Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*

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Synopsis

Increases in water temperature and fish size should increase standard metabolism and food demand. Stream-dwelling trout may then, despite the increased cost of swimming, seek faster water where food is more abundant. We tested these predictions with juvenile steelhead trout, *Salmo gairdneri*, in a California stream and found that increased fish size and water temperatures did result in the increased selection of microhabitats with high water velocities. Faster water provided proportionally larger amounts of drifting invertebrate food. Higher velocity, shallower, and coarser substrate microhabitats also enabled fish to capture prey from portions of the water column substantially faster and more productive than at their resting positions. Velocities selected in this stream were similar to those which would result in a doubling of metabolic rate. Models evaluating trout habitat and effects of modifications should take energetic factors into account.

Introduction

Recently, efforts have been made to use microhabitat preferences to model the impacts of flow regimes on trout, especially in regulated streams (Stalnaker 1979). Habitat quality models, based on structural features (velocity, depth and substrate), have been developed (Main 1978) that assume microhabitat choice to be relatively fixed. However, microhabitat choice may vary in different environments. For example, Smith (1982) found trout density within sections of several small, cool streams (13–17° C) to be unrelated to water velocity, but in warmer streams (19–23°) density was strongly dependent on velocity. Even within the warm streams the patterns were different: density increased exponentially with velocity in two of the streams but was highest at intermediate velocities in a third, more productive, stream.

Water velocity is an important factor determining trout distribution in streams (Baldes & Vincent 1969, Lewis 1969), because trout generally maintain feeding stations within or beneath fast water where they are able to prey on drifting invertebrates (Chapman &Bjornn 1969, Jenkins et al. 1970, Waters 1972, Elliot 1973). Since foraging behavior is related to velocity, velocities utilized should vary in different environments or at different times just as prey choice, time and effort foraging, and other components of foraging behavior do. In particular, velocity choice should vary in response to several energetic factors: (1) water temperature, which affects standard metabolic rate (Beamish 1964) and thus food demand; (2) fish size,

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which also affects standard metabolic rate; (3) abundance and availability of drift organisms; and (4) cost of swimming. We report results of a study undertaken to determine the effects of water temperature and fish size on velocity preferences of juvenile steelhead trout, *Salmo gairdneri*, and to assess the relative benefits (drift availability) and costs (swimming energy) of using feeding stations of different water velocities.

Study area

Uvas Creek is a tributary of the Pajaro River, which empties into Monterey Bay in central California (approximate latitude 37° N, longitude 122° W). The stream is small, with width ranging from 4 to 12 m. Summer unregulated base flows average less than 0.05 m^3 sec^{-1}. The stream is moderately basic (pH 8.2), hard (140 mg l^{-1} as $CaCO_3$) and conductive (310 μohms). Flows in the lower portion of the stream are regulated by Uvas Reservoir. Water stored there is released for instream percolation, and downstream flows are relatively stable throughout the summer (0.2 to 0.3 m^3 sec^{-1} in 1978). Releases are from the bottom of the reservoir, but because the reservoir is nearly drained in most years, water temperatures below the reservoir are about equal to those above the reservoir by August and remain warm until November.

The study area is located between 2 and 7 km downstream from the reservoir. Gradient within the study area is about 0.2%, and pool to riffle ratios vary between 3 to 1 and 8 to 1, resulting in relatively low invertebrate drift rates (Waters 1972). In the upper portion of the study area average mid-day shade is about 60%, but it decreases to less than 5% at the lower boundary. Average water temperature increases downstream. Water temperatures within the study area reach a maximum of 23 to 25° C in summer, and can still reach 18 to 22° C as late as October. Releases from the reservoir are moderately turbid, especially in late summer, but clarity increases downstream as silt settles or is trapped by epibenthic algae.

