



Influence of Habitat Manipulations on Interactions Between Cutthroat Trout and Invertebrate Drift

Author(s): Margaret A. Wilzbach, Kenneth W. Cummins and James D. Hall

Source: *Ecology*, Vol. 67, No. 4 (Aug., 1986), pp. 898-911

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1939812>

Accessed: 13/11/2013 17:34

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

INFLUENCE OF HABITAT MANIPULATIONS ON INTERACTIONS BETWEEN CUTTHROAT TROUT AND INVERTEBRATE DRIFT¹

MARGARET A. WILZBACH AND KENNETH W. CUMMINS

*Center for Environmental and Estuarine Studies, Appalachian Environmental Laboratory,
University of Maryland, Frostburg, Maryland 21532 USA*

AND

JAMES D. HALL

Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. The objectives of this study were to examine the interactions 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. Short-term relative growth rates of cutthroat trout, experimentally confined in stream pools, were greater in a logged than in a forested section of stream. Differences in growth rates were attributed to differences among pools in invertebrate drift density, and to differences in trout foraging efficiency that were related to differences between the sections in the amount of overhead shading and substrate crevices. Mean percentages of introduced prey captured by trout were greater in logged control pools and pools of both sections whose bottoms were covered with fiberglass screening to eliminate substrate crevices than in forested control pools and logged pools that were artificially shaded. A logarithmic relationship was found between trout foraging efficiency and surface light of pools.

Drift density significantly increased relative to controls in pools from which trout were removed in the logged reach, but not in the forested section. This may result from habitat features in the logged section that favor greater trout foraging success and the occurrence of behaviorally drifting prey taxa, which represent a predictable food supply for the trout.

Key words: *foraging efficiency; logging; Salmo clarki; stream drift; stream habitat; trout food habits; trout predation.*

INTRODUCTION

Laboratory studies (Glass 1971) and field manipulations in experimental ponds (Crowder and Cooper 1982) suggest that growth rates of fish in lentic environments are greatest at an intermediate level of habitat complexity (e.g., extent of vascular plant beds, density of substrate crevices). 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 (Ware 1973, 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 1985). Behavioral drifters are frequently polyvoltine species characterized by rapid turnover, 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).

¹ Manuscript received 6 February 1985; revised 12 August 1985; accepted 25 September 1985.

Allan (1983) 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 avoid capture successfully. Although the 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 (Slobodkin 1961, Reisen 1975, Pritchard 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 determine stream habitat complexity to a large degree (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, large amounts of in-channel wood (boles and root wads) characteristically 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 ri-

parian 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 yr) 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 ≈ 800 m. The forested section was located >300 m from the downstream end of the logged section. A site description is provided in Wilzbach and Hall (1985). 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 0.01 m/s with a Montedoro Whitney digital flowmeter at the surface, middepth, and bottom. Maps were drawn to scale and pool volumes were determined planimetrically. Mean (\pm SD) pool surface area was 3.2 ± 1.2 m²; pool volumes ranged from 0.753 to 2.875 m³ (\bar{X} = 1.63 m³, 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 >1° on any given day.

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

Five to 14 trout, ranging in size from 90 to 200 mm, were reintroduced into each of the other pools. Trout densities were adjusted so that trout densities and biomass per unit pool volume (approximately six fish and 122 g/m³) were fairly constant. In no instance was the number of trout introduced into a pool greater than the number of trout that previously inhabited that pool. Migration of trout to or from pools was prevented by blocking the head and tail of each pool with 1.3-cm (one-half inch) mesh hardware cloth. From prior observations we determined that the trout exhibited at least seasonal microhabitat fidelity, and we therefore feel 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 millimetre and weighed to the nearest 0.1 g, and the left side of each fish was photographed for later identification (Bachman 1984).

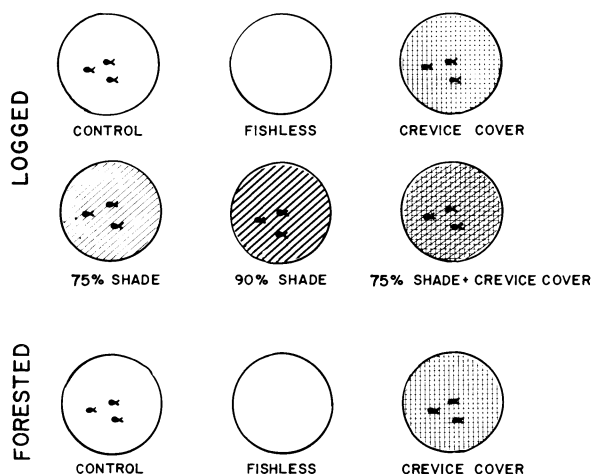


FIG. 1. Experimental design. Pool manipulations were replicated twice. Fish symbols indicate pools where cutthroat trout were re-introduced. "Crevice cover" refers to pools whose bottoms were covered with fiberglass screening to eliminate substrate crevices.

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) The pool was artificially shaded with overhead nylon screen that reduced surface light by $\approx 75\%$, (2) The pool was artificially shaded with screen that reduced surface light by $\approx 90\%$, (3) The bottom was lined with 1-mm mesh fiberglass screening to eliminate substrate crevices (hereafter termed "crevice-covered pools"), and (4) The pool was shaded with 75% screening and the crevices covered (Fig. 1). Similarly, the substrates of two pools in the forested section were covered with screening. Treatments were arbitrarily assigned to pools. 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 tied 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 buttoner button fasteners (Dennison). The screening did not alter topography of the pool bottom, but it did effectively eliminate substrate crevices.

