Determinants of Diet of Brook Trout (*Salvelinus fontinalis*) in a Mountain Stream

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Feeding rates, time of feeding, and prey choice of brook trout (*Salvelinus fontinalis*) were studied in Cement Creek, Colorado, in 1975–77. On each of five dates from early June to late September, I collected trout at intervals over a 24-h period, along with samples of invertebrate drift and benthos. Although substantial individual variation was observed in time of feeding and prey choice, feeding during the day appeared to predominate. The period of peak feeding shifted from 18:00–22:00 in June–July to earlier hours in August–September. The average number of prey per predator declined over the season and trout relied more heavily on terrestrial forms as aquatic taxa became more rare. The weight of food eaten per day was ~ 3–4 × the average amount observed per stomach.

The numerical abundance of prey in the diet was significantly correlated with abundance of prey in the drift. Except for a few trout which ingested large, rare prey, this was also true for prey composition by biomass. Large taxa tended to be consistently overrepresented in trout diet and small taxa underrepresented. Several prey species shifted from underrepresentation in trout diets to overrepresentation as they grew in size. Abundance and size of prey, along with individual specialization by trout presumably as a result of experience, are suggested as primary determinants of trout diet.

Key words: brook trout, *Salvelinus fontinalis*; stream, predator-prey, aquatic insects

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L'article qui suit décrit une étude menée dans le ruisseau Cement, au Colorado, en 1975–77, sur les taux et moments de l'alimentation, et sur le choix des proies de l'omble de fontaine (*Salvelinus fontinalis*). À chacune de cinq dates du début de juin à la fin de juillet, j'ai capturé des ombles de fontaine à divers intervalles sur une période de 24 h, en même temps que des échantillons de dérive d'invertébrés et de benthos. Bien qu'il y ait variation individuelle substantielle du moment de l'alimentation et du choix des proies, les ombles semblent se nourrir surtout le jour. La période d'alimentation de pointe passe de 18:00–22:00 en juin–juillet à des heures plus hâtives en août–septembre. Le nombre moyen de proies par prédateur diminue au cours de la saison, et, à mesure que les taxa aquatiques se font plus rares, l'omble de fontaine dépend de plus en plus de formes terrestres. Le poids de nourriture consommée quotidiennement est approximativement de 3 à 4 fois la quantité moyenne observée par estomac.

L'abondance numérique des proies dans le régime alimentaire montre une corrélation significative avec l'abondance des proies dans la dérive. Ceci est également vrai de la composition des proies par biomasse, sauf dans le cas de quelques ombles qui avaient avalé des grandes proies rares. Les taxa abondants ont tendance à être uniformément surreprésentés, et les taxa moins abondants, à être sous-représentés dans le régime des ombles de fontaine. Plusieurs espèces proies, à mesure qu'elles croissent, passent de l'état de sous-représentation à celui de surreprésentation. Ces observations laissent penser que l'abondance et la taille des proies, de même qu'une spécialisation individuelle des ombles, probablement due à l'expérience, seraient les principaux déterminants du régime alimentaire de l'omble de fontaine.

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SELECTION of prey by a predator clearly relates to maximizing fitness for the individual through choice of an appropriate diet (Pyke et al. 1977), and potentially may determine structure of the prey community through selective removal of certain species (Connell 1975). Salmonids are important predators in cold-water streams, sometimes the only vertebrate predator, and have been the subject of numerous feeding studies. Despite this, relatively little is known about the factors governing prey choice by salmonids under natural conditions, or the effect of their predatory activity on stream-dwelling invertebrates. The large literature on feeding of salmonids often characterizes feeding as opportunistic. Prey include a diversity of forms; large items are preferred, and new prey appear in the diet as they become available (Allen 1941; Elliott 1967; Metz 1974). While this general pattern appears accurate, further study is needed to relate precisely the observed composition of the diet to prey abundance, prey size, and other factors. In addition, most previous studies have been limited to a single time of year, and so have not resolved seasonal trends adequately nor taken advantage of seasonal comparisons to elucidate factors governing prey choice.

The primary goals of the present study were to describe food consumption by brook trout (*Salvelinus fontinalis*) under natural conditions, to determine the daily and seasonal pattern of feeding activity, and to investigate factors affecting choice of prey.

Description of Site

Cement Creek, Gunnison County, Colorado, is a high-elevation, stony-bottom stream which originates in snow melt at 3600 m and joins the East River at 2600 m. Allan (1975) described the stream in detail. Three species of salmonids, cutthroat trout (*Salmo clarki*), brown trout (*S. trutta*), and brook trout maintain breeding populations; rainbow trout (*Salmo gairdneri*) are stocked for anglers. Brown trout are abundant below 2900 m and brook trout above that elevation, while cutthroat trout are found primarily above 3200 m.

The study site was located in a meadow at 3100 m where brook trout strongly predominated. In this region, the main stream-bank vegetation was *Salix* spp. Stream width was 3.5–4 m, depth was 10–30 cm, and current typically ranged from 20 to 60 $cm \cdot s^{-1}$ except during peak runoff when values were in excess of 1 $m \cdot s^{-1}$.

