——— 1922a - On the septal and pharyngeal glands of the Microdrili (Oligochaeta). *Trans. roy. Soc. Edinb.* 53:241—264, pl. 53.
——— 1922b - Contributions to the morphology, classfication and Zoogeography of the Indian Oligochaeta IV. On the diffuse production of sexual cells in a species of *Chaetogaster* (fam. Naididae). *Proc. zool. Soc. London* 1922. 1—2:109—188, pl. 1—6.
——— 1923 - Oligochaeta. The Fauna of British India. London. xxiv+518 p, 262 fig.
——— 1924 - On some Indian Oligochaeta, with a description of two new genera of Ocnirodrilinae. *Rec. Indian Mus.* 26:317—365, 2 fig, pl. 21—23.
——— 1925a - Oligochaeta from various regions. *Proc. zool. Soc. London* 1925, 3—4:879—907, pl. 1—3.
——— 1925b - On some Oligochaeta mainly from Assam, South India and the Andaman Islands. *Rec. Indian Mus. Calcutta* 23:43—74, pl. 3—4.
——— 1929 - The Oligochaeta of the Indawgyi Lake (Upper Burma). *Rec. indian Mus.* 31:225—240.
——— 1930 - The Oligochaeta. Oxford. xvi+978 p, 242 fig.
——— 1931a - Oligochaeta from Basil and Paraguay. *J. Linn. Soc. London* 37:294—326, pl. 17—18.
——— 1931b - Oligochaeta from Burma, Kenya, and other parts of the world. *Proc. zool. Soc. London* 1931, 1—2:33—92.
——— 1931c - Oligochaeta from the Malay Peninsula *J.F.M.S. Mus. Kuala Lumpur* 16:261—285.
UDE, H. - 1929 - Oligochaeta F. Dahl: Die Tierwelt Deutschlands 15:1—132, 165 fig. Jena.
WEERKONN, A. C. J. & E. L. SAMARASINGHE. - 1958 - Mesofauna of soil of a paddy field in Ceylon. Preliminary survey. *Ceylon J. Sci. (Biol. Sci.)* 1, 2:155—170.

Benthic Animals and Foods Eaten by Brook Trout in Archuleta Creek, Colorado

by

EDWARD B. REED[1] & GEORGE BEAR[2]

(with 1 fig.)

INTRODUCTION

Brook trout (*Salvelinus fontinalis*) was introduced into Colorado many years ago. The species has thrived in the small mountain streams of the state, often to the virtual exclusion of other trouts. Frequently brook trout in small mountain streams develop rather dense populations of smallsized individuals. The question may be raised, how are these populations supported?

This study relates the stomach contents of brook trout to the benthos of a small mountain stream in south central Colorado.

A mile-long section of Archuleta Creek, a tributary of Cochetopa Creek, rising in the mountains about 30 miles southeast of Gunnison, Saguache County, Colorado, was chosen for the study area. Archuleta Creek is a small meandering stream with pronounced cut banks and sand bars. In the upper reaches of the study area, the banks are .5 to 1m high. At the lower end of the area, the banks rise as much as 2.15m above the stream level. Toward the lower end of the study area many springs enter the creek and the increased volume has allowed the stream to cut deeply into the sandy soil.

The creek has many pools separated by shallow riffles. The pools have soft clay bottoms, whereas the substrate of the riffles is of small stones and pea-sized gravel.

Archuleta Creek flows through a mountain valley characterized by

[1] Assistant Professor, Zoology Department, Colorado State University, Fort Collins, Colorado.
[2] Game Biologist, Colorado Game, Fish, and Parks Department, Fort Collins, Colorado

Received November 5th, 1964.