Invertebrate drift was sampled at dawn, midday, dusk, and midnight from the tail of each pool at the beginning and termination (after 6 or 8 wk) of the experiment, and at midday at the mid-point (after 3 or 4 wk). Each drift net was positioned in the thalweg (principal current pathway) 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 $250 \mu\text{m}$. Current velocity was measured in front of each net at the time of sampling. Samples were collected over a 1-h period at each

sampling time, and were preserved in 70% ethanol. 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 by observation (K. W. Cummins and M. A. Wilzbach, *personal observation*). Total lengths were measured at $12\times$ magnification to the nearest millimetre, and biomass was estimated from available length-mass regressions (Coffman 1963, Mackey 1977, Rogers et al. 1977, Smock 1980, K. W. Cummins and M. A. Wilzbach, *personal observation*).

Trout were collected from each pool with a barbless hook and line 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% ethanol for later identification. The trout were measured, weighed, photographed, and released into their respective pools. Comparison of the spot patterns on the left side of each fish permitted 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 mass per day, were then estimated according to the formula:

$$\frac{(M_f - M_i)}{\left[\frac{(M_f + M_i)}{2}\right]} \cdot T^{-1} \cdot 100$$

where M represents mass; i = initial; f = final; T = time between samplings, in days.

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 $250\text{-}\mu\text{m}$ net placed immediately upstream for the duration of a feeding trial. Four group sizes (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-min trials each from a feeding apparatus (Fig. 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. After this pulse of drift subsided, a net was placed at the head of each pool to prevent further influx of drift. A series of light readings at the surface of each pool was taken with a LI-COR light meter immediately before and after each feeding session, and averaged to obtain an estimate of surface light. All feeding trials were conducted during daylight hours (1400–1700).

Tail beat frequencies of individual trout were determined by underwater observation during and after feeding trials to obtain an indirect estimate of energy 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 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 ($100 \times [\text{feeding} - \text{holding}]/\text{holding}$) 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 ($P < .05$, Mann-Whitney U test) (Fig. 3). This suggests that the findings of Ware (1972), Allan

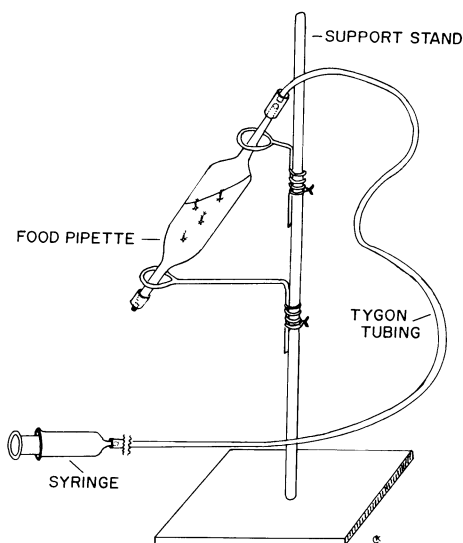


FIG. 2. Apparatus used in trout feeding trials. Apparatus consists of a replaceable volumetric pipette into which the specified number of prey animals (mosquito larvae) is drawn. Pipette is held in place with a clear plexiglass ring stand, and is attached with 15 m of Tygon tubing to a syringe hand-operated by observer. Group of prey is forced by air into the water column.

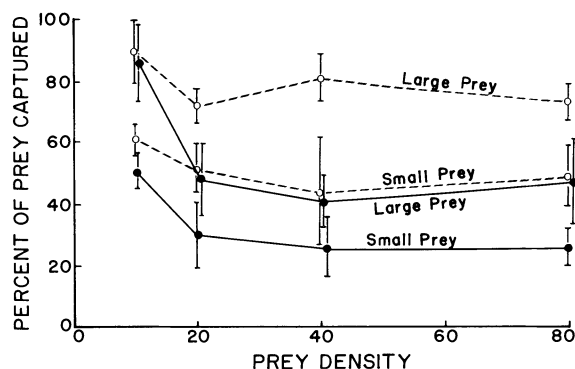


FIG. 3. Relationship between prey density and percent of introduced prey that were captured by feeding trout. Large prey were 7–10 mm; small prey were 3–5 mm. ○ logged control pools; ● forested control pools. Vertical bars represent ± 1 SD; $n = 6$.

(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 ($P < .05$, Mann-Whitney U test), but this result was not significant for small prey. Foraging efficiency on small prey in control pools of the logged section was nearly identical to the efficiency with which trout in the forested section (control pools) captured large prey.

Although absolute numbers of introduced prey captured increased with size of the introduced prey group, the proportion of prey captured tended to be greatest at the lowest prey level (10 animals per group) in both sections, and within a site and prey size class, was fairly similar at all other levels. This result was significant ($P < .05$, 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 level of 10 animals per introduced group was deleted from subsequent estimations of mean capture efficiency. From previous sampling (Wilzbach and Hall 1985), the average daytime flux of drift into the logged and forested pools was 73 and 51 individuals/3 min, respectively. Thus, capture efficiency was estimated within a range of prey densities naturally encountered by the trout.

