

EFFECTS OF TURBIDITY ON FORAGING EFFICIENCY AND GROWTH OF
SALMONIDS IN NATURAL SETTINGS

by

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ABSTRACT

Effects of Turbidity on Foraging Efficiency and Growth of Salmonids in Natural Settings

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Elevated turbidity and suspended sediment loads have been documented to negatively effect salmonids and their habitats. Laboratory studies have demonstrated the effect of elevated turbidity levels on the physiology and behavior of salmonids.

However, the effects of turbidity on fish in a natural setting are largely uncertain. The goal of this study was to extend the understanding of turbidity effects to natural settings in coastal northern California where impacts to salmonids may occur both as a result of impaired visual capability and reduced prey availability. I compared foraging success and growth of rainbow trout/steelhead (*Oncorhynchus mykiss*) in reaches immediately above and below a sediment point source in each of two tributaries of the Mad River (Maple and Cañon creeks) during small storm events in 2004-2005 and 2005-2006. Movements of tagged individuals within and between reaches of Maple Creek were monitored using paired fixed antennas at the upper and lower ends of each reach.

Increases in turbidity above background levels did not appear to have substantial negative effects on the feeding success or growth of salmonids. Fish actively fed during small storm events, as evidenced by stomach fullness values. Feeding was predominantly from the benthos, on oligochaetes and salmonid eggs, rather than from the drift. Growth of tagged individuals showed no apparent relationship with median reactive distance, and varied widely among sampling dates. Fish moved considerably during storm events,

most often in an upstream direction. Retention of tagged individuals within a sampling reach was low.

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INTRODUCTION

The North Coast Hydrologic Region of California is characterized by high rates of uplift, high rainfall, and unstable rock types, which produce high natural sediment yields (Mount 1995). Land use activities, including logging and associated road-building, have exacerbated natural conditions to create some of the highest sediment yields measured within the United States. The increased sediment supply from land use activities is dominated by fine-grained silt and clay particles, which move through streams and rivers as suspended load and contribute to turbidity. Turbidity, which is caused by the presence of suspended and dissolved organic and inorganic matter in the water column, is an expression of the optical properties of a sample that cause light rays to be scattered and absorbed rather than transmitted in straight lines through a sample (ASTM International 2002). Turbidity is usually measured in nephelometric turbidity units (NTU), and these are used as a surrogate for the less easily measured suspended sediment content (Davies-Colley and Smith 2001).

Turbidity and high suspended sediment loads are associated with negative effects on salmonids and their habitats (as summarized by Newcombe and McDonald 1991 and Waters 1995), and are thus of concern to management agencies seeking to reverse well-documented declines in Pacific salmon throughout the Northwest (e.g. Nehlsen et al. 1991; Brown et al. 1994; Busby et al. 1996). Many states have established turbidity standards for protection of fish and freshwater resources that place limits on turbidity increases above “natural background levels”. In California, for example, the Northcoast Regional Water Quality Control Board established basin wide regulations that turbidity

should not be increased more than 20 percent above naturally occurring background levels (Northcoast Regional Water Quality Control Board 2001). While turbidity is a crucial property in water quality regulation, applying the standards and evaluating their utility in alleviating biological problems are challenging for a number of reasons. Among these are: 1) problems with instrumentation and repeatability of turbidity measurements (Duchrow and Everhart 1971; USGS 2000; Gray and Glysson 2003); 2) difficulties in establishing background levels due to legacy effects from historic events and because unaltered systems display wide ranges of turbidity over space and time (Lloyd 1987); and 3) incomplete understanding of the linkage between turbidity and biological response.

Our understanding of salmonid response to turbidity, in particular, is still incomplete. Most studies have been conducted in laboratories, and there are significant difficulties in extrapolating laboratory results to natural settings (Everest et al. 1987). Laboratory settings may not adequately reflect field conditions, such as prey availability, habitat complexity, and the biotic environment (e.g., intra-or interspecific competitors or predators). Nor do laboratory experiments reveal cumulative effects or synergistic interactions among variables that potentially affect salmonid response. Environmental variables that may affect salmonid response to turbidity include sediment particle characteristics, duration, magnitude, frequency and timing of exposure (Servizi and Martens 1992), temperature, species and life stage of fish, availability of and access to refugia (Sedell et al. 1990), and natural background turbidity. Salmonids apparently have the ability to cope with some level of background turbidity at certain life stages, as they are found in streams receiving glacial melt and often utilize turbid estuaries (Gregory and

Northcote 1993). The extent to which they can tolerate increased sediment loading and turbidity above background levels, however, is not clear.

Effects of increasing sediment loads and turbidity on salmonids range from lethal to sublethal (Newcombe and McDonald 1991), and arise from physiological stress (e.g., gill trauma, changes in blood sugar levels and osmoregulatory function, susceptibility to disease), loss of spawning and rearing habitat that accompany sediment deposition, and alteration of behaviors (e.g., avoidance, territoriality, and foraging) that affect salmonid growth and survival. Behavioral alteration in particular has been studied exclusively in laboratory settings, and findings have sometimes been inconsistent.

With respect to foraging behavior, several laboratory studies have reported an inverse relationship between turbidity and feeding efficiency or prey ingestion (e.g., Berg 1982, Berg and Northcote 1985, Sweka and Hartman 2001a). As salmonids are visual predators that feed largely on invertebrate drift, this relationship is associated with a decrease in their reactive distance to prey as turbidity increases. Berg (1982) found that turbidity as low as 20 NTU reduced salmonid foraging effectiveness and delayed their response to food. In contrast, Sigler et al. (1984) and Gregory (1988) found that foraging rates of salmonids were greater in slightly (31 NTU) to moderately (45 NTU) turbid water than in clearer water. Increased foraging may result from a reduced risk of predation in more turbid water (Barrett et al. 1992; Abrahams and Kattenfeld 1997; Gregory and Levings 1998; Johnson and Hines 1999).

In natural settings, increased foraging rates at moderate levels of turbidity may also reflect increased prey capture by subordinate individuals as territorial structure

breaks down (Berg and Northcote 1985), or it may result from increases in availability of drifting invertebrates (Rosenberg and Wiens 1978; Shaw and Richardson 2001) or other prey sources. Salmonid growth is a function of both food availability and the metabolic costs of obtaining and processing food. The net effect of turbidity on salmonid growth is likely to depend on a variety of interactions among fish, their competitors and predators, and their food supply. Because laboratory experiments cannot duplicate the full context of natural settings, increased understanding of turbidity effects on salmonid feeding and growth requires field investigation.

The paucity of studies of salmonid response to turbidity in natural settings is not surprising, as sampling fish, their prey, and their habitat during the high-discharge storm events that generate turbidity is challenging. Because the timing of storm events and sediment inputs cannot be predicted, sampling schedules must be opportunistic rather than fixed. The ability to control factors through experimental structures such as enclosures is very limited, as these are not likely to remain intact during large storms.

One experimental design that offers promise of increasing understanding of salmonid response to above-background turbidity in natural settings involves evaluating salmonid response in reaches above and below likely point sources of sediments during storms. Provided that upstream and downstream reaches are reasonably similar in discharge and other stream characteristics, differences in salmonid response between reaches could be reasonably attributed to turbidity if the fish do not move between reaches. This design has not been previously used in turbidity studies.

To evaluate the effect of turbidity on salmonid feeding during storm events, I compared prey availability, feeding success, and diet composition of rainbow trout/steelhead (*Oncorhynchus mykiss*) between reaches that were upstream and downstream from point sources of sediments in two streams in coastal northern California. I also evaluated the relationship between salmonid growth and median reactive distance in each reach of the two streams. Finally, in one of the streams, I tracked movements of tagged rainbow trout/steelhead during storms within and between reaches to determine directionality and movement of fish within and between reaches.

STUDY SITES

This study was conducted in Cañon and Maple creeks, which are tributaries of the Mad River in coastal northern California (Figures 1 and 2). Cañon Creek is a 4th order stream which drains a 42.3 km² catchment to the mouth at the Mad River. Maple Creek is a 4th order stream which drains a catchment of 40.4 km². The study reaches established within each of these two streams were similar in stream size, upstream catchment area (37.2 and 30.4 km² in Cañon and Maple creeks, respectively), gradient (2 percent), and channel morphology. Channel substrate in Cañon Creek was composed primarily of small and large cobble, with few boulders and a moderate amount of large wood structures. Channel substrate in Maple Creek was composed primarily of small and large cobble with numerous boulders and few large wood structures.

Study areas in both streams flow through forests of coastal redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) which are managed for timber production. Riparian areas are dominated by red alder (*Alnus rubra*) with interspersed willow (*Salix* spp.), bigleaf maple (*Acer macrophyllum*), California bay (*Umbellularia californica*), and conifers. Apart from rainbow trout/steelhead, other aquatic vertebrates in the study areas include coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*), prickly sculpin (*Cottus asper*), Pacific lamprey (*Lampetra tridentata*), coastal giant salamander (*Dicamptodon tenebrosus*), and tailed frogs (*Ascaphus truei*).

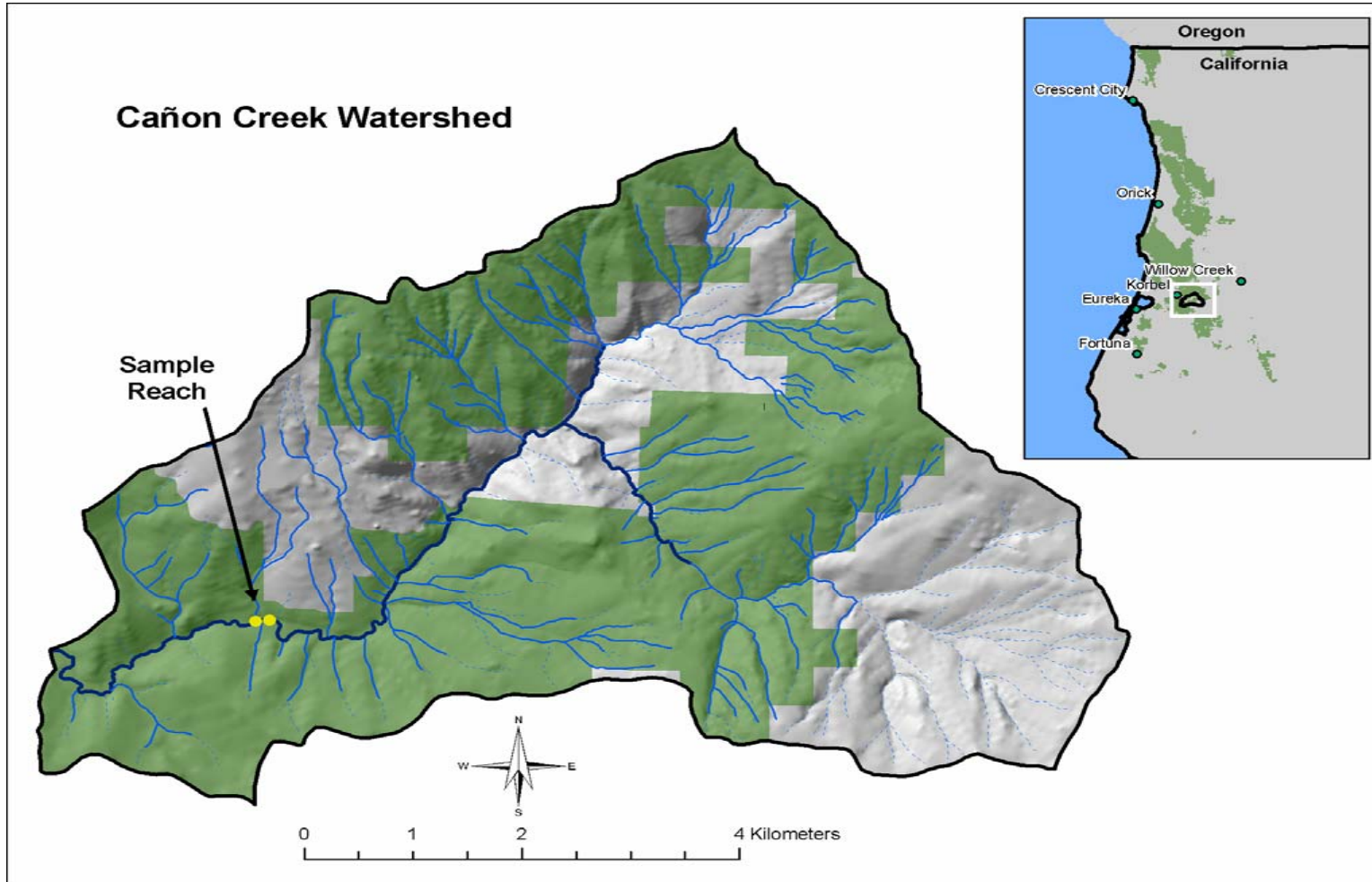


Figure 1. Cañon Creek watershed with sampling reach locations.

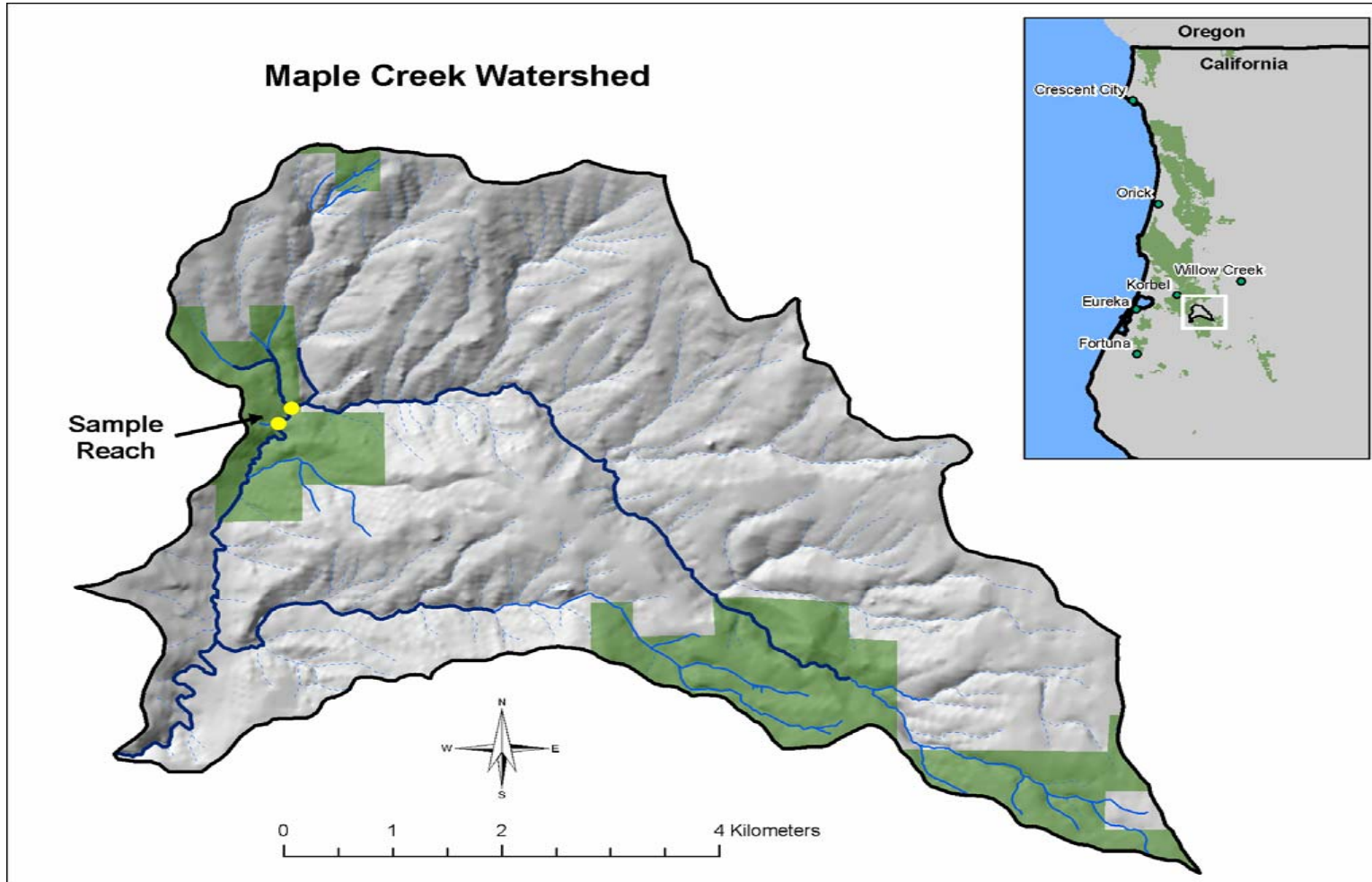


Figure 2. Maple Creek watershed with sampling reach locations

The regional climate is maritime with mild, dry summers and cool, wet winters. Average annual precipitation exceeds 120 cm, most of which falls as rain between November and March. Water temperature typically ranges from 10 – 18 °C in summer and 5 – 11 °C in winter in the two streams. Winter stream flows during the study averaged 4.4 m³/s and 3.9 m³/s at Cañon Creek and Maple Creek, respectively. Peak flows exceeded bank full events in each creek during both of the sampling years. High rainfall, unstable geology, logging, and anthropogenic activities combine to deliver large amounts of sediment to the study areas. Over the course of this study, summer turbidity levels averaged less than 1 nephelometric turbidity units (NTU), while background winter levels were 6 to 12 NTUs and at times exceeded 300 NTUs in the winter in each of the creeks. Typically, storm-generated turbidity drops to pre-storm levels within approximately 4 days of its peak, creating an average of 6-7 days of elevated turbidity per storm.