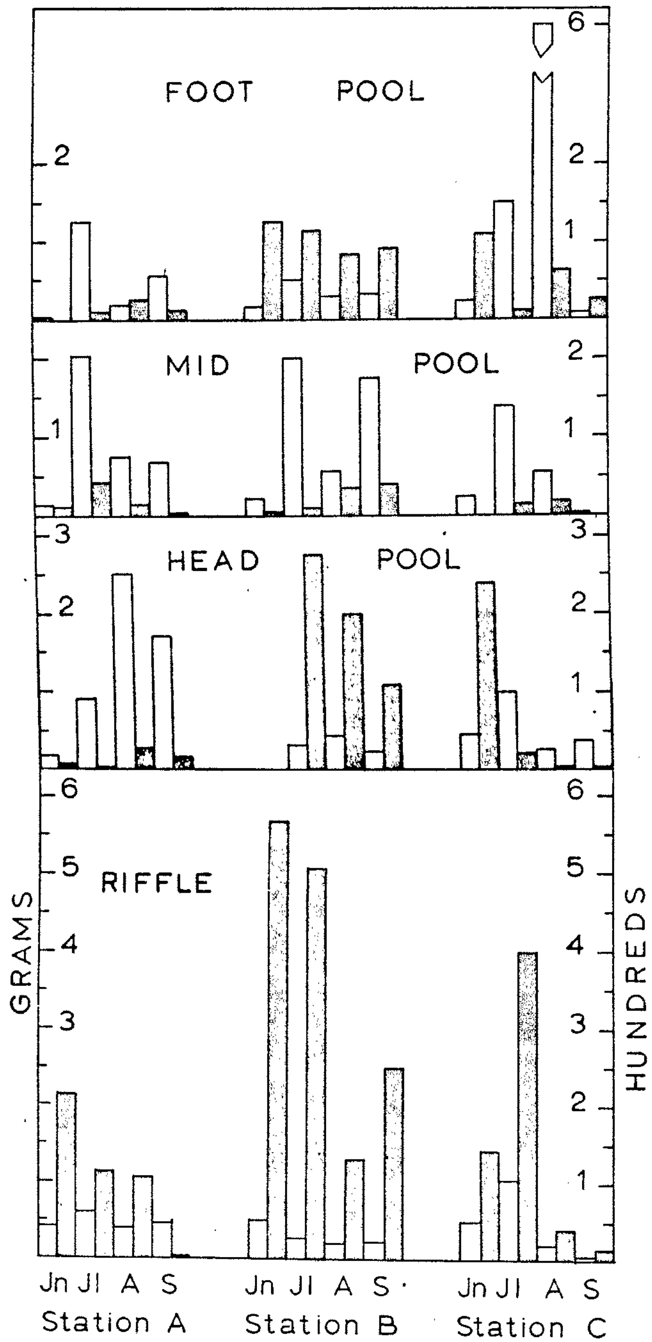

Figure 1. The standing crop of bottom fauna at three stations on four sampling dates in Archuleta Creek, Colorado. Open bars are numbers of organisms and stippled bars are wet weights of organisms per square foot.

Big Sage (*Artemisia tridentata*) and various bunch grasses, at an elevation of 2900m. Immediately adjacent to the stream are meadows of grasses and sedges.

Water temperatures never differed by more than 1.5 degrees between stations A and B on any sampling date although temperature fluctuated between 18.0 and 13.6°C for the entire period. However, water temperatures at station C were rarely less than 3 and occasionally as much as 5 degrees colder than the other two stations.

Methods

Sampling was done at monthly intervals from mid-June to mid-September, 1961. Usually 100 brook trout were taken by fly rod on each of four sampling dates. The fish were sexed, weighed and measured. Stomachs were removed and stored in 5% formalin for later analyses. Total volume of contents of each stomach was measured by water displacement in a graduated cylinder; food items were then sorted and identified. The percentage of total volume of each stomach was estimated for each food category.

A Surber sampler was used to sample the benthic fauna at the same time that fish stomachs were collected. Three stations each consisting of a pool and adjoining riffle were selected within the study area. On each sampling date four samples were taken from each station: at the head or upstream end of the pool, mid-pool area, foot or downstream end of the pool and on the riffle. In all, 48,09 sq. m bottom samples were obtained. Organisms were sorted and preserved in 5% formalin for later identification. The numbers and total weights were recorded for each type of bottom organism.

Results

Seasonal trends in the standing crops of benthic animals are evident from Figure 1. Riffles were characterized by few individuals of high weight. The mid-pool habitat was poorest both in numbers and in weight of organisms. The general trend of low numbers in June rising to peaks in July or August and then declining in September would be expected as insects developed and emerged, leaving the stream.

When samples from the sub-habitats within each station are combined, it is clear that the stations varied in their standing crops (Table I). Stations A and C were similar in numbers of organisms, but those at C weighed about twice as much as those at A. Fewest organisms were collected at B, but here the weight was much greater than at either of the other stations. About 60% of the weight of all organisms collected at B was due to riffle-dwelling animals; however, the weight of pool-dwelling organisms was also greater at B than at A or C.