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 1985). 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

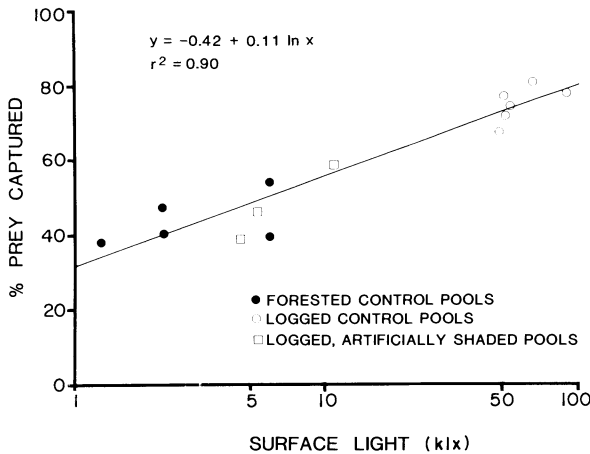


FIG. 4. Relationship between foraging efficiency of cutthroat trout, expressed as mean percent of prey captured, and mean surface light of pools at the time feeding trials were conducted. The relationship is based on data from this study and Wilzbach and Hall (1984) for foraging efficiency on large (7–10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

between replications was not significant ($P > .10$, 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 poor relationships were found between the percent of fish feeding and pool volume ($r^2 = 0.15$), between the percent of prey captured and the number of fish feeding ($r^2 = 0.07$), and between the percent of prey captured and mean velocity in the plume of the feeding apparatus ($r^2 < 0.01$).

Using data from feeding trials obtained both years (this study and Wilzbach and Hall 1985), we found a strong relationship ($r^2 = 0.90$; significant F test for slope, $P < .01$) between mean foraging efficiency of the trout and the natural logarithm of mean surface light at the time feeding trials were conducted (Fig. 4). This relationship is based on data for large prey over a range of prey densities (20–80 animals per introduced group) 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. 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 (photon flux density of $3.0 \times 10^{15} \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) 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 ($P < .05$, 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 ($P < .15$, multiple comparisons (Dunn 1964; Fig. 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 ($P < .15$). Relative to pools in which shading alone was manipulated, the covering of substrate crevices increased foraging efficiency. Percentages of prey capture by trout were similar in crevice-covered pools of the forested section and in crevice-covered, shaded pools of the logged section (Fig. 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, 1973) finding that total food consumption and predation intensity of rainbow trout (*Salmo gairdneri*) varied inversely with substrate complexity.

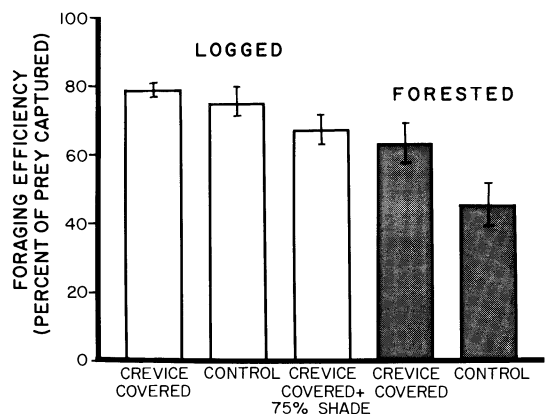


FIG. 5. Foraging efficiency of cutthroat trout, expressed as percent of prey captured, in control and crevice-covered pools (pools whose bottom was covered with fiberglass screening to eliminate substrate crevices) of the logged and forested sections of a stream, and crevice-covered plus shaded (75%) pools of the logged section. Foraging efficiency for each treatment is based on averages of prey captures from two pools on large (7–10 mm) prey and densities ranging from 20 to 80 animals per introduced prey group. $n = 9$ –18. Vertical bars represent ± 2 SE.

Trout foraging energetics

The relationship between trout size and tail beat frequency during holding, standardized for flow (centimetres per second), was weak ($r^2 = 0.32$). Similarly, no relationship was found between trout size and the percent increase in tail beat frequency at feeding relative to holding periods ($r^2 < 0.01$). 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. Tailbeat frequencies estimated in this study are within the range of tailbeat frequencies reported for rainbow trout by Feldmuth and Jenkins (1971), and 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. 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 energy 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 ($P < .05$, Kruskal-Wallis). RGR was greatest in the logged control pools (0.55% body mass per day), and least in the forested control pools (0.04% dry mass per day) (Fig. 7). Differences within pools in RGR between the first and second halves of the experiment were not significant ($P > .10$, Mann-Whitney U test), nor were differences significant among replications ($P > .10$, 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 ($P < .15$, multiple comparisons [Dunn 1964]). This result corresponds with differences observed in the length-mass 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-mass relationship for cutthroat trout in the logged section was $\log_{10} M = -4.67 + 2.87 \log_{10} L$ ($n = 66$, $r^2 = 0.98$). In the forested section, the length-mass relationship was $\log_{10} M = -4.65 + 2.81 \log L$ ($n = 33$, $r^2 = 0.96$). Trout of the same length in the logged section weighed significantly more than did trout in the forested section ($P < .05$, Wilcoxon's signed ranks test). Relative to the energy expenditures involved in foraging at an intermediate level of efficiency, the lower energy expenditures associated with the high-

