments. - Treatment turbidity levels were created using soil obtained from the banks of Roaring Creek, a native brook trout stream in Preston County, WV. The soil was suspended by agitation in a bucket, creating a turbid solution. This solution was added to the head tank until a desired turbidity treatment level was reached in the artificial stream. A LaMotte 2020 turbidimeter was used to measure turbidity in NTU's.

Water depth was either 15 or 25 cm within the artificial stream. In the first five reactive distance trials, the depth was 25 cm and turbidity treatment levels were approximately 0, 10, 15, 20, and 25 NTU's. In 25 cm of water depth, it was not possible to accurately view the fish at turbidities above 25 NTU's. Water depth was then lowered to 15 cm which enabled continued testing of fish up to approximately 40 NTU's. Two additional sets of three fish were tested at turbidity levels of approximately 0, 10, 15, 20, 25, 30, 35, and 40 NTU's. Analysis of covariance (ANCOVA) was used to detect differences in maximum reactive distance between depths.

Feeding trials were conducted with live prey. Housefly larvae (*Musca domestica*) were used as prey items. Larvae were 10.3 ± 0.2 mm (± SE) in length. These larvae were small enough so that a fish could consume several without becoming satiated, yet large enough to be seen with the video-camera. Since the larvae normally sank quickly, air was injected into each before a feeding trial began. Thus, the view of both predator and prey could be maintained. Larval prey were used in the first five reactive distance trials at 25 cm of water depth and two additional sets of trials in 15 cm of water depth.

In addition to the standard reactive distance experiments, the effect of prey color was examined. Two more sets of trials (three fish in each) were run using frozen adult flies (11.7 ± 0.2 mm length) to see if prey color had any effect on reactive distance. Adult flies were black while larvae were white. These trials were conducted at 15 cm water depth and ANCOVA was used to detect differences in reactive distances between adult and larval prey.

Feeding Trials. - A feeding trial lasted approximately 20 minutes during which time 25-30 housefly larvae were sequentially placed in the viewing area by rinsing them down a delivery tube. After each prey item was released, the monitor was observed and the fate of the prey item was recorded. A prey recognition was defined as any action a fish took in reacting or orientating to a prey item. An attack was considered a pursuit of a prey item. If the fish struck and took the prey item into its mouth, it was considered a capture. If after capturing, a fish did not reject the prey item, it was considered an ingestion. The next prey item was not offered until the previous one was either consumed or passed through the back of the viewing area. The proportion of prey items recognized, proportion of recognized prey attacked, proportion of attacked prey captured, and proportion of captured prey ingested was recorded. Unconsumed prey was captured in a net at the rear of the viewing area.

With the light color of the artificial stream, there was not sufficient contrast to allow observation of the light colored prey at low turbidities. To remedy this problem, a black plastic mat (0.8 x 0.6 m) was placed on the tank bottom in the front portion of the viewing area.

At the end of a feeding trial, turbid water was added to the head tank until the next highest turbidity treatment was reached. Fish were again allowed to acclimate to this treatment for twelve hours, and were then tested again. Two trials, each at a different treatment level, were conducted per day until the final treatment level was reached. At this time, the fish were removed, anesthetized, and marked by clipping adipose fins to avoid re-testing the same individuals in subsequent trials. The artificial stream and head tank were then prepared for the next set of fish to be tested. It was not believed that testing the fish at sequential turbidity levels influenced the results in any way. In a similar study with rainbow trout, Barret et al. (1992) found that sequential application of treatment levels resulted in no difference in reactive distance compared to randomized treatments and this also simplified experimental logistics. One reactive distance trial at 0.57 NTU was eliminated from the data set because the brook trout seemed lethargic and did not react readily to prey. This was the first trial in a sequence for this group of fish and they may not have been acclimated to the testing environment. In the following trial at 17.6 NTU, they did not show any signs of stress or lethargy.

Reactive Distance Estimation. - Feeding video was reviewed and frame capture software (Multimedia Studio Pro®) was used to capture a particular video image at the instant a fish first recognized a prey item. The moment a fish made an indication of recognition of a prey item the image was captured and imported to MS Paint®. At this time marker was placed on both the fish and prey item. This documented which fish first recognized the prey item and eliminated any confusion about the location of the prey item in the image. The image was saved for later reactive distance measurement.

Interactive Data Language (IDL 5.0 from Research Systems © 1997) software was used to measure reactive distance. A 20 cm long piece of bright yellow poster board was placed on one of the cross supports of the artificial stream as a reference target (Fig. 1). The IDL program would import a saved image of a predator-prey encounter and would identify the reference target. By enumerating the number of pixels along the 20cm length of the reference target, the distance between fish and prey could be estimated.

In testing this method on known lengths within the viewing area, it was found that all estimates from the IDL program were 20% lower than actual values because the reference target was closer to the camera lens than objects in the viewing area. Estimates were corrected by the equation $Y = 1.25(X)-.52$ ($R^2=0.98$) where: Y was the actual length, and X was the estimated length. Further testing of this method showed that mean differences between estimated and actual lengths were 0.52 ± 0.3 (± 95% C.I.) cm.

Statistical Analysis. - Data were analyzed with windows based SAS®. I used linear and nonlinear regression to model changes in reactive distance and foraging success with increasing turbidity. Analysis of covariance was used to compare water depths and prey types.

Results

25 cm Water Depth. - Brook trout showed a significant reduction in maximum reactive distance with increasing turbidity ($F=102.75$, $p<0.01$). A simple linear model described the data well ($R^2=0.83$), but residual analysis showed that at intermediate turbidities the observed values for reactive distance consistently fell below predicted values. An exponential model, $R_{max} = A*e^{(-B*NTU)}$, was then used to describe the data and increased the fit of the model (Table 1). Brook trout in clear water (NTU<5.0) had a mean maximum reactive distance of 80.73 ±12.86 (± 95% C.I.) cm and this decreased to an average maximum of 18.59 ± 2.34 (± 95% C.I.) in the highest turbidities, approximately 25 NTU's. Variation among fish in maximum reactive distance was greatest at low and intermediate turbidity levels and decreased as turbidity increased (>20 NTU).

25 vs. 15 cm Water Depth. - Reduction of depth in the artificial stream from 25 cm to 15 cm permitted observation of the brook trout at higher turbidities. Comparison of the data obtained from both depths at treatment levels less than 26 NTU's showed no difference in maximum reactive distance between depths (ANCOVA: F=0.44, p = 0.51). The data from both depths was then pooled to create a model describing reactive distance ranging from 0 to 40 NTU's (Fig. 2). Reactive distance appeared to asymptote near 10 cm at turbidity levels greater than 25 NTU's.

Prey Color. - Brook trout reactive distance was significantly lower for dark colored, adult prey than for the light colored, larval prey (ANCOVA: F=8.77, p<0.01). Model intercepts were significantly different, while slopes were equal (Table 1 and Fig. 3).

Foraging Success. - Increased turbidity and reduced reactive distance resulted in a decreased proportion of prey recognized by brook trout (ANOVA: F=112.28, p<0.01). Furthermore, prey recognition rate was significantly higher in shallower water than in deeper water (ANCOVA: F=9.42 $p<0.01$). Fewer adult prey were recognized than larval prey at both depths (ANCOVA: F=20.66, $p<0.01$). In clear water (NTU<5.0), nearly all larval prey items were recognized. At elevated turbidities the proportion of prey items recognized decreased in a linear fashion for both depths and prey types (Fig. 4 and Table 2).

Although the proportion of prey recognized decreased, the proportion of recognized prey items that were attacked did not differ with depth, turbidity, or prey type (ANCOVA: depth F=2.10, p=0.15; turbidity F=1.48, p=0.23; prey type F=2.31, p=0.13)(Fig. 5). The proportion of attacked prey items that were captured also did not differ significantly with depth (ANCOVA: F=3.37, p=0.07), turbidity (ANCOVA: F=0.08, p=0.77), or prey type (ANCOVA: F=2.48, p=0.12). In fact, all larval prey that were attacked in 15 cm of water depth were captured (Fig. 5). Turbidity decreased the proportion of adult prey items captured which were ingested (ANCOVA: F=8.20, p=0.01), but had no influence on proportion of larval prey captured which were ingested in either 25 or 15 cm (Fig. 5).

Encounter Rates. - For comparison of the possible influence of turbidity on foraging of brook trout, encounter rates were modeled with the Gerritsen and Strickler (1977) model using observed reactive distances for adult prey. The encounter rate model is given by the equation:

$$E = ((\pi R^2 N_H)/3)*((v^2+3u^2)/u)$$

where: E is the encounter rate in numbers per second, R is the predator's reactive distance, N_H is the prey density, v is the predator's swimming speed, and u is the prey's swimming speed. Brook trout are drift feeders and capture drifting prey by ambush, so v was set to 0, and u was set to 0.06 m/s which was the velocity of prey drifting in the artificial stream. The prey density, N_H, was set to that found within the viewing area of the tank while feeding, 1.38 prey/m^3.

The reactive distance, R, is the highest order variable in the model and thus any changes in R produce the greatest relative change in encounter rate. Encounter rates then follow a similar function to that of reactive distance (Fig. 6), $E = ae^{(-b*NTU)}$ where: E is the encounter rate in numbers per second, a = 0.18, and b = -0.12. As a means of evaluating trade-offs between increased drift rate and reduced reactive distance at elevated turbidity, the Gerritsen and Strickler (1977) model was solved for prey density (N_H) (Fig. 7). Density must increase exponentially to maintain a constant encounter rate between brook trout and prey. For example, prey density must increase by a factor of 4, from 1 prey item/m^3 at 0 NTU to 4 prey items/m^3 at 10 NTU and by a factor of 14 to 14 prey items/m^3 at 20 NTU to maintain the same encounter rate as seen in clear water.

Discussion

Reactive Distance. - As expected, reactive distance of brook trout decreased as turbidity increased. Visual observation of the brook trout during feeding trials showed that the fish with the longest reactive distances at elevated turbidity levels tended to hold nearer the surface. The result was a decrease in reactive distance corresponding to a nonlinear model. Under turbid conditions, the brook trout held nearer the surface where light intensities would be greatest in an effort to compensate for a decrease in visual acuity. Others have found similar results with different species. Gradall and Swenson (1982) found brook trout to be less associated with substrate in turbid water and to increase activity in turbid waters. Mathews (1984) also noted that larval shad tend to emigrate toward the surface under turbid conditions. This is most likely in an effort to maintain visual acuity by movement to the surface where light intensities would be greatest.

The curvilinear relationship between reactive distance and turbidity found in this study indicates that turbidity has its greatest effect at the lower treatment levels (0-15 NTU). Miner and Stein (1996) also showed a nonlinear reduction in reactive distance for bluegill (*Lepomis macrochirus*) with the majority of reduction in reactive distance occurring from 0-5 NTU. Barret et al. (1992), however, described the decrease in reactive distance of rainbow trout with increasing turbidity as a linear function.

Rainbow trout have been believed to suppress brook trout abundance in Appalachian streams (Larson and Moore 1985) possibly due to competition. To further observe how reactive distance compares between brook trout and rainbow trout, I also analyzed my data using linear regression of the mean reactive distances found during each feeding trial as Barret et al. (1992) did for rainbow trout (Fig. 8). Only means for turbidity levels less than 35 NTU’s were used because Barret et al. (1992) did not have data for rainbow trout greater than this level. The equation of the linear model describing brook trout reactive distance was $Y = 51.46 – 1.66X$ and the equation describing rainbow trout reactive distance was $Y = 52.81 – 1.09X$ (Barret et al. 1992) where: Y = reactive distance and X = turbidity. The slope for the brook trout model was significantly greater from that given for rainbow trout ($t = 4.08$, $p<0.01$), but the intercepts were equivalent ($t = 0.52$, $p > 0.1$). However, a linear model does not appropriately describe how turbidity influences mean brook trout reactive distance. Residual analysis shows that in intermediate turbidity ranges, observed means consistently fall below those predicted by the linear model. Therefore, the reactive distance of these two salmonid species differs in response to increasing turbidity. This greater visual acuity of rainbow trout than brook trout may be one mechanism responsible for the perceived competitive advantage of rainbow trout.

Prey color had a significant influence on brook trout reactive distance. Although the rate of decrease in reactive distance with larval prey and adult prey was equal, adult prey were recognized at significantly lower distances than were larval prey. Salmonids are known to select for larger available prey (Wilzbach et al. 1986; Young et al. 1997) and the reactive distance of rainbow trout increases with prey size (Ware 1972). In this experiment, adult and larval prey were of similar size. Wilzbach et al. (1986) believed trout to select for surface drift due to increased contrast between prey and background. All prey items offered to brook trout in this experiment floated on the surface where the fish could see a contrast between a prey item and the outside environment. A greater contrast between larval prey and the outside environment may be responsible for the perceived difference in reactive distance between prey types. Thus, differences in prey recognition due to color, as well as size, could alter the taxon selectivity of brook trout under turbid conditions in nature.

I feel that my methods for measuring reactive distance were more accurate than any other means reported in the literature. Others have estimated reactive distance through visual observation with the use of some type of reference device of known lengths (Nicieza and Metcalfe 1997; Miner and Stein 1996), or through a wire grid placed above the fish (Barret et al 1992). The use of computer software in my study to measure reactive distance would be expected to reduce bias due to observer error and yield more precise measurements.

Foraging Success. - As turbidity increased and reactive distance decreased, the proportion of prey items that were recognized also decreased. Although maximum reactive distance measurements were not different between depths, fish in 15 cm of water recognized a significantly greater proportion of prey items than did fish in 25 cm of water. Maximum reactive distance measures were similar between depths since the fish with greatest distances held closer to the surface where light intensities would be greatest. I suggest that the difference between depths in the proportion of larval prey recognized is due to greater light intensity near the bottom of the artificial stream when the water was at 15 cm depth, permitting fish holding closer to the bottom to recognize prey which those in 25 cm of depth may not have seen. Also, a lower proportion of adult prey items were recognized at all treatment levels due to the reduced reactive distance with adult prey as compared to larval prey. The proportion of prey items recognized for both depths and prey types decreased at nearly the same rate. Barret et al. (1992) also noted a decrease in foraging strikes at elevated turbidities for rainbow trout.

Once a prey item was recognized, turbidity, depth, and prey type had no effect on the proportion of recognized prey items that were attacked, or the proportion of attacked prey items that were captured. Turbidity, however, had a significant influence on the proportion of adult prey captured that was ultimately ingested. Brook trout often rejected captured prey one or more times before ingesting it. After rejecting it, the trout would often swim toward the bottom and then return to capture it again. Perhaps fish would lose sight of the darker colored, adult prey, or perhaps adult prey was not as palatable as larval prey.

It appears that reduced prey consumption by brook trout as a function of turbidity was governed primarily by a turbidity induced decrease in prey recognition. Several studies have found that other species show reduced consumption and slower growth rates in turbid water than in clear water (Redding et. al. 1987; Sigler et. al. 1984; Birtwell et. al. 1984). In a study of coho salmon, Redding et al. (1987) used an index of intestinal fullness (0-3, with 3 representing a full intestine) to compare consumption across different turbidity levels. They found that after seven days exposure to suspended sediment mean indices were 2.8 for fish in clear water, 2.3 for fish in 0.3-0.6 $mg \cdot L^{-1}$ suspended sediment, and 0.8 for fish in 2-3 $mg \cdot L^{-1}$ suspended sediment. When compared to fish reared in clear water, Sigler et al. (1984) found approximately a 75% decrease in growth rate for coho salmon and a 62% decrease in growth rates for steelhead reared in turbid water of 49 NTU compared to those reared in clear water.

