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ROLE OF ALLOCHTHONOUS DETRITUS IN THE TROPHIC STRUCTURE OF A WOODLAND SPRINGBROOK COMMUNITY[1]

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Abstract. The community trophic structure of Morgan's Creek, Meade County, Kentucky was analyzed through regular measurement of standing crops of the chief potential sources of plant materials available to the animals (suspended particulate, attached particulate, and allochthonous leaf materials) and an examination of their gut contents. The most important food was allochthonous leaf materials, which occurred as suspended material in the water, as a component of materials attached to the streambed, and as whole leaves and fragments. Diatoms were the only other important source of plant materials and constituted the greatest proportion of the attached organic fraction.

Mean standing crop measurements of potential foods for five sampling stations ranged from 0.6 to 1.0 kcal/m^3 for suspended particulate organic matter; 12 to 19 kcal/m^2 for attached particulate organic matter; and 4.7 to 13 kcal/m^2 for allochthonous leaf materials. Comparison of standing crop data with previous findings indicates that the values generally are within the known ranges for flowing waters. Analysis of gut contents and determination of the principal pathways of energy flow in the stream indicate that imported organic matter in the form of allochthonous leaf materials provides the main source of energy for the primary consumers and, indirectly, for the entire benthic community of Morgan's Creek. Of the 37 taxa of animals studied, 24 were herbivores, 5 omnivores, and 8 carnivores. In general, detritus made up from 50 to 100% of all the materials ingested by both the herbivores and omnivores. The total number of benthic animals was comprised of 14% herbivores, 83% omnivores, and 3% carnivores. *Gammarus minus* was the single most important member of the fauna. It contributed 81% of the total number of invertebrates, and well over 90% of its diet consisted of allochthonous leaf detritus.

Introduction

It has been known for a number of years that dead organic matter may be ingested by aquatic invertebrates. However, only comparatively recently was it realized that allochthonous detritus can play an important role in the economy of aquatic ecosystems (Jones 1949, 1950; Dunn 1954; Elton 1956; Teal 1957; Odum and Smalley 1959; Brown 1961; Darnell 1961, 1964; Hynes 1961, 1963; Nelson and Scott 1962; Chapman and Demory 1963; Minckley 1963; Egglishaw 1964). The present study provides further evidence of the importance of allochthonous detritus to the benthic communities of flowing waters, and explores the role of this food in the trophic economy of a relatively simple system, a woodland springbrook.

At present the only other study relating specifically to the role of detritus in stream productivity is that of Nelson and Scott (1962) on the Middle Oconee River, Georgia. Nelson and Scott measured standing crops of the major sources of primary food and of the bottom fauna over an entire

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year. They were able to show that the primary consumer organisms derived 66% of their energy from allochthonous organic matter. However, their study was restricted to a single, isolated riffle; and they lacked information on the specific food habits of the fauna. To my knowledge, the present investigation on Morgan's Creek is the first of its kind to concern an entire stream.

The problem of determining the role of detritus in Morgan's Creek was approached from two different aspects: the first, from the standpoint of potential sources of plant materials available to the animals; the second, from the standpoint of foods eaten by the fauna. As will be seen, treatment of the potential sources of food divided itself most readily into three categories: 1) suspended organic matter, 2) attached organic matter, 3) allochthonous leaf material. Data for the present study were obtained between 1 February 1963 and 26 September 1964.

Description of Study Area

Morgan's Creek is a small stream (modal discharge 0.007 m^3/sec; range 0.005–0.35) which arises as a spring at the mouth of Morgan's Cave in Otter Creek Park, Meade County, Kentucky. The stream flows approximately 0.8 mile (1,335 m) through a narrow, thickly wooded valley to empty into the Ohio River near river mile 638. A detailed description of the stream and sampling stations will be presented in a subsequent publication (see also Minshall 1965).

Eight permanent sampling stations were established along the length of the stream. Five of the stations may be broadly classed as fast-water riffle areas. Cumulatively they represent conditions over about 78% of the stream, and it is with these stations that the present study is concerned. Station I is at the source; station III, 360 m downstream; station IV, 460 m; and stations VI and VII, 860 and 1,150 m below the source, respectively. Some supplementary data for station V, one of the few permanent pools in the stream, have also been used.

The upper one-third of the stream (stations I–III) and the region around station VII are covered by a dense canopy of deciduous vegetation during most of the growing season. From station IV to below station VI most of the riparian vegetation has been removed. This has reduced the amount of allochthonous leaf material supplied directly to the stream in that area.

General Considerations

In the present study, detritus is considered to be any "material of organic origin permanently incapable of reproduction" (Strickland 1960; p. 5) and includes "dead fragments of plants; partially decomposed, finely divided, plant material; and a certain amount of dead animal matter" (Kendeigh 1961; p. 54). Animal detritus was not often seen in Morgan's Creek or taken in the regular samples. It is quite likely that dead invertebrates in the stream are eaten or decompose soon after death. This makes it difficult to assess the importance of this component directly. In the present study no attempt was made to distinguish dead animals from living ones, since the difference of the two in food value probably is negligible. Amorphous animal detritus also was not treated separately, since on a biomass basis this could constitute only a small percentage of the total detrital complex.