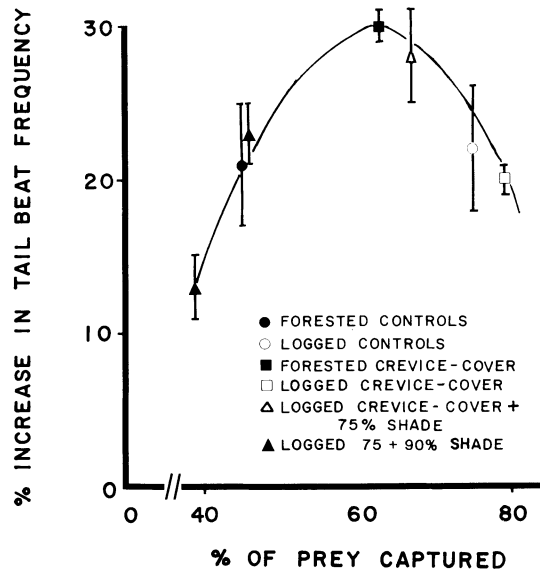


FIG. 6. Relationship between foraging energetics and foraging efficiency (percent of prey captured) of cutthroat trout in six types of stream pools. "Crevice-cover" means that the bottom of the pool was covered with fiberglass screening to eliminate substrate crevices. Energy expenditures are indexed by the percent increase in tail beat frequency of trout engaged in feeding relative to holding ($100 \times [\text{feeding} - \text{holding}] / \text{holding}$); $n = 10$ –15 observations per treatment. Foraging efficiency is based on averages of prey capture from two pools on large prey with prey densities ranging from 20–80 animals per introduced prey group ($n = 9$ –18 groups). Curve was fitted by inspection.

est foraging efficiencies (Fig. 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 ($P < .15$, multiple comparisons, Dunn 1964) (Fig. 7). In the logged section, RGR of trout in crevice-covered pools was lower, but not significantly, relative to control pools. The lack of an increase in RGR of trout in logged, crevice-covered pools 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 energy 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 partially eaten 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. Potential trout predators sighted within the study

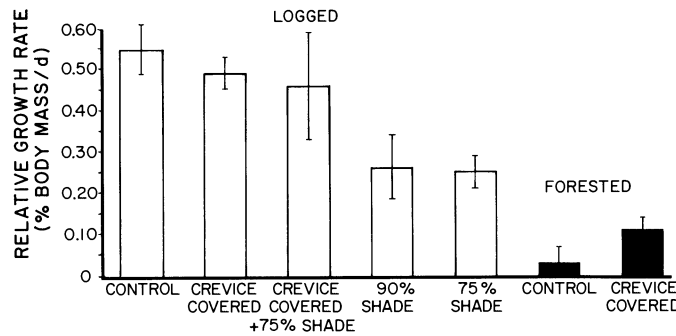


FIG. 7. Mean relative growth rates of trout from control and manipulated pools in the logged and forested sections. "Crevice cover" as in Fig. 5. Means are derived from growth rates estimated for individual trout collected during the first and second halves (3 or 4 wk each) of the experiment from two replicate pools. Vertical bars represent ± 1 SD.

area included Belted Kingfishers, fishers (*Martes pennanti*), black bear, and garter snakes (*Thamnophis* spp.).

Because of large variation in trout growth in crevice-covered and shaded pools, the differences in RGR of trout between logged control pools and crevice-covered plus shaded pools were not significant ($P > .15$, multiple comparisons, Dunn 1964), 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 faster ($P > .10$, t test), than larger fish (>150 mm) (\bar{X} 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 ($P > .15$, multiple comparisons), but a reduction in RGR of trout relative to other logged pools ($P < .15$) was associated with artificial shading (without the addition of crevice cover) (Fig. 7). The mean RGR of trout in pools with artificial shading was less than half that of trout in logged control pools. The effect of substrate manipulations in the logged section was not as dramatic, suggesting that surface light plays a relatively much greater role in affecting trout growth in this system than does structural complexity of the substrate. In the forested section, even though elimination of crevices resulted in an almost threefold increase in RGR of trout compared to the RGR of trout in control pools, the increased growth was considerably below the range found for trout in the better lighted logged section.

Data suggest that although habitat features influence trout foraging efficiency, differences in habitat-related foraging efficiencies are insufficient to account for observed differences in trout growth. If such were the case, for example, the RGR of trout in forested crevice-covered pools would equal that found for trout in crevice-covered plus shaded pools of the logged section, and this was not observed. Differences in prey availability between the sections are needed in addition to provide a more complete explanation for the observed differences in trout growth.

Differences in mean RGR among treatments were strongly correlated with differences in mean density of daylight drift ($P < .05$, Kendall's rank correlation) (Fig. 8). Estimates of mean density of daylight drift were obtained by averaging, over the two pools of a treatment, the densities of individuals 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 <1 mm in length were insignificantly represented (always $<1\%$ by numbers or biomass) in trout stomachs, these were excluded from density estimates to reflect prey availability to trout better. 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 more accurately estimates prey availability for stream-dwelling cutthroat trout than does the benthos.