Methods

Drift, benthos, and trout samples were collected on five occasions over a 22-mo period between September 30 1975 and June 6 1977. Trout were collected by electroshocking at roughly 3-h intervals over 24 h. At each 3-h interval an attempt was made to collect six trout, two each of small (<10 cm), medium (10–15 cm), and large (>15 cm) size. All trout were measured for length and weight, and stomachs were preserved in 10% formalin for later analysis. Sampling dates, number, and size range of trout collected are given in Table 1. Sizes were relatively uniform, except that trout collected on June 6 1977 were smaller on the average.

Drift samples were collected at eight 3-h intervals over 24 h using a single net of 0.3-mm mesh with an opening of 0.1 m^2. Drift sampling was not always over the same 24-h period as the trout collections, but was close enough (≤10 d) for valid comparison. Depending upon sampling date, between 6.0 and 10.7% of flow passed through the net. On September 30 1975 the net was submerged continuously for 24 h, and contents were removed at 3-h intervals and later analyzed in their entirety. However, on other dates nets were submerged for only 1 h (at eight 3-h intervals over 24 h), and contents were subsampled, usually 25 or 50% depending upon conditions. Counting of replicate samples and use of replicate nets (Allan unpublished data) indicated that this procedure adequately described drift.

Benthos was sampled once at midday on each sampling date by taking 12 Surber samples using a net of 0.3-mm mesh and 0.093-m^2 area. Each total sample comprised 1.12 m^2. The same sampling stations located in stony-bottom riffles were used throughout the study; the drift station was 20 m upstream from the benthos station.

Taxa were identified to the level of species (occasionally genus) for aquatic insects except Diptera, which were identified to family. Prey recovered from trout stomachs were measured as well as counted. Then the dry weight of stomach contents was estimated using regressions of body weight on head width of aquatic insects (Allan unpublished data), and by drying and weighing miscellaneous items for which no regression equation was available. A 25% weight loss due to preservation was assumed for these latter items. Most prey items were aquatic insects for which dry weight was reliably estimated. Thus the estimates of biomass ingested also should be

TABLE 1. Number and size of brook trout collected on five occasions. For all trout, the relationship between weight and length is described by $W = 0.012\,L^{2.98}$.

Sampling date		Length (cm)			Weight (g)		
	N	$\bar{X}$	Min	Max	$\bar{X}$	Min	Max
Sept. 30–Oct. 1 1975	46	16.2	9.6	29.4	64.4	10.7	308.4
July 7–8 1976	45	16.5	11.0	26.5	60.9	13.5	202.4
Aug. 9–10 1976	45	17.2	11.8	22.9	66.1	21.4	157.1
Sept. 8–9 1976	46	17.0	8.9	26.5	66.0	8.7	197.3
June 6–7 1977	44	15.9	7.0	22.5	46.6	4.0	120.0

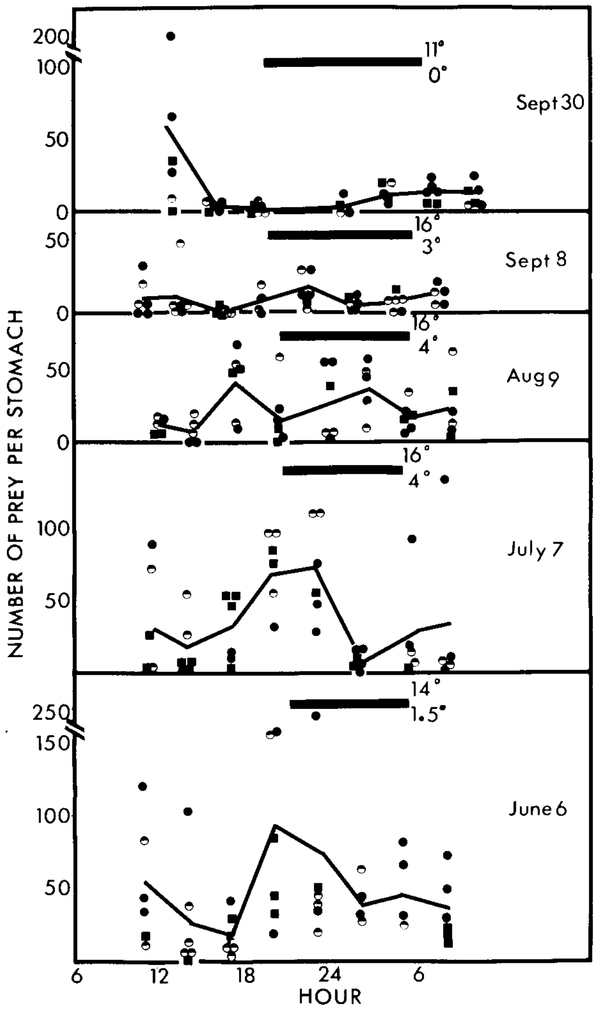

FIG. 1. Observed number of prey per stomach from individual trout collected at 3-h intervals over 24 h. ● = trout >50 g, ○ = 25–50 g, ■ = <25 g. Solid line connects means, solid bar denotes darkness. Maximum and minimum temperature as noted.

quite reliable. However, head capsules often are digested more slowly than the rest of the prey. Thus this method may estimate something more than the actual dry weight of food remaining, and less than the total meal eaten unless that meal was very recent so all head capsules were intact.