No attempt was made to measure or evaluate the dissolved organic matter component, since it appears to be insignificant as a direct source of food to most of the aquatic macrofauna (Krogh 1931; Prosser and Brown 1961; see also reviews by Welch 1952; Fogg 1959). However, recent studies (Slater 1954; Sorokin 1964; Warren et al. 1964) have revealed that dissolved organic matter can stimulate the production of certain bacteria and other microorganisms, which in turn provide food to the macroconsumers.

Suspended foods occur primarily in the particulate form and consist of particulate plant materials, organic substances adsorbed on inert particles, and living and dead microorganisms (Prosser and Brown 1961). In the present study, "suspended food" refers to the total particulate complex of organic materials of particle size 4–158 μ present in the water. Particulate organic material in the water probably is more important as a food source than the dissolved or colloidal organic matter because of its availability to filter-feeding organisms (Nelson and Scott 1962). For all practical purposes, especially in small streams, this fraction may be considered as largely detrital in nature.

Potential food materials on the stream bottom are contained in the aufwuchs community and in the detritus. The situation in Morgan's Creek was somewhat simplified by the absence of vascular plants from the stream proper, and by the limited abundance or restricted occurrence of mosses and algae other than diatoms. Since any sample of organic material taken from the stream bottom was likely to contain both algae and detritus, it was not feasible to distinguish between the living and dead components in measurements of the standing crops of particulate matter. Consequently, only values for the total attached complex of organic materials were obtained by the method employed. As used here, attached particulate organic matter includes primarily the aufwuchs community, especially the algae, and the closely associated detrital material. In Morgan's Creek, the algal portion is essentially diatomaceous and the detritus largely of terrestrial origin. Further insight into the composition of the attached fraction was obtained by microscopic analyses. However, the techniques employed did not distinguish the bacteria (see Rodina 1963).

The dominant potential source of food in Morgan's Creek is allochthonous leaf detritus from the surrounding woodland. This category includes all recognizable leaf materials, from whole leaves to fine particles. Since leaf stems and veins and bark usually were left unaltered during the relatively short time they remained in the stream, they were considered inedible and were removed from the sample whenever feasible. No attempt was made to measure rates of utilization or removal by drift, although losses from the latter especially may be considerable. The standing crop measurements are believed to be representative of amounts available to the benthic consumers at any given "moment" in time.

METHODS

Potential foods

Suspended organic matter.—Water samples for determination of suspended particulate organic matter were collected in 2-liter polyethylene bottles at monthly intervals from April 1963 through August 1964 (excluding August 1963, and April and June 1964). The water was passed through a No. 10 plankton net before treatment. Total carbon content was measured by quantitative dichromate oxidation (Strickland and Parsons 1960; p. 113–121). From 500 to 1,000 ml of water was filtered, depending on the amount of suspended material present.

The theoretical aspects of quantitative dichromate oxidation have been extensively reviewed and applied to limnological analyses by Maciolek (1962). The extinction of the yellow dichromate solution after reduction by the organic matter was determined with a Bausch and Lomb Spectronic-20 colorimeter. Sintered glass filters with a porosity of 4–8 μ were used for concentrating the samples before oxidation. Results are expressed in kilocalories, based on a caloric equivalent for glucose of 3.8 kcal/g. Whenever the determinations could not be carried out immediately, the samples were filtered and then frozen until analyzed. The determination of oxidizable organic matter is considered a realistic measure of the amount of energy stored as food (Strickland and Parsons 1960).

Attached organic matter.—Quantitative samples (4 cm^2) for attached particulate matter were taken with a Young sampler (Welch 1948) from flat stones in the riffle areas. Two such samples were taken monthly at each station sampled from February 1963 through September 1964. One set of samples was concentrated in a Foerst centrifuge, preserved in 5% formalin, and used for estimation of total cell numbers. Total cell counts were made with a Sedgewick-Rafter counting cell, at a magnification of 100× (Welch 1948). The second set of samples was refrigerated immediately after collection and taken to the laboratory for estimation of total carbon content, as discussed above.

Allochthonous leaf material.—Quantitative samples, containing both leaves and benthic organisms, were collected in biweekly intervals from February 1963 through September 1964 (excluding one each in November 1963, and January, March, and August 1964). Each sample was of 5 min duration and was secured by vigorously disturbing the stream bottom with the feet and allowing the current to carry the dislodged material into a fine-meshed (24 threads/cm) net. The samples were preserved with 5% formalin in the field. Animal and plant materials were separated in the laboratory, and the plant material was placed in tared containers for drying.

An estimate of the area represented by a 5-min sample at each of the stations was obtained from measurements made 19 July 1963 and 17 July 1964. The length and width of the portion of streambed disturbed during 5 min of collecting were measured. The areas covered in the two collections were approximately: I – 6·1, 5·5; III – 7·7, 6·1; IV – 5·7, 5·1; VI – 5·2, 4·8; and VII – 14·9, 13·3 m^2, respectively. Animal numbers and plant biomass were converted to values per square meter on the basis of these conversion factors.

