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[Note]

Winter Feeding Success of Stream Trout under Different Streamflow and Turbidity Conditions

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Abstract.—To investigate the relationship between turbidity and trout feeding success in natural systems, we sampled the stomach contents of resident rainbow trout *Oncorhynchus mykiss* and coastal cutthroat trout *O. clarkii clarkii* under different streamflow and turbidity conditions during winter in two northwestern California streams (total sample size = 161). Feeding success generally did not differ sharply for fish collected under low versus high streamflow and turbidity conditions. Bioenergetics modeling suggested that feeding success on average did not reach maintenance levels for seven of eight sets of samples, but extensive feeding on oligochaetes during one period of elevated streamflow resulted in positive energy balances. Occasional peaks in food intake could greatly influence the energy budgets and growth of trout in mild-winter systems. Under some natural conditions, trout appear able to achieve relatively high feeding success when turbidity limits visibility.

Stream-dwelling trout *Oncorhynchus* spp. can feed throughout the winter (Maciolek and Needham 1952; Cunjak and Power 1987; Cunjak et al. 1987), although low temperatures (<5°C) can impede assimilation (Cunjak et al. 1987). However, trout in the southern portions of their native ranges live in systems with comparatively mild winter temperatures. Particularly if temperatures are warm enough to permit relatively efficient assimilation, the winter energetics of trout in such systems might differ substantially from the energetics of trout in colder regions (Cada et al. 1987).

Although higher water temperatures increase assimilation efficiency, metabolic demands also rise. Can trout in warmer systems obtain adequate food to meet these demands? Drift rates of aquatic invertebrates can reach annual maxima during high winter streamflows in streams with relatively warm winter temperatures (Romero et al. 2005), but turbidity often increases sharply with discharge. While Arndt et al. (2002) documented the ability of Atlantic salmon *Salmo salar* to feed during summer floods when turbidity peaked in the range of 40–60 nephelometric turbidity units (NTU), turbidity in streams draining managed lands in western North America commonly exceeds this range, such that feeding by salmonids may be impaired. Additionally, while terrestrial invertebrates constitute a substantial portion of the annual energy budget for some stream-dwelling trout (Kawaguchi and Nakano 2001), in some streams terrestrial input drops to a minimum in winter (Kawaguchi and Nakano 2001; Romero et al. 2005).

In this study, we quantified winter feeding success for trout in two streams with relatively mild winters. Our study included an attempt to estimate the effects of streamflow and associated elevated turbidity on feeding success. Specifically, we compared stomach contents from resident rainbow trout *O. mykiss* and coastal cutthroat trout *O. clarkii clarkii* under paired high and low streamflow and turbidity conditions in two northwestern California streams where streamflow and turbidity were continuously monitored.

Study Sites

Jacoby Creek drains into Humboldt Bay in the Coast Range of northwestern California. We collected fish for this study in a reach at an elevation of around 250 m draining about 1,500 ha. The stream channel (average width, about 4 m) in the sampling reach alternates between shallow riffles with a gradient of 1–2% and pools with maximum depths around 1.25 m. The substrate is predominantly gravel and cobble. The drainage receives most precipitation as rain from October to April, and annual rainfall exceeds 120 cm. Summer base flow is less than 0.05 m^3/s, and winter storms produce discharges greater than 10 m^3/s. Bankfull discharge (recurrence interval, 1.5 years) is approximately 14 m^3/s. Turbidity often exceeds 500 nephelometric turbidity units (NTU) during storms and remains above 100 NTU for extended periods (>1 d). The slope of the turbidity-to-discharge relationship is steep [turbidity (NTU) = 46·discharge (m^3/s) (r^2 = 0.91)]. Water temperatures in Jacoby Creek remain fairly mild year round, rarely dropping below 6°C in winter or exceeding 18°C in summer. Daily mean temperatures on the days we collected fish for this study ranged from 7.2°C to 12.3°C.

