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MICROSESTON DYNAMICS IN A SIMPLE SIERRA NEVADA LAKE-STREAM SYSTEM

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(Accepted for publication October 12, 1967)

Abstract. Suspended organic particles in a small, precipitous drainage were studied primarily in regard to trophic ecology. Headwater and seepage sources in the 6.5-km (4-mile) system contained minimal quantities (< 2 gcal/liter or 0.5 mg/liter dry wt) mainly of organic detritus. Maximum concentration (> 12 gcal/liter or nearly 3 mg/liter dry wt) appeared in the stream as effluent phytoplankton from the single lake located near the headwaters. A progressive decrease in cellular microseston below the lake was accompanied by an increase in detritus. The cell loss was due mostly to trophic uptake by filter-feeding simuliid larvae which were capable of removing 60% of the suspended algae within a 0.4-km section of stream. Downstream gain of organic detritus resulted from external contributions (e.g. streamside vegetation), abetted by decompositional processes within the stream, including digestion by aquatic invertebrates. Autochthonous material was considerably less important quantitatively as seston than allochthonous (lacustrine and terrestrial). Sedimentation and physicochemical loss were secondary to trophic uptake in seston removal. Destruction of cellular material by turbulent flow was directly proportional to stream gradient and was clearly evident only where a prolonged gradient existed in excess of 5%. Because all loss-causing factors operate selectively on cellular material, organic detritus would be expected as the chief microseston component of streams isolated from lake outflow.

INTRODUCTION

One striking difference in the trophic aspect of ecology between limnetic and rapidly flowing waters is that the basic autochthonous production (producer and primary consumer levels) in streams is confined almost exclusively to the substrate. Stream plankton exists only as an accidental member (tychoplankton) of the biocoenosis. Even in the absence of a true phytoplankton population, many stream bottom-dwelling consumers depend directly upon suspended particulate organic matter for nourishment. Therefore, the existence of suspended particles is of considerable importance to stream trophic ecology. Slow-flowing and very large rivers must be excluded from this trophic concept inasmuch as they display character intermediate between lenitic and fast-flowing waters, particularly in having a characteristic potamoplankton population (cf. Williams 1962).

Welch (1952) discusses running waters mostly in terms of rivers, which do not compare in many respects with the mountain stream of this investigation. However, some features mentioned are most pertinent, such as Cilleuls' description of general characteristics of plankton from rivers with rapid flow (Welch 1952, p. 422). The first of these characteristics is: "Presence of mineral and organic detritus which nearly always surpasses the plankton in quantity." Subsequent researchers (e.g., Cushing 1964) have substantiated this observation. Plankton *per se* therefore constitutes the less abundant fraction of suspended matter. In view of this circumstance, it is more accurate to describe the particulate organic matter of stream water as "seston" (cf. Reid 1961, p. 101), thereby including both living and nonliving particles.

A statement of even greater significance (Welch 1952, p. 424) concerns Kofoid's work on the Illinois River before the turn of the century: "Filter-paper catches indicate the presence, on the average, of a plankton 3.3 times the volume of that taken by the silk net. Leakage through the silk

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is therefore a matter of some volumetric importance." This condition is evident in Sierra streams, perhaps even to a greater extent, and probably occurs in most streams. The microscopic component of the seston, or microseston, thus constitutes most of the total suspended organic matter. It is unfortunate that the few published stream seston measurements (e.g., Chandler 1937; Cushing 1964; Peterson 1956) concern net catches that only partly describe its abundance and quality. Some of the most enlightening indications of stream seston quality are to be found among descriptions of gut contents of filter-feeding invertebrates (e.g., Anderson and Dicke 1960; Grenier 1948; Jones 1949, 1950; Peterson 1956), especially with reference to black fly larvae that consume principally microseston.

A general observation from Welch (1952) and other ecological works is that stream "plankton" undergoes progressive downstream changes, usually both in abundance and composition. Hence, there is much interest and discussion on the reasons for such changes.

The first direct approach to stream microseston study made by the senior author was a cursory survey of a 16-km (10-mile) portion of the Convict Creek drainage in the Sierra Nevada Range. The unpublished data indicated striking downstream variations in the concentration and composition of microseston that appeared to result from certain environmental factors (lacustrine influence, topography, streamside vegetation). Thereafter, an investigation was made of the temporal fluctuations of microseston at a single station on Convict Creek that was subject to lacustrine influence (Maciolek 1966). The present investigation was initiated as an extension of these in order to examine microseston in a small, simple drainage where factors of supply and removal might be more discernible and measurable, and where trophic influence could be observed more closely. It concerns Laurel Creek in the central Sierra Nevada, which was studied during the summer and autumn of 1963.

This work constitutes part of the limnological program of the Sierra Nevada Aquatic Research Laboratory, a facility of the U.S. Bureau of Sport Fisheries and Wildlife near Bishop, California. We gratefully acknowledge the aid of the laboratory staff, Messrs. R. S. Nielson, N. Reimers, and H. D. Kennedy, in accomplishing the study and evaluating the manuscript. We are indebted to the following persons for identification of organisms: W. C. Day, Ephemeroptera; D. C. Denning, Trichoptera; C. L. Hogue, Blepharoceridae; S. G. Jewett, Jr., Plecoptera; S. S. Roback, Tendipedidae; B. V. Peterson, Simuliidae; G. W. Prescott, the diatom *Stephanodiscus*.

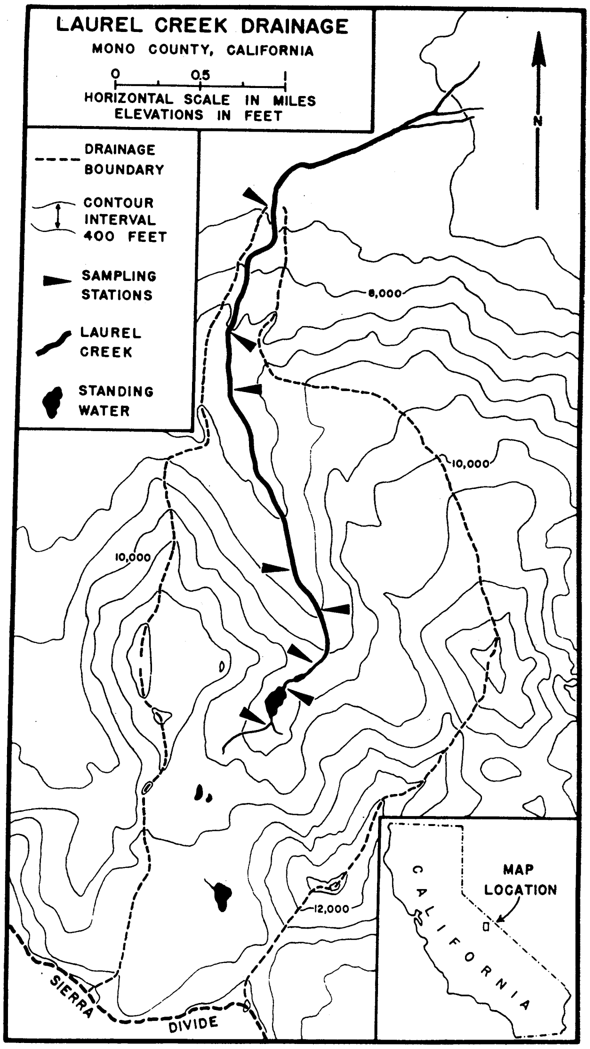

FIG. 1. Topographic map of Laurel Creek drainage.

DRAINAGE BASIN

Laurel Creek Drainage (Fig. 1) is situated along the steep eastern escarpment of the central Sierra Nevada Mountains in Mono County, California. It is a narrow, unbranched basin oriented north-south, with an area of about 2.3 km^2 (6 miles^2). Its southern boundary is the main Sierra Divide, which has an average elevation of 3,506 m (11,500 ft) in this locality. To the north, the basin forms a broad outwash plain, where it joins the upper Owens River valley. This outwash plain has an elevation of 2,200 m (7,200 ft), the lowest of the basin. The highest point occurs at the 3,824 m (12,544 ft) summit of Bloody Mountain, a peak whose sheltered slopes hold perennial snows. The striking surface features shown in Figure 2 are the result of tectonic activity, inten-

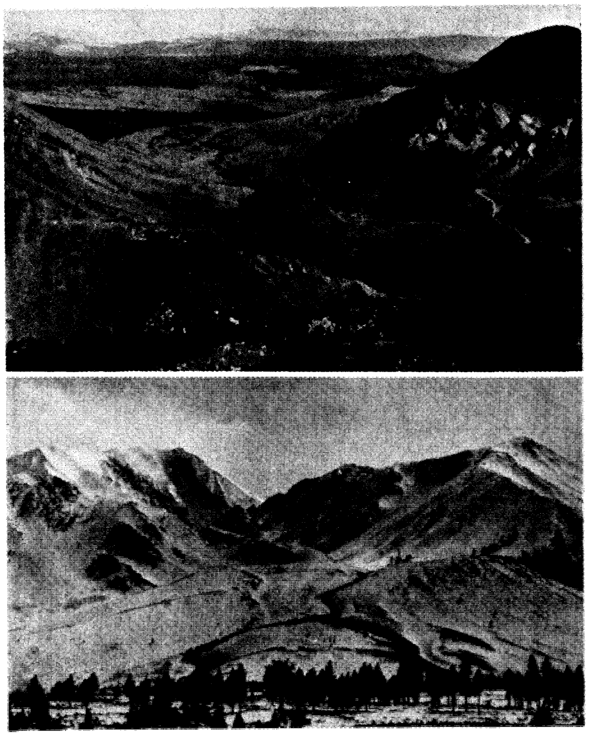

FIG. 2. Views of Laurel Creek drainage. Top (A) Looking north and downstream along the glaciated valley: station C is at pond outlet in bottom center and station G is where arc of terminal moraine disappears behind a lateral moraine in upper center of picture. Bottom (B) Looking south at terminal moraine and upwards toward Bloody Mountain before spring thaw: station G occurs at top of moraine where stream appears, and station H is where stream disappears behind foreground pine trees.

sive glaciation, and substrate lithology described by Rinehart and Ross (1964). The south and west parts of the basin consist of granitic material common to most of the range. The central area displays a contrasting exposure of metasedimentary rock (chiefly hornfels, crystalline limestone, and associated scree) of the Paleozoic age. Mixed alluvium (glacial till and outwash) predominate in the northern part of the drainage.

Much of the terrestrial vegetation is associated with the stream, which is described in detail later. Elsewhere, the vegetation is limited by poor edaphic development and climatic severity. Whitebark pine krumholz (*Pinus albicaulis*) prevails above 3,300 m (11,000 ft). The south end of the basin consists of a porous, boulder-strewn granitic bench containing a few isolated tarns, and a scattering of pines (*P. albicaulis, P. Murrayana*). In middrainage, mature stands of pines and hemlock (*Tsuga mertensiana*) are found. Below 2,700 m (9,000 ft), xeric shrubs such as sagebrush (*Artemisia* sp.), bitterbrush (*Purshia* sp.), and mountain mahogany (*Cercocarpus* sp.) characterize the prevailing semidesert conditions.

Compared to adjacent drainages, Laurel Creek Basin is small and culturally insignificant. Although the upper half lies within the High Sierra Wilderness Area, the basin is not connected with the Sierra trail network. Recreational usage is light, consisting of summer angling, restricted to the lower part of the stream, and fall hunting. Sporadic mining activity (Rinehart and Ross 1964) during the past few decades and occasional use of the main valley as a summer cattle range represent other cultural influences on this otherwise pristine drainage basin.

CREEK AND STUDY AREA

Laurel Creek, has a unique surface flowage compared to adjacent streams which eventually merge into the Owens River system. It arises from springs and seepages at about 3,050 m (10,000 ft) and flows about 8 km (5 miles) to a porous area on the outwash plain at 2,100 m (7,200 ft), where it seeps back into the earth. The portion of stream selected for study, comprising about 6.4 km (4 miles) of this surface flowage, is shown as an annotated profile in Figure 3. A descent of nearly 730 m (2,400 ft) in 6.4 km (4 miles) gives the study stream a precipitous, average gradient of 11%. Stream gradients vary between sampling stations from 1% to 22%. The low gradients occur in the headwater area, which contains the only standing water of the system. The sites of stations A and B were selected for measurement of the influent and effluent of Laurel Lake. It has an area of 3.2 ha (8 acres) and a mean depth of 6.8 m (22.3 ft). Plankton production seems to have increased in recent years, as indicated by increasing turbidity and standing crop, making it

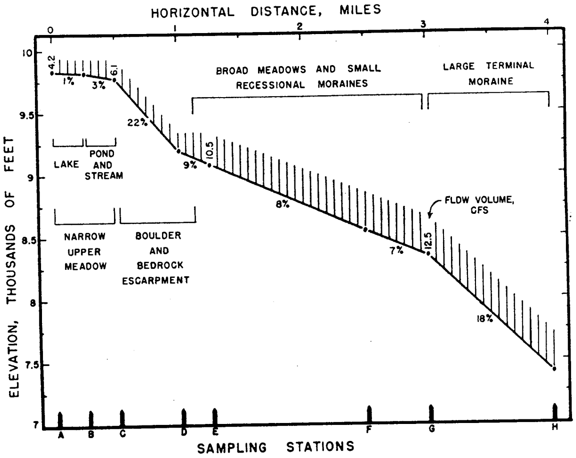

FIG. 3. Profile of Laurel Creek through study area, and average July–August flow volumes as indicated by vertical bars. Included are gradient percentages and descriptions of prominent landscape features.

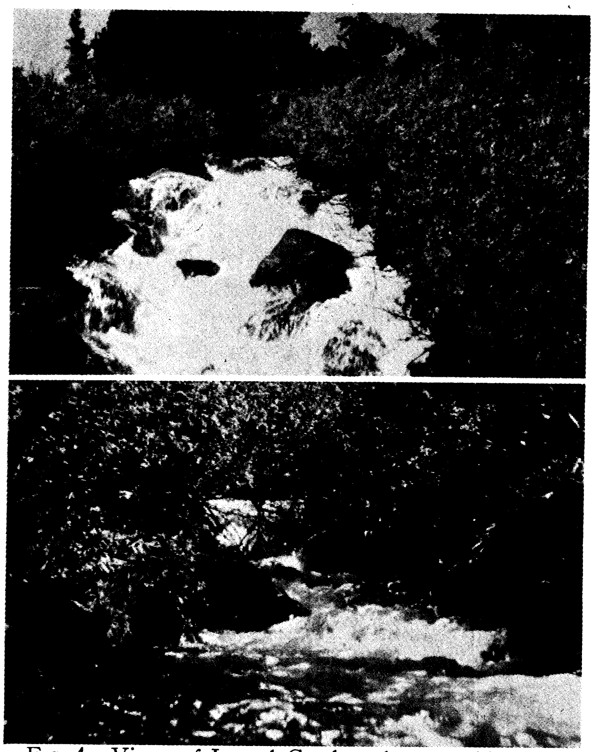

Fig. 4. Views of Laurel Creek and streamside vegetation. Top (A.) Below station C the stream begins descent of escarpment where a moderately dense border of willows occurs and gradient averages 22%. Bottom (B.) Near terminal station H the gradient is 18% and the stream flows under a dense canopy of alders, waterbirches, and willows.

considerably less oligotrophic than other lakes of the area.

Below Laurel Lake, in section B-C, there is a pond of about 0.4 ha (1 acre) in area, which occupies almost one-third of the interstation distance (Fig. 2A). This pond is not considered truly lacustrine because of its shallowness (ca. 4.5 m [15 ft] maximum depth), lack of fine sediments, and high rate of water exchange (a few hours at average flow compared to a few months for Laurel Lake).

The stream next descends a steep escarpment (Fig. 3, interstation C-D and Fig. 4A) and enters a broad, strongly-glaciated valley about 3 km (2 miles) long (Fig. 2A and Fig. 3, interstation D-G). The valley contains meadow areas separated by small, bouldery recessional moraines. The creek meanders slightly in these meadows. Through the final mile of study area (G-H), the stream plunges down the face of a steep terminal moraine with an average gradient of 18% (Fig. 2B).

Streamside vegetation is considered an important source of microseston (Maciolek 1966). It varied considerably in density and type along Laurel Creek. Above station C, there were spotty growths of shrubby willow (*Salix*) and alder (*Alnus*). The stream was partly enclosed by more continuous stands of willow (Fig. 4A) and stunted aspen (*Populus*) between station C and the middle of section E-F. From there to station G, open grassy areas and stands of large aspen occurred. The terminal section (G-H) was densely canopied (Fig. 4B) with alder, willow and waterbirch (*Betula*).

The stream bed is stable, consisting mainly of rubble and boulders with some sandy areas through the meadows. Aquatic vegetation is limited to thin epilithic algal films (diatoms of the genera *Diatoma, Syrnedra, Gomphonema*), occasional trailing strands of filamentous Chlorophyta (e.g., *Spirogyra*) and Chrysophyta (*Hydrurus*), and scattered gelatinous *Nostoc* colonies. Small trout (*Salmo gairdneri* and *S. aqua-bonito*) and char (*Salvelinus fontinalis*) are the only aquatic vertebrates present.

Flow volumes are difficult to measure with accuracy in Laurel Creek, and therefore were determined at only four locations in the study area. These have been averaged for July and August, and extended by interpolation for presentation in Figure 3. Most of the flow originates in the upper third of the study area, primarily around and above the lake but also along interstation section D-E where rivulets and spring seepages join the mainstream over a diffuse area. Seasonal fluctuation is large; maximum flows generally occur in late June or early July, decreasing by half in late August. Late October flows are only 20% or 25% of the maximum runoff. Even at high flows, Laurel Creek appears clear because the water contains little suspended material. Water temperatures varied between 4°C at station A and 13°C at station H during the study period. Chemical constituents of the stream water were not determined but can be inferred from lake-water analyses. One such series was reported by Maciolek and Kennedy (1964), and others were made subsequently. They indicate that the water is of the calcium-bicarbonate type, with pH slightly above neutrality, specific conductance between 62 and 76 micromhos/cm^2, and total dissolved solids between 50 and 62 mg/liter.

Methods

Eight sampling stations were established at 400- to 1,600-m (¼ to 1-mile) intervals along the section of stream between the elevations of 2,200 and 3,000 m (7,300 and 9,700 ft) (Figs. 1 and 3). The two uppermost stations were positioned with respect to the single lake (inlet and outlet);

the remaining six were selected on the basis of major changes in stream biotopes, which are essentially related to topography. Topographic data were obtained from the U.S. Geological Survey, Mt. Morrison Quadrangle, 15-minute series.

Sampling was done on three dates: on 18 July, soon after the lake was ice-free and runoff was near maximum; on 29 August, when summer conditions of warm weather and moderate flow prevailed; and on 23 October, with stream flow low and winter conditions imminent. On all dates, water samples were collected from each station for microseston analysis. In July and August, stream flows were measured at four stations (Fig. 3) with a Price-type current meter, and stream invertebrates were sampled randomly throughout the study area. Most bottom fauna collections were made with a Surber stream-bottom sampler as directed in Welch (1948) at 17 locations in July and 22 locations in August. The bottom sampler could not be used between stations C and D, and at a few other locations, because of the steepness and rockiness of the streambed. In such areas, the stream splashed violently through a jumble of large boulders. Smaller rocks were retrieved from these stream sections, submerged portions measured, and the specimens removed with forceps. These were preserved in 70% alcohol for sorting and enumeration at the laboratory.

Water samples were taken by allowing plastic bottles to fill while held submersed and moved laterally in the current. Samples for compositional analyses were taken in separate bottles and fixed immediately with acid Lugol's iodine (Edmondson 1959, p. 1,200). Sampling was done serially downstream over a period of 4–6 hr. Velocity of the stream below the pond was approximately equal to the collection schedule so that nearly the same watermass was sampled at each of the six lower stations.

Quantitative analyses of total microseston were done by dichromate oxidation of filtered residues, generally following the procedure outlined by Maciolek (1962). The water samples were first prefiltered through a 350-μ mesh screen to eliminate occasional large particles. Volumes of about 400 ml were then vacuum-filtered through prefired, 2.4 cm glass fiber pads (H. Reeve Angel and Co., No. 934–AH), and the residues were oven-dried at 90°C before analysis. Tests have shown that these pads retained at least 95% of the particles present relative to membrane filters of 0.45 μ pore size. Prefiring of the pads, 2–4 hr at dull red heat, was necessary to reduce their inherent oxygen consumption. Pads with residues were oxidized in pyrex test tubes with 1.4 ml of 0.25 N dichromate and 3.0 ml of concentrated H_2SO_4, the reaction being maintained for 3 hr at 100°C. Despite prefiring, the pads retained a small oxygen demand, and it was necessary to add an unused pad to each reagent blank. Values for the oxygen consumed in the reactions were converted to gram calories using the relationship 1 mg oxygen = 3.4 gcal, and then expressed per liter. Less accurate weight conversions (1 mg oxygen = 0.75 mg ash-free organic matter) were also made (for discussion, see Maciolek 1962). The analyses were performed in duplicate for each sample, with an average precision within ±4% and an estimated (caloric) accuracy within ±10%.

Compositions and area-weighted numerical abundances of the microseston were determined from microscope mounts of filtered residues. Slides were prepared by filtering 50- to 150-ml portions of the fixed samples through standard 25-mm membrane filters (Millipore Filter Co., Type HA), staining the residues with fast green, flushing them with 25% clear corn syrup, and mounting them under cover slips in undiluted syrup. This technique was expeditious in preparing slides and produced semipermanent mounts of fair quality. However, the membrane base was initially foggy and required curing by diffusion loss of water for a few weeks before the material could be examined critically. Osmotic differences may have induced an initial plasmolysis in some algal cells, but they apparently regained turgor and form during the curing period, with no evidence of damage. In the determination of simuliid food habits, slides were prepared in the above manner from aqueous suspensions of the combined digestive-tract contents of several larvae selected at random.

Microseston particles were enumerated in both quality and size categories, size referring to the approximate area occupied by each particle viewed. Thus, abundant species of algae were tallied individually and their areas calculated. Less abundant forms of algae and detrital material were tallied separately in three diameter classes: $< 10\ \mu$, 10–25 μ, and $> 25\mu$. An average area was assumed for each particle in its class. Ten or more fields of view were counted on each slide, depending upon particle density. The result was an area-weighted count which yielded semiquantitative information on the composition of microseston. These counts were calculated to a per-liter basis to enable interstation comparisons. Three compositional categories were ultimately established: diatoms (the most abundant algae), other algae (but including occasional microzoans), and organic debris.

TABLE 1. Taxonomic list of aquatic invertebrates and their relative numerical abundances in Laurel Creek on July and August sampling dates

Aquatic invertebrates	Stream sections[a] sampled July 16				Stream sections[a] sampled August 21			
	A	B-D	D-G	G-H	A	B-D	D-G	G-H
Filter feeders:								
Diptera								
Simuliidae								
Simulium arcticum								
Simulium canadense	+	numerous				very numerous	++	++
Prosimulium onychodactylum								
Trichoptera								
Hydropsychidae								
Arctopsyche sp.		+	+				+	
Nonfilter feeders:								
Diptera								
Blepharoceridae								
Agathon comstocki				+				
Deuterophlebiidae								
Deuterophlebia nielsoni							+	
Tendipedidae								
Diamesa nr. *nivoriunda*	++	+++	+		+	+	+++	+
Tipulidae								
Tipula sp.	+							
Ephemeroptera								
Baetidae								
Ephemerella doddsi			+				+	
Ephemerella coloradensis							+	+
Ephemerella hystris		+	+					
Baetis bicaudatis?	++	++	++	+			+	
Baetis sp.?					+	++	++	++
Heptageniidae								
Rithrogena brunnea?			++	+				
Iron longimanus		++	+			+	++	+
Iron sp.						+	++	
Plecoptera								
Nemouridae								
Nemoura frigida		+	+				+	
Perlidae								
Acroneuria californica			+			+	+	
Trichoptera								
Limnephilidae								
Ecclisomyia bilera (Larvae and pupae)	+	+	++			+	+	+
Rhyacophilidae								
Rhyacophila sp.	+	+	++		+	+	++	
Glossosoma alascense (larvae and pupae)			+				++	
Amphipoda								
Gammarus sp.						+		
Hydracarina	+							
Nematoda		+					+	
Oligochaeta		+				+		
Tricladida								
Dugesia sp.	+		+			+		+

[a] Compare with Figures 1 and 3

In addition, proportional counts were made for two diatoms in order to evaluate their downstream changes in abundance. Viable *Stephanodiscus* cells (i.e., with protoplasm) occurring at each station were calculated as the percentage of total (with and without protoplasm) *Stephanodiscus* frustules observed. Similarly, intact *Asterionella* frustules at each station were enumerated as the percentage of total frustules (intact and broken) present for that diatom. Such ratios were independent for each station and resulted in an enumeration that avoided the various errors associated with "counts per unit volume", including dilution and possible loss by sedimentation.

INVERTEBRATE FAUNA

The bottom fauna of Laurel Creek was surveyed to determine taxonomic composition and abundances, inasmuch as these factors are of great importance to the trophic structure of the stream. Difficulties of collection (see Methods) and inadequacies of sampling techniques permitted the establishment, only in a very broad manner, of relative numbers of the faunal forms at different locations in the stream. These data are presented in Table 1. Organisms are listed taxonomically as either filter feeders or nonfilter feeders, according to feeding habits described in the literature (Hynes 1961; Jones 1950; Pennak 1953; Usinger 1956). Although food habits of stream fauna have been described similarly, it is not possible to list them with certainty without examination of the organisms' gut contents. Many forms apparently change diets according to available food (Jones 1949, p. 151; Jones 1950, p. 169; Slack 1936, p. 107–111; Ross 1944, p. 4).

Occurrence and relative abundance of each organism in different stream sections are indicated in Table 1 by plus signs. This tally is based on the number of individuals found per unit area of substrate, ranging from scarce (+) to abundant (+++). Two dipterans were among the most numerous forms: *Simulium arcticum,* described in detail below, and *Diamesa nivoriundo,* which occurred in silty tubes on the surfaces of submerged rocks. Other organisms found most frequently were mayflies in the genera *Baetis* and *Iron.*

Suspended organic matter is utilized directly by that group of stream fauna usually referred to as passive or filter feeders. This survey of macrofauna included two forms of possible significance; net-spinning caddisfly larvae (Hydropsychidae) and black fly larvae (Simuliidae). However, the utilization of microseston by hydropsychid larvae in Laurel Creek is questionable. Close inspection of their net structure indicated minimum apertures, on the order of a few tenths of a millimeter, sufficiently large to pass the particulate matter considered here as microseston. Moreover, dissection of a few larval caddis guts showed that they had been feeding on large particles, consisting of entire or fragmented insects and relatively large strands of filamentous algae.

Simuliid larvae are considered by many to feed indiscriminately on suspended particulate matter by means of their head fans (Grenier 1948, p. 302; Jones 1950, p. 170; Puri 1925, p. 298; Tonnoir 1925, p. 216; Zahar 1951, p. 41). Exceptions to this opinion (e.g. Petersen 1956), suggest that abnormal conditions and possible insufficiency of suspended food may cause the larvae to feed by means other than filtration. One qualification to the indiscriminate feeding habit was noted by Anderson and Dicke (1960), who reported larvae rejecting "larger" particles. That the filter fans of these insects are effective in straining the most minute particles from water is evidenced by Fredeen's (1964) successful culturing of these larvae on suspensions of yeast and bacteria. Thus, simuliids can be considered as prime utilizers of microseston.

FIG. 5. Simuliids in late August. Top (A.) Larvae and some pupae on metasedimentary rock from vicinity of station B. Bottom (B.) Larvae on aluminum plate removed from stream bed near station F.

Larval simuliids are common in Sierra streams. Their abundance and distribution in Laurel Creek during this study were important in determining the trophic relationship of microseston. The impossibility of precise or even reliable sampling, a problem discussed by Zahar (1951), necessitates a description of their occurrence in relative terms. In July, they occurred in moderate abundance in the upper portion of the stream but were scarce in the lower part. By late August, however, extremely dense populations appeared locally, chiefly within section B-C. A simuliid-encrusted rock, removed from the stream bed at station B, is shown in Figure 5A. Most stream rubble in that locality, as well as submerged willow branches and roots, and trailing strands of filamentous algae were coated similarly with larvae and a few pupae. It was noted that these larvae showed a distinct preference for the dark metasedimentary rocks which were more numerous than whitish granitic rocks at that location. Larvae were also quite abundant in the lower half of the study area in late August. Figure 5B illustrates larvae occupying a discarded aluminum plate in the vicinity of station F. It was the only instance noted where larvae showed preference for a light-colored substrate, suggesting that surface texture may be an important attachment factor. Such larval densities occurred locally in the lower stream area, but never as extensively as in section B-C. By October, virtually all the larvae in section B-C had pupated and most of these had emerged. At that time, simuliid larvae were rare above station D, but moderate to large numbers prevailed below station E. In general, considerable temporal and local variations characterized the simuliid populations of the creek during the 14-week study period.

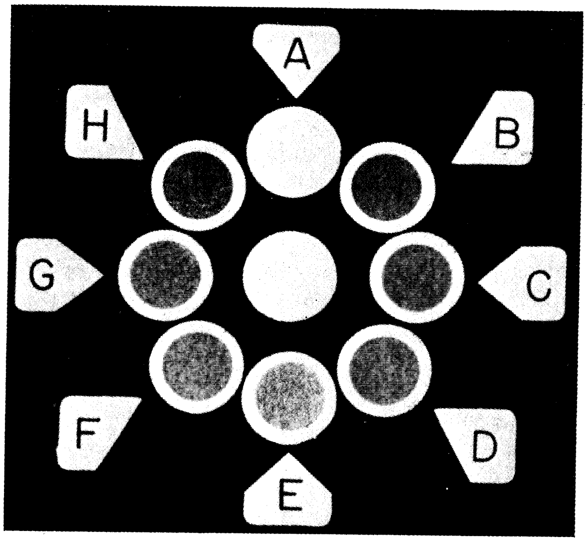

Fig. 6. Glass fiber filter pads with residues from equal volumes of water taken in October from each station. Unused 2.4 cm pad appears in center.

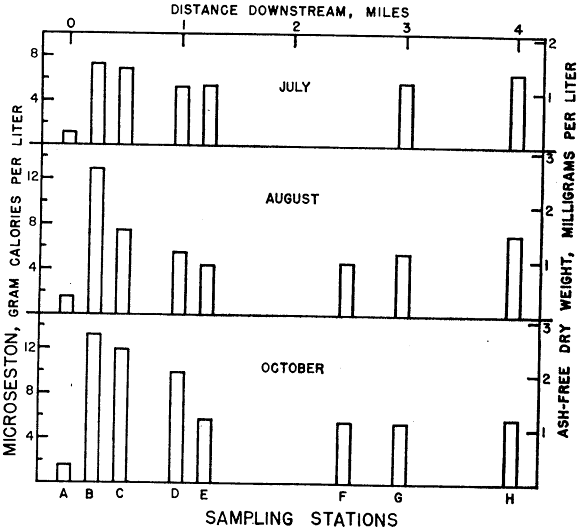

Fig. 7. Concentrations of microseston at each station for each sampling date as determined by quantitative oxidation. Ordinates are scaled for organic energy content (left) and its approximate weight equivalent (right).

Microseston Abundance and Composition

A rough approximation of the abundance and composition of microseston occurring at each station was apparent by visual comparison of the residues filtered for quantitative analysis. One such series of fresh residues (October) is shown in Figure 6. Lake inlet water (station A) contained only a few humic-brown detrital particles. Effluent lake water (station B) produced a dense yellow-green residue of phytoplankton. The intensity of algal pigment color decreased progressively at succeeding stations, and the brownish hue increased with increasing numbers of humified detrital particles. At station H, the residue was a rich, medium-brown color, and photosynthetic pigment was no longer apparent. Thus, residue color differences represented changing microseston qualities, and the amounts (thicknesses) of residues on the filters suggested relative quantities.

More precise quantitative estimates, obtained by oxidative analyses of such residues, are given in Figure 7. Microseston concentrations are indicated as energy units (gram calories per liter) on the left ordinate, and their approximate weight equivalents are scaled on the right ordinate. Laurel Lake, although oligotrophic, had a profound influence on the downstream abundance of microseston. Approximately seven times as much particulate matter existed in the effluent stream during the season as in the inlet water. Extreme values for these locations are 1.2 gcal/liter in the inlet water at station A in July, and 13.2 gcal/liter in the outlet water at station B in October. The lower concentration of microseston in lake effluent water (B) in July compared to the later dates reflects mainly the greater water discharge early in the season. For the rest of the stream, the patterns on all three dates exhibited a general similarity, with maximal values at station B, decreasing downstream toward the middle of the study area, and then increasing to the terminal station (H). The most striking change in microseston quantity was a sharp decrease between stations B and C in August, which was not evident in July or October.

The preceding description of microseston quantities deals with concentrations, or relative abundances. In a strict sense, such values cannot be used to compare accurately different locations or different sampling dates when the volume of flow has changed. A condition of changing flow existed in Laurel Creek as both downstream and seasonal flow fluctuations did occur. It is important to note that much of the downstream flow increment concerned water with a paucity of microseston, similar to that at station A. The resulting dilution of mainstream microseston caused an apparent reduction when its abundance was measured as concentration. Required, then, is a measure of absolute abundance. This problem was treated briefly by Maciolek (1966), wherein absolute quantity was expressed as discharge, or amount of microseston passing a given point on the stream per unit time (i.e. gcal/sec). In other words, concentration times flow volume eliminates the relative (unit volume) factor.

The accuracy of absolute abundance measurements in Laurel Creek is limited by flow estimates, which are much less accurate than concentration determinations. The flow data in Figure 3, however, suffice to permit a general description of absolute abundances. By combining and rounding off the average flows and microseston concentrations for the July and August dates, the following downstream pattern for relative and absolute abundances is derived:

Station	Concentration *gcal/liter*	Discharge *gcal/sec*
A	1.5	180
B	10.0	1,600
C	7.0	1,200
D	5.5	1,000
E	5.0	1,500
F	—	—
G	5.5	2,000
H	7.0	2,400

Comparing the concentrations and the discharge for the same stations, note that the overall downstream pattern does not change much except that discharge shifted the minimum midsection abundance in an upstream direction. More important, however, is the greater amount of microseston appearing as discharge in the terminal portion of the stream. Expressed as concentration, station H was equal to station C, but actually it had twice the absolute amount of C because of doubled flow volume.

It is possible to view microseston concentrations in Figure 7 grossly as discharges by assuming and applying flow factors for each sampling date. July flow was about twice the volume of that in August and about four times the October volume. Approximate July, August, and October discharges are thus obtained by multiplying the concentration values by 4, 2, and 1, respectively. Discharges derived in this manner were somewhat greater in July than in August and considerably larger than in October. In assessing the relative merits of describing microseston abundances as either concentration or discharge, it should be remembered that the two show no difference in a situation of unchanging flow volume. Since the concentration of organic particles can be measured more precisely and with greater facility, and because it is very likely a more significant factor to the consumer organisms than is discharge, concentration would appear to be generally the more useful and important measure of microseston abundance.

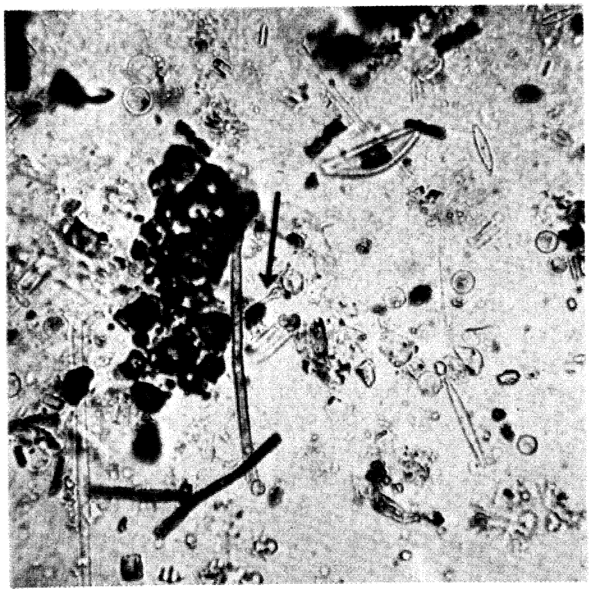

FIG. 8. Photomicrograph of microseston at station H in July. Arrow is 40 μ long and indicates end of broken *Asterionella* frustule partly obscured by detritus. Small circles are *Stephanodiscus* frustules in valve view (rectangular in girdle view).

Microscopic appraisal of the slide-mounted microseston showed a variety of particle types, such as bacteria, intact and empty algal cells, pollen exines, epithelial plant tissue, rhizoids, appendages and other exoskeletal fragments of invertebrates, and a large amount of unidentifiable (probably humified) organic debris. A representative view of such material appears in Figure 8. For convenience in enumeration and description, the particles were classified into one of three major component groups as described in Methods and indicated in Figure 9. The composition and abundance of the microseston at each station for each sampling date are shown here. Areas of the circles are proportional to the total amount of micro-

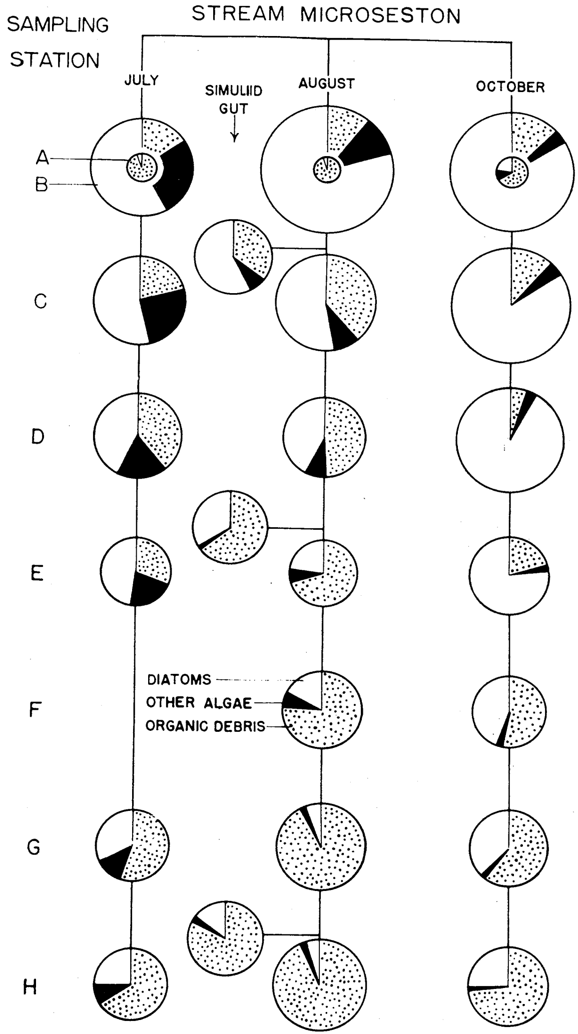

FIG. 9. The composition of microseston at each station and of simuliid larvae digestive tract from three locations in the stream. The areas of the circles, except those for the simuliid larvae, represent abundance of particles determined by area-weighted microscopic counts and are partitioned into three major particle classes as indicated at station F and described in text.

seston as determined by the previously described area counts, giving secondary (semiquantitative) measures of relative abundance which agree quite closely with the concentration patterns established by dichromate oxidation shown in Figure 7.

The circles are, in effect, pie charts with each sector proportional to the amount of microseston in each major component group. They show the nature of downstream changes in microseston composition, as suggested by the gross appearance of filtered residues of Figure 6. Lake inlet water (A) contained mostly detrital particles, and cellular material predominated in the outlet (B). The extremes in numbers of cells occurred between these two stations, the averages being 1.4×10^5 cells per liter of inlet water and 3.42×10^7 cells per liter of effluent water. Downstream from the lake, there was a progressive diminution of cellular particles with a concomitant increase in debris. This cell loss was most severe in August immediately below the lake and in the lower half of the study area in October. The gain in debris was sufficient to cause its predominance at the lowermost two or three stations on all sampling dates.

Included in Figure 9 are the seston components of simuliid guts from three locations to illustrate their nonselective feeding in Laurel Creek. The areas of these circles have no significance. The importance of simuliid feeding upon microseston is considered in the following section of this report.

MICROSESTON LOSSES

One of the most striking features of the Laurel Creek microseston pattern was the downstream decrease in the concentration of cellular material that originated in the lake. This loss can be attributed, *a priori,* to trophic utilization by stream invertebrates, to sedimentation, and to physical damage incurred during turbulent transport. In assessing the fate of effluent limnoplankton in Michigan streams, Chandler (1937) considered dilution as a loss factor. As was pointed out earlier, however, dilution only causes an apparent loss when particulate matter is measured in terms of relative abundance.

It is possible to describe instances of true loss from the data of this study. The circumstances permitting this evaluation were a temporary fluctuating population of seston feeders (simuliids), large differences in water turbulence among the interstation sections, and an abundance of certain