MATERIALS AND METHODS

Sampling Design

Two 200-m reaches were established in each of the two streams, with one reach upstream and one reach downstream of a direct source of sediment that was likely to produce differences in turbidity between the upstream and downstream reaches during storms. This design allowed me to evaluate turbidity effects on fish growth and foraging within streams, with other stream attributes held reasonably constant. In Cañon Creek, the sediment source was a small bank slump 75 m up a small tributary 60 m above and 42 m below the downstream and upstream reach, respectively. In Maple Creek, sediment originated from numerous small slumps in a tributary (Bear Creek, 12 m below the upstream reach) and a small and large landslide 25 and 50 m downstream of the tributary, respectively. The downstream reach of Maple Creek was located 127 m below the upstream reach. Downstream reaches were located a minimum of 50 meters downstream of the sediment sources to allow for complete mixing of sediment inputs into the mainstem channel.

Turbidity Sampling and Habitat Characterization

Turbidity was measured from paired turbidity monitoring stations, which were installed in the reaches above and below the identified point sources of sediments in the two streams. Each station consisted of a DTS-12 turbidimeter, a Druck PDCR 1230 pressure transducer, fixed WaterMark graduated stage plates, and a Cambell CR510x or CR10x data-logger. Turbidity and stage height were continuously measured at 10-minute

intervals throughout the entire study and grab samples were taken at regular intervals to calibrate turbidimeter readings. Stream discharge measurements were taken at various stage levels throughout the study to establish stage-discharge relationships at each reach. Discharge was estimated using the velocity-area method (Gore 1996) in a straight section of each reach near the fixed graduate stage plates. Velocity was measured with a Price AA or mini current meter with topset rod.

Habitat within each reach was characterized to compare temperature and habitat volume and availability of cover between upstream and downstream reaches. Temperature was measured at 10 minute intervals using a Hobo water temp pro data logger. Habitat units were classified as shallow or deep pool and riffles, and the length, width, and maximum depth of each unit was measured. Dimensions of cover structures were measured using a stadia rod to estimate percent cover by area provided within each reach. Cover structures that were distinguished included small (< 10 cm diameter, < 1 m length) and large (> 10 cm diameter at one end, > 1 m length) woody debris, overhanging terrestrial vegetation, and bank and rock undercuts.

Fish Sampling

All procedures on vertebrates were approved by the Humboldt State University Institutional Animal Care and Use Committee (protocol # NO. 04/05.F63.A and amendments). Rainbow trout/steelhead were sampled during storm events in the winter/spring periods of 2005 and 2006 to obtain diet samples and to measure growth and movement of tagged individuals. Sampling occurred on the falling hydrograph limb of

storms to ensure that diet samples represented prey consumption during times of increased turbidity. Sampling events were selected when the turbidity was elevated above background winter levels for a minimum period of 48 h, to allow for complete digestion of food consumed during a lower turbidity. A minimum of three-four weeks was maintained between sampling events to reduce collecting and handling stress to fish. Due to the time involved for collecting and processing fish, only one stream was sampled per storm event. Four storm events each were sampled in Cañon and Maple creeks over the course of study. The largest storm events could not be sampled because of sampling inefficiency at high flows and for safety considerations. The storm events that I sampled were smaller than bank-full events.

Fish were sampled in each reach using a backpack electroshocker. A single pass of electro-fishing proceeded in either an upstream or downstream direction. To minimize handling stress, fish were sampled within 50 m sections at a time. Captured individuals were anesthetized with carbon dioxide (Alka-Seltzer Gold) before measuring fork length (FL) to the nearest mm and wet mass to the nearest 0.1 g. Stomach contents of fish > 70 mm FL were sampled by gastric lavage. Stomach contents were washed onto a 500 μ m sieve and fixed in 70 percent ethanol. Fish greater than 70 mm FL were also implanted with passive integrated transponder (PIT) tags. Individuals < 100 mm were implanted with 12 mm full-duplex tags, while individuals > 100 mm FL received 23 mm half-duplex tags. PIT tagging and/or scanning for the presence of tags occurred in fall 2004 and 2005 prior to the beginning of storm seasons, in summer 2005 and 2006 after the

storm season for each year had passed, as well as during all storm event samples. Upon recovery from anesthesia, fish were returned to the locations of capture.

Fish movements in Maple Creek were monitored to evaluate whether fish implanted with 23 mm half-duplex tags remained within the study reaches during storm events. Paired radio-frequency identification fixed-antenna arrays were installed at the upper and lower ends of upstream and downstream reaches prior to the 2005-2006 sampling season (Figure 3). Each pair of antenna consisted of a half-duplex radio-frequency identification reader with antenna multiplexer and two antenna tuner modules constructed by Oregon RFID (Portland, OR). Copper wire was buried under the substrate and then looped back across the stream and connected at both ends to the tuner module. Shielded twin-axial cable ran from the tuner to the radio-frequency identification reader where readings were stored on a Palm data logger. Antennas were placed in channel cross-sections that were 10 m or less in bank-full width, with the top and bottom of the antenna loop less than 1.2 m apart. Read ranges measured at regular intervals averaged approximately 0.45 m from each antenna loop. Readings between pairs of antennas were used to establish direction and timing of movements.

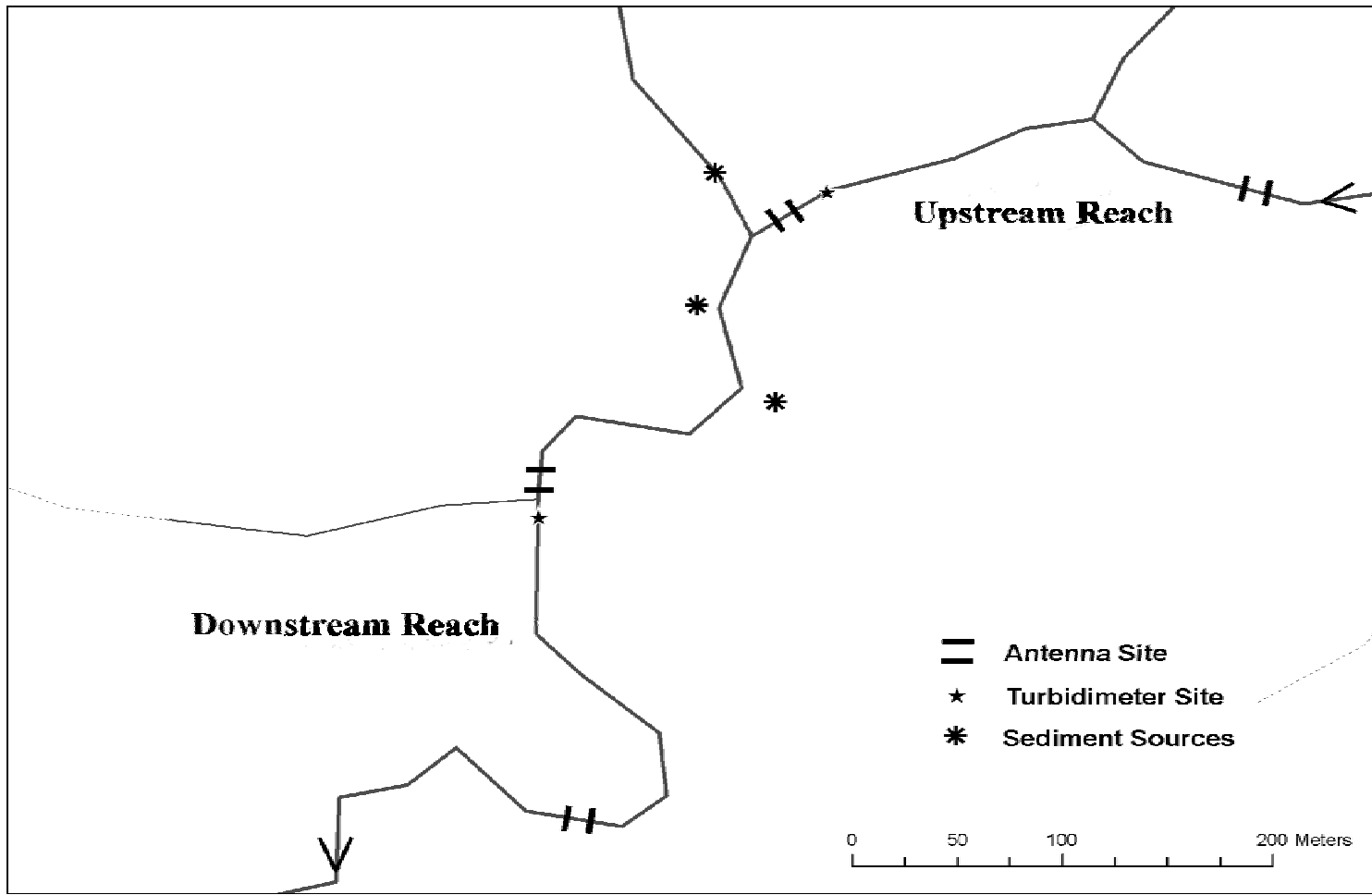


Figure 3. Schematic diagram showing the placement of radio-frequency identification antenna arrays and turbidity stations in the upstream and downstream reaches of Maple Creek.

Invertebrate Sampling and Processing

Invertebrate drift was sampled to estimate prey availability. Prey availability was expressed as drift biomass (dry), in mg/m^3 . Drift sampling occurred concurrently with fish sampling during storm events. In each reach, drift was sampled during daytime hours for 2-5 h with a single 363 μm mesh net that was 99 cm long with a 1587 cm^2 rectangular opening. To minimize impact from electro-shocking, the net was placed at the upstream end of a reach at the bottom of a riffle, and the bottom lip of the net was 10 cm above the substrate. Nets were never fully submerged. Volume of water filtered by each net during the sampling period was estimated from average velocity, length of exposure, and exposed cross-sectional area of the net. Average velocity was estimated based on stage-discharge relationships. At the end of the sampling period, net contents were washed in a 500 μm sieve and fixed in 70 percent ethanol.

Invertebrate drift samples and fish stomach contents were sorted, identified, and measured in the laboratory using a dissecting microscope. Body lengths were measured to the nearest 0.1 mm from the front of the head to the tip of the abdomen. Individual body lengths were converted to estimates of dry mass using taxon-specific relationships provided by K.W. Cummins (Humboldt State University, Institute for River Ecosystems) and M.A. Wilzbach (United States Geological Survey, California Cooperative Fish Research Unit). Relationships are shown in Appendix A. Organisms were identified to order and, if possible, to family. However, to simplify analysis and interpretation of drift and fish stomach data, individuals were classified into 9 prey categories: Ephemeroptera,

Plecoptera, Trichoptera, Diptera, other aquatic invertebrates, Oligochaeta, terrestrial invertebrates not including Oligochaeta, salmonid eggs, and vertebrates.

Data Analysis

Because I was able to replicate the sampling design of up-and downstream of point sources of sediments in only two streams and within stream sample sizes were small, my data were analyzed graphically rather than statistically. I graphically compared response variables between upstream and downstream reaches within each stream. Upstream and downstream reaches were assumed to differ primarily in turbidity, although I also compared differences in habitat volume and percent cover between sections. Because turbidity has been shown to reduce capture success for drift-feeding fish through a reduction in reactive distance, I converted turbidity values to reactive distance (cm) and used the average or median reactive distance in some analyses in order to express turbidity in units that were directly relevant to fish feeding. Turbidity (NTU's) was converted to reactive distance using the equation developed by Sweka and Hartman (2001a) from laboratory studies on brook trout (25.35 ± 6.65 g) foraging, where:

$$\text{Reactive Distance} = 90.14 * e^{(-0.08*NTU + 0.0007*NTU^2)}$$

Sweka and Hartman (2001a) used fish that were larger, on average, than in this study and one size class of prey (10.3 ± 0.2 mm). This may confound true reactive distances for various size classes of fish under different turbidity levels. It does however, provide for a rough estimate of reactive distance to allow a comparison of effects between sampled reaches.

Turbidity data for each sampling event were averaged for each reach from data collected over a 30 h period ending with the completion of biological sampling. This time period was chosen to allow for gastric evacuation of prey consumed by fish at pre-storm levels of turbidity.

The response variables in my study included prey availability, fish feeding success, diet preference, growth and movement. Feeding success of the fish was represented by stomach fullness (Miller and Sadro 2003). To standardize the amount of food consumed among individuals of varying size, I expressed stomach fullness as dry mass of stomach contents (mg) divided by the wet mass of individual fish (g).

Differences between upstream and downstream drift mass and stomach fullness were plotted against differences in reactive distance and sampling dates to detect trends in food availability and foraging success. Drift composition was described as the percentage of mass of each prey category from the collective total of all sampling events in each stream reach from both sampling years ($n = 4$). Diet preference was assessed by comparing the relative percentage of each prey category within fish stomachs and within the drift.

Growth was expressed as specific growth rate (G), which was estimated as:

$$G = \left(\frac{\ln W_t - \ln W_0}{t} \right) * 100, \text{ where } W_t \text{ is the final mass (grams), } W_0 \text{ is the initial mass}$$

(grams), and t is the growth period (days).

