Ecology, 63(5), 1982, pp. 1444–1455

THE EFFECTS OF REDUCTION IN TROUT DENSITY ON THE INVERTEBRATE COMMUNITY OF A MOUNTAIN STREAM[1]

J. DAVID ALLAN
Department of Zoology, University of Maryland, College Park, Maryland 20742 USA

Abstract. An experimental reduction in trout density was carried out for 4 yr to determine whether the numbers or species composition of aquatic invertebrates would be affected. In a Colorado stream, the standing crop of trout (mainly *Salvelinus fontinalis*) prior to this study was 4.86 g/m^2, typical of infertile trout streams. Repeated electroshocking of a 1220 m long experimental section kept trout stocks at 10–25% of this initial value during the summers of 1975–1978.

Density of invertebrates in the benthos (number of invertebrates per square metre) showed no consistent differences between the trout removal section and upstream and downstream control sections for the majority of taxa examined. Drift density (number of invertebrates per 1000 cubic metres) also failed to show an effect of the trout removal. Some taxa were significantly more abundant at one site than another, but this was attributable to changes along the stream gradient or differences in phenology among the sites rather than experimental reduction of trout. As trout stomach content analysis revealed very intensive grazing on a few taxa of aquatic insects, their failure to increase in the trout removal section was unexpected.

Statistical analysis showed that because of the variability of the system, a doubling or halving of numbers must occur to be detectable. Within these limits, it is concluded that removal of trout had no significant effect on the prey community, and two explanations are offered. Trout may actually consume only a small fraction of total prey, although this conclusion is limited by inability of current techniques to sample the benthos fully. It is also likely that because streams do not provide areas where fish are predictably absent, the invertebrate community is highly adapted to fish predation and so is not sensitive to manipulations in fish density.

Key words: aquatic insects; benthos; drift; field experiment; predator; prey; Salvelinus fontinalis; *stream.*

INTRODUCTION

The ecology and feeding of stream-dwelling salmonids has been studied extensively, from the standpoint of the fish. Production and population dynamics (Northcote 1969), growth and metabolism (Hoar et al. 1979), and food consumption and composition of diet (Elliott 1973, Allan 1981) compose a voluminous literature. Relatively little attention has been paid to the role of fish from the viewpoint of the invertebrate community. As a consequence it is not known whether trout severely limit invertebrate abundance and perhaps determine community composition as Paine (1966) showed for the top predator, a starfish, in a marine intertidal community. Some authors (e.g., Mann 1978) have concluded that invertebrate stocks are very heavily grazed, which suggests that the presence or absence of trout would substantially alter prey densities. Others (e.g., Mundie 1974) have speculated that food may be well in excess of requirements.

The principal goal of this study was to determine whether the presence or absence of the top predator, trout, affected the numbers or species composition of the prey community, invertebrates, in a mountain stream. An indirect answer to this question may be provided by a comparison of amount eaten to amount available, and Allan (1982*b*) makes such an analysis. The most direct approach is either to add or remove trout in a field experiment, as reported in the present paper.

No demonstrable increase in population numbers or change in species composition compared to control sections resulted from a 4-yr experimental reduction in numbers of trout. Because trout apparently consumed a substantial fraction of prey present (Allan 1982*b*), and only a few species comprised the majority of their prey, this was unexpected. It is suggested that actual invertebrate densities must be substantially underestimated to account for this discrepancy, and that invertebrates in streams are highly adapted to the presence of fishes, with the result that changes in predation pressure do not markedly alter the prey community.

EXPERIMENTAL DESIGN

The basic concept was to reduce predation by trout in one section of stream relative to natural control sections, and determine whether invertebrate populations were affected. The trout removal (TR), or experimental, section was a 1220-m length of stream (Fig. 1). The 700-m section upstream from the upper end of the TR section was designated the upstream control (UC); the first 1000 m downstream from the lower end of the TR section formed the lower control

[1] Manuscript received 15 September 1980; revised 1 October 1981; accepted 8 October 1981.

(LC). The three sections appeared similar in habitat and cover. The sampling station within the experimental section was ≈200 m from the downstream end. Downstream displacement or drift of invertebrates in streams is well known and potentially could cause enough dispersal through section TR to mask any experimental response. The intent was to provide ≈1000 m, as nearly trout free as possible, above the sampling station in the experimental section.

The null hypothesis (H_0) was that there would be no change in numbers or species composition within section TR. The most likely alternative hypothesis (H_A) was that invertebrates would increase in abundance when released from predation. However, it is possible that an alternate predator or competitive dominant might increase, thereby causing the decline of other species. Thus it seemed more cautious to broaden H_A to include any change in TR compared to control sections.

The study area lies between altitudes of 3000 and 3200 m in Cement Creek, Gunnison County, Colorado, USA. It is a stony-bottom, high-gradient mountain stream in which trout are the only fish present. Brook trout (*Salvelinus fontinalis* Mitchill), brown trout (*Salmo trutta* L.), and cutthroat trout (*S. clarki* Cope) maintain breeding populations, and rainbow trout (*S. gairdneri* Richardson) are stocked during summer, but below this elevation. The stream is in open meadow throughout the study region, with *Salix* spp. along the stream bank. Stream width was typically 3.5–4.5 m. Allan (1975) described the stream in detail.

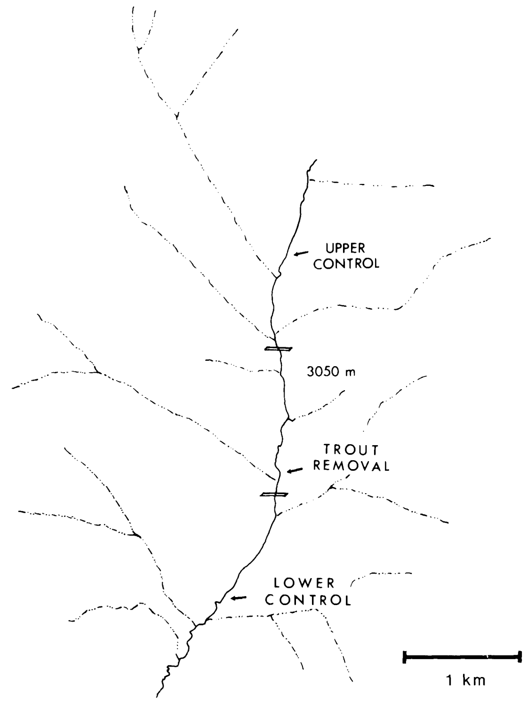

FIG. 1. Map of Cement Creek, Gunnison County, Colorado, USA, showing trout removal section (1220 m long, between fences) and upper and lower control sections. Approximate locations of sampling sites are indicated by arrows. Dashed lines are intermittent streams which usually contain running water.

