

AN ABSTRACT OF THE THESIS OF

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Title: Prey Availability Overrides Cover in Determining Growth and
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The abundance and biomass of cutthroat trout (Salmo clarki) have been found to be greater in logged than in forested streams of the Oregon Cascades. Although certain prey taxa increase in abundance following logging, habitat stability generally decreases and cover structures are removed. Research was conducted to examine the manner in which habitat features interact with the prey base to result in greater abundance of the trout in logged streams.

Cutthroat trout were more effective in foraging on experimentally introduced prey (Culex spp. larvae) in a logged section of Grasshopper Creek (Lane Co., Oregon) than in a forested section. The differences in efficiency were related to prey size and to the amount of overhead shading and substrate crevices. Mean percentages of prey captured by trout were greater in logged control pools and crevice-covered pools of both sections than in forested control pools. Artificial shading of logged pools reduced capture success by the trout to levels found for trout in forested pools.

Relative growth rates of cutthroat trout experimentally confined in pools were also greater in the logged than in the forested reach. Differences in growth rates were primarily due to differences between the reaches in invertebrate drift density. Higher drift density

in the logged section probably reflected a greater habitat instability that increases the probability that benthic fauna will occur in the water column where they are more available as prey.

Drift density significantly increased relative to controls in trout-excluded pools in the logged reach, but not in the forested section. This may have resulted from habitat features in the logged section that favor greater trout foraging success, and from the occurrence of a greater relative proportion of behaviorally drifting prey taxa, which represent a predictable food source.

In laboratory experiments, food abundance played a relatively greater role than did cover in determining the abundance of cutthroat trout. In trials of one week duration, few introduced trout emigrated from channels having high food abundance, irrespective of the amount of cover. In channels with low food abundance, no, or very few, trout remained, irrespective of the amount of cover. These results support field data that suggest that, in spite of reduced cover, cutthroat trout are more numerous in logged than in forested sites in response to a greater foraging return.

PREY AVAILABILITY OVERRIDES COVER IN DETERMINING
GROWTH AND ABUNDANCE OF STREAM-DWELLING CUTTHROAT TROUT

by

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PREY AVAILABILITY OVERRIDES COVER IN DETERMINING GROWTH
AND ABUNDANCE OF STREAM-DWELLING CUTTHROAT TROUT

CHAPTER I

INTRODUCTION

Although species diversity of stream communities correlates well with structural complexity of the habitat (e.g. Rabeni and Minshall 1977, Gorman and Karr 1978, Hart 1978, Williams 1980), correspondence between habitat complexity and abundance of a particular taxon may be poor or non-existent. In headwater streams of the Oregon Cascades, for example, cutthroat trout (Salmo clarki) are more numerous in structurally simple, logged sites than in complex, forested ones (Aho 1977, Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983). This has been previously explained on the basis of an increased abundance in logged sites of some benthic invertebrate taxa (Hawkins et al. 1983). Primary productivity of small forested streams of the Pacific Northwest is typically light-limited (Gregory 1980); opening of the canopy that attends clearcut logging increases in-stream algal production and the abundance of invertebrates that utilize certain of the enhanced algae as a food resource.

Cutthroat trout, however, must respond to concomitant effects on habitat and their prey base that are imposed by the riparian setting. Removal of the mature riparian vegetation by logging increases light levels to the channel and reduces bank stability as a result of loss of root binding of soil particles. If logging procedures include removal of large woody debris from the stream channel, small sediment sizes are most frequently exported from the

reach. The channel bottom becomes more homogeneous and, if equal gradient systems are compared, may become less stable because of the loss of substrate packing that is a feature of mixed substrate sizes (Pfankuch 1975). For cutthroat trout, these effects may translate into a loss of cover and a greater habitat instability (Swanson and Lienkaemper 1978). The manner in which cover and habitat instability interact with the food base to result in a greater abundance of trout has not been previously examined.

Prey abundance is not synonymous with prey availability if trout are not able to detect or capture all potential prey items. Snorkeling observations and analyses of trout stomach contents indicated that cutthroat trout in the study sites were feeding predominantly on drifting invertebrates in the water column and at the surface. In chapter two, classification of invertebrate taxa according to propensity to appear in the water column is suggested as an approach to evaluating prey availability to cutthroat or other drift-feeding trout. The relationship between habitat features and invertebrates exhibiting a behavioral tendency to drift is examined in this chapter, and a hypothesis is proposed that links drift abundance, trout production, and habitat instability.

Apart from an indirect effect realized through the prey base, habitat and particularly cover features may influence trout by affecting their ability to exploit the prey base. Results of pilot studies that examined trout foraging efficiency in a logged and forested section of stream, and the influence of overhead shading on foraging efficiency are reported in chapter two. The results of an

expanded study to examine the influence of overhead shading, substrate crevices, and interactions between these on foraging efficiency and growth of cutthroat trout are presented in chapter three. The impact of trout predation on drift composition is also examined in this chapter. If foraging efficiency varies with habitat complexity, predation intensity exerted by trout is expected to vary as well.

To the extent that cover features simultaneously reduce foraging efficiency of trout and provide protection to them from predation or physical disturbances, a trade-off exists between costs and benefits of foraging in a particular habitat. Research findings that both growth and density of cutthroat trout are greater in cover-poor sites than in sites with abundant cover suggest that trout populations place a greater relative weight on foraging gain. Microhabitat use and emigration of cutthroat trout from laboratory channels were examined under varying combinations of food abundance and cover to evaluate the relative importance of food abundance and cover in determining habitat distribution. The results reported in chapter four clearly show the overriding influence of food abundance.

CHAPTER II

PREY AVAILABILITY AND FORAGING BEHAVIOR OF CUTTHROAT TROUT IN
AN OPEN AND FORESTED SECTION OF STREAM

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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 and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983). In Mack Creek, Oregon, 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, algal 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 and Lienkaemper 1978) that reduces local stream power (Sedell et al. 1978), retains organic and inorganic material (Bilby 1981), and produces habitat complexity. Together with

rooted bank 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 increase the probability of major channel changes 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. II. 1). Cutthroat trout in these streams are more likely food limited than habitat limited.

This explanation is facile, however, for two reasons. First, 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 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 and Sutherland 1976) to regulate or constrain the abundance and composition of the invertebrate prey assemblages that develop in an area (Fig. II. 2). Composition of an invertebrate assemblage, as well as its abundance, are 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 differences in trout population parameters 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. Many other predator-prey studies in a variety

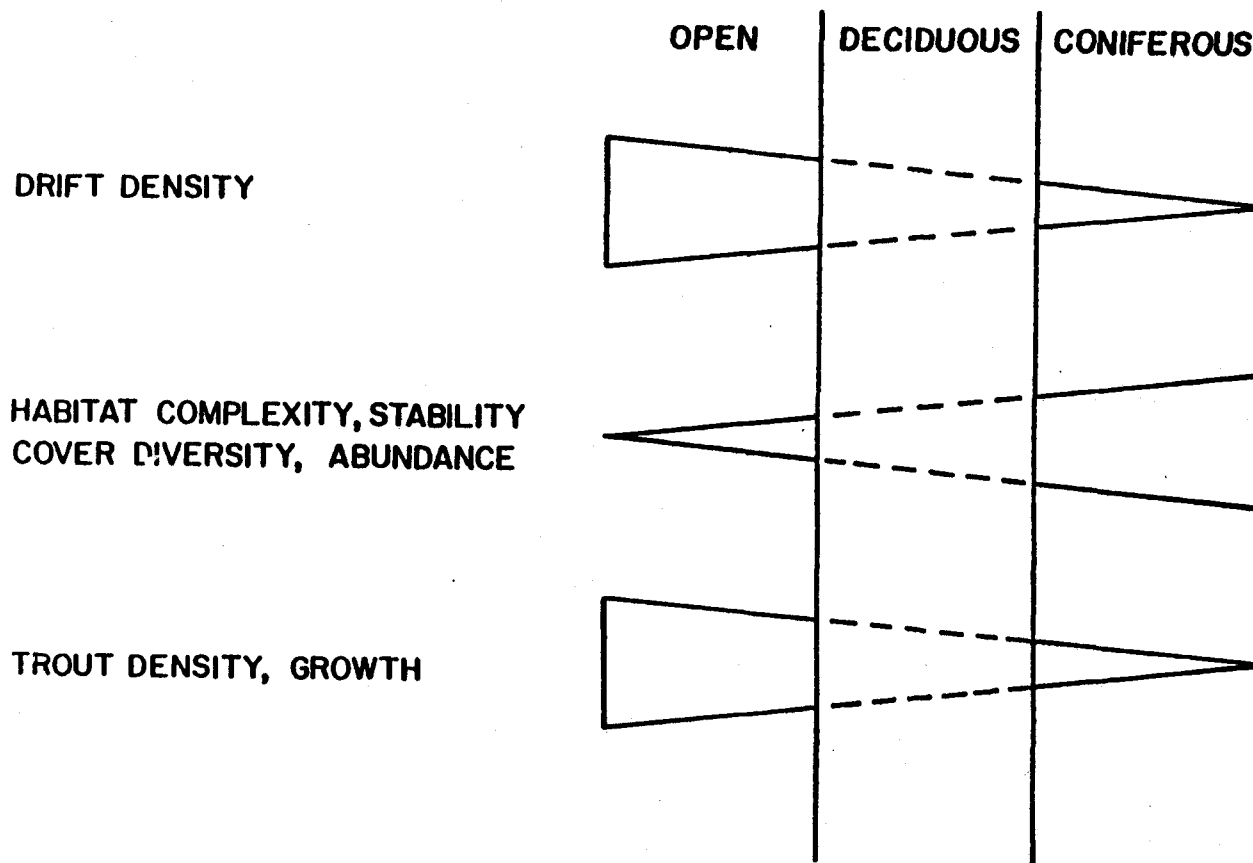


Fig. II. 1. Predicted relationships among trout population parameters, prey abundance, and habitat characteristics with a change in age of the riparian vegetation.

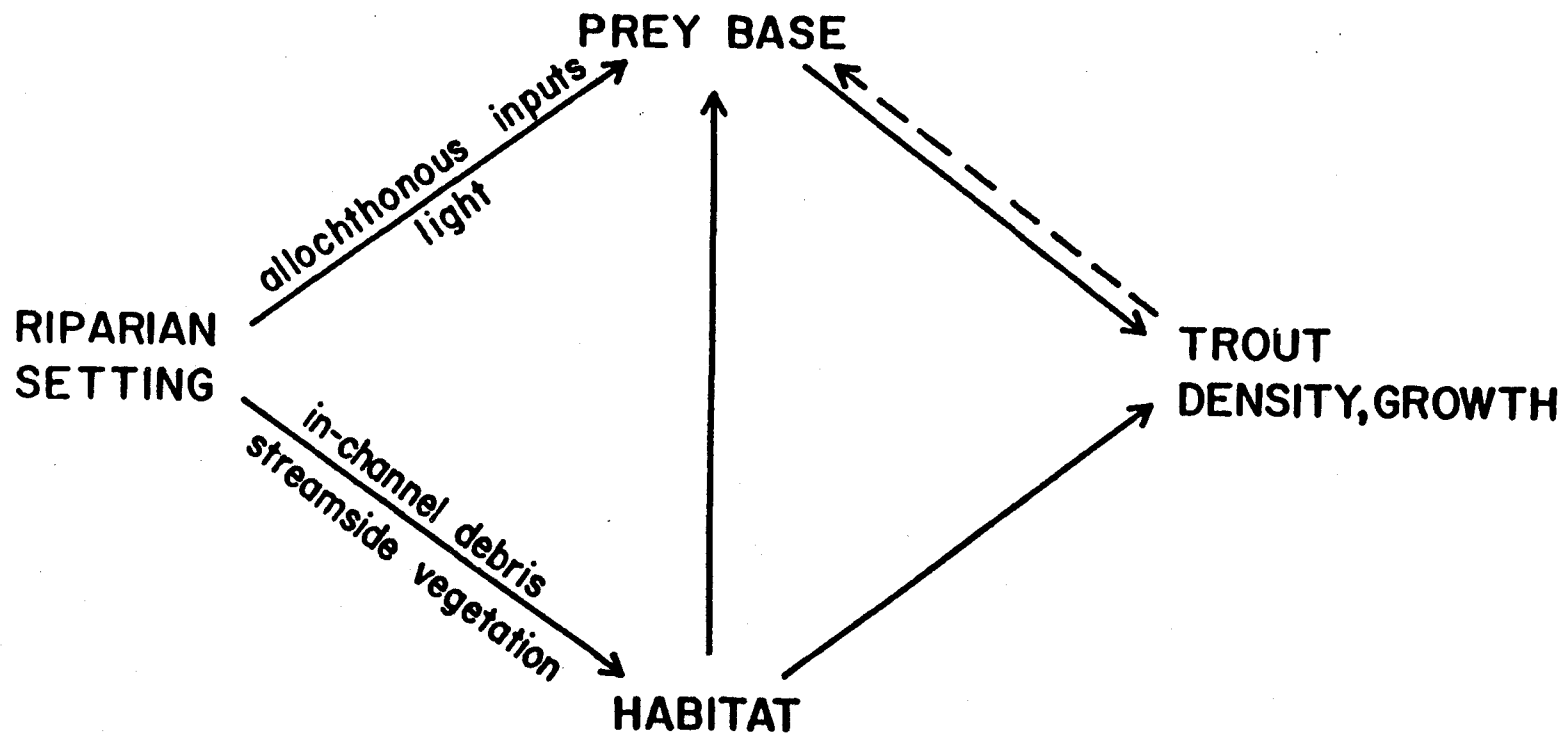


Fig. 11. 2. Conceptual model relating influence of the riparian setting on trout density and growth through the prey base and habitat. ∞

of ecosystems have shown habitat to be significant. For example, Menge (1978) 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 (7 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. The study reaches consist of a series of riffles or rapids and plunge pools. The old-growth section is highly modified by wood debris. A debris torrent occurred approximately 5 to 10 yrs previous several thousand meters upstream of the clear-cut section. It is buffered from the study reach by an intact old-growth reach. Each study section was approximately 150 m in length. Study sections were separated by approximately 800 m. The old-growth section was located more than 300 m from the end of the clear-cut. 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.