Results

Feeding Rates

The number of recognizable prey items per stomach varied from 0 to a maximum of 250 in trout >15 cm, 190 in trout 10–15 cm, and 85 in trout <10 cm. Substantial variation clearly exists in the observed number of prey per stomach among sampling intervals and dates (Fig. 1). With some exceptions, one can find individual trout containing large numbers of prey and others containing few or none at almost any time over the diel cycle.

The strongest temporal pattern is apparent in the collections of June 6, July 7, and September 30. In June and July there was a definite peak in number of prey observed at 20:00–24:00 (solid line in Fig. 1), with a possible second peak in late morning. The major peak appears to precede nightfall or perhaps coincide with it. However, feeding activity already had increased substantially by 20:00 when light levels were still in the range of 10^3 lx. On August 9 the pattern was more variable, but at least suggests a peak in feeding activity in late afternoon and around 24:00. On September 8, feeding rates were low with no apparent periodicity. On September 30, feeding rates again were low, but showed a midday peak.

The temporal pattern of feeding activity appeared to change seasonally. In June and July feeding activity was greatest in early evening. By August this periodicity was less pronounced, and late afternoon feeding was apparent. In early September, feeding activity was aperiodic, and in late September it was greatest at midday. Thus a gradual shift from feeding near dusk to feeding during the day seems to have occurred.

The estimates of dry weight of stomach contents for each individual trout are not presented here, as they showed a pattern similar to that in Fig. 1. In addition, number of prey ingested should better represent bouts of feeding activity. The main discrepancies between the estimates of numbers ingested vs. weight ingested were associated with the infrequent availability of very large prey. The early morning of July 8 was the only occasion on which earthworms were ingested by a number of trout, perhaps because this was the only sampling period during which it rained. The early morning of October 1 was the only occasion on which a number of trout ingested trout eggs, as this was a period of spawning activity. These few large items resulted in enormous contributions to biomass of diet.

In addition to a seasonal change in time of feeding, there was a clear seasonal decline in number of prey per stomach (Fig. 2). This occurred in each size-class of trout. The only exception is the >50-g trout on September 30, and is due to some individuals ingesting substantial numbers of trout eggs.

The seasonal pattern of feeding activity was analyzed in terms of biomass to estimate total food consumption per 24 hours. Following Elliott and Persson (1978), I estimated daily food consumption as:

$$\text{daily ration } (C_{24}) = 24 \cdot \bar{S} \cdot R$$

where $\bar{S}$ is the mean amount of food in the stomach over the 24-h period, and R is the exponential rate of gastric evacuation for brown trout, determined from Elliott (1972), for the average temperature over the 24-h period.

The estimate of daily ration (C_{24}) generally exceeded the average observed weight of stomach contents ($\bar{S}$) by a factor of 3–4 (Table 2). The maximum observed weight of stomach contents was similar to the estimate of daily ration. This is reasonable, as time to 90% gastric evacuation is close to 1 d at the water temperatures encountered, and at least some individuals should be collected shortly after ingesting a full meal. Daily ration increased with trout size, as expected, and decreased seasonally in the smaller trout. For the largest trout there was no decline in biomass ingested over season, in contrast to results for numbers eaten (Fig. 2). The main reason

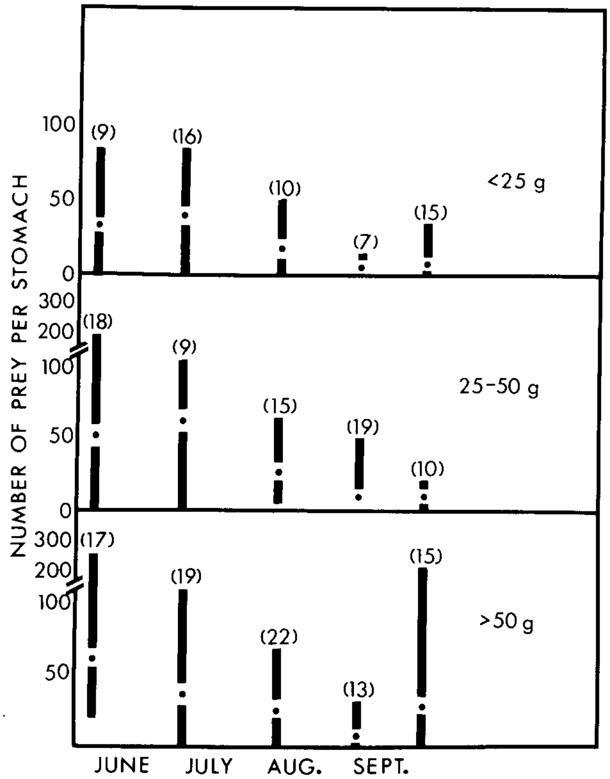

FIG. 2. Prey consumption by trout. Mean and range of number of recognizable prey per stomach of trout collected at 3-h intervals over 24 h. Sample size in parentheses. Top panel = trout <25 g; middle panel = trout 25–50 g; bottom panel = trout >50 g.