Direct measurements of leaf dry weights were made to the nearest 10^{-2} g on an electric single-pan balance. These values were converted to kilocalories on the basis of a dry weight caloric equivalent. Measurements of the caloric equivalent of the leaves were made with an adiabatic bomb calorimeter (Parr Instrument Company 1960) on a composite sample of terrestrial leaf materials collected from the stream. The estimation of caloric values based on an established conversion factor, as done in the present study, appears to be a valid procedure (Bocock 1964). All gravimetric measurements for bomb calorimetry were made with a torsion balance with a stated accuracy of 5 mg, after the samples had been dried in an oven at 60°C and allowed to cool to room temperature in a desiccator.

Foods eaten

The second aspect emphasized in the investigation of the role of detritus in the trophic economy of Morgan's Creek was that of the actual foods eaten by the fauna. These data were obtained by quantitative analysis of gut contents, supplemented by direct observation in the field.

Brown (1961) has reviewed a number of methods for the estimation of food materials in gut samples. In the present study, specimens of invertebrates for gut samples were taken when moderate to large individuals were available. Only those whose guts contained ingested materials were used. The anterior portion of the gut was removed intact and the contents extracted and teased apart with fine needles. A number of guts (usually 5–10) for a particular species were pooled together in vials, according to the month in which they were collected (see Borgeson 1963). Composite samples from guts containing primarily finely divided materials were shaken vigorously, and subsamples were drawn off with a large-bore dropper. Several drops were placed on a glass slide, and the slide was heated gently to evaporate the excess water. A permanent mount was then made by adding nonresinous mounting medium (Turtox CMC–10) and a cover slip. The prepared slides were examined by the strip-count method, under a compound microscope (400×), with at least 300 items being counted in each case. The data are expressed as percentages of the total number counted. Composite samples from guts in which most of the material consisted of recognizable pieces and fragments were emptied into a small petri dish backed with 1-mm graph paper and were examined under a dissecting microscope. The various components were separated and then spread out evenly over the grid. The percentage composition of each component was estimated on the basis of the proportion of the grid it covered. The results of gut analyses for the various months were averaged to obtain the values given in Figure 2.

Results

Tables containing the complete results of the standing crop measurements and of the gut content analyses are available in an unpublished dissertation (Minshall 1965). These are summarized below, and the mean values are plotted in Figures 1 and 2.

Potential foods

The mean values (Fig. 1A) for suspended particulate, attached particulate, and allochthonous leaf materials all increased from stations I to IV and leveled off or decreased slightly between stations IV and VI. At station VII there was a marked decline in leaf detritus and an increase in the amount of suspended organic matter, resulting from inundation of the area by the Ohio River and the deposition of sediments. The flood waters annually remove large amounts of leaf material and deposit silt and finely divided organic matter, which are eroded away during the remainder of the year. Standing crops of attached organic materials were only a little less than at station VI.

Suspended organic matter.—With few exceptions, the content of particulate organic matter suspended in the water was lowest at station I and increased downstream (Table I; Fig. 1A),

Table I. Range and mean of standing crops of organic matter in Morgan's Creek, Meade County, Kentucky

Type organic matter	Station I	III	IV	VI	VII
Suspended particulate (kcal/m³)	0.1–2.9 (0.6)	0.4–1.9 (0.7)	0.2–1.7 (0.7)	0.1–1.4 (0.6)	0.3–2.3 (1.1)
Attached particulate (kcal/m²)	2.5–24 (12)	5.3–28 (13)	4.7–27 (19)	4.7–27 (16)	3.4–26 (16)
Allochthonous leaf (kcal/m²)	0–39 (8.8)	0.4–53 (10)	0.9–50 (13)	0.5–54 (11)	0.4–20 (4.7)

indicating some production of this material within the stream. Noticeable peaks occurred in June and July 1963 and January and July 1964 (Fig. 1B). It is noteworthy that the summer peaks correspond to lows in the allochthonous leaf fraction, whereas the winter high occurred during a similar peak in the attached particulate component. The summer peaks agree with the findings of Nelson and Scott (1962), who noted a higher quantity of suspended particulate detritus during the summer than during the winter. They attributed this to certain streambed-stream discharge relationships (principally those involving the scouring and flushing of previously accumulated detritus) and to more rapid decomposition of organic fragments at higher summer temperatures. The January 1964 high could be due to the sloughing off of attached materials, which were especially abundant at that time. Except for these peaks and a low in May 1963, most of the monthly averages for the entire stream fell within the range 0·4 to 0·7 kcal/m³.

Attached organic matter.—Monthly averages of the organic matter contained in the attached particulate fraction were highest in midwinter (Fig. 1B), but no trends were evident. The greatest average concentration of attached particulate organic matter was supported by station IV (Table I), but the relationship was much more variable than is indicated by the averages. The averages