Snorkeling 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 snorkeling 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 m² and a mesh size of 0.250 mm, were submerged for one hour for each sample at varying times of day. 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 spp. 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 spp. 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 daytime 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 ($p < 0.05$, Mann-Whitney U test) (Fig. II. 3). These data do not directly reflect habitat differences between sites in and of themselves because variables concerning prey food resources may also contribute to differences. Allan (1985) found that differences in discharge often account substantially for variation in drift density. In the Grasshopper Creek sites, discharge and the range of current velocities encountered were similar. The relationship between drift density and current was not significantly different between sites ($p > 0.10$, 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). The Pfankuch method is designed to predict sediment yield at high flows, and is based on qualitative ranking of several features of a stream channel and its banks that relate to the likelihood of sediment displacement. At low flow, a higher percentage of taxa that occur in

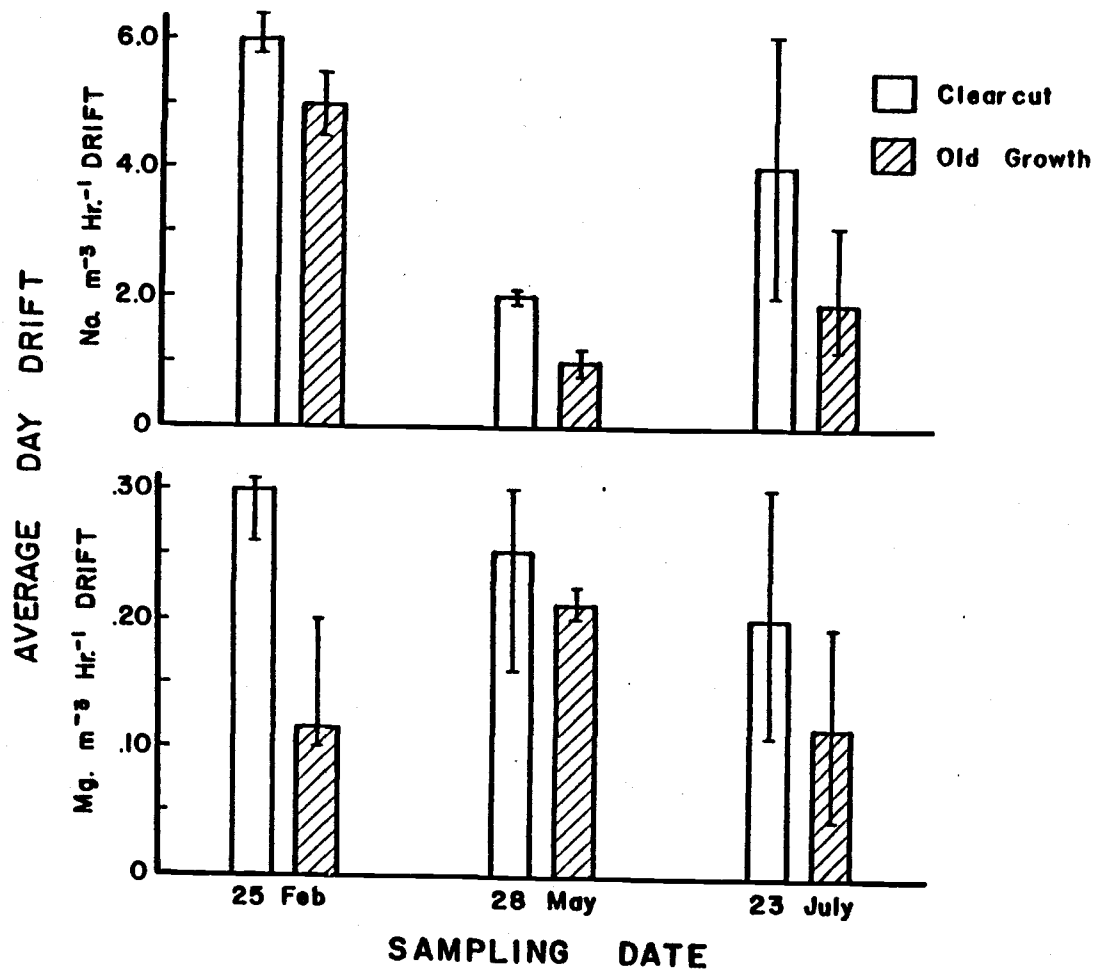


Fig. II. 3. Density and biomass of average day drift in a clear-cut and old-growth section of Grasshopper Creek at high (February and May) and low (July) flows, 1983. Vertical bars indicate range of values, $n = 2 - 5$.

the drift behaviorally (Fig. II. 4) in the clear-cut than in the old-growth section is probably related to 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 food resource of high quality and with a rapid turnover. The predominant behavioral drifting invertebrates collected in this study were Baetis bicaudatus and Orthocladiinae chironomids. Benthic composition, although not examined in this study, has been found by Hawkins et al. (1983) to be more diverse in forested than in open stream sites. 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. A more diverse benthic fauna, including a greater proportion of univoltine and longer-lived species adapted to substrates less prone to shifting, occurs in old-growth stream sites in response to a greater microhabitat and food diversity. At high flows the relative percent of behavioral drifters in the clear-cut section decreased because more accidental drifters became dislodged.

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 constant food supply drifting at predictable times each day. Even at high flows, although the percentage of behavioral drift decreases in the clear-cut relative to low flow periods, absolute numbers of all drift are greater than in

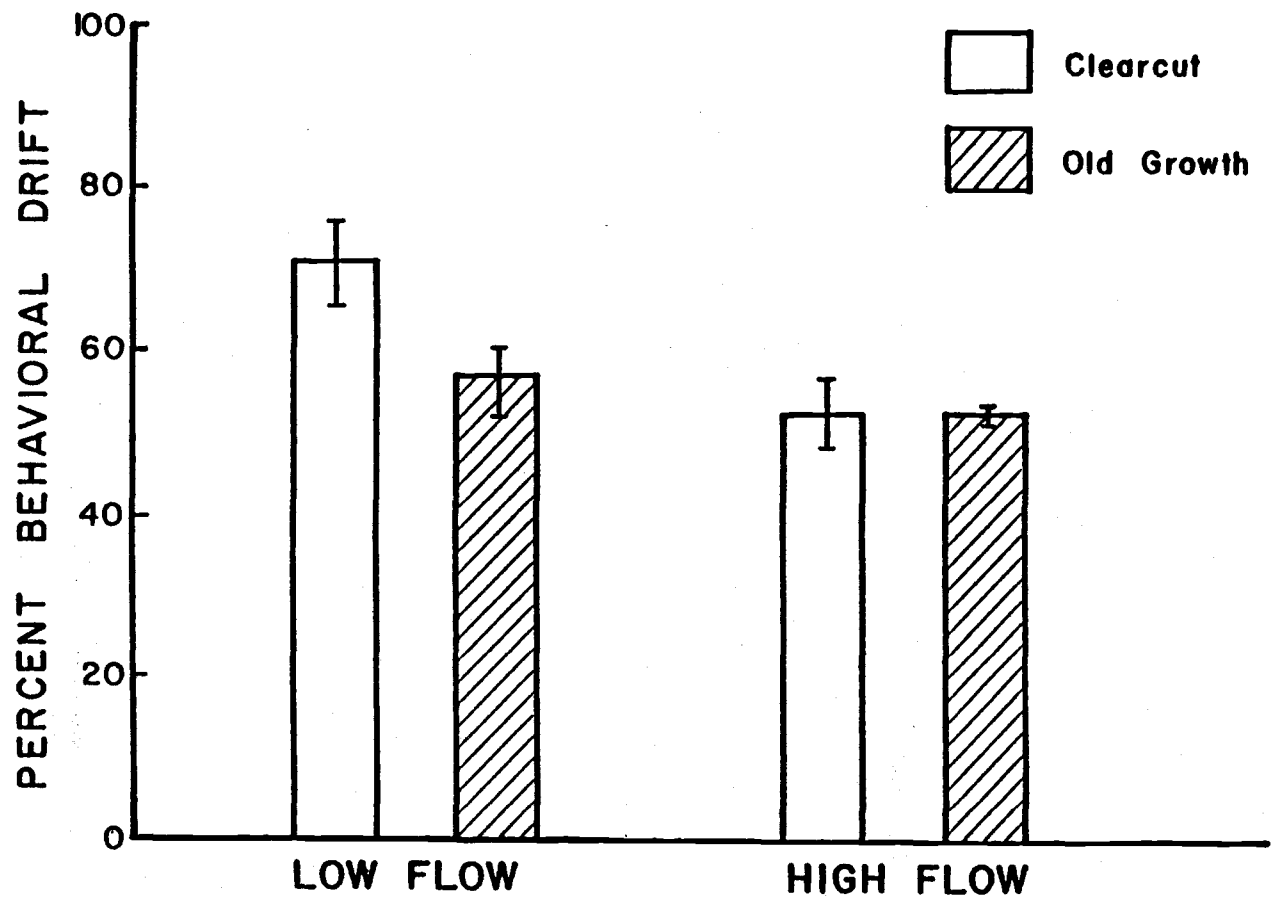


Fig. II. 4. Percent of behaviorally drifting invertebrates that occurred in drift samples collected in the old-growth and clear-cut section during high and low flows. Vertical bars indicate CV, n = 4 - 5.

the old-growth section (Fig. II. 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. If drift abundance increases with increasing habitat instability, we hypothesize that 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. II. 5). Once some threshold is reached, greater habitat instability may not increase the supply of drift until the habitat becomes so unstable that invertebrates cannot be maintained in the reach at all.

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 greater than 1 yr old ($n = 109$) 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

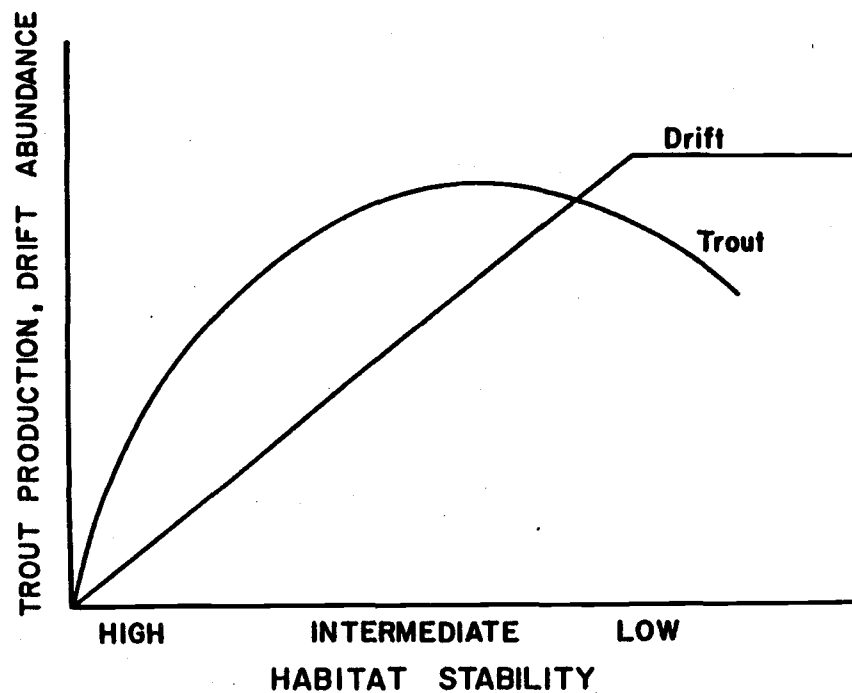


Fig. II. 5. Proposed relationship between trout production and drift abundance along a gradient of habitat instability. At a level of habitat instability greater than is represented in the figure, drift abundance is expected to sharply decline as the habitat becomes so unstable that invertebrates cannot be maintained. At a high level of habitat stability, trout production and drift abundance are hypothesized to be maintained at low (but not zero) levels.

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 and Hall 1981, Hawkins et al. 1983). An assumption affecting these studies is that capture efficiencies 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 may moderate harsh physical conditions such as high flows and sediment movement or decrease 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 spp. larvae) and observing the number of captures during a three minute trial. The number of fish per unit pool volume (one fish per 0.14 m^3) was the same at the two 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 efficiency 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 was 51 and 73 animals, respectively, per three minutes at that time of year.

In both sites, capture efficiency was highest at the lowest density and was fairly constant at high densities (Fig. II. 6). At higher prey densities (> 10 prey per 3 minutes), capture efficiency was greater in the clear-cut pool. Surface light was approximately 40 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. II. 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 10. A 40-fold reduction in light in the old-growth pool resulted in a 36% reduction in average capture efficiency.

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

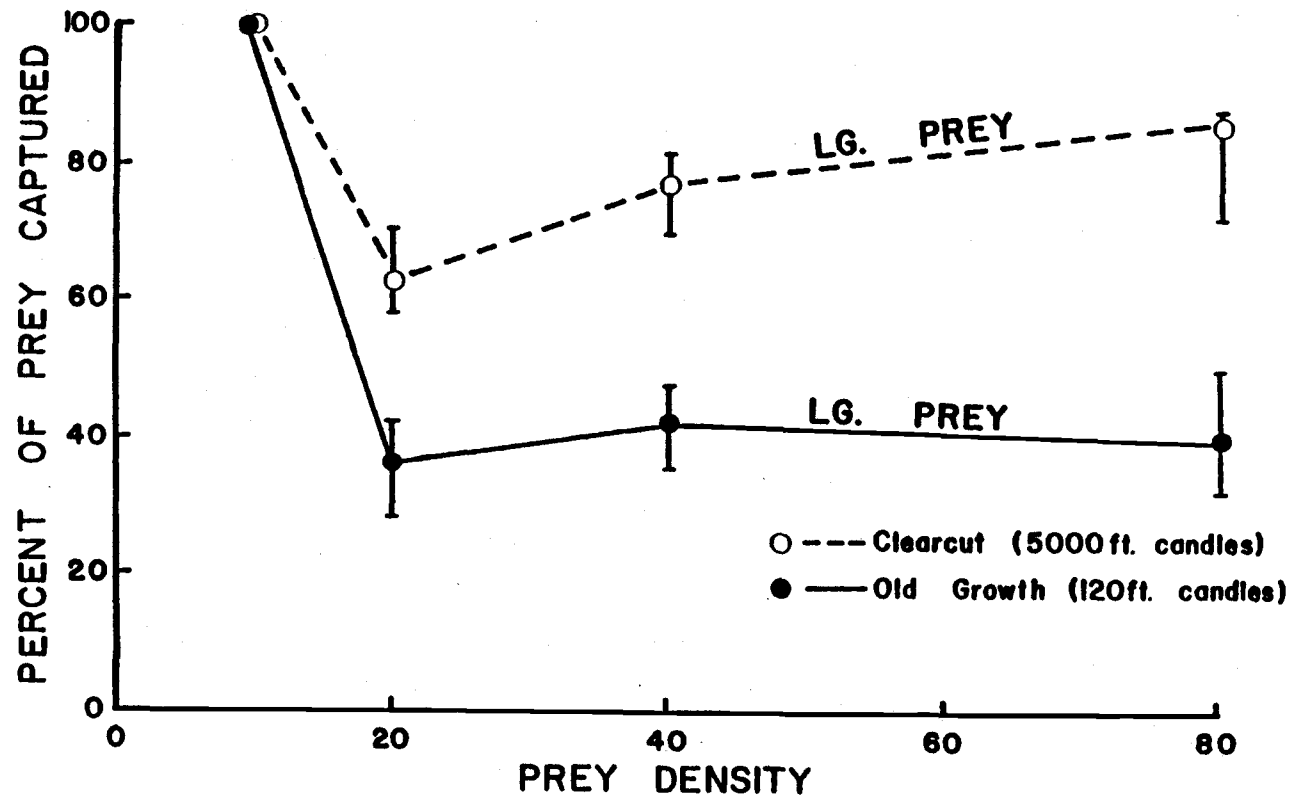


Fig. II. 6. Percent of prey captured by cutthroat trout at varying prey densities in an old-growth and clear-cut pool. Large (10 mm) *Culex* sp. larvae were introduced in a randomized order during feeding trials of three minutes each. Vertical bars indicate range of value, $n = 2 - 3$. Surface light readings for each pool were measured with a Gossen® light meter at the time feeding trials were conducted.