Fish movements during each storm event in Maple Creek were counted and categorized as: 1) upstream movement within a reach; 2) downstream movement within a reach; 3) movement from the upstream reach to the downstream reach; and 4) movement

from the downstream reach to the upstream reach. Differences in pattern and timing of fish movements between the upstream and downstream reaches were analyzed by plotting the number of fish in each movement category against storm events and peak discharges.

RESULTS

Turbidity and Habitat Characterization

Differences in turbidity between upstream and downstream reaches during high-flow events in Cañon and Maple creeks were not similar (Table 1). Despite efforts to locate the downstream reach of Cañon Creek below a direct source of sediment, the upstream and downstream reach within Cañon Creek did not substantially differ in turbidity on any of the four sampling dates. Within Maple Creek, the downstream reach was more turbid than the upstream reach on all four sampling dates. The greatest difference in turbidity was realized during the storm event sampled on 22-Mar-2005, when the downstream reach was 73 percent more turbid than the upstream reach. This increased turbidity in the downstream reach was associated with an estimated reduction of 5 cm in reactive distance by foraging trout. The greatest difference in reactive distance between upstream and downstream reaches was 7 cm, which was observed in Maple Creek during the 13-Mar-2006 sampling event. In both creeks, turbidity in downstream reaches ranged between 17 – 69 NTUs during all sampling events (with reactive distance ranging between 12 and 30 cm), while turbidity in upstream reaches ranged between 14 – 63 NTUs (with reactive distance ranging between 12 – 35 cm). Based on data from all sampling dates and reaches, a positive relationship was observed between turbidity and discharge ($R^2 = 0.64$, $b = 7.67$). Differences in discharge between the upstream and downstream reach of each stream were slight.

Table 1. Sampling date, peak discharge, turbidity, and fish reactive distance in upstream and downstream reaches of Cañon and Maple creeks during storm events in 2005 and 2006. Fish reactive distance was estimated from Sweka and Hartman (2001a).

	Date	Reach	Discharge (m ³ /s)	Temperature (°C)	Turbidity (NTU)	Reactive Distance (cm)
Cañon	5-Jan-2005	Upstream	11.9	7	17	30
		Downstream	12.5	7	17	30
	31-Mar-2005	Upstream	18.3	9	47	13
		Downstream	20.0	8	49	12
	5-Jan-2006	Upstream	15.7	9	63	12
		Downstream	16.4	10	60	12
	27-Mar-2006	Upstream	9.5	8	20	25
		Downstream	10.2	8	20	26
Maple	22-Mar-2005	Upstream	8.4	8	40	17
		Downstream	9.0	8	69	12
	7-Feb-2006	Upstream	13.8	8	27	19
		Downstream	15.0	8	31	16
	13-Mar-2006	Upstream	3.8	5	14	35
		Downstream	4.0	5	17	28
	18-Apr-2006	Upstream	7.2	7	17	29
		Downstream	7.8	6	21	24

Habitat structure and volume were comparable between upstream and downstream reaches within the two creeks. The upstream reach of Cañon Creek contained 7 pools and 5 riffles and was composed of 68 percent pools and 32 percent riffles by surface area, while the downstream reach contained 7 pools and 3 riffles and was composed of 54 percent pools and 46 percent riffles. In-stream cover measured 4.7 percent and 4.2 percent of surface area in the upstream and downstream reach, respectively. The upstream reach of Maple Creek contained 5 pools and 6 riffles and was composed of 46 percent pools and 54 percent riffles by surface area, while the downstream reach contained 9 pools and 5 riffles and was composed of 69 percent pools and 31 percent riffles. Instream cover measured 3.4 percent of surface area in the upstream reach and 3.5 percent at the downstream reach.

Prey Availability

Drift biomass did not vary consistently between upstream and downstream reaches, or with turbidity, among sampling dates in either Cañon or Maple Creek (Figures 4 and 5). Although the range in drift biomass was comparable between the two creeks, mean drift biomass was greater in the two reaches of Maple Creek (mean = 0.093 mg/ m³, SD = 0.055, n = 8) than in the Cañon Creek reaches (mean = 0.047, SD = 0.023, n = 8). In both creeks, drift biomass tended to be greater later in the storm season (March and April) than earlier. The lowest drift biomass was observed in February in Maple Creek. Over all sampling dates and reaches, a negative relationship was observed between drift biomass and discharge (n = 16, R² = 0.45, b = -0.02).

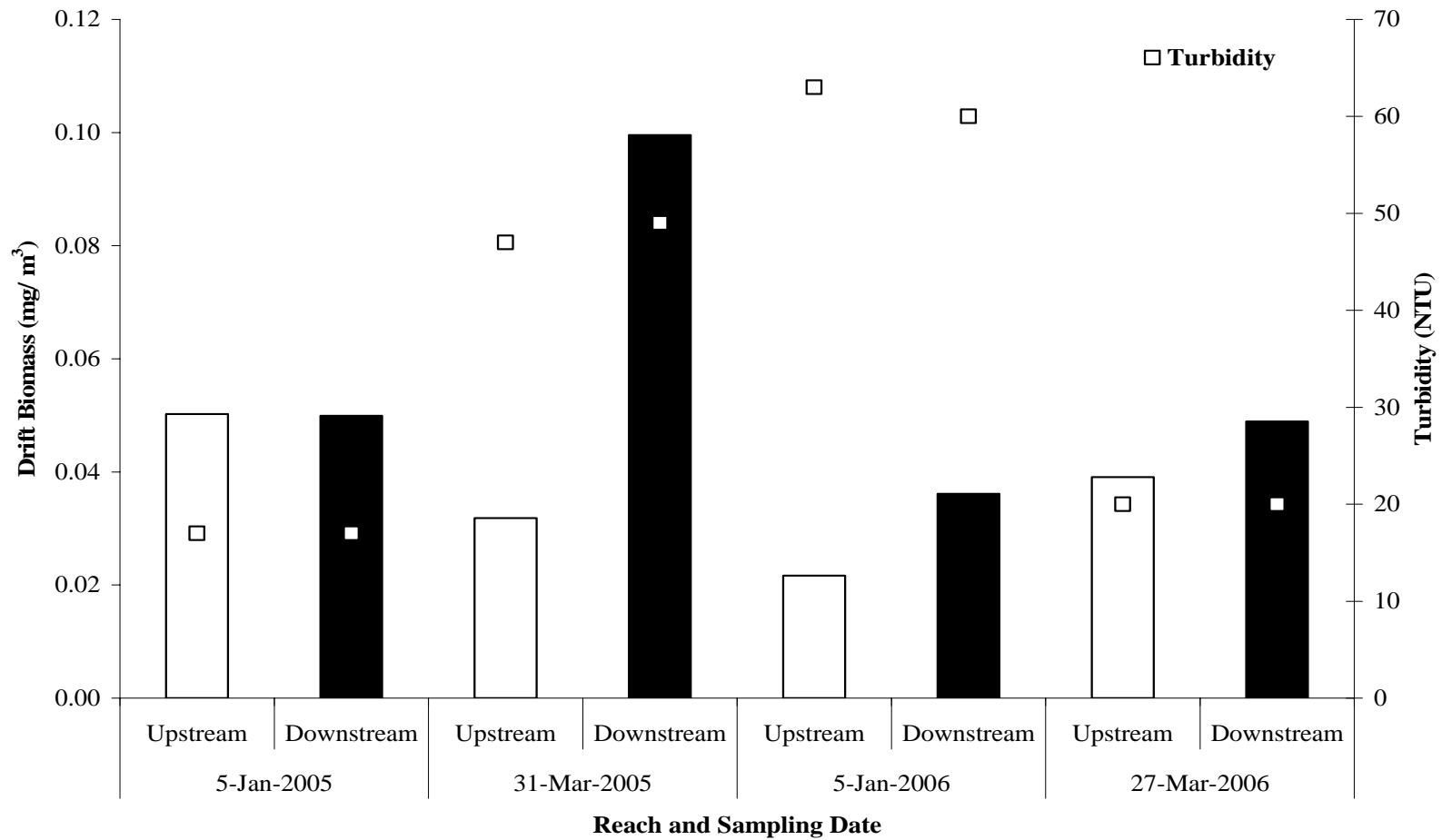


Figure 4. Drift biomass and turbidity in upstream and downstream reaches of Cañon Creek during 4 storm events in 2005 and 2006.

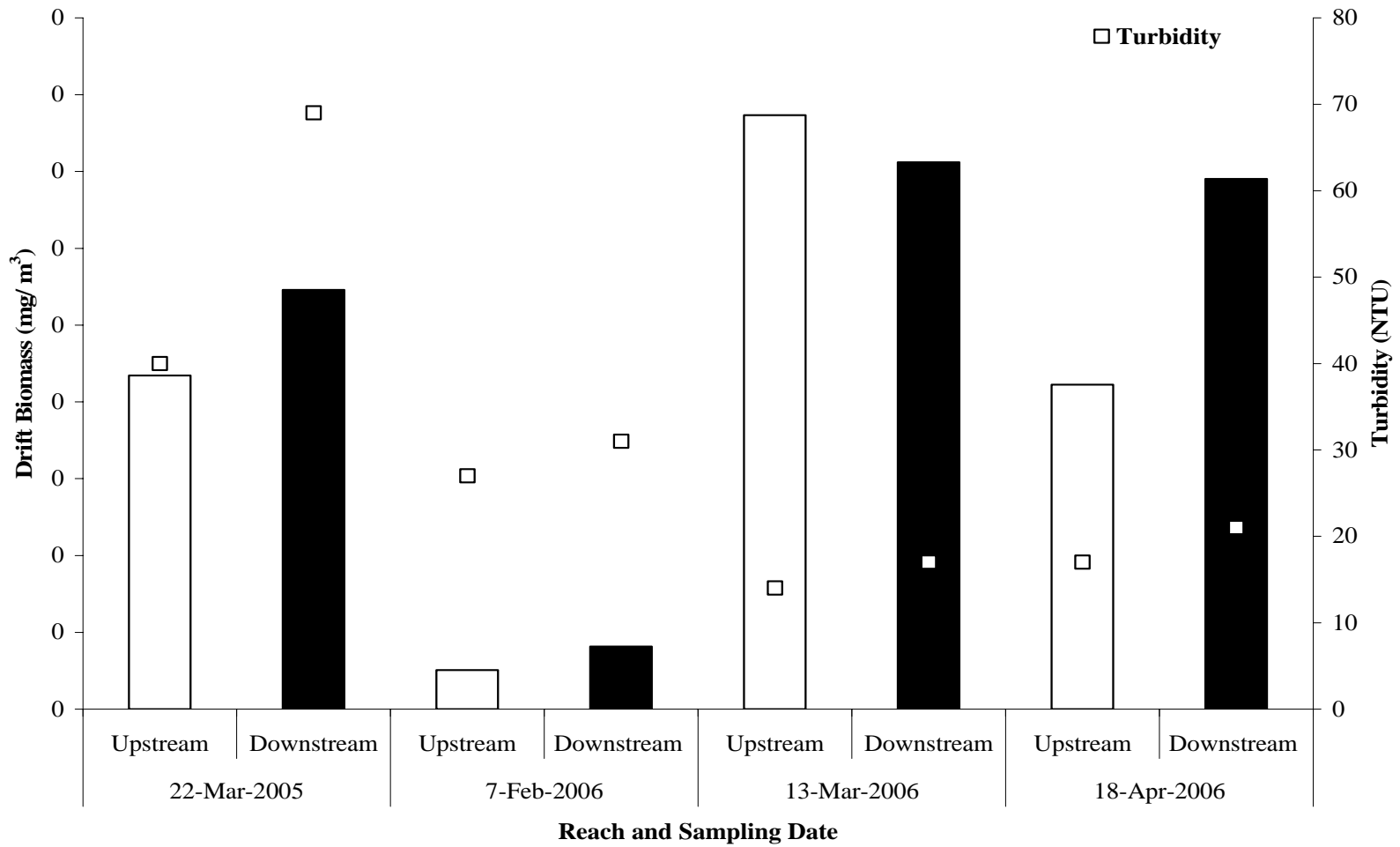


Figure 5. Drift biomass and turbidity in upstream and downstream reaches of Maple Creek during 4 storm events in 2005 and 2006.

Composition of the drift varied widely among all sampling dates and between the upstream and downstream reaches of both creeks. Based on data combined over sampling dates, the upstream reach of Cañon Creek contained higher proportions by mass of Ephemeroptera, Plecoptera, and Diptera, while the downstream reach drift was dominated by Trichoptera, other aquatic and other terrestrial invertebrates (Figure 6). In Maple Creek, the upstream reach contained higher proportions by mass of Trichoptera, Ephemeroptera and other aquatic invertebrates, whereas the downstream reach contained larger proportions of Diptera and other terrestrial species (Figure 7). Averaged among sampling dates and reaches, organisms of terrestrial origin composed 15 percent and 11 percent of the total drift biomass in Cañon and Maple creeks, respectively. The percentage by mass of terrestrial organisms in the drift was considerably greater in March and April than in January and February sampling dates.

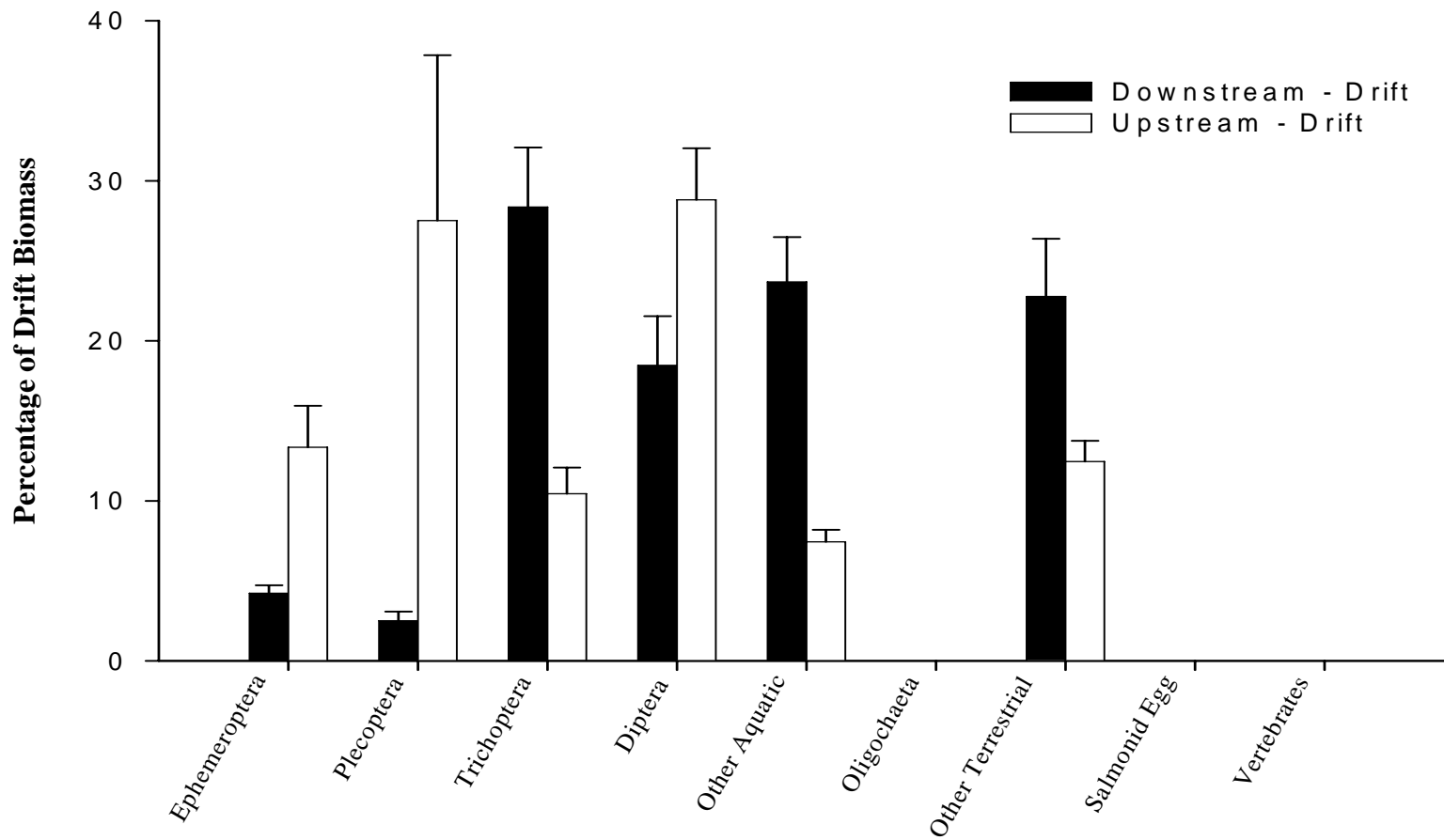


Figure 6. Percentage, by mass, of prey categories in the drift at Cañon Creek averaged over all sampling dates (n = 4). Oligochaeta represents only terrestrial species. Vertical lines represent standard deviation.