Encounter rates between predator and prey are strongly dependent on the reactive distance of the predator (Gerritsen and Strickler 1977). Slight changes in reactive distance result in pronounced effects on encounter rates. In turbid waters, the Gerritsen and Stickler (1977) model would predict that encounter rates should decrease as turbidity increases. In theory, prey consumption should decrease in a similar manner to reactive distance. For a brook trout to compensate for reduced encounter rates with prey, prey density must increase significantly or the fish must begin to actively search for prey. Active searching would reduce the net energy gain from each prey item consumed and could also make the fish more vulnerable to predation.

In natural streams, invertebrate drift has been found to increase with turbidity independent of flow. This is a result of decreased light reaching the streambed causing night-active diel drift photoperodicity (Waters 1995), whereby under conditions of decreased light penetration, invertebrate drift densities increase. Birtwell et al. (1984) found as turbidity increased, so did invertebrate drift, yet arctic grayling had less in their stomachs. The potential drift energy which could be gained by fish under turbid conditions may be damped by their inability to detect prey. Field studies should be conducted relating turbidity to invertebrate drift densities and brook trout stomach contents.

Conclusions.- Increased sediment loading in streams due to timber harvest, road construction, and other land-use practices may not be sufficient to cause deleterious effects on stream habitat or invertebrate densities, but could significantly increase mean turbidity levels. Turbidity effects on fish energy acquisition may be seen long before effects of sediment deposition on prey production or spawning potential. High gradient streams may have enough flow to prevent deposition of sediment which could deplete available spawning gravel. However, in streams with increased mean turbidity levels, avoidance of turbid waters may lead to significant emigration and absence of fish in long stream reaches (Waters 1995). The fish which stay may show slower growth rates and decreased recruitment due to decreased forage efficiency. This may affect production and population dynamics of brook trout as well as other stream-dwelling fishes. Such sublethal impacts of sedimentation upon brook trout and other fish populations may be partly responsible for perceived declines in production of streams throughout North America.

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Table 1. Reactive Distance Parameters. Brook trout showed a negative exponential decrease in reactive distance described by the model Y = Ae^(-B*Turbidity in NTU's) where: Y = maximum reactive distance, A = intercept, B = exponential coefficient, and NTU = turbidity.

Depth	Prey type	Parameter Description	Value±95% C.I.	N	R^2
25	Larvae	A: Intercept	87.42±9.33	23	0.88
		B: Coefficient e^(-B*NTU)	0.07±0.01		
15	Larvae	A: Intercept	84.28±9.14	16	0.95
		B: Coefficient e^(-B*NTU)	0.06±0.01		
Pooled Depths	Larvae	A: Intercept	85.44±6.3	39	0.90
		B: Coefficient e^(-B*NTU)	0.06±0.01		
15	Adult	A: Intercept	65.99±9.22	18	0.90
		B: Coefficient e^(-B*NTU)	0.06±0.01		

Table 2. Foraging Success Parameters. Linear models of foraging success, Y = A+B(NTU) where: Y = proportion, A = intercept, and B = slope. All larval prey items which were attacked in 15 cm depth were captured.

Proportion of:	Depth	Prey type	A: Intercept ±95% C.I.	B: Slope ±95% C.I.	N	P value	R^2
Prey Recognized	25	Larvae	0.935 ±0.115	-0.021±0.009	25	0.0001	0.64
	15	Larvae	1.053±0.123	-0.019±0.001	16	0.0001	0.84
	15	Adult	0.729±0.149	-0.014±0.006	16	0.0002	0.59
Recognized Prey Attacked	25	Larvae	0.982±0.042	-0.001±0.003	25	0.4540	0.02
	15	Larvae	1.007±0.037	-0.001±0.003	16	0.2030	0.11
	15	Adult	0.974±0.074	-0.001±0.005	16	0.6440	0.01
Attacked Prey Captured	25	Larvae	0.978±0.068	-0.002±0.004	25	0.2760	0.05
	15	Larvae	1	0	16	*	*
	15	Adult	0.943±0.063	0.001±0.003	16	0.4730	0.03
Captured Prey Ingested	25	Larvae	0.981±0.091	-0.004±0.006	25	0.1160	0.10
	15	Larvae	0.987±0.037	-0.001±0.001	16	0.8340	0.01
	15	Adult	1.057±0.139	-0.007±0.005	16	0.0110	0.34

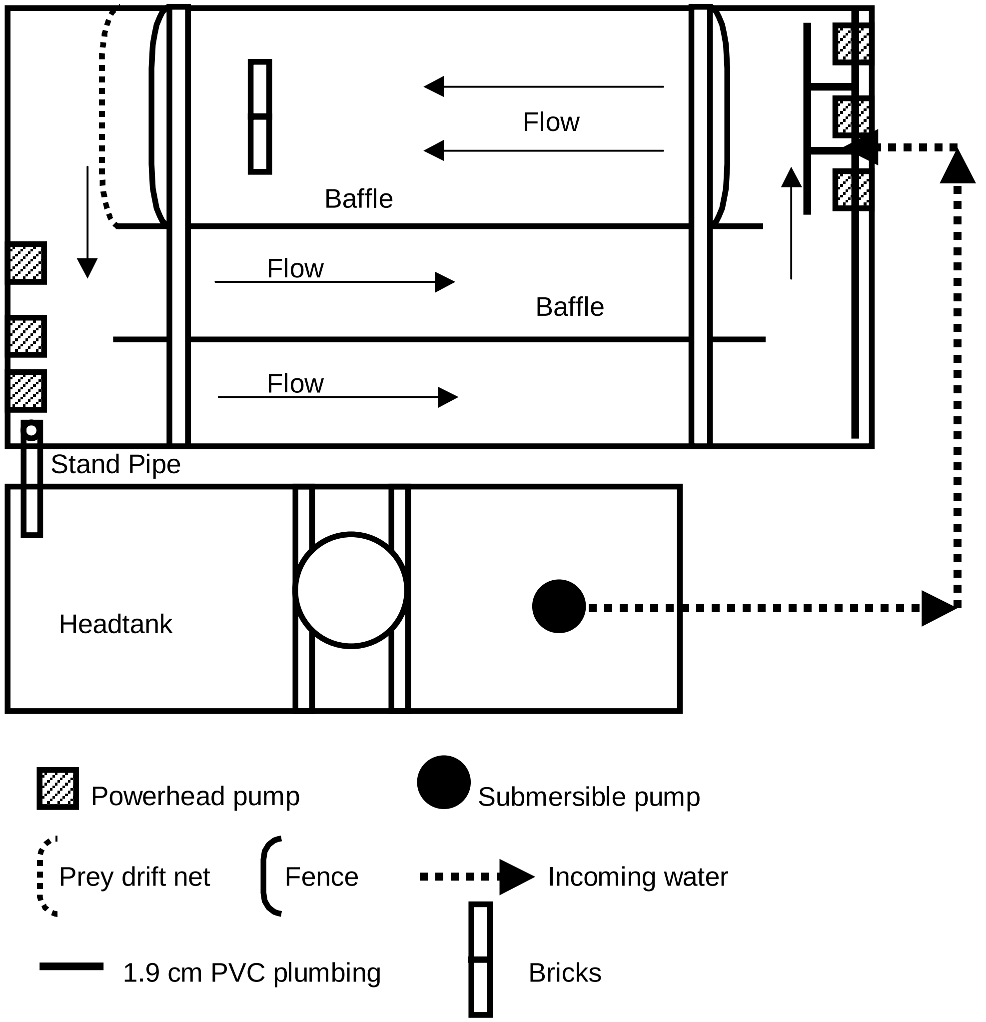

Figure 1. Overhead view of artificial stream design. See *Methods: Artificial Stream Design* for description.

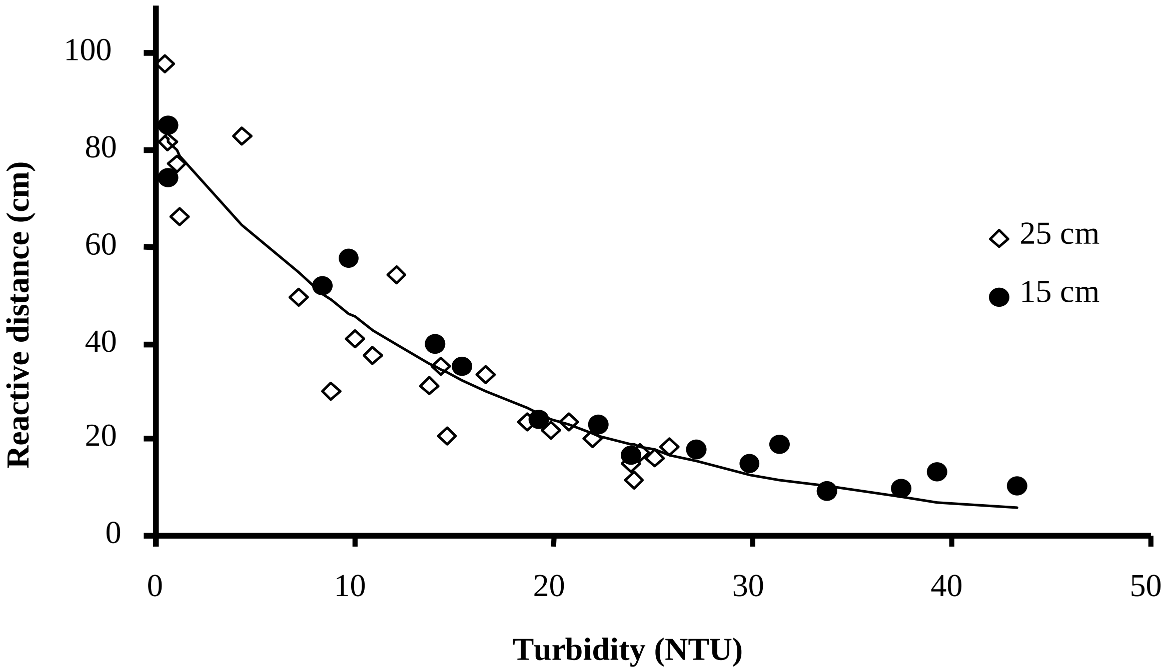

Figure 2. Model describing brook trout maximum reactive distance from 0 to 43 NTU. Data from both depths and all turbidity levels was pooled.

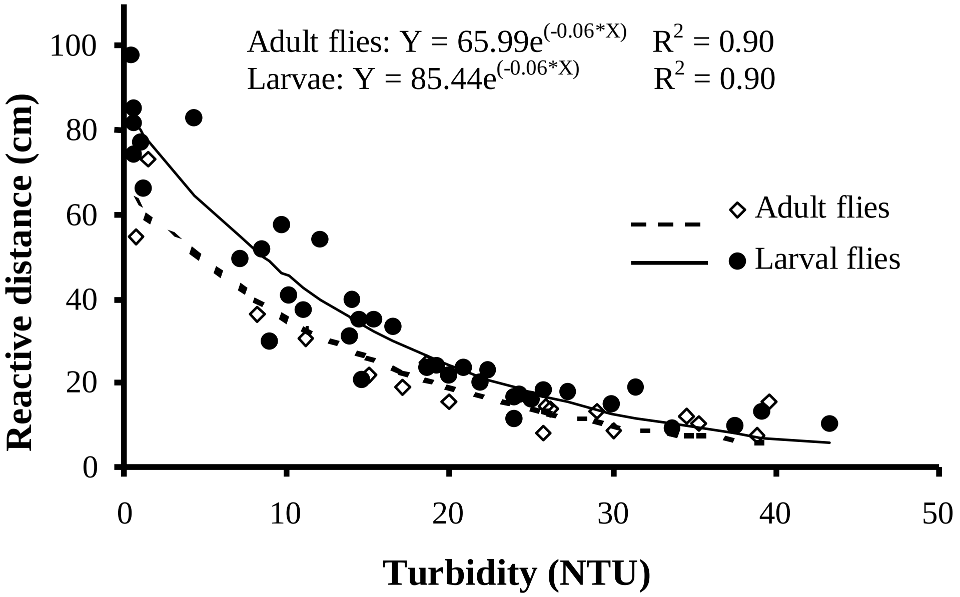

Figure 3. Effect of prey type on maximum reactive distance of brook trout. Maximum reactive distances for dark colored, adult prey were significantly lower than those for light colored, larval prey. Model intercepts were different (F=8.7708, $p<0.01$), while slopes were the same.

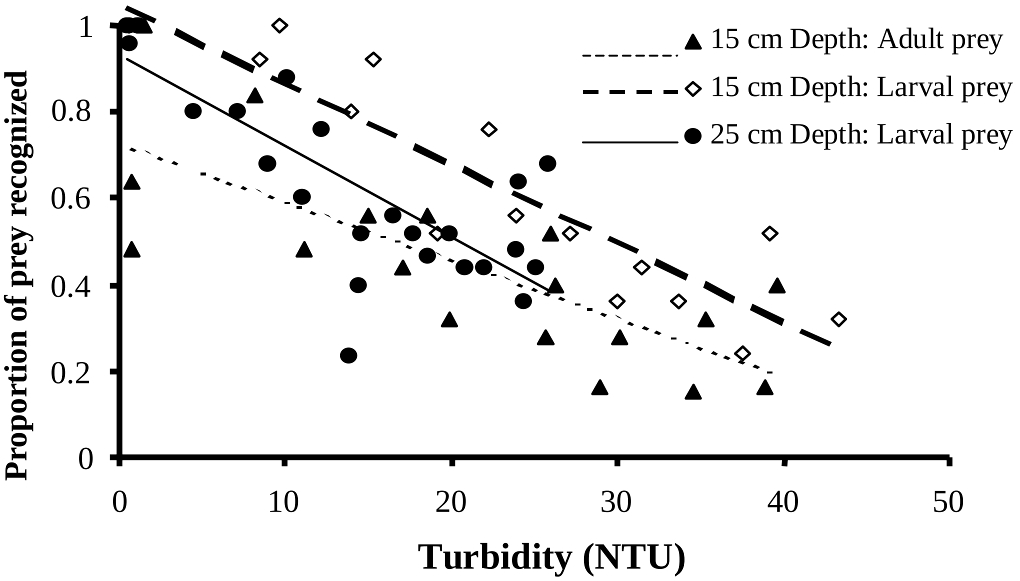

Figure 4. Proportion of prey recognized (Y) in a given turbidity (X). Each data point represents the proportion of offered prey recognized by at least one of the three brook trout during a trial. ANCOVA showed that depth (F=9.42, p<0.01), prey type (F=20.66, p<0.01) , and turbidity (F=112.28, p<0.01) were all significant factors with the greatest proportion of prey recognized being larval prey in 15 cm water depth.