TABLE 2. Estimated amounts of food in stomach (S) and daily ration (C_{24}) in mg dry weight of brook trout collected on various dates.

	June 6–7	July 7–8	Aug. 9–10	Sept. 8–9	Sept. 30–Oct. 1
<25 g trout					
S mean	22.8	17.8	13.4	4.6	5.0
Standard error	7.5	4.1	4.2	2.2	1.3
N	8	16	8	5	14
Maximum	60.9	45.8	38.8	10.1	13.7
C_{24}	63.5	69.2	52.1	17.0	11.2
25–50 g trout					
S mean	43.8	152.5	27.1	16.7	27.2
Standard error	14.0	70.1	5.1	11.1	14.7
N	18	11	15	16	11
Maximum	224.9	790.0	76.8	180.0	149.3
C_{24}	132.5	592.8	105.4	61.9	60.8
>50 g trout					
S mean	60.9	396.3	26.3	13.3	76.0
Standard error	11.6	202.2	5.7	5.8	24.3
N	17	18	21	25	15
Maximum	186.8	2954.7	78.0	74.1	282.5
C_{24}	184.2	1540.8	102.3	49.0	169.7

appears to be the above-mentioned ingestion of large items by some trout on July 8 and October 1. It is difficult to know if these infrequent events are representative or obscure the usual trend. If the data of Table 2 are recalculated to omit these few large items, the pattern closely resembles that in Fig. 2.

COMPOSITION OF PREY

Effect of prey abundance — Drift samples provide the main estimate of prey abundance used here. It was chosen because drift may vary over the diel cycle, perhaps affecting prey availability and also because total drift usually correlates with total benthic abundance.[1] The diel periodicity of drift on each sampling date is shown in Fig. 3. A nocturnal peak is evident on all dates except September 11. This peak typically occurs immediately after dark (but see September 30) and may reach $\simeq 10 \times$ the daytime average.

The diel pattern of feeding (Fig. 1) shows little or no resemblance to the diel drift rate (Fig. 3). If trout fed when prey were most numerous, the curve of feeding rate should mirror the curve of drift rate, but be extended to the right because of time required for gastric evacuation. However, when Fig. 1 and 3 for June and July collections are compared, it is clear that the peak in feeding activity precedes the peak in drift activity, indicating predusk feeding. The August data are consistent with the interpretation that trout exploited the small midday increase in drift (composed 15–30% of emerging blackflies), and about 1/3 by numbers of trout stomach contents was emerging blackflies and other insects. Little can be said about periodicity from the September 8 data, as neither drift nor trout feeding showed a discernible pattern. On September 30 feeding peaked at midday, while drift peaked at night.

While the diel pattern of feeding and drift do not correlate, the seasonal decline in number of prey ingested (Fig. 1) parallels the seasonal decline in total drift rates (Fig. 3) and also the seasonal decline in benthic densities (see footnote 1). I calculated an average number of prey per trout stomach for each date, pooling different size-classes of trout because the sampling program was designed to take a standard array of sizes (cf. Table 1) for correlation with drift rate (no./h) based on the entire 24-h collection. A positive relationship was found between number of prey consumed and drift rate ($r^2 = 0.75$, $P < 0.05$). Both are high early in the year and decline throughout the season. This relationship suggests a dependence of feeding rate on total prey abundance.

Prey abundance and species composition of diet — For each sample date, I compared the frequency of a particular prey species in the diet to its frequency in the environment. For the former I used total prey from all trout stomachs collected on a given date, pooling trout size and sampling time. Size of prey consumed by the three size-classes of trout did not differ when only the common aquatic insects were considered. Occasionally very large tipulids, adult beetles, annelids, and other terrestrial items were eaten, and then only by the largest trout.

[1]The complete set of tabular data is available at a nominal charge from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada, K1A 0S2.