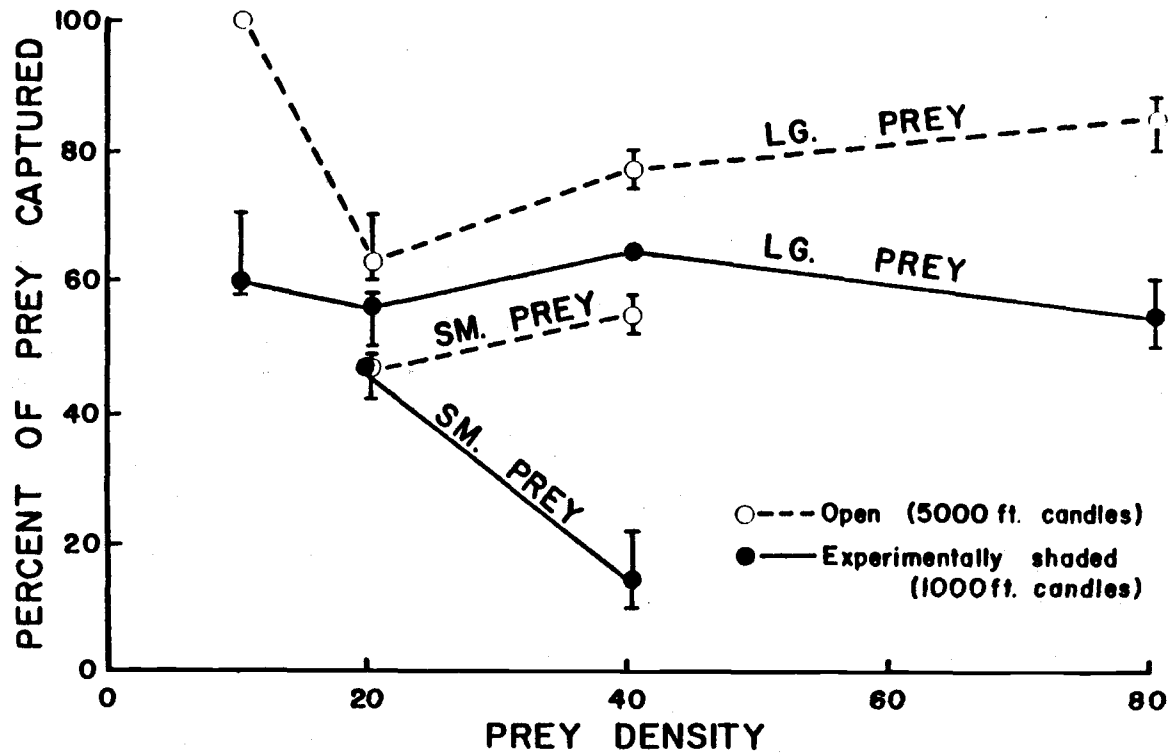


Fig. II. 7. Percent of prey captured by cutthroat trout at varying prey densities and large (10 mm) and small (5 mm) sizes in a clear-cut pool under artificial shading and natural conditions. Culex sp. larvae were introduced in a randomized order during feeding trials of three minutes each. Vertical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

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 at high flows or predation. Trout populations are perhaps more abundant in clear-cut streams, but they may also be more susceptible to reduction in abundance from unpredictable physical disturbances or from predation.

CHAPTER III

INFLUENCE OF RIPARIAN-RELATED HABITAT MANIPULATIONS ON
INTERACTIONS BETWEEN CUTTHROAT TROUT AND INVERTEBRATE DRIFT

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Introduction

Laboratory studies (Glass 1971) and field experiments in artificial ponds (Crowder and Cooper 1982) suggest that growth rates of fish in lentic environments are greatest at an intermediate level of habitat complexity. The diversity and abundance of invertebrate prey are often greatest at high habitat complexity (Crowder and Cooper 1982). Fish growth, however, may be limited as a result of prey refuges provided by structural complexity, a reduced foraging efficiency, and behavioral deterrents to feeding (Glass 1971, Savino and Stein 1982). At low levels of habitat complexity, although foraging effectiveness is high, prey availability is low and fish risk total depletion of prey, as well as an increased risk of mortality from their own predators (Hall and Werner 1977, Mittelbach 1981, Werner et al. 1983).

These findings may not apply to cutthroat trout (Salmo clarki) and other drift-feeding fish in stream habitats. As in lentic habitats, diversity of benthic invertebrate assemblages in streams is correlated with structural complexity (e.g. Rabeni and Minshall 1977, Hart 1978, Williams 1980). But because benthic taxa and life stages vary widely in propensity to occur in the drift, relationships between benthic diversity or abundance and prey availability are often not direct. Prey availability may be greater in unstable, structure-poor stream settings than in complex habitats, as substrate features and a greater relative abundance of periphyton that characterize the former (Fisher 1983) may favor the occurrence of behavioral drifters (Wilzbach and Hall 1984). Behavioral drifters are characterized by

rapid turn-over, polyvoltine species such as Baetis spp., which exhibit a diel pulse in drift activity (Waters 1965). If both prey availability and foraging efficiency are greater in 'simple' habitats, growth of cutthroat trout should be greater in these sites than in habitats of either intermediate or high complexity.

The effect of trout predation on its prey base should be greatest in stream habitats of low complexity as well. Although several studies (e.g. Brooks and Dodson 1965, O'Brien 1979, Gilinsky 1984) have shown that fish strongly regulate prey composition in ponds or lakes, the available data for streams are ambiguous or support an opposite conclusion (Griffiths 1981, Allan 1982, 1983). Allan proposed that failure of stream fish to regulate benthic or drifting invertebrate prey may result because there are no areas in streams where fish are predictably absent, and that invertebrates have therefore evolved mechanisms to successfully avoid capture. Although reasons why stream fish have not counter-evolved increased hunting skills are not clear, the impact of stream fish predation on its prey base may be insignificant for other reasons as well. As with many invertebrates, aquatic insects exhibit a negative exponential survivorship curve (Pritchard 1978, 1980), with as much as 90% or more of the mortality occurring within the first few instars. These instars are outside the size range that stream fish typically select for or are able to detect and capture. If this is the case, stream fish predation may be an insignificant source of invertebrate mortality. If habitat complexity, however, influences the capture success of stream

fish and the range of prey sizes cropped, the generality of this proposal may be restricted.

The age and floristic characteristics of the riparian setting act in concert with and may override geomorphic processes to largely determine stream habitat complexity (Swanson et al. 1982, Cummins et al. 1984). This regulatory role is mediated by standing bankside vegetation and large woody debris in the stream channel that is derived from riparian vegetation (Swanson and Lienkaemper 1978). In unperturbed, forested stream reaches, particularly in the Pacific Northwest, characteristically large amounts of in-channel wood (boles and root wads) act as retention structures for organic and inorganic inputs, decrease gradients through a stair-stepping effect, and create a diversity of pools and other microhabitat types (Swanson and Lienkaemper 1978, Cummins et al. 1983). Together with overhead shading from bank vegetation, in-channel debris provides abundant cover for trout, directly and indirectly through effects on sediment size distribution. Removal of wooded riparian vegetation through logging, particularly if it involves removal of in-channel debris, typically results in stream 'channelization', with an attendant loss of both structural complexity and cover.

Previous studies (Aho 1977, Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983) have documented that the abundance and biomass of cutthroat trout are greater in logged headwater (stream order <4) stream reaches of the Oregon Cascades than in sites bordered by mature assemblages of riparian vegetation. However, the effects of riparian-related habitat features on the foraging activity and growth

of the trout in logged and forested stream reaches have not been examined.

The objectives of this study were to examine the interaction of the riparian setting (logged vs. forested) and prey availability on the prey capture efficiency and growth of cutthroat trout and to determine if the riparian setting influences the impact of trout predation on drift composition.

Methods

The study was conducted from June through August 1984 in a recently logged (7 yrs) and a downstream forested (450+ yr old-growth stand) section of Grasshopper Creek, a third order stream at 1000 m elevation in the western Cascade Mountains in Oregon. The study sites were separated by approximately 800 m. The forested section was located more than 300 m from the downstream end of the logged section. A site description is provided in Wilzbach and Hall (1984). Resident (non-anadromous) populations of cutthroat trout are the only fish species present in each section.

Twelve pools in the logged section and six pools in the old-growth section were selected for study. Pool selection was based on similarity of pool depth and volume. Pool length and width, depths, and velocities were determined by survey, in which line transects were established at the head, middle, and tail of the pool. Depths and current velocities were measured every 0.5 m on each transect. Current was determined to the nearest 0.01m/sec with a Montedoro Whitney® digital flowmeter at the surface, mid-depth, and bottom.

Maps were drawn to scale and pool volumes were determined planimetrically. Mean pool surface area was 3.2 m^2 , $SD=1.2$; pool volumes ranged from 0.753 to 2.875 m^3 ($\bar{x} = 1.63 \text{ m}^3$, $SD = 0.72$; mean maximum depth was 0.66 m , $SD= 0.18$. Water temperatures were monitored in the pools with Taylor® maximum-minimum mercury thermometers. Temperatures ranged from 10° to 15°C throughout the experiment. Differences in temperature among pools in the logged and forested sections were never greater than 1°C on any given day.

Trout were removed from each of the selected pools by underwater capture or by barbless flies on hook and line. They were kept excluded from two pools in each site to enable examination of effects of trout predation on drift composition (Fig. III.1).

Five to 14 trout, ranging in size from 90 to 200 mm, were re-introduced into each of the other pools. Trout densities were adjusted such that trout densities and biomass per unit pool volume (approximately 6 fish and $122\text{g}/\text{m}^3$) were fairly constant. In no instance was the number of trout introduced into a pool greater than the number of trout that previously inhabited each pool. Migration of trout to or from pools was prevented by blocking the head and tail of each pool with 1/2-in. (1.27-cm) mesh hardware cloth. From prior observations we determined that the trout exhibited at least seasonal microhabitat fidelity, and we feel therefore that the enclosures did not greatly interfere with the natural foraging movements of the fish. Before introduction to a pool, trout were measured to the nearest mm, weighed to the nearest 0.1 g and the left side of each fish was photographed for later identification (Bachman 1984).

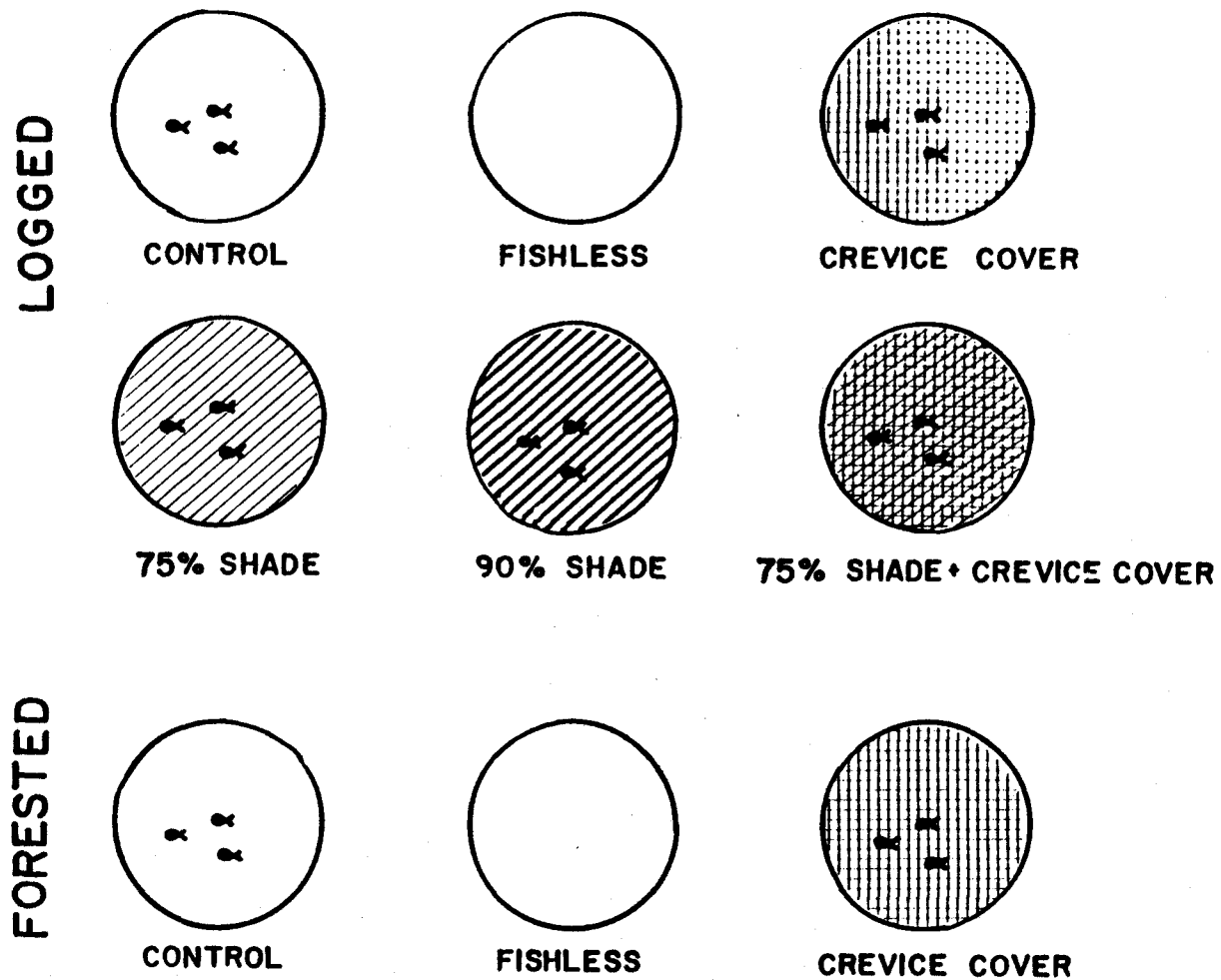


Figure III. 1. Experimental design. Pool manipulations were replicated twice. indicates pools where cutthroat trout were re-introduced.

To determine if surface light and/or substrate crevices affect trout foraging activity, two pools each in the logged section were manipulated in one of the following ways: 1) artificially shaded with overhead nylon screen that reduced surface light by approximately 75%, 2) artificially shaded with screen that reduced surface light by approximately 90%, 3) the bottom was lined with 1 mm mesh fiberglass screening to eliminate substrate crevices, and 4) shaded with 75% screening and the crevices covered (Fig. III. 1). Similarly, the substrates of two pools in the forested section were covered with screening. We hypothesized that substrate crevices should act to decrease foraging effectiveness by impeding a trout's field of vision and that artificial shading and crevice cover should have counteracting effects.

Overhead shade cover was held in place with lines tethered to bankside vegetation. Screening positioned over pool substrates was anchored with small rocks placed at screen borders and the panels of screen were fastened together with plastic buttoneers (Dennison®). The screening did not alter topography of the pool bottom, but it did effectively eliminate substrate crevices.

Invertebrate drift was sampled at dawn, mid-day, dusk, and mid-night from the tail of each pool at the beginning and termination (after 6 or 8 weeks) of the experiment, and at mid-day at the midpoint (after 3 or 4 weeks). Each drift net was positioned in the thalweg to capture most of the organisms exiting a pool. Drift nets had a mouth area of 0.0234 m^2 and a mesh size of $250 \text{ }\mu\text{m}$. Current velocity was measured in front of each net at the time of sampling.

Samples were collected over a 1 hr period at each sampling time, and were preserved in 70% alcohol. Individuals were later separated into the lowest taxonomic category feasible and into drift categories (accidental and behavioral). Animals classified as behavioral drifters were identified from the literature and from unpublished observations (Cummins and Wilzbach). Total lengths were measured in 1-mm intervals at 12X and biomass was estimated from available length-weight regressions (Cummins and Wilzbach, unpubl.; Coffman 1967, Mackey 1977, Rogers et al. 1977, Smock 1980).

Trout were collected from each pool by hook and line with barbless flies at the midpoint and termination of the experiment. Stomach contents of each fish were removed by flushing the foregut with a syringe and were preserved in 70% alcohol for later identification. The trout were measured, weighed, photographed, and released back into their respective pools. Comparison of the photographed spot patterns on the left side of each fish body enabled recognition of individual trout at successive sampling times (Bachman 1984). Relative growth rates (RGR, Waldbauer 1968) of individual trout, expressed as the percent increase in body weight per day, were then estimated according to the formula:

$$\left[\frac{(W_f - W_i)}{(W_f + W_i)} \right] \cdot T^{-1} \cdot 100$$

where W represents weight; i = initial; f = final;

T = days between sampling times.

Feeding experiments were conducted in each pool to examine the influence of habitat features on prey capture efficiency of trout,

independently of differences in prey availability among pools. In these experiments, incoming drift was blocked from each pool by a 250- μ m net placed immediately upstream for the duration of a feeding trial. Four densities (10, 20, 40, and 80 animals) and two size classes (small [3-5 mm] and large [7-10 mm]) of Culex spp. (Culicidae) larvae were introduced in a randomized order during 3-minute trials each from a feeding apparatus (Fig. III. 2) placed at the head of each pool. The number of feeding trout and the total number of prey captures were determined by a snorkeling observer located 1-2 m downstream of the feeding fish. Because Ware (1972) found that searching behavior of trout may be controlled by a critical rate of food capture, feeding response of the trout was triggered prior to the beginning of feeding trials by manually dislodging the substrate above each pool to accelerate the flow of drift. A series of light readings at the surface of each pool were taken with a Lycor[®] light meter immediately before and after each feeding session, and they were averaged to obtain an estimate of surface light. All feeding trials were conducted during daylight hours (1400-1700 hrs.).