Little Jones Creek drains into the Middle Fork Smith River in the Siskiyou Mountains of northwestern California. We collected fish for this study in a reach

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at an elevation of about 300 m draining about 2,200 ha. The stream channel (average width, about 5 m) in the sampling reach consists of long stretches of riffle and run habitat with gradients of around 2% punctuated by pools with maximum depths between 1.5 and 2.0 m. Cobble and gravel are the most common substrata. The drainage receives most precipitation as rain from October to April, and annual rainfall exceeds 335 cm. Summer base flow is less than 0.20 m^3/s, and winter storms produce discharges greater than 15 m^3/s. Bankfull discharge is approximately 22 m^3/s. Turbidity in Little Jones Creek exceeds 100 NTU for only short periods (<1 d) during storms. The turbidity : discharge relationship is comparatively flat, the slope being only 2.5 (r^2 = 0.68). Similar to Jacoby Creek, water temperatures in Little Jones Creek typically fall between 6°C and 18°C; the means for the days we sampled fish for this study ranged from 7.3°C to 8.9°C.

The sampling reaches in Jacoby and Little Jones creeks lie upstream of natural barriers to upstream passage of fish. The fish assemblages in the study reaches consist solely of resident populations of trout: rainbow trout in Jacoby Creek and coastal cutthroat trout in Little Jones Creek.

Methods

To investigate the effects of different streamflow and turbidity conditions on the winter feeding success of trout in our study streams, we collected stomach contents on different dates paired by contrasting physical conditions but separated by as little time as possible. Using a backpack electrofisher to capture fish, we collected two paired sets of samples in each creek between 11 January 2000 and 26 March 2003. We made all fish collections between 1030 and 1600 hours. Collections at high and low streamflows and turbidity within each pair were separated by 7 to 24 d. The sample collections included stomach contents of trout from small (fork length [FL] < 100 mm; $N = 9$–13 trout) and large (FL $\geq$ 100 mm; $N = 9$ or 10 trout) size-classes. The two size-classes represented age-0 versus age-1 and older trout. We sedated fish with sodium bicarbonate; recorded FL to the nearest millimeter and wet mass to the nearest 0.01 g; and collected stomach contents by means of gastric lavage. Gastric lavage has had 98% removal efficiency when tested on salmonids in the size ranges we sampled (Light et al. 1983). We preserved stomach contents with 70% ethanol. After fully recovering in a bucket of freshwater, each fish was returned to the habitat in which it was captured.

Laboratory processing of stomach contents included identification, enumeration, and measurement of invertebrates using a dissecting microscope with an ocular micrometer. We converted individual body lengths to estimates of dry mass by applying taxon-specific relationships provided by K. W. Cummins (Humboldt State University Institute for River Ecosystems) and M. A. Wilzbach (U.S. Geological Survey California Cooperative Fishery Research Unit). Because many of the oligochaetes we found in samples were broken into pieces, we dried and weighed oligochaetes rather than relying on body length : dry mass relationships. We summarized the data by fish size-class (FL < 100 mm and FL $\geq$ 100 mm). To describe stomach fullness, we computed the mean dry mass of stomach contents per wet mass of fish (mg/g). We also summarized the taxonomic composition of the diet by mass, pooling samples by size-class and sample collection.

To evaluate stomach contents samples in terms of energetics, we first estimated minimum maintenance requirements (the energy required to maintain mass for 1 d) by applying a simplified version of the Wisconsin bioenergetics model (Hanson et al. 1997) with parameters for rainbow trout (Railsback and Rose 1999). The model we used includes standard and active metabolism but ignores egestion and excretion. For each sample set and size-class, we ran the model for a 1-d time step using a fish with the mean body mass for that sample collection. For the range of water temperatures during the sample periods in this study, gut evacuation in trout requires around 3 d (Sweka et al. 2004), so in these calculations we used the mean water temperature from midnight 2 d before the sampling time to the sampling time. We further assumed that fish incurred costs of swimming at 20 cm/s for 4 h/d. Our day and night winter observations of cutthroat trout in Little Jones Creek provided the basis for this assumption; estimates of overall energetic requirements of the fish were not highly sensitive to the extent of swimming activity, in that swimming costs under the assumption above contributed only about 12% of estimated daily maintenance energy requirements. We then estimated daily energy intake from the sampled stomach contents by assuming 20 J/dry mg (Cummins and Wuycheck 1971) and then multiplying by an assimilation efficiency factor (0.72) from Elliott (1976) and a temperature-dependent gastric evacuation rate from Sweka et al. (2004).

