

Use of Benthic Prey by Salmonids under Turbid Conditions in a Laboratory Stream

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Abstract.—The negative effect of turbidity on the reactive distance of salmonids has been well established. However, determining the consequences of this relationship for overall feeding success remains problematic, as successful foraging by salmonids across a broad range in turbidity has been observed under a variety of conditions. Previous laboratory and field observations suggest that benthic feeding by salmonids in flowing water affects the turbidity dependence of foraging success. Two experiments were conducted in a laboratory stream to quantify benthic feeding success of salmonids across turbidity treatments ranging from 0 to 400 nephelometric turbidity units (NTU). In one experiment, cutthroat trout *Oncorhynchus clarkii* and coho salmon *O. kisutch* were offered the same nonliving prey in the drift and on the stream bottom; in the second experiment, cutthroat trout were offered only live oligochaetes moving along the stream bottom. In the first experiment, benthic feeding success of both cutthroat trout and coho salmon at 100 NTU was at least 70% of their feeding performance in clear water (i.e., 0 NTU), whereas neither species fed at 400 NTU. In the second experiment, benthic feeding success of cutthroat trout at 150 NTU was about 35% of their performance in clear water but dropped to near 0% at 200 NTU; no feeding was observed at 400 NTU. Passive integrated transponder tag detections suggested that cutthroat trout activity increased over the range of 0–150 NTU. Although drift and benthic foraging success decreased over the examined turbidity range, the results suggest that both cutthroat trout and coho salmon are capable of feeding from the benthos in relatively turbid, flowing water. The importance of this ability for salmonid populations will be influenced by the turbidity regime, food availability patterns, and hydraulic complexity of the systems they occupy.

Various human activities can alter the suspended-sediment regime of surface waters, thereby creating a variety of consequences for aquatic food webs. One specific link of special concern is the effect of elevated turbidity on the foraging success of animals (e.g., salmonids) that partially rely on visual cues for feeding. Support for this concern comes from experiments documenting negative relationships between turbidity and (1) the distance at which salmonids react to prey in the water column (e.g., Barrett et al. 1992; Gregory and Northcote 1993; Vogel and Beauchamp 1999; Sweka and Hartman 2001a); (2) prey consumption by salmonids (DeRobertis et al. 2003); and (3) salmonid growth (Sigler et al. 1984; Shaw and Richardson 2001; Sweka and Hartman 2001b).

Under some conditions, however, salmonids appear able to at least partially mitigate the strong effect of turbidity on the visual detection of prey. Several laboratory experiments involving various floating, planktonic, and benthic prey have revealed no strong relationship between salmonid foraging success and turbidity (Sweka and Hartman 2001b; DeRobertis et al. 2003; Rowe et al. 2003) or have reported greater

foraging success in elevated turbidity than in clear water (Gregory and Northcote 1993). Most laboratory observations of nonsignificant or positive turbidity effects on fish foraging success have come from experiments with standing water. However, Sweka and Hartman (2001b) observed that brook trout *Salvelinus fontinalis* in a laboratory stream with modest water velocity (6 cm/s) were able to maintain foraging success on floating prey over a turbidity range from 0 to 40 nephelometric turbidity units (NTU); however, greater activity associated with foraging at the higher turbidity levels resulted in lower growth rates. Field observations of gut fullness (Arndt et al. 2002; White and Harvey 2007) have not detected strong differences in foraging success for salmonids in streams during relatively turbid (~25–75 NTU) versus relatively clear water conditions, but variation in food availability probably influenced these results.

Previous research has left unanswered questions about the foraging abilities of salmonids in turbid, flowing water. Laboratory observations of successful benthic feeding in highly turbid, standing water (e.g., Rowe et al. 2003, who observed rainbow trout *Oncorhynchus mykiss* feeding on benthic chironomid larvae at turbidity levels up to 320 NTU) and field observations of feeding from the benthos under turbid stream conditions (Tippets and Moyle 1978) suggest that the ability of salmonids to feed from or near the

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stream bottom in flowing water deserves additional study. In this study, we first quantified foraging success of cutthroat trout *O. clarkii* and coho salmon *O. kisutch* offered both drifting and benthic prey across turbidity levels ranging from 0 to 400 NTU. After observing consumption of oligochaetes by salmonids under high-streamflow, high-turbidity conditions in natural streams (White and Harvey 2007), we conducted a second experiment to quantify cutthroat trout success in foraging for oligochaetes moving along the stream bottom at turbidity levels of up to 400 NTU.