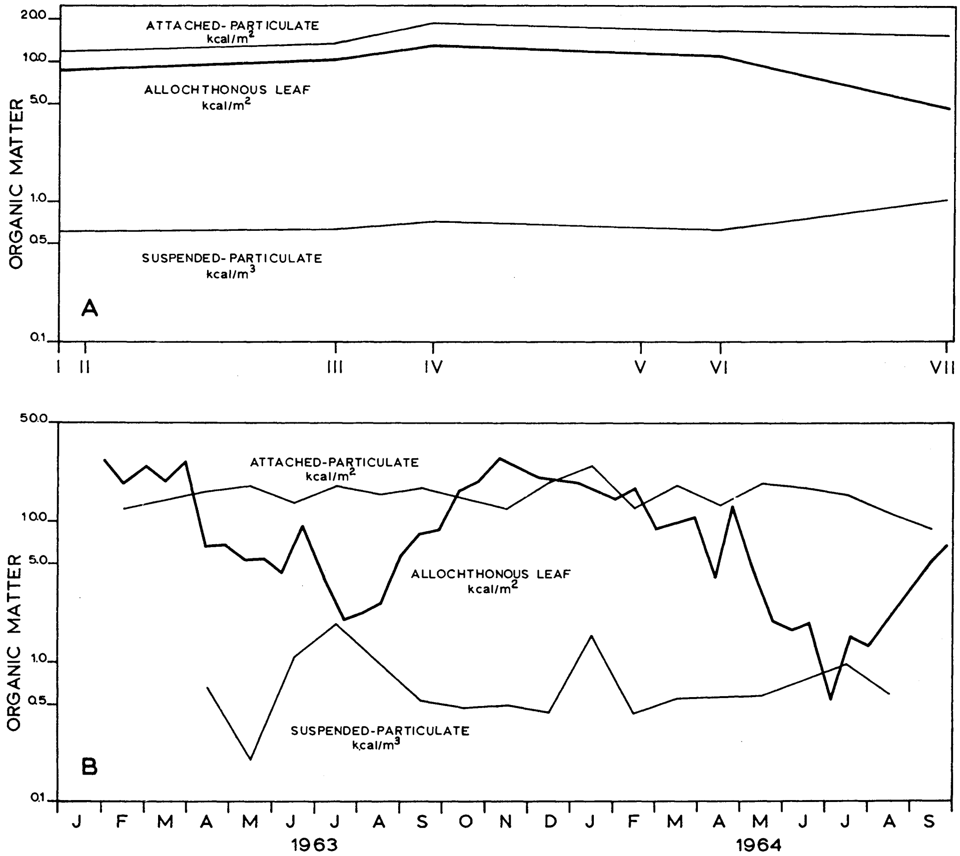

FIG. 1. Longitudinal (A) and seasonal (B) variations in the average amount of organic matter in the three principal fractions of plant material, Morgan's Creek, Meade County, Kentucky.

for each station agree with the general impression obtained by direct observations, in that stations IV and VI were the most, and station I, the least productive. The averages are also in agreement with the results of McIntire and Phinney (1965) who found that light-grown periphyton communities were more productive than shade-grown ones.

A microphytobenthoic ooze (Nelson and Scott 1962), consisting of amorphous detritus and its attendant bacterial-protozoan populations, frequently was abundant in quiet-water areas of Morgan's Creek as a flocculent deposit or intermixed with inorganic sediments. It made up the most important component of the particulate organic matter on the stream bottom at station V. The organic content of the ooze at station V, though not given in Table I, ranged from 4·7 to 27 kcal/m² during the study period, with a mean of 19 kcal/m². Lowest values were recorded in February of both years, and values greater than 25 kcal/m² were obtained in September and October 1963 and March and May 1964.

Allochthonous leaf material.—The most abundant sources of allochthonous material in Morgan's Creek were leaves of sycamore (*Platanus occidentalis*), oak (*Quercus bicolor, Q. marilandica, Q. montana, Q. Muhlenbergii, Q. Prinus, Q. rubra,* and *Q. velutina*), maple (*Acer saccharinum* and *A. saccharum*), and elm (*Ulmus americanus*). On the average, leaf detritus (apart from that contained in the suspended and attached portions) was most abundant at station IV and least abundant at station VII (Table I). The average for station V, though not given in the table, was 7·5 kcal/m², based on a 12-month average. The decline in leaf materials below station IV and continuing through station VI shows the effect of the reduction of the riparian vegetation in this area; upstream and wind-blown supplies prevented the level from becoming reduced appreciably. The cause of the further decline at station VII (flooding by the Ohio River) was mentioned previously.

There was a good seasonal pattern in the amount of allochthonous leaf material, with a high in late autumn-early winter and a low in midsummer (Fig. 1B). The entire sequence follows the facts of leaf litter production, utilization, and export already documented for deciduous forests (see Ovington 1965 for references). As could be expected, the quantity of dead-leaf material varied with discharge and degree of wind action. This is reflected by the ups and downs shown in Fig. 1B. Significant deviations from the norm occurred only during periods of unusually high discharges, e.g., during a flood which devastated the entire community of Morgan's Creek in March 1964 (Minshall 1965). Thus, measurements of standing crops appear to reflect the algebraic sum of inflow and outflow for any particular time of the year (i.e., net production); as such they should give a good indication of amounts available to the consumers. At no time during the year was leaf detritus completely absent from the stream. Fresh materials (initially as elm and then sycamore leaves) began to be added as early as the beginning of August.