The creek supports highly variable numbers of juvenile steelhead. None were present in 1976 or 1977 because drought prevented access by sea-run adults, but the 1978 stock was the highest recorded from 1972 to 1980. No resident (nonanadromous) trout are present in the study area, and since Uvas Creek steelhead become smolts in one year (Smith 1982), only a single year class is present in any given year. The stream also supports abundant Sacramento suckers, *Catostomus occidentalis*, riffle sculpins, *Cottus gulosus*, and several species of minnows, including Sacramento squawfish, *Ptychocheilus grandis*. No direct interactions between the steelhead and other species were noted, although other species may affect overall drift rates (Smith in preparation).

Methods

Velocity preferences

Trout within the study area, especially the larger ones, were usually associated with riffle (surface broken) or run (fast water with most of surface smooth) areas, where surface turbulence or vegetation provided overhead cover and blocked visibility from above. Therefore, we made over 90% of the microhabitat preference determinations by using an underwater viewer while wading or crawling along the bottom. We used a mirror attachment to obtain a periscopic view in the shallow riffles, but because of difficulties in approaching feeding trout in very shallow riffles, no determinations were made with the viewer at depths less than 25 cm. Most of the sampling took place from September through December 1978, although additional work was done during late April and early May 1980 to collect data on small fish (<6 cm).

We checked microhabitat positions by working upstream through all pool, run and riffle habitats at each of three sites within the study area. When a fish was located, its focal point, or relatively fixed swimming position, was determined by observing its movements for at least 3 minutes. We used a thin calibrated pole for reference to measure or estimate depth of water at the focal point, distance of the fish from the substrate and fish size. Bottom type, degree of shading, and overhead cover were also

recorded. Velocity was measured with a Marsh McBirney flowmeter, and readings were taken at the focal point, and (for about half of the fish) at feeding loci. Feeding loci were the points to which fish moved to intercept drifting prey. These points were upstream from, and usually higher in the water column than, the focal point. Sometimes we did not measure velocity at the time the fish was encountered, but instead marked the focal point with a numbered metal washer and determined velocity later (usually during the same day and always at the same flow rate, as determined by a water height marker).

Cross-sectional transects were run at the three sites to determine relative availability of microhabitat for comparison with fish choices. Thirty-three transects were made at each site and data were recorded every 0.5 m. Velocity readings in these transects were taken at 5 cm above the bottom, since that was the most frequent focal point distance. We sampled the study area by electrofishing (Smith-Root type V and VIII) to provide data on general habitat (riffle, run and pool) distributions and size composition of trout for comparisons with visual results.

Water temperatures during observations were recorded and 24 h mean temperatures were calculated by using these records and data from maximum-minimum thermometers at the sites. Comparisons of velocities chosen at different temperatures are based upon data from different sites and/or sampling dates. The average temperatures at the downstream end of the study area were 3–4° C higher than those at the other two sites. Lower temperature values at all sites also came with the cooling of water in fall. Any increase in fish size during this cooling period would slightly counteract any temperature effect, but mean size of fish observed did not significantly change during the period of cooling. In spring 1980, data for fish less than 6 cm were recorded within a three week period when mean water temperature was stable; these data were used only to compare focal points of different sized fish.

Invertebrate drift

At each of the three sites drift nets were used to determine the relationship of drift volume to velocity and to see if the three sites had substantially different drift rates. At each site twelve drift nets (18 × 36 cm mouth, 70 cm long with 0.3 mm mesh) were placed within a single riffle and associated downstream pool and run, and widely distributed to represent a considerable range of velocities. Placement was checked with dye releases and adjusted to insure that no net interfered with the drift of another. All nets were placed 2.5 cm off the bottom, and none extended above the water surface; consequently surface drift and benthic movements were not sampled. Velocity was measured at a point 10 cm off the bottom and 20 cm forward from the center of the net mouth.

Sampling was conducted on three overcast days (November 8, 11, 12, 1978) and at approximately the same starting time (1000 h) at each site. During sampling, nets were in place for two 1 h periods, separated by about two hours. Even with the short sampling periods, nets in faster water tended to clog with fine particulate organic matter, possibly reducing their effectiveness. Sorting was done in the field, because the live invertebrates could be seen more easily than preserved invertebrates among the leaves and other detritus. Invertebrates were counted and their relative volume in each sample was estimated by using a mayfly 0.5 cm long as a volume reference unit [similar to the point system of Windell (1971)].