Because the composition and abundance of drift are clearly of key importance to trout growth, the data were analyzed in detail with reference to the availability of this food source to trout. Differences in densities and biomasses of daytime drift were nonsignificant with respect to sampling time (dawn, noon, or dusk) ($P > .05$, Kruskal-Wallis), and data were thus combined over these times to obtain an average of daytime drift on the beginning and final dates (Table 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 ($P < .01$, Wilcoxon's signed ranks test). 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 daytime drift (Table 1) varied signifi-

cantly among treatments ($P < .05$, Friedman non-parametric ANOVA with sampling dates as blocks). There was no significant difference in daytime drift among the sampling dates ($P > .10$, Kruskal-Wallis), 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, daytime drift densities were similar among the control, crevice-covered, and crevice-covered plus shaded pools. These pools exhibited greater daytime drift densities ($P < .01$) 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 ($P < .05$) 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 in flow rates among the pools, which resulted in differing volumes of water sampled by the drift nets. To represent actual prey availability to trout, that is, the number of prey items passing through a "feeding window" per unit time, data (Table 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 1985 and Fig. 10). The distance travelled by drifting invertebrates has been reported to be often < 10 m (McLay 1970, Elliott 1971, Otto 1976), but perhaps as great as 50–60 m (Waters 1965). Because the study sections were separated by at least 800 m, it is unlikely that abundance of drift in the downstream forested reach was impoverished by trout predation in the upstream logged reach.

Biomass of daytime drift was similar between the first two sampling dates, but significantly lower on the last date ($P < .05$, Wilcoxon's signed ranks test). Biomass of nighttime drift was also lower on the final than on the beginning sampling date. Differences among treatments in biomass of daytime drift for the first two sampling dates were nonsignificant ($P > .20$, 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. Larger individuals usually were of terrestrial origin and they were well represented in both logged and forested sections. Occurrence of terrestrial invertebrates in the drift was probably a function of proximity of suitable terrestrial habitat (i.e., overhanging vegetation or woody debris). In the logged section, terrestrial inputs were dominated by Hymenoptera and Hemiptera that were associated with streamside willow (*Salix* spp.), and in the forested reach, wood-associated Coleoptera were abundant.

A proposed conceptual model relating trout growth to prey availability and to foraging efficiency and energetics is presented in Fig. 9. The strong correlation existing between prey density and trout growth (Fig.

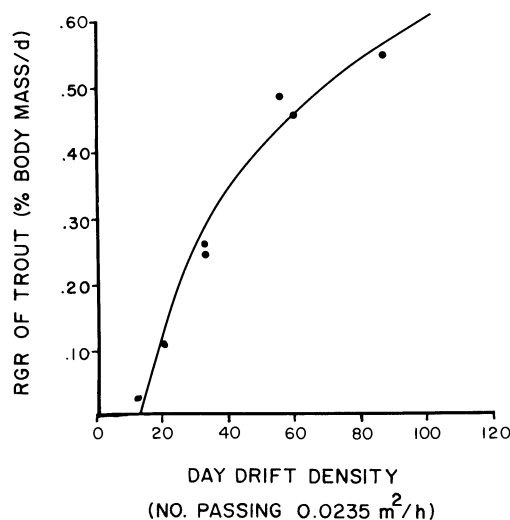


FIG. 8. Relationship between mean density of daylight drift and mean relative growth rates of trout from pools in the logged and forested sections. Drift density is based on averages for each treatment from two drift samples (drift net mouth area = 0.0235 m^2) collected at dawn, noon, and dusk on the beginning and final sampling dates, and at noon at the midpoint of the experiment ($n = 14$ samples). Individuals 1 mm in length were excluded from density estimates. Mean relative growth rates of trout are based on averages from two pools of growth estimated for individual trout ($n = 10\text{--}21$ individuals per treatment). Curve was fitted by inspection.

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. 6) suggests that energy expenditures for foraging may increase at the intermediate level of foraging efficiency, and decrease at high and low foraging efficiencies. Given equal prey densities, 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. Growth, however, would probably not decrease in this situation, as net energy intake would remain high. 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 availability, foraging efficiency, and foraging energetics are all in turn related to habitat characteristics. Overhead shading and structural complexity of pool substrates, for example, decreased foraging efficiency (Figs. 4 and 5).

TABLE 1. Numbers and biomass of drift samples collected from paired replicated pools in the logged and forested sections on three sampling dates. "Crevice-cover" refers to pools whose bottoms were covered with fiberglass screening to eliminate substrate crevices.

Treatments	Beginning								Middle			
	Day*				Night†				Day‡			
	No. inds.		Biomass (g)		No. inds.		Biomass (g)		No. inds.		Biomass (g)	
	\bar{X}	CV	\bar{X}	CV	\bar{X}	CV	\bar{X}	CV	\bar{X}	CV	\bar{X}	CV
Logged												
Control	126	23	3.78	111	78	87	14.64	26	33	40	1.95	56
Trout removal	48	62	2.57	110	86	29	9.03	48	22	25	4.54	101
Crevice-cover	69	41	6.11	110	91	59	14.36	74	30	99	7.99	130
75% shade	42	34	9.19	107	288	77	45.97	96	53	76	7.81	41
90% shade	11	10	4.41	87	41	120	5.83	13	86	115	3.63	123
Crevice-cover + shade	45	68	5.33	102	309	100	52.56	10	97	73	3.41	72
Forested												
Control	15	69	0.53	101	27	52	2.66	11	31	45	1.95	31
Trout removal	34	56	1.35	101	36	15	3.52	17	92	84	11.24	65
Crevice-cover	34	68	1.60	62	87	59	8.68	10	28	71	1.52	80

* At the beginning and end of the experiment, day values of drift represent means of samples collected at dawn, noon, and dusk ($n = 6$).