Tail beat frequencies of individual trout were determined by underwater observation during and after feeding trials to obtain an indirect estimate of energetic expenditures involved in foraging. Hunter and Zweifel (1971) and Feldmuth and Jenkins (1973) established that a consistent linear relationship exists between tail beat frequency and swimming speed. Feldmuth and Jenkins (1973) suggest that energy expenditures of trout in natural stream habitats can then be estimated from published data (e.g. Rao 1968) on metabolic rates at

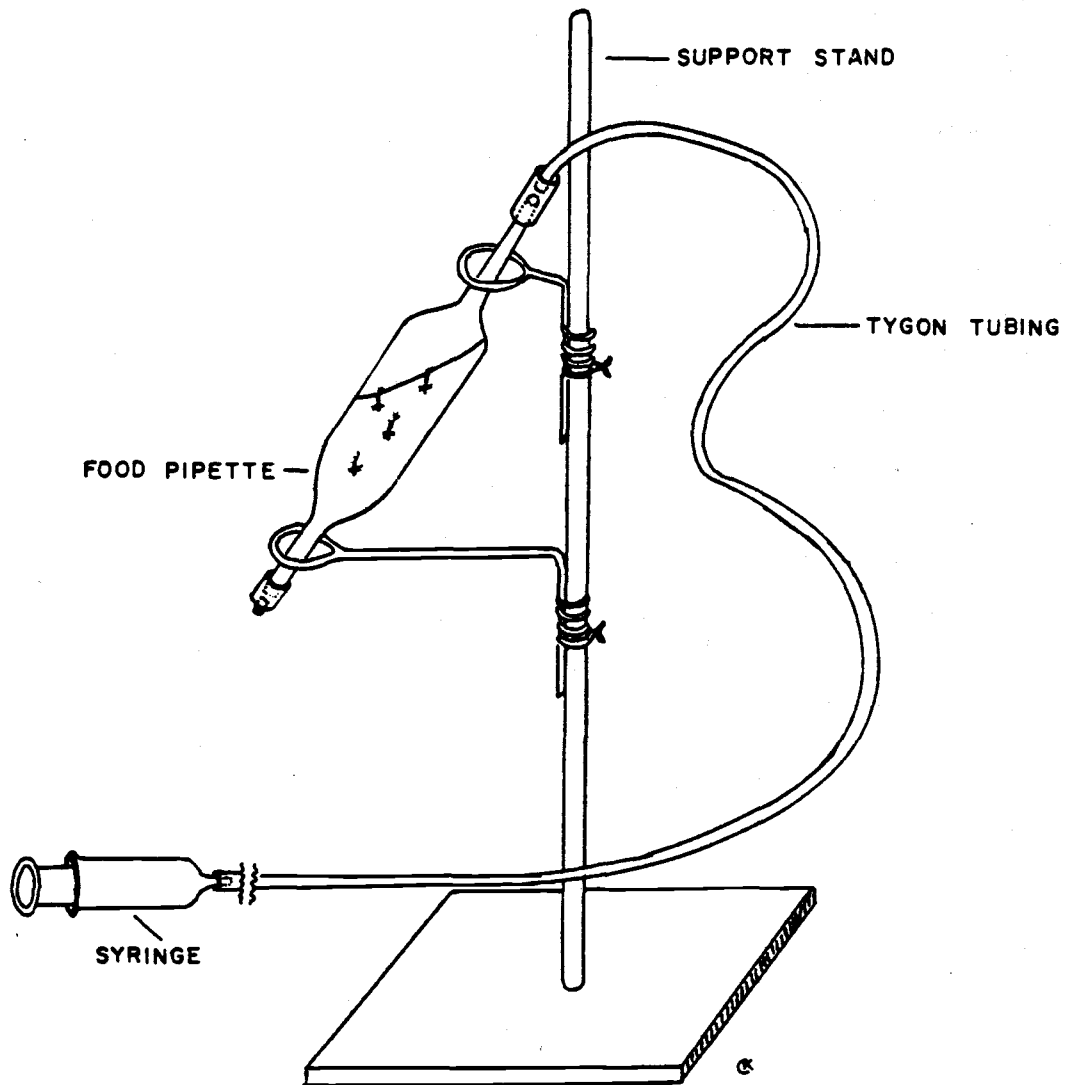


Figure III. 2. Apparatus used in trout feeding trials. Apparatus consists of a replacible volumetric pipette into which prey animals are drawn. Pipette is held in place with a clear plexiglass ring stand, attached with 15 m of Tygon® tubing to a syringe hand-operated by observer. Prey are forced by air into the water column.

various swimming speeds. Tail beat frequencies for fish of known size were determined during holding (non-feeding) and feeding periods. Feeding periods included activities involved in search, capture, and return to focal position.

The percent increase in tail beat frequencies at feeding relative to holding periods $[(\text{feeding} - \text{holding}) / \text{holding} \times 100]$ was calculated to obtain an estimate of energy expenditures involved in foraging. This measure was used to standardize among pools for the influence of current on the energy expenditures associated with holding position.

Results and Discussion

Prey capture efficiency of trout

In control pools of both the logged and the forested section, foraging efficiency of the trout, expressed as the percent of total prey captures by all feeding fish, was greater for large (7-10 mm) than for small (3-5 mm) prey ($p < 0.05$, Mann-Whitney U test) (Fig. III.3). This suggests that the findings of Ware (1972), Allan (1978), Ringler (1979), Wankowski (1981) and others that trout are generally size-selective may be partly based on greater foraging efficiency on larger prey. The foraging efficiency of trout in control pools in the logged section was greater than that of trout in forested control pools for large prey ($p < 0.05$, Mann-Whitney U test), but this result was not significant for small prey. Foraging efficiency on small prey in controls pools of the logged section was nearly identical to the efficiency with which trout in the forested section (control pools) captured large prey.

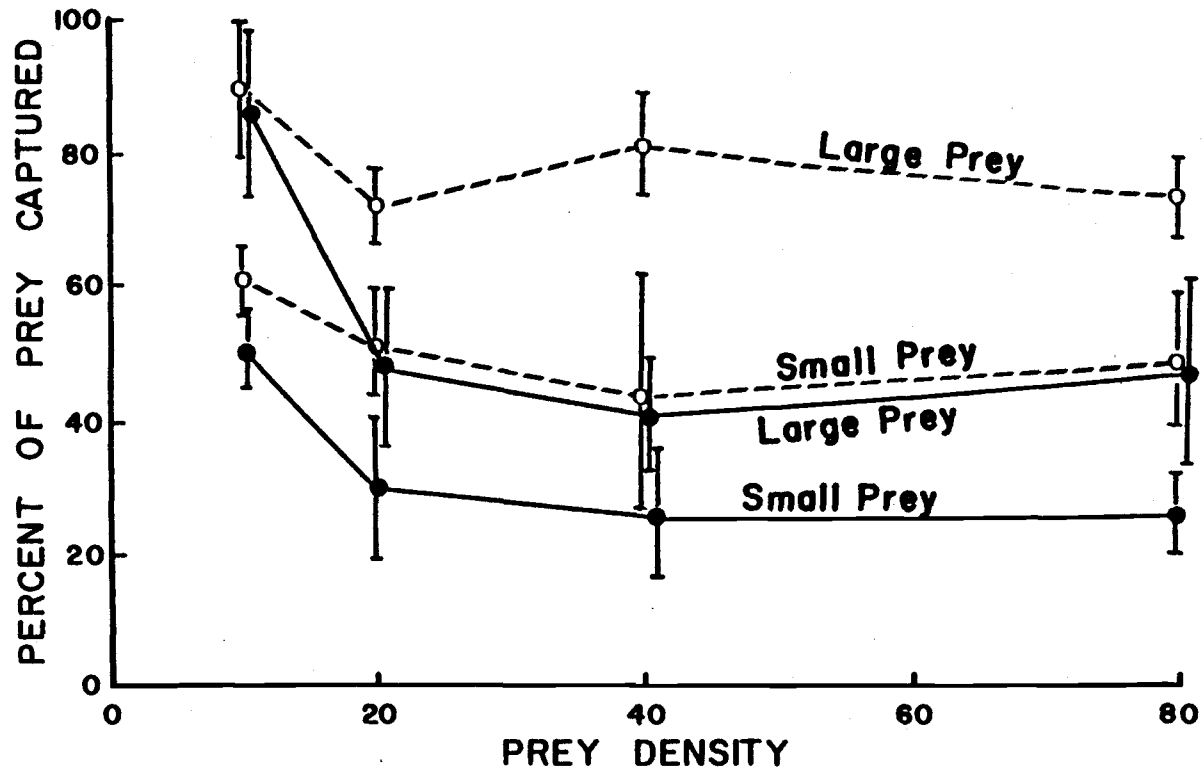


Figure III. 3. Relationship between prey density and percent of introduced prey (*Culex* spp. larvae) that were captured by feeding trout. Large prey were 7-10 mm; small prey were 3-5 mm. Vertical bars represent SD, n=6. Symbols: ○ - logged control pools; ● - forested control pools.

Although the absolute number of introduced prey captured increased with prey density, the proportion of prey captured tended to be greatest at the lowest prey density (10 animals) in both sections, and within a site and prey size class, was fairly similar at all other densities. This result was significant ($p < 0.05$, Mann-Whitney U test) for large and small prey in the forested section. In order to restrict comparisons to a range in which foraging efficiency was independent of prey density, the percent of prey captured at a prey density of 10 was deleted from subsequent estimations of mean capture efficiency.

The effects of prey size and density on foraging efficiencies are similar to results obtained from feeding trials conducted in the same manner and at the same site during the previous year (Wilzbach and Hall 1984). As before, the foraging efficiency within a pool during a feeding session neither increased nor decreased with time, indicating that neither learning nor satiation influenced the results. The difference in efficiencies between replications was not significant ($p > 0.10$, Mann-Whitney U test) for any treatment, nor was the difference in efficiency within a pool between dates of feeding trials.

Comparison of the percentage of prey captured among treatments is not appropriate unless differences in pool volumes or current profiles or in the number of trout feeding did not affect the results. This appears to be the case, as no relationship was found between the percent of fish feeding and pool volume, between the percent of prey captured and the number of fish feeding, or between the percent of prey capture and mean velocity in the plume of feeding apparatus.

Using data from feeding trials obtained both years (this study and Wilzbach and Hall 1984), we found a strong relationship ($R^2 = 0.90$; significant F-test for slope, $p < 0.01$) between mean foraging efficiency of the trout and the logarithm of mean surface light at the time feeding trials were conducted (Fig. III. 4). This relationship is based on data for large prey over a range of prey densities (20-80 animals) from control pools or pools in which artificial shading was the only manipulation. The artificial shading employed in pools of the logged study section was generally effective in reducing light levels of the pools to those characteristic of the forested section during daylight hours (Fig. III. 4).

It is not known if the relationship between foraging efficiency and surface light remains log-linear or perhaps exhibits a threshold response at light levels lower than those tested. We were unable to see well enough during crepuscular light conditions to conduct feeding trials at those times. In laboratory feeding experiments, Henderson (1982) demonstrated that Dolly Varden charr (Salvelinus malma) were able to detect prey at lower irradiance levels than cutthroat trout. The reactive distance of both species to prey increased as irradiance increased from a threshold level (3.0×10^{15} photons $m^{-2}s^{-1}$ for cutthroat trout, independent of prey type or characteristics), below which prey were not detected.

Foraging efficiency of trout in logged and forested pools differed among treatments ($p < 0.05$, Kruskal-Wallis). In the forested reach, mean foraging efficiency of trout in crevice-covered pools was greater than the efficiency of trout in control pools ($p < 0.10$,

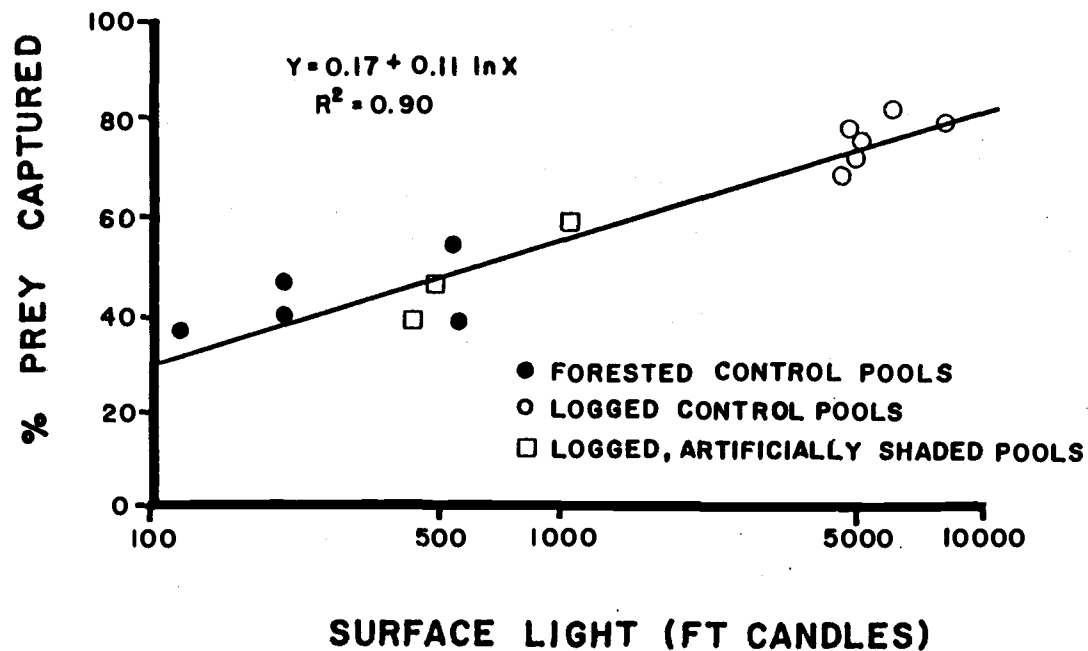


Figure III. 4. Relationship between foraging efficiency of cutthroat trout, expressed as mean percent of prey captured, and mean surface light of pools at the time feeding trials were conducted. The relationship is based on data from this study and Wilzbach and Hall (1984) for foraging efficiency on large (7-10 mm) prey over prey densities ranging from 20-80 animals, from control pools or pools in which artificial shading was the only manipulation. Each point represents 6-9 feeding trials in one pool.

multiple comparisons (Dunn 1964) (Fig. III.5). A similar result was found in the logged section, but was not significant. The addition of 75% shading to crevice-covered pools in the logged section, however, significantly reduced foraging efficiency of trout relative to that for trout in pools in which crevice cover alone was manipulated ($p < 0.10$). Relative to pools in which shading alone was manipulated, the addition of crevice cover increased foraging efficiency. Percentages of prey capture of trout were similar in crevice-covered pools of the forested section and in crevice-covered plus shaded pools of the logged section (Fig. III. 5). These results generally support our hypotheses that substrate crevices should act to decrease foraging effectiveness by impeding a trout's field of vision and that artificial shading and crevice cover should have counteracting effects. These results are also in agreement with Ware's (1972) finding that total food consumption and predation intensity of rainbow trout (Salmo gairdneri) varied inversely with substrate complexity.