Other potential foods.—Plant materials other than diatoms and allochthonous leaves which might provide food for the benthos of Morgan's Creek are the moss *Hygroamblystegium irriguum* and the algae *Cladophora glomerata* and *Vaucheria. sp. H. irriguum* was common from station I through III, where it began to decline, and was absent below station IV. *C. glomerata* was restricted to a small portion of the stream above station III. Growths appeared as early as October and reached their peak about mid-April; its disappearance from the stream corresponded to development of the leaf canopy. *Vaucheria* (presumably *geminata*) was restricted to station I. Periods of high discharge had a deleterious effect, wearing the wooly mats down to short stumps.

Foods eaten

The important benthic invertebrate components of the three general consumer categories (herbivore, omnivore, carnivore) are listed in Table II. Not listed, but included among the carnivores, were the fishes *Semotilus atromaculatus* (Mitchill) and *Rhinichthys atratulus* (Hermann). Of the 37 taxa studied, 24 were herbivores, 8 carnivores, and 5 omnivores.

Herbivores.—A striking feature of *Asellus* (both *A. brevicaudus* and *A. intermedius* Forbes) was that the entire gut, from mouth to anus, usually was filled with amorphous detritus. The nature of this material did not vary markedly in texture or general composition from end to end. Apparently digestion is only partial in these animals and there is much waste, or they utilize the associated microorganisms and not the detritus as such. This may explain why the feces of *Asellus* can provide nutriment for *Gammarus minus* (Minckley 1963) and certain mayflies (Brown 1961).

All species of mayflies examined were found to be strictly herbivorous. Detritus and diatoms were the most important foods eaten, although bits of filamentous algae were found occasionally. On the basis of these findings and those of Burks (1953), Chapman and Demory (1963), and others, those species whose guts were not analyzed during this study were arbitrarily classed as herbivores and assumed to have food habits similar to those of the species that were examined.

The plecopterans *Nemoura delosa* and *N. vallicularia* are herbivores and, in Morgan's Creek, ate primarily leaf material. It is probable that *Leuctra sibleyi* and *Allocapnia rickeri* have food habits similar to *Nemoura* in Morgan's Creek. Species of the genus *Leuctra* are believed to be entirely herbivorous (Hynes 1941; Jones 1949, 1950). *Allocapnia* is also herbivorous and feeds on decaying vegetation (principally leaves) and diatoms (Needham et al. 1937).

TABLE II. Consumer groups and their actual and relative numerical abundance in Morgan's Creek, Meade County, Kentucky, February 1963 through September 1964. An asterisk (*) denotes those taxa whose food habits were not investigated in the present study

Consumer groups	Total numbers[a]	% of total	Mean no./m²[b]
HERBIVORES	52534	13.54	
Tubificidae	2421	0.60	3.3
Asellus (mainly *A. brevicaudus* Forbes)	12969	3.36	10.6
Ephemeroptera	19532	5.02	
Baetis amplus Traver*	9755	2.51	32.7
Baetis herodes Burks	4863	1.25	6.9
Baetis phoebus McDunnough	1572	0.40	4.4
Epeorus pleuralis (Banks)	1356	0.35	2.9
Centroptilum rufostrigatum McDunnough	1326	0.34	3.2
Pseudocloeon carolina Banks*	387	0.10	1.2
Paraleptophlebia moerens McDunnough*	237	0.07	0.7
Plecoptera	248	0.06	
Nemoura (mainly *N. delosa* Banks)	108	0.03	0.6
Allocapnia rickeri Frison*	87	0.02	1.0
Leuctra sibleyi Claassen*	53	0.01	0.4
Ectopria sp. (larvae)*	457	0.12	0.7
Trichoptera	308	0.08	
Neophylax autumnus Vorhies	241	0.06	0.7
Glossosoma intermedium (Klapálek)	67	0.02	0.4
Diptera	16583	4.27	
Tendipedidae	14234	3.63	11.8
Simulium sp.	1315	0.33	2.5
Tipulidae*	236	0.06	0.5
Pericoma sp.*	204	0.05	0.9
Dixa sp.*	92	0.02	0.5
Other*	502	0.13	0.8
OMNIVORES	320976	82.60	
Gammarus minus Say	315947	81.30	234.2
Orconectes rusticus rusticus (Girard)	485	0.13	0.8
Cambarus tenebrosus Hay	181	0.05	0.3
Diplectrona modesta Banks	3764	0.97	5.7
Rhyacophila parantra Ross	599	0.15	1.0
CARNIVORES	13283	3.41	
Phagocata gracilis gracilis (Haldeman)	11971	3.08	10.2
Isoperla clio (Newman)	360	0.09	0.9
Isogenus decisus Walker	49	0.01	0.3
Nigronia fasciata (Walker)	126	0.03	0.4
Sialis joppa Latreille	92	0.02	0.4
Antocha saxicola Osten Sacken*	685	0.18	1.2

[a]Totals from stations I, III, IV, VI, and VII combined.
[b] $\left[\frac{\text{Total numbers from all 5-min samples}}{\text{Frequency of occurrence in the samples}}\right] / \text{Average area represented by a 5-min sample } (7.0\ \text{m}^2)$

The stone-case Trichoptera in Morgan's Creek, *Glossosoma intermedium* and *Neophylax autumnus,* both restricted their diets to plant material. Diatoms were of only secondary importance in *G. intermedium,* but in *N. autumnus,* they were nearly equal in importance to detritus on several occasions.