METHODS

Physical measurements

Temperature was measured with a maximum-minimum recording thermometer at about weekly intervals during the summer season, and when possible at other times of the year. Current was measured periodically with a pygmy current meter, and total discharge was calculated from triplicate current and depth readings at three points across the stream.

Invertebrate sampling

Benthos.—The benthos was sampled using a Surber sampler of mesh size 0.3 mm. At each site, 12 individual samples (area = 0.093 m^2) were collected in a 3 × 4 grid across the stream by moving upstream 1–2 m after each row of 4 samples was collected across the stream width. The total sample size was 1.12 m^2. I attempted to choose riffle areas <20–30 cm deep, except when high flows forced me to sample in deeper water (40–50 cm in some instances). A sample size of 12 was chosen, as preliminary estimates of variability indicated that precision increased markedly with sample size up to 10–15 samples, and more slowly thereafter. As the initial intent was to rely on nonparametric statistics, and for ease of sample sorting, all 12 Surber samples were combined into a single sample at the time of collection in 1975 and 1976. However, in order to have an estimate of precision associated with each sample, in 1977 and 1978 each of the 12 samples per site was sorted separately.

Samples were preserved in 10% formalin with some rose bengal added to facilitate later sorting. All samples were sorted in their entirety and stored in an alcohol-glycerine solution. All invertebrates were counted and identified to the lowest taxonomic level feasible (generally to species, except in the Diptera where the family level was used).

Drift.—The drift was sampled using nets of mesh size 0.3 mm suspended from steel bars driven into the substrate. Care was taken that nets did not contact the bottom. Each net had a square opening of 0.1 m^2, a length of 2 m, and was joined to the frame by a 20-cm sleeve of smooth Dacron® to minimize the likelihood of insects crawling out of the net. Nets were slightly greater in area ≈0.2–0.5 m behind the opening to minimize turbulence at the net mouth. Two nets were used at each site and sampled over a 24-h period. Contents were preserved as described for benthos.

Flow through the nets was estimated from the product of percent of net opening submerged, area of net opening, and current estimated within the mouth of the net. Three estimates of current were made at the

TABLE 1. Estimated trout numbers in experimental section of Cement Creek at beginning of removal experiment (1975) and in subsequent years. Date is date of first fishing, C_i is the i^{th} catch, $\hat{N}$ (with 95% CL) is the estimated number in the 1220-m section, and $\hat{p}$ is the estimated capture probability.

Date	Catch					$\hat{N}$ and 95% CL	$\hat{p}$
	C_1	C_2	C_3	C_4	C_5		
8 July 1975							
<12-cm trout	23*	72	68	32	27	261.9 ± 46.8	.30
>12-cm trout	83	68	56	29	38	385.2 ± 73.6	.22
Total						647.1 ± 120.4	
9 July 1976	115	54	31			235.0 ± 26.5	.47
25 June 1977	111	50				202.0 ± 37.1	.55
6 July 1978	100	93	45	42		382.9 ± 66.9	.28

* Not included in estimate of $\hat{N}$.

beginning and end of each sampling interval, and averaged. Any loss of filtering efficiency was noted from beginning and end current readings; for the most part none occurred. Drift density (numbers drifting per 1000 cubic metres of discharge) was calculated by dividing number of invertebrates captured in an interval by volume (cubic metres) of water sampled, multiplied by 1000.

Drift sampling procedures were varied during the study in an effort to reduce the effort of sample sorting. In all cases I collected eight paired samples at 3-h intervals over 24 h. In 1975, nets were submerged for the entire 3-h sampling interval. Because number of invertebrates collected was often very large, and some loss of net-filtering efficiency was observed, in subsequent years I used 1-h sampling periods at 3-h intervals. The only exception to the 1-h sampling period occurred near the height of spring runoff, when net clogging would allow only a 20-min sample. Because of the well-known nocturnal increase in drift, I took care to time the first evening sampling interval to begin just after nightfall.

Drift samples generally were subsampled with a plankton splitter prior to removal of invertebrates. The range of subsample sizes was 12.5–100%, and in most instances 25 or 50% was subsampled. Invertebrates were counted and stored as described for benthos.

Trout

Two fences were erected 1220 m apart in a meadow at 3050 m (Fig. 1) to form the experimental section. Fences were 2.5-cm vinyl-coated chain link secured to steel fence posts driven into the stream bed. Locations were chosen for wide, shallow, and as uniform as possible bottom configuration to increase the effectiveness of the barrier. A flexible wire screen extending up to the surface was then placed on the upstream side of the chain link fence, so that current held it in place. This screen was bent at a right angle so that ≈0.5 m was flush with the stream bottom, and then covered with stones. Thus a barrier was created which reduced the likelihood that trout could penetrate underneath the fence. The screen was 2.5-cm mesh under high flow conditions (July) and 1.3-cm mesh when lower flow permitted. Fences were installed about 1 July of each year and removed in mid- to late September. As spring runoff peaked in mid-June, it was not feasible to install fences earlier.

Trout were collected by electroshocking (pulsed DC). To census the population and also to remove trout from the 1220-m experimental section, repeated (two to five) electroshocking efforts were made in an upstream direction. Trout were kept alive and later released elsewhere, or killed for length and mass data. All fish were measured (fork length in millimetres), and the mass of each sample was determined to the nearest 0.1 g on a triple-beam balance.

As each individual catch tends to be large, relative to the population, in stream electrofishing, the catch-removal method is appropriate for estimation of numbers (Seber and Le Cren 1967, Seber 1973:309). Because it has been reported that the probability of capturing small trout is lower than that for large trout (e.g., McFadden 1961), I separated my estimates into two size-classes (<12 cm, >12 cm) where it improved the precision of the estimates.

RESULTS

Physical measurements

Water temperature was 0°C from early November until late April. Maximum summer temperatures were 15°–18°, typically with a diel range of 10–12°. Low flow conditions in 1977 resulted in warmer temperatures compared to 1978, a high flow year. Discharge (cubic metres per second) in Cement Creek typically peaked in mid-June, followed by a decline throughout the summer. Differences between years were evident: 1975 and 1978 both were high-discharge years, 1976 somewhat lower, and 1977 registered extremely low flows. In excess of 70% of the total annual discharge typically occurred between mid-May and mid-July. Further documentation of temperature, discharge, and water chemistry are available from the author on request, and in Allan (1975).