TABLE I

Total numbers and weights of benthic organisms collected in four habitats at three stations on Archuleta Creek.

	Head		Pool Mid		Foot		Riffle		Station totals	
Station	No.	Wt.*	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
A	525	1.02	357	1.37	207	0.96	182	8.93	1271	12.28
B	94	10.70	449	1.68	125	8.43	114	29.14	782	49.95
C	205	5.29	215	0.84	797	4.15	181	11.98	1398	22.26
Total	824	17.01	1021	3.89	1129	13.54	477	50.05	3451	84.49

* wet weight in grams

Sub-habitats within the stations varied in size of standing crop. Head- and foot-pools contained a much greater total weight than did the mid-pools (Table I). The riffles held the fewest individuals, but greatly exceeded the other habitats in weight of standing crop.

TABLE II

Composition of benthic fauna in different habitats in Archuleta Creek as a percentage of total numbers and weight of organisms collected.

	Pools							
	Head		Mid		Foot		Riffle	
	No.	Wt.	No.	Wt	No	Wt.	No.	Wt.
Ephemeroptera	1.5	*	*	*	1	*	17	*
Plecoptera	*	*	*	*	*	*	4	*
Trichoptera	0	0	*	1	0	0	4	1
Tipulidae	5.8	87.3	*	27.5	3	74.7	22.3	85
Tendipedidae	33	2	30.5	8	24.5	2	5	*
other Diptera	1	1	1	4	*	1	7	*
Coleoptera	3	*	*	*	1	*	17	*
Oligochaeta	53.2	8.2	65.5	57	68	20	17	12
Amphipoda	1.5	*	1	1	3	1	3	*
Miscellaneous	*	*	*	*	*	*	2	*

*present but comprising less than 1 % of total

Larvae of Craneflies (Tipulidae) clearly dominated the bottom samples on a weight bases (Table II). Midges (Tendipedidae) were numerically important in the pools, but not in the riffles. Oligochaetes

made up over half of the numbers of bottom organisms taken from the pools and about one fifth of those collected on the riffles. The substantial percentage of weight of mid-pool organisms attributed to aquatic earthworms was due to a few large individuals. Mayflies (Ephemeroptera) and aquatic beetles (Coleoptera) each contributed to the numbers of riffle organisms as largely as did the oligochaetes; however, both groups were much less important in weight.

TABLE III

Total numbers of different kinds of benthic organisms collected at three stations on Archuleta Creek.

	June	July	Aug.	Sept.
Ephemeroptera	37	36	24	11
Plecoptera	8	13	2	6
Trichoptera	10	13	0	0
Tipulidae	95	59	30	7
Tendepididae	36	516	207	105
other Diptera	7	30	12	14
Coleoptera	22	57	7	43
Oligochaeta	80	541	917	409
Amphipoda	9	7	14	34
Miscellaneous	0	0	4	16

Some seasonal trends in benthic organisms may be seen in Table III. Tipulid and caddisfly (Trichoptera) larvae and the naiads of may- and stoneflies (Plecoptera) were most numerous in the bottom samples collected in June and July and decreased thereafter. Perhaps this is due to the emergence of adults of the latter two and movements of the former two to sites of pupation. Tendipedid larvae, "other Diptera", Coleoptera larvae and oligochaete numbers were relatively low in June, increased to a peak in July or August and then decreased. Amphipods, on the other hand, were present in low numbers in the early samples and were still increasing in September.

No significant differences between male and female brook trout from Archuleta Creek in regard to total length and weight were found (Table IV). The ratio of males to females, while varying somewhat during the summer, was essentially 1 : 1.

A sub-sample of ten males and ten females was taken at random from the fish obtained on each sampling date. No significant differences between the sexes in regard to diet were found. The items appearing with the greatest frequency in the stomachs of males likewise appeared most frequently in the stomachs of the females. Small differences in estimated volumes of food items were considered to be more likely due to chance or sampling error than to actual differences in feeding habits or preference.

TABLE IV

Total lengths and weights of brook trout from Archuleta Creek.