Simulium guts contained the full spectrum of plant materials, but detritus always constituted a preponderant amount of the total volume. The *Simulium* population studied by Chapman and Demory (1963) was similar to that of Morgan's Creek, feeding principally on detritus and occasionally taking some diatoms. The data on the food habits of the Tendipedidae are very incomplete and are based on collections from March only. Tendipedidae larvae are primarily herbivorous and feed on algae, higher aquatic plants, and detritus (Pennak 1953).

Omnivores.—*G. minus* had the widest repertoire of known foods of any organism in the creek (Table III). Leaf detritus was the most important component, but animals were regularly taken. *G. minus* probably eats anything that is available (Minckley and Cole 1963), including other *G. minus.*

TABLE III. Summary of laboratory and field data of foods eaten by the principal omnivore and carnivore groups in Morgan's Creek, Meade County, Kentucky. The food items are listed in order of importance

Taxon	Known food items in Morgan's Creek
Omnivores	
Gammarus	Detritus, *Asellus*, baetine mayflies, Tendipedidae, Trichoptera (*Diplectrona, Glossosoma*), *Gammarus*
Cambarus	Detritus, baetine mayflies (*Centroptilum*), Tendipedidae, *Gammarus, Phagocata*
Orconectes	Detritus, Tendipedidae, baetine mayflies, Trichoptera (*Glossosoma*)
Rhyacophila	Detritus, diatoms, *Phagocata*
Diplectrona	Detritus, diatoms, unidentified animal remains
Carnivores	
Phagocata	*Gammarus, Asellus*, unidentified animal remains
Isogenus	Baetine mayflies, Tendipedidae
Isoperla	Tendipedidae, *Epeorus*, Trichoptera, baetine mayflies, *Asellus, Allocapnia*
Sialis	Trichoptera (*Diplectrona?*), *Gammarus*
Nigronia	*Gammarus, Asellus, Ectopria*, unidentified amorphous material
Rhinichthys	*Gammarus*, Tendipedidae, terrestrial insect larvae, Oligochaeta, Decapoda
Semotilus	*Gammarus*, Tendipedidae, terrestrial insect larvae and adults, Trichoptera (*Rhyacophila*), *Asellus, Phagocata*

Leaf detritus was the chief plant material eaten by the crayfishes, and baetine mayflies and Tendipedidae were the main animal foods found in the guts. *Gammarus* remains were relatively abundant in one *Cambarus* collected in November 1963. In the August composite sample of 10 *Orconectes,* amorphous detritus made up an estimated 75% of the gut contents by volume; animal materials constituted the remainder and included 32 mayflies and 8 tendipedids.

Vegetable matter was the most important component eaten by *C. tenebrosus* and *O. rusticus* in nearby Doe Run, Kentucky (Prins 1965). Detritus, primarily from tree leaves, made up most of the diet, although at times aquatic vascular plants and algae were important. Among the invertebrates eaten, *Gammarus* and *Asellus* were important; but in biomass the animal component was seldom significant. Both species tended to be opportunists, but there was some indication that *O. rusticus* fed more extensively on amorphous materials than did *C. tenebrosus* (Prins 1965 and personal communication).

Most caddisfly larvae are omnivorous and eat anything available. Such forms as *Diplectrona* (Hydropsychidae) eat a preponderance of sessile diatoms and other small organisms, but they also eat insect larvae and, under crowded conditions, are cannibalistic (Ross 1944). *Rhyacophila* generally is considered a carnivore (Ross 1944; Chapman and Demory 1963), but limited analyses of guts from Morgan's Creek specimens indicate that plant materials, particularly detritus, may be important, at least at times. *R. parantra* in Morgan's Creek were observed ingesting *Phagocata.*

Carnivores.—Information on the food habits of *Phagocata gracilis* was obtained solely from observations made in the field. *G. minus* was the most common food item in the diet of *P. gracilis,* and *A. brevicaudus* appeared to be next in importance. Teal (1957) found that *P. gracilis* is strictly predaceous and feeds on live or recently dead animals. In the present study when injured *Gammarus* were placed together with *P. gracilis* in a tray, they were quickly sought out and devoured.

Analysis of the food of *Isogenus decisus* and *Isoperla clio* in Morgan's Creek, particularly of *I. decisus,* was hampered by the lack of suitable specimens. Nevertheless, it appears that animal matter made up 75–100% of the gut contents of both species; the remaining material probably was derived from the guts of the prey or was incidental to ingestion of the animals. No *Gammarus* remains were found in the guts, and on several occasions *I. clio* was observed to pass over *Gammarus* in preference to mayflies.

The guts of most of the *Nigronia* examined were only partially full, and most of the contained material was of indeterminate nature. It is possible that *Nigronia* feeds infrequently and utilizes the material rather slowly. This would explain why the larval stage is fairly long, yet contains "surprisingly few" instars (Pennak 1953). *Sialis* and *Nigronia* are both active predators and probably eat any animal they can catch. Minckley (1963) found that *Nigronia* (his *Chauliodes*) ate considerable amounts of terrestrial invertebrates in addition to benthic animals.