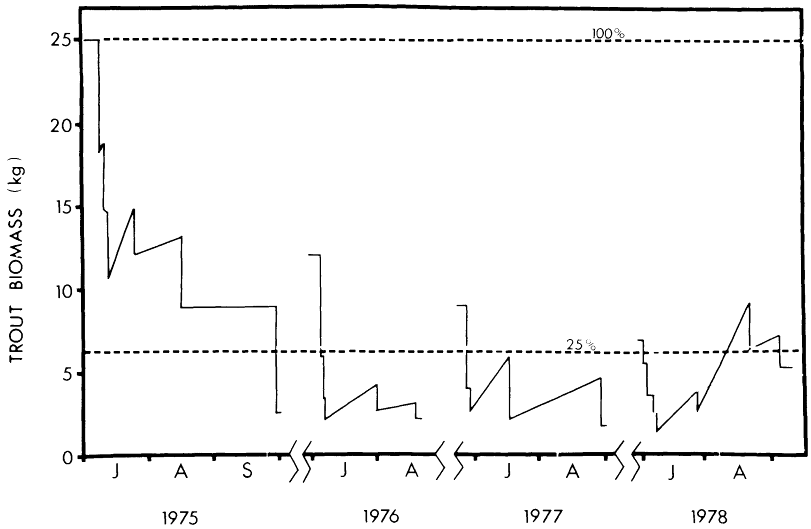

FIG. 2. Standing crop biomass (wet mass) of trout in the experimental (trout removal) section, summers of 1975–1978. Horizontal dashed lines represent 100 and 25% of initial biomass.

Trout

During the initial trout census and removal from the experimental section, five electrofishing sweeps were made between 8 July and 15 August 1975. A plot of cumulative catch vs. catch for <12-cm trout revealed that this size-class was very underrepresented in the first electrofishing, presumably because of high flow and inexperience. Accordingly, the numbers of this size-group were estimated from the second through fifth electrofishings, while number of trout >12 cm was estimated separately from all five collections. The estimates (with 95% CL) are 261.9 ± 46.8 trout <12 cm, and 385.2 ± 73.6 trout >12 cm, for a total of 647.1 ± 120.4 trout in the 1220-m section (Table 1). A slightly higher point estimate, 661 trout, is obtained by the graphical method of Seber and Le Cren (1967). On 27 September 1975, a final collection under low-flow conditions brought the number of trout collected to 616. Thus by the end of the first summer, 93–95% of the estimated initial population had been captured. Brook trout (*Salvelinus fontinalis*) comprised 95.5% of the trout present, with about equal numbers of brown (*Salmo trutta*) and cutthroat trout (*S. clarki*) in the remainder.

The relation between wet mass (M, in grams) and fork length (L, in centimetres) was determined to be:

$$M = 0.012\, L^{2.98} \qquad (1)$$

($r^2 = .98$) based on 244 brook trout collected at various times from 1975 to 1978. Individual regressions from collections on different dates did not differ significantly, and so were pooled.

As all trout were measured when collected, it was possible to convert all population estimates to biomass using Eq. 1. The few brown and cutthroat trout were presumed to conform to the same regression, and this seemed reasonable based on inspection of the data. Applying the mass distribution obtained from the 616 captured trout to the point estimate of 647.1 trout gives an estimated biomass of 25.18 kg. Based on an estimated stream area of 5182 m^2, the standing crop of trout was 4.86 g/m^2 at the beginning of this experiment. Censuses conducted in other years from source to mouth of Cement Creek were consistent with this estimate.

TABLE 2. Friedman's nonparametric ANOVA for trends in benthic densities (number per sample) among upper control (UC), trout removal (TR), and lower control (LC) sections. For each taxon, density was ranked among the three sections on each of 16 dates. Significant differences between means based on an a posteriori comparison of ranked sums (Hollander and Wolfe 1973:151) are indicated by inequality signs.

Taxon	*P*	Result
Ephemeroptera		
Baetis bicaudatus	NS >.1	
Cinygmula sp.	NS >.5	
Epeorus longimanus	<.01	UC < TR = LC
Ephemerella coloradensis	NS >.1	
E. infrequens	NS >.05	
Rhithrogena hageni	NS >.5	
Plecoptera		
Alloperla spp.	NS >.1	
Perlodidae	NS >.5	
Zapada haysi	NS >.1	
Trichoptera		
Rhyacophila acropedes	<.025	UC < TR = LC
R. valuma	<.05	UC > TR = LC
Diptera		
Chironomidae	NS >.5	
Simuliidae	NS >.1	
Total aquatic invertebrates	NS >.5	

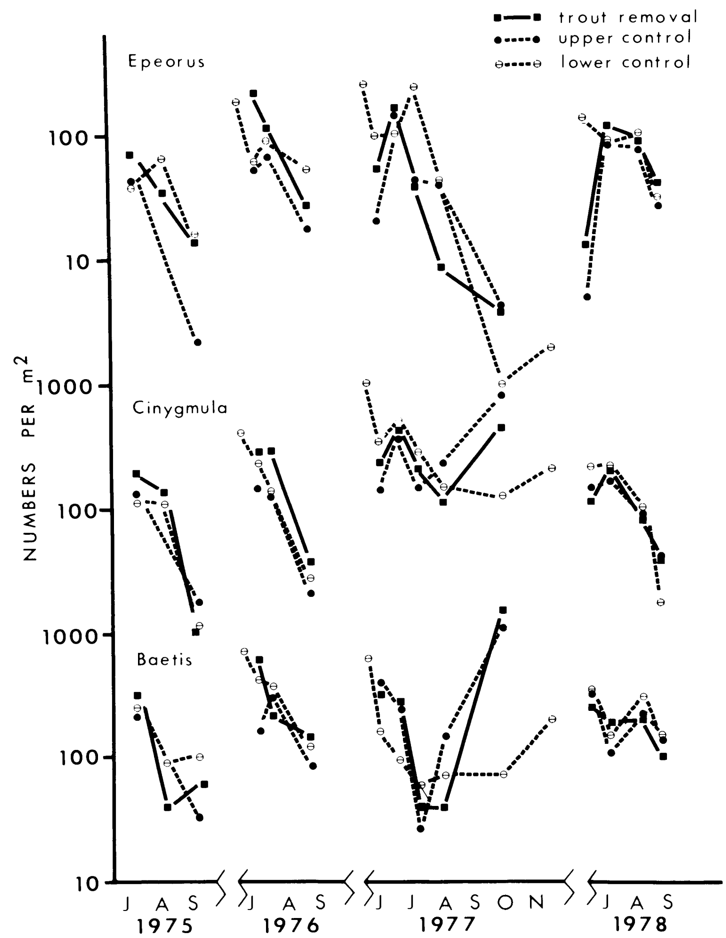

FIG. 3. Number of individuals per square metre in the trout removal (■———■), upper control (●- - -●), and lower control (⊖- - -⊖) sections over 4 yr. Lower panel: *Baetis bicaudatus*; middle panel: *Cinygmula* sp.; upper panel: *Epeorus longimanus*.