Methods

Laboratory stream and study animals.—To explore the effects of turbidity on foraging success with an emphasis on benthic or near-benthic prey under lotic conditions, we conducted two experiments in a laboratory stream. The stream was a 75-cm-wide channel configured in a recirculating rectangle (4.00 m long \times 2.75 m wide). Water depth was 50 cm, and velocity in the middle of the water column ranged from 15 to 25 cm/s. Chillers maintained water temperature between 9°C and 13°C (mean = 11.3°C). Cutthroat trout used for both experiments were collected by backpack electrofishing in Tectah Creek, a tributary to the lower Klamath River in Del Norte County, California. We obtained coho salmon for experiment 1 from Rock Creek Hatchery, Oregon. We held the fish in a pair of 625-L circular tanks before each experiment. While in holding, fish received an ad libitum ration of dry trout pellets and various frozen fish foods.

Fish handling procedures were similar for both experiments. Several days before beginning an experiment, we measured each fish and inserted a passive integrated transponder (PIT) tag into its body cavity. Before each feeding trial, fish were acclimated to treatment turbidity levels for 18–24 h in holding tanks that shared a water source with the laboratory stream. We withheld food during the acclimation period to standardize hunger. Before each trial, individual fish were allowed 15 min for acclimation in the experimental arena. After completing each trial, we collected stomach contents by gastric lavage, returned each fish to the holding tanks, and administered an ad libitum feeding. Individual fish were tested at all treatment levels; we allowed individuals a minimum of 48 h for recovery between trials.

We manipulated turbidity by using material collected from an exposed bank of a local stream. We created slurries of this material by agitating several liters of the soil in 20-L buckets filled with water. We then added the solution to the artificial stream to achieve the desired turbidity treatments as measured by a DTS-12

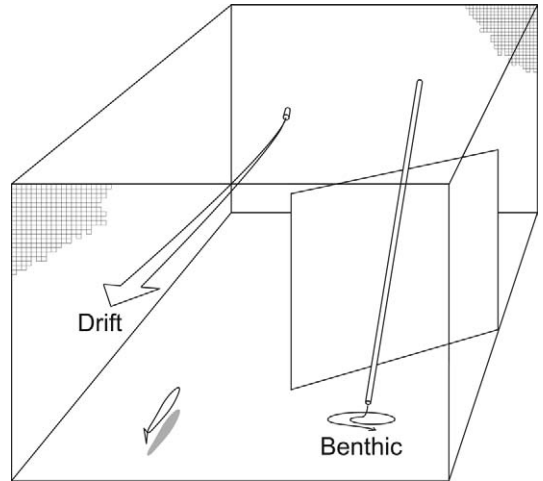


FIGURE 1.—Schematic diagram of the arena in a laboratory stream used to measure the influence of turbidity on drift and benthic foraging success of juvenile cutthroat trout and coho salmon.

turbidity sensor (FTS, Inc., Blaine, Washington). Water movement in the stream kept most of the fine sediment suspended. Turbidity was monitored continuously during all trials. We maintained treatment levels by adding more suspended sediment or sweeping the bottom of the stream with a broom. Within-trial mean turbidity differed from desired treatment values by an average of 3.4%.

Experiment 1.—In the first experiment, individual cutthroat trout ($n = 13$, mean fork length [FL] = 81 mm, range = 71–95 mm) and young-of-the-year (age-0) coho salmon ($n = 14$, mean FL = 78 mm, range = 69–85 mm) were given two feeding options: water column drift and benthic prey. Each fish completed two 15-min feeding trials at each of six turbidity levels (0, 25, 50, 100, 200, and 400 NTU) in a 1-m-long experimental arena. We selected treatment levels to include turbidities that would address the steep gradient in reactive distance to drifting prey observed in previous studies (in the range of 0–50 NTU; e.g., Sweka and Hartman 2001a) and to include the higher-turbidity levels that were anticipated to capture the upper limits of benthic feeding. Treatments were ordered haphazardly (0, 25, 100, 400, 200, and finally 50 NTU). Plastic-mesh fences established the upstream and downstream boundaries of the arena and a deflector on one side created a velocity shelter (Figure 1). The dark-green fiberglass bottom of the stream served as the substratum for this experiment. The arena was illuminated by a 100-W incandescent reflector light suspended 1.25 m above the water's surface and natural light through windows on two sides of the