Metabolic costs

The models of Weihs (1973) and Ware (1978) suggested that a swimming effort which doubles metabolic rate is energetically optimal for covering distance. Winberg (1956) has also suggested that routine or field metabolism is about twice the standard (resting) metabolic rate. We calculated swimming velocities which would double metabolic rate according to Weihs' model, using the cost of swimming data of Brett & Glass (1973). We used their data for sockeye salmon, *Oncorhynchus nerka*, rather than available data for rainbow trout be-

cause they studied small fish similar to those we encountered. These estimates were then compared with focal point velocities to determine whether effort by Uvas Creek fish was compatible with energetically efficient swimming.

Metabolism increases with fish size, and both metabolism and digestion rate increase with temperature (Elliot 1975, 1979, Windell et al. 1976). Elliot (1975, 1979) used data for brown trout, *Salmo trutta*, and combined these effects for various fish sizes and temperatures to estimate satiation requirements (amount of food demand or minutes feeding per meal) and maximum daily food demand for trout. We used his models to estimate satiation requirements for Uvas Creek trout and compared them with trout focal point velocity choices.

Results

Focal point velocities

Young steelhead selected focal points where water velocities were higher than those typically available in Uvas Creek (Fig. 1). Most fish for which focal points were determined were in deeper riffles and runs or at the heads of pools (mean depth was 59 cm). However, our results probably underestimated mean water velocities at focal points, since most of the faster water (velocities greater than 30 cm sec^{-1}) was in riffles less than 30 cm deep. These areas were not adequately observed with the underwater viewer, but were heavily used; over 40% of all fish and over 60% of those longer than 12 cm (standard length) taken by sampling with an electrofisher came from shallow water.

When fish size was checked against focal point water velocity preferences (Fig. 2) the expected increase in mean velocity with fish size was found for fish to a length of 10 cm. The general equivalence of water velocity choices for still larger fish is possibly due to selective sampling. Most of the larger fish were in shallow, unsampled riffles.

We found that focal point velocities also increased at higher temperatures (Fig. 3). Although the study was conducted over a period of over 4 months, fish sizes did not significantly change within sites for different dates and temperatures. However, fish from the lowermost site consistently averaged about 15% larger than those at other sites. At the lower site a 10° C increase (from 10.5 to 20.5° C) in mean temperature resulted in a 64% increase in mean water velocities at focal points. At the other 2 sites a 9° C increase (from 8 to 17° C) resulted in a 180% increase in focal point velocity.

Of focal points examined, 93% were within 10 cm of the substrate, and 72% were within 5 cm. Fish moved forward, and usually upward, to intercept drifting prey moving at velocities equal to, or

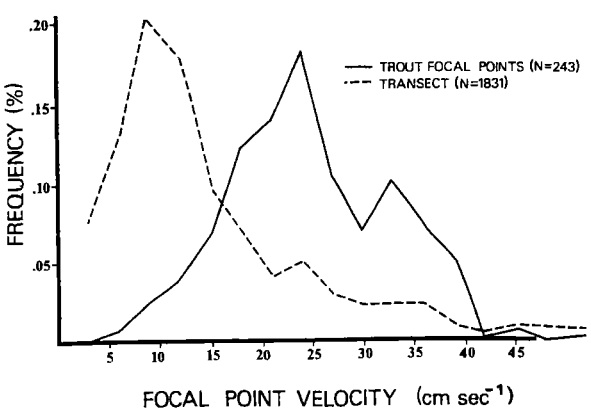

Fig. 1. Focal point velocity choices for trout at three sites in Uvas Creek, compared with results of transects of available habitat.