From electrofishing returns each year, it was possible to estimate the population of trout in the experimental section at the beginning of the 1976, 1977, and 1978 seasons (Table 1). Numbers ranged from 31–59% of the original value on about 1 July of each year owing to invasion of the experimental section during the winter and perhaps especially during spring runoff. The estimates obtained by separate treatment of $<$12-cm and $>$12-cm trout were very close to estimates based on all trout combined, and only the estimates based on total trout are presented.

The estimated biomass of trout present in the experimental section was estimated from electrofishing and length-frequency data throughout the 4-yr study (Fig. 2). On any date, numbers present prior to electrofishing were estimated from $\hat{N}$ = (number captured) $\div \hat{p}$, where $\hat{p}$ was based on data from an occasion when repeated electrofishings were conducted under similar flow conditions. Number remaining was estimated as $\hat{N}$—number caught, and all figures were then converted to biomass. Values were highest at the beginning of each summer, but were not as high as numbers alone (Table 1) would suggest because most of the trout were small. After the first week in July, biomass present was generally in the range of 10–25% of initial biomass.

Invertebrates

Benthic collections.—Benthic densities were estimated in the trout removal and the two control sections on each of 16 dates between 30 July 1975 and 11 September 1978. Samples were collected at the lower control site on some additional dates to better define population fluctuations.

Average numbers per square metre are presented for *Baetis bicaudatus*, *Cinygmula* sp., and *Epeorus longimanus* (Ephemeroptera) in Fig. 3, and for the stonefly *Zapada haysi*, the Chironomidae, and the Simuliidae in Fig. 4. For some 31 data sets where 12 replicates were sorted separately, 95% confidence intervals were calculated from $\log(x + 1)$ transformed data. They are omitted from Figs. 3 and 4 for clarity.

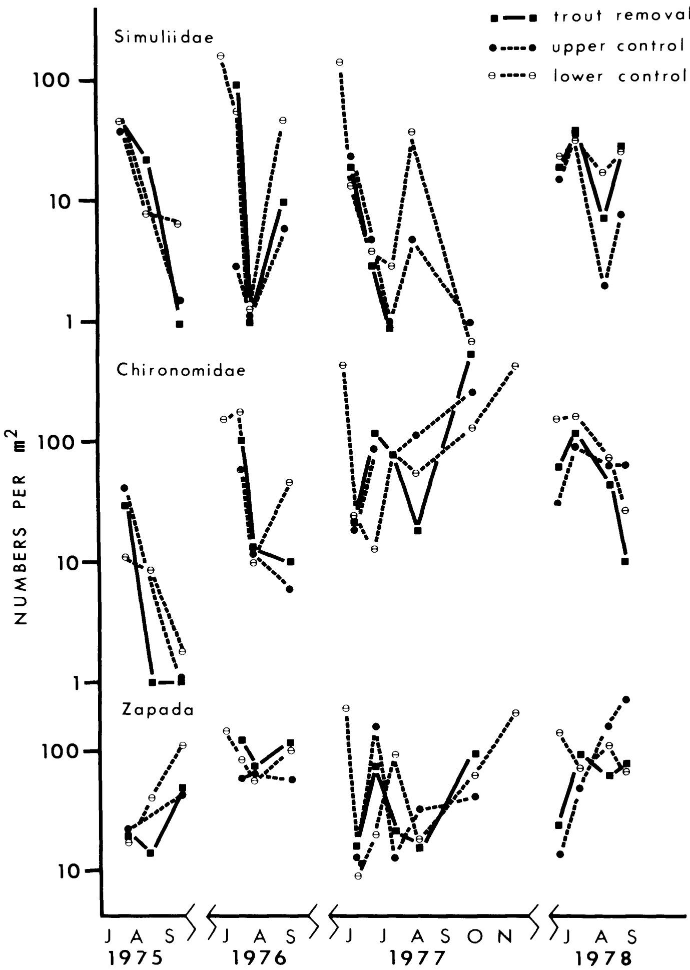

FIG. 4. Number of individuals per square metre in the trout removal (■———■), upper control (●- - -●), and lower control (⊖- - -⊖) sections over 4 yr. Lower panel: *Zapada haysi*; middle panel: Chironomidae; upper panel: Simuliidae.

Typical 95% confidence intervals were ± 50% of the mean (J. D. Allan, *personal observation*). The minimum detectable difference between means is discussed in a later section. Seasonal fluctuations typically encompassed three orders of magnitude. Densities also varied among years, perhaps owing to annual variation in water discharge.

None of the six taxa presented in Figs. 3 and 4 showed a consistent trend toward more individuals in the trout removal section compared to the two controls. However, it is clear that on some dates, at least two of the sites differed substantially. On 12 October 1977, for example, *Baetis* density at the lower control site was exceeded by *Baetis* density at the other two sites by at least an order of magnitude.

To determine whether densities were consistently greater at one site compared to the others, I used Friedman's nonparametric test in which dates were treated as blocks, and mean density at each of three sites was ranked for each collecting date. Of 14 taxa examined (Table 2), 3 showed significant differences among ranked densities: *Epeorus longimanus* (Ephemeroptera), *Rhyacophila acropedes*, and *R. valuma* (Trichoptera). The results with *E. longimanus* appeared consistent with release from predation. However, significance was obtained primarily because there were consistently fewer individuals at the upper control site, while numbers were not significantly greater in TR compared to LC (Table 2). A similar interpretation seems appropriate for the *R. acropedes* result, while *R. valuma* generally decreased in a downstream direction. Thus while three species showed significant differences among sites, they did not provide convincing evidence of release from predation.

For nine dates in 1977–1978 where individual replicates were sorted separately, I compared densities by one-way analysis of variance among the three sites. All data were transformed to logarithms ($\log[x + 1]$ when zero observations were present). Six taxa were

TABLE 3. Results of one-way ANOVAs among upper control (UC), trout removal (TR), and lower control (LC) for 1977–1978 benthic densities. Means which differed significantly (.05) by the a posteriori SNK test are indicated by inequality signs.