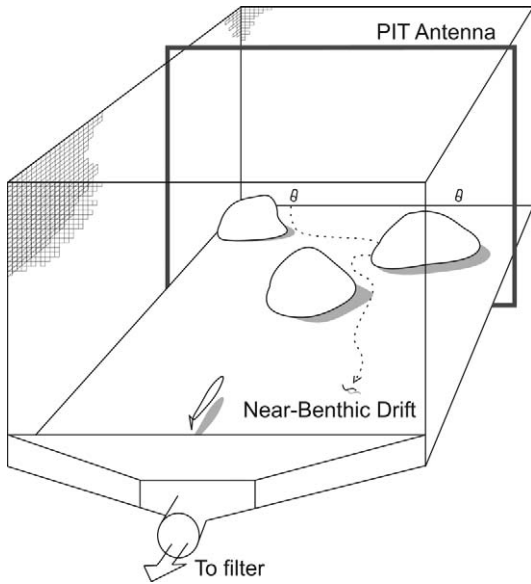


FIGURE 2.—Schematic diagram of the arena in a laboratory stream used to measure the influence of turbidity on juvenile cutthroat trout acquisition of mobile, near-benthic prey (oligochaetes). Fish were passive integrated transponder (PIT) tagged, and the antenna was used to detect fish activity during the trials.

stream, which together provided about 280 lx (International Commission on Illumination photopic spectrum) at the surface of the water. Two black-plastic panels (40×15 cm) placed just above the water's surface in the rear corners of the arena provided overhead cover for fish.

Both drifting and benthic food consisted of thawed, neutrally buoyant, 2-mm-long pieces of frozen mysid shrimp. To distinguish the two prey sources in diet samples, we randomly selected in each trial either drifting or benthic prey for staining with tetracycline solution. Drifting food was introduced through a tube situated 20 cm off the bottom at the front fence (on the side opposite the deflector wall), and the food passed through the unit at 20–25 cm/s. Uneaten drifting food passed through the rear enclosure fence and was collected on fine-mesh screens downstream of the arena. Benthic food was introduced behind the deflector wall via a tube located 2 cm off the bottom. Benthic food normally remained on the bottom until eaten or until the trial ended; sometimes the benthic food swirled in small eddies. Occasionally, benthic prey became entrained in the current and were quickly washed from the experimental arena. Because this process occurred near the downstream end of the enclosure, benthic prey entrained in the current were unlikely to have been consumed as drift. Five drifting

and five benthic prey items were introduced through the feeding tubes at randomly selected times during each 15-min trial, with the constraint that deliveries of individual items were separated by at least 5 s. At the end of a trial, we removed fish from the experimental arena with a dip net, anesthetized them with CO_2 , collected stomach contents by gastric lavage, enumerated the consumed prey, and identified the prey source (drift or benthos) by inspecting each item under ultraviolet light. Before beginning another trial, we thoroughly swept the arena with a fine-mesh dip net to collect any uneaten benthic food and cleaned the downstream collector screens.

We analyzed experiment 1 as a two-factor experiment (turbidity and fish species) with repeated measures on one factor (turbidity). We separately analyzed drift and benthic feeding success and explored their relationship by analyzing within-trial differences. Inspection of variation within treatment combinations indicated no need for data transformation.

Experiment 2.—The second experiment challenged juvenile cutthroat trout ($n = 18$, mean FL = 116 mm, range 98–136 mm) to feed on live oligochaetes that tumbled along the stream bottom (coho salmon were not available for this experiment). Each fish in the experiment completed two 10-min feeding trials—one with bare sand substrate and one with three cobbles added to the upstream end of the arena to increase habitat complexity—at each of six turbidity levels from 0 to 400 NTU. Turbidity levels were the same as in experiment 1 except that a 150-NTU treatment was used instead of the 25-NTU treatment. We made this change because experiment 1 suggested a sharp decline in benthic feeding success between 100 and 200 NTU. To reduce confounding of turbidity treatments and treatment history, two groups of fish were subjected to the treatments in different sequences (group A: 0, 200, 50, 100, 150, and 400 NTU; group B: 200, 50, 100, 150, 400, and 0 NTU). Within a turbidity level treatment, we assigned the initial substratum treatment at random and completed feeding trials for all fish before switching to the other substratum treatment. For this experiment, we fabricated a 1-m-long, 0.6-m-wide arena with plastic-mesh front, back, and sides and a solid bottom (Figure 2). The entire arena was suspended so that it could be lifted nearly out of the stream to facilitate capture and removal of fish. A combination of natural and artificial light yielded 280 lx at the water's surface. A black-plastic panel (20×40 cm) located just above the water's surface at the rear of the arena provided overhead cover for fish.