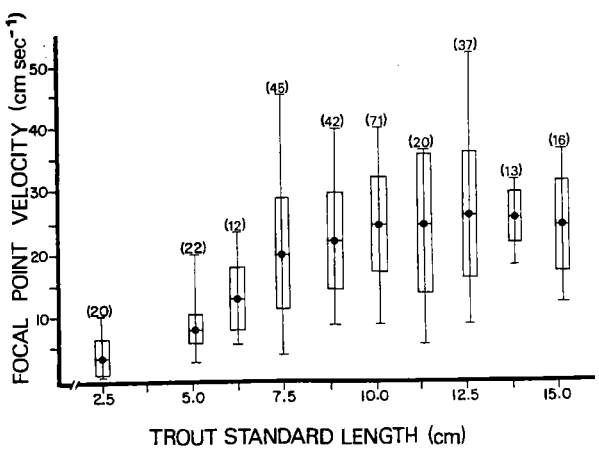

Fig. 2. Means, ranges, and 95% confidence intervals for water velocities at focal points for Uvas Creek trout of different standard lengths. Numbers in parentheses are sample sizes.

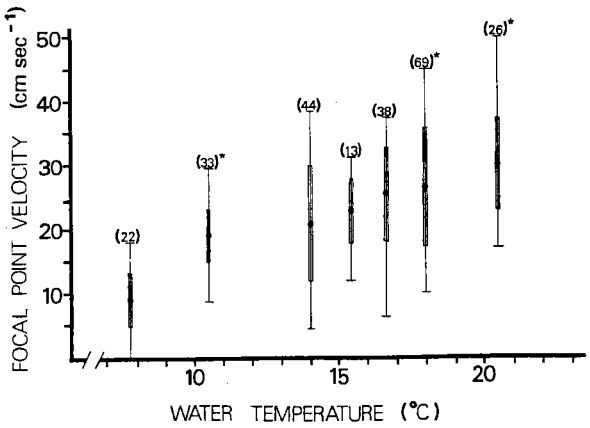

Fig. 3. Means, ranges, and 95% confidence intervals for water velocities at focal points of Uvas Creek trout at different 24 h mean water temperatures. Data with * is from lowermost study site.

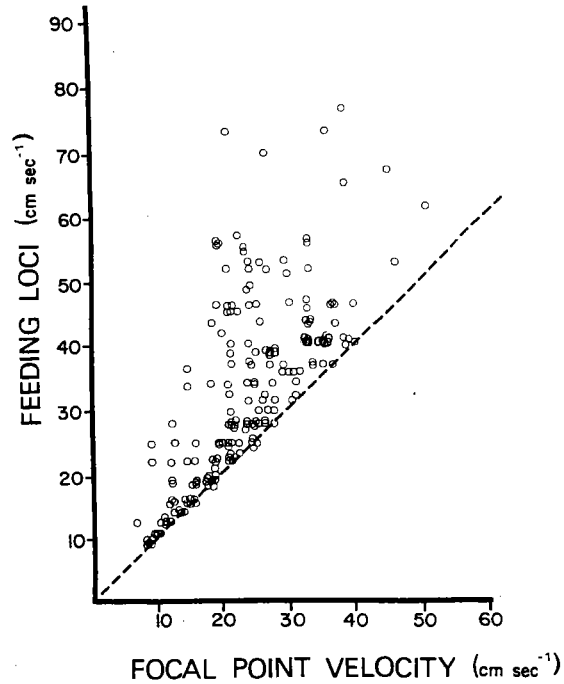

Fig. 4. Feeding loci water velocities for Uvas Creek trout having different focal point water velocities.