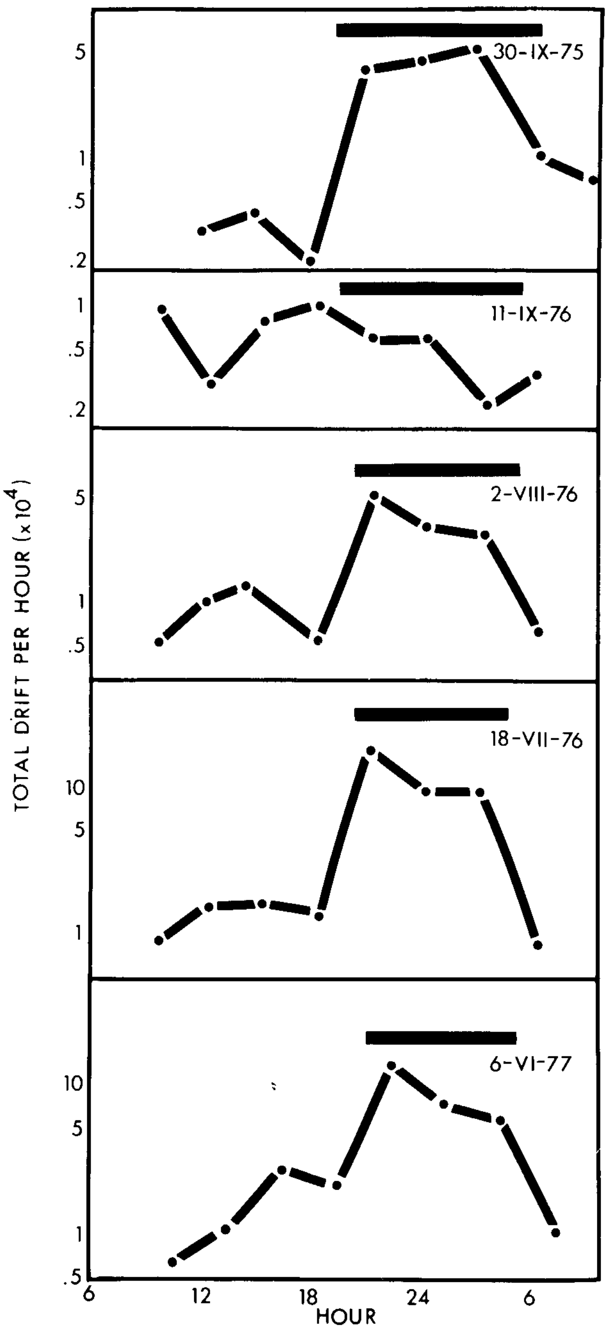

FIG. 3. Total numbers drifting per hour throughout season for comparison with trout collections. Solid bar denotes darkness.

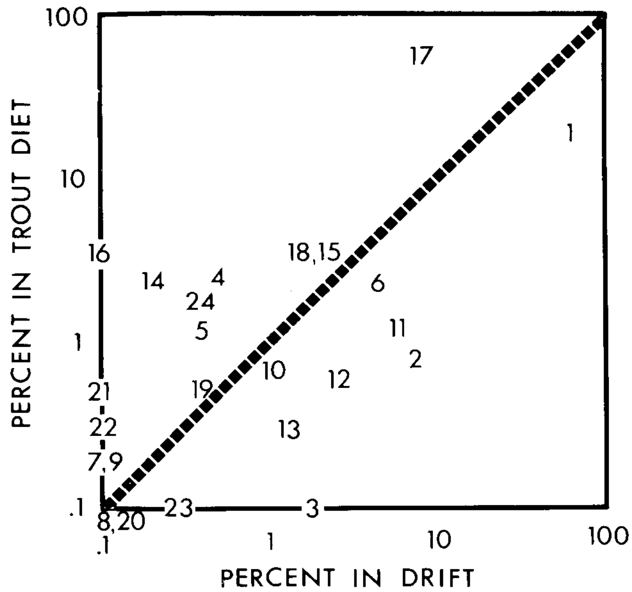

FIG. 4. Relationship between percent composition of prey items consumed by trout and percent composition of drift. Data of June 6–7 1977. Total recognizable prey from the stomachs of 44 trout = 2135. Spearman's r_s = 0.46, $P < 0.05$. 1 = *Baetis bicaudatus*, 2 = *Cinygmula* sp., 3 = *Epeorus longimanus*, 4 = *Rhithrogena hageni* and *R. robusta*, 5 = *Ephemerella infrequens*, 6 = *E. coloradensis*, 7 = *E. doddsi*, 8 = *Paraleptophlebia vaciva*, 9 = *Ameletus velox*, 10 = *Alloperla* spp., 11 = *Zapada haysi*, 12 = Perlodidae, 13 = other Plecoptera, 14 = *Brachycentrus* sp., 15 = *Rhyacophila* spp., 16 = other Trichoptera, 17 = Simuliidae, 18 = Chironomidae, 19 = other Diptera, 20 = *Heterliminus* sp., 21 = other Coleoptera, 22 = Acari, 23 = emerging aquatic insects, 24 = terrestrial invertebrates, 25 = trout eggs.

The numerical abundance of prey in the environment was estimated from total 24-h drift, which in effect emphasizes nighttime proportions. Separation of results into day and night drift did not change the conclusions, so totals were judged adequate.

To determine if trout were feeding on particular species in accord with their relative abundance, I plotted log percent representation of each prey item in trout stomachs against log percent representation of the same item in the drift (Fig. 4–8). If drift is a good indicator of prey abundance and trout take prey roughly in proportion to their relative abundance, the points should fall on the 45° line.

Although there is considerable scatter which requires further consideration, the points tend to be distributed along the 45° axis. Many items are about the same order of magnitude of abundance in the diet of trout and in the drift. On each date, the Spearman rank correlation coefficient is significant (see figure captions). Common items in drift are common in the diet of trout, and rare items are correspondingly rare.

Typically, mayflies (*Baetis*, *Cinygmula*, *Rhithrogena*, Ephemerellidae) and dipterans (especially Simuliidae) predominated. Simuliids and *Baetis* were very frequent prey in June–July (Fig. 4 and 5), and surface drift (terrestrial and emerging insects) were consumed heavily in August–September (Fig. 6–8).