We used live oligochaetes (25–50 mm total length) as the prey item in experiment 2. The worms were

slightly negatively buoyant and tumbled along the bottom with the current at 10–15 cm/s. Unlike the smaller prey items in experiment 1, uneaten worms did not pass readily through the mesh at the downstream end of the arena. Therefore, we constructed a broad funnel that spanned the lower 4 cm of the rear fence and attached it to a pump and filter to remove uneaten worms from the arena. We introduced worms through two tubes placed 2 cm off the bottom along the front enclosure fence. In each 10-min trial, five worms were dispensed at randomly selected times through randomly selected tubes, again with a 5-s minimum separation between deliveries. Oligochaetes required 140 s on average to pass through the experimental unit. At the end of a trial, we raised the arena, removed the fish and collected the stomach contents using gastric lavage. Before beginning another trial, we thoroughly swept the arena with a fine-mesh dip net to collect any uneaten worms.

We installed a PIT tag antenna (Figure 2) to provide information on fish activity and position in experiment 2. The antenna registered tag detections when fish occupied the upstream half of the experimental arena. As a measure of fish activity, we quantified the number of detections that were separated from the previous detection by at least 4 s. This 4-s separation between detections was selected to balance (1) the goal of minimizing inclusion of distinct detections that occurred with little or no fish movement and (2) the goal of minimizing exclusion of distinct detections that reflected notable fish movement.

Feeding success data were assessed using a repeated-measures analysis of variance (ANOVA) with group as an among-subject factor and turbidity and substrate as within-subject factors. We also evaluated all interactions between and among turbidity, substrate, and group. Proportional data were arcsine-square root transformed. Tag detection data were analyzed with the same statistical approach but did not require transformation.

Results

Experiment 1

For both cutthroat trout and coho salmon, turbidity affected foraging success differently for drifting versus benthic prey (Figure 3). Fish exploited both sources of food in clear water, usually by maintaining position in the water column near the downstream end of the arena and making forays to capture either drifting or benthic prey. Consumption of drifting prey fell sharply as turbidity increased from 0 to 50 NTU but remained above zero (feeding success = 14% for cutthroat trout, 8% for coho salmon) at 100-NTU turbidity. Benthic foraging success for both species generally exceeded

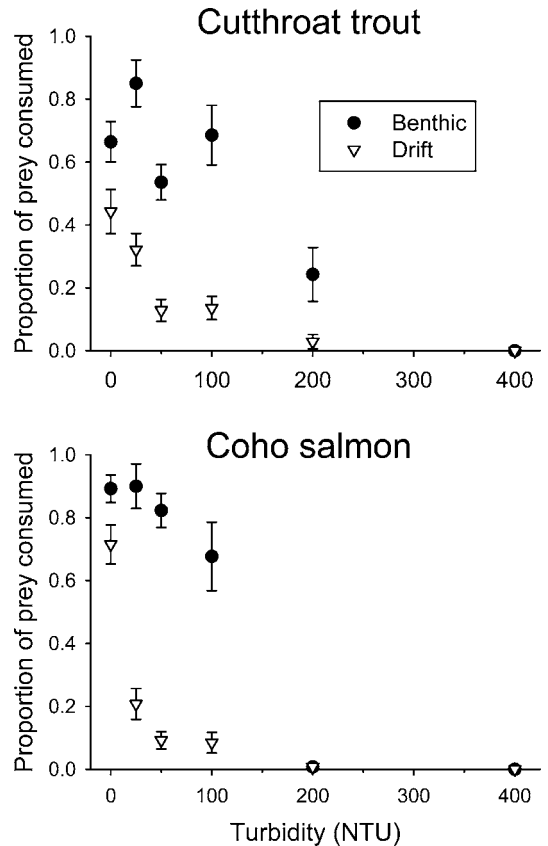


FIGURE 3.—Mean (\pm SE) feeding success (proportion of prey consumed) for cutthroat trout and coho salmon that were offered both drifting and benthic prey during 15-min trials across six turbidity treatments (in nephelometric turbidity units [NTU]) within a laboratory stream (experiment 1).