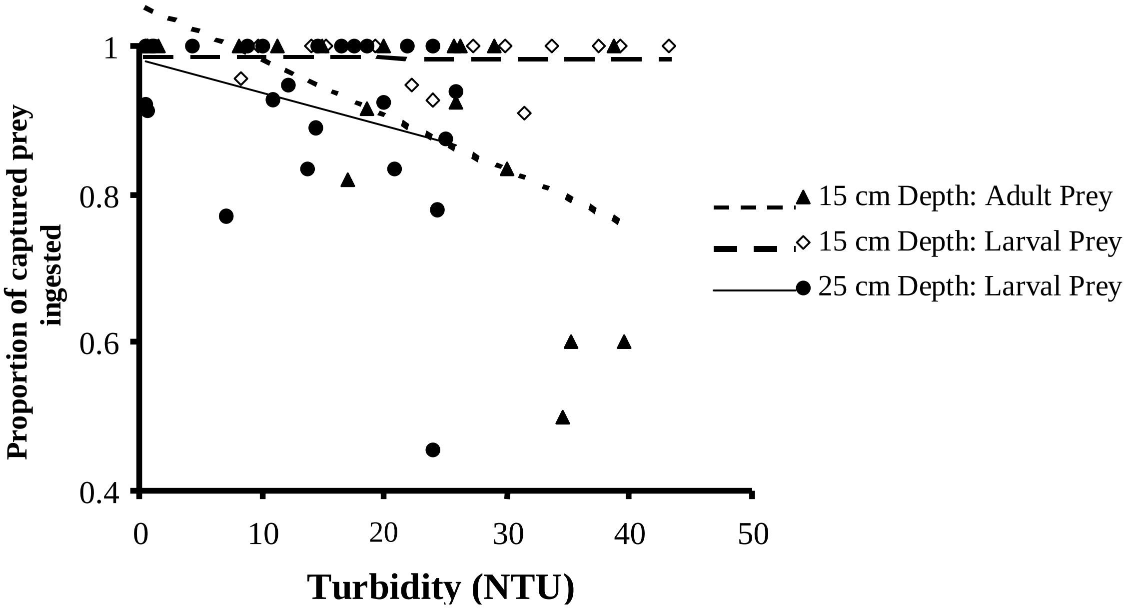

Figure 5. Effects of turbidity on the proportion of captured prey ingested. The proportion of adult prey captured which were ingested (F=8.20, p=0.01) decreased significantly with increasing turbidity, but this was not evident with larval prey at either depth.

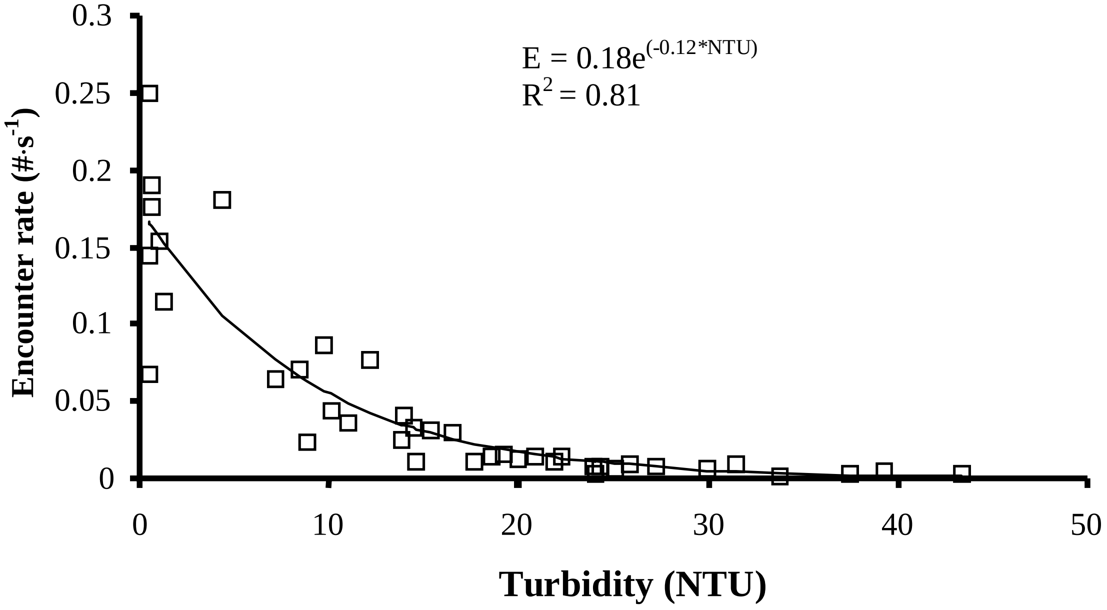

Figure 6. Encounter rates between brook trout and prey with increasing turbidity. Encounter rates were calculated using the Gerritsen and Strickler model (1977). The model predicts that as turbidity increases the encounter rate between predator and prey approaches 0.

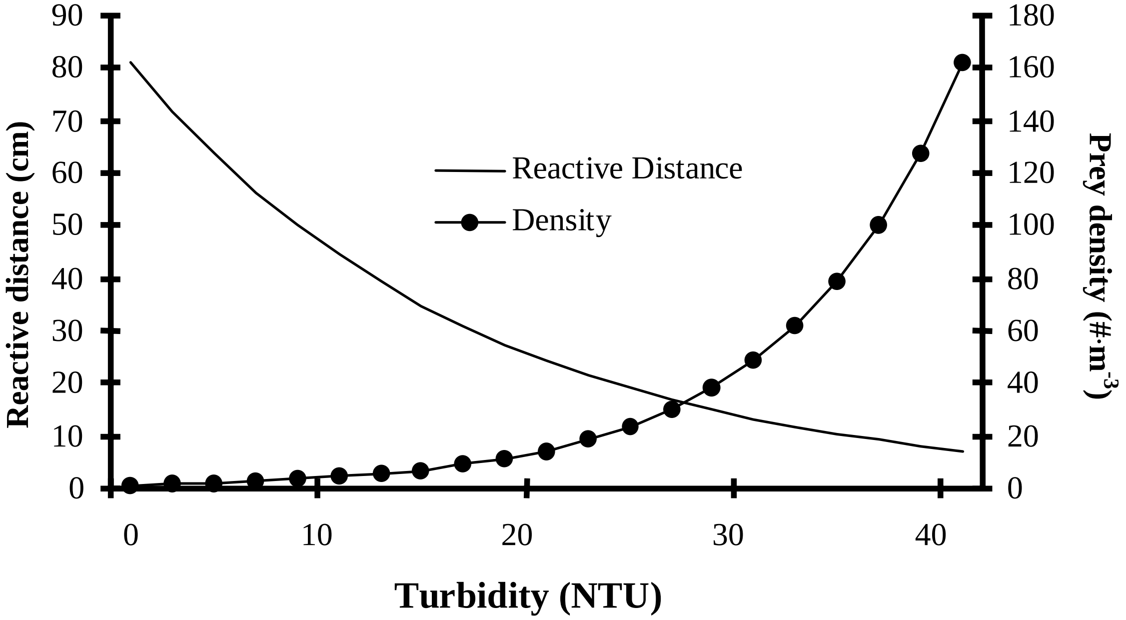

Figure 7. Relationship between brook trout reactive distance and prey density necessary to maintain constant encounter rates between predator and prey. Density data represent that needed to maintain a mean encounter rate of 0.16±0.05 prey·s^{-1} calculated for brook trout in clear water (<5 NTU).

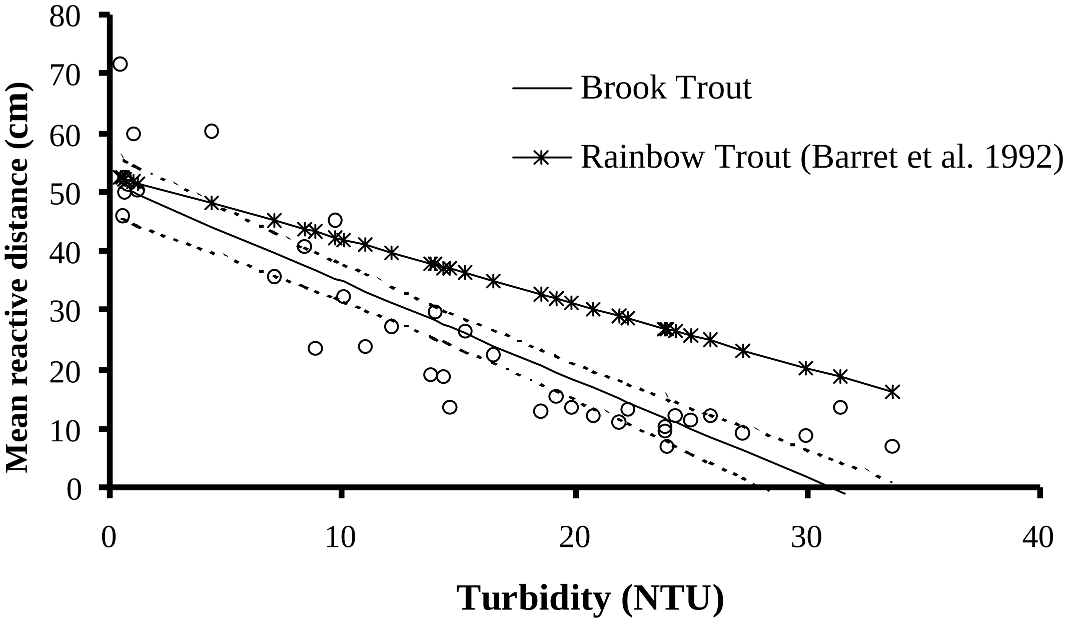

Figure 8. Comparison of mean brook trout and mean rainbow trout reactive distance (Barret et al. 1992). Dashed lines represent 95% confidence intervals for the brook trout model.

Chapter 2:

Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling

Abstract

Brook trout (*Salvelinus fontinalis*) were held in an artificial stream to observe the influence of turbidity on mean daily consumption and specific growth rates. Treatment turbidity levels ranged from clear (<3.0 NTU's) to very turbid water (>40 NTU's). Observed mean daily specific consumption rates were standardized to the mean weight of all brook trout tested. Turbidity had no significant effect on mean daily consumption, but specific growth rates decreased significantly as turbidity increased. Brook trout in turbid water became more active and switched foraging strategies from drift feeding to active searching. This switch was energetically costly and resulted in lower specific growth rates in turbid water as compared to clear water. Bioenergetics simulations were run to compare observed growth to that predicted by the model. Observed growth values fell below those predicted by the model and the difference increased as turbidity increased. Abiotic factors, such as turbidity, which bring about changes in the activity rates of fish, can have implications for the accuracy of predicted growth by bioenergetics models.

Introduction

Salmonids are visual predators and turbidity is believed influence their foraging efficiency. Steelhead (*Oncorhychus mykiss)* and coho salmon (*Oncorhynchus kisutch*) have shown decreased growth rates when reared in turbid water (Sigler et al. 1984). Also, coho salmon actively avoid turbid waters (Bisson and Bilby 1982). Reactive distance of rainbow trout (*O. mykiss*) has been found to decrease linearly and the reactive distance of brook trout (*Salvelinus fontinalis*) has been found to decrease exponentially as turbidity increases in artificial stream channels (Barret et al. 1992; Sweka 1999).

Although decreased growth rates in turbid waters have been attributed to an inability to detect prey and subsequent decrease in consumption, few studies have quantified daily consumption in salmonids under turbid conditions. Brook trout have been shown to become more active in turbid waters (Gradall and Swenson 1982), which could be a mechanism promoting increased feeding activity during periods of high invertebrate drift in natural streams. However, in another drift feeder, arctic grayling (*Thymallus articus*), a decrease in stomach contents was found in fish in turbid waters despite increased invertebrate drift (Birtwell et al. 1984).

Activity represents a significant portion of a fish’s energy budget. Changes in activity confound predictions of bioenergetics models because the activity component of the model is assumed to be constant (Boisclair and Legget 1989). Kerr (1982) hypothesized that the energy allocated to activity was positively related to the quantity of food consumed for actively foraging fish. This was also confirmed by Boisclair (1992) who found a positive logarithmic relationship between activity rates and feeding rates. These findings were based on observations of fish in still water. Brook trout typically utilize a drift feeding strategy in streams, whereby they hold in a single position or focal point, leave the focal point to intercept prey, and then return to the original focal point (Grant 1990; Fausch 1984). Under a drift feeding strategy, the current velocity at the focal point governs activity and the energy required maintaining position. However, Gradall and Swenson (1982) found that brook trout become more active under turbid conditions. Abiotic factors, such as turbidity, which alter the activity of fish could have profound effects on the accuracy of predictions from bioenergetics models.

Brook trout are the top predators in Appalachian headwater stream communities, and are often the only fish species present in such streams. Land-use practices such as timber harvest, mining, and road construction may result in increased sediment loads in headwater streams. Although much research has focussed on the effects of deposited sediment as a limiting factor for brook trout spawning potential, turbidity may be an important yet relatively unexamined factor also contributing to perceived decline of brook trout production in Appalachian streams. In this study, I sought to answer the following questions in flowing water: (1) how does turbidity influence brook trout mean daily consumption in streams; (2) how are specific growth rates influenced by turbidity; and (3) if brook trout become more active in turbid waters (Gradall and Swenson 1982), what effect will this have on their energy budget; and (4) what are the implications for bioenergetics modeling of stream-dwelling salmonids.

Materials and Methods

All experiments were conducted in an artificial stream. Brook trout were tested at sequential treatment levels of turbidity ranging from clear water (<5.0 NTU’s) to >40

NTU's (nephelometric turbidity units). Each trial lasted at least five days with five to six trials at different turbidity levels conducted on each fish. A subsample of the brook trout tested were videotaped while foraging to quantify changes in activity with increasing turbidity.

Artificial Stream Design.- Consumption and growth experiments were conducted in a 1.2 x 2.4-m steel tank (Fig. 1). A 1.8-m removable baffle was installed, separating the tank into two 0.6-m wide sections with fences (1 cm^2-mesh) at each end. One fish was placed in each of the sections. The artificial stream was surrounded by a curtain to minimize outside disturbance. Current ($0.06\ m \cdot s^{-1}$) was created with three powerhead pumps placed in front of each section. Drift nets were placed downstream of the fencing to catch uneaten prey.

Water temperatures were maintained at $12.0 \pm 0.5^{\circ}C$ within the artificial stream. Water was chilled in a head tank with a 16 amp Fridgid Units chiller and a 6 amp submersible pump was used to deliver chilled water to the artificial stream.

Fish.- Brook trout were obtained from Bowden Fish Hatchery, Bowden, West Virginia. Mean total length at the beginning of testing in clear water was 132.0 ± 28.6 mm (mean ± SE; range 77 – 179 mm) and mean weight was 31.1 ± 18.6 g (4.6 – 71.2 g). A wide range of fish sizes were used to determine the effect of size on consumption and to estimate allometric consumption parameters. These allometric consumption parameters were later used for standardization of specific consumption rates to the overall mean body weight of brook trout across trials. Brook trout energy density was estimated from percent dry weight mass of a separate sample of 15 fish using lake trout (*Salvelinus* *namaycush*) energy constant regression parameters as in Hartman and Brant (1995a). Mean energy density was 6481.3 ± 156.3 J·g^{-1} (mean ± SE) wet weight.

Prey.- Trials were conducted using live housefly larvae (*Musca domestica*) as prey. Larvae were 10.3 ± 0.2 mm in length and had an energy density of 8426.4 ± 90.4 J·g^{-1} wet weight as calculated from Cummins and Wuycheck (1971). Air was injected into the larvae with a syringe before being offered to the brook trout, making the larvae float and ensuring that any unconsumed prey entered the drift net for retrieval. To be sure that the larvae would float, they were dropped in an container of water and only those which floated were offered to the brook trout.

Experimental Procedure.- Unlike other growth experiments in turbid water, which measured growth in groups of salmonids (e.g. Sigler et al. 1984), I observed daily consumption and growth in individual brook trout. I felt that mean consumption determined by measuring consumption in groups of fish would be biased due to possible competitive dominance by a few individuals. Before beginning experimentation, each brook trout was anesthetized with tricane methanesulfonate (MS-222), weighed on an analytical balance to the nearest 0.01g, total length measured to the nearest mm, and placed into one of the sections of the artificial stream. Individuals were allowed to acclimate to the testing environment for twelve hours before testing began.