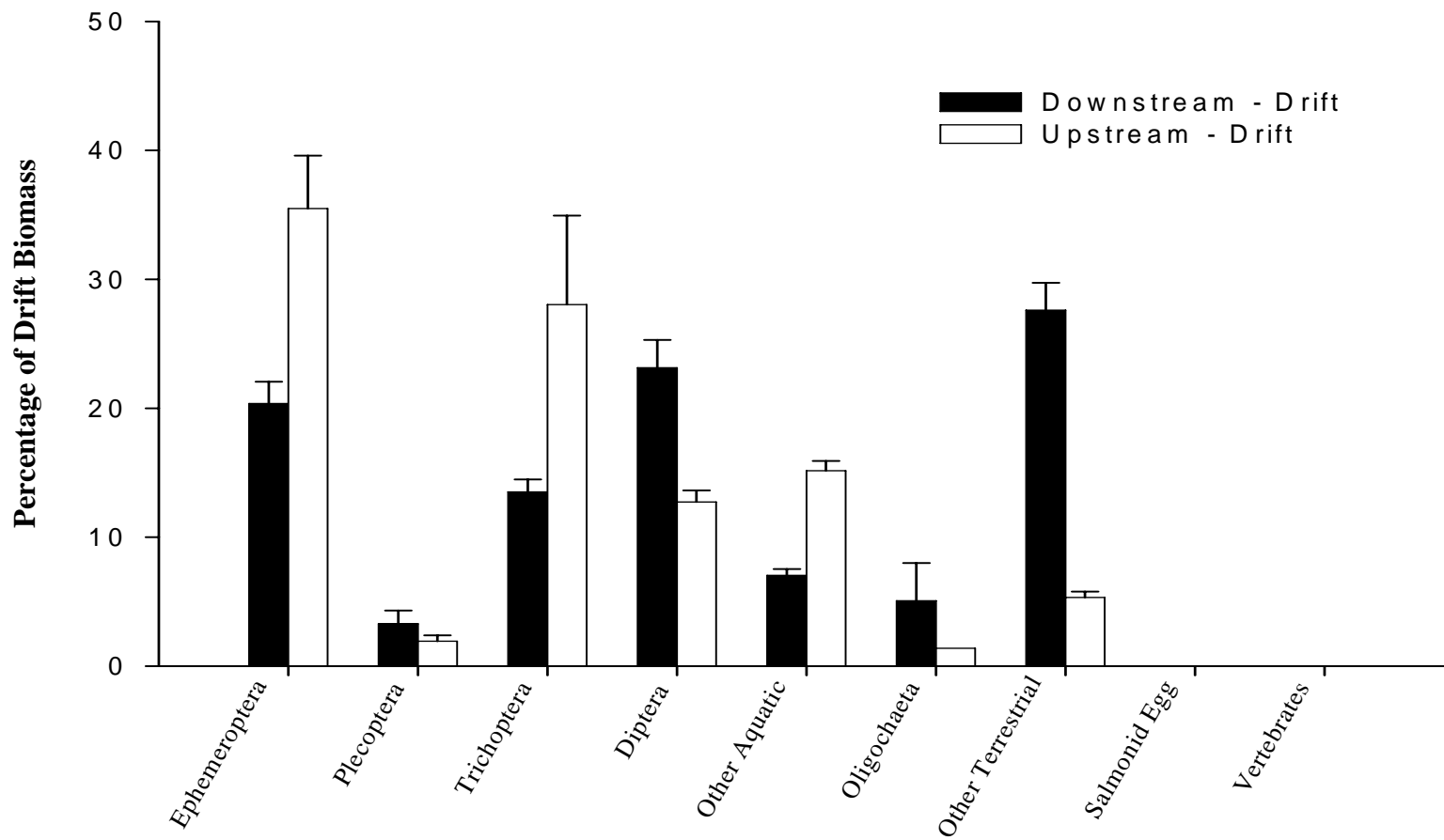


Figure 7. Percentage, by mass, of prey categories in the drift at Maple Creek averaged over all sampling dates (n = 4). Oligochaeta represents only terrestrial species. Vertical lines represent standard deviation.

Feeding Success and Diet Preference of Rainbow Trout/ Steelhead

Rainbow trout/steelhead in upstream and downstream reaches of Cañon and Maple creeks actively fed during the sampled storm events, as evidenced by their stomach fullness (Figures 8 and 9). Across all reaches and dates, stomach content weights of the fish were similar in Cañon and Maple creeks. Mean stomach content weight of the fish in Cañon was 87 mg (range = 0.2 to 601 mg) and 62 mg in Maple Creek (range = 0.3 to 1172 mg). Mean mass of fish from which stomach contents were drawn was 18.6 g (SD = 19.84, n = 104) in Cañon Creek and 10.9 g (SD = 7.5, n = 88) in Maple Creek. In Maple Creek, mean stomach fullness was greater in the more turbid downstream reach than in the upstream reach on all sampling dates. This difference was particularly large during the 7-Feb-2006 storm. In Cañon Creek, where differences in turbidity between reaches was negligible, differences in stomach fullness between the upstream and the downstream reach were not consistent among dates. A large difference in stomach fullness was observed between the upstream and downstream reach during the 5-Jan-2005 storm.

Differences in stomach fullness of rainbow trout/steelhead between upstream and downstream reaches were not associated with differences in drift biomass between the reaches in either Cañon Creek or Maple Creek (Figures 10 and 11). In Cañon Creek, the difference in reactive distance of the fish to their prey between the upstream and downstream reach was small, while in Maple Creek, this difference was greater.

Comparison of diet composition of the rainbow trout/steelhead with drift composition in the upstream and downstream reaches of Cañon and Maple creeks revealed that drifting invertebrates of aquatic origin did not dominated the prey base of

fish (Figures 12 and 13). In Cañon Creek, salmonid eggs accounted for 71 percent and 82 percent

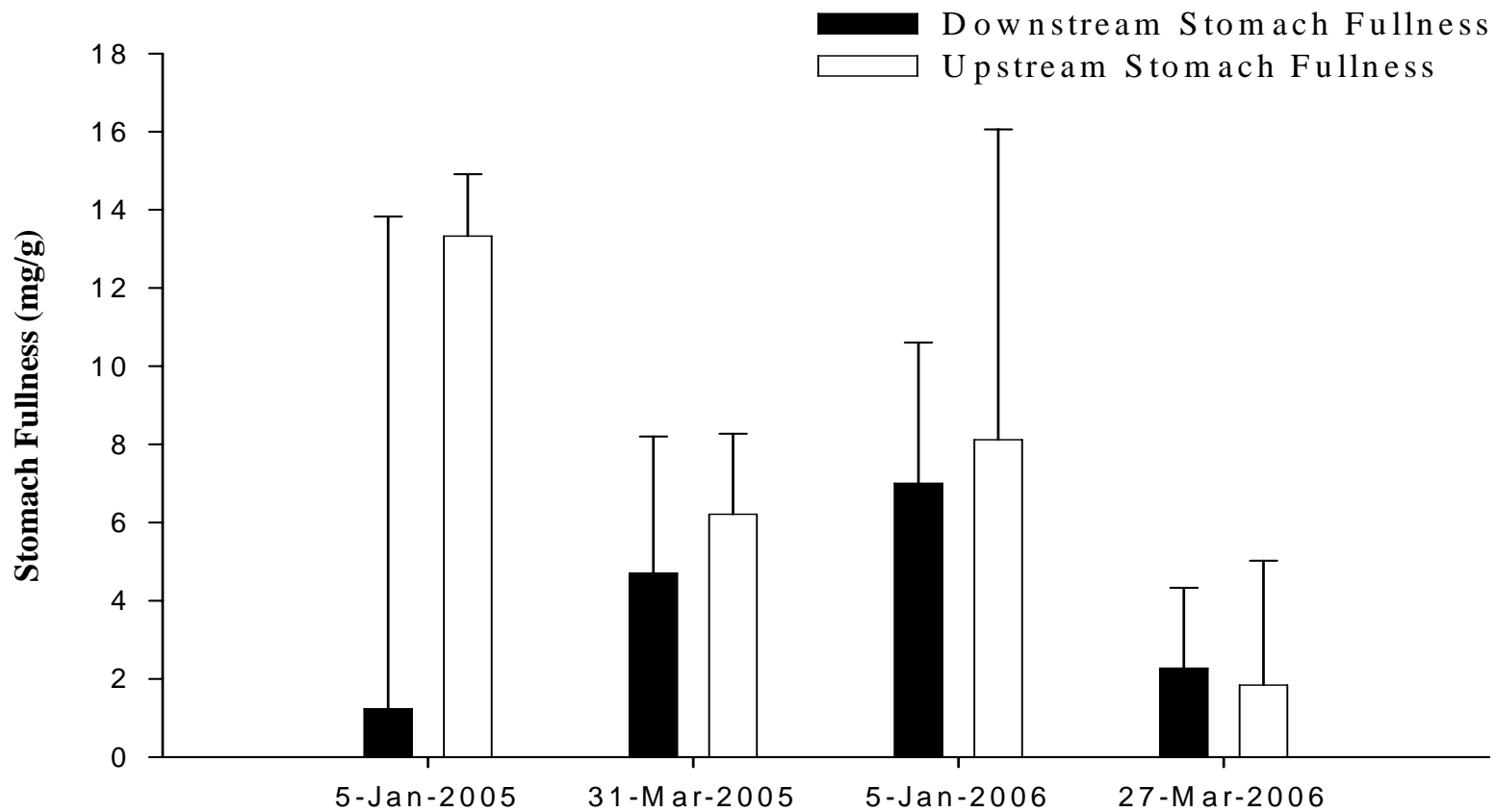


Figure 8. Mean stomach fullness, expressed as dry mass of gut contents per wet mass of fish, of rainbow trout/steelhead in the upstream and downstream reach of Cañon Creek during 4 storm events in 2005 and 2006. Vertical lines represent standard deviation. Sample size is shown in parentheses.

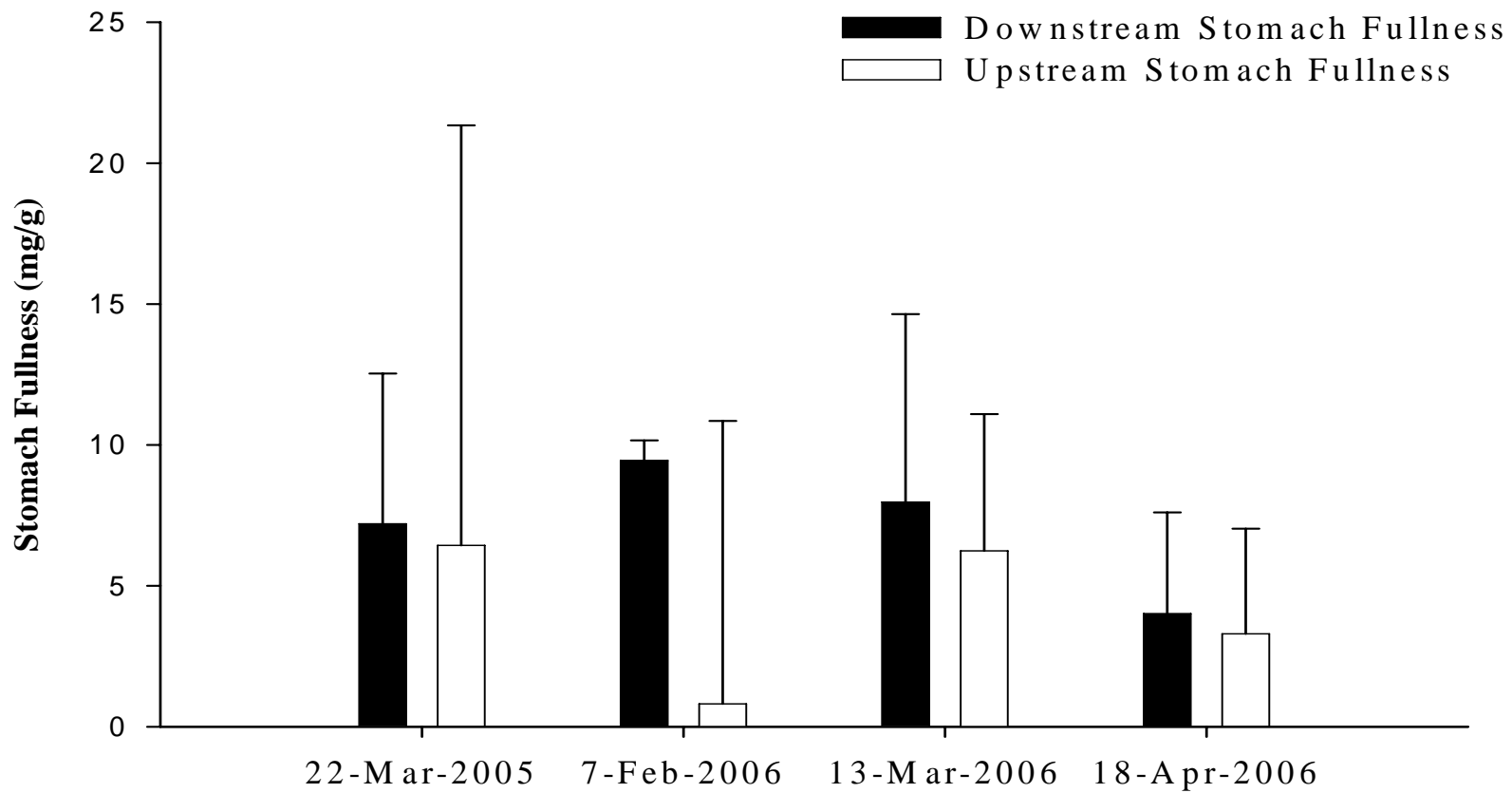


Figure 9. Mean stomach fullness, expressed as dry mass of gut contents per wet mass of fish, of rainbow trout/steelhead in the upstream and downstream reach of Maple Creek during 4 storm events in 2005 and 2006. Vertical lines represent standard deviation. Sample size is shown in parentheses.

