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Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream

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With 7 figures in the text

Introduction

Previous research has established that the density and biomass of cutthroat trout (*Salmo clarki*) are greater in open, recently logged (clear-cut) stream sites of the Pacific Northwest (U. S. A.) than in sites bordered by more mature deciduous or coniferous forest (AHO 1977; MURPHY & HALL 1981; MURPHY et al. 1981; HAWKINS et al. 1983). In Mack Creek, for example, both biomass and density of cutthroat trout were approximately twice as great in an unshaded, early second growth section than in an upstream old-growth section (AHO 1977). The explanation advanced for this finding is related to differences in food abundance (HAWKINS et al. 1983). Primary production of small shaded streams of the Pacific Northwest is typically light-limited (GREGORY 1980). Opening of the canopy increases algal production; at least some invertebrate populations increase with an increase in high-quality food resources, and the trout track changes in prey abundance. The influence on trout population parameters of habitat differences that occur with a difference in riparian setting has not been examined.

The nature of the riparian setting may exert a considerable control on stream channel morphology and trout habitat. In-channel woody debris derived from riparian vegetation is an important and characteristic structural element of unperturbed streams. It creates a stepped gradient (SWANSON & LIENKAEMPER 1978) that reduces local stream power (SEDELL et al. 1978), acts to retain organic and inorganic inputs (BILBY 1981), and produces habitat complexity. Together with rooted bankside vegetation, large woody debris lends stability to the stream channel and provides cover for trout.

Habitat changes that accompany clear-cut logging are likely to destabilize the channel, and thus be deleterious to trout. By implication, if food abundance increases and habitat suitability decreases with a change in age of the riparian stand, increases in trout abundance in clear-cut stream sections are best explained on the basis of food (Fig. 1). Cutthroat trout in these streams are more likely food limited rather than habitat limited.

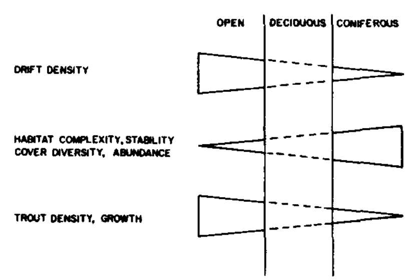

Fig. 1. Predicted relationships among trout population parameters, prey abundance and habitat characteristics with a change in age of the riparian vegetation.

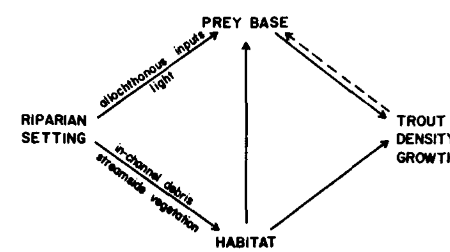

Fig. 2. Conceptual model relating influence of the riparian setting on trout density and growth through the prey base and habitat.

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This explanation is facile, however, for two reasons. The first is that the food supply is not independent of habitat structure. Increases in prey abundance in clear-cut streams are attributable in part to an increase in system productivity that follows from an opening of the canopy and a change in the nature of allochthonous inputs. But spatial and temporal aspects of habitat structure act jointly with system productivity (MENGE & SUTHERLAND 1976) to regulate or constrain the abundance and composition of the invertebrate prey assemblages that develop in an area (Fig. 2). Composition of an invertebrate assemblage, as well as its abundance, is of significance in that different taxa and life stages are not equally susceptible to predation from trout.

The second reason that food alone may be insufficient to explain difference in trout population parameters that exist among sites differing in riparian setting is that habitat features, independently of prey abundance or productivity, may influence the ability of trout to exploit the prey base. MENGE (1978), for example, found that the predation intensity exerted by *Thais lapillus* on its prey in a rocky intertidal community was independent of prey or predator abundance and varied with environmental and habitat variables.

In this paper we explore 1) differences in prey availability that co-occur with differences in habitat structure between an old-growth and a clear-cut section of a stream, and 2) the influence of habitat structure on the ability of cutthroat trout to exploit invertebrate prey.

Methods

Research was conducted during 1982 and 1983 in a recently logged (4 yrs.) and a downstream old-growth (approx. 400 yrs.) section of Grasshopper Creek, a third order stream at 1000 m elevation in Lane County, Oregon. Each study site was approximately 150 m. Cutthroat trout are the only fish species present at each site.