Turbidity treatment levels were created by mixing sediment collected from the banks of a local stream in a bucket and adding the solution to the head tank until a desired treatment level was reached. Fish were initially held at given treatment for a duration of seven days and fed four times daily. A pilot study in clear water showed that trials could be shortened to a duration of five days and two feedings per day with no difference in mean daily consumption. This simplified experimental logistics and shortened experimental time. During each feeding period, three turbidity measurements were taken with a Lamotte 2020 turbidimeter and the median recorded. For a given feeding period, turbidity was maintained within 4 NTU's of the desired treatment level through periodic agitation of the head tank and addition of more turbid water.

Prey items were offered to the brook trout in an amount greater than the maximum consumption predicted for lake trout (*Salvelinus namaycush*) of similar sizes at experimental temperatures. Consumption parameters from Stewart et al. (1983) were used in Fish Bioenergetics 3.0® (Hansen et al. 1997) to determine maximum consumption, and brook trout were offered an amount greater than the value predicted by the model each day. This amount averaged 5% greater than the amount necessary for maximum consumption, which ensured that the fish were offered more prey than they could consume during each day of testing. Larvae were blotted dry and were offered to the fish by rinsing them down a delivery tube at the front of each section of the artificial stream. Once a prey item was offered, another was not offered until the previous one was consumed or drifted though the back of the section into the drift net. After all prey were offered, uneaten prey were collected from the drift nets, blotted dry, and weighed once more to calculate the amount consumed by each fish. Brook trout never consumed all the prey items that were offered.

To standardize the rate of gastric evacuation, fish were given 12 hours before re-weighing and measuring to determine growth over the trial duration. Fish were then placed back into their respective sections of the artificial stream and tested at the next highest treatment turbidity level. The weights and lengths at the end of the previous trial were used as the starting weights and lengths at the beginning of the next trial (i.e., the end weight of trial *n* equaled the start weight of trial *n+1*).

A total of ten fish were tested. While testing the first three fish, treatment turbidity levels ranged from clear water to approximately 25 NTU with mean treatment levels of turbidity at 0.8, 6.1, 10.1, 14.8, 20.3, and 25.6 NTU. I initially felt that this would be high enough to show a difference in mean daily consumption as Sigler et al. (1984) found that this level was enough to cause a reduction in coho salmon growth. However, I did not observe a significant change up to 25 NTU's (See results), so I then tested fish at turbidity levels ranging from clear water to >40 NTU's with five treatment levels run on each fish to see if turbidity would have an effect at these higher levels.

Movement Experiment. - Visual observation of the brook trout feeding showed that as treatment turbidity increased, the fish began to move more often and to actively search for prey. To quantify movement, the last four fish tested were videotaped during feeding experiments. Each fish was videotaped during three randomly chosen feeding periods throughout each treatment using a Sharp E550 View Cam mounted above each section. Turbidity levels for each trial were approximately 0.6 (clear water), 10, 20, 30, and 40 NTU's. In review of the video, frame capture software (Multimedia Studio Pro®) was used to capture a particular frame at the instant a fish first recognized a prey item. A computer-generated grid (32 quadrants, each 18 x 18 cm) was then transposed onto the section of the tank and the location of the fish when recognizing a prey item was recorded.

Statistical Analysis.- Nonlinear regression was used to determine the effect of body size on mean daily consumption for brook trout in clear water (the control). The allometric consumption model was used to describe the relationship between consumption and body size (Kitchell et al. 1977).

$$C = CA(W^{CB})$$

Where: C = consumption in $g{\cdot}g^{-1}{\cdot}d^{-1}$, CA = the intercept of the allometric mass function, and CB = the slope of the allometric mass function. Because individual fish were tested over several weeks, and grew as testing continued, CA and CB parameters found in clear water were used to standardize observed daily consumption values to the overall mean weight of all fish used in all experiments as in Hartman and Brandt (1995b).

Analysis of variance and regression analysis was used to determine the influence of turbidity on mean daily consumption, specific growth rates, and number of quadrants used to forage within sections of the artificial stream. Significance was set at an alpha level of 0.05.

Simulations were run using Fish Bioenergetics 3.0® software to compare observed growth rates to those predicted by the model for lake trout. All lake trout respiration, egestion, and excretion parameters were used in the simulations (Stewart et al. 1983). I used lake trout parameters because of the close systematic relationship between brook trout and lake trout (both are in the same genus) and the similar temperature requirements for each species. Consumption parameters of CA and CB determined for brook trout in clear water (this study) replaced those of the lake trout. I assumed that 10% of the prey wet weight was indigestible. The model was fit to observed total consumption from the laboratory experiments and differences between observed and predicted values for growth at the end of a trial were analyzed using linear regression on mean trial turbidity.

Results

Experiments in clear water showed a weak relationship between mean daily consumption and weight of the brook trout. Larger fish had lower specific consumption rates than smaller fish. Allometric parameters of CA and CB for the equation $C = CA(W^{CB})$ were 0.130 and –0.201 respectively (Fig. 2).

The experimental allometric consumption parameters were then used to standardize brook trout consumption to the overall mean weight of fish tested (37.44 ±6.02 g). Brook trout did not show a significant difference in adjusted mean daily consumption with increasing turbidity (Fig. 3; F=1.36, p=0.25). Because of the relatively poor association between mean daily consumption in clear water and mean fish weight ($r^2 = 0.12$), and the large difference between lower and upper 95% confidence intervals for the CB parameter (Lower 95% C.I. = -0.344; Upper 95% C.I. = -0.058), I also standardized mean daily consumption rates using lake trout CA and CB parameters (Stewart et al. 1983; CA = 0.0589 and CB = -0.307). Again, turbidity showed no significant influence on mean daily consumption (F = 0.236, p = 0.63).

Specific growth rates decreased significantly with increasing turbidity (Fig. 4; F = 23.758, $p < 0.01$). Mean specific growth rates in clear water were 0.046 ± 0.001 (mean ± SE) $g \cdot g^{-1} \cdot d^{-1}$ while those at the highest treatment levels (≥ 38 NTU's) were 0.020 ± 0.003 $g \cdot g^{-1} \cdot d^{-1}$. Brook trout specific growth rates thus showed a 57% decrease from clear water to the highest treatment levels.

The movement study showed that the number of quadrants within each section of the artificial stream used to forage increased significantly (F = 17.31, $p<0.01$) with increasing turbidity (Fig.5) despite much variation between fish at intermediate treatment levels (10-20 NTU's). In clear water, 75% of the fish used three or fewer quadrates to forage, while one of the fish tended to move more frequently and forage from various locations in clear as well as turbid water.

Bioenergetics simulations gave predicted trial end weights for each fish based on the total amount of prey consumed. Observed values consistently fell below those predicted by the model and the difference increased as turbidity increased (Fig.6; F = 29.72. $p < 0.01$). Mean observed growth in clear water was 26% lower than that predicted by the bioenergetics model, while mean observed growth in the highest treatment level (NTU>40) was 56% lower than that predicted by the bioenergetics model.

Discussion

The results I obtained were contrary to what was expected. Turbidity had no significant influence on brook trout mean daily consumption. Reactive distance has a strong influence on encounter rates between predator and prey and turbidity has been shown to decrease the reactive distance of fish (Barret et al. 1992; Miner and Stein 1996). According to the Gerritsen and Strickler (1977) model, decreased reactive distance leads to decreased encounter rates. For drift feeding fishes like brook trout, decreased reactive distance under turbid conditions would be expected to decrease the volume of water searched per unit time. This should eventually result in decreased consumption rates.

One means by which a predator could compensate for a decrease in reactive distance is to increase swimming activity. Gradall and Swenson (1982) found that in water of 7.1 FTU's (formazin turbidity units) brook trout activity increased and association with cover and substrate decreased. (Benfield and Minello (1996) give a conversion of FTU to NTU where FTU = 1.25·NTU. Therefore, 7.1 FTU's = 8.8 NTU's). Increasing the time spent moving increases the chance of encountering potential prey by increasing the total volume of water searched. For brook trout in this study, a switch in foraging strategy was observed. In clear water, typical drift feeding behavior (Grant 1990) was observed where a fish would recognize a prey item, strike at that prey item, and return to the original holding position. As the water became more turbid, fish tended to utilize more of the available area of the tank to forage. The number of locations used to forage increased significantly as turbidity increased. By using more locations as holding positions, the brook trout increased their chance of recognizing potential prey, thus compensating for decreased reactive distance with increasing turbidity. Although foraging locations were quantified for only four brook trout, I feel that their behavior is representative of all tested fish based on observation while conducting feeding trials.

The transition from a typical drift feeding strategy to an active searching strategy took place between 10 and 20 NTU where the greatest variation in the number of quadrants used to forage occurred. At these levels of turbidity, the fish were faced with a choice of holding in a single location which may decrease the number of prey recognized, or utilizing more of the tank and increasing the chance of prey detection. At higher turbidity levels (30-40 NTU's), lower variation in the data and a higher mean number of quads used suggests that active searching for prey was the primary foraging strategy.

Although active searching for prey may compensate for decreased visual acuity in turbid waters, this strategy is energetically taxing. Net return per unit effort in foraging would be expected to decrease when switching from a typical drift feeding strategy to an actively searching strategy as the activity required to capture each prey item increases (Boisclair and Sirois 1993, Boisclair and Legget 1989). This can be seen in the decrease in brook trout specific growth rates with increasing turbidity. Reduced growth rates seen in fishes under turbid conditions may not only be a result of decreased visual acuity, but also a result of the increased amount of energy required to locate prey.

The brook trout grew over treatment levels, and it may be argued that this growth could account for the decrease in specific growth rate. However, regression of specific growth rate on body weight for brook trout tested in clear water showed no correlation between fish size and specific growth rate ($F = 1.36$, $p = 0.28$). Therefore, I believe that the reduction in specific growth rates under turbid conditions is due to the treatment effect rather than possible allometric changes in growth rates.

The bioenergetics model simulations illustrated the influence of turbidity on the energetic return per unit effort. In clear water, trial end weights were slightly below those predicted by the bioenergetics model. The $0.06\text{-m}\cdot\text{s}^{-1}$ current velocity in the artificial stream not taken into account by the bioenergetics model can explain the difference. As turbidity increased, the difference between trial end weights predicted by the model and those observed increased significantly, thus indicating a more energetically costly situation as the brook trout switched from a drift feeding strategy to an active searching strategy.

The comparison of observed growth to that predicted by the bioenergetics model points out simplification in the assumptions of the bioenergetics model. The model assumes constant rates of activity, which is seldom the case. Activity plays a significant role in a fish's energy budget (Boisclair and Sirois 1993). Changes in abiotic factors, such as turbidity, can influence fish behavior, leading to changes in activity independent of temperature fluctuations. These changes in activity can strongly influence the accuracy of predicted growth by bioenergetics models. With the difference between observed and predicted growth over the relatively short duration of the experiments in this study, caution should be warranted when using bioenergetics models to predict growth in natural populations of stream-dwelling fish over longer time periods, especially where turbidity is elevated or variable, or where other abiotic conditions are common.

Decreased growth rates in turbid water in other salmonids have been attributed to decreased visual acuity and thus decreased consumption (Sigler et al. 1984). In another set of experiments (Sweka 1999, *see Ch1.*), I found that the reactive distance of brook trout decreased exponentially with increasing turbidity. The decrease in reactive distance was expected to translate into a decrease in mean daily consumption. Although visual acuity may result in decreased consumption rates in salmonids, growth rates may not only be governed by consumption, but also by activity. In this study, turbidity did not directly influence brook trout growth rates through reduced mean daily consumption, but caused behavioral changes in activity, which were energetically costly.

Increased sediment loading to streams may not be sufficient to alter habitat and substrate, but may markedly change mean or stormflow turbidity levels (Barret et al. 1992). Thus, although spawning habitat and invertebrate biomass may be unaffected, turbidity can decrease growth rates in fish through decreased visual acuity and subsequent changes in feeding behavior in an effort to compensate for the decreased ability to detect prey under turbid conditions. Factors such as turbidity, and its influence on activity, complicate application of bioenergetics models describing stream-dwelling fish in the field, and an overestimation of potential growth may result. The results found here suggest that turbidity can decrease brook trout growth through allocation of energy for changes in activity rather than for growth.

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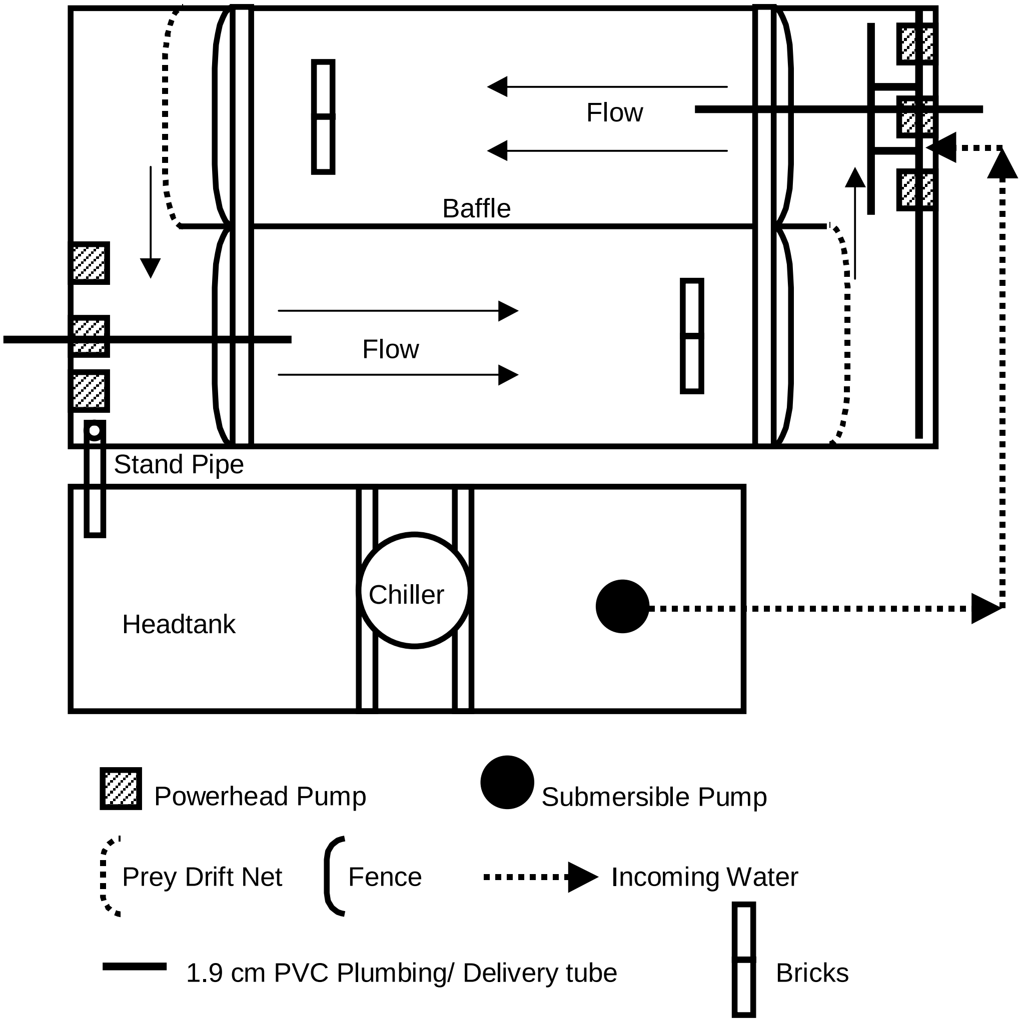

Figure 1. Overhead view of artificial stream design. See *Methods: Artificial Stream Design* for description