50% in the range of 0–100 NTU. However, relatively low benthic foraging success was observed for cutthroat trout at 50 NTU; this resulted from anomalously low success (30%) on one date (feeding success was >80% for the other 3 dates). Lacking any apparent explanation for the pattern, we did not exclude those data from the analyses. Some fish foraged from the benthos at 200 NTU, particularly cutthroat trout (Figure 3; Table 1), but neither species consumed prey in the 400-NTU treatment.

The ANOVA highlighted the significance of turbidity for both drift and benthic foraging success ($F = 37.8$; $df = 4, 100$; both $P < 0.001$). The turbidity factor had four degrees of freedom because we excluded the 400-NTU treatment from analysis due to the 0% feeding success. Although species was not a significant factor in either drift or benthic foraging success ($F = 1.7$; $df = 1, 25$; both $P > 0.20$), a significant species \times

TABLE 1.—Percentage of juvenile salmonids that consumed prey presented in a laboratory stream at different turbidity levels (in nephelometric turbidity units [NTU]) during two experiments. Experiment 1 percentages include coho salmon and cutthroat trout that fed on drifting prey, benthic prey, or both. Experiment 2 percentages describe only cutthroat trout consumption of live oligochaetes that moved along the bottom.

| Turbidity (NTU) | Experiment 1 | | Experiment 2 (cutthroat trout only) |
|-----------------|--------------|-----------------|-------------------------------------|
| | Coho salmon | Cutthroat trout | |
| 0 | 100 | 100 | 93 |
| 25 | 100 | 100 | |
| 50 | 100 | 100 | 68 |
| 100 | 85 | 93 | 68 |
| 150 | | | 70 |
| 200 | 8 | 57 | 13 |
| 400 | 0 | 0 | 0 |

turbidity level interaction was indicated ($F = 4.8$; $df = 4, 100$; $P < 0.002$ for both drift and benthic foraging success). Inspection of Figure 3 reveals that the interspecific difference was largest for drifting prey in clear water; coho salmon foraged on drift more successfully than did cutthroat trout under 0-NTU conditions.

Finally, for experiment 1, analysis of the difference between benthic and drift feeding also revealed a strong turbidity effect ($F = 24.5$; $df = 4, 100$; $P < 0.001$) and a significant species \times turbidity interaction ($F = 4.6$; $df = 4, 100$; $P = 0.002$). The significant interaction term reflects interspecific variation in the difference between benthic and drift feeding success at 25, 50, and 100 NTU, which were greater for coho salmon than for cutthroat trout (Figure 3).

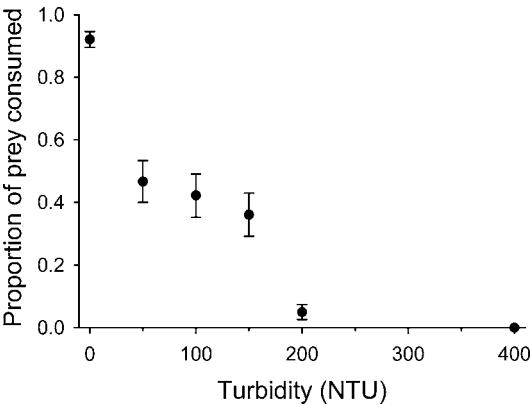


FIGURE 4.—Mean (\pm SE) feeding success (proportion of prey consumed) for cutthroat trout that were offered live, mobile oligochaetes during 10-min trials across six turbidity treatments (in nephelometric turbidity units [NTU]) within a laboratory stream (experiment 2).