Taxon	Sampling date								
	16 Jun 77	5 Jul 77	25 Jul 77	17 Aug 77	12 Oct 77	5 Jul 78	23 Jul 78	23 Aug 78	11 Sep 78
Baetis bicaudatus	NS	LC < TR	NS	TR < UC	LC < TR = UC	NS	NS	NS	NS
Cinygmula sp.	UC < TR = LC	NS	NS	TR < UC	LC < TR = UC	NS	NS	NS	NS
Epeorus longimanus	UC < TR = LC	NS	LC > TR = UC	NS	NS	LC > TR = UC	NS	NS	NS
Zapada haysi	NS	NS	LC > TR = UC	NS	NS	LC > TR = UC	NS	NS	TR < UC
Chironomidae	NS	LC < TR	NS	TR < UC	TR > UC = LC	LC > TR = UC	NS	NS	TR < UC
Simuliidae	NS	NS	...*	...	...	NS	...	...	...

* Number too few for analysis.

chosen for this analysis based on their importance in trout diet and relatively infrequent zero observations.

Of the 48 separate ANOVAS, fully 17 (35%) showed a significant difference among sites at the .05 level. A posteriori comparisons made by the Student-Newman-Keuls (SNK) test (Sokal and Rohlf 1969) allowed determination of which means differed significantly (Table 3). For example, TR > UC = LC would be expected as a result of release from predation. Only the Chironomidae on 12 October 1977 showed this result, although 5 of the remaining 16 significant effects were due to higher densities in the trout removal section compared to one control section. However, the pattern of these significant differences is not consistent within a species over time; rather, on a particular date one site differs from the other two for several taxa. On 5 July 1978, for example, *E. longimanus*, *Z. haysi*, and the Chironomidae were each more abundant at the upper control site compared to the other two sites. Either chance selection of a rich location or seasonal phenology seem to be more likely explanations than do differences in trout density.

In summary, analyses of trends in invertebrate densities by a nonparametric test over 4 yr and by F tests on nine dates in 1977–1978, failed to reveal a significant difference between the trout removal and two control sections. While a particular species may differ in mean density between some pairs of sites, no consistent trend emerges.

Drift collections.—Drift samples were collected at the experimental and the two control sites (Fig. 1) over a 24-h period on 12 sampling dates between 13 August 1975 and 24 August 1978. Results were calculated as drift density, or numbers per 1000 cubic metres of

TABLE 4. Drift densities (numbers per 1000 cubic metres) estimated by two replicate nets (1, 2) at two sites (TR = trout removal; LC = lower control) for the 24-h period 18–19 August 1976.

	Invertebrates (number/1000 m^3)			
	TR 1	TR 2	LC 1	LC 2
Invertebrates				
Baetis bicaudatus	9260.6	8080.0	14 870.5	14 474.7
Cinygmula sp.	425.5	474.1	405.7	555.7
Epeorus longimanus	404.0	303.0	440.5	588.0
Ephemerella coloradensis	209.5	206.3	244.6	246.2
E. infrequens	96.1	78.1	82.5	147.0
Total Ephemeroptera	10 591.6	9202.8	16 213.1	16 066.6
Alloperla spp.	243.4	68.7	396.7	220.1
Perlodidae	29.5	139.4	15.5	206.9
Zapada haysi	342.9	251.0	493.9	361.5
Total Plecoptera	615.7	464.7	906.0	811.7
Rhyacophila acropedes	5.7	13.0	9.0	16.9
R. valuma	4.3	9.3	2.6	6.3
Total Trichoptera	21.8	48.3	63.8	63.2
Simuliidae	1631.9	2013.5	3286.6	3262.9
Chironomidae	519.5	515.1	404.4	774.4
Total aquatic invertebrates	13 875.0	12 480.3	22 001.8	21 420.8
Terrestrial invertebrates	133.6	72.4	332.9	310.6
% of discharge sampled	5.29	6.44	7.93	4.84
Discharge (m^3/s)	0.58		0.68	

water sampled, to correct for differences in flow among sites. This figure was obtained by dividing total individuals collected over 24 h by total discharge for the same period, and so represents an average of day and night values. Although two replicate nets were used, I routinely analyzed only one net at each site because of the effort involved. On 18 August 1976, however, the contents of both nets were analyzed at two sites (TR, LC) to determine reliability of estimates. Replicate estimates of drift density were independent because each was based on a separate estimate of numbers captured and flow through the net. In general, results differed between the two sites more than between the two replicates, and numbers were greater at site LC (Table 4). The replicate samples at site LC were based on sampled water volumes that differed by nearly a factor of two, yet gave quite similar estimates. The eight individual estimates that provide the 24-h total were compared by split-plot ANOVA (between sites, times within sites, T × S). Total invertebrates and most major taxonomic groups were significantly more abundant at site LC.

Because of the lack of information on within-site variation in drift density, apart from that reported above, statistical analysis was by nonparametric methods only. As with benthic estimates, the drift density was ranked among the three sites on each of 12 dates to test whether numbers were consistently higher at one site compared to the others. Of the 14 taxa examined (Table 5), five showed significant differences among sites. Four of these clearly were density changes along the stream gradient. Only *Rhithrogena hageni* showed a tendency to increase in TR compared to both controls (but not significantly with respect to LC), and possibly this species benefitted from reduced trout density. However, higher densities of *R. hageni* in the TR section were most apparent in 1975–1976, and less apparent thereafter, which appears inconsistent with the continuing reduction in trout biomass (Fig. 2).

In summary, comparison of drift density among the three sites did not indicate higher drift from the TR section compared to the two controls. Some taxa showed significantly different drift densities among stream sections, but the pattern was more consistent with some factor or factors acting parallel to the stream gradient than with reduction in trout density.

TABLE 5. Friedman's nonparametric ANOVA for trends in drift density (numbers per 1000 cubic metres) among upper control (UC), trout removal (TR), and lower control (LC) sections. For each taxon, density was ranked among the three sections on each of 12 dates. Significant differences between means based on an a posteriori comparison of ranked sums (Hollander and Wolfe 1973:151) are indicated by inequality signs.