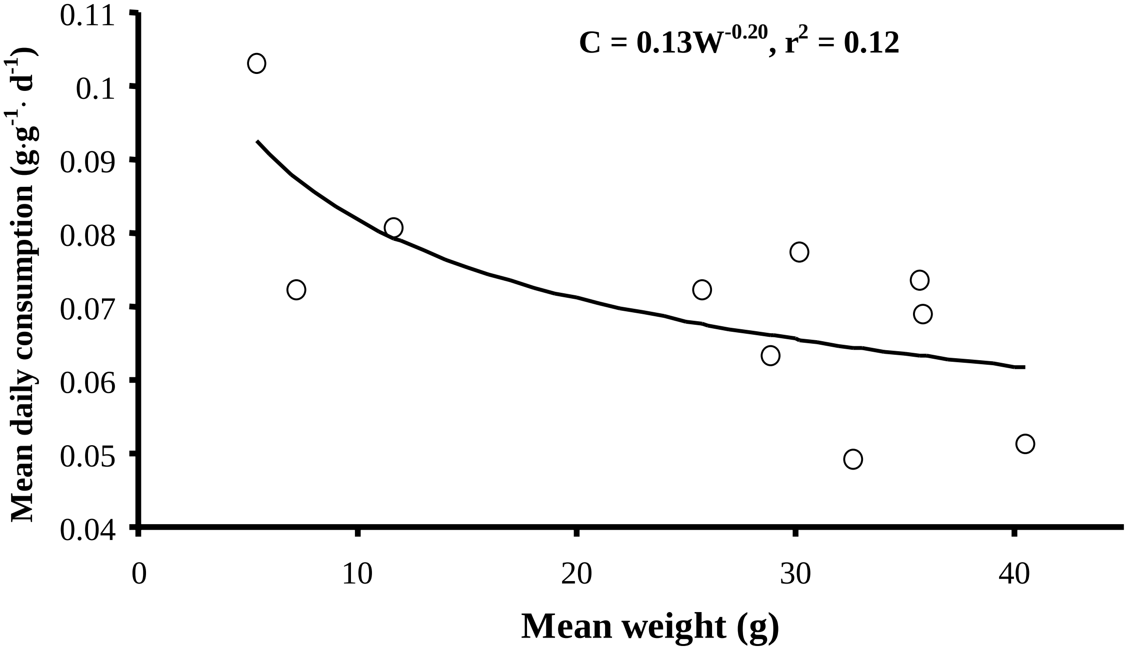

Figure 2. Regression of mean daily consumption (C) on mean weight (W) of brook trout tested in clear water. The 95% C.I. on CA was ±0.052 and the 95% C.I. on CB was ±0.143.

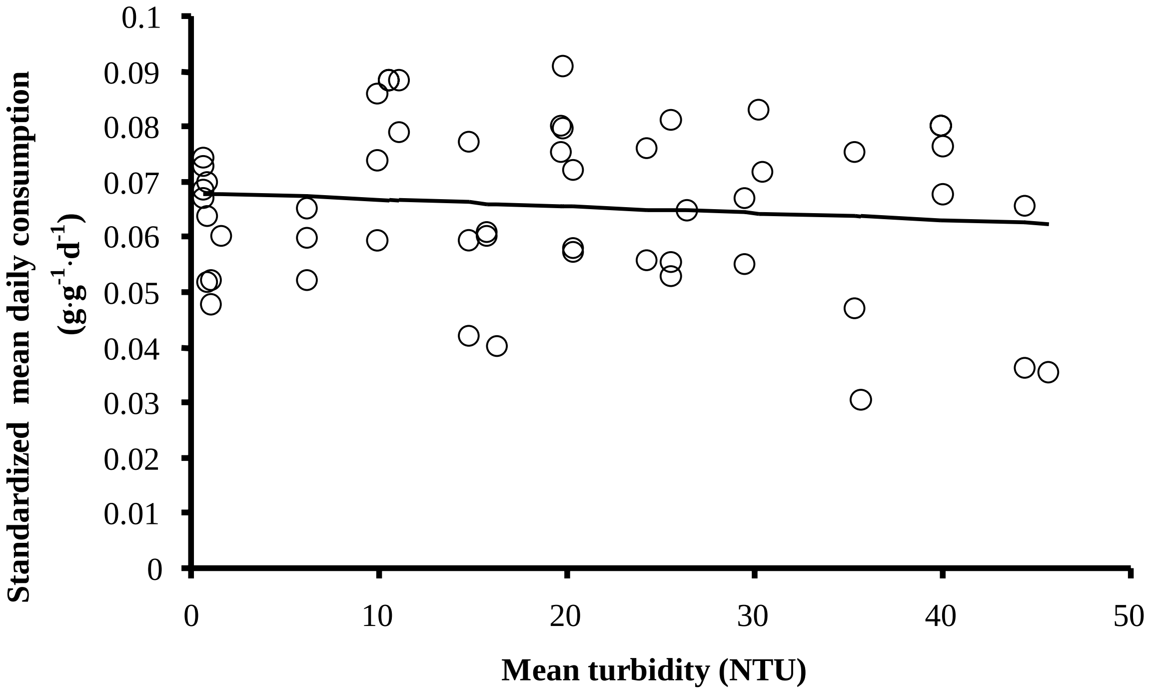

Figure 3. Regression of standardized mean daily consumption values on mean turbidity level for each trial. Turbidity did not have a significant influence on mean daily consumption (F=1.36, p=0.25).

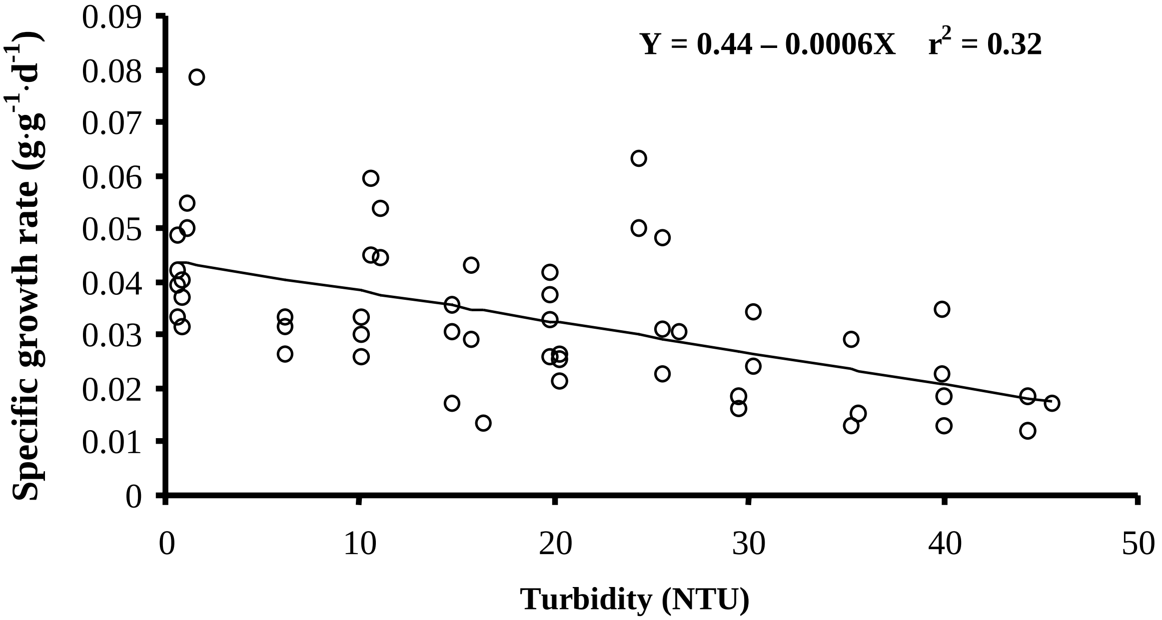

Figure 4. Regression of specific growth rate (Y) standardized on mean trial turbidity (X). Specific growth rates decreased significantly with increasing turbidity (F=23.76, $p<0.01$).

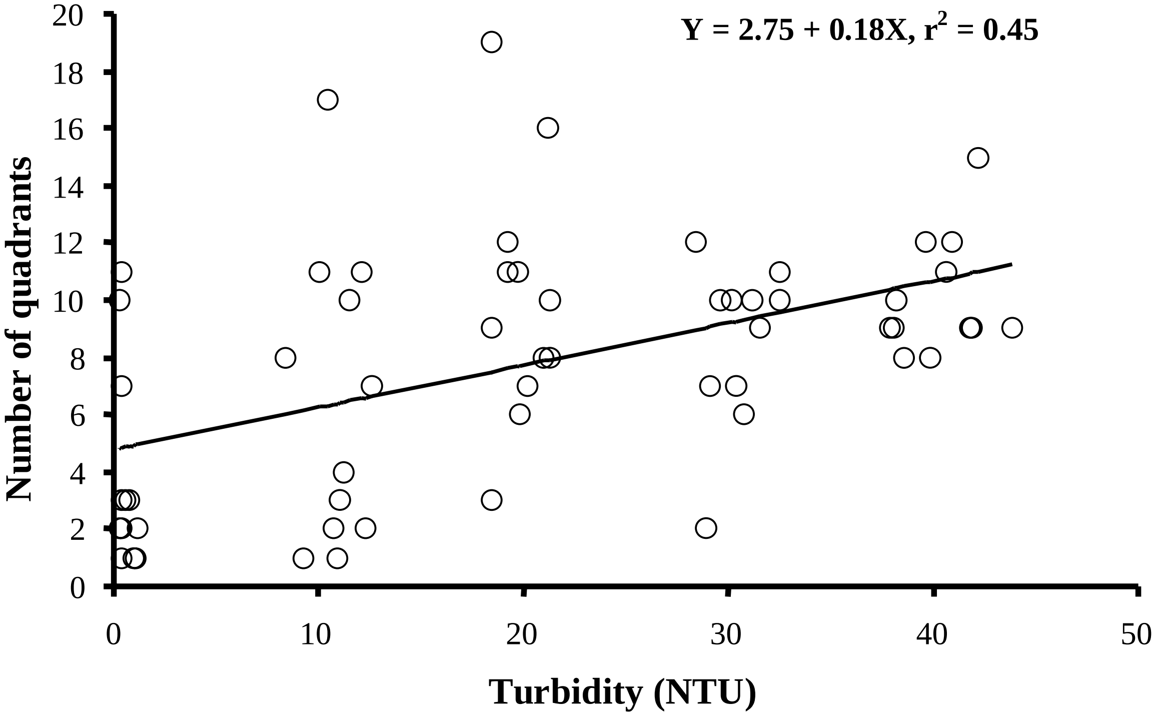

Figure 5. Regression of the number of quadrants used to forage (Y) on turbidity (X). Each point represents the number of quadrants used by brook trout to forage during one taping session. The number of quadrants used to forage within the artificial stream increased significantly as turbidity increased (F=17.31, $p<0.01$).

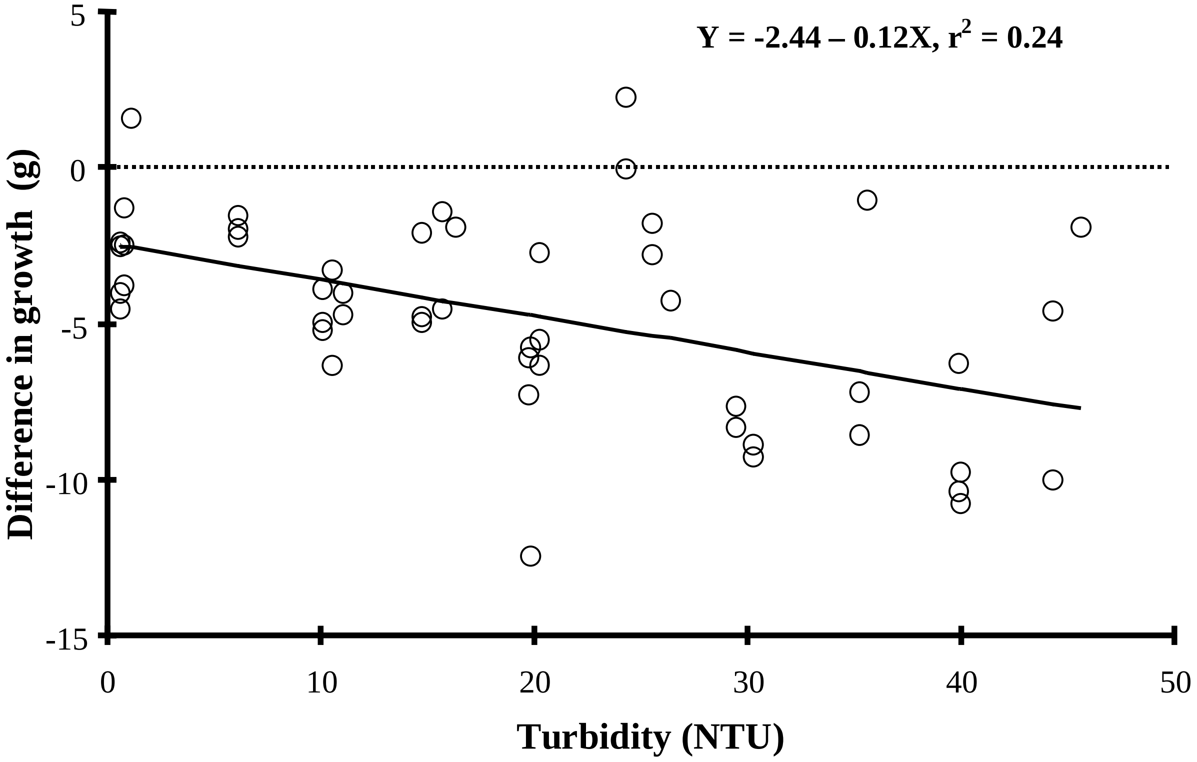

Figure 6. Regression of the difference (Y) in observed trial end weights and those predicted from the bioenergetics model on turbidity (X). As turbidity increased, the difference between observed growth and that predicted by the model increased significantly with observed values being lower than those predicted by the model (F=29.72, p<0.01).

Chapter 3:

Comparison of the Foraging Abilities of Cold and Warmwater Predatory Fish Under Turbid Conditions

Abstract

Turbidity has been shown to impair the feeding abilities of fish and most research has been focused on coldwater species, particularly salmonids. In this study I compared the effects of turbidity on a cold and a warmwater predatory species. Brook trout (*Salvelinus fontinalis*) and smallmouth bass (*Micropterus dolomieu*) were held in an artificial stream to determine how turbidity influenced reactive distance, foraging success, and encounter rates with prey. Because the species were of different size, absolute measures of reactive distance were standardized to mean total lengths. Both species showed a significant decrease in reactive distance, in terms of body lengths, with increasing turbidity and the reactive distance of brook trout decreased at a faster rate than that of the smallmouth bass. With the decrease in reactive distance, the proportion of prey which were recognized by each species also decreased. However, after recognition, turbidity had no influence on the success of foraging attempts. Encounter rates between predator and prey are strongly influenced by reactive distance, and I predict that encounter rates would decrease more rapidly for brook trout than for smallmouth bass with increasing turbidity. This study showed that the foraging abilities of species adapted to cold and warmwater habitats differ in response to increasing turbidity and that turbidity would have a greater

influence on species adapted to clear water conditions than on those adapted to more turbid conditions.

Introduction

Increased sediment loading can have negative impacts on fish production through reduction of available spawning gravel (Davies and Nelson 1993; Hartman et al. 1996) and reduction of invertebrate density. Although relatively large sediment loads may be required to significantly alter stream substrate, small inputs can raise the amount of suspended sediment and markedly increase turbidity (Duchrow and Everhart 1971). Turbidity seldom reaches levels that would be lethal to fish in natural systems, suggesting that its effects result from behavioral responses (Gradall and Swenson 1982).