Trout foraging energetics

The relationship between trout size and tail beat frequency during holding, standardized for flow ($\text{cm}^{-1} \cdot \text{sec}^{-1}$), was weak ($R^2 = 0.44$). Similarly, no relationship was found between trout size and the percent increase in tail beat frequency at feeding relative to holding periods. This was in agreement with Bachman's (1984) finding that, for brown trout (Salmo trutta), differences in tail beat frequency with fish size were insignificant relative to differences in activity state. Tail beat frequencies estimated in this study are

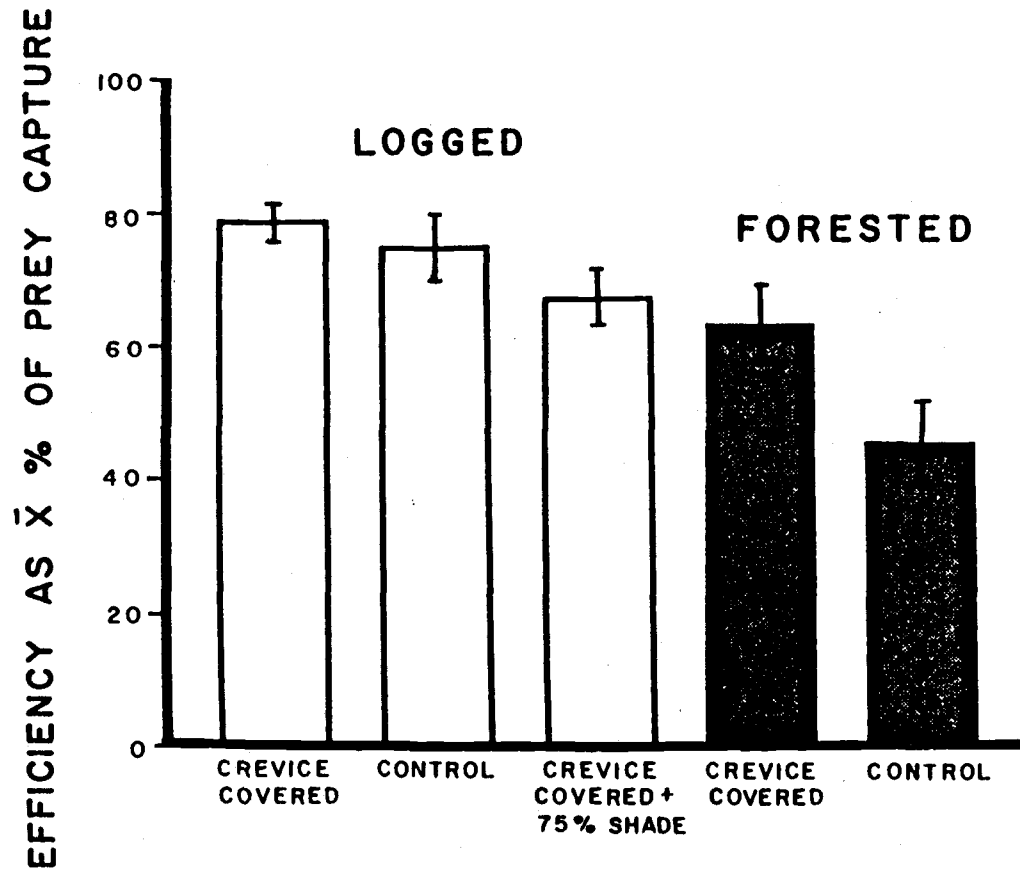


Figure III. 5. Foraging efficiency of cutthroat trout, expressed as mean percent of prey captured, in control and crevice-covered pools of the logged and forested sections, and crevice-covered plus shaded (75%) pools of the logged section. Foraging efficiency for each treatment is based on averages from 2 pools of prey captures on large prey and densities ranging from 20-80. n=9-18. Vertical bars represent 2 SE of the mean.

within the range of tail beat frequencies reported for rainbow trout by Feldmuth and Jenkins (1971), and are somewhat higher than values reported by Bachman (1984) for brown trout.

The percent increase in tail beat frequencies at feeding relative to holding periods, averaged over all fish in a pool, was greatest at an intermediate level of observed foraging efficiency (Fig. III. 6). At low foraging efficiency, trout probably do not detect enough prey to stimulate active foraging. At high foraging efficiency, as prey density and visibility increase, prey capture likely is effected with lower energetic output. The foraging area probably contracts at high foraging efficiency to a space immediately surrounding the holding or focal point position.

Growth rates of trout and prey availability

Short-term relative growth rates of trout (RGR) differed significantly among treatments ($p < 0.05$, Kruskal-Wallis). RGR was greatest in the logged control pools (0.55% body weight per day), and least in the forested control pools (0.04% dry weight per day) (Fig. III. 7). Differences within pools in RGR between the first and second halves of the experiment were not significant ($p > 0.10$, Mann-Whitney), nor were differences significant among replications ($p > 0.10$, Kruskal-Wallis). Data were thus combined over sampling dates and replications to obtain mean relative growth rates for each treatment. Regardless of treatment, the RGR of trout in logged pools was significantly greater than the RGR of trout in forested pools in all cases ($p < 0.10$, multiple comparisons [Dunn 1964]). This result corresponds with differences

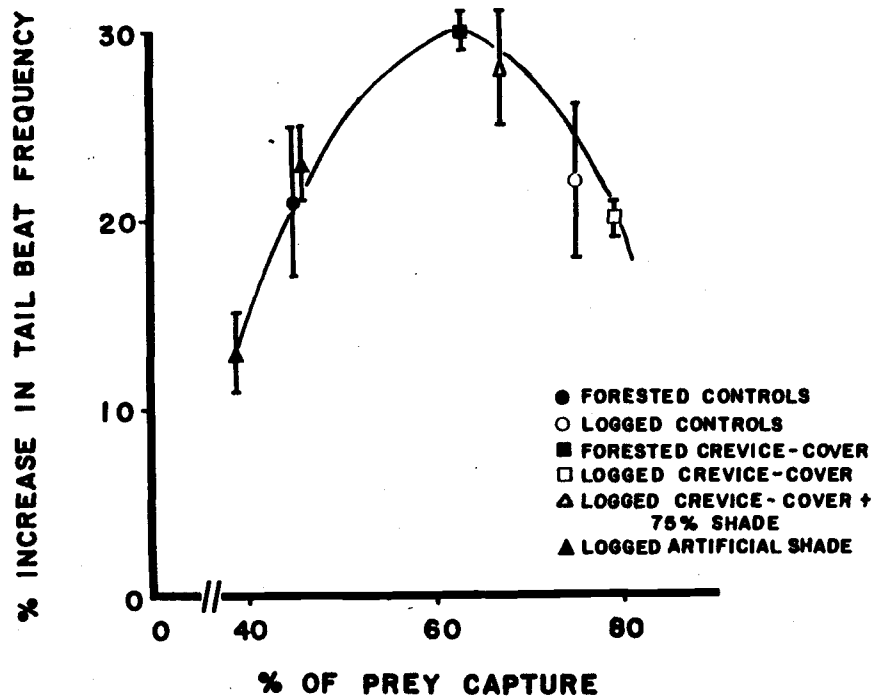


Figure III. 6. Relationship between foraging energetics and foraging efficiency of cutthroat trout. Energy expenditures are indexed by the percent increase in tail beat frequency of trout engaged in feeding relative to holding (feeding-holding/holding * 100); n = 10 - 15 observations per treatment. Foraging efficiency is based on averages from 2 pools of prey capture on large prey with densities ranging from 20-80 (n = 9 - 18). Curve was fitted by inspection. Vertical bar represents S.D.

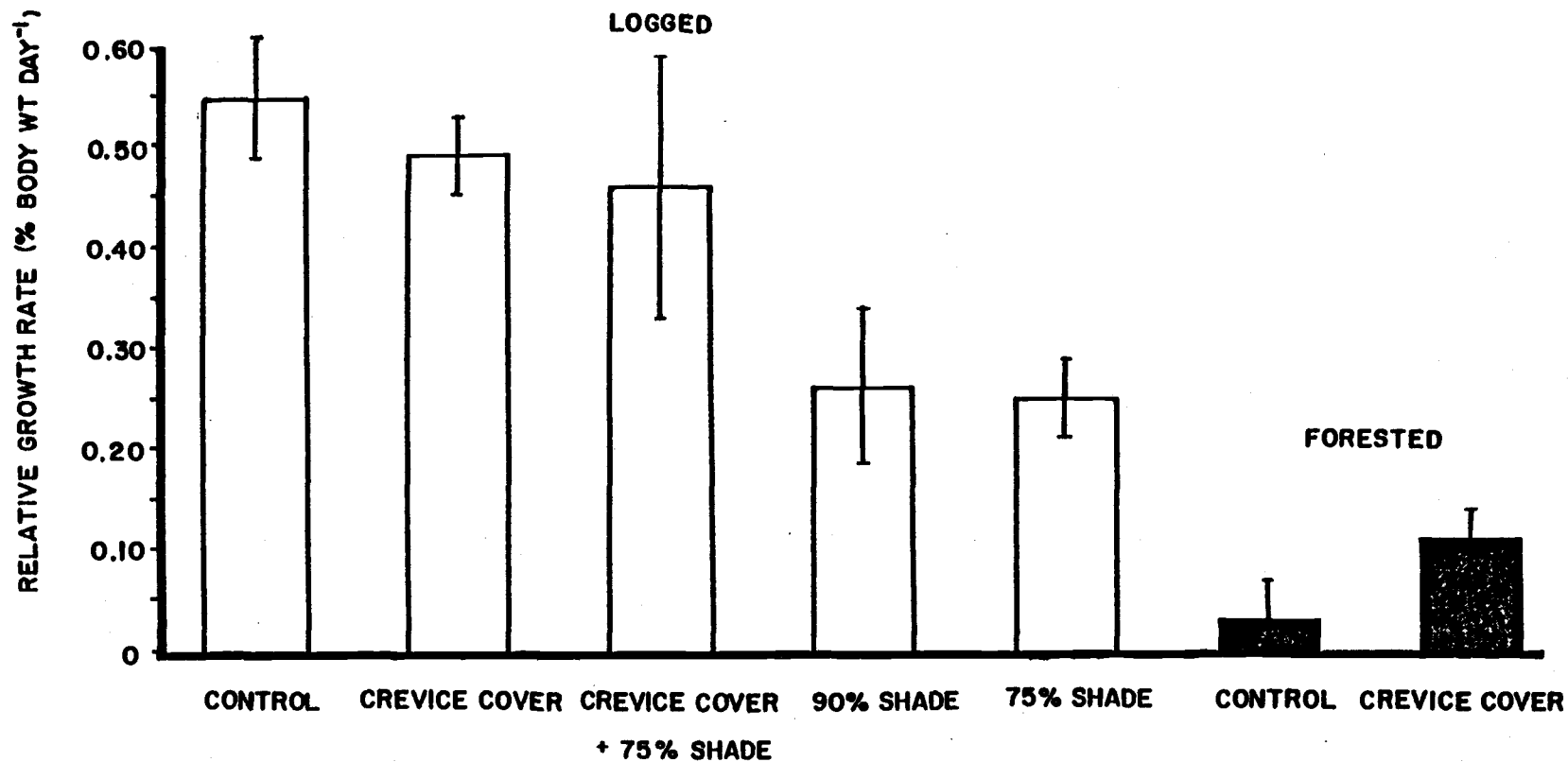


Figure III. 7. Mean relative growth rates of trout from control and manipulated pools in the logged and forested sections. Means are derived from growth rates estimated for individual trout collected during the 1st and 2nd halves (3-4 weeks each) of the experiment from 2 replicate pools. Vertical bar represents S.D.

observed in the length-weight relationship of cutthroat trout between the logged and forested study reaches. Based on data derived from trout captured prior to the initiation of the field experiment, the length-weight relationship for cutthroat trout in the logged section was $\log_{10}W = -4.67 + 2.87 \log_{10}L$ ($n = 66$, $R^2 = 0.98$). In the forested section, the length-weight relationship was $\log_{10}W = -4.65 + 2.81 \log_{10}L$ ($n = 33$, $R^2 = 0.96$). Based on average weights from the regression, trout of a given length in the logged section weighed more than did trout in the forested section. Relative to the energetic expenditures involved in foraging at an intermediate level of efficiency, the lower energetic expenditures associated with the highest foraging efficiencies (Fig. III.6) also corresponded with the highest observed trout growth rates (logged control and crevice-covered pools).

The covering of substrate crevices resulted in an increase in the RGR of trout over that found for control pools in the forested section ($p < 0.15$, multiple comparisons). In the logged section, RGR of trout in crevice-covered pools decreased, but not significantly, relative to control pools. The lack of an increase in RGR of trout in crevice-covered pools in the logged section may have resulted from an increased overhead visibility and hence vulnerability of the trout to predation. The trout in the logged crevice-covered pools were observed to stay in the turbulent pool inlet, where predation risk would be minimized by reduced visibility but where energetic costs of maintaining position were much greater. Evidence of an increased mortality risk of trout was apparent in the loss of four trout in the

logged section (36% of total) and two trout in the forested section (20% of total) from crevice-covered pools over the course of the experiment. The corpse of a trout that had evidently been killed by a predator was found at the margin of a logged crevice-covered pool. No trout were lost from other pools. Because of large variation in trout growth in crevice-covered plus shaded pools, differences in RGR of trout between logged control pools and crevice-covered plus shaded pools were not significant ($p > 0.15$, multiple comparisons), nor were they significant between logged crevice-covered pools and crevice-covered plus shaded pools. Some of the variation is attributable to differences in RGR with fish size. Small fish (< 125 mm) generally grew faster, but not significantly, than larger fish (> 150 mm) (mean RGR = 0.32%, SD = 0.21 and 0.26%, SD = 0.17 respectively).

Differences in RGR of trout between logged pools with 75 and 90% shading were not significant ($p > 0.15$, multiple comparisons), but a reduction in RGR of trout relative to other logged pools ($p < 0.15$) was associated with artificial shading (without the addition of crevice cover).

Differences in mean RGR among treatments were correlated with differences in mean density of daylight drift ($p < 0.05$, Kendall's rank correlation) (Fig. III. 8). Drift density estimates were revised by multiplying drift densities by mean foraging efficiency for a given treatment to better reflect actual prey consumption. This resulted in a correlation with RGR with a greater level of significance ($p < 0.03$). Estimates of mean density of daylight drift were obtained by averaging, over the two pools of a treatment, the densities of indivi-

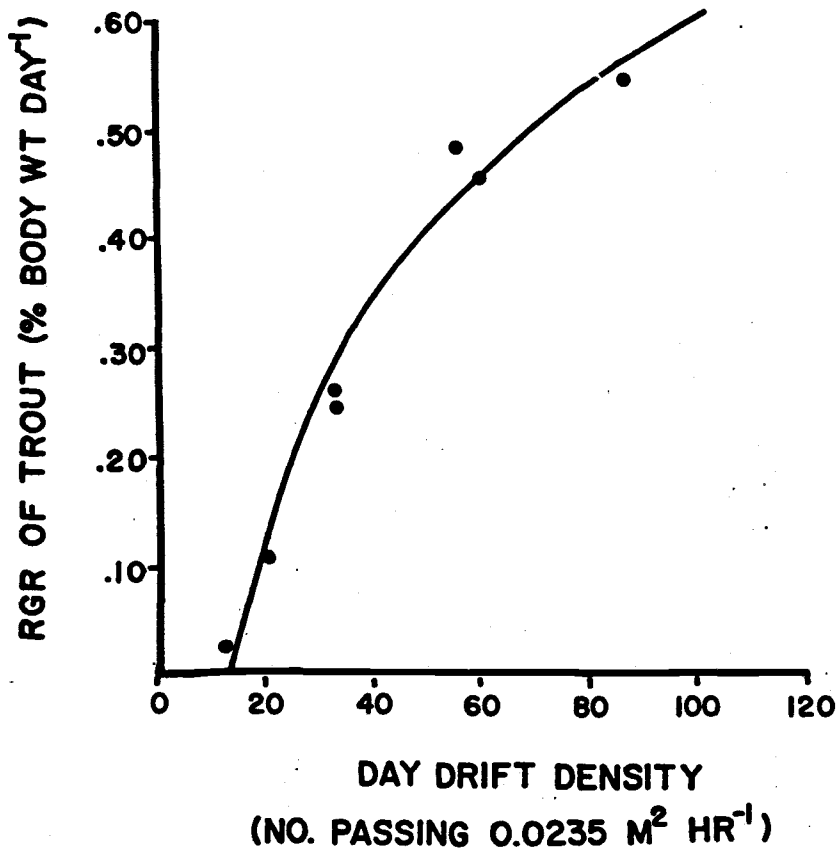


Figure III. 8. Relationship between mean density of day drift and mean relative growth rates of trout from pools in the logged and forested sections. Drift density is based on averages for each treatment from two drift samples collected a dawn, noon, and dusk on the beginning and final sampling dates, and at noon at the midpoint of the experiment (n=14). Individuals < 1 mm in length were excluded from density estimates. Mean relative growth rates of trout are based on averages from 2 pools of growth estimated for individual trout (n=10-21 per treatment). Curve was fitted by inspection.

duals passing into each drift net at dawn, noon, and dusk on each of two sampling dates (beginning and end of the experiment), and at noon at the midpoint of the experiment. Because prey individuals less than 1 mm in length were insignificantly represented (always < 1% by numbers or biomass) in trout stomachs, these were excluded from density estimates to better reflect prey availability to trout.