	Total Length (inches*) No. fish	Mean (Range)	SD.	Weight (grams) No. fish	Mean (Range)	SD.
	Males			Males		
June	59	6.90 (4.25— 9.25)	1.13	59	52 (10—118)	23.19
July	52	6.59 (4.24— 8.75)	1.14	52	47 (10— 92)	20.94
August	50	7.07 (4.50—10.13)	1.07	50	56 (13—144)	24.64
September	40	6.82 (3.38— 9.38)	1.40	40	54 (7—127)	31.39
	Females			Females		
June	42	6.97 (5.75— 9.00)	0.82	42	51 (28—100)	18.84
July	50	6.77 (4.75— 8.88)	0.72	50	47 (20— 99)	13.71
August	50	6.84 (5.75—12.25)	1.00	50	52 (27—338)	42.54
September	44	6.85 (4.88—12.13)	1.38	44	54 (16—260)	44.12
All Males	201	6.85 (3.38— 9.38)	1.18		52 (7—127)	24.94
All Females	186	6.86 (4.75—12.25)	0.99		51 (16—338)	32.66
All Fish	387	6.85 (3.38—12.25)	1.09		51 (7—338)	28.89

*1 inch = 2.54 cm

Apparently during the period of this study the brook trout of Archuleta Creek (at least those subject to capture by artificial flies and flyrod) were a homogeneous population in regard to length, weight and diet.

From Table V it is at once evident that on a volume basis terrestrial insects were the most important item in the diet of the trout. Terrestrial insects as used here does not include species having aquatic immature stages. Aquatic beetles and midges were frequently fed upon and beetles were, surprisingly, the second most important item in average volume. Mayfly naiads, caddisfly larvae and oligochaetes appeared most frequently in stomachs obtained early in the summer. The significance of this in regard to the worms is doubtful since they are probably quickly digested and therefore not recognizable for long in stomach samples. Plecoptera naiads and the larvae of "other Diptera" (mostly tabanids) increased in frequency in the stomach samples as the summer progressed. No seasonal trend was evident in regard to amphipods or plant material.

DISCUSSION

Benthic organisms taken in the Surber sampler may be compared with the contents of the brook trout stomachs thusly:

TABLE V

Foods of brook trout taken from Archuleta Creek expressed as percentages of total volume of stomach contents and frequency of appearance in stomachs.

	June Vol.	June Freq.	July Vol.	July Freq.	August Vol.	August Freq.	September Vol.	September Freq.	Average Vol.	Average Freq.
Terrestrial Insects	44	82	47	76	40	80	43	70	44	74
Ephemeroptera	2	9	*	*	*	*	2	12	*	7
Plecoptera	*	1	0	0	*	1	*	6	*	2
Trichoptera	5	18	2	9	*	2	1	4	2	3
Tipulidae	12	29	10	26	16	33	10	23	12	28
Tendipedidae	8	75	5	69	9	80	10	83	8	77
Other Diptera	*	9	*	14	*	9	3	27	*	14
Coleoptera	14	74	18	74	16	99	13	76	15	78
Oligochaeta	1	16	*	12	*	2	*	5	4	9
Amphipoda	3	24	2	20	4	25	4	13	3	20
Miscell.	*	15	*	24	3	14	6	37	2	22
Plants	10	48	9	50	6	37	6	40	8	44

* present but comprising less than 1 % of the total

1) Mayflies and caddisflies started relatively high and decreased in both bottom and stomach samples as the summer progressed.

2) Craneflies were high in June and decreased in bottom samples but remained at about the same frequency in the stomachs.

3) Stoneflies decreased in numbers in the bottom samples during the summer, but appeared more frequently in the stomachs.

4) Midges and beetles were low in early bottom samples, then increased and subsequently decreased, but appeared in about the same frequency in stomach samples. However, both appeared to be more important in the diet of the trout than the bottom sampling alone would indicate. The beetles may not be truly benthic or perhaps are adept at dodging the sampler.

5) Amphipods increased in the benthic samples as the summer progressed, but were not utilized more frequently by the trout.

6) Tipulids which made up most of the weight of the benthic organisms did not comprise a correspondingly high percentage of the trout diet. Perhaps the craneflies were generally unavailable to predation or perhaps were not palatable to the fish.

The problems of how accurately Surber samples reflect the actual numbers and composition of stream benthic populations are well known. Our limited number of samples were not taken with the intention of adding new information to the problems of statistical adequacy of bottom sampling nor were we concerned particularly with the relative composition of the diet except insofar as it elucidates the source of the trouts' diet. The relationship between the frequency with which food items are taken and the apparent availability of items is of interest but our data are not adequate to pursue this further.

What we do wish to attract attention to is the presence of relatively large numbers of top level carnivores in an aquatic community which apparently provides only about one half of their support.