Effects of turbidity on fish behavior may include avoidance and redistribution, changes in activity, and decreased foraging success. Steelhead (*Onchorynchus mykiss*) and coho salmon (*O. kisutch*) avoid turbid water (Sigler et al. 1984; Bisson and Bilby 1982). Larimore (1975) found that turbidity caused young smallmouth bass (*Micropterus dolomieu*) to be displaced downstream due to the loss of visual orientation. Such avoidance behavior could leave long stream reaches devoid of fish (Waters 1995). Elevated turbidity has been shown to decrease consumption and growth rates of bluegill (*Lepomis machrochirus*), coho salmon, steelhead, and arctic grayling (*Thymallus arcticus*) (Gardner 1981; Berg and Northcote 1985; Sigler et al. 1984; and McLeay et al. 1987). Reduced consumption and growth in fishes under turbid conditions has been attributed to decreased reactive distance with subsequent reduction in predator-prey encounters (Barret et al. 1992; Gardner 1981; Vinyard and O’Brien 1976). However, Gradall and Swenson (1982) found brook trout (*Salvelinus fontinalis*) activity increased under turbid conditions and they hypothesized that this may be a mechanism to promote increased feeding when invertebrate drift would be expected to be high.

More attention has been given to how turbidity effects coldwater species, particularly salmonids, than to how it effects warmwater species (Waters 1995). This may be due to the perception that warmwater streams are generally more turbid than coldwater streams and that their species have evolved mechanisms to deal with chronically turbid conditions (Waters 1995). According to the river continuum concept, species assemblages shift from cold to warmwater species as stream temperature increases with increasing stream order. Also, large rivers may be permanently turbid due to increased suspension of fine particulate organic matter and sediment (Vannote et al. 1980).

In the Appalachians, brook trout and smallmouth bass are top predators in cold and warmwater habitats, respectively. Although information exists in the literature on the effects of turbidity on the foraging ability of other cold and warmwater species, direct comparison under the same experimental conditions is lacking. Thus, the objective of this study was to compare the effects of turbidity on the reactive distance, foraging success, and encounter rates with prey of predatory species representing cold and warmwater habitats.

Methods and Materials

Brook trout and smallmouth bass were held in an artificial stream to determine how turbidity effects reactive distance and foraging success. The fish were tested at sequentially increasing turbidity levels and all feeding trials were videotaped. The video was analyzed to determine reactive distance and foraging success.

Artificial Stream Design.- The artificial stream used to measure reactive distance was a 1.2 x 2.4 m galvanized steel tank (Fig. 1) The tank had a 1.8 m removable baffle installed in the center which separated the tank into two longitudinal sections. Fish were contained in each section by fences of 1 cm^2 mesh galvanized wire fencing material positioned at the upstream and downstream end of each section. This created a viewing area of 1.0 x 0.6 m. The artificial stream was surrounded by a curtain to minimize outside disturbance. Current ($0.06\ m \cdot s^{-1}$) within the artificial stream was created with three powerhead pumps placed in the front of each section.

Water temperatures were maintained at 12.2 ± 0.1 C° (mean ± SE) while testing brook trout and 23.6 ± 0.1 C° while testing smallmouth bass. These temperatures were within optimum ranges for each species (Coutant and DeAngelis 1983; Piper et al. 1982). Water was chilled in a head tank with a 16 amp Firdgid Units® chiller and a 6 amp submersible pump was used to deliver chilled water to the artificial stream.

Fish.- Brook trout were obtained from Bowden State Fish hatchery, Bowden, WV and smallmouth bass were obtained from both a private fish hatchery and from Aarons Creek, Monongalia Co., WV. I used hatchery raised brook trout because wild brook trout were difficult to acclimate to a laboratory environment. No differences were found in the results obtained from hatchery and wild smallmouth bass. Brook trout were 136 ± 2 mm (mean ± SE; range: 113 – 151 mm) and smallmouth bass were 99 ± 2 mm (range: 87 – 115).

My experimental protocol for reactive distance measurement differed from others reported in the literature. Here, three similar sized fish of a species were tested at a time. Other studies have measured reactive distance using only a single fish (Vinyard and O'Brien 1976; Barret et al. 1992). A single fish may not react to a prey item when it is first seen, but may wait until the prey drifts closer to react. This could give an underestimate of maximum reactive distance. By testing three fish at once, a competitive situation was established. The fish first recognizing a potential prey item was at a competitive advantage over the other two by striking at that prey item before it was recognized by the other fish. The result would be a measure of maximum reactive distance.

To begin each experiment, three fish were anesthetized with MS-222, weighed, measured, and placed into one of the viewing portions of the artificial stream. Each set of three fish was given at least twelve hours to acclimate to the artificial stream before testing began.

Videotaping of Foraging Behavior.- Recording of reactive distance and foraging behavior was done with a Sharp E550 view cam. The camera was mounted on the ceiling of the lab, 2 m above the viewing area of the artificial stream. The camera was connected to a computer and the image of the tank and fish could be viewed on the monitor using Media Studio Pro software® while videotaping foraging trials.

Feeding Trials. - Treatment turbidity levels were created using soil obtained from the banks of Roaring Creek, a native brook trout stream in Preston County, WV. The soil was suspended by agitation in a bucket, creating a turbid solution. This solution was added to the head tank until a desired turbidity treatment level was reached in the artificial stream. Turbidity was maintained within ± 3 NTU’s of a target treatment level. A LaMotte 2020 turbidimeter was used to measure turbidity in NTU's.

Brook trout were tested in 15 and 25 cm of water depth while smallmouth bass were tested in only 15 cm water depth. In the first five reactive distance trials for brook trout, the water depth was 25 cm and treatment turbidity levels were approximately 0, 10, 15, 20, and 25 NTU’s. At this depth it was not possible to accurately view the fish at turbidity levels above 25 NTU’s. The water depth was then decreased to 15 cm which enabled continued testing of fish up to approximately 40 NTU’s. There was no difference in maximum brook trout reactive distance between 15 and 25 cm of water depth for treatments levels up to 25 NTU’s (ANCOVA: $F = 0.44$, $p = 0.51$) and the data from both depths was pooled for further analysis.

Feeding trials were conducted with live prey. Housefly larvae (*Musca domestica*) were used as prey items. Larvae were 10.3 ± 0.2 (mean ± SE) mm in length. These larvae were small enough so that a fish could consume several without becoming satiated, yet large enough to be seen with the videocamera. Since the larvae normally sank quickly, air was injected into each before a feeding trial began. Thus, view of both predator and prey could be maintained.

With the light color of the artificial stream, there was not sufficient contrast to allow observation of the light colored prey at low turbidities. To remedy this problem, a black plastic mat (0.8 x 0.6 m) was placed on the tank bottom in the front portion of the viewing area.

A feeding trial lasted approximately 20 minutes during which time housefly larvae were sequentially placed in the viewing area by rinsing them down a delivery tube. Brook trout were offered 25-30 prey items and smallmouth bass were offered 10-15 prey. Fewer prey were offered to the smallmouth bass because of their smaller size compared to brook trout, and I did not want to satiate them which could affect later trials. After each prey item was released, the monitor was observed and the fate of the prey item was recorded. A prey recognition was defined as any action a fish took in reacting or orientating to a prey item. An attack was considered a pursuit of a prey item. If the fish struck and took the prey item into its mouth, it was considered a capture. If after capturing, a fish did not reject the prey item, it was considered an ingestion. The next prey item was not offered until the previous one was either consumed or passed through the back of the viewing area. The proportion of prey items recognized, proportion of recognized prey attacked, proportion of attacked prey captured, and proportion of captured prey ingested was recorded. Unconsumed prey was captured in a net at the rear of the viewing area.

At the end of a feeding trial, turbid water was added to the head tank until the next highest turbidity treatment was reached. Fish were again allowed to acclimate to this treatment for twelve hours, and were then tested again. Two trials, each at a different treatment level, were conducted per day until the final test level was reached. At this time, the fish were removed, anesthetized, and marked by fin clipping to avoid re-testing the same individuals in subsequent trials. The artificial stream and head tank were then prepared for the next set of fish to be tested. I assumed that testing the fish at sequential turbidity levels influenced the results in any way. In a similar study with rainbow trout, Barret et al. (1992) found that sequential application of treatment levels resulted in no difference in reactive distance compared to randomized treatments and this also simplified experimental logistics. One reactive distance trial with brook trout at 0.57 NTU was eliminated from the data set because the brook trout seemed lethargic and did not react readily to prey. This was the first trial in a sequence for this group of fish and they may not have been acclimated to the testing environment. In the following trial at 17.6 NTU's, they did not show any signs of stress and lethargy.

Reactive Distance Estimation. - Feeding video was reviewed and frame capture software (Multimedia Studio Pro®) was used to capture a particular video image at the instant a fish first recognized a prey item. The moment a fish made an indication of recognition of a prey item the image was captured and imported to MS Paint®. At this time marker was placed on the fish and one on the prey item. This documented which fish first recognized the prey item and eliminated any confusion about the location of the prey item in the image. The image was saved for later reactive distance measurement.

Interactive Data Language (IDL 5.0 from Research Systems © 1997) software was used to measure reactive distance. A 20 cm long piece of bright yellow poster board was placed on one of the cross supports of the artificial stream as a reference target (Fig. 1). The IDL program would import a saved image of a predator-prey encounter and would identify the reference target. The distance between fish and prey could be estimated by enumerating the number of pixels along the 20cm length of the reference target.

In testing my method on known lengths within the viewing area, I found that all estimates from the IDL program were 20% lower than actual values because the reference target was closer to the camera lens than objects in the viewing area. Estimates were corrected by the equation $Y = 1.25(X)-.52$ ($R^2=0.98$) where: Y was the actual length, and X was the estimated length (cm). Further testing of this method showed that mean differences between estimated and actual lengths were 0.52 ± 0.3 (± 95% C.I.) cm.

Statistical Analysis.- In the analysis, I only used the maximum reactive distance recorded during each feeding trial because I wanted to establish an upper bound on reactive distance for each species. Data were analyzed with windows based SAS®. I used linear and nonlinear regression to model changes in reactive distance and foraging success with increasing turbidity. Analysis of covariance was used to determine differences between species. Because the brook trout were significantly larger than the smallmouth bass tested (Paired t-test: $t = 12.2$, $p<0.01$), I also compared reactive distances standardized to terms of body length by dividing the maximum reactive distance by the mean total length of each group of three fish in a given trial. In all statistical tests, alpha was set at 0.05.

Results

Reactive Distance.- Absolute maximum reactive distance decreased exponentially with increasing turbidity for both species (ANOVA: F = 286.77, $p < 0.01$) and species were not significantly different (ANCOVA: F = 0.92, p = 0.34) (Figure 2). This decrease was described by the negative exponential model, $R = ae^{(-b \cdot NTU)}$ where: R is the reactive distance, a is the model intercept, and b is the slope and NTU is the turbidity. However, when reactive distance was standardized to terms of body lengths, The rate of decrease was greater for brook trout than for smallmouth bass (ANCOVA: F = 15.37, $p < 0.01$) (Figure 3). Intercepts of the models were similar between species, with overlap of 95% confidence intervals on the parameter estimate, but slopes were different with no overlap of 95% confidence intervals (Table 1).

Foraging Success.- Increasing turbidity had a significant influence on the proportion of prey that were recognized, but had no influence on foraging success after recognition. The proportion of prey items which were recognized decreased significantly for both species (ANOVA: F = 73.44, $p<0.01$), but no difference was found between species (ANCOVA: F = 1.66, p = 0.20) (Figure 4). Once recognized, turbidity had no influence on the proportion of recognized prey attacked (ANOVA: F = 0.01, p = 0.94) and there was no difference between species (ANCOVA: F = 1.49, p = 0.23). During one trial with smallmouth bass at a turbidity treatment level of 0.62 NTU, only 66% of the prey items that were attacked were captured. This resulted in an increase in the proportion of attacked prey captured with increasing turbidity (ANOVA: F = 4.55, p = 0.04). This data point was determined to be an outlier with the maximum normed residual test (MNR test)

($MNR_{14} = 0.695$, $p < 0.01$) and was dropped from the data set. Further analysis showed that turbidity had no influence on the proportion of attacked prey which were captured (ANOVA: F = 2.59, p = 0.11) and there were no differences between species (ANCOVA: F = 0.26, p = 0.61). Finally, turbidity had no influence on the proportion of captured prey which were ingested (ANOVA: F = 3.023, p = 0.09), also with no difference between species (ANCOVA: F = 0.37, p = 0.55).

Predator-Prey Encounter Rates. – The Gerritsen and Strickler (1977) encounter rate model was used to determine encounter rates with prey for both brook trout and smallmouth bass. The encounter rate model is given by the equation:

$$E = ((\pi R^2 N_H)/3)*((v^2+3u^2)/u)$$

where: E is the encounter rate in numbers per second, R is the predator's reactive distance, N_H is the prey density, v is the predator's swimming speed, and u is the prey's swimming speed. Brook trout and smallmouth bass in this study used a drift feeding strategy whereby they captured prey by ambush so v was set to 0. Further, u was set to 0.06 m/s which was the velocity of prey drifting in the artificial stream. The prey density, N_H, was set to that found within the viewing area of the tank during the experiments, 1.38 prey/m^3.

Reactive distance of both species was standardized to the overall mean total length of all fish of both species tested (117.3 mm). This was accomplished by multiplying maximum reactive distance in terms of body length found during each feeding trial by the overall mean length. The standardized reactive distances were then converted to meters for use in the model.

The reactive distance, R, is the highest order variable in the model and thus any change in R produce the greatest relative change in encounter rate. Encounter rates then follow a similar function to that of reactive distance (Fig. 5), $E = Ae^{(-B*NTU)}$ where: E is the encounter rate in numbers per second, A is the intercept of the model, and B is the slope or rate of decrease. Like reactive distance, encounter rates also differed between species (ANCOVA: $F = 5.60$, $p = 0.02$). Model intercepts were similar between species, but slopes were different with a higher rate of decrease for brook trout.

As a means of evaluating trade-offs between increased drift rate and reduced reactive distance at elevated turbidity, the Gerritsen and Strickler (1977) model was solved for prey density (N_H) (Fig. 6). Density must increase exponentially to maintain a constant encounter rate between fish and prey and this increase would have to be greater for fish like brook trout whose reactive distance decreases more rapidly than fish like smallmouth bass. In this analysis, prey density would have to increase by a factor of 125 for brook trout and by a factor of 30 for smallmouth bass in order to maintain the same encounter rates at the highest treatment turbidity levels as in clear water.

Discussion

Reactive Distance. –To make species comparisons, I standardized absolute reactive distance measurements into terms of body lengths due to the difference in size between the brook trout and smallmouth bass tested. Visual resolution in fish increases with fish size as the eye and its components change during postembryonic development (Walton et al. 1992). Visual resolution in bluegill (*Lepomis macrochirus*) has been shown to increase rapidly at small sizes (27-50 mm: standard length) and the rate change diminishes in larger fish (> 50 mm) (Breck and Gitter 1983; Li et al. 1985).

Reactive distance decreased significantly for both species with increasing turbidity. After standardization of reactive distances to body lengths, brook trout and smallmouth bass showed similar reactive distances in clear water. However, with increased turbidity, the reactive distance decreased at a significantly greater rate for brook trout than smallmouth bass. Both species showed a curvilinear relationship between reactive distance and increasing turbidity. Others have also shown reactive distance to decease in a similar manner. Bluegill reactive distance decreases as a curvilinear function with the greatest reduction at low turbidity levels (Vinyard and O'Brien 1976; Miner and Stein 1996). Barret et al. (1992), however, found rainbow trout reactive distance to decrease linearly with increasing turbidity.