The chief vertebrate predators in Morgan's Creek were *Semotilus atromaculatus* and *Rhinichthys atratulus,* although other fishes, salamanders, and frogs were also present, some in significant numbers. *Semotilus* and *Rhinichthys* fed mainly on *Gammarus* and Tendipedidae, but *Gammarus* generally was the more important, both numerically and volumetrically. One *Rhinichthys,* typical of a size range commonly collected in Morgan's Creek (60 mm body length), contained 14 *Gammarus;* another taken the same day (11 May 1964) contained the remains of at least 61 tendipedids. *Semotilus* and *Rhinichthys* apparently ate whatever was most available. *Semotilus* utilized surface drift materials more effectively, since it was more active than *Rhinichthys* and able to swallow most of its natural foods in one gulp; *Rhinichthys* was less adept in the open water and did best in the riffles, where it fed off the bottom.

Results of the gut analyses are summarized in Figure 2. The dominant and consistent importance of detritus in the herbivore and omnivore groups is striking; diatoms were the only other plant material eaten in any significant amounts. The organisms eaten by the carnivores (Table III)

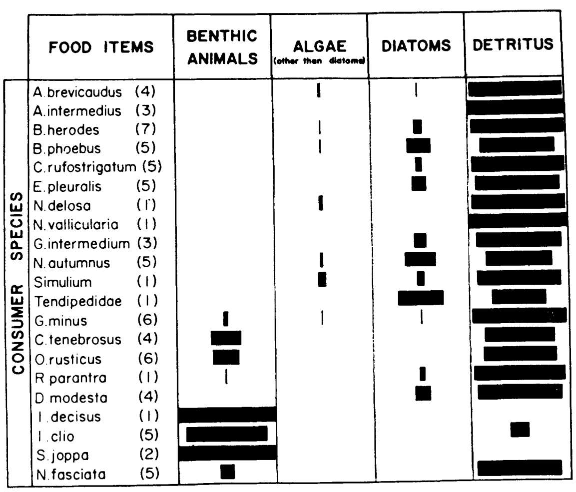

FIG. 2. Trophic spectra for important consumer species in Morgan's Creek, Meade County, Kentucky. For each species the total of all food items equals 100%, which is also the width of the column for each food category (see Darnell 1961). The numbers in parentheses denote the total months for which specimens were examined.

in Morgan's Creek were chiefly detrital feeders. The regular occurrence of Ephemeroptera, Tendipedidae, and *Gammarus* in the guts of the secondary consumers is noteworthy since they were among the most abundant groups in the creek (Table II) and were all important consumers of detritus.

DISCUSSION

Comparison with other studies

The ranges for each of the three major fractions of organic matter in Morgan's Creek are given in Table IV, which also permits a comparison with

TABLE IV. Comparison of values for organic matter in Morgan's Creek, Meade County, Kentucky, with those from previous studies

Locality	Amount
SUSPENDED ORGANIC MATTER (kcal/m³)	
Morgan's Creek, Ky. Range of 14 monthly averages	0.2–1.9
Wisconsin River at Prairie du Sac Dam (November and July, respectively) (Birge and Juday 1926)	5.1–13[a]
Middle Oconee River, Ga. Range of 14 monthly measurements (Nelson and Scott 1962)	40–235[a]
ATTACHED ORGANIC MATTER (kcal/m²)	
Periphyton in shoal areas of alpine lakes (Maciolek 1962, Maciolek and Kennedy 1964)	0.1–2.3
Morgan's Creek, Ky. Range of 20 monthly averages	8.9–20
Periphyton in artificial streams (Kevern 1963)	39–48[b]
Periphyton in artificial streams (McIntire and Phinney 1965)	
Light-grown	213–604[c]
Shade-grown	119–604[c]
ALLOCHTHONOUS LEAF MATERIAL (kcal/m²)	
Morgan's Creek, Ky. Range of 39 biweekly averages	0.6–28
Middle Oconee River, Ga. Range of 14 monthly measurements (Nelson and Scott 1962)	10–170[a]

[a]Assuming 1 mg organic matter equals 5 cal (Maciolek 1962).
[b]Assuming 1 mg algal organic matter equals 4.5 cal (Kevern and Ball 1965).
[c]Assuming 1 mg organic matter as periphyton equals 4.1 cal (McIntire and Phinney 1965).

the findings of other workers. Nelson and Scott (1962) noted a linear relationship in the Middle Oconee River, Georgia, between the amount of suspended organic material and stream flow but could detect no seasonal variations. Their values ranged from 8 to 47 mg/liter (40–235 kcal/m³), with the majority of the samples having 10–20 mg/liter (50–100 kcal/m^3). Although these are considerably higher than the values obtained from Morgan's Creek, they may be explained by differences in water origin and by the greater size (average discharge 8·07 m^3/sec versus a modal discharge of about 0·01 m^3/sec for Morgan's Creek) and drainage of the Middle Oconee (398 $miles^2$ versus 2–3 $miles^2$ for Morgan's Creek).

Comparison of values for attached particulate organic matter indicates that the values from Morgan's Creek are about one-half to one-third as large as those obtained for periphyton in artificial streams after 30 days of growth (data from Kevern 1963), but are considerably more than those obtained by Maciolek (1962; Maciolek and Kennedy 1964) for periphyton growths in the shoal areas of oligotrophic alpine lakes. Results from a recent study by McIntire and Phinney (1965), also for a laboratory stream, yield much higher values than any previous study and possibly represent the upper level of conditions to be encountered.