Each stream reach was surveyed and the locations of habitat types and cover features were drawn to scale on a map. Depth-contoured pool areas were determined with a planimeter, and volumes were calculated.

Snorkelling observations were used to estimate trout density as well as to examine microhabitat use and feeding behavior.

Drift samples were collected to estimate prey availability at each site because snorkelling observations indicated that all trout other than fry fed predominantly on the water column and surface drift. Replicated drift samples (n = 2—5) were collected during high (February and May) and low (July) flows in 1983. Nets, with a mouth area of 0.025 m^2 and a mesh size of 0.250 mm, were submerged for one hour for each sample. To enable identification of taxa that displayed pulsed diel drift activity, paired drift samples were collected four times daily on the May sampling date.

Feeding experiments were initiated in July 1983 to evaluate prey exploitation efficiency of trout in the clear-cut and old-growth sections. Four densities (10, 20, 40, and 80) and two size classes (5 and 10 mm) of *Culex* sp. larvae were introduced in a randomized order during three minute trials each from an observer-controlled feeding apparatus into the thalweg of a pool in each section. The number of prey captures was observed from a location 1—2 m downstream of the feeding fish. Feeding response of the trout was triggered prior to the release of *Culex* sp. by dislodging the substrate and producing a stream of drift. During the trials, a 0.250 mm net placed immediately upstream blocked off incoming drift.

Results and discussion

Prey availability

Density and biomass of average day drift, expressed as numbers and biomass collected per hour per volume of water sampled, were greater in the clear-cut than in the old-growth section at both high and low flows (Fig. 3). These data do not reflect well habitat differences between sites in and of themselves because variables concerning prey food resources may also contribute to differences. ALLAN (1984) found that differences in discharge often account substantially for variation in drift density. In these sites discharge and the range of current velocities encountered were similar. The relationship between

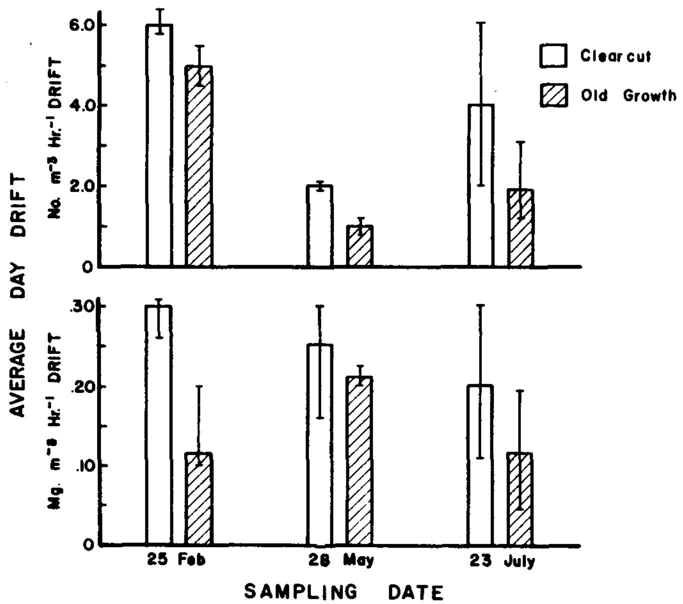

Fig. 3. Density and biomass of average day drift in a clear-cut and old-growth section of Grasshopper Creek at high (February and May) and low (July) flows, 1983. Vertical bars indicate range of values, n = 2—5.

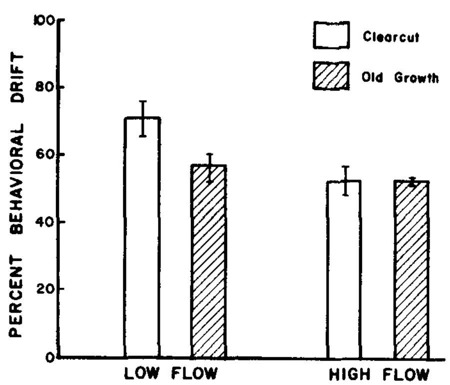

Fig. 4. Per cent of behaviorally drifting invertebrates that occurred in drift samples collected in the old-growth and clear-cut section during high and low flows. Vertical bars indicate CV, n = 4—5.