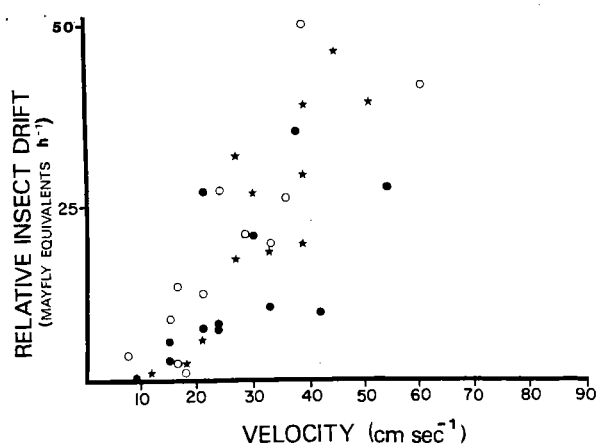

Fig. 5. Relative insect drift at different water velocities at three sites in Uvas Creek.

greater than, the velocity at their focal point (Fig. 4). No trout were observed feeding on the bottom. At low velocities (8–20 cm sec^{-1}) the difference between velocities at the focal and feeding points was usually small, but at higher velocities (above 30 cm sec^{-1}) it averaged 31%. One reason for this difference was that slower focal points were usually in deeper water, where velocity changed less with small increases in height in the water column. A second reason was that focal points in slower water were usually associated with finer substrates of sand and small gravel. In faster water, focal points were more often associated with coarse gravel and rubble, which produced small, slow-water pockets near the substrate.

Invertebrate drift

Among the three sites sampled for invertebrate drift we found the same pattern of response to velocity (Fig. 5). Volume of drifting invertebrates captured by the nets increased in a manner compatible with either a linear or slightly curvilinear response to velocity. If a linear relation is assumed, there was a threshold, near 10 cm sec^{-1}, below which drift was negligible. If these drift net results accurately represent food available to feeding trout, a fish should be able to more than double food intake by feeding in water moving at 30 cm sec^{-1} rather than at 20 cm sec^{-1}. A further shift to 40 cm sec^{-1} water would gain the fish an additional 60% in available food. The apparent lack of drift at velocities below 10 cm sec^{-1} in Uvas Creek may account for the near absence of feeding trout at such low velocities (Fig. 1).

Metabolic costs

Although energy costs increase with swimming speed, the efforts we found for Uvas Creek fish were not excessive. When compared with swimming velocities which would double metabolic rate (Table 1), focal points showed close agreement, except for fish of small sizes. Small fish were actually working less than that necessary to produce the field metabolism of Winberg (1956).

When water velocities at focal points were compared with satiation requirements for fishes of different sizes or fish at different temperatures (Fig. 6), the responses were similar. Velocities utilized generally increased with satiation requirements, but at higher requirements the rate of change for velocity choice diminished. At the largest fish sizes there was no change, possibly due to inability to sample these fish adequately.

Table 1. Water velocities (body lengths sec^{-1}) at focal points for Uvas Creek trout versus swimming velocity at which swimming cost would double metabolic rate. Metabolic cost is from Brett & Glass (1973) for sockeye salmon at 16° C.

Total length (cm)	Focal velocity (Mean ± SD)	Velocity to double metabolism
3.3	1.3 ± 0.6	2.9
6.7	1.3 ± 0.5	2.5
8.1	1.6 ± 0.6	2.2
9.5	2.1 ± 1.0	2.1
10.9	2.1 ± 0.7	1.9
12.2	2.1 ± 0.7	1.8
13.6	1.8 ± 0.8	1.8
15.0	1.8 ± 0.7	1.7
16.4	1.6. ± 0.3	1.6
17.7	1.4 ± 0.4	1.5

Discussion

Uvas Creek, like most streams, is a complex environment of varying depths, substrates, pool and riffle sizes, velocities and amounts of overhead cover. Despite the importance of these structural features, the energetic role in trout microhabitat choice is clear and substantial. The drifting invertebrates upon which all the trout fed were more

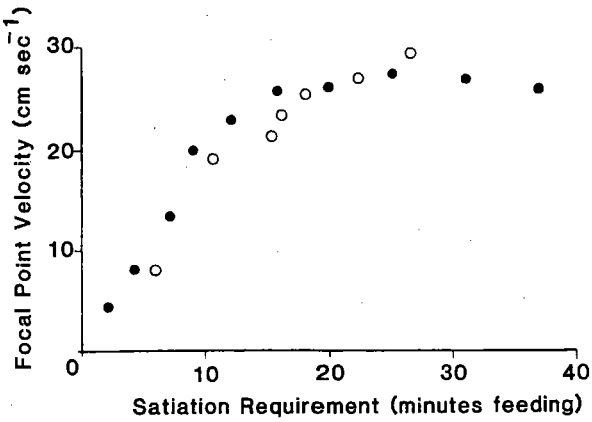

Fig. 6. Focal point water velocity choices of Uvas Creek trout at estimated satiation requirements (from Elliot 1975, 1979) for different fish sizes (●) and water temperatures (○).