Because the composition and abundance of drift is clearly of key importance to trout growth, the data were analyzed in detail with reference to their availability to trout. Differences in densities and biomasses of daytime drift were insignificant with respect to sampling time (dawn, noon, or dusk) ($p > 0.05$, Wilcoxon), and data were thus combined over these times to obtain an average of day drift on the beginning and final dates (Table III. 1). Snorkeling observations revealed that, after the midpoint of the experiment, several trout had immigrated into one of the trout removal pools in the forested study section; drift data for this pool were deleted on the final sampling date.

Both densities and biomasses of drift samples were greater at night than during the day ($p < 0.01$, Wilcoxon). This supports a well-documented nocturnal increase in drift, and, for behavioral drifters, may reflect an adaptation for predator avoidance. Allan (1978), for example, observed that within a taxon, larger individuals, which are more vulnerable to predation, are more likely to drift at night.

Densities of day drift (Table III. 1) varied significantly among treatments ($p < 0.05$, Friedman nonparametric ANOVA with sampling dates as blocks). There was no significant difference in daytime drift

Table III. 1. Mean density and biomass of drift samples collected from replicated pools in the logged and forested sections on three sampling dates. Coefficients of variation are indicated in parentheses. At the beginning and end of the experiment, day values of drift represent means of samples collected at dawn, noon, and dusk (n=6). At the midpoint of the experiment, day values represent means of samples collected only at noon (n=2). Values for night drift are from samples collected at midnight (n=2).

Treatments	BEGINNING				MIDDLE		END				
	Day		Night		Day		Day		Night		
	#	g	#	g	#	g	#	g	#	g	
LOGGED											
Control	126(23)	3.78(111)	78(87)	14.64(26)	33(40)	1.95(56)	111(37)	1.36(94)	83(79)	3.35	
Trout Removal	48(62)	2.57(110)	86(29)	9.03(48)	22(25)	4.54(101)	14(35)	0.29(67)	15(34)	0.75(90)	
Crevice- Cover	69(41)	6.11(110)	91(59)	14.36(74)	30(99)	7.99(130)	75(106)	3.43(77)	85(106)	4.17(62)	
75% Shade	42(34)	9.19(107)	288(77)	45.97(96)	53(76)	7.81(41)	30(53)	8.25(222)	170(71)	5.28(77)	
90% Shade	11(10)	4.41(87)	41(120)	5.83(13)	86(115)	3.63(123)	19(35)	1.39(102)	102(97)	7.27(126)	
Crevice- Cover + Shade	45(68)	5.33(102)	309(100)	52.56(10)	97(73)	3.41(72)	46(30)	0.65(90)	65(39)	2.65(88)	
FORESTED											
Control	15(69)	0.53(101)	27(52)	2.66(11)	31(45)	1.95(31)	20(87)	0.73(152)	36(108)	2.64(79)	
Trout Removal	34(56)	1.35(101)	36(15)	3.52(17)	92(84)	11.24(65)	*14(31)	*0.68(95)	*19	*1.67	
Crevice- Cover	34(48)	1.60(62)	87(59)	8.68(10)	28(71)	1.52(80)	13(99)	0.80(111)	26(24)	2.02(91)	

*Data are not replicated because of trout immigration into one of the pools from which they were excluded.

among the sampling dates ($p > 0.10$, Wilcoxon), and sampling dates were combined to examine differences in density among treatments. Multiple comparison of treatment ranks (Gibbons 1976) indicated that, within the logged study section, day drift densities were similar among the control, crevice-covered, and crevice-covered plus shaded pools. These pools exhibited greater day drift densities ($p < 0.01$) than logged pools with 75 and 90% shading, which were similar in drift density to forested trout-removal pools. These pools, in turn, exhibited greater drift density ($p < 0.05$) than were found in the forested control and crevice-covered pools, and logged trout-removal pools. Some of the variability among and within treatments can be attributed to differences between the pools in the volume of water sampled by the drift nets. To represent actual prey availability to trout, data (Table III. 1) were uncorrected for flow. In general, when corrected for flow, drift densities were greater in the logged than in the forested section at both high and low flow periods (Wilzbach and Hall 1984).

Biomass of day drift was similar between the first two sampling dates, but significantly lower on the last date (Wilcoxon $p < 0.05$). Biomass of night drift was also lower on the final than on the beginning sampling date. Differences among treatments in biomass of day drift for the first two sampling dates were insignificant ($p > 0.20$, Friedman nonparametric ANOVA). Lack of correspondence in trends exhibited by drift density in comparison with biomass is largely attributable to differential treatment effects on invertebrates of aquatic vs. terrestrial origin. Because larger individuals usually

were of terrestrial origin, their presence in a drift sample was essentially independent of treatment effects. Occurrence of terrestrial invertebrates in the drift was probably a function of proximity of suitable terrestrial habitat (i.e. overhanging vegetation or woody debris).

A proposed conceptual model relating trout growth to prey availability and to foraging efficiency and energetics is presented in Fig. III. 9. The strong correlation existing between prey density and trout growth (Fig. III. 8) suggests that prey availability is the most important and direct factor positively affecting trout growth. An increase in prey availability may effect a decrease in energy expenditures involved in foraging, as the foraging range of the trout contracts. Energy expenditures involved in foraging in turn should be negatively related to growth rates. Comparison of the percent increase in tail beat frequency with feeding and foraging efficiency (Fig. III. 6) suggests that energy expenditures of foraging may increase at an intermediate level of foraging efficiency, and decrease at high and low foraging efficiencies. An increase in foraging efficiency should result in an increase in growth rates. The relationship between prey availability and foraging efficiency is uncertain. In the trout feeding trials, foraging efficiency was generally greatest at the lowest prey density and fairly constant over all other densities. In natural situations, foraging efficiency should decrease at very high prey densities as the trout become swamped. At very low prey densities (providing the prey are large enough), the trout may be able to remove nearly all those entering their feeding 'window'. Prey

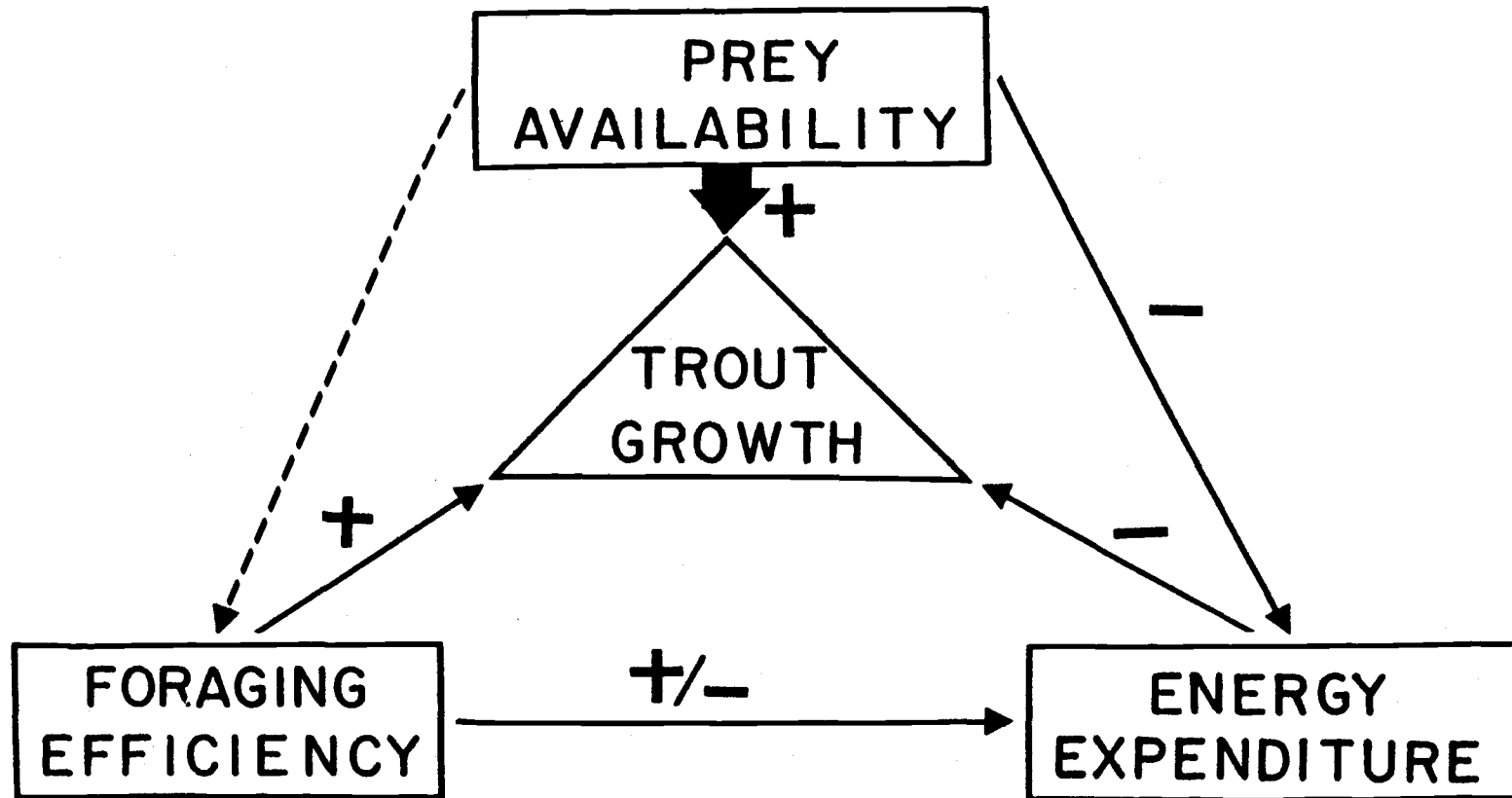


Figure III. 9. Proposed model relating trout growth to prey availability and to foraging efficiency and energetics. +/- signs indicate positive and negative correlations. Arrow width represents intensity of the relationship. Dashed line indicates uncertain relationship.

availability, foraging efficiency, and foraging energetics are all in turn related to habitat characteristics. The influence of overhead shading and of substrate crevices on foraging efficiency was demonstrated in trout feeding trials. Foraging energetics are affected by current profiles and by proximity of current refuges and concealment from feeding positions. Prey availability is determined at least in part by habitat features, such as current velocity, substrate size and stability.

Effect of trout predation on prey

We observed an increased density per unit volume of daytime drift in the trout removal pools of the logged and forested reaches after the beginning of the experiment (Fig. III. 10). These results are contrary to Allan's (1982) finding that reduction in trout density did not result in an increase in drift density. At the beginning of the experiment, drift samples were taken within two days of trout introductions to the control pools. Because feeding rates of trout were probably reduced as a result of handling, we expected drift densities at the beginning to be similar between the control and trout removal pools. This expectation was realized. At the midpoint and end of the experiment, day drift densities were significantly greater in the trout removal pools than in the control pools of the logged section ($p < 0.05$, Mann-Whitney U test). Although a slight increase in day drift density in trout removal pools of the forested section was apparent (Fig. III. 10), differences between control and trout removal pools were not significant. Because several trout were observed in one of

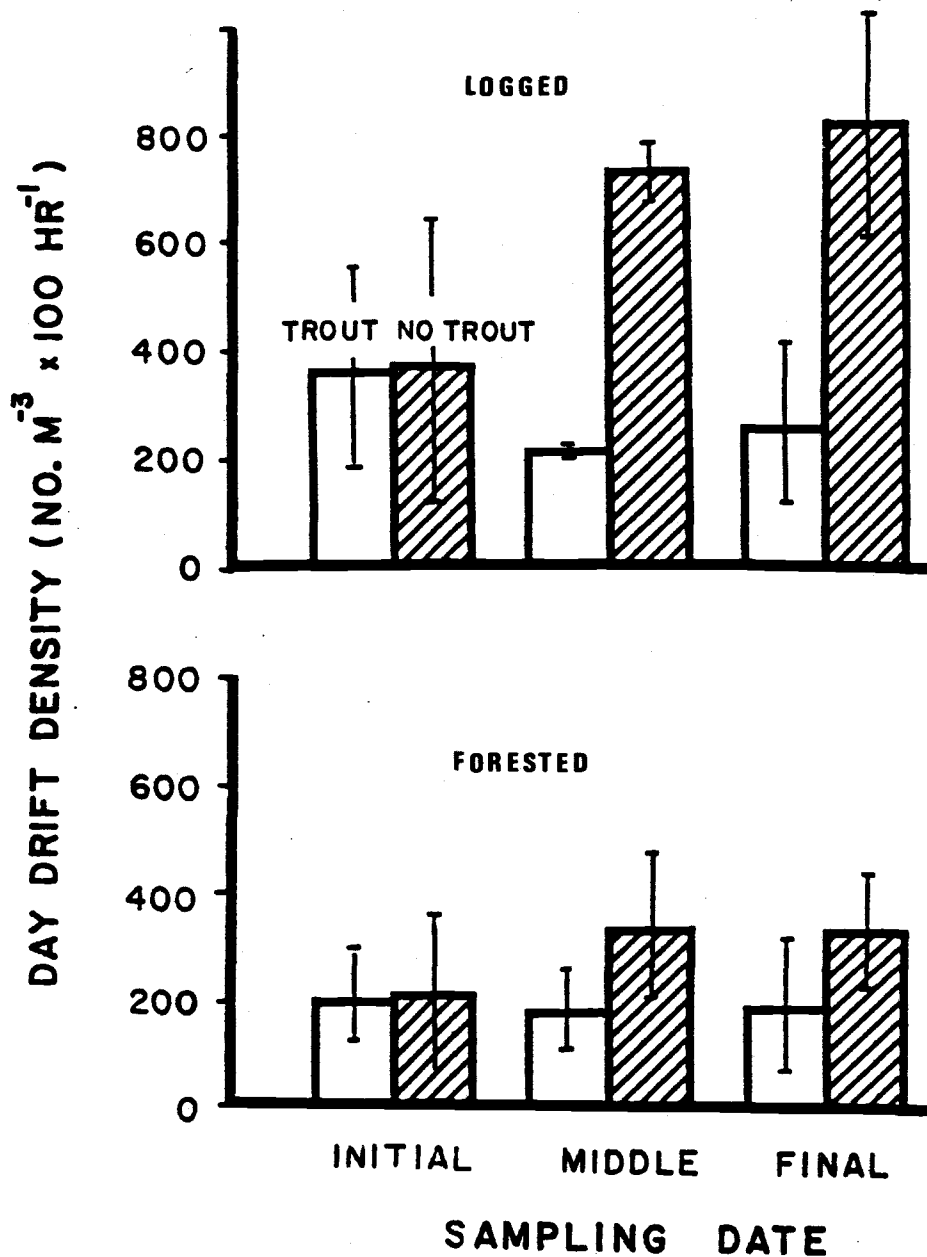


Figure III. 10. Density of day drift in control and trout removal pools in the logged and forested section on each of 3 sampling dates. Drift density, corrected for differences in flow among pools and dates, represents mean no. of individuals collected from drift samples at dawn, noon, and dusk on the beginning (n=6) and final (n=6) sampling dates, and at noon at the midpoint of the experiment (n=2). Except for the logged, trout removal pool on the final sampling date, drift samples were taken from two pools for each treatment. Vertical bars represent S.D.

the forested, trout removal pools after the midpoint of the experiment, drift densities from this pool on the final sampling date were excluded from the analysis. This may have influenced the observed lack of significance.