For the study duration, streamflow and turbidity readings were taken every 10 min at gauge stations located in the sampling reach of each stream. To characterize streamflow and turbidity conditions during the time fish were consuming the items we collected in the stomach samples, we again used the time period from midnight 2 d before sampling to the time of sampling. We restricted the turbidity characterization to readings taken between sunrise and sunset, assuming

turbidity would significantly affect trout feeding primarily during daylight hours. To further refine our description of conditions, we computed weighted means for both turbidity and streamflow, deriving weightings from a temperature-specific equation estimating the proportion of an initial meal remaining over time (Sweka et al. 2004). The time intervals used to compute weighted mean turbidity included sunrise to sample time on the day of sampling, daylight hours on the previous day, and daylight hours 2 d prior. For streamflow, we did not exclude nighttime, so we took each interval back to midnight on the previous day. Weightings were calculated using the midpoints of each time interval. For example, weighting for streamflow data for one of the sampling periods was 0.49 for the day of sampling, 0.34 for the day before, and 0.17 for 2 d prior.

Results

We collected 161 samples of trout stomach contents across a broad range of physical conditions in Jacoby and Little Jones creeks. While weighted mean turbidity did not exceed 8 NTU before all four low-streamflow collections, weighted mean turbidity exceeded 69 NTU before three of the four high-streamflow collections (Figure 1). These differences in turbidity probably reflect strong differences in reactive distance to drifting prey for the trout we sampled (Table 1). The physical conditions during the first pair of collections from Little Jones Creek reflected the weakest contrast within pairs: streamflow substantially exceeded winter base flow on the "low streamflow/turbidity" sampling date, while weighted mean turbidity equaled 21 NTU on the "high streamflow/turbidity" sampling date (Figure 1).

The stomach contents for all sample collections indicated that resident trout in Jacoby and Little Jones creeks fed during winter at both low and high streamflow and turbidity (Figure 1). We did not detect consistent differences in dry mass of stomach contents associated with low versus high streamflows (Figure 1). The first pair of samples from Little Jones Creek (LJ Pair 1), however, differed from the other pairs of samples. For the dry mass of stomach contents from smaller fish (FL < 100 mm), LJ Pair 1 means did not differ between streamflows (t-test: df = 17, $P = 0.31$) but were three- to fourfold higher than the means for all other collections (Figure 1). For samples from larger fish in LJ Pair 1, the mean dry mass of stomach contents at high streamflow exceeded the accompanying value for low streamflow (and all other sample collections) by at least threefold.

Diet components varied considerably, both within and between pairs (Figure 2). In general, however, aquatic invertebrates tended to dominate the diet during

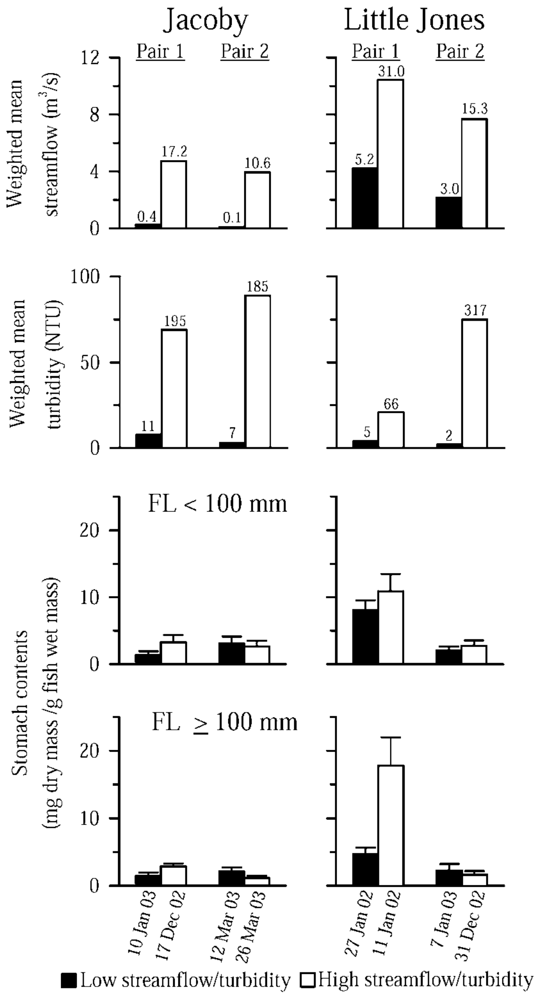

FIGURE 1.—Stomach contents by size-class with accompanying weighted mean streamflow and turbidity before sampling for low- and high-streamflow pairings in Jacoby and Little Jones creeks. The numbers above the streamflow and turbidity bars indicate the peak values over the 3 d before sampling; the error bars for stomach content data indicate SEs.

low discharges, Ephemeroptera nymphs and Trichoptera larvae forming large proportions of most samples. During high streamflow, terrestrial oligochaetes were the largest component of the diet, constituting on average 43% of the dry mass consumed. Oligochaetes made up 90% of the stomach contents in the sample set with the highest mean relative dry mass consumed.