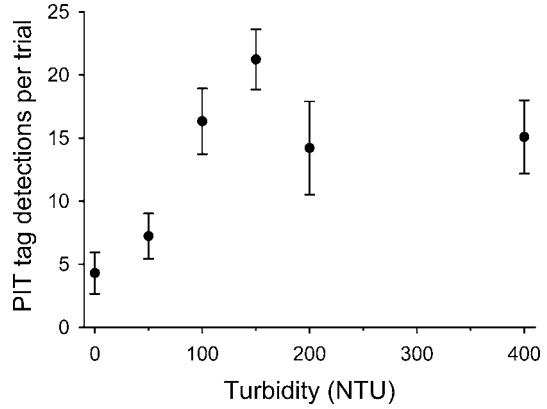


FIGURE 5.—Mean (\pm SE) number of passive integrated transponder (PIT) tag detections (those separated by >4 s) for individual cutthroat trout monitored during 10-min foraging trials across six turbidity treatments (in nephelometric turbidity units [NTU]) within a laboratory stream (experiment 2).

Experiment 2

Turbidity strongly influenced the foraging success of cutthroat trout feeding on oligochaetes tumbling along the stream bottom (Figure 4). In clear water, fish consistently captured almost all available prey. In this treatment, fish usually held a position near the downstream end of the experimental arena and made forays of up to 50 cm to capture prey. Fish had moderate feeding success at turbidity levels of 50–150 NTU, near-zero success in the 200-NTU treatment, and no prey captures in the 400-NTU treatment (Table 1).

The ANOVA revealed the significant effect of turbidity on foraging success ($F = 42.4$; $df = 4, 137$; $P < 0.001$), but no other factor was significant ($P > 0.05$). For group B foraging over complex substrate at 0 NTU (1 of 24 group \times substrate \times turbidity treatment combinations), most of the earthworms delivered to the arena became lodged on the substrate near the arena’s upstream end, where they were found at the end of the trials. The spurious results from that treatment combination were therefore excluded from the analysis. We also excluded the results of the 400-NTU treatment.

Patterns in PIT tag detection indicated differences in the behavior of cutthroat trout across turbidity treatments. Fish in clear water rarely moved to the upstream end of the experimental arena. However, under turbid conditions, the fish occupied the upper portion of the arena more frequently and were more active (Figure 5). The ANOVA clearly indicated the influence of turbidity on tag detections ($F = 6.8$; $df = 5, 162$; $P < 0.001$), but group, substrate, and the various

interaction effects were not significant. This analysis excluded the treatment combination noted above (group B foraging over complex substrate at 0 NTU), and data were missing for seven other combinations of group, turbidity, and substrate because of problems with the apparatus.

Discussion

The decline in drift feeding success with increasing turbidity in experiment 1 generally parallels the documented decline in reactive distance of drift-feeding salmonids as turbidity increases (Barrett et al. 1992; Sweka and Hartman 2001a). However, coho salmon and cutthroat trout had slightly greater drift feeding success at 50 and 100 NTU than would be predicted from extrapolations of the relationship between reactive distance and turbidity at 0–40 NTU (Barrett et al. 1992; Sweka and Hartman 2001a). A strong link between drift feeding success and reactive distance should be expected when water velocity prevents fish from having lengthy encounters with individual prey items, as in experiment 1. Our results obtained under relatively high velocity contrasted with those of previous studies in standing or slow-moving water, where elevated turbidity had no effect (Sweka and Hartman 2001b) or a positive effect (Gregory and Northcote 1993) on salmonid foraging success. Both visual and nonvisual cues may have contributed to drift feeding success at 50 and 100 NTU. Gregory and Northcote (1993) found that Chinook salmon *O. tshawytscha* reacted to the visual cues from live prey in turbid (100-NTU), standing water; Rowe et al. (2003) documented that rainbow trout fed on live chironomid larvae in total darkness. Although offering both drifting and benthic prey within single trials may have led to underestimation of the ability of fish to feed on either prey type, fish in our study clearly did not specialize on one prey type while feeding at 0–100 NTU. The relatively slow rate of food delivery during the trials probably influenced this result.

In contrast to the results for drift feeding, turbidity in the range of 50–100 NTU did not severely inhibit benthic feeding by juvenile salmonids in experiment 1. These results generally correspond to those reported for juvenile Chinook salmon in turbidity treatments of 35, 70, and 150 NTU in aquaria (Gregory and Northcote 1993), where fish fed on live *Tubifex* given the opportunity to burrow into a glass-bead substratum. However, results for benthic feeding from our experiment 1 and the study by Gregory and Northcote (1993) revealed a greater turbidity effect above about 100 NTU than was observed in another study that included benthic feeding by rainbow trout on live prey in standing water (Rowe et al. 2003). In the latter study,

feeding rates on two kinds of benthic prey occupying flat surfaces were unaffected by turbidity of 0–320 NTU, although size selectivity for one prey type (mayfly larvae) was affected at higher turbidity levels.