Effects of prey size — Additional clues regarding the factors affecting prey choice can be discerned from inspection of outlier species in Fig. 4–8 and consideration of the role of size in explaining this variation. Some taxa are consistently overrepresented, some underrepresented, and others change their representation seasonally.

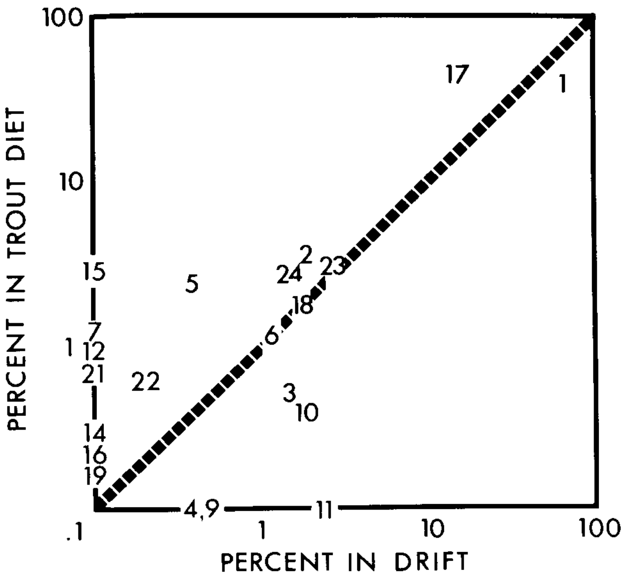

FIG. 5. The relationship between percent composition of prey items consumed by trout and percent composition of drift. Data of July 7–8 1976. Total recognizable prey from the stomachs of 45 trout = 1643. Spearman's $r_s = 0.51$, $P < 0.05$.

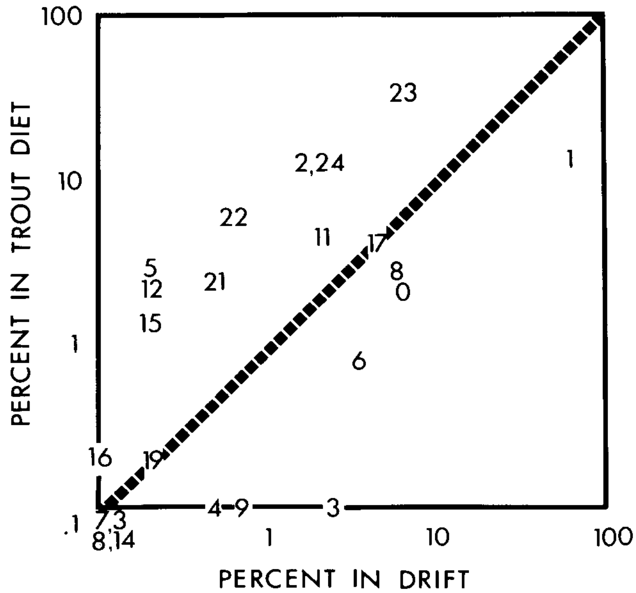

FIG. 6. The relationship between percent composition of prey items consumed by trout and percent composition of drift. Data of August 9–10 1976. Total number of recognizable prey from the stomachs of 45 trout = 1045. Spearman's $r_s = 0.67$, $P < 0.01$.

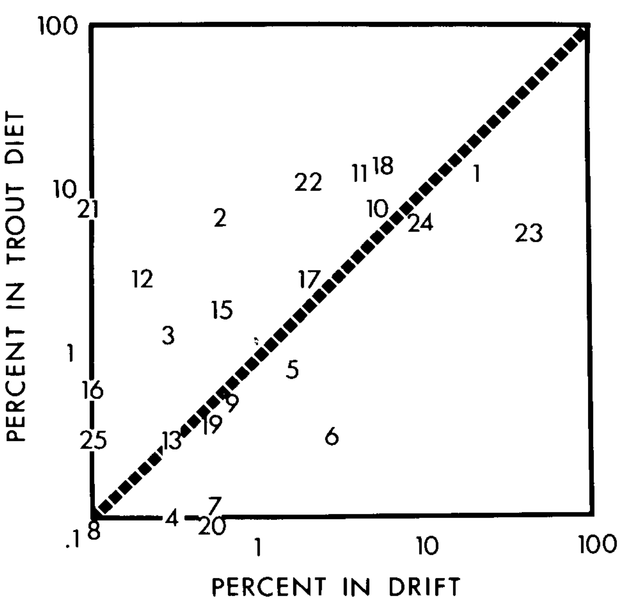

FIG. 7. The relationship between percent composition of prey items consumed by trout and percent composition of drift. Data of September 8–9 1976. Total recognizable prey from the stomachs of 46 trout = 390. Spearman's $r_s = 0.68$, $P < 0.01$.