A considerable literature relevant to the food habits of brook trout has accumulated. It is not necessary to review it exhaustively here; however, certain papers may be profitably mentioned.

WISEMAN (1951) examined, throughout the summer of 1946, 64 brook trout and compared the stomach contents with catches from Surber bottom samples in small streams in the Medicine Bow Mountains of Wyoming. He considered the organisms taken in the bottom sampling as being available to the fish. Diptera larvae and mayfly naiads made up 81% of the numbers of bottom organisms collected. Diptera larvae and adults and mayfly naiads and adults comprised 88% of the numbers of organisms found in stomachs. From this WISEMAN concluded that his data lent "credence to the generally accepted impression that brook trout are 'opportunists'" as pointed out earlier by NEEDHAM (1930).

DINEEN (1951) compared the food habits of sculpins and trout in a Michigan stream and noted (p. 642) "with the exception of oligochaetes, the common bottom organisms were consumed by the trout and sculpins in proportion to their availability". DINEEN had only a small number of brook trout which were all collected in the autumn. He indicated that perhaps surface feeding might be important at other seasons of the year.

ALLEN & CLAUSSEN (1960) examined the stomach contents of 62 brook trout recovered when a Wyoming beaver pond was drained. They found no difference in feeding between the sexes. Adult and immatures of beetles, dipterans and mayflies comprised most of the stomach contents.

SMITH (1961) noted that terrestrial insects were, at times, common food items of brook trout in a Nova Scotia lake. SMITH also found that the amphipod *Hyalella*, although abundant in some bottom samples was not used extensively as food by the fish.

BENSON (1953) examined the stomach contents of 420 brook trout taken from the Pigeon River, Michigan, by anglers during the summer of 1953. Caddisflies, mayflies, and oligochaetes were generally high in early samples then declined as the summer progressed. Diptera were high in early samples, then declined and finally increased in frequency in stomachs. Orthoptera were used extensively for a time in midsummer. BENSON mentioned the availability of adult dipterans but did not distinguish between terrestrial and aquatic.

NEEDHAM (1930) studied the food habits of brook trout in New York, examining 251 fish taken over a one-year period. His general conclusion was that for the year about two-thirds of the diet came from the water and one-third from the land. Caddis, mayflies and dipterans made up two-thirds of the aquatic food. Terrestrial foods were extensively used from April through November, but were most heavily used in August (52% of diet), September (64%) and October (63%). NEEDHAM did not differentiate between dipterans that were completely terrestrial and those having aquatic immature stages. We question the inclusion of adult mayflies with truly terrestrial insects.

TEBO & HASSLER (1963) reported that terrestrial insects and aquatic adults made up slightly more than one-half the total number of organisms consumed by 33 brook trout in North Carolina.

RICKER (1930) found that over 50% of the total food taken by 1000 Ontario brook trout was terrestrial. RICKER suggested that in some streams terrestrial insects might be substituted for aquatic foods when evaluating resources of streams in relation to trout production.

CLEMENS (1928) noted the importance of terrestrial insects in the diet of New York brook trout, particularly during the warm months. He considered the adults of aquatic larvae as being terrestrial insects. CLEMENS further believed that a stream could be regarded as a closed system, probably in the sense that the adult insects eaten by fish were returning to the system from which they had drawn much of their energy.

It is clear that under some circumstances, brook trout utilize considerable quantities of terrestrial insects. However, not all food (and energy) taken in at the stream surface is unequivocably terrestrial. Mayflies pass the entire naiad existence feeding in the water and do not feed as flying adults. Hence the energy contained in the body of a mayfly is returned to the ecosystem from whence it came when the fly is eaten by a trout. Other insects which possess aquatic immature stages feed in various ways as flying adults, thus when one of these is eaten by a trout part of the energy within the insect returns to the system where the energy was first captured and part is the addition of new energy to the aquatic ecosystem.

ALLEE et al. (1949, p. 495) point out that "one of the fundamental causes of adaptive utilization of the space-time community lattice is the drive for nourishment" and that food is obtained from the organisms' environment.

In the current trend of ecological analysis in terms of trophic relations between different feeding levels and in energy flow between levels, it is important to consider the additional energy derived by the aquatic ecosystem from the surrounding terrestrial system.

LINDEMAN (1942) suggested that the further removed an organism is from the initial source of energy in the trophic level series, the less probable will be its sole dependence upon the preceding level as a source of energy. This appears to be true of the Archuleta Creek brook trout. They fed on herbivorous, carnivorous and omnivorous invertebrates both aquatic and terrestrial.