Taxon	*P*	Result
Ephemeroptera		
Baetis bicaudatus	NS (>.5)	
Cinygmula sp.	<.01	LC < TR = UC
Epeorus longimanus	NS (>.5)	
Ephemerella coloradensis	NS (>.1)	
E. infrequens	NS (>.1)	
Rhithrogena hageni	<.05	UC < TR = LC
Plecoptera		
Alloperla spp.	NS (>.1)	
Perlodidae	<.05	UC > TR = LC
Zapada haysi	<.01	UC > TR = LC
Trichoptera		
Rhyacophila acropedes	NS (>.1)	
R. valuma	NS (>.1)	
Diptera		
Chironomidae	<.01	LC < TR = UC
Simuliidae	NS (>.1)	
Total aquatic invertebrates	NS (>.05)	

DISCUSSION

Adequacy of the trout removal experiment

In assessing results, one wishes to know the extent of the reduction in predation accomplished in the experimental section. Initial density is known moderately well, with the 95% confidence interval ± 18.6% of the estimated mean. Because mass can be estimated from length with high precision, values expressed as biomass are nearly as good. There is possible systematic bias if trout differ markedly in catchability, leading to underestimates of 15 or even 30% (Bohlin and Sundström 1977). No assessment of this bias is feasible, however.

The amount of trout remaining in the experimental section over the course of this study, expressed as biomass (Fig. 2), reveals that a very substantial reduction was accomplished. From early July until autumn when temperatures and feeding rates decline markedly (Allan 1981), trout biomass is only 10–25% of the initial value. During May and June, however, feeding rates can be quite high (Allan 1981), and biomass expressed as a percentage of initial value was 48% (1976), 36% (1977), and 28% (1978). Overall, the reduction in predator abundance was substantial but not complete. It is possible that the remaining trout fed at a higher rate; however, inspection of length-mass relationships did not indicate such an effect (J. D. Allan, *personal observation*).

Cement Creek, because of its high altitude, might be expected to be relatively unproductive. This is generally true, although probably the study area is typical of less-fertile salmonid streams anywhere (see reviews by Waters 1977, Chapman 1978). The standing crop biomass from the experimental section of Cement Creek (4.9 g/m^2), and production estimated by the graphical method of Allen (1951: 3.1 $g \cdot m^{-2} \cdot yr^{-1}$), are fairly typical values.

Invertebrate response

In this experiment, the null hypothesis (H_0) of no difference among sites cannot be rejected. I conclude

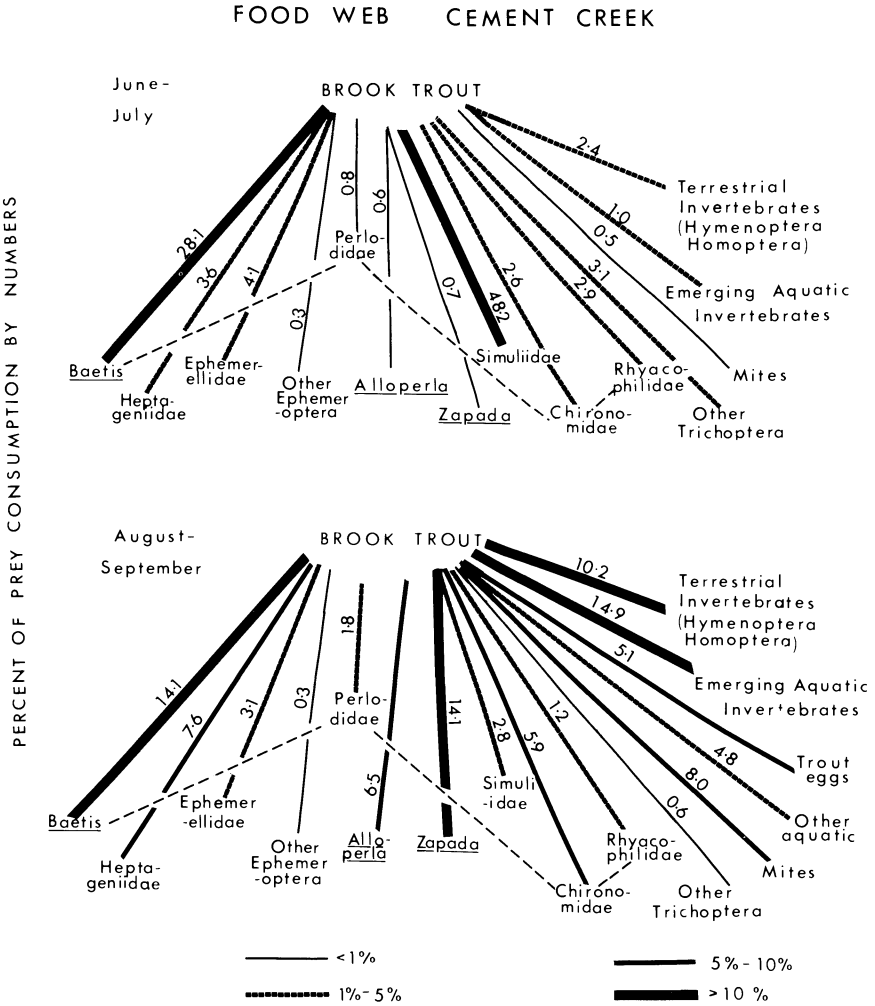

FIG. 5. Food web in Cement Creek in early and late summer, based on stomach analysis of trout and stoneflies (Plecoptera) over seasons.

that the presence or absence of trout did not play a major role in determining abundance or species composition of aquatic invertebrates in this stream. Whether or not the taxa under investigation are heavily preyed upon by trout, and whether or not the data are adequate to detect a difference, if one exists, are important concerns in accepting such a conclusion.

Some a priori insight into the likely effects of trout can be gained from knowledge of the food web. Extensive analysis of the food of brook trout provided estimates of the relative importance of different species in trout diet (Allan 1981). Two collections in June and July were similar to one another, as were three collections in August and September (Fig. 5). The diet of invertebrate macropredators is indicated by dashed lines from evidence presented in Allan (1982*a*) and Thut (1969).

The food web of spring and early summer showed very heavy reliance on *Baetis bicaudatus* and larval blackflies (Simuliidae). Together these comprised 76.3% of total numbers eaten. The food web of late summer and autumn differed in that emerging insects and terrestrial prey were more important (25.1%), the plecopteran *Zapada haysi* was 14.1% of total prey eaten, as was *B. bicaudatus*, while larval simuliids were unimportant. If one uses the frequency that a prey item appears in trout stomachs as a likely indication of the effect of the trout removal experiment, then clearly certain species should especially benefit from release from predation. These include *B. bicaudatus*, *Z. haysi*, and the Simuliidae. However, a very abundant species might withstand very intense predation, and a rare species might actually experience a greater proportional effect. The perlodid stoneflies are comparatively rare, and are of large size, which increases risk of predation (Allan 1978). They also are the principal invertebrate predators.