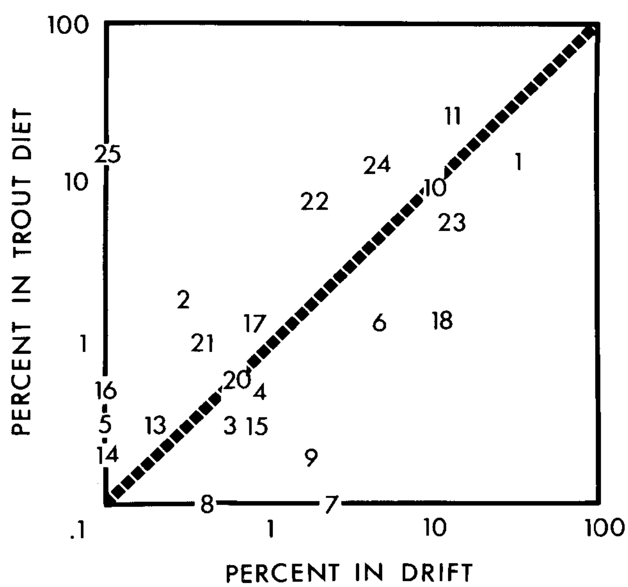

FIG. 8. The relationship between percent composition of prey items consumed by trout and percent composition of drift. Data of September 30–October 1 1975. Total recognizable prey from the stomachs of 46 trout = 624. Spearman's $r_s = 0.48$, $P < 0.05$.

Perhaps surprisingly, because it is invariably a major constituent of the diet, *Baetis bicaudatus* is consistently underrepresented. In addition, *Epeorus longimanus*, *Ephemerella coloradensis*, *Ameletus velox*, and emerging aquatic insects (with the striking exception of Fig. 6) all show varying degrees of underrepresentation. At least in the last instance, small size seems implicated. The emerging adults were predominantly small Chironomidae on most dates; when larger

Simuliidae predominated in August they were overrepresented in the diet.

The taxa which tend to be overrepresented include large items (trout eggs, "other" Coleoptera and Trichoptera, *Rhyacophila* spp., *Ephemerella infrequens*, Perlodidae), and/or items conspicuous on the surface (terrestrial invertebrates). Mites, and to a lesser extent *Brachycentrus*, may be overrepresented in trout diets because of individual conspicuousness due to contrast. Mites are often red or orange and are unusual in their daytime drift activity. *Brachycentrus* cases often are on stone surfaces in shallow riffles and are easily seen by the human observer.

A number of taxa are overrepresented on some sampling dates and not on others. The Chironomidae seem to fit this pattern, although for the most part they do not fall far from the 45° line, and I have no explanation for the observed variation between dates. Representation of certain other taxa (*Cinygmula* sp., *Rhithrogena* spp., *Ephemerella doddsi*, *Alloperla* spp., and *Zapada haysi*) changes according to the stage of their life cycle, that is, according to size. *Rhithrogena* completes its life cycle earliest, by the beginning of July, and is one of the largest mayflies (10–15 mg dry weight for a mature nymph). While always rare, it is overrepresented in the diet of trout collected June 6, and strongly underrepresented thereafter. The other taxa follow a similar pattern but differ in timing because of their particular life cycles.

The ratio percent in diet/percent in drift is positively correlated with body size (mg dry wt) for these five species (Fig. 9: $P < 0.001$ by Olmstead and Tukey's corner test of association, Sokal and Rohlf 1969). Overall, prey less than 0.1 mg were avoided, those larger than 1.0 mg were positively selected, and electivity increased proportional to dry weight. Neither *Z. haysi* nor *Alloperla* spp. showed a clear relationship between electivity and size within the taxon. At least in the case of *Alloperla* spp., this is explainable in part by lack of adequate taxonomic resolution. Several species with probably different growth patterns were lumped together, and in addition, the size composition of *Alloperla* spp. in the drift varied between day and night (cf. Allan 1978), making difficult the quantification of average size of *Alloperla* occurring in the drift.

Thus it appears that size is a useful second factor in predicting the representation of a taxon in the diet of trout. At least part of the scatter around the 1:1 line is explainable by body size, which in turn may be related to stage of life cycle.

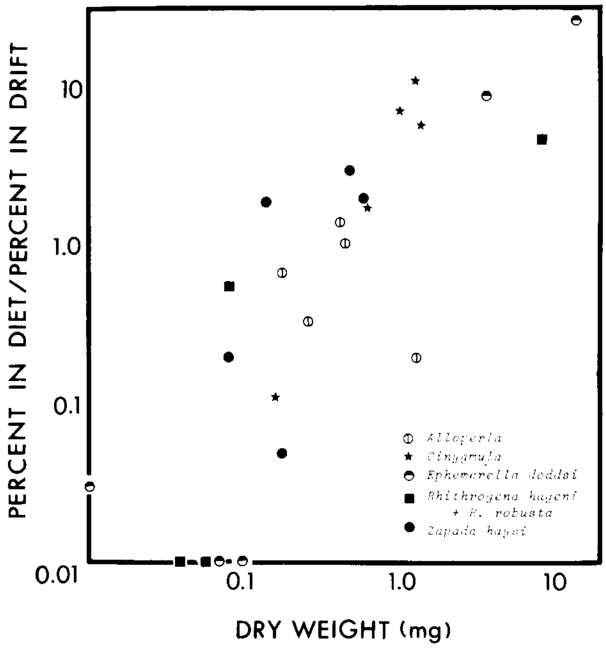

FIG. 9. The ratio percent in diet : percent in drift (AF of Allen 1941, E′ of Ivlev 1961) increases with increasing body size for five taxa which changed their representation in trout diet over the season.