Size distribution of the drift shifted toward relatively larger individuals in trout removal pools relative to control pools ($p < 0.01$, Chi-square) (Fig. III. 11). This effect was most pronounced in the forested section. The shift in distribution can be accounted for by the selectivity of prey sizes eaten by the trout (Fig. III. 11, Table III. 2). Given the observed shift in size distribution of drift in trout removal pools and the evident selectivity of trout for large prey, it was surprising that differences in biomass of drift samples between control and trout removal pools were not significant in either the logged or forested sections on any sampling date ($p > 0.05$, Mann-Whitney U test). Lack of correspondence between drift density and biomass reflected the chance occurrence in control pools of a few large terrestrial invertebrates that had escaped capture by trout.

Differences in species composition of the drift were also observed between trout removal and control pools. Community resemblance was estimated with the percent similarity index, (PS) (Pimentel 1979). This measure is influenced by numerical abundance as well as by the presence or absence of particular taxa. The index ranges from 0 (completely dissimilar) to 100 (composition and numerical abundance of taxa identical between communities). PS between control and trout removal pools was 40 in the logged section and 47 in the forested section. PS between trout removal pools in the logged

Table III. 2. Mean length and weight of individual invertebrates from trout foreguts (n=10-12) and from drift samples collected from replicated pools at the midpoint of the experiment.

	TROUT DIETS		DRIFT	
	mm \pm SE	mg \pm SE	mm \pm SE	mg \pm SE
Logged Control	3.91 \pm 0.08	0.473 \pm 0.043	1.83 \pm 0.08	0.071 \pm 0.027
Logged Crevice-Cover	3.56 \pm 0.07	0.540 \pm 0.061	1.13 \pm 0.09	0.124 \pm 0.072
Forested Control	3.63 \pm 0.06	0.906 \pm 0.090	1.24 \pm 0.14	0.048 \pm 0.024
Forested Crevice-Cover	2.88 \pm 0.07	0.657 \pm 0.102	1.39 \pm 0.16	0.053 \pm 0.004

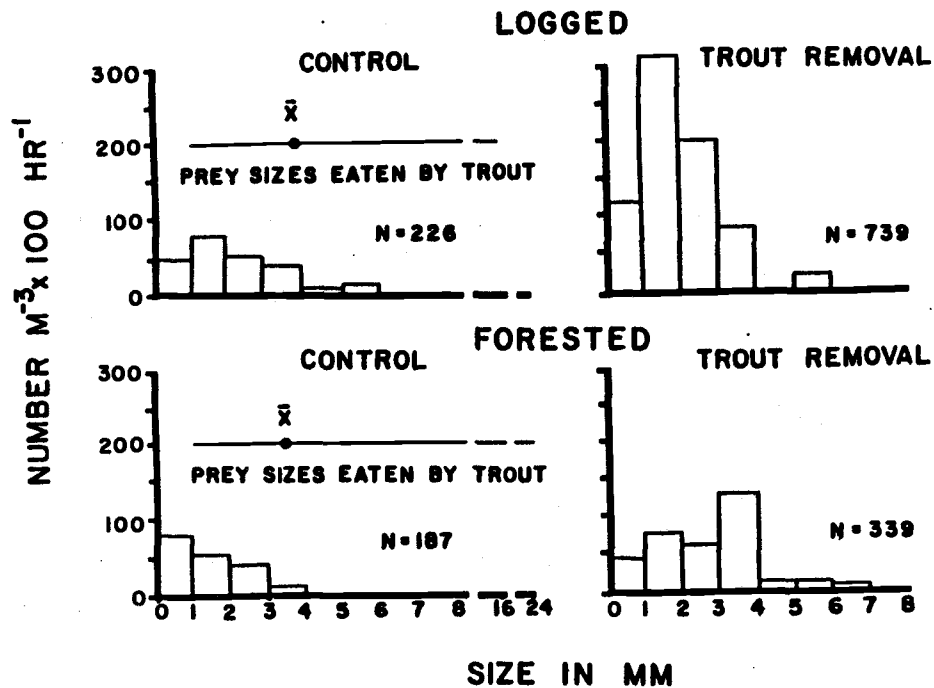


Figure III. 11. Size distribution of invertebrates in drift samples from control and trout removal pools in the logged and forested sections. Means are derived from replicate samples taken at noon during the midpoint of the experiment, corrected for differences in flow among pools. Mean and range of prey sizes found in trout foregut samples on the same date are shown above each graph (n=10-12 trout foreguts per treatment).

and forested section was 63. These values were determined from noon drift samples taken at the midpoint of the experiment. PS between replicate samples within a treatment was greater than 72 in all cases, and replicate samples were combined to represent the drift 'community' for a given treatment. Control pools of the logged and forested section were more similar to each other than either was to its respective fishless pair. Drift composition was least similar between the logged control and trout removal pools, supporting the conclusion that the impact of trout predation on drift composition was greater in the logged than in the forested reach. Some of the dissimilarity is attributable to the presence in the trout removal pools of invertebrate predator taxa, including the Tanypodine midges (Chironomidae, Diptera) and Rhyacophila spp. (Rhyacophilidae, Trichoptera). Differences in drift density of Baetis spp. between treatments also contributed to the dissimilarity. Total numbers of Baetis spp. were 114 and 384, respectively, in the logged control and trout removal pools.

A greater percentage of Baetis in stomach contents of trout than in the drift samples from logged control pools (Table III. 3) suggests active selection of trout for this taxa. Baetis spp. are behavioral drifters, and are an important and predictable component of the drift. They were present in every trout stomach examined (n = 62), and were present in all but four of 162 drift samples taken in both logged and forested sections throughout the experiment. Active selection of trout for this taxa may occur as a result of experience (Ware 1981).

In the forested section, the percentage of Baetis spp. in trout diets and in the drift were similar, and Orthocladiinae midges,

Table III. 3. Percent of drift components in trout diets and in drift samples in logged and forested control pools. Data are from replicated drift samples and trout foregut contents (n=10-12) collected at noon at the midpoint of the experiment.

	LOGGED		FORESTED	
	% in Diet	% in Drift	% in Diet	% in Drift
Total Behavioral drift	63	63	34	43
<u>Baetis</u> spp.	28	19	28	27
*Orthocladiinae	32	32	4	15
Total Accidental drift	16	37	18	47
Total Surface drift	21	0	48	10
Aquatic Origin	14	0	34	6
Terrestrial Origin	7	0	14	4

* excluding Tanypodinae

another important group of behavioral drifters, were selected against by trout (Table III. 3). Relative to other components of the drift, these behavioral drifters are characterized by a small size. Lack of positive selection by trout in the forested section for behavioral drifters may result from a reduced capture efficiency on small individuals (Fig. III. 1).

The percentage of trout diets comprised of surface drift was much greater in the forested than in the logged section (Table III. 3). Activity associated with emergence and contrasts or highlights provided by the air/water interface may greatly improve prey detection by trout in forested reaches. Trout appeared to actively select for surface drift in both sections, but because drift nets were not positioned to effectively sample surface drift, this suggestion needs further work.

Although lower growth rates of trout were observed in the forested reach (Fig. III. 7), the mean number of prey items and total biomass of gut contents were greater, but not significantly, than in the logged reach (51 [SD=36] vs. 28 [SD=19]; 37.0g [SD=39.1] vs. 8.9g [SD=4.7], respectively; n = 10-12). Because of lower levels of surface light, trout in forested reaches may be more constrained to feed during the middle of the day.

The lack of a significant reduction in drift density from trout predation in the forested reach appears to result from 1) habitat features such as overhead shading that reduce foraging efficiency of the trout and may restrict periods of foraging activity and 2) twice the percentage of terrestrial invertebrates that comprise trout diets

relative to that observed in the logged reach. A greater impact of trout predation on drift composition in the logged section may reflect habitat features that favor both greater foraging efficiency (Fig. III. 1) and a greater relative proportion of a constant food supply drifting at predictable times each day (behavioral drift) (Table III. 4, Wilzbach and Hall 1984). In spite of an increased foraging efficiency, however, small (< 1 mm), early instar insects, for which probability of mortality is very high, were insignificantly represented in trout diets. Further study is needed to determine if the trout are removing large individuals that are critical to the reproduction and continued survival of the insect populations. Unanswered as well is the relationship of drift assemblages to the benthic community from which they are largely derived. Many of the insects collected from drift samples and from trout foreguts were observed to be heavily parasitized with nematodes. This agrees with the findings of Statzner and Bittner (1983) that drifting Gammarus were more heavily parasitized than benthic individuals. It is possible that many of the drifting animals might have been 'lost' from the benthic community in any case.

Findings that trout growth (Fig. III. 8) and abundance (Wilzbach and Hall 1984) are strongly correlated with drift abundance suggest that populations of cutthroat trout are food-limited in the stream reaches studied. This would appear to be inconsistent with a finding that trout predation may not strongly regulate the prey community in structurally complex streams. The apparent discrepancy, if in fact real, may result because drift abundance and prey availability are not

equivalents. Habitat features that influence the ability of trout to detect and capture prey and the energy costs of doing so restrict the range of drift that can be utilized. Incorporation of information concerning habitat features and their influence on foraging efficiency with data on drift composition appears to be the most promising approach for evaluating the food support base for populations of wild trout.

CHAPTER IV

RELATIVE ROLES OF FOOD ABUNDANCE AND COVER IN DETERMINING
THE HABITAT DISTRIBUTION OF STREAM-DWELLING CUTTHROAT TROUT

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Introduction

Habitat features, including overhead shading and substrate complexity or associated crevices, have been demonstrated to reduce foraging efficiency of stream fishes, presumably by impairing detection of prey (Ware 1972, Wilzbach et al. 1984). As these features also provide shelter from predation and physical disturbances, a trade-off may exist between potential costs and energetic return of foraging. Experimental elimination of substrate crevices, for example, increased foraging efficiency of cutthroat trout (Salmo clarki) relative to that found for trout in control pools, but probably resulted in an increased mortality (Wilzbach et al. 1984). Habitat use and foraging behavior of stream fish are expected to adaptively balance these rewards and risks, and Dill (1983) reviewed considerable empirical evidence that suggests that this is the case.

Difficulties in incorporating predation risk into models of foraging behavior or habitat use arise because the units of measurement (i.e. risk of mortality vs. caloric or nutritional gain) are not comparable, and Dill (1983) has proposed that one possible solution may lie in observation of fish response to a variety of risk/reward combinations. The choices made by the fish provide a biologically relevant basis for weighting the two factors. In a recent experimental test that followed this approach, Werner et al. (1983) demonstrated that, in the presence of a predator (largemouth bass, Micropterus salmoides), small bluegill (Lepomis macrochirus) in artificial ponds grew slower and restricted their habitat use to areas

of low foraging profitability. Interactions between growth and density were not examined, as densities were adjusted to compensate for mortality from predation.

Research findings that cutthroat trout are more numerous in cover-poor, logged streams of the Oregon Cascades than in forested streams with abundant cover (Aho 1977, Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983), and that prey availability and foraging efficiency of the trout are likewise greater in logged streams (Wilzbach and Hall 1984), suggest that interpretations of Werner et al. (1983) may not be sufficient when applied to salmonids in stream environments. The intensity of predation on the trout in these streams is not known, but from sightings of avian, reptilian, and mammalian predators at several study sites, at least some risk of a predation in logged pools may be inferred (Wilzbach et al. 1984).

This study was designed to evaluate the relative contribution of food abundance and of cover in determining habitat distribution of cutthroat trout. Microhabitat use and emigration of trout from laboratory channels were examined under varying conditions of food abundance and cover.

Methods

The experiment was conducted in June and July 1984 in recirculating stream channels designed and constructed by Reeves et al. (1983). The channels were oval-shaped, approximately 18 m in total length, and had a water capacity of 5.9 m³. A 3-m section of each channel that contained a paddle wheel and heating and cooling elements

was separated from the test area with screening. Escape traps were positioned at these upstream and downstream boundaries. The experimental portion of each channel consisted of an alternating series of riffles and pools, with water velocities ranging from 0 to 10 cm/sec. Water temperature was maintained at 11° C throughout the experiment. The photoperiod was set for a 12-h day.

In trials of one week duration each, ten cutthroat trout, ranging in size from 10 to 15 cm, were introduced into a channel. Wild trout were obtained from Grasshopper Creek (Lane County, Oregon) by capture with barbless fly on hook and line. Trout were obtained from the same stream in which previous studies of habitat influence on foraging efficiency and growth of the trout were conducted. Captured trout were measured to the nearest millimeter, weighed to 0.1 g, and photographed for later identification (Bachman 1984, Wilzbach et al. 1984). To acclimate the trout to the water supply and to allow time for recovery from handling stress, they were placed in a holding tank maintained at stream temperature for 48 hrs prior to introduction to the channel.

In one treatment, trout were fed a high level of food (high food), 15% of the total trout biomass daily, and were given abundant cover (high cover). The trout were fed frozen brine shrimp (Artemia spp.) at dawn, noon, and dusk from a food delivery system that simulated natural drift by introducing the food from numerous ports along the entire length of the channel bottom (Reeves et al. 1983). Cover consisted of simulated undercut banks in the form of wood shelters, and large crevices formed by arrangements of bricks. The channel bot-

tom was covered with sand and gravel in the pools, and with small rock (5-8 cm) in the riffles. Cover structures were added to only the upstream half of the channel to provide the trout with a choice in the use of cover.

A second treatment consisted of high food and low cover. In this treatment, the cover structures were removed. A third treatment consisted of low food abundance, and high levels of cover (cover structures added to the upstream half of the channel). At low food abundance trout were fed 5% of their total biomass daily. From pilot experiments, this was determined to be a food level sufficient to maintain short-term survival of the trout but not provide for growth. A fourth treatment consisted of low food abundance and low cover. All treatments were repeated once. To simulate a predation risk and reinforce the use of cover, a battery-powered toy 'scuba diver', 200 mm in length, was made to swim through each channel several times at random. Although not in the legion of predators naturally encountered by the trout, the 'scuba diver' effectively frightened the fish.

Trout use of microhabitat was monitored throughout each trial prior to feeding periods. Trout were observed from the center viewing area of the channels through openings in suspended black plastic curtains that covered the channel sides and allowed viewing of the fish without disturbing them (Reeves et al. 1983). Individual trout were identified from photographs by comparison of the lengths and the spotting pattern on the body. The tops of the channels were covered with plastic sheets to prevent fish from jumping out. Escape traps were

checked three times daily. Emigrants were measured, weighed, and removed from the channels.

Results and Discussion

Micro-distribution

When provided with high food abundance, trout used simulated cover structures. Little change in the distribution of trout was observed between the beginning and end of the trials (Fig. IV. 1). Habitat distribution of the trout did not differ by time of day ($p > 0.10$, Kruskal-Wallis).

When food abundance was low, however, trout left cover structures after 3 days (Fig. IV. 1). The percentages of trout that occurred in association with cover differed significantly between high and low food treatments ($p < 0.01$, Kolmogorov-Smirnov). The failure of trout to remain associated with cover structures when food abundance is low is consistent with the finding that, in the cover-rich, forested section of Grasshopper Creek, which has a low abundance of food, no relationship existed between numbers of trout inhabiting a pool and a qualitative ranking of cover ($p > 0.05$, Kendall's rank correlation).