abundant in fast water, and as food demand increased with increasing fish size or water temperature, the fish responded by feeding in faster water. Juvenile atlantic salmon, *Salmo salar*, have also been shown to have distributions which are both size dependent and related to drift abundance (Wankowski & Thorpe 1979). For faster water and for larger fish our data are limited and uncertain because of our inability to sample fast, shallow riffles. However, Alley (1977), working on a large, warm California stream, found that larger rainbow trout (mean = 18.9 cm total length) chose focal velocities nearly twice as fast (45 cm sec^{-1} in 1976) as those we found. Size-dependent velocity responses for steelhead and chinook salmon, *O. tshawytscha*, were also found by Everest & Chapman (1972).

The possible benefits of feeding in faster water are substantial; in Uvas Creek a shift from 20 to 30 cm sec^{-1} would more than double drifting invertebrates. However, feeding fish in Uvas Creek, or elsewhere, are not all in the fastest water for several reasons:

1) Swimming cost may increase faster than food benefits. The effort of Uvas Creek trout did not generally exceed that which would double their resting metabolic rate (Table 1), and exponential cost increases of swimming may restrict effort to a point near or below this level. At higher tempera-

tures the relative metabolic cost of swimming decreases because swimming costs are relatively constant, but standard metabolism increases with temperature. Fish in warmer water can more profitably increase their activity.

2) Ability to react to and capture prey may restrict feeding efficiency at high velocities. In a moderately turbid stream Tippets & Moyle (1978) found that trout juveniles, with low metabolic rates and presumably in slow water, fed on drift, but adults fed on epibenthos. For adults the turbid conditions probably prevented their reacting to, and feeding on, fast-water drift; consequently drift-feeding had to be abandoned. Similar conditions can operate in heavily shaded streams; in Uvas Creek most focal points, even in generally shaded stream sections, were sunlit. At higher velocities, turbulence may also hinder prey capture.

3) Satiation can be achieved without hard work if prey are abundant, or if metabolic rate or digestive rate are low. Elliot (1975) found that for brown trout at low temperatures, a single short meal during the peak drift period was sufficient for satiation. At higher temperatures more rapid digestion allowed two meals per day. In Uvas Creek, due to high temperatures and low drift rates, fish apparently were feeding continuously. Because size differences in satiation requirements are great (Elliot 1979), small fish may rapidly become satiated, even at low drift rates. Comparisons of high and low drift streams should find large differences in fish focal points.

4) Fish may be able to reduce effort by maintaining a focal point in slow water, near the bottom or near obstructions, and still feed on fast-water drift. In this study we found that this differential averaged 31% at higher velocities; in faster water or with coarser substrate the difference should increase. Both Alley (1977) and Dettman (1978) found that trout focal points were often associated with slower pockets around boulders.

Because energetics can be so important in microhabitat choice, structural models of trout and salmon habitat (Main 1978) should consistently work well only among streams of similar productivity and temperature. Models in which temperature and productivity indices are used may prove to be more generally predictive (Binns & Eiserman 1979). Since metabolism varies with size, models must also account for size classes. Velocities suitable for supporting small, smolt-sized steelhead and salmon may be insufficient for spawning-sized fish necessary to sustain a resident trout stock.

Energetic models have obvious applications to maintaining and improving habitat quality. Not only do they show how quantity of flow may affect trout under various circumstances, but they also suggest that qualitative changes in flow, such as reducing temperature or turbidity or the addition of habitat structures, can improve habitat quality.

Acknowledgements

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