The ratios of mean stomach content energy values to estimated maintenance requirements revealed that the trout in our study probably experienced energy deficits throughout the winter (Table 1). We estimated that for all but LJ Pair 1, the energy value of the mean stomach contents represented less than half of the daily

TABLE 1.—Physical conditions and trout feeding success during pairs of sampling periods in Jacoby and Little Jones creeks. The weighted mean reactive distances were computed with methods parallel to those for weighted mean turbidity (described in the text) and relied on the reactive-distance-to-turbidity equation in Sweka and Hartman (2001) plus the assumption of a reactive distance of 9 cm with turbidity ≥51 NTU.

	Jacoby Creek				Little Jones Creek			
	Pair 1		Pair 2		Pair 1		Pair 2	
Variable	Jan 10, 2003	Dec 17, 2002	Mar 12, 2003	Mar 26, 2003	Jan 27, 2000	Jan 11, 2000	Jan 7, 2003	Dec 31, 2002
Streamflow category	Low	High	Low	High	Low	High	Low	High
Mean (range) temperature (°C)	11.6 (10.1–13.5)	8.6 (7.0–10.3)	7.9 (6.9–9.0)	8.3 (7.4–9.3)	8.0 (7.0–8.9)	7.8 (7.2–8.6)	8.6 (7.8–10.3)	8.8 (8.4–9.3)
Weighted mean reactive distance (cm)	49	12	71	15	67	32	80	17
Proportion of daily maintenance requirement met by stomach contents								
FL < 100 mm	0.1	0.3	0.3	0.3	0.9	1.2	0.2	0.3
FL ≥ 100 mm	0.2	0.4	0.3	0.2	0.8	2.8	0.3	0.2