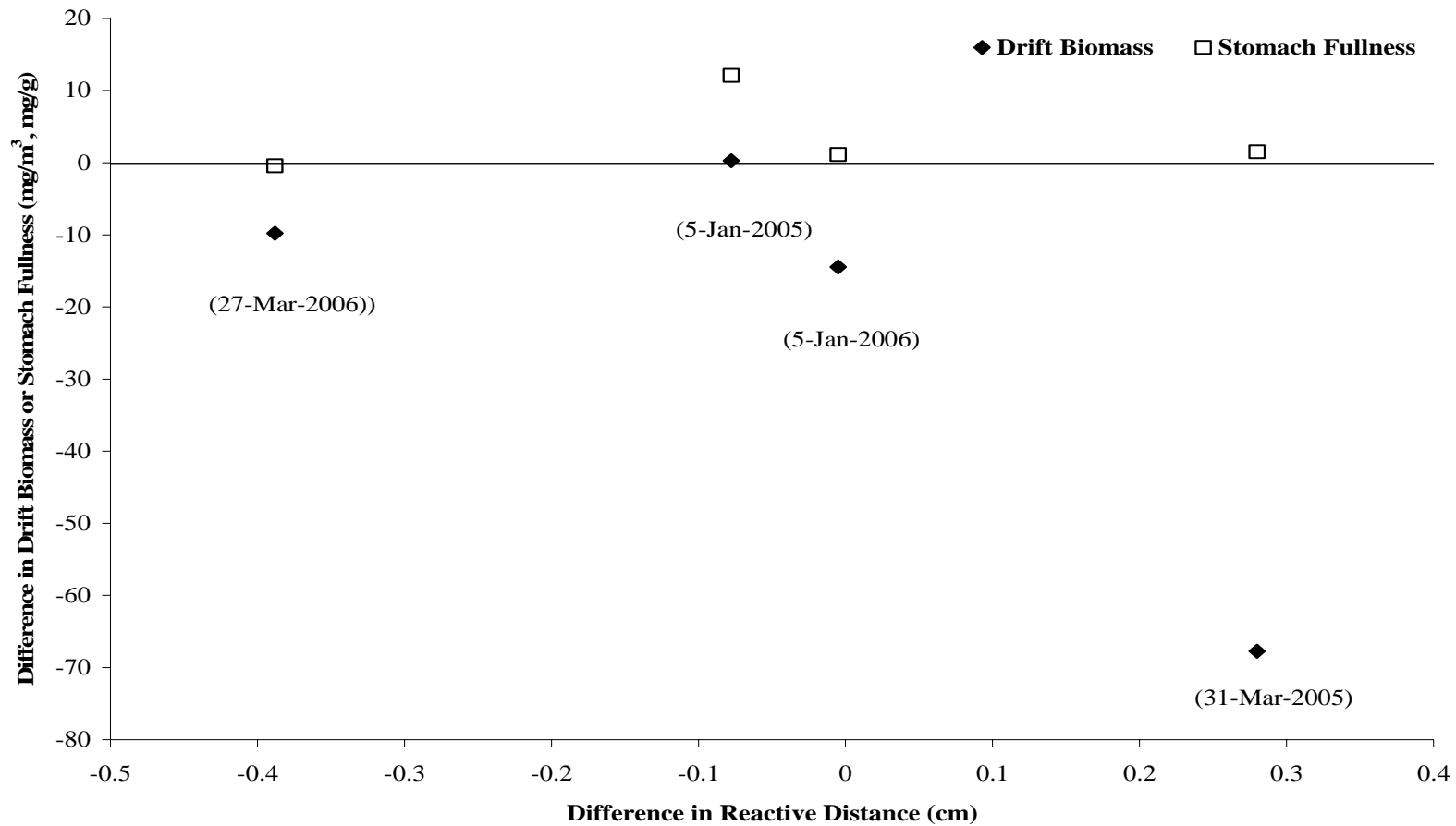


Figure 10. Differences in drift biomass and stomach fullness of steelhead trout in the downstream reach from the upstream reach of Cañon Creek, plotted against the difference in reactive distance of the fish on each of 4 storm events. Plotted points portray the relationship between feeding success and availability of drift.

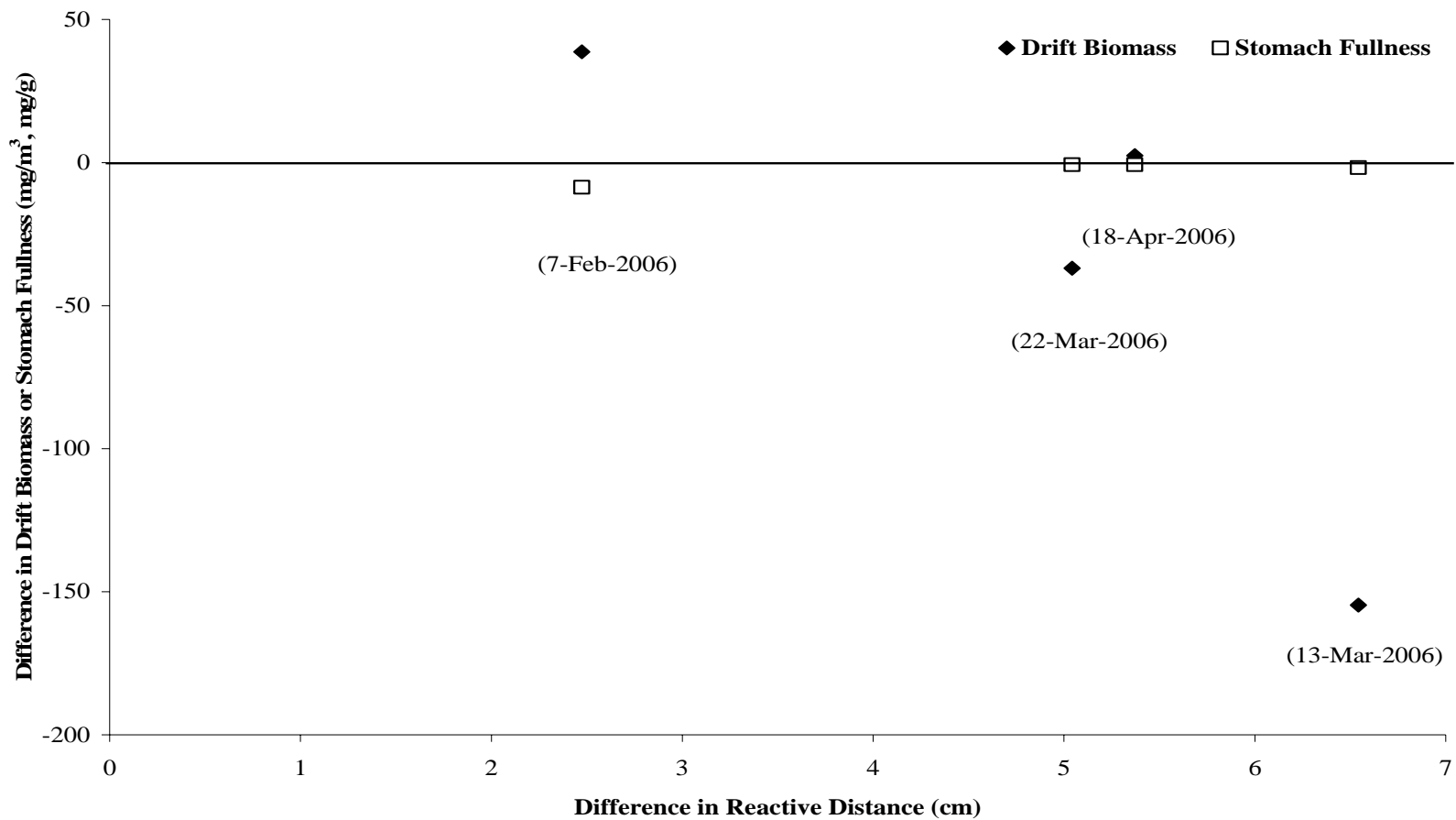


Figure 11. Differences in drift biomass and stomach fullness of steelhead trout in the downstream reach from the upstream reach of Maple Creek, plotted against the difference in reactive distance of the fish on each of 4 storm events. Plotted points portray the relationship between feeding success and availability of drift.

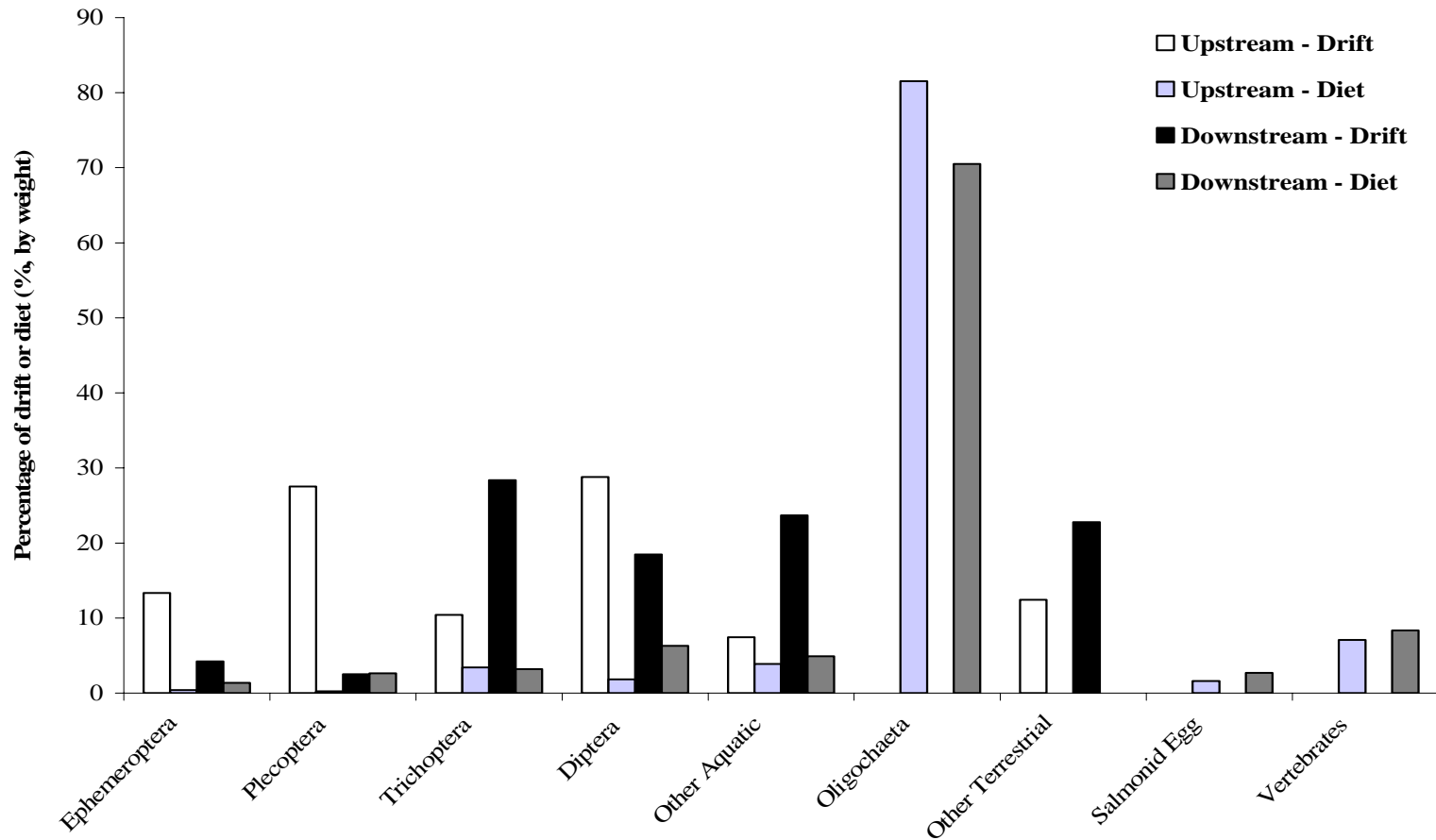


Figure 12. Percentage, by mass, of prey categories that were consumed by steelhead trout and that were available within the drift in the upstream and downstream reach of Cañon Creek. Data are averaged over 4 sampling dates. Oligochaeta represents only terrestrial species.

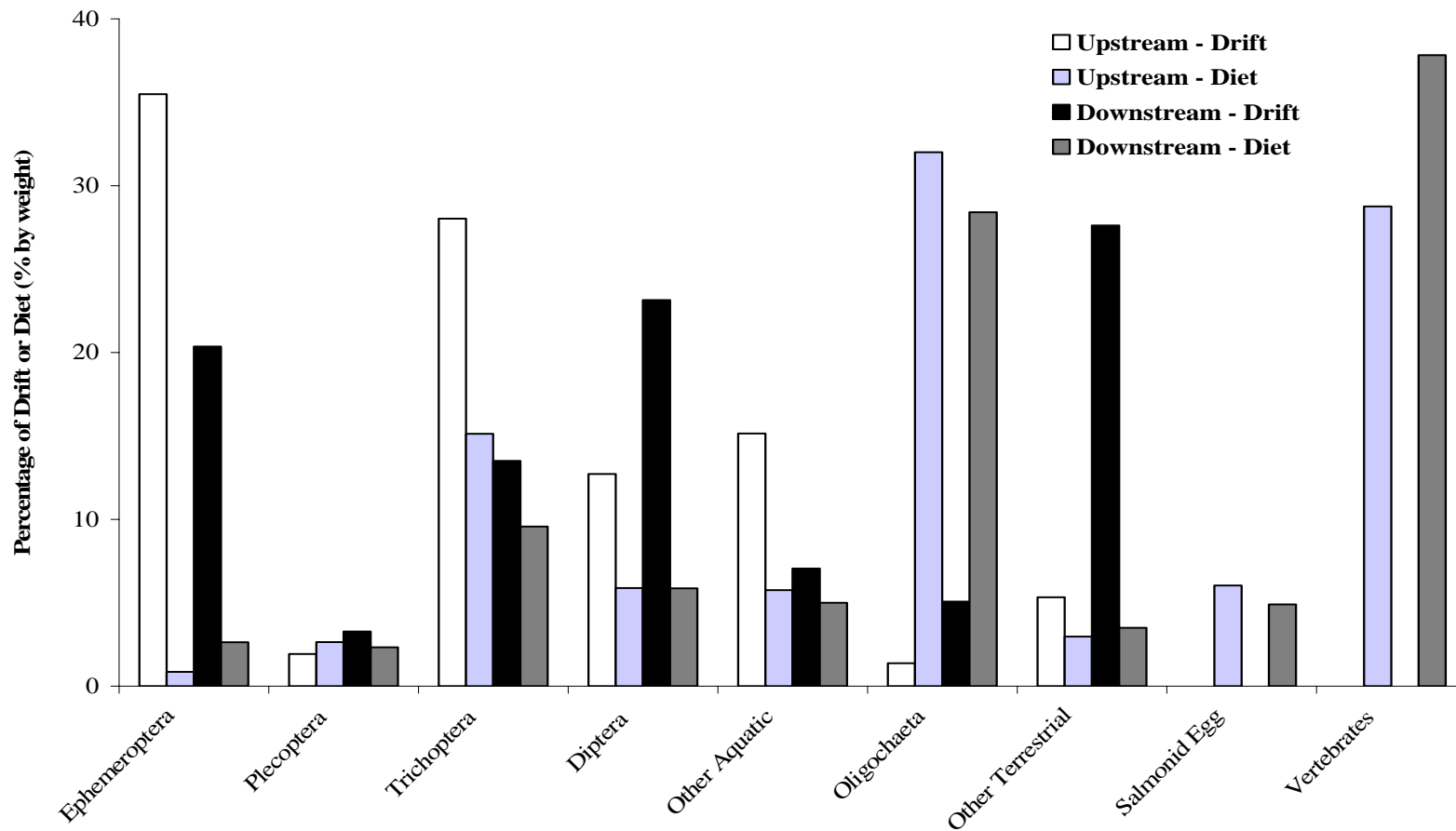


Figure 13. Percentage, by mass, of prey categories that were consumed by steelhead trout and that were available within the drift in the upstream and downstream reach of Maple Creek. Data are averaged over 4 sampling dates. Oligochaeta represents only terrestrial species.

of the biomass of food consumed in the upstream and downstream reach, respectively. In Maple Creek, fish consumed a greater proportion of drifting organisms than in Cañon Creek. Despite large differences in the proportions of drifting prey categories between upstream and downstream reaches, differences in the proportions of consumed prey items between the reaches was slight. The primary prey base in both reaches of Maple Creek was dominated by salmonid eggs and terrestrial oligochaetes.