Differences in reactive distance, in terms of body length, between species may be accounted for by differences in eye size and morphology. To further explore the relationship of reactive distance with eye size, I measured the eye diameter and total length of a sample of 30 brook trout and 30 small mouth bass of varying lengths encompassing the size range of each species tested. An eye diameter:body length (E:B) ratio was then established for each fish. Regression of E:B ratios on total length showed no change in E:B ratios with increasing fish size for either species (brook trout: $F = 0.40$, $p=0.53$; smallmouth bass: $F=2.45$, $p = 0.13$). Smallmouth bass did, however, have significantly higher mean E:B ratios (0.066 ± 0.001, SE) than did brook trout (0.047 ± 0.001, SE) (paired t-test: $t = 18.05$, $p < 0.01$). Huber and Rylander (1992) suggest that resolving power in fish eyes depends on the number of retinal receptors per visual angle, which is a function of eye size. Thus, differences in reactive distance, in terms of body length, between fish species may be a function of the eye size compared to body length.

Predatory fish feeding under low light conditions possess visual adaptations to such conditions. Walleye (*Stitzostedion vitreum*), which are efficient predators under low light conditions, possess such visual adaptations. These adaptations include a large eye size, arrangement of retinal rods into macroreceptors, and a tapetum lucidium which reflects light back to photoreceptors (Vanderbyllaardt 1991). Trout do not have such adaptations (Vinyard and Yuan 1996). Warmwater streams, of higher stream order are typically more turbid than cold water streams of lower stream order (Waters 1995). Smallmouth bass, which inhabit these warmwater streams, may have evolved some of the same visual adaptations as walleye for feeding under low light conditions. Histological studies of the eye are needed to determine the exact mechanism by which warmwater predatory fish may have greater visual acuity under low light conditions compared to coldwater predatory fish.

Foraging Success. – With the decrease in reactive distance with increasing turbidity, the proportion of prey which were recognized also decreased for both species. Barret et al. (1992) also noted that rainbow trout attacked fewer prey at elevated turbidities. No differences were found between species even though turbidity had less of an influence on smallmouth bass reactive distance in terms of body lengths. If the smallmouth bass had been equal to the brook trout in size, I would expect absolute reactive distance values to be greater than those of brook trout since reactive distance increases with fish size (Li et al. 1985). This would be expected to result in a greater proportion of prey being recognized in turbid water. Absolute measures of reactive distance (in cm) were not significantly different between species (ANCOVA: F = 0.92, p = 0.34) with much overlap in reactive distance models at turbidities greater than 10 NTU's. This accounts for the lack of difference between species in the proportion of prey recognized. After recognition, turbidity had no influence on the foraging success of either species.

Reduced prey consumption by brook trout and smallmouth bass as a result of increasing turbidity was governed by a reduction in the ability to recognize potential prey. Other studies have found reduced consumption and slower growth rates in turbid water than in clear water (Benfield and Minello 1996; Easton et al. 1996; Vinyard and Yuan 1996; Sigler et al. 1984). The consumption rate of gulf killifish (*Fundulus grandis*) on grass shrimp (*Palaemonetes pugio*) decreased 60% when feeding in turbid water of 100 NTU's compared to clear water (Benfield and Minello 1996). In a field study comparing annual variation in juvenile smallmouth bass diets, Easton et al. (1996) attributed reduced stomach fullness of juvenile smallmouth bass during one year to increased frequency of flooding and the resulting turbid conditions. Vinyard and Yaun (1996) found Lahonton cutthroat trout (*Oncorhynchus clarki henshawi*) predation of *Daphinia magna* to decrease linearly with an 80% reduction at 25 NTU's compared to clear water. The growth rates of steelhead (*O. mykiss*) decreased 75% and the growth rates of coho salmon (*O. kisutch*) to decreased 62% when reared in turbid water of 49 NTU compared to those reared in clear water (Sigler et al. 1984). An exception to this general trend was found by Vandenbyllaardt et al. (1991) where juvenile walleye (< 85 mm fork length) consumed more fathead minnows (*Pimephales promelas*) at turbidity levels ranging from 7 to 121 NTU's than in clear water. Walleye are well adapted to feeding under low light conditions compared to other fishes as discussed earlier.

Encounter Rates.- Calculated encounter rates with prey decreased for both species as reactive distance decreased. Under natural conditions of turbidity, invertebrate drift is know to increase through night-active diel drift photoperiodicity (Waters 1995), whereby under conditions of decreased light penetration, invertebrate drift densities increase. This raises the question as to how much of an increase would be necessary to maintain the same encounter rates in turbid water as in clear water. The calculated necessary prey density under turbid conditions would have to be much higher for brook trout than for smallmouth bass (Figure 6). This also point outs the importance of reactive distance in encounter rates with prey. Slight changes in reactive distance result in pronounced effects on encounter rates (Gerritsen and Strickeler 1977). Thus, turbidity would be expected to have a greater influence on potential prey consumption by brook trout than by smallmouth bass.

Conclusions. – Turbidity had significantly different effects on the foraging abilities of brook trout and smallmouth bass. Within a watershed, brook trout are restricted to the headwaters where water temperature are cool enough for their existence. As stream order increases, water temperature increases as the river continuum concept suggests (Vannote et al. 1980). Cold water species, like brook trout, are replaced by warmwater species, such as smallmouth bass, as top predators. Mean turbidity levels also increase with the increase of suspended fine particulate organic material and increases in primary production (Vannote et al. 1980). Here, I have shown how turbidity has a greater influence on a species adapted to clear water conditions, brook trout, than on one which is adapted to more turbid water conditions, smallmouth bass. Although increased sediment loading will have negative impacts on the foraging abilities of predatory fish in all habitats along the river continuum, the effects would likely be greater for fish inhabiting headwater reaches.

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Table 1: Model parameters for brook trout and smallmouth bass for reactive distance standardized to body length. The fitted model was $R = a \cdot e^{(-b \cdot NTU)}$ where: R is the reactive distance in body lengths, a is the model intercept, b is the model slope, and NTU is turbidity. Intercepts were similar between species, but slopes were significantly different with no overlap of 95% confidence intervals.

Species	**Parameter**	**Value**	**Lower 95% C.I.**	**Upper 95% C.I.**	**r^2**
Brook trout	a (Intercept)	6.348	5.818	6.878	0.89
	b (slope)	0.064	0.055	0.072	
Smallmouth bass	a (Intercept)	6.560	6.034	7.085	0.86
	b (slope)	0.046	0.041	0.052	

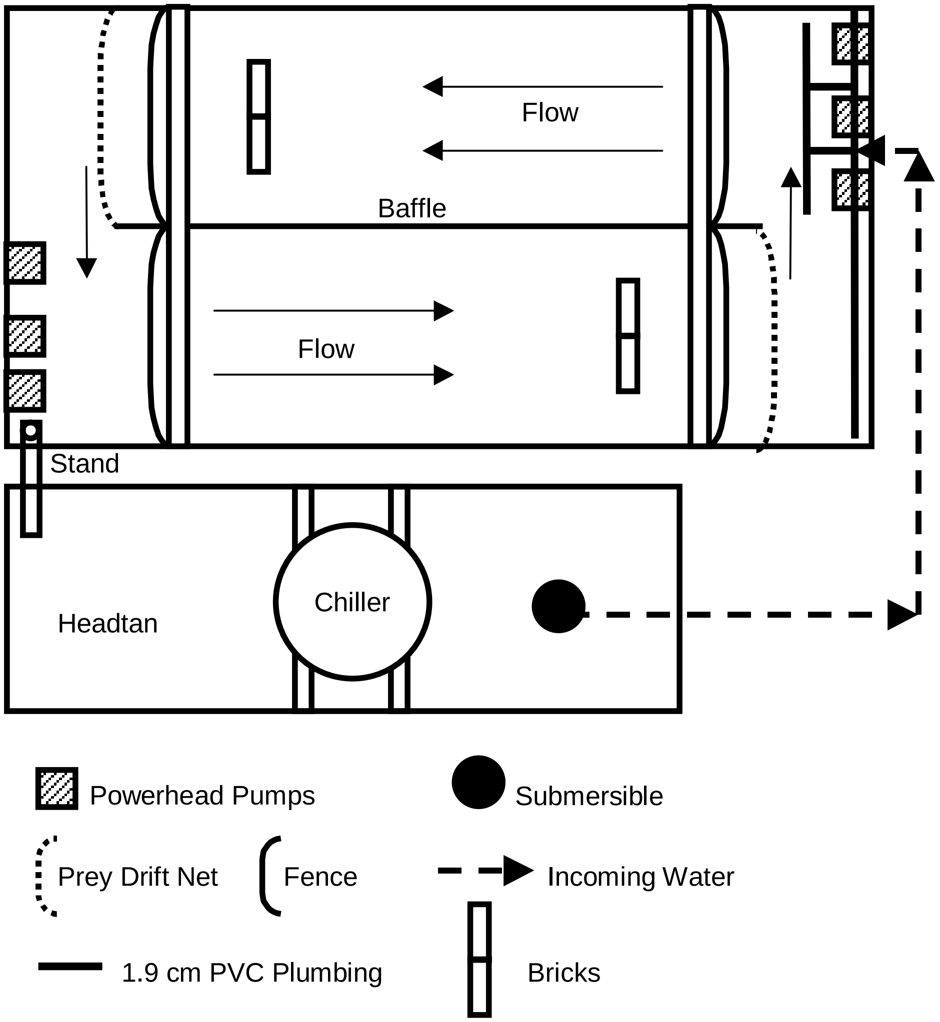

Figure 1. Artificial Stream Design. See Methods and Material – *Artificial Stream Design* for description.

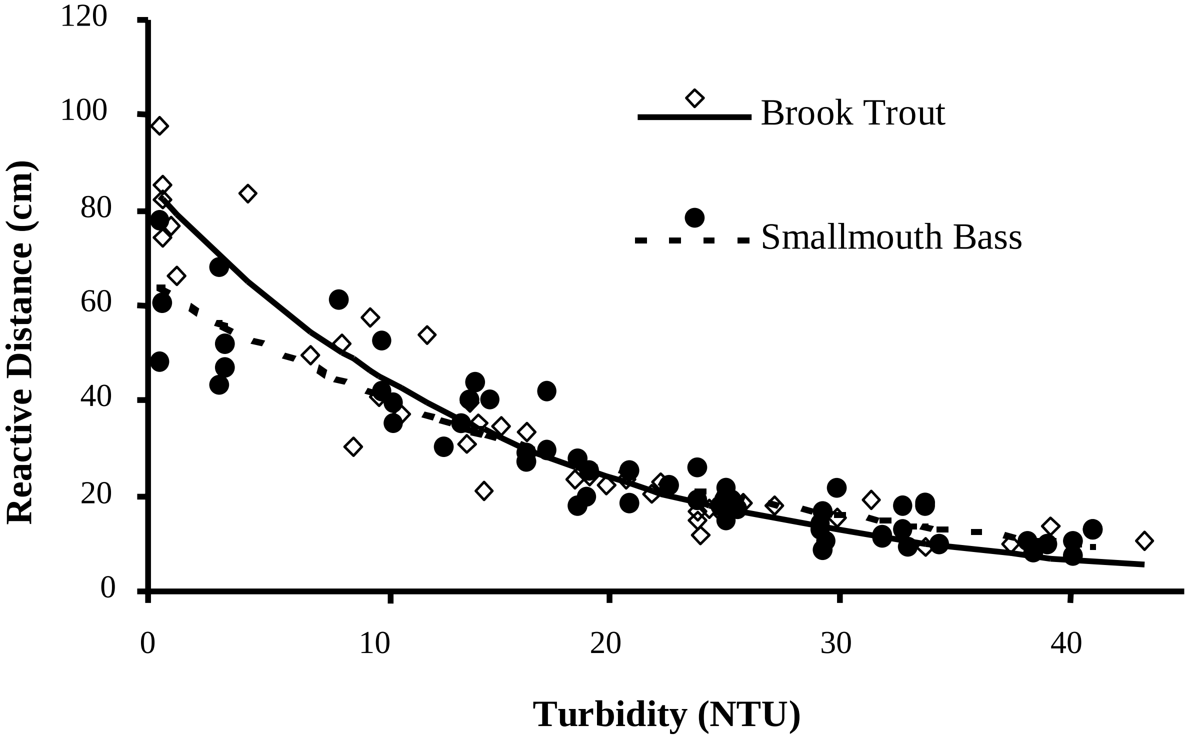

Figure 2. Absolute measures of reactive distance for brook trout and smallmouth bass. Both species showed a significant reduction in reactive distance with increasing turbidity (ANOVA: F= 286.77, $p < 0.01$), but there were no significant differences between species (ANCOVA: F = 0.92, $p < 0.34$).

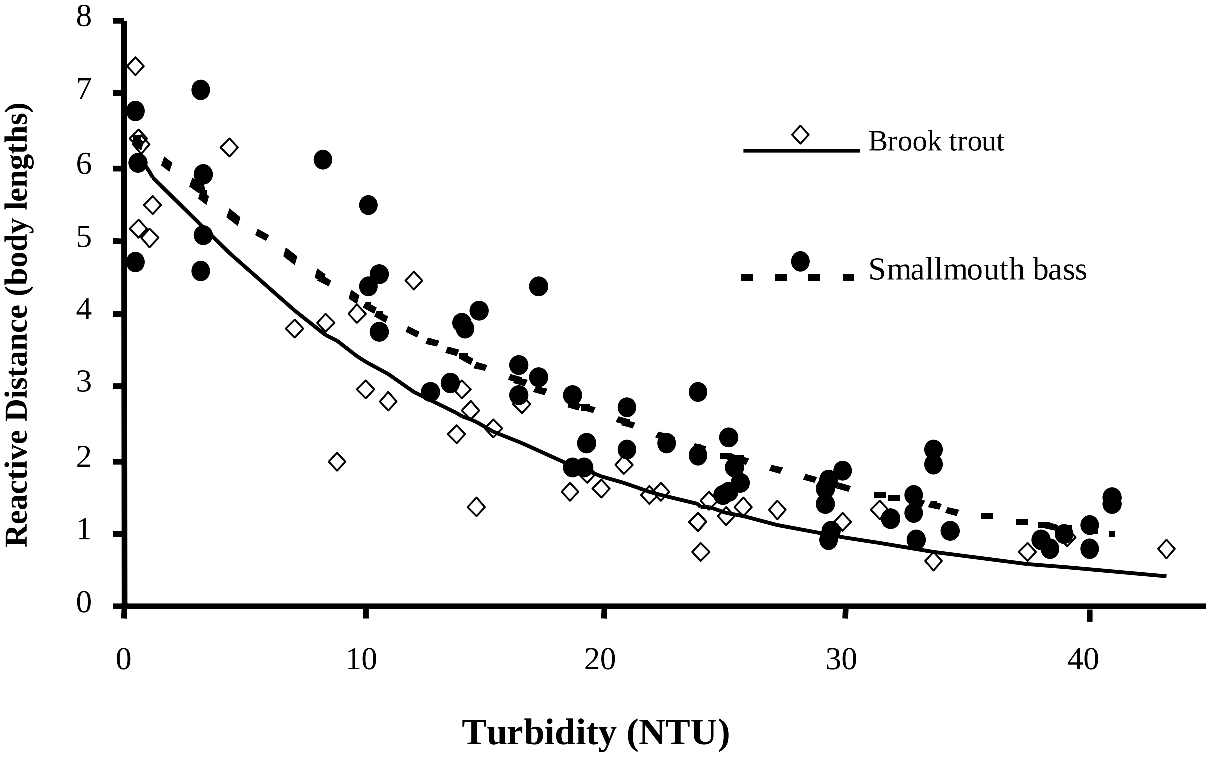

Figure 3. Reactive distance standardized to total body length. In terms of body length, reactive distance decreased at a greater rate for brook trout than for smallmouth bass (ANCOVA: F = 15.37, $p < 0.01$). Intercepts of the models were similar between species, but slopes were different.