† Values for night drift are from samples collected at midnight ($n = 2$).

‡ At the midpoint of the experiment, day values represent means of samples collected only at noon ($n = 2$).

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

Foraging energetics are affected by current profiles and by proximity of current refuges and concealment from feeding positions, and therefore structurally complex habitats reduce energy costs of trout. Prey availability is determined at least in part by habitat features, such as current velocity, substrate size and stability, and apparently by logging (Table 1).

Effect of trout predation on prey

When expressed on a volume basis, consistent with Allan (1982), density of daytime drift in trout removal pools of the logged and forested reaches increased after the beginning of the experiment (Fig. 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 2 d 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, daytime drift densities were significantly greater in the trout removal pools than in the control pools of the logged section ($P < .05$, Mann-Whitney U test). Although a slight increase in daytime drift density in trout removal pools of the forested section was apparent (Fig. 10), differences between control and trout removal pools were not significant. Because several trout were observed in one of 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 in both the logged and forested sections ($P < .01$, chi-square) (Fig. 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. 11, Table 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 ($P > .05$, 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 and forested sections 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 > 72 in all cases, and replicated samples were combined to represent the drift "community" for a given treatment. Control pools of

TABLE 1. Continued.

End							
Day*				Night†			
No. inds.		Biomass (g)		No. inds.		Biomass (g)	
\bar{X}	CV	\bar{X}	CV	\bar{X}	CV	\bar{X}	CV
111	37	1.36	94	83	79	3.35	
14	35	0.29	67	15	34	0.75	90
75	106	3.43	77	85	106	4.17	62
30	53	8.25	222	170	71	5.28	77
19	35	1.39	102	102	97	7.27	126
46	30	0.65	90	65	90	2.65	88
20	87	0.73	152	36	108	2.64	79
14§	31	0.68	95	19		1.67	
13	99	0.80	111	26	24	2.02	91

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 was 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 3) suggests active selection of trout for this taxon. *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 4 of 162 drift

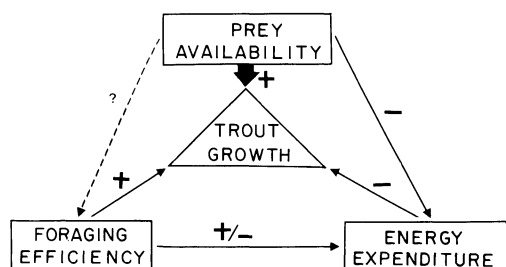


FIG. 9. Proposed model relating trout growth to prey availability and to foraging efficiency and energetics. +/- signs indicate positive and negative correlations. Arrow width represents intensity of the relationship. Dashed line indicates uncertain relationship.

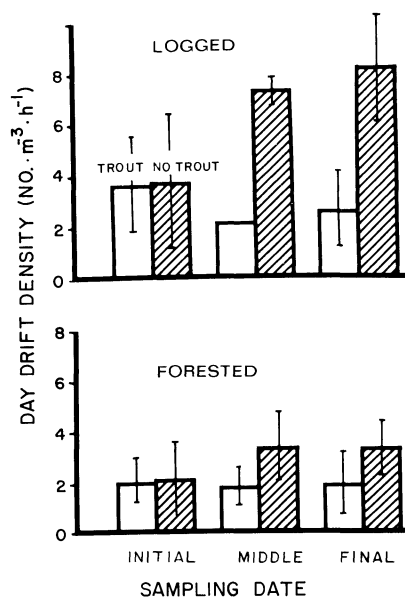


FIG. 10. Density of day drift in control and trout removal pools in the logged and forested section on each of three sampling dates. Drift density, corrected for differences in flow among pools and dates, represents mean number of individuals collected from drift samples at dawn, noon, and dusk on the beginning ($n = 6$) and final ($n = 6$) sampling dates, and at noon at the midpoint of the experiment ($n = 2$). Except for the forested trout removal pool on the final sampling date, drift samples were taken from two pools for each treatment. Vertical bars represent ± 1 SD.

samples taken in both logged and forested sections throughout the experiment. Active selection of trout for this taxon may occur as a result of experience (Ware 1971).

In the forested section, the percentage of *Baetis* spp. in trout diets and in the drift were similar, and Orthocladiinae midges, another important group of behavioral drifters, were selected against by trout (Table 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. 3).

The percentage of trout diets composed of surface drift was much greater in the forested than in the logged section (Table 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 appear to select actively for surface drift in both sections, but because drift nets were not positioned to sample surface drift effectively, this suggestion needs further examination.