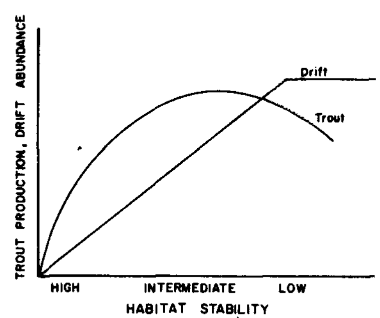

Fig. 5. Proposed relationship between trout production and drift abundance along a gradient of habitat instability.

drift density and current was not significantly different between sites ($p > 0.05$, Wilcoxon Rank Sum test), and the interrelationship between drift density and current combined

for both sites was not very strong ($r^2 = 0.26$, $n = 10$). Current was measured at the mouth of the drift net; a stronger relationship might result if current were measured at the drift source area.

Stability of the clear-cut section, evaluated by the PFANKUCH (1975) method, is rated as fair (numerical score = 92); the old growth section received a rating of good (numerical score = 75). A higher percentage in the clear-cut than in the old-growth section at low flow of taxa that occur in the drift behaviorally (Fig. 4) reflects a greater habitat instability in this reach. Behavioral drifters, defined as organisms showing a diel pulse in drift activity (WATERS 1965), are characterized by polyvoltine species, many of which, such as *Baetis* spp., are periphyton feeders. As a group, they are well-adapted to unstable habitats and a rapid turnover, high-quality food resource. The predominant behavioral drifting invertebrates collected in this study were *Baetis bicaudatus* and Orthocladiinae chironomids. The lower percentage of behavioral drifters in the old-growth section probably reflects their reduced relative density as a component of a more diverse benthic fauna. Benthic composition, although not examined in this study, has been found by HAWKINS et al. (1982) to be more diverse in forested than in open stream sites. A more diverse benthic fauna, including a greater proportion of univoltine and longer-lived species adapted to stable substrates, occurs in old-growth stream sites in response to a greater microhabitat and food diversity. At high flows the relative per cent of behavioral drifters in the clear-cut section decreases as more of the benthos becomes accidentally dislodged by turbulent flow and substrate movement.

The significance to trout of differences in relative percentages of behavioral drifters between the clear-cut and old-growth section is that behavioral drifters represent a more predictable food supply. Even at high flows, although the percentage of behavioral drift decreases in the clear-cut relative to low flow periods, absolute numbers are greater than in the old-growth section (Fig. 3). Interestingly, trout were observed actively feeding in the clear-cut section at high flows in winter and they were concealed and inactive in the old-growth section. A gradient of increasing feeding activity of trout was observed in a 100 m transition area between the old-growth and clear-cut area. The most probable explanation for this observation is related to differences in prey availability between sites. To the extent that drift abundance increases with increasing habitat instability, trout production may also increase with instability up to a threshold where energetic costs of feeding exceed benefits derived from an increased food supply (Fig. 5).

Habitat influence on foraging activity of cutthroat trout

Habitat structure may influence foraging activity of trout in the sense that trout may be constrained for energetic reasons to certain microhabitats irrespective of prey distribution. The clear-cut section of Grasshopper Creek, for example, is best described as an alternating series of rapids and plunge or lateral scour pools. All of the cutthroat trout (n = 109) observed in this section were located in pools, which constitute only 34% of the total area (181 m^2). Pools in the old-growth section constitute 40% of the total area (186 m^2). In this section, where in-channel debris decreases local gradients and riffles are more prevalent, 10% of all observed trout (n = 99) occurred in non-pool habitats.

The difference in density of cutthroat trout between sites is not as striking as differences reported in studies based on electroshocking (AHO 1977; MURPHY & HALL 1981; HAWKINS et al. 1983). An assumption affecting these studies is that capture efficiencies

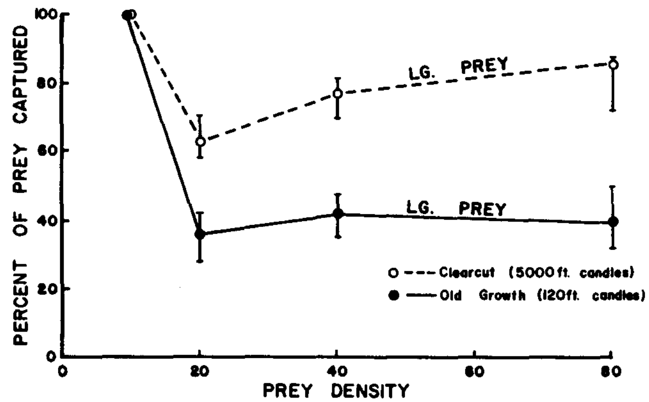

Fig. 6. Per cent of prey captured by cutthroat trout at varying prey densities in an old-growth and clear-cut pool. Large (10 mm) *Culex* sp. larvae were introduced in a randomized order during feeding trials of three minutes each. Vertical bars indicate range of value, n = 2—3.

are equal in open and forested sites. Inasmuch as forested stream channels are often much more structurally complex, this assumption deserves examination.