While *B. bicaudatus*, *Z. haysi*, the Perlodidae, and the Simuliidae each may be expected on a priori grounds to benefit from reduced trout density, none of these taxa provide any basis for rejecting H_0. Thus the conclusion that trout have no effect on abundance of invertebrates does not appear to stem from choosing inappropriate taxa for comparison.

In view of the considerable variability that characterizes stream benthos, it seems reasonable to ask how large a difference in numbers between sites must be to be detectably different. To determine this minimum detectable difference, I used the a posteriori SNK test which is based on the error mean square (EMS) of the one-way ANOVA with three treatments and 12 replicates used in Table 3. The EMS of log-transformed data was quite consistent and independent of mean density for each taxon examined. The antilogarithm of the amount by which two means of log-transformed data must differ is the "times-divide" factor (Elliott 1977) by which one arithmetic mean must exceed another. For *B. bicaudatus*, *E. longimanus*, and *Cinygmula* sp., mean densities at some pair of the three sites must differ by a factor of 1.9 on the average for rejection of H_0 at the .05 level (Fig. 6). As the inset of Fig. 6 shows, the times-divide factor in any given data set will vary around this average value. Although this minimum detectable difference could not be estimated for 1975–1976, there was no indication that it varied between sampling dates or between years for the 1977–1978 data.

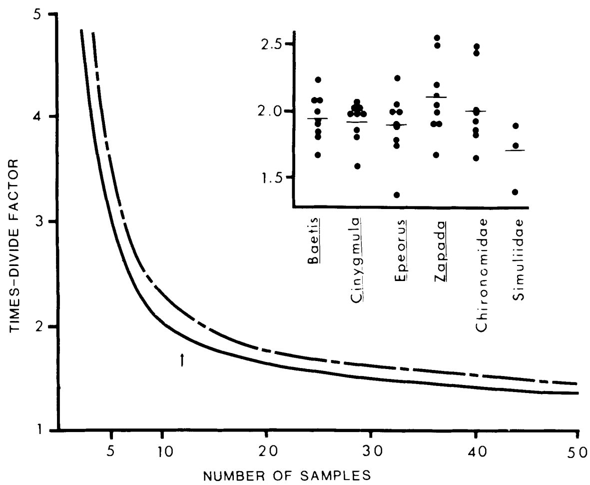

FIG. 6. The multiple that one mean must be of a second mean (times-divide factor) in order to differ significantly (P = .05), as a function of sample size. Result applies where three treatments are compared and the goal is to distinguish one mean from the other two. For 12 replicates per treatment (arrow, this study), roughly a doubling or halving is required. Solid line = *Baetis bicaudatus*, *Cinygmula* sp., and *Epeorus longimanus*; Dotted line = *Zapada haysi*. Results for Chironomidae were intermediate. Inset shows actual times-divide factor from the F tests of the Table 3 ANOVAs; horizontal line is mean of points.

Thus, for the design used, roughly a doubling or halving of abundance is required to reject the null hypothesis. As Fig. 6 shows, the inherent variability of stream benthos allows increased precision only with very substantial effort. This magnitude for a minimal detectable difference, and its dependence on sample number, may be fairly typical of field data from other systems as well (Eberhardt 1978).

The drift data did not permit an estimate of how large a difference may be detected, because of lack of replication. However, replicated samples of drift are generally more consistent than are replicate samples of benthos (Chutter 1975: Table 4). Had higher drift densities resulted from the reduction in trout predation, this increase should have been detectable by the nonparametric test used, at a level of discrimination comparable to or better than that possible with the benthic data.

Predation and community composition

It has been suggested that predation is of overriding importance in determining community organization (Connell 1975). This view appears especially well supported by studies of marine and freshwater ecosystems using manipulation experiments and comparisons of natural communities with and without the presence of certain species (e.g., Paine 1966, Dodson 1970). However, it is hardly plausible that removal of a species chosen at random will affect the structure of an entire community, and many species may be "weak interactors" in the terminology of Paine (1980). Paine defines a strong interactor as one whose absence or removal results in pronounced changes in other species. Such an effect is especially likely with a predator that plays a key role in controlling a particular prey, and where that prey is competitively superior to other species in the food web.

In a general review of food consumption by fish in nature, Mann (1978) concluded that food stocks usually are very intensively grazed. In his classic study of the Horokiwi Stream, New Zealand, Allen (1951) concluded that trout consumed 40–150 times the standing stock of invertebrates present. Further studies showed that figure to be high by a factor of two to three, but did not change the central point of very heavy utilization of available food. Warren et al. (1964) established that trout production could be increased in an experimental stream by increasing the benthic biomass through sucrose addition, and Brocksen et al. (1968) observed a decrease in benthic densities with increasing biomass of stoneflies and sculpins. Elliott (1973) concluded that trout were getting enough food in excess of maintenance requirements to permit growth on only one of three sampling dates.

Mundie (1974), in contrast, calculated that drift rates were sufficient to support 10 times the number of salmon fry present in a British Columbian stream, although he added the qualification that there is no knowledge of the amount current drift contributes to future feeding. The extent to which invertebrates are cropped by fish may have been underestimated in the past, based on recent indications (Hynes et al. 1976) that total benthic density commonly is underestimated due to the distribution of invertebrates deep in the substratum.

In summary, a controversy remains as to whether trout heavily graze their prey or subsist on the surplus; any resolution is made particularly uncertain by the potentially very substantial underestimation of food available, especially in stony streams. Nonetheless, the weight of evidence lies closer to the view that trout crop a significant, rather than a trivial, fraction of their prey.

Other fish manipulation experiments have caused few changes. Macan (1966, 1977) studied the effects of addition and removal of brown trout (*Salmo trutta*) on the fauna of a moorland pond. Some larger species which inhabit open water (tadpoles, *Notonecta*) were markedly reduced, while much of the fauna, especially that which lived in vegetation, was little affected. Gowing and Momot (1979) stocked brook trout (*Salvelinus fontinalis*) at different densities in three small lakes in Michigan, and found that crayfish (*Orconectes virilis*) recruitment and production did not vary among the lakes. Zelinka (1974, 1976) compared benthos and drift in three sections of a small stream in Czechoslovakia having natural, high (186% by numbers of natural density *Salmo trutta*, 135% *Cottus poecillopus*) and low (7% *S. trutta*, 73% *C. poecillopus*) fish densities. Total numbers of Ephemeroptera in the benthos actually increased slightly where fish were added, although fewer large nymphs occurred and drift decreased. The overall effect appeared slight.