Although lower growth rates of trout were observed in the forested reach (Fig. 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); 37.0 g (SD = 39.1 g) vs. 8.9 g

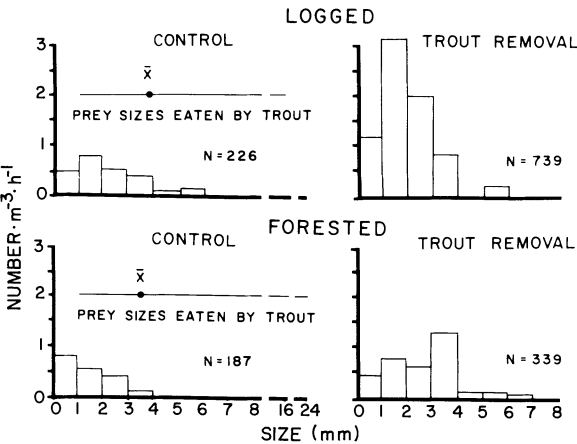


FIG. 11. Size distribution of invertebrates in drift samples from control and trout removal pools in the logged and forested sections. Means are derived from replicate samples taken at noon during the midpoint of the experiment, corrected for differences in flow among pools. Mean and range of prey sizes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

(SD = 4.7 g), respectively; $n = 10\text{--}12$ trout foreguts per treatment]. 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 (Figs. 4 and 5) and a greater relative proportion of a constant food supply drifting at predictable times each day (behavioral drift) (Wilzbach and Hall 1984:Table 4). 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 in the logged section are removing large individ-

uals 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. 8) and abundance (Wilzbach and Hall 1984) are strongly correlated with drift abundance suggest that populations of cutthroat trout are food-limited in the forested stream reach 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 such as shading and substrate complexity 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.

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, although cover-related habitat features 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 demonstrated that food abundance was of overriding importance (Wilzbach 1985). Habitat selection by fish should adaptively balance rewards and risks of foraging (Dill 1983). Assuming there is a risk of mortality which is reduced by substrate crevices and shading, the habitat response of trout to recent, anthropogenic disturbances such as logging may be nonadaptive.

TABLE 2. Mean length and mass of individual invertebrates ($\bar{X} \pm \text{SE}$) from trout foreguts ($n = 10\text{--}12$ per treatment) and from drift samples collected from replicated pools at the midpoint of the experiment.

	Trout diets		Drift	
	Length (mm)	Mass (mg)	Length (mm)	Mass (mg)
Logged control	3.91 ± 0.08	0.473 ± 0.043	1.83 ± 0.08	0.071 ± 0.0027
Logged crevice-covered*	3.56 ± 0.07	0.540 ± 0.061	1.13 ± 0.09	0.124 ± 0.072
Forested control	3.63 ± 0.06	0.906 ± 0.90	1.24 ± 0.14	0.048 ± 0.024
Forested crevice-covered*	2.88 ± 0.07	0.657 ± 0.102	1.39 ± 0.16	0.053 ± 0.004

* “Crevice-covered” pools were those whose bottoms were covered with fiberglass screening to eliminate substrate crevices.

TABLE 3. Percent of drift components in trout diets and in drift samples in logged and forested control pools. Data are from replicated drift samples ($n = 2$) 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
<i>Baetis</i> 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 Tanyptodinae.

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, following an initial increase in abundance after logging, may decline to levels lower than those characteristic of streams bordered by old-growth forests.

Spatial as well as temporal considerations may also restrict the generality of results found in this study. This study was conducted in a high-gradient, head-water 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.

CONCLUSIONS

1) Cutthroat trout were more effective in foraging on experimentally introduced prey in a logged than in a forested section of a Northwestern mountain stream. Differences in foraging efficiency were related to light levels and to substrate crevices. Artificial shading of

logged pools reduced capture success by the trout to levels found for trout in forested pools, and a strong logarithmic relationship was observed between foraging efficiency and mean surface light. Experimental elimination of substrate crevices increased foraging efficiency of trout in both sections of the stream, most likely because the field of vision of the trout was increased.

2) Although habitat features such as surface light influenced foraging efficiency of the trout, differences in foraging efficiency were insufficient to account fully for differences in trout growth between the sections. 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. Higher growth rates of trout in the logged section appear to be due primarily to a greater abundance of their prey base of invertebrate drift.

3) 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. This may have resulted from habitat features in the logged section that favor trout foraging success (e.g., more light due to canopy removal and less crevice habitat), and from 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.

ACKNOWLEDGMENTS

Research was supported by grant BSR 811-24-55 from the Ecosystem Studies Program of the National Science Foundation (Riparian Contribution Number 21) and by Contract Number DE-FG05-85EV60301 from the Environmental Sciences Division of the Department of Energy. We thank Mike and Steve Cummins for field assistance, Steve Cummins for computer programming, and Karan Fairchild for sorting drift samples. We also thank Drs. S. V. Gregory, B. A. Menge, F. J. Swanson, T. F. Waters, and an anonymous reviewer for critical review of the manuscript. This is Contribution Number 1691-AEL.