Specific habitat features, particularly those that provide cover for trout, may also affect trout foraging activity. Cover in the form of in-channel debris or overhead shading, for example, is beneficial to trout to the extent that it moderates harsh physical conditions and/or decreases conspicuousness to predators, but it may also decrease foraging effectiveness of trout by impeding prey capture. We examined prey capture efficiencies of trout in a representative old-growth and clear-cut pool by introducing different densities of prey (*Culex* sp. larvae) and observing the number of captures during a three minute trial. The number of fish per unit pool volume (one fish · 0.14 m^{-3}) was the same between sites (old-growth: pool volume 1.104 m^3, 8 fish; clear-cut: pool volume 2.100 m^3, 15 fish). No regular pattern of increase or decrease in the efficience of prey capture during successive trials was apparent, indicating that neither learning nor satiation influenced the results. Prey densities introduced were in the range of those naturally encountered by the trout. Average daytime flux of drift into the old-growth and clear-cut pool is approximately 51 and 73 animals, respectively, per three minutes.

In both sites, the pattern of capture efficiency was highest at the lowest density and was fairly constant at high densities (Fig. 6). At higher prey densities (> 10 prey), capture efficiency was greater in the clear-cut pool. Surface light was approximately forty times greater in the clear-cut than in the old-growth pool. To examine the extent to which light contributed to differences in prey capture efficiency, feeding trials were repeated in the clear-cut pool under artificial shading that reduced light five-fold. In these trials, two size classes (5 and 10 mm) were introduced. Under both light conditions, all small prey were captured less efficiently than were large prey (Fig. 7). Shading generally reduced efficiency; the lowest percentage of prey captures occurred with small prey under shaded conditions.

The relationship between feeding efficiency and surface light is apparently non-linear or perhaps involves a threshold response. A five-fold reduction in surface light in the clear-cut pool resulted in an 18 % reduction in average capture efficiency at prey densities greater than ten. A forty-fold reduction in light in the old-growth pool resulted in a 36 % reduction in average capture efficiency.

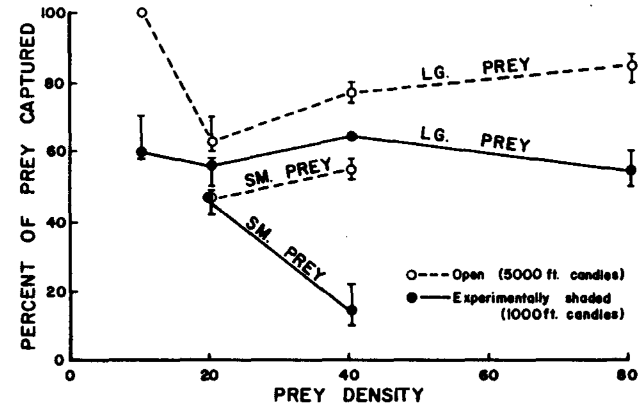

Fig. 7. Per cent of prey captured by cutthroat trout at varying prey densities and large (10 mm) and small (5 mm) sizes in a clear-cut pool under artificial shading and natural conditions. *Culex* sp. larvae were introduced in a randomized order during feeding trials of three minutes each. Vertical bars indicate range of values, n = 2—3.

Data from the feeding trials suggest that shading and perhaps other habitat differences can influence the efficiency with which trout exploit their prey base; and that a trade-off may be involved between foraging efficiency and protection from predators or physical disturbance.

The explanation for an increased abundance of cutthroat trout in clear-cut streams appears to be related to food. Habitat structure, however, plays a role in the sense that 1) habitat instability may increase the probability that invertebrates will occur in the drift where they are more available to be eaten by trout (Waters 1969), and 2) loss of cover structures may promote efficient foraging. The cost to trout of more food and more efficient foraging is a greater risk of mortality from physical displacement or predation. Trout populations are perhaps more abundant in clear-cut streams, but they may also be less stable.

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