DARNELL (1961)in studying trophic relations in Lake Pontchartrain, Louisiana, found that apparently the consumers depended greatly upon allochthonus primary productivity and that the lake was trophically unbalanced.

We suggest that the community of Archuleta Creek is likewise trophically unbalanced in that much of the support for the top level carnivores is derived from outside the community. MINCHLEY (1963) found that in Doe Run, a spring fed stream in Kentucky, trophic unbalance in the sense that the fauna depended more on allochthonus debris increased with increasing distance from the source.

Utilization of large amounts of terrestrial insects by the brook trout may confer a degree of stability to the community which otherwise might be lacking. The use of outside sources of food by the fish reduces their dependence on lower trophic levels in the stream and provides alternate pathways along which energy may flow. The situation in Archuleta Creek may be analagous to that in a salt marsh studied by TEAL (1962). In the marsh the range of kinds of plants and animals is limited but trophic stability is achieved by broad unrestricted feeding habits.

Whatever the paths of energy flow or amount of community stability, this study points up a danger inherent in sampling one trophic level and making inferences about other levels.

Sampling of either the bottom fauna or fish alone in Archuleta Creek could lead easily to an erroneous conclusion. The presence of large numbers of top level consumers might bring about an overs estimate of the amount of food produced within the stream ecosystem- Sampling the benthic animals could lead to unwarranted conclusions regarding the amount of food available to, and utilized by, the trout.

SUMMARY

On each of four dates in summer 1961, approximately 100 brook trout (*Salvelinus fontinalis*) were taken by flyrod from Archuleta Creek, a small mountain stream in south-central Colorado. Simultaneously benthic animals were sampled with a Surber sampler at three stations. Four habitats were sampled at each station.

The riffle habitat yielded the greatest weight of bottom organisms, 50.05 grams (about 3 to 4 times as much as the head- and foot-pool areas respectively); mid-pools were the poorest habitat in weight of organisms, 3.89 grams.

Approximately three fourths of the trout stomachs contained terrestrial insects which composed about 45% of the volume of the stomach contents. Thus nearly one half of the trouts' support came from outside the aquatic ecosystem.

LITERATURE

ALLEN, G. H. & G. CLAUSSEN. - 1960 - Selectivity of food by brook trout in a Wyoming beaver pond. *Trans. Amer. Fish. Soc.* 89: 80—81.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK & K. P. SCHMIDT. - 1949 - Principles of animal ecology. W. B. Saunders Co., Philadelphia.

BENSON, N. G. - 1953 - Seasonal fluctuations in the feeding of brook trout in the Pigeon River, Michigan. *Trans. Amer. Fish. Soc.* 83: 76—83.

CLEMENS, W. A. - 1928 The food of trout from the streams of Oneida County, New York State. *Trans. Amer. Fish. Soc.* 58: 183—197.

DARNELL, R. M. - 1961 - Trophic spectrum of an estuarine community, based on studies of Lake Ponchartrain, Louisiana. *Ecology* 42: 553—568.

DINEEN, C. F. - 1951 - A comparative study of the food habits of *Cottus bairdi* and associated species of Salmonidae. *Amer. Mid. Nat.*, 46: 640—645.

LINDEMAN, R. L. - 1942 - The trophic-dynamic aspect of ecology. *Ecology* 23: 399—418.

MINCKLEY, W. L. - 1963 - The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildlife Monographs*, 11: 1—124.

NEEDHAM, P. R. - 1930 - Studies on the seasonal food of brook trout. *Trans. Amer. Fish. Soc.* 60: 73—

RICKER, W. E. - 1930 - Feeding habits of speckled trout in Ontario waters. *Trans. Amer. Fish. Soc.* 60: 64—72.

SMITH, M. W. - 1961 - Bottom fauna in a fertilized natural lake and its utilization by trout (*Salvelinus fontinalis*) as food. *Verh. int. Ver. Limnol.* 14: 722—726.

TEAL, J. M. - 1962 - Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614—624.

TEBO, JR., L. B. & W. W. HASSLER. - 1963 - Food of brook, brown, and rainbow trout in streams in western North Carolina. *J. Elisha Mitchell Sci. Soc.* 79: 44—53.

WISEMAN, J. S. - 1951 - A quantitative analysis of foods eaten by eastern brook trout. *Wyoming Wild Life* 15, 10: 12—17.