Discussion

Timing and Rate of Feeding

Brook trout in Cement Creek fed more during the day than at night, although some night feeding must have occurred to explain the ingestion of annelids and trout eggs. The interpretation of feeding activity from diel changes in stomach contents is difficult because of the length of time required for gastric evacuation (Eggers 1977). Other authors have reported feeding activity to be greatest at midday and especially in the evening (Elliott 1967, 1970, 1973; Metz 1974), and to be continuous over 24 h (Allen 1951; Jenkins et al. 1970; Bisson 1978). Perhaps the strongest conclusions from this study are that individual trout vary considerably when they feed (Fig. 1), and there is no apparent synchrony of feeding with the nighttime peak in drift.

The average number of prey per stomach (Fig. 2) is similar to values reported by Elliott (1967) of 12.1 for 0^+, 15.2 for 1^+, and 27.4 for 2^+ age trout. The seasonal decline is not reported elsewhere, but is consistent with frequent reports of a change in diet from aquatic to terrestrial items as the former become rarer during the summer (Hunt 1975).

The five dates of observation on the food of trout actually span 22 mo. The assumption that these can be treated as representing a seasonal series seems valid on the basis of the data. The June 1977 and July 1976 results resemble one another more closely than either resembles results from other dates.

The actual amount of food consumed in mg dry weight per day could be estimated only speculatively because of lack of laboratory studies on brook trout digestion and the diel temperature fluctuation in Cement Creek. Estimates of daily ration (C_{24}) typically were 30–40% of the maximum daily ration which would be ingested by a brown trout of the same size (Elliott 1975). A few larger trout ingested maximum meals that were at least twice the weight of the maximum daily ration of a brown trout of comparable size. However, if figures are computed excluding the earthworms and trout eggs, maximum ingestion again is 30 to 40% of the maximum that a brown trout will ingest in captivity. Since only 5% of the 226 trout examined ingested these large items, the lower figure probably represents the usual condition. Thus, despite the abundance of aquatic invertebrates as evidenced by drift collections, trout were feeding well below maximum rations and much of the food must not be truly available to them. Additionally, this analysis, while speculative, points to the importance of capitalizing on occasional, large items.

Elliott (1973) calculated that the level of feeding provided energy in excess of resting metabolic needs on only one of three collection dates. Both Jenkins et al. (1970) and Tippets and Moyle (1978) concluded that food was insufficient for trout in the streams studied. The present study indicates that food may be in short supply to trout despite an evident abundance of invertebrates.

Determinants of Prey Composition

A number of authors have concluded that salmonids feed selectively, usually based on prey size (e.g. Allen 1941; Metz 1974; Allan 1978), but perhaps more generally on any characteristic which enhances surface visibility (such as surface drift in hydroptilid larva, suggested by Mundie 1969). The importance of prey size and predator experience have been demonstrated in the laboratory by Ware (1971, 1972) and Ringler (1979). However, it is uncertain how readily results from the laboratory may be applied to natural conditions, as adequate light, easily visible prey and experience with standard feeding conditions typify the former but not the latter (Ringler 1979).

The present study indicates that if one wishes to predict the composition by numbers of prey in trout diet purely from an examination of prey available, one would be more accurate ranking prey by abundance than by size (Fig. 4–8). Most prey ingested were of intermediate size (*Baetis*, Simuliidae, emerging and terrestrial forms), and for ≃ 95% of the 226 trout examined, most of the biomass ingested came from such prey.

Additionally, as Fig. 9 shows, some of the variation from the 45° line of Fig. 4–8 is explainable by prey size. As a result, vulnerability to predator varies with stage of life cycle. In other streams where large, stonecase caddis flies are more common than in Cement Creek, selection of these items by larger trout is especially strong (Elliott 1967, Tippets and Moyle 1978).

A third factor described well by Bryan and Larkin (1972) is individual variation in feeding habits. In the present study, water mites were a significant component of trout diet despite their small size. However, two of the 226 trout examined accounted for one-third of the mites eaten, and nine trout accounted for nearly two-thirds. Most trout ate none. As the ability to perceive particular prey at distance increases with experience and does not appear to transfer to other prey (Ware 1971), it is not surprising that a good deal of individual specialization is observed.

Inclusion of some prey in the diet appears inexplicable. The smallest *Baetis* nymph or chironomid larvae which appears in the drift runs a small but real risk of being eaten, even by a trout whose meal clearly is dominated by much larger items. Offered a choice of prey size under defined laboratory conditions, brown trout preferred larger items but continued to ingest small prey at a low rate (Ringler 1979).

Three factors discussed above, abundance and size of prey, and individual specialization by the predator, explain much of the diversity of prey observed in the diet of trout. Differential use of habitat, perhaps mediated through intraspecific interactions, is an additional factor not considered here. The selective behavior of trout raises the possibility that the activity of this predator may affect the makeup of the prey community. An effect on diel activity of prey as a function of prey size has been described by Allan (1978), but the effect on abundance or species composition is unknown.

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