LITERATURE CITED

- Aho, R. S. 1977. A population study of the cutthroat trout in an unshaded and shaded section of stream. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Allan, J. D. 1978. Trout predation and the size composition of stream drift. *Limnology and Oceanography* 23:1231–1237.
- . 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology* 63:1444–1455.
- . 1983. Predator-prey relationships in streams. Pages 191–229 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: application and testing of general ecological theory*. Plenum, New York, New York, USA.
- Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society* 113:1–32.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of the plankton. *Science* 150:28–35.
- Coffman, W. P. 1963. Community structure and trophic relations in a small woodland stream, Linesville Creek,

- Crawford County, Pennsylvania. Dissertation. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**:1802–1813.
- Cummins, K. W., G. W. Minshall, J. R. Sedell, C. E. Cushing, and R. C. Petersen. 1984. Stream ecosystem theory. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **22**:1818–1827.
- Cummins, K. W., J. R. Sedell, F. J. Swanson, G. W. Minshall, S. G. Fisher, C. E. Cushing, R. C. Petersen, and R. L. Vannote. 1983. Organic budgets for stream ecosystems: problems in their evaluation. Pages 299–354 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: application and testing of general ecological theory*. Plenum, New York, New York, USA.
- Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:398–408.
- Dunn, O. J. 1964. Multiple comparisons using rank sums. *Technometrics* **6**:241–252.
- Elliott, J. M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. *Oecologia (Berlin)* **6**:350–379.
- Feldmuth, C. R., and T. M. Jenkins. 1973. An estimate of energy expenditure by rainbow trout (*Salmo gairdneri*) in a small mountain stream. *Journal of the Fisheries Research Board of Canada* **30**:1755–1759.
- Fisher, S. G. 1983. Succession in streams. Pages 7–27 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: application and testing of general ecological theory*. Plenum, New York, New York, USA.
- Gibbons, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart, and Winston, New York, New York, USA.
- Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* **65**:455–468.
- Glass, N. R. 1971. Computer analysis of predation energetics in the largemouth bass. Pages 325–363 in B. C. Patten, editor. *Systems analysis and simulation in ecology*. Volume I. Academic Press, New York, New York, USA.
- Griffiths, R. W. 1981. The effect of trout predation on the abundance and production of stream insects. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.
- Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* **106**:545–555.
- Hart, D. D. 1978. Diversity in stream insects: regulation by rock size and microspatial complexity. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **20**:1376–1381.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Riparian canopy and substrate composition interact to influence the abundance of salmonids, sculpins, and salamanders in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:1173–1185.
- Henderson, M. A. 1982. An analysis of prey detection in cutthroat trout (*Salmo clarki clarki*) and Dolly Varden charr (*Salvelinus malma*). Dissertation. University of British Columbia, Vancouver, British Columbia, Canada.
- Hunter, J. R., and J. R. Zweifel. 1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *United States National Marine Fisheries Service Fishery Bulletin* **69**:253–266.
- Mackey, A. P. 1977. Growth and development of larval Chironomidae. *Oikos* **28**:270–275.
- McLay, C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *Journal of the Fisheries Research Board of Canada* **27**:359–370.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**:1370–1386.
- Murphy, M. L. 1979. Predator assemblages in old-growth and logged sections of small Cascade streams. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* **38**:137–145.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* **110**:469–478.
- O'Brien, J. W. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *American Scientist* **67**:572–581.
- Otto, C. 1976. Factors affecting the drift of *Potamophylax cingulatus* (Trichoptera) larvae. *Oikos* **27**:93–100.
- Pimentel, R. A. 1979. Morphometrics, the multivariate analysis of biological data. Kendall/Hunt, Dubuque, Iowa, USA.
- Pritchard, G. 1980. Life budgets for a population of *Tipula sacra* (Diptera: Tipulidae). *Environmental Entomology* **5**:165–173.
- Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting micro-distribution of stream benthic insects. *Oikos* **29**:33–43.
- Rao, G. M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Canadian Journal of Zoology* **46**:781–786.
- Reisen, W. K. 1975. Quantitative aspects of *Simulium virgatum* Coq. and *S. species* life history in a southern Oklahoma stream. *Annals of the Entomological Society of America* **68**:949–954.
- Ringler, N. H. 1979. Prey selection by drift feeding brown trout (*Salmo trutta*). *Journal of the Fisheries Research Board of Canada* **36**:392–403.
- Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America* **70**:51–53.
- Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* **111**:255–266.
- Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart, and Winston, New York, New York, USA.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* **10**:375–383.
- Statzner, B., and A. Bittner. 1983. Nature and causes of migrations of *Gammarus fossarum* Koch (Amphipoda)—a field study using a light intensifier for the detection of nocturnal activities. *Crustaceana* **44**:281–291.
- Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. Campbell. 1982. Land-water interactions: the riparian zone. Pages 267–291 in R. L. Edmonds, editor. *Analysis of coniferous forest ecosystems in the western United States*. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.
- Swanson, F. J., and G. W. Lienkaemper. 1978. Physical consequences of large organic debris in streams of the Pacific Northwest. *United States Forest Service General Technical Report PNW-69*.
- Waldbauer, G. 1968. The consumption and utilization of food by insects. *Advances in Insect Physiology* **5**:229–288.
- Wankowski, J. W. J. 1981. Behavioral aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate, drifting prey. *Animal Behaviour* **29**:557–571.
- Ware, D. M. 1971. Predation by rainbow trout (*Salmo*

- gairdneri*): the effect of experience. Journal of the Fisheries Research Board of Canada **28**:1847–1852.
- . 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada **29**:1193–1201.
- . 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada **37**:787–797.
- Waters, T. F. 1965. Interpretation of invertebrate drift in streams. Ecology **46**:327–334.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540–1548.
- Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. Limnology and Oceanography **25**:166–172.
- Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences **42**:1668–1672.
- Wilzbach, M. A., and J. D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **22**: 2516–2522.