Growth

Specific growth rates of rainbow trout/steelhead in Cañon and Maple creeks did not differ substantially between upstream and downstream reaches, and were not detectably related to median reactive distance (Figures 14 and 15). In Cañon Creek, growth averaged 0.48 percent/day (SD = 0.35, n = 20) in the upstream reach and 0.40 percent /day (SD = 0.38, n = 19) in the downstream reach. In Maple Creek, growth averaged 0.32 percent /day (SD = 0.37, n = 35) in the upstream reach and 0.29 percent /day (SD = 0.41, n = 31) in the downstream reach. The interval over which growth was measured ranged from 66 to 446 days in Cañon Creek and from 34 to 250 days in Maple Creek. Growth estimates and dates of tagging and recapture for each fish in the upstream and downstream reaches of the two streams are given in Appendix B and C. Fish which were recaptured in a reach different from the reach in which they were tagged were not included in this analysis, nor were fish from Maple Creek that were detected to have moved between reaches in between captures. In Cañon Creek, 40 of 382 tagged individuals were recaptured with 4 individuals being recaptured multiple times. In Maple

Creek, 63 of 350 tagged individuals were recaptured with 6 individuals being recaptured multiple times.

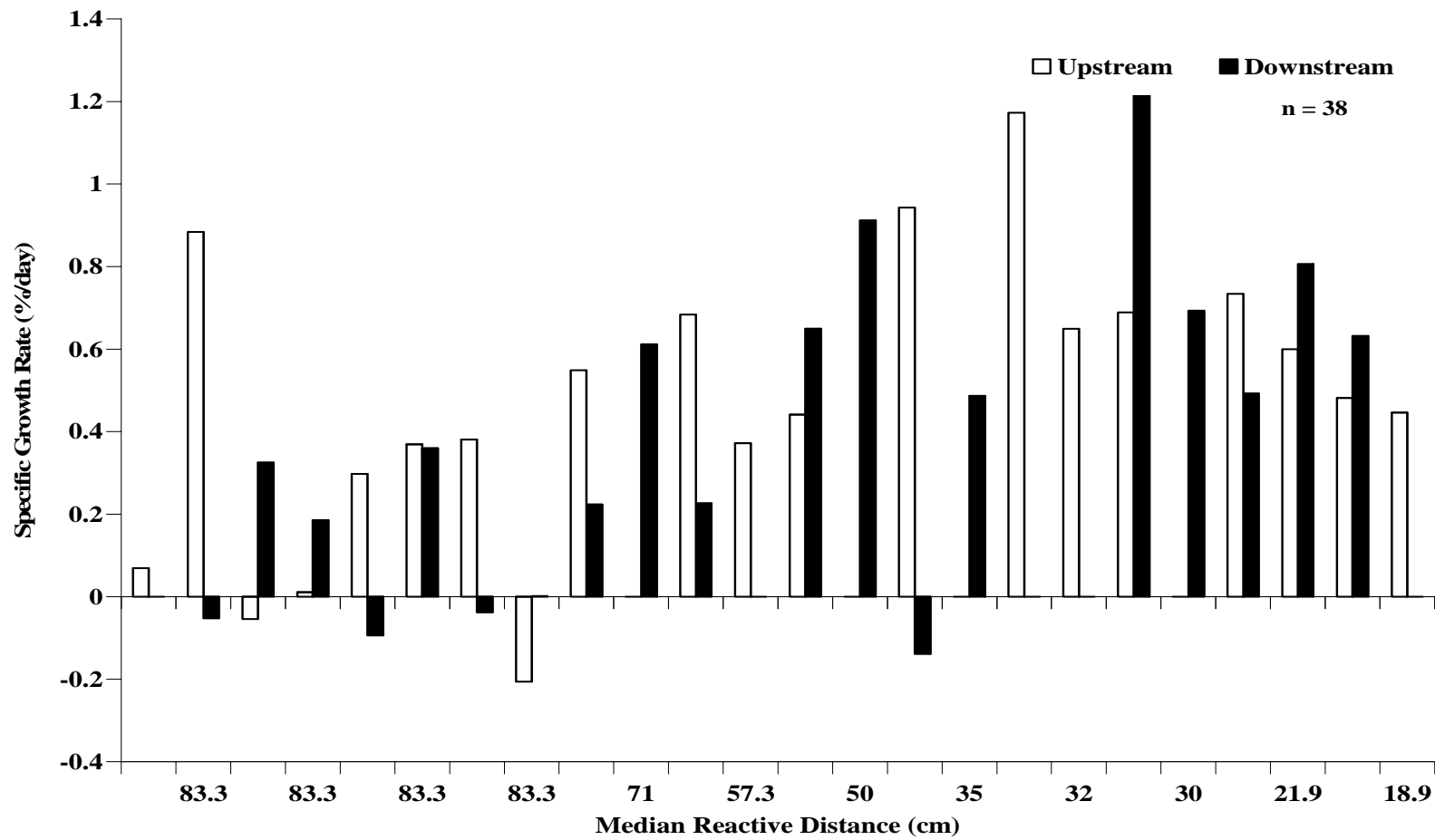


Figure 14. Specific growth rates of rainbow trout/steelhead in Cañon Creek, plotted against median reactive distance, from time of first capture to subsequent recaptures.

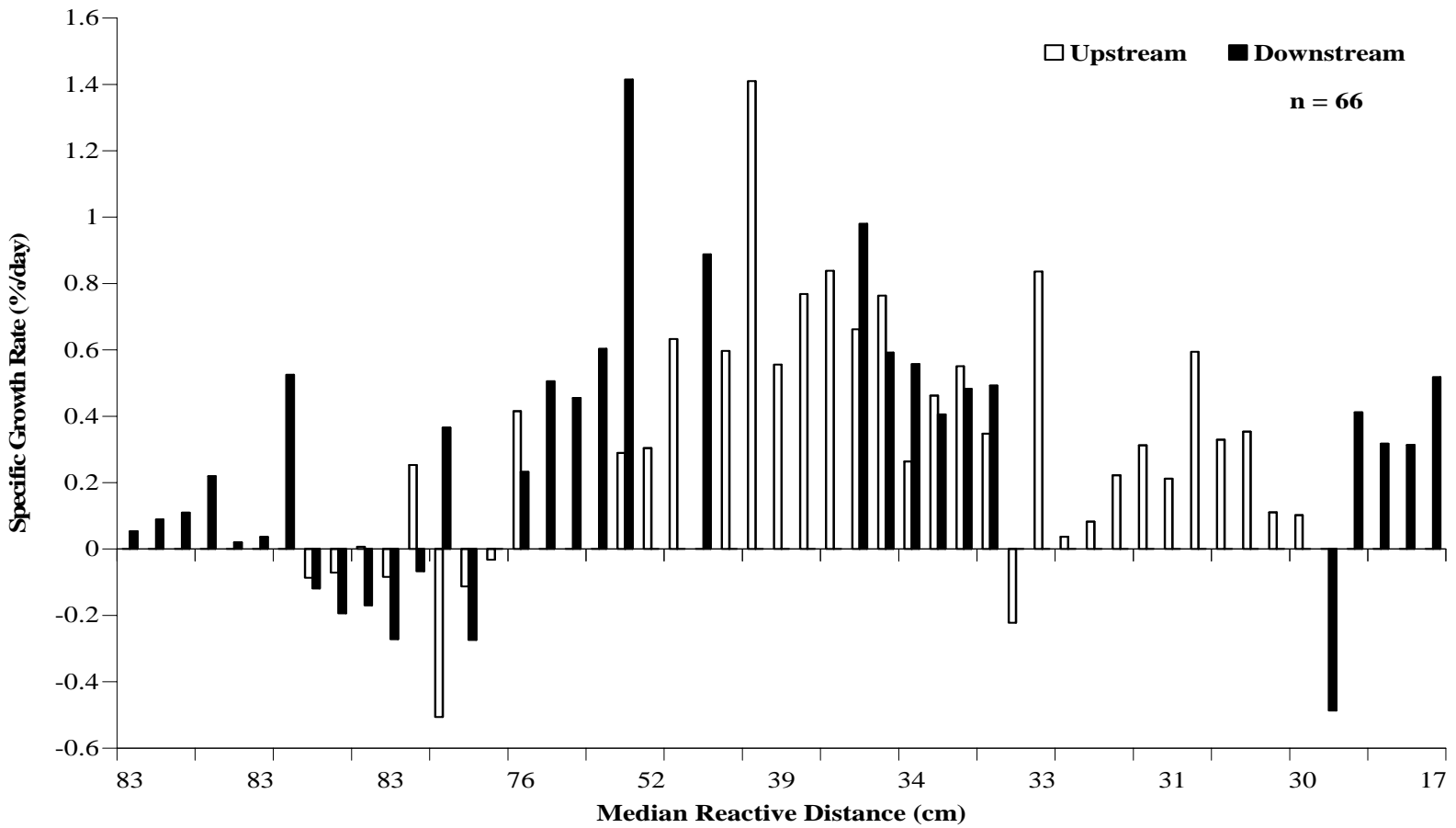


Figure 15. Specific growth rates of rainbow trout/steelhead in Maple Creek, plotted against median reactive distance, from time of first capture to subsequent recaptures.

Movement of Fish within Maple Creek

Movements of rainbow trout/steelhead during storm events in Maple Creek differed between the upstream and downstream reach, but did not vary consistently with turbidity and associated discharge (Figures 16 and 17). In the upstream reach, movements were detected from 78.7 percent of 47 tagged individuals. Of the total number of movements that were detected ($n = 52$), 46 percent were in an upstream direction within the reach, and 32 percent were in a downstream direction within the reach. Twenty-two percent of the upstream fish movements were to the downstream reach. In the more turbid downstream reach, movements were detected from 51.2 percent of 41 tagged individuals. All of the total number of movements that were detected ($n = 32$) were in an upstream direction only. Forty-three percent of these were localized within the reach, and 57 percent involved fish movement to the upstream reach. Four fish moved between reaches multiple times within a single storm event. These all originated from the upstream reach.

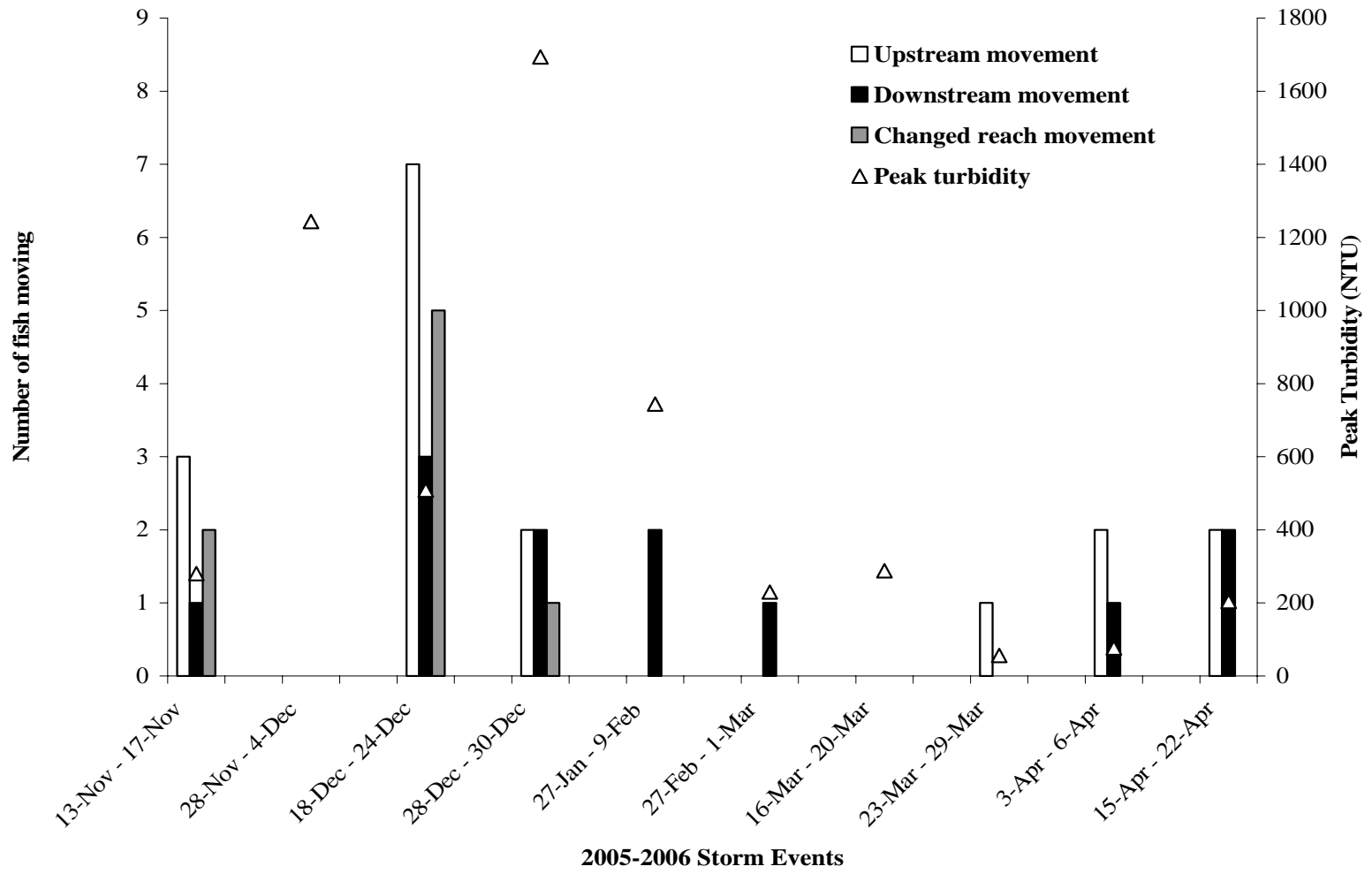


Figure 16. Fish movement and peak turbidity in the upstream reach of Maple Creek during storm events in 2005 and 2006.