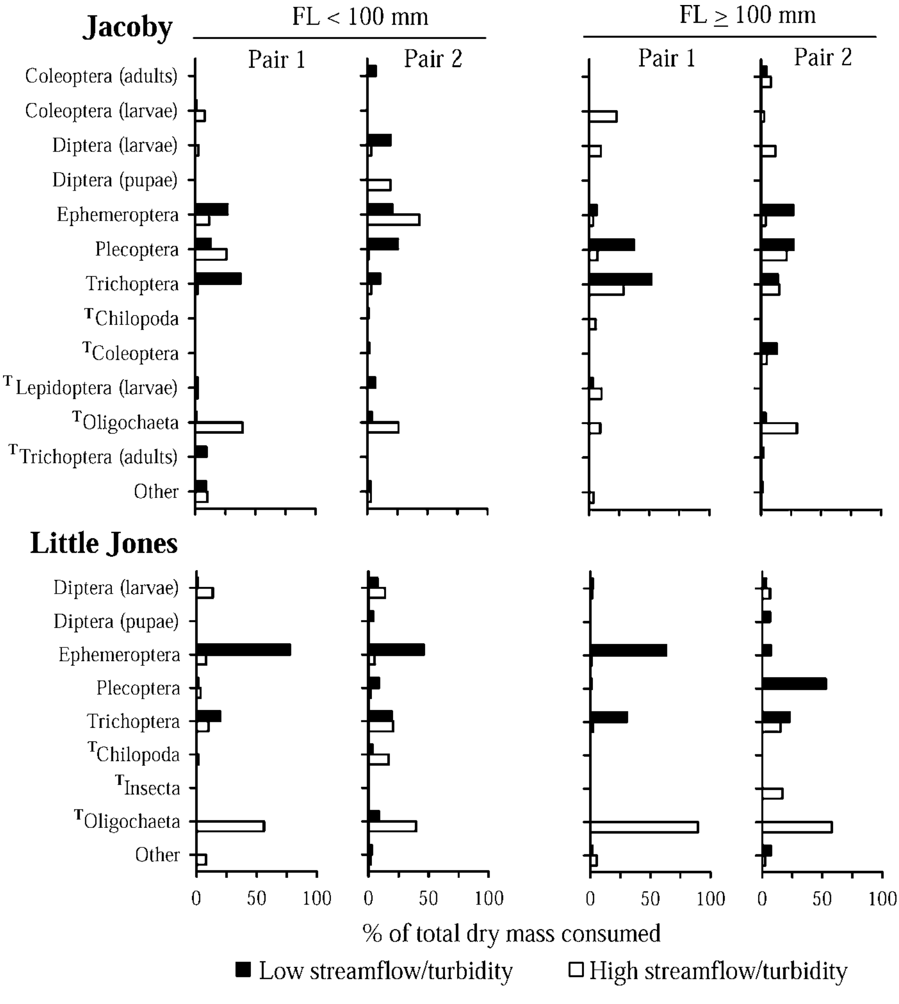

FIGURE 2.—Diet composition by fish size-class for low- and high-streamflow pairings in Jacoby and Little Jones creeks. The "other" category includes taxa that contributed less than 5% of the total dry mass consumed in all samples within a creek; superscripted *T*s denote terrestrial fauna.

maintenance ration. For LJ Pair 1, however, stomach contents of trout in the small size-class were close to or slightly exceeded the daily maintenance ration at both high and low streamflow and turbidity. For the larger fish, stomach contents nearly met the maintenance ration for the low streamflow, low-turbidity samples and exceeded that ration by nearly threefold for the high streamflow, high-turbidity samples.

Discussion

Like trout in cold-winter streams (Cunjak and Power 1987; Cunjak et al. 1987), the trout in this study appeared to commonly experience energy deficits during winter. However, these deficits did not appear more severe during conditions with relatively high streamflow and turbidity, and the only sample set with mean stomach contents that significantly exceeded maintenance intake was collected during an event with moderately high flow and turbidity on Little Jones Creek. These observations, parallel to the results of Arndt et al. (2002) for Atlantic salmon feeding during summer floods, indicate that under some natural conditions, salmonids may overcome the strong effect of turbidity on reactive distance to drifting prey (Barrett et al. 1992; Sweka and Hartman 2001). In some natural settings, trout may exploit benthic (or "proxi-benthic") prey using nonvisual cues. Laboratory studies have documented successful benthic feeding by salmonids under turbid conditions in standing water (Gregory and Northcote 1993; Rowe et al. 2003).

The results from both study streams suggest that oligochaetes become more available during high streamflows and remain detectable during moderate to high turbidity. The potential for pulses of oligochaetes in winter provides a possible contrast with previous studies documenting arthropod-dominated terrestrial subsidies for stream-dwelling trout during summer and fall (Kawaguchi and Nakano 2001; Romero et al. 2005). Occasional, profitable feeding opportunities could be an important component of the energy budget of trout in winter. Estimates from the energetics model we used suggest that an average cutthroat trout of 100 mm or longer in Little Jones Creek (32 g), consuming the mean dry mass we measured for fish of 100 mm or longer from that stream during low streamflow, would lose 6% of its body mass per month given typical winter temperatures. However, addition of a single feeding of the highest mean dry mass consumed in Little Jones Creek would allow that fish to maintain its mass over the month, and addition of two such feedings would result in growth of more than 7%. Of course, these estimates are highly speculative, given uncertainty in influential assumptions related to the cost of swimming, and additional parameter and equation uncertainty in the model (Railsback and Rose 1999). They do not incorporate the possibility of higher metabolic costs during floods. For example, although Arndt et al. (2002) did not detect an effect of summer floods on feeding success for Atlantic salmon, analysis of RNA : DNA ratios in that study indicated that floods caused brief reductions in growth rate of 20–30%.

The energy gained through winter feeding might be an important part of the year-round energy budget for trout in mild-winter systems. Similar to trout in colder systems, the trout in Jacoby and Little Jones creeks appear to be unable to meet maintenance energy requirements during much of the winter. However, sporadic feeding success during winter storms could significantly increase survival, growth, or fecundity, particularly for spring-spawning species such as steelhead (anadromous rainbow trout), rainbow trout, and cutthroat trout.

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