These studies provide some corroborating evidence of lack of response of a freshwater invertebrate community to manipulation of predation by fish. The conspicuous top predator in at least several instances has proven to be a weak interactor (Macan 1966, Zelinka 1974, Thorp and Bergey 1981). Possibly this was because no competitive dominant existed or was affected, or because refuges in the substratum greatly reduce the foraging efficiency of fishes. An additional, speculative explanation is that the fauna has adapted so well over evolutionary time to predation by fish, that community make-up is little affected by changes in fish density. Streams by their anastomosing nature do not provide habitats where fish are predictably absent, in contrast to ponds. Nor is spatial patchiness likely to be sufficiently stable over time, because of the randomizing effects of drift, to allow a potential prey to complete its life cycle without encountering predators. The result may be a fauna highly adapted to fish predation and therefore less subject to its influence. This adaptation includes at least small size, cryptic coloration, and nocturnal activity. Some stream invertebrates show a greater propensity to nocturnal drift as they increase in size (Steine 1972, Allan 1978, Fjellheim 1980) and thus suffer greater risk of selective predation (Ringler 1979). The primary effect of fish predation may be in limiting the foraging activity of stream invertebrates, rather than their numbers, much as Stein and Magnuson (1976) demonstrated in laboratory experiments with bass and crayfish.

Acknowledgments

I am grateful to the Colorado Division of Wildlife, and especially W. Burkhardt and R. Sherman, for permission and generous assistance in conducting this study. J. Kuhar, D. Robison, R. Koons, L. Dyott, E. O'Doherty, and M. Rollence helped in field and laboratory work. R. Baumann, O. Flint Jr., and P. Carlson aided with identifications. In the course of this work I have benefitted from discussions with numerous individuals, but I especially thank C. O. Berg, J. M. Elliott, and T. T. Macan. Research supported by National Science Foundation grants DEB-75-03396 and DEB-77-11131, and the University of Maryland Biomedical Research Fund. I am grateful to the Freshwater Biological Association, Windermere Laboratory, England, for space and library facilities.

Literature Cited

Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology **56**:1040–1053.

———. 1978. Trout predation and the size composition of stream drift. Limnology and Oceanography **23**:1231–1237.

———. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences **38**:184–192.

———. 1982*a*. Feeding habits and prey consumption of three setipalpian stoneflies (Plecoptera) in a mountain stream. Ecology **63**:26–34.

———. 1982*b*, *in press*. Food consumption by trout and stoneflies in a Rocky Mountain stream, with comparison to prey standing crop. *In* T. Fontaine and S. Bartell, editors. Dynamics of lotic ecosystems. Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.

Allen, K. R. 1951. The Horokiwi Stream: a study of trout population. Fisheries Bulletin 10, New Zealand Marine Department, Wellington, New Zealand.

Bohlin, T., and B. Sundström. 1977. Influence of unequal catchability on population estimates using the Lincoln index and the removal method applied to electro-fishing. Oikos **28**:123–129.

Brocksen, R. W., G. E. Davis, and C. E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. Journal of Wildlife Management **32**:51–75.

Chapman, D. W. 1978. Production in fish populations. Pages 5–25 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

Chutter, F. M. 1975. Variation in day time drift of a Natal River. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen **19**:1728–1735.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities. Pages 387–404 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography **24**:131–137.

Eberhardt, L. L. 1978. Appraising variability in population studies. Journal of Wildlife Management **42**:207–238.

Elliott, J. M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia (Berlin) **12**:329–347.

———. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Scientific Publication Number 25, Freshwater Biological Association, Windermere Laboratory, England.

Fjellheim, A. 1980. Differences in drifting of larval stages of *Rhyacophila nubila* (Trichoptera). Holarctic Ecology **3**:99–103.

Gowing, H., and W. T. Momot. 1979. Impact of brook trout (*Salvelinus fontinalis*) predation on the crayfish *Orconectes virilis* in three Michigan lakes. Journal of the Fisheries Research Board of Canada **36**:1191–1196.

Hoar, W. S., D. J. Randall, and J. R. Brett. 1979. Bioenergetics and growth. Volume VIII. Fish physiology. Academic Press, New York, New York, USA.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. J. Wiley and Sons, New York, New York, USA.

Hynes, H. B. N., D. D. Williams, and N. E. Williams. 1976. Distribution of the benthos within the substratum of a Welsh mountain stream. Oikos **27**:307–310.

Macan, T. T. 1966. The influence of predation on the fauna of a moorland fishpond. Archiv für Hydrobiologie **61**:432–452.

———. 1977. The influence of predation on the composition of fresh-water animal communities. Biological Reviews **52**:45–70.

Mann, K. H. 1978. Estimating the food consumption of fish in nature. Pages 250–278 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

McFadden, J. T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildlife Monographs **7**:1–73.

Mundie, J. H. 1974. Optimization of the salmonid nursery stream. Journal of the Fisheries Research Board of Canada **31**:1827–1837.

Northcote, T. G., editor. 1969. Symposium on salmon and trout in streams. Institute of Fisheries, University of British Columbia, Vancouver, British Columbia, Canada.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1980. Food webs: linkage, interaction strength and community structure. Journal of Animal Ecology **49**:667–686.

Ringler, N. H. 1979. Prey selection by drift feeding brown trout (*Salmo trutta*). Journal of Fisheries Research Board of Canada **36**:392–403.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Charles Griffin, London, England.

Seber, G. A. F., and E. D. LeCren. 1967. Estimating population parameters from catches large relative to the population. Journal of Animal Ecology **36**:631–643.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco, California, USA.

Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology **57**:751–761.

Steine, I. 1972. The number and size of drifting nymphs of Ephemeroptera, Chironomidae and Simuliidae by day and night in the River Stranda, Western Norway. Norwegian Journal of Entomology **19**:127–131.

Thorpe, J. H., and E. A. Bergey. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology **62**:365–375.

Thut, R. N. 1969. Feeding habits of larvae of seven *Rhyacophila* species with notes on other life history features. Annals of the American Entomological Society **62**:894–898.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research **10**:91–164.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. Journal of Wildlife Management **28**:617–660.

Zelinka, M. 1974. Die Eintagsfliegen (Ephemeroptera) in Forellenbachen der Beskiden. III. Der Einfluss des verschiedenen Fischbestandes. Vestnik Ceskoslovenske spolecnesti Zoologicje **38**:76–80.

———. 1976. Mayflies (Ephemeroptera) in the drift of trout streams in the Beskydy Mountains. Acta entomologica bohemoslovaca **73**:94–101.