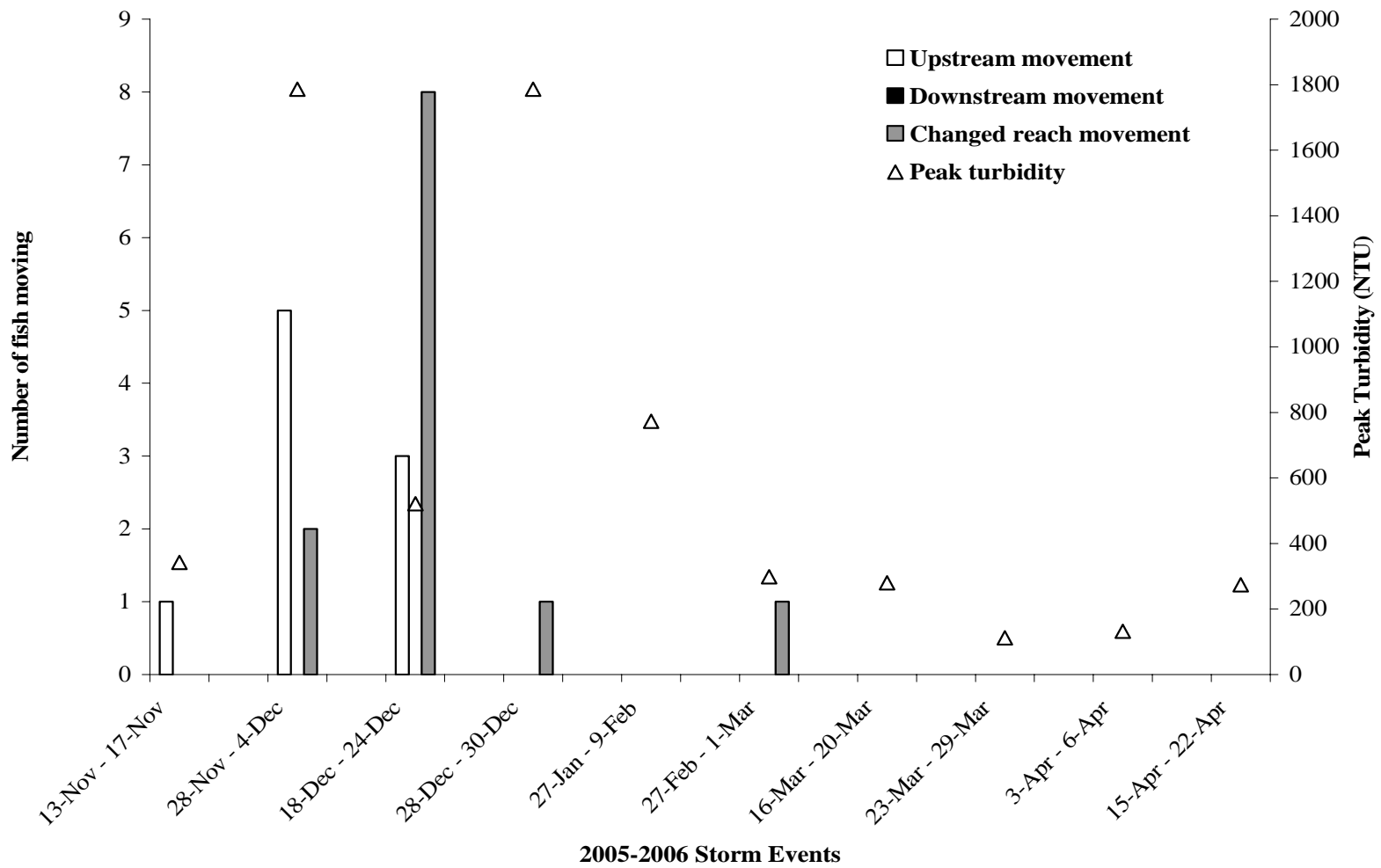


Figure 17. Fish movement and peak turbidity in the downstream reach of Maple Creek during storm events in 2005 and 2006

DISCUSSION

Despite effort to locate differences in storm-generated turbidity between upstream and downstream reaches, I only observed large differences in turbidity between the upstream and downstream reach in 1 of 4 sampling events on Maple Creek. In Cañon Creek, upstream and downstream reaches did not substantially differ on any of the sampling dates. Lack of consistently large differences in turbidity between upstream and downstream reaches diminished my ability to attribute differential fish response between the reaches solely to turbidity. Visible differences in turbidity between upstream and downstream reaches of the two streams were observed during larger storms, but higher flows prevented me from being able to sample at these times. My findings were restricted to turbidities that ranged from 17 – 69 NTU's and discharges of 3.8 – 20m³/ s. Despite these sampling limitations, my findings add to an understanding of salmonid response to turbidity during storm events in natural settings.

For example, stomach fullness data suggested that rainbow trout/steelhead were actively feeding within the ranges of discharge, and turbidity that I sampled, even at low temperatures. On three sampling dates, stream temperatures were below 7 ° C, and stream temperatures on all sampling dates were 10 ° C or lower. Several studies have documented that salmonids continue to feed during low temperatures (e.g. Bremset 2000, Cunjak 1988, Giannico and Healey 1998), with relatively more individuals feeding at night than during the day (Bradford and Higgins 2001, Fraser et al. 1995, Gries et al. 1997, and Meyer and Gregory 2000). Nocturnal feeding has been hypothesized to result from reduced metabolic needs and higher daytime predation risk at cold temperatures

(Heggenes et al. 1999). Even though almost all of the prey items I encountered in fish stomach samples were fully intact, reduced digestion at low temperatures (Koski and Kirchhofer 1982), did not allow me to make inferences about the diel timing of fish feeding.

Irrespective of the timing of fish feeding, the lack of correspondence that I observed between drift biomass and stomach fullness, or between drift composition and diet composition, suggests that fish were not feeding within the water column during storm events. The oligochaetes and salmonid eggs that dominated the diets of fish from both streams were undoubtedly procured by benthic feeding. As such, invertebrate drift is not sufficient as an index of prey availability during periods of high flows and turbidities. Sweka and Hartman (2001b) also observed a lack of correspondence between drift composition and diet composition of brook trout during winter. While stream salmonids typically feed predominantly on drifting invertebrates (Elliott 1973, Waters 1965), drift feeding may become too energetically costly at higher flows and turbidities because swimming performance and reactive distances to prey are reduced.

Provided that benthic prey sources of aquatic or terrestrial origin are available that can be located and consumed by fish, benthic feeding need not inhibit fish growth. Minakawa and Kraft (1999) noted the important role that high rainfall and flooding played in making food available for juvenile coho salmon in both off-channel and creek habitats in late fall and early winter. Tschaplinski and Hartman (1983) found that during small, winter storm events, juvenile coho salmon were able to take advantage of alternative food sources as they moved into inundated vegetation, floodplains, and other

sources of refuge. In this study as well, the majority of fish that I captured were located along cut banks, inundated vegetation and around instream structures, where they presumably had access to nearby supplies of benthic prey that were sufficient to sustain growth.

Studies have reported a negative effect of turbidity on fish growth. Shaw and Richardson (2001) found that growth of rainbow trout fry decreased linearly with the duration of turbidity pulses (0-6 h at 23 NTUs) in short-term (19-d) experiments conducted in streamside channels. Sigler et al. (1984) reported that growth of steelhead and coho salmon was slower and emigration was greater in artificial channels that were maintained at varying levels of turbidity than in channels with clear water. Fish growth in my study was highly variable and showed no detectable relationship with median reactive distance. This finding, however, is likely confounded by seasonal differences in growth. Because fish recaptures were low and I was not willing to risk fish health through frequent electro-shocking, I was unable to measure growth over equal time intervals between reaches. Growth estimates were made over intervals ranging from 34 – 446 days. Strong seasonal growth differences have been documented in stream salmonids in coastal northern California, with growth considerably greater during the winter-spring period than during the summer (Wilzbach et al. 2005). Thus in my study, growth estimates that encompassed periods of reduced or negative growth will likely be lower than estimates made over shorter intervals when growth was higher. Nonetheless, the absence of a relationship between fish growth and median reactive distance suggested

that the effect of turbidity on fish growth was not strong enough to override seasonal differences in growth that may have occurred.

Avoidance of turbidity through emigration that was observed by Sigler et al. (1984) appears to be a common response of all life stages of salmonids (Bisson and Bilby 1982). In this study, I observed considerable movement of fish during storm events, but the extent of movement did not vary consistently with discharge and associated turbidity. Berg and Northcote (1985) found that juvenile coho salmon did not avoid moderate turbidity increases when background levels were low, but exhibited significant avoidance when turbidity exceeded a threshold that was relatively high (> 70 NTU). This level of turbidity was temporarily exceeded, by pulses of sediment, in the storm events used to analyze fish movements. While I found that fish movement from the more turbid downstream reach always gave rise to upstream movement, McLeay et al. (1984, 1987) reported that salmonids moved downstream to avoid turbid areas. The limited number of useable antenna readings that I obtained, coupled with low recapture rates of tagged fish, suggests that fish movement in my study may have been more extensive than I was able to document. Irrespective of the direction in which movement occurred, the likelihood of movement suggests that future studies of salmonid response to turbidity should not address feeding alone (e.g. through field enclosure experiments), but will need to consider feeding and movement together.

LITERATURE CITED

- Abrahams, M. V., and Kattenfeld, M. G. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* 40:169-174.
- ASTM International. 2002. ASTM International Book of Standards, Section Eleven, Water and Environmental Technology, Volume 11.02.
- Barrett J.C., G.D. Grossman, and J. Rosenfeld. 1992. Turbidity induced changes in reactive distance of rainbow trout. *Transactions of the American Fisheries Society* 121:437-443.
- Berg, L. 1982. The effect of exposure to short-term pulses of suspended sediment on the behavior of juvenile salmonids. Pages 177-196 *in* G.F. Hartman et al., editors. *Proceedings of the Carnation Creek workshop: a ten-year review*. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, Canada.
- Berg, L. and T.G. Northcote. 1985. Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon following short-term pulses of suspended sediment. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1410-1417.
- Bisson, P.A. and R.E. Bilby. 1982. Avoidance of Suspended Sediment by Juvenile Coho Salmon. *North American Journal of Fisheries Management* 4: 371-374.
- Bradford, M.J. and P.S. Higgins. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:365–374.
- Bremset, G. 2000. Seasonal and diel changes in behaviour, microhabitat use and preference by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Environmental Biology of Fishes* 59: 163-179.
- Brown, L. R., P. B. Moyle, and R. M. Yoshiyama. 1994. Historical decline and current status of coho salmon in California. *North American Journal of Fisheries Management* 14(2):237-261.
- Busby, P. J., T. C. Wainwright, and G. J. Bryant. 1996. Status review of west coast steelhead from Washington, Oregon and California. NOAA technical memorandum NMFS-NWFSC-27. National Marine Fisheries Service. Seattle, WA. 275 pp.

- Cunjak, R.A., 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Canadian Journal of Fisheries and Aquatic Sciences 45: 2156–2160.
- Davies-Colley, R.J. and D.G Smith. 2001. Turbidity, suspended sediment, and water clarity: A review. The Journal of the American Water Resources Association 37:1085-1101
- Duchrow, R.M. and W.H. Everhart. 1971. Turbidity measurement. Transactions of the American Fisheries Society 4:682-690.
- Elliott, J.M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. Oecologia 12:329-347.
- Everest, F.H., R.L. Beschta, J.C. Scrivener, K.V. Koski, J.R. Sedell, and C.J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98-142 in E.O. Salo and T.W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington Institute of Forest Resources, Seattle, Washington.
- Fraser, N.H.C., J. Heggenes, N.B. Metcalfe, and J.E. Thorpe. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Canadian Journal of Zoology 73:446-451.
- Giannico, G.R. and M.C. Healey. 1998. Effects of flow and food on winter movements of juvenile coho salmon. Transactions of the American Fisheries Society 127: 645-651.
- Gray, J.R. and G.D. Glysson, 2003. Proceedings of the Federal Interagency Workshop on turbidity and other sediment surrogates, April 30-May 2, 2002, Reno, Nevada: U.S. Geological Survey, Circular 1250, 56 p.
- Gries, G., K.G. Whalen, F. Juanes, and D.L. Parrish. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. Canadian Journal of Fisheries and Aquatic Sciences 54:1408-1413.
- Gore, J.A. 1996. Discharge Measurements and Streamflow Analysis. Pages 53-74. In F.R. Hauer and G.A. Lamberti, editors. Methods in stream ecology. Academic Press. Burlington, MA 01803.

- Gregory, R.S. 1988. Effects of turbidity on benthic foraging and predation risk in juvenile chinook salmon. Pages 65-73 in C.A. Simenstad, editor. Effects of dredging on anadromous Pacific coast fishes. Workshop proceedings, September 8-9, 1988. Washington Sea Grant Program, University of Washington, Seattle, USA.
- Gregory, R.S. and C.D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275-285.
- Gregory, R.S. and T.G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*O. tshawytscha*) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences 50:233-240.
- Heggenes, J., J.L. Bagliniere and R.A. Cunjak. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8:1-21.
- Johnson, J.E. and R.T. Hines, 1999. Effect of suspended sediment on vulnerability of young razorback suckers to predation. Transactions of the American Fisheries Society 128(4):648-655.
- Koski, K.V. and D.A. Kirchhofer. 1982. A stream ecosystem in an old-growth forest in Southeast Alaska. Part IV: food of juvenile coho salmon, (*O. kisutch*) in relation to abundance of drift and benthos. Pages 81-87 in W.R. Meehan, T.R. Merrell Jr. and T.A. Hanley, editors. Proceedings of a symposium on fish and wildlife relationships in old-growth forests, April, 1982. Juneau, Alaska.
- Lloyd, D.S. 1987. Turbidity as a water quality standard for salmonid habitats in Alaska. North American Journal of Fisheries Management 7:34-45.
- McLeay, D.J., G.L. Ennis, I.K. Birtwell and G.F. Hartman. 1984. Effects on Arctic grayling (*Thymallus arcticus*) of prolonged exposure to Yukon placer mining sediment: a laboratory study. Canadian Technical Report of Fisheries and Aquatic Sciences 1241.
- McLeay, D.J., I.K. Birtwell, G.F. Hartman and G.L. Ennis. 1987. Responses of Arctic grayling (*Thymallus arcticus*) to acute and prolonged exposure to Yukon placer mining sediment. Canadian Journal of Fisheries and Aquatic Sciences 44:658-673.
- Meyer, K.A. and J.S. Gregory. 2000. Evidence of concealment behavior by adult rainbow and brook trout in winter. Ecology of Freshwater Fish 9:138-144.

- Miller, B.A. and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546-559.
- Minakawa, N. and G.F. Kraft. 1999. Fall and winter diets of juvenile coho salmon in a small stream and an adjacent pond in Washington State. *Journal of Freshwater Ecology* 14:249-254.
- Mount, J.F. 1995. California rivers and streams: the conflict between fluvial process and land use. University of California Press, Berkeley CA.
- Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- Newcombe, C.P. and D.D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management* 11:72-82.
- North Coast Regional Water Quality Control Board. 2001. Water quality control plan for the Northcoast region. North Coast Regional Water Quality Control Board, Santa Rosa, CA.
- Rosenberg, D.M. and A.P. Wiens. 1978. Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river. *Water Research* 12:753-763.
- Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford, and C.P. Hawkins. 1990. Role of refugia in recovery from disturbance: modern fragmented and disconnected river systems. *Environmental Management* 14:711-724.
- Servizi, J.A. and D.W. Martens. 1992. Sublethal responses of coho salmon (*Oncorhynchus kisutch*) to suspended sediments. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1389-1395.
- Shaw E.A. and J.S. Richardson. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2213-2221.
- Sigler, J.W., T.C. Bjornn, and F.H. Everest. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. *Transactions of the American Fisheries Society* 113:142-150.