The only comparable data for allochthonous leaf material are those from the study by Nelson and Scott (1962). It is evident that the range of allochthonous detritus values from Morgan's Creek overlaps the lower end of the range for the Middle Oconee River values. In general, larger streams, somewhat independent of extraneous influences and with appreciable discharges, might be expected to have smaller standing crops of allochthonous detritus than would small creeks. Therefore, it is likely that a thick bed of *Podostemum* growing on the riffle studied by Nelson and Scott acted as a net, which trapped and held more detrital material than normally would be the case. No such holding device was present in Morgan's Creek.

Of 14 measurements made by Neslon and Scott, 11 yielded values less than 500 mg/500 cm^2. These give an average of 250 mg/500 cm^2 (approximately 25 kcal/m^2), which seems much more reasonable in view of the present data. Excluding their extremely high values, which occurred in April and May and apparently were due to catkins, the data of Nelson and Scott give some indication of a seasonal trend for allochthonous plant detritus, with a high in November and a low in June. Nevertheless, the seasonal pattern is much less pronounced than that of Morgan's Creek.

Detritus and the trophic economy of Morgan's Creek

It is apparent from the data already presented that the chief potential sources of food for the primary consumers in Morgan's Creek are included in the suspended particulate, attached particulate, and allochthonous leaf fractions. The importance of each fraction will vary with the feeding habits and food preferences of the organisms. However, on a quantitative basis, allochthonous leaf detritus is by far the most important potential source in Morgan's Creek; in addition to the direct role that it plays, allochthonous leaf detritus also serves as a major reservoir for detrital components of both the suspended and attached fractions. Because of the manner in which the problem was approached, it was not possible to separate the detrital component of the attached particulate matter from the aufwuchs complex. However, consideration of the total cell standing crop and of the composite nature of the attached particulate fraction indicates that the total contribution of the allochthonous materials to the overall economy of the stream is many times that of the aufwuchs community. Though no measurements of algal biomass in Morgan's Creek are available, cell numbers also indicate that the biomass of the algae always was less than that of leaf detritus. These conclusions agree with evidence obtained from field observations.

The trophic economy of Morgan's Creek is built upon two major sources of primary foods: living materials, chiefly diatoms, and nonliving materials in the form of imported leaf litter. Although both energy flow routes exist in the stream, the detrital pathway appears to be by far the more important of the two. Over 95% of the total numerical standing crop of benthic organisms is tied up in the form of herbivores and omnivores (Table II). The most important of these is *Gammarus minus,* which dominated the community in terms of both numbers and biomass. *G. minus* contributed 81·3% of the total number of invertebrates collected during the study, and well over 90% of its diet consisted of detritus. *Asellus,* the second most abundant invertebrate in the stream (3.3% of total), consumed 96–100% allochthonous plant materials. The Ephemeroptera and herbivorous Diptera made up 5·0 and 4·3% of the benthic community, respectively. From 50 to 100% of the foods ingested by these animals was in the form of detritus. The crayfish *Orconectes rusticus* and *Cambarus tenebrosus,* although not numerically so important, were the largest invertebrates in the stream and consumed correspondingly large amounts of food; 30–100% of the food material in their guts was terrestrial leaf detritus.

As could be expected from the fundamental role of detritus as a major source of plant material, its importance permeates the entire community. These relationships are best shown in the form of a food web (Fig. 3) summarizing the principal pathways of energy flow in Morgan's Creek.

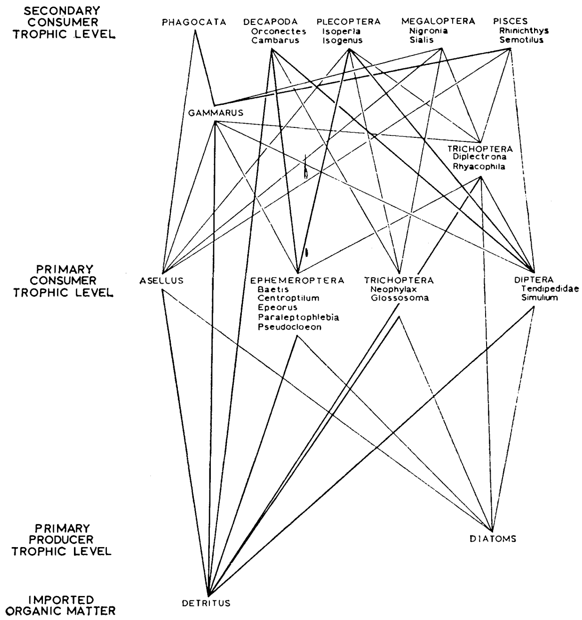

FIG. 3. Trophic structure and major pathways of energy flow in Morgan's Creek, Meade County, Kentucky. The heavy lines designate primary pathways and the lighter lines secondary routes.

Ricker (1934) and Jones (1949; see also Odum 1959, p. 50) used similar diagrams in their interpretations of data from the Mad River, Ontario, and the River Rheidol, Wales, respectively. It is noteworthy that in Morgan's Creek the secondary consumers represent the "top" trophic level and consequently are terminal points in the energy flow sequence.

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