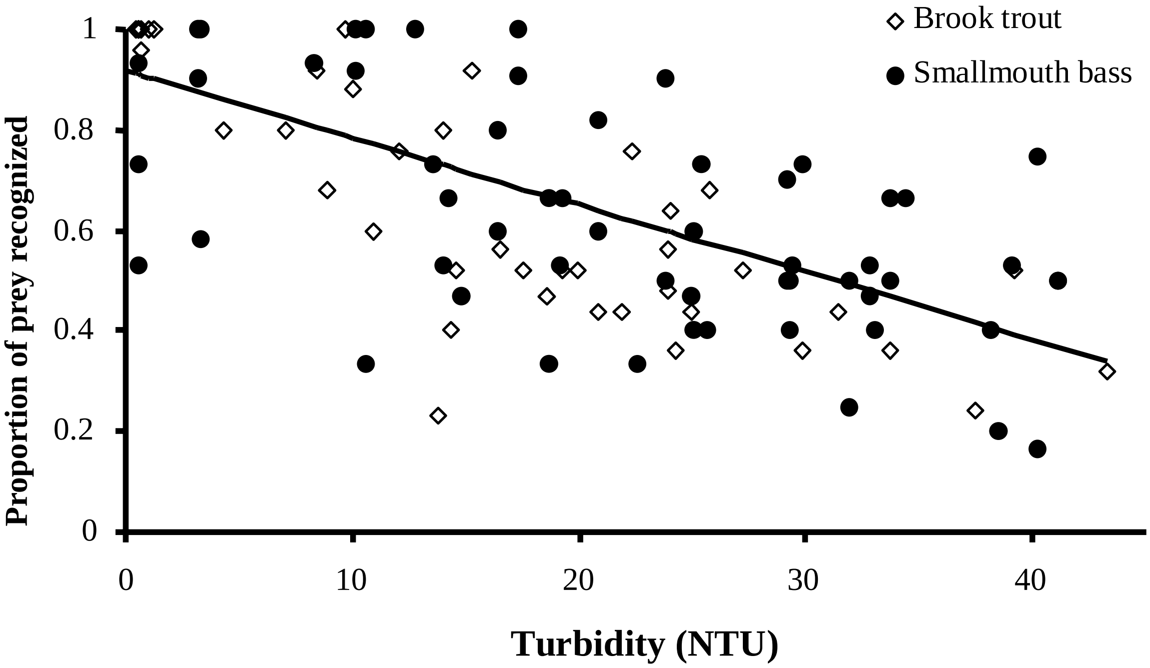

Figure 4. Proportion of prey recognized. The proportion of prey recognized by both species decreased with increasing turbidity (ANOVA: F = 73.45, p <0.01), but there were no differences between species.

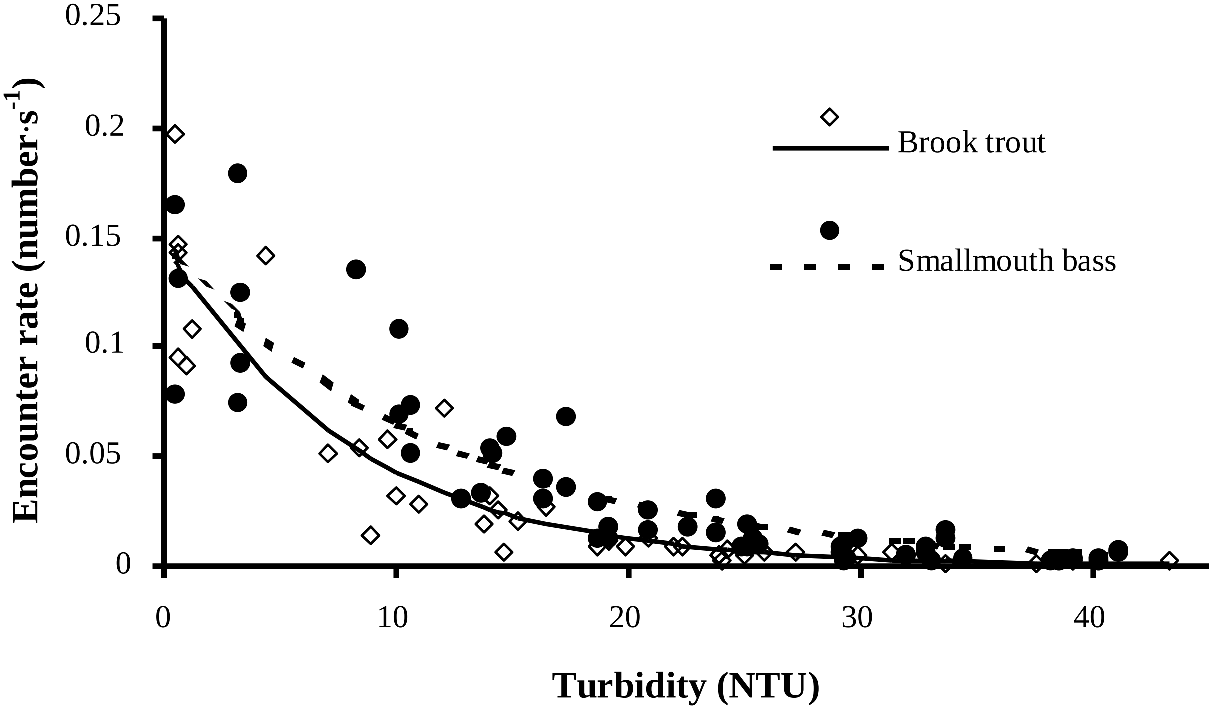

Figure 5. Encounter Rates. Turbidity had a significant influence on encounter rates for both species (ANOVA: F = 169.87, $p < 0.01$), and species were different with a faster rate of decrease for brook trout (ANCOVA: F = 5.60, $p = 0.02$).

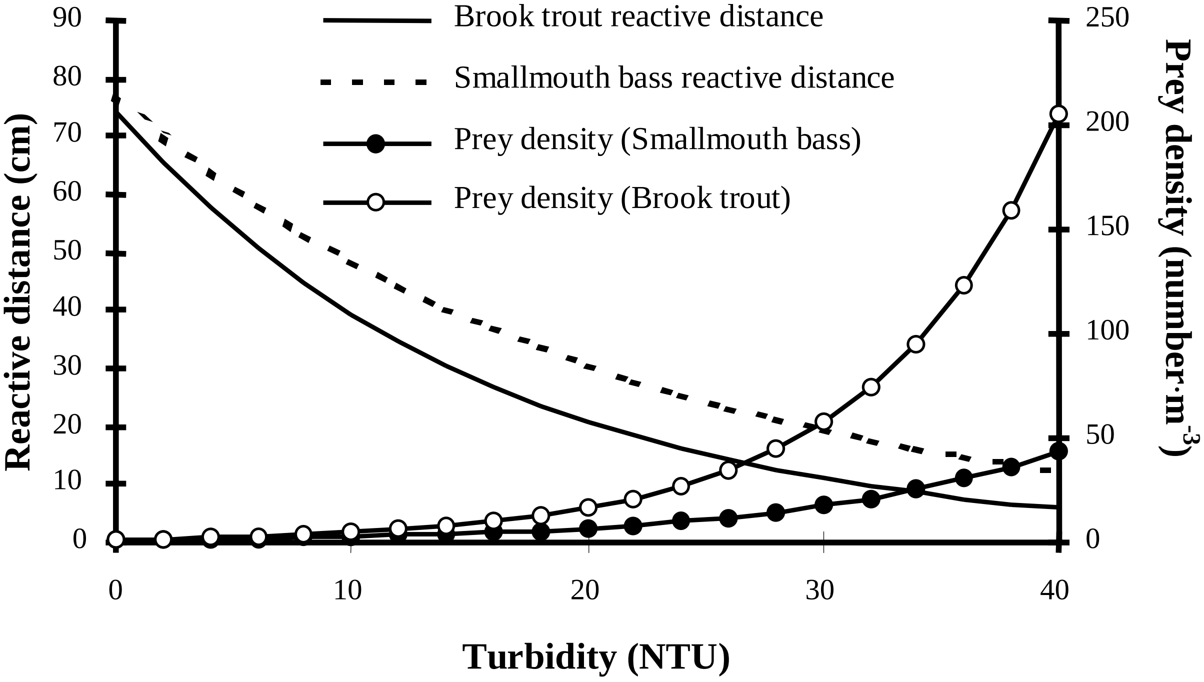

Figure 6. Relationship between reactive distance and the prey density. When reactive distance is standardized to the overall mean total length of all fish tested, brook trout showed a 92% reduction in reactive distance, while smallmouth bass showed an 84% reduction in reactive distance from clear water to the highest treatment level (≈ 40 NTU). Because of the difference between species in reactive distance, prey densities would have to increase by a factor of 125 for brook trout and by a factor of 30 for smallmouth bass in order to maintain the same encounter rates with prey in turbid water as in clear water.

Summary and Conclusions

Brook trout reactive distance decreased exponentially with increasing turbidity and this decrease may alter the taxon selectivity of fish in the field. Here, I have shown that brook trout recognize light colored prey (larval houseflies) at longer distances than dark colored prey (adult houseflies). (Smallmouth bass would not feed readily on adult prey for unknown reasons, therefore my results on the effect of prey color are restricted to brook trout.) In an experiment with various sized *Daphnia pulex* and turbidity levels, Vinyard and O'Brien (1976) found that bluegill (*Lepomis macrochirus*) recognized large individuals at greater distances than small individuals at a given level of turbidity. However, the rate of reactive distance decrease with increasing turbidity was greater for larger prey. In another study with bluegill, Miner and Stein (1993) found that under low-light conditions, bluegill consumed proportionately more large zooplankton. Thus, as turbidity increases, fish may be forced to become more opportunistic foragers by decreasing selectivity and capturing prey which are more readily seen.

The exponential decrease in reactive distance for brook trout was expected to result in decreased daily consumption values through decreased encounter rates with prey. Also, during reactive distance experiments, fewer prey were captured at elevated treatment levels. It was then expected that consumption during the growth and consumption experiments should also decrease and result in a decrease in specific growth rate for brook trout.

Specific growth rates did decrease with elevated turbidity, but not by the expected mechanism, decreased consumption. During consumption and growth experiments, brook trout mean daily consumption was not affected by turbidity, but in order to maintain the same consumption rates in clear as well as turbid water the brook trout switched foraging strategies. The fish typically fed from a single focal point in clear water, but began to actively search for prey in more turbid water. Gradall and Swenson (1982) noted that brook trout became more active in turbid water, which was also the case in these experiments. By increasing the time spent moving, the brook trout increased the chance of encountering each prey item offered. Thus, although turbidity reduced reactive distance, specific growth rates did not decrease due to decreased prey consumption, but rather due to the increased activity associated with capturing each prey item.

Three fish were tested at a time during reactive distance and foraging success experiment, while only one fish was tested at a time during growth and consumption experiments which may explain why fewer prey were recognized and consumed with increasing turbidity during reactive distance and foraging success experiments. While reviewing the reactive distance video, many aggressive interactions between the three brook trout were observed and it appeared that each fish established and defended a territory within the artificial stream. With the decrease in reactive distance at elevated turbidity levels, prey items may have drifted between established territories of the brook trout and went unseen by any one of the three fish. However, when conducting consumption and growth experiments with only one fish at a time, there was no need for the fish to establish a territory, and the single fish could move about the tank without competitive interactions with other fish. Thus, the observed switch in brook trout foraging strategies with elevated turbidity may not only be a function of turbidity, but also a function of predator density.

Marchand and Boisclair (1998) also suggest that consumption rates may be dependent on the density of fish. They conducted enclosure experiments where brook trout were held in 8 m^3 enclosures at densities of four and eight brook trout per enclosure (thus, 1 $fish \cdot m^{-3}$ and 0.5 $fish \cdot m^{-3}$). The fish fed on zooplankton within the enclosures. Zooplankton densities did not differ between experimental groups, but they found that total energy consumption by fish in the four fish enclosures was 15% higher than that of fish in the eight fish enclosures. The density of brook trout in my reactive distance and foraging success experiments was 3 $fish \cdot 0.108\ m^{-3}$ (approximately 27 $fish \cdot m^{-3}$) which would suggest more competitive interactions than those found in Marchand and Boisclair's (1998) study.

Changes in activity can have profound influences on the energy budget of fish. An assumed constant rate of activity, an over-simplification in bioenergetics models, is rarely the case. The work of Boisclair (Boisclair and Legget 1989; Boisclar 1992; and Boisclair and Sirois 1993) addresses the importance of activity in consumption and growth rates of fish and how the Kitchell (1977) bioenergetics model can give biased estimates of prey consumption for actively foraging fish. Boisclair and Legget (1989) point out that the Kitchell (1977) model is a valuable tool when activity costs would be negligible for ambush type predators. However, in the experiments here, the model failed to account for changes in brook trout activity when the fish abandoned a typical drift feeding strategy (an ambush strategy) due to increasing turbidity. As turbidity increased, predicted growth of the brook trout based on total prey consumption less accurate. Consumption rates of fish have been found to increase with an increase in activity (Kerr 1982; Boisclair and Legget 1989) which may help to negate the effects of turbidity.

Typically in nature, turbid episodes are accompanied by increased flow and are short lived in small streams. During such conditions, salmonids seek refuge in areas of lower flow close to the streambed (Pert and Erman 1994) or in areas of more habitat complexity such as those with large woody debris (Harvey 1998). Although more complex habitats may provide refuge, foraging efficiency is decreased in such habitats (Wilzbach et al. 1986). Decreased foraging efficiency within refuge areas coupled with a decrease in visual acuity could result in decreased or even no prey consumption by fish. Upon return of favorable conditions for efficient foraging, compensatory growth (Hayward et al. 1997) could act as a mechanism diminishing the effects of the period of reduced prey consumption during a turbid episode. The results of this study do not account for increased flow, which is commonly seen during turbid events in the field, and further experimentation that combines increased turbidity with increased flow is needed to determine the additive effects of both.

This research has also shown that the effects of turbidity differ between species adapted to different habitats. The rate of decrease for smallmouth bass reactive distance was less than that of brook trout. These results suggest that elevated turbidity may have a greater effect on the foraging abilities of predatory fish found in cold, headwater streams than on those found in warmwater streams of higher order and typically higher natural turbidity (Vannote et al.1980). The observed difference between species may be a function of eye size and its light gathering abilities (Huber and Rylander 1992). Smallmouth bass had a larger eye diameter for a given body length than did brook trout.

Aside from the effects of sediment on the reproductive potential of stream-dwelling fish, sediment can effect fish production through decreased encounter rates with prey. Encounter rates with potential prey are governed by the density of the prey and the reactive distance of the predator (Gerritesen and Strickler 1977). Streams with chronically high turbidity levels will most likely have high bed loads of sediment. The highest production of benthic invertebrates, which are most available to fish as food, occurs in heterogeneous substrate of pebble and cobble riffles (Waters 1995). Increased bed loads of sediment fill the interstitial spaces of such substrate reducing benthic production and the density of prey in the drift. The combined effects of decreased prey abundance in streams with turbidity problems and decreased ability to detect prey during turbid episodes can either decrease the amount of prey consumed, or increase the activity required in capturing a prey item thus decreasing the energetic profit per prey item.

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