- Sweka, J.A. and K.J. Hartman. 2001a. Influence of turbidity on brook trout reactive distance and foraging success. *Transactions of the American Fisheries Society* 130:138-146.
- Sweka, J.A. and K.J. Hartman. 2001b. Fall and winter brook trout prey selection and daily ration. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 55: 8-22.
- Tschaplinski, P.J. and G.F. Hartman. 1983. Winter distribution of juvenile coho salmon (*O. kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwintering survival. *Canadian Journal of Fisheries and Aquatic Sciences* 40:452-461.
- USGS. 2000. Guidelines and standard procedures for continuous water-quality monitors: site selection, field operation, calibration, record computation, and reporting. R.J. Wagner, H.C. Matraw, G.F. Fritz and B.A. Smith. U.S. Geological Survey Techniques of Water-Resources Investigations Report 00-4252 (<http://water.usgs.gov/pubs/wri/wri004252/>). U.S. Geological Survey, Reston, Virginia, USA.
- Waters, T.F. 1965. Invertebrate drift-ecology and significance to stream fishes. Pages 121-134 *in* T.G. Northcote, editor. Symposium on salmon and trout in streams. H.R. MacMillan Lecture Series, University of British Columbia, Institute of Fisheries, Vancouver, BC.
- Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society. Bethesda, Maryland.
- Wilzbach, M.A., B.C. Harvey, J.L. White, and R.J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 62:58-67.

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Appendix A. Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$.

Coefficient a	Coefficient b	Invertebrate taxa	Life stage
0.001230	3.5800	Ephemeroptera	Adult
0.001849	3.4570	Ephemeroptera	Larvae
0.002809	3.0360	Plecoptera	Adult
0.004303	3.0610	Plecoptera	Larvae
0.017650	2.9030	Trichoptera	Adult
0.002299	3.0790	Trichoptera	Larvae
0.037140	2.3660	Diptera	Adult
0.001135	2.7508	Diptera	Larvae
0.000115	3.4780	Diptera	Pupae
0.002581	2.9930	Collembola	Adult
0.004303	3.0610	Isopoda	Adult
0.003300	2.3200	Diplopoda	Adult
0.003300	2.3200	Chilopoda	Adult
0.004303	3.0610	Amphipoda	Adult
0.004303	3.0610	Megaloptera	Larvae
0.017650	2.9030	Lepidoptera	Adult
0.047360	2.6810	Coleoptera	Adult
0.001453	3.6110	Coleoptera	Larvae
0.085350	0.2160	Coleoptera (terrestrial)	Adult
0.044780	2.9290	Araneae	Adult
0.020838	2.4070	Hymenoptera	Adult
0.020838	2.4070	Hymenoptera	Larvae
0.039726	2.7610	Acari	Adult
0.049887	2.2700	Hemiptera	Adult
0.049887	2.2700	Hemiptera	Larvae
0.036589	2.6960	Homoptera	Adult
0.036589	2.6960	Homoptera	Larvae
0.002809	3.0360	Thysanoptera	Adult

Appendix A. Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$ (continued).

Coefficient a	Coefficient b	Invertebrate taxa	Life stage
0.001135	2.7508	Pulmonata	Adult
0.287200	1.0000	Hirudinea	Adult
0.003300	2.3200	Oligochaeta	Adult
0.001423	3.0525	Dicamptodontidae	Larvae
0.078882	3.0525	Salmonidae	Fry
0.001423	3.0525	Salmonid eggs	egg

Appendix B. Specific growth rates (G) of rainbow trout/steelhead in the upstream and downstream reaches of Cañon Creek.

Reach	Capture date	Re-capture date	Weight before (g)	Weight after (g)	Total days	Median Reactive Distance (cm)	G (%/d)
Upstream	1-Aug-2005	7-Oct-2005	4.10	5.25	67	83	0.369
Upstream	1-Aug-2005	7-Oct-2005	23.20	23.37	67	83	0.011
Upstream	1-Aug-2005	7-Oct-2005	7.20	8.79	67	83	0.298
Upstream	1-Aug-2005	7-Oct-2005	7.60	7.33	67	83	-0.054
Upstream	1-Aug-2005	7-Oct-2005	5.20	7.51	67	83	0.549
Upstream	1-Aug-2005	7-Oct-2005	20.20	17.60	67	83	-0.206
Upstream	1-Aug-2005	7-Oct-2005	6.40	8.26	67	83	0.381
Upstream	1-Aug-2005	7-Oct-2005	5.10	9.22	67	83	0.884
Upstream	1-Aug-2005	7-Oct-2005	10.10	10.58	67	83	0.069
Upstream	5-Jan-2005	31-Mar-2005	9.60	21.40	85	46	0.943
Upstream	31-Mar-2005	1-Aug-2005	10.00	15.80	123	57	0.372
Upstream	5-Jan-2006	27-Mar-2006	8.50	12.20	81	19	0.446
Upstream	7-Oct-2005	5-Jan-2006	6.02	17.30	90	32	1.173
Upstream	5-Jan-2005	5-Jan-2006	5.10	61.80	365	59	0.683
Upstream	7-Oct-2005	27-Mar-2006	4.74	10.80	171	22	0.482
Upstream	7-Oct-2005	27-Mar-2006	5.70	15.90	171	22	0.600
Upstream	7-Oct-2005	27-Mar-2006	7.75	27.20	171	22	0.734
Upstream	7-Oct-2005	1-Jun-2006	5.02	25.70	237	32	0.689
Upstream	7-Oct-2005	1-Jun-2006	5.07	23.60	237	32	0.649
Upstream	1-Aug-2005	1-Jun-2006	15.80	60.40	304	50	0.441
Downstream	1-Aug-2005	6-Oct-2005	10.90	12.63	66	83	0.223
Downstream	1-Aug-2005	6-Oct-2005	11.40	11.41	66	83	0.001
Downstream	1-Aug-2005	6-Oct-2005	24.30	23.70	66	83	-0.038
Downstream	1-Aug-2005	6-Oct-2005	6.20	7.86	66	83	0.359
Downstream	1-Aug-2005	6-Oct-2005	23.20	21.81	66	83	-0.094
Downstream	1-Aug-2005	6-Oct-2005	16.20	18.31	66	83	0.186
Downstream	1-Aug-2005	6-Oct-2005	30.00	37.17	66	83	0.325
Downstream	1-Aug-2005	6-Oct-2005	11.80	11.40	66	83	-0.052

Appendix B. Specific growth rates (G) of rainbow trout/steelhead in the upstream and downstream reaches of Cañon Creek (continued).

Reach	Capture Date	Re-capture date	Weight before (g)	Weight after (g)	Total Days	Median Reactive Distance (cm)	G (%/d)
Downstream	27-Mar-2006	1-Jun-2006	6.30	11.50	66	50	0.912
Downstream	27-Mar-2006	1-Jun-2006	16.80	25.80	66	50	0.650
Downstream	31-Mar-2005	1-Jun-2005	5.30	11.60	62	32	1.263
Downstream	31-Mar-2005	1-Aug-2005	18.40	24.30	123	59	0.226
Downstream	31-Mar-2005	6-Oct-2005	5.50	17.47	189	72	0.612
Downstream	5-Jan-2006	27-Mar-2006	18.80	16.80	81	49	-0.139
Downstream	6-Oct-2005	5-Jan-2006	10.08	15.70	91	35	0.487
Downstream	6-Oct-2005	27-Mar-2006	11.40	33.80	172	20	0.632
Downstream	6-Oct-2005	27-Mar-2006	7.35	29.40	172	20	0.806
Downstream	6-Oct-2005	27-Mar-2006	5.32	12.40	172	20	0.492
Downstream	6-Oct-2005	1-Jun-2006	6.82	35.50	238	30	0.693

Appendix C. Specific growth rates (G) of rainbow trout/steelhead in the upstream and downstream reaches of Maple Creek.

Reach	Capture date	Re-capture date	Weight before (g)	Weight after (g)	Total days	Median Reactive Distance (cm)	G (%/d)
Upstream	5-Aug-2005	30-Sep-2005	4.90	5.81	56	52	0.304
Upstream	5-Aug-2005	30-Sep-2005	7.90	9.29	56	64	0.289
Upstream	5-Aug-2005	30-Sep-2005	6.30	7.26	56	83	0.253
Upstream	5-Aug-2005	30-Sep-2005	7.00	6.68	56	83	-0.084
Upstream	5-Aug-2005	30-Sep-2005	5.10	5.12	56	83	0.007
Upstream	5-Aug-2005	30-Sep-2005	13.40	13.16	56	78	-0.032
Upstream	5-Aug-2005	30-Sep-2005	24.60	23.64	56	83	-0.071
Upstream	5-Aug-2005	30-Sep-2005	23.20	29.28	56	76	0.416
Upstream	5-Aug-2005	30-Sep-2005	24.70	23.53	56	83	-0.087
Upstream	5-Aug-2005	30-Sep-2005	45.30	42.54	56	83	-0.112
Upstream	5-Aug-2005	30-Sep-2005	46.00	34.64	56	83	-0.506
Upstream	18-Apr-2006	7-Jun-2006	4.20	8.50	50	41	1.410
Upstream	13-Mar-2006	18-Apr-2006	7.50	7.60	36	33	0.037
Upstream	13-Mar-2006	18-Apr-2006	7.40	10.00	36	33	0.836
Upstream	13-Mar-2006	18-Apr-2006	3.90	3.60	36	33	-0.222
Upstream	11-May-2005	30-Sep-2005	9.40	23.09	142	48	0.633
Upstream	7-Feb-2006	13-Mar-2006	25.50	26.40	34	30	0.102
Upstream	13-Mar-2006	7-Jun-2006	9.50	18.40	86	39	0.769
Upstream	20-Jan-2006	7-Feb-2006	30.10	25.10	18	17	-1.009
Upstream	14-Apr-2005	30-Sep-2005	5.10	14.00	169	41	0.598
Upstream	22-Mar-2005	11-May-2005	7.90	9.40	50	34	0.348
Upstream	7-Feb-2006	18-Apr-2006	6.70	7.10	70	33	0.083
Upstream	7-Feb-2006	7-Jun-2006	10.30	22.80	120	39	0.662
Upstream	7-Feb-2006	7-Jun-2006	18.50	50.60	120	39	0.838
Upstream	22-Mar-2005	5-Aug-2005	11.60	24.70	136	39	0.556
Upstream	30-Sep-2005	7-Feb-2006	4.23	6.70	130	31	0.354
Upstream	30-Sep-2005	7-Feb-2006	13.86	18.50	130	31	0.222
Upstream	30-Sep-2005	7-Feb-2006	6.74	14.60	130	31	0.595
Upstream	30-Sep-2005	13-Mar-2006	9.09	10.90	164	31	0.111

Appendix C. Specific growth rates (G) of rainbow trout/steelhead in the upstream and downstream reaches of Maple Creek (continued).

Reach	Capture date	Re-capture date	Weight before (g)	Weight after (g)	Total days	Median Reactive Distance (cm)	G (%/d)
Upstream	30-Sep-2005	13-Mar-2006	4.78	8.20	164	31	0.329
Upstream	30-Sep-2005	13-Mar-2006	6.50	9.20	164	31	0.212
Upstream	30-Sep-2005	13-Mar-2006	23.53	39.30	164	31	0.313
Upstream	30-Sep-2005	7-Jun-2006	9.20	36.50	250	34	0.551
Upstream	30-Sep-2005	7-Jun-2006	4.80	32.40	250	34	0.764
Upstream	30-Sep-2005	7-Jun-2006	47.30	150.10	250	34	0.462
Upstream	30-Sep-2005	7-Jun-2006	28.46	55.00	250	34	0.264
Downstream	5-Aug-2005	29-Sep-2005	4.40	5.38	55	83	0.366
Downstream	5-Aug-2005	30-Sep-2005	5.70	7.65	56	83	0.525
Downstream	5-Aug-2005	30-Sep-2005	6.90	6.98	56	83	0.021
Downstream	5-Aug-2005	30-Sep-2005	5.20	5.88	56	83	0.219
Downstream	5-Aug-2005	30-Sep-2005	5.20	5.53	56	83	0.110
Downstream	5-Aug-2005	30-Sep-2005	5.90	6.20	56	83	0.089
Downstream	5-Aug-2005	30-Sep-2005	23.40	21.89	56	83	-0.119
Downstream	5-Aug-2005	29-Sep-2005	26.70	25.73	55	83	-0.067
Downstream	5-Aug-2005	29-Sep-2005	35.80	30.83	55	83	-0.272
Downstream	5-Aug-2005	30-Sep-2005	32.60	33.59	56	83	0.053
Downstream	5-Aug-2005	30-Sep-2005	17.60	17.96	56	83	0.036
Downstream	5-Aug-2005	29-Sep-2005	43.00	38.66	55	83	-0.193
Downstream	5-Aug-2005	29-Sep-2005	23.00	19.78	55	83	-0.274
Downstream	5-Aug-2005	30-Sep-2005	22.00	20.00	56	83	-0.170
Downstream	18-Apr-2006	6-Jun-2006	5.90	11.80	49	62	1.415
Downstream	11-May-2005	5-Aug-2005	21.30	35.80	86	68	0.604
Downstream	11-May-2005	29-Sep-2005	18.00	24.97	141	79	0.232
Downstream	7-Feb-2006	13-Mar-2006	5.90	5.00	34	25	-0.487
Downstream	13-Mar-2006	6-Jun-2006	21.20	45.10	85	44	0.888
Downstream	7-Feb-2006	6-Jun-2006	4.70	15.10	119	39	0.981
Downstream	21-Mar-2005	11-May-2005	33.40	43.50	51	17	0.518
Downstream	21-Mar-2005	29-Sep-2005	10.80	28.51	192	69	0.506

Appendix C. Specific growth rates (G) of rainbow trout/steelhead in the upstream and downstream reaches of Maple Creek (continued).

Reach	Capture date	Re-capture date	Weight before (g)	Weight after (g)	Total days	Median Reactive Distance (cm)	G (%/d)
Downstream	21-Mar-2005	30-Sep-2005	8.50	20.47	193	69	0.455
Downstream	30-Sep-2005	7-Feb-2006	21.89	32.90	130	23	0.313
Downstream	30-Sep-2005	13-Mar-2006	4.87	8.20	164	23	0.318
Downstream	29-Sep-2005	13-Mar-2006	10.74	21.20	165	23	0.412
Downstream	30-Sep-2005	6-Jun-2006	5.58	19.00	249	34	0.492
Downstream	30-Sep-2005	6-Jun-2006	5.50	18.30	249	34	0.483
Downstream	30-Sep-2005	6-Jun-2006	7.57	20.80	249	34	0.406
Downstream	30-Sep-2005	6-Jun-2006	9.01	36.10	249	34	0.557
Downstream	30-Sep-2005	6-Jun-2006	6.73	29.40	249	34	0.592