Several factors probably contribute to the variation in these examples of salmonids feeding on benthic prey in turbid, standing water or on benthic prey exhibiting little or no movement in flowing water (experiment 1). These factors include the use of different prey, variation in the complexity of the substratum, and possibly interspecific differences in feeding capability. Experiment 1 provides some evidence for the last factor in that some differences were detected, mainly greater drift feeding success by coho salmon in clear water and greater benthic feeding success by cutthroat trout in the 200-NTU treatment. However, because the individuals of the two species used in our experiment had very different histories (wild cutthroat trout versus hatchery coho salmon), we cannot conclude that results of the experiment reflect consistent interspecific differences. The general similarity in patterns for the two species probably deserves greater emphasis.

Experiment 2 included live, mobile, near-benthic prey in an attempt to approach natural conditions more closely than in experiment 1. Lower feeding success on benthic prey in experiment 2 than in experiment 1 at 50 and 100 NTU is probably explained by prey movement. However, the ability of cutthroat trout to feed on mobile, near-benthic oligochaetes under 50-, 100-, and 150-NTU conditions could be valuable in the wild. These results correspond with field observations that oligochaetes can be an important component of trout diets under high-streamflow, high-turbidity conditions (White and Harvey 2007).

Experiment 2 also yielded a pattern of increasing activity by juvenile cutthroat trout as turbidity increased from 0 to 150 NTU. This result extends the relationship between salmonid activity and turbidity documented for brook trout over the turbidity range of 0–40 NTU (Sweka and Hartman 2001b) and in treatments of less than 10 NTU (Gradall and Swenson 1982). In experiment 2, the energetic cost of increased activity compounded the reduced feeding success at 50–150 NTU relative to the costs and benefits of feeding in clear water. Although increasing activity to increase encounter rates with prey under turbid conditions is a logical explanation for the results of experiment 2 (Sweka and Hartman 2001b), increasing activity with increasing turbidity might also result from the perception of lower predation risk (Gregory 1993; Sweka and Hartman 2001b).

Measuring turbidity's effects on fish foraging success and activity in laboratory settings leaves us several steps away from evaluating the consequences

of elevated turbidity for the energetics of fish in real streams. Where turbidity increases with streamflow, concurrent changes in the taxonomic composition, density, and distribution of available prey might be expected as a result of processes like increased entrainment of invertebrates (Poff and Ward 1991; Lancaster et al. 2006), mobilization of the streambed (Gibbins et al. 2007), or inundation of floodplains (Benke 2001). Such processes may yield prey availability patterns similar to those successfully exploited by salmonids in the laboratory, such as increases in the density of large, floating prey (Sweka and Hartman 2001b); relatively immobile, benthic prey (experiment 1); or large, mobile benthic prey (experiment 2). Indeed, two field studies have documented similar gut fullness in salmonids under various streamflow and turbidity conditions (Arndt et al. 2002; White and Harvey 2007). However, one of those studies (Arndt et al. 2002) included information on RNA : DNA ratio that suggested a reduction in fish growth under high-streamflow, high-turbidity conditions even though gut fullness was maintained; the reduction in growth may have been attributable to higher activity costs. Considerable variation among systems in feeding success and activity cost under turbid conditions should be expected. For example, greater hydraulic complexity might increase (1) the availability of flow refugia for fish (Pearsons et al. 1992), (2) microhabitats that tend to concentrate prey, and (3) prey abundance during high streamflow. All of these factors could serve to mitigate the challenge of detecting prey in turbid water.

Possible relationships among elevated turbidity, channel morphology, food availability, and other factors influencing fish population dynamics raise questions about prioritizing restoration activities when fish populations are a key concern. Although considerable uncertainty remains, the demonstrated ability of salmonids to feed under turbid, lotic conditions on benthic and near-benthic prey suggests that restoration plans with a narrowly focus on reducing turbidity are unlikely to be optimal in streams that do not exhibit persistent extreme (e.g., >100-NTU) levels of turbidity. However, in many cases, restoration efforts with the broader goal of reducing sediment supply rates may benefit fish by reducing turbidity and by increasing channel complexity through reduction of sediment storage in stream channels.

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