When cover structures were absent, cutthroat trout were randomly distributed throughout the channels, and individual trout changed locations frequently. Differences in the percentage of trout that were positioned in the upstream half of each channel were not significant between high and low food treatments ($p > 0.10$, Kolmogorov-Smirnov).

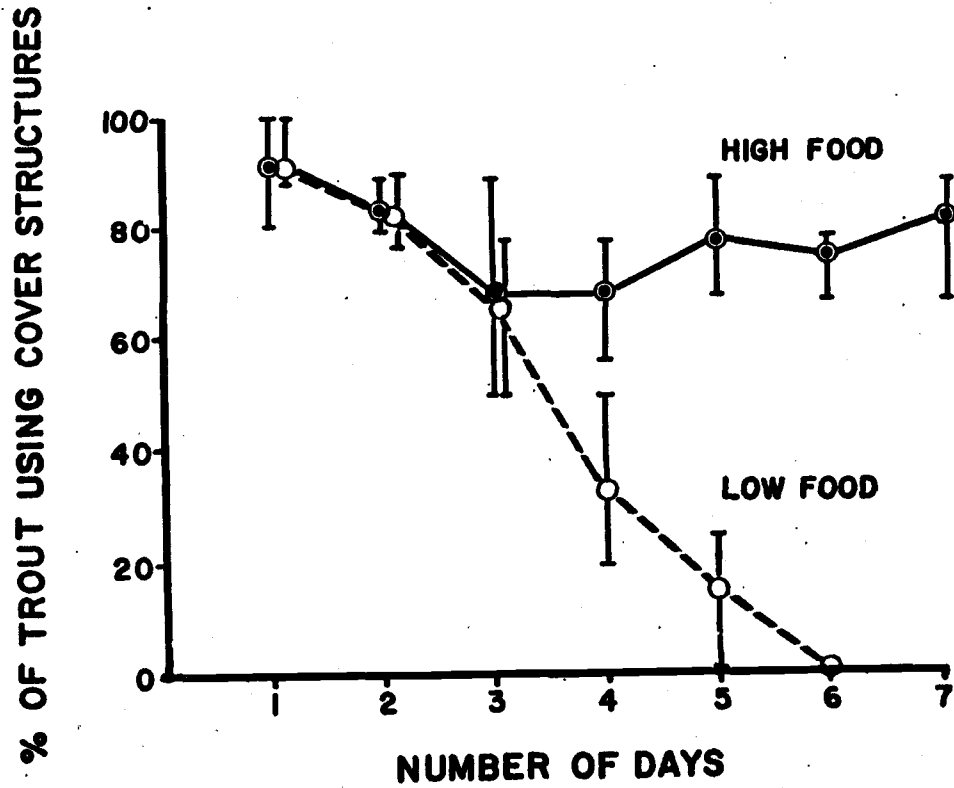


Figure IV. 1. The percent of trout present in a channel on a given day that were using cover under conditions of high and low food abundance. Vertical bars represent range of values. n = 6 observations.

Emigration

Classifications by food abundance and cover were significantly associated ($p < 0.01$, 2×2 contingency table). When food abundance was high, the mean number of trout remaining in channels at the end of one week was greater at high than low cover (Fig. IV.2). When food abundance was low, the number of trout remaining was greater at low than high cover. Regardless, however, of the amount of cover, the number of trout remaining in channels was greater with high than with low food abundance. There was little variation between replications within a treatment.

In all trials, at least one trout emigrated from the channel, suggesting that initial densities exceeded the carrying capacity. Stocking densities (approximately 3.4 trout/m^3 of pool), however, were slightly below densities of trout that were observed in the field (3.7 trout/m^3 of pool in the logged section of Grasshopper Creek). The majority (over 70%) of trout that emigrated from the lab channels exited into the downstream traps. This is consistent with the notion that displaced cutthroat trout may in general be more likely to attempt to relocate downstream rather than upstream, as energetic costs should be much less.

When provided with a high ration of food, the relative growth rate of trout was greater in channels with high cover than with low cover, but the difference was not statistically significant (Table IV. 1). However, when provided with a low ration of food, trout tended to lose a greater amount of their body weight in channels with high

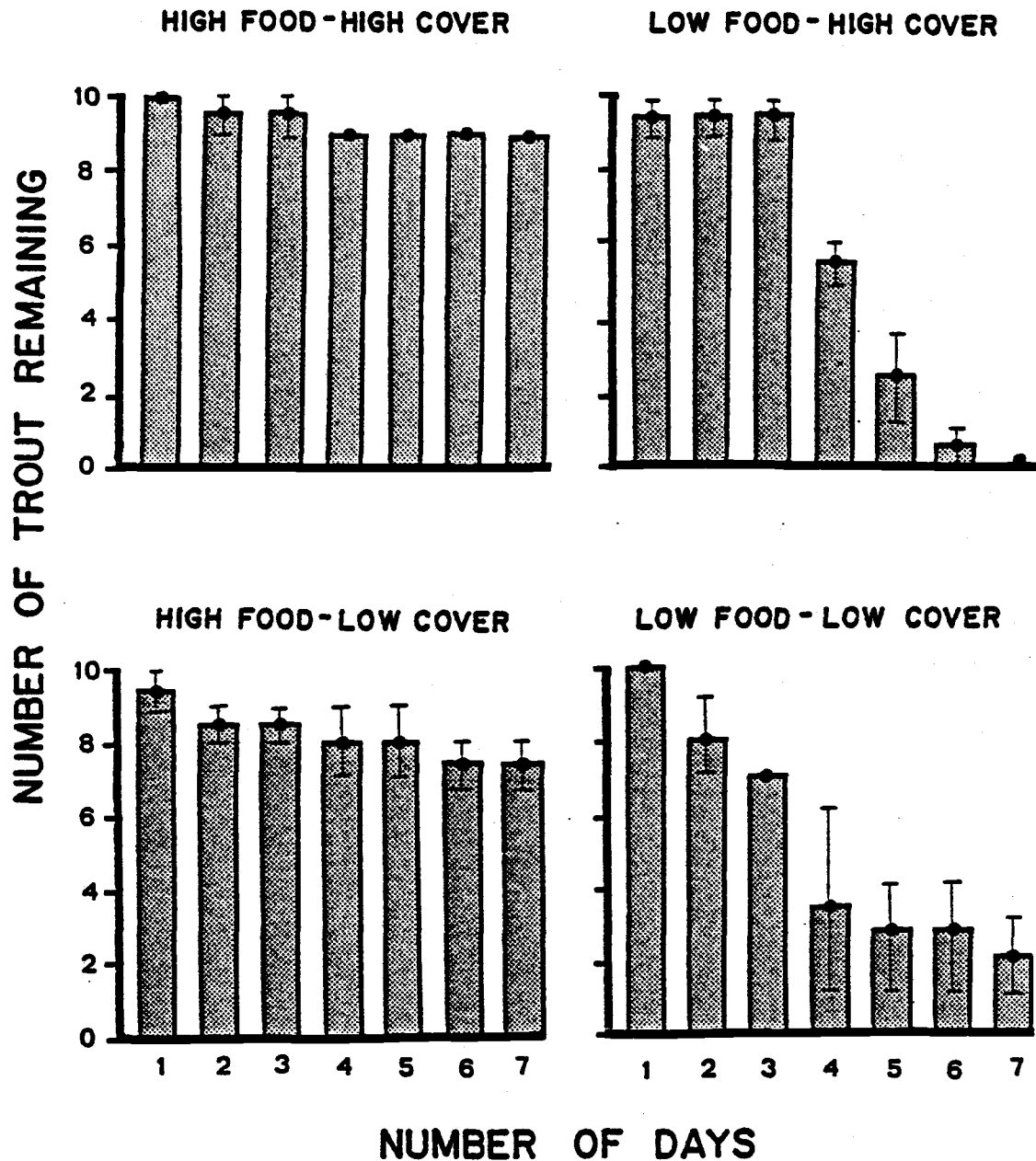


Fig. IV. 2. Mean number of cutthroat trout remaining in channels on each day of a trial under different combinations of food abundance and cover. Vertical bars indicate range of values. All treatments were repeated once.

Table IV.1. Relative growth rate \pm S.D. of cutthroat trout remaining in channels at least 3 days. Sample size is indicated in parentheses. Relative growth rate (final minus initial weight divided by mean weight, divided by number of days, times 100) is expressed as percent body weight per day.

	HIGH FOOD	LOW FOOD
HIGH COVER	0.39 \pm 0.41 (19)	-1.53 \pm 1.06 (19)
LOW COVER	0.24 \pm 0.34 (16)	-1.13 \pm 1.15 (14)

cover. This may result from a decreased foraging efficiency associated with abundant cover (Wilzbach et al. 1984), or from behavioral deterrents to feeding in complex habitats (Glass 1971, Savino and Stein 1982). Overall, growth rates of the trout differed significantly between treatments that provided high and low food abundance ($p < 0.01$, Mann-Whitney U test) (Table IV. 1), indicating that the differences in food rations were biologically meaningful to the trout.

Trout emigrated from channels when weight loss approached a fairly narrow band of 4.0 to 5.5% of the body weight (Table IV. 2). Trout that emigrated on the first day may have left the channels for reasons unrelated to food abundance, and showed approximately the same weight loss as trout remaining in the channels after 7 days under low food abundance. Trout remaining in the channels after 7 days under conditions of high food abundance gained weight.

Results of this study corroborate field data suggesting that prey availability is more important than cover in determining distribution and abundance of cutthroat trout in the Oregon Cascades. Assuming that predation poses at least some risk of mortality to trout, an implication of this conclusion is that habitat response of trout to recent, man-made disturbances may be non-adaptive. Alternatively, trout populations in cover-poor and cover-rich streams may simply adopt different strategies for dealing with environmental uncertainty. Longer-term studies, encompassing estimates of reproduction through several year classes, will be necessary to determine which alternative may apply.

Table IV. 2. Weight change \pm S.D. of cutthroat trout that emigrated from channels after 1 to 6 days, and that remained in the channels throughout a 7-day trial. Weight change was measured as final minus initial weight, divided by initial weight, * 100.

No. of Days	Weight change \pm S.D. (% Body weight)	n
1	-2.43 \pm 1.18	9
2	-5.50 \pm 3.00*	2
3	-5.57 \pm 2.50	17
Emigrants		
4	-5.33 \pm 1.51	8
5	-5.20 \pm 3.19	5
6	-4.00 \pm 2.00*	2

7 low food	-2.50 \pm 2.38	4
Residents		
high food	+2.94 \pm 4.14	33

* range

CHAPTER V

CONCLUSION

Considerable effort has been devoted to attempting to account for variation in the abundance of salmonid populations among streams (see review by Hall and Knight 1981). The general research approach has centered on an examination of either physical factors, or less commonly, on biological factors including prey availability, competition, or predation. Implicitly or explicitly, the physical and biological factors have usually been treated as if they represent dichotomous elements, either of which, but not both, may limit population abundance.

Previous studies of logging impacts on populations of cutthroat trout, for example, have largely considered only effects on the trout that derive from changes in the food base. Although the habitat changes that accompany logging may be striking, the influence of these on the trout has not been well examined. The general focus of the research reported in this thesis was to examine how habitat features interact with the food base to result in an increased abundance of cutthroat trout in logged streams.

The results of trout feeding experiments reported in chapters two and three revealed that the foraging efficiency of trout on introduced prey was greater in a recently logged than in a downstream forested section of Grasshopper Creek. This was found to be related to the amount of overhead shading and to substrate crevices. Artificial shading of pools in the logged section resulted in a decrease in the

foraging efficiency of trout, and a strong logarithmic relationship was observed between foraging efficiency and mean surface light of pools at the time feeding trials were conducted. Experimental elimination of substrate crevices in pools in both the logged and forested sites resulted in an increase in trout foraging efficiency, most likely because the field of vision of the trout may have been increased.

Although habitat features such as surface light appear to influence the foraging efficiency of trout, these features were insufficient to fully account for differences in trout growth that were observed between the two sections. As reported in chapter three, the relative growth rates of trout experimentally confined in control and manipulated pools were greater in the logged than in the forested section, regardless of treatment. Differences in prey availability between the sections are needed in addition to provide a more complete explanation for the observed differences in trout growth.

A strong correlation was found between the relative growth rate of the trout and mean drift density. Drift density was used in this study as an estimate of prey availability, because snorkeling observations indicated that the trout were feeding predominantly in the water column on drifting invertebrates of aquatic and terrestrial origin, rather than on the benthos. Few studies have reported a significant relationship between trout growth and the standing crop of benthic invertebrates. The strong correlation between trout growth and drift density found in this study suggests that drift density may

more accurately estimate prey availability for stream-dwelling cutthroat trout than does the benthos.

Drift densities were found to be greater in the logged than in the forested section of Grasshopper Creek at both high and low flow periods. This probably reflected both a greater abundance in the logged section of high quality, algal food sources, and a greater habitat instability that may increase the probability that benthic invertebrates will occur in the drift, where they are more available to be eaten by trout. The relative proportion of invertebrates exhibiting a behavioral tendency to drift was also greater at low flow in the logged section. In contrast to 'accidental' drift, behavioral drift is available as a food source to trout at predictable times each day. For this reason, the timing of trout feeding activity may be adapted to the diel periodicity of behavioral drift.

Coincident with a greater foraging efficiency of trout, the effect of trout predation on drift abundance was greater in the logged than in the forested study reach. The few field studies that have examined effects of fish predation on aquatic insects in streams have produced ambiguous results or have concluded that fish predation does not regulate prey abundance. These studies have not, however, examined the influence that habitat features might have on predation intensity. In this study, as reported in chapter three, drift abundance in the logged section was three times greater in pools from which trout were excluded than in control pools. Differences in drift abundance between trout removal and control pools in the forested section were not significant. The striking effect of trout predation on

drift abundance in the structure-poor logged section may have resulted from habitat features that favor both greater foraging success and a greater proportion of a predictable (behavioral drift) food supply. Longer-term studies are needed, however, to determine if effects of trout predation on their prey base are persistent.

Although cover-related habitat features have been demonstrated to reduce the foraging efficiency of trout, these features also provide shelter from predation or physical disturbances. Results of a laboratory experiment to evaluate the relative roles of food abundance and of cover in determining the abundance of trout within a site indicated that food abundance appears to be of overriding importance. This is consistent with the finding that cutthroat trout were more abundant in the cover-poor logged section than in the forested reach, which had a greater abundance of cover but a lower availability of food. Habitat selection by fish is expected to adaptively balance rewards and risks of foraging (Dill 1983). Assuming that a risk of mortality is present, an implication of this study is that habitat response of trout to recent, man-made disturbances such as logging may be non-adaptive.

Results of this study should not be construed to mean that effects of clear-cut logging on populations of cutthroat trout or other salmonids will always be beneficial. Several caveats deserve mention. First, little is known about salmonid response to habitat and food conditions at later stages of riparian recovery. When second-growth vegetation begins to shade the stream channel, beneficial effects of increased light levels on the food resource base and on trout foraging efficiency will be quickly lost. Murphy (1979), for

example, found that biomass and species richness of vertebrate and invertebrate predators tended to be lower in second-growth than in clear-cut streams, and equal to or lower than amounts in old-growth streams. Reversal of adverse habitat changes that may attend logging are likely to require a greater length of time if, for example, inputs of large woody debris are needed to stabilize the channel. As watersheds are increasingly maintained in a stage of second-growth vegetation, trout populations may decline following an initial increase in abundance after logging to levels lower than those characteristic of streams bordered by old-growth forests.

Spatial as well as temporal consideration may also restrict the generality of results found in this study. This study was conducted in a high-gradient, headwater stream, and only small patches of the watershed were logged. Increased erosional inputs from logging were not retained because of the steep gradient, and adverse temperature effects were not realized. In lower gradient streams, or in streams in which the entire watershed is logged, sediment deposition or elevated temperatures may exacerbate other habitat changes. Effects of logging on salmonid populations appear to depend on an interaction between habitat structure and the prey base. The outcome in a given stream is likely to depend on the site-specific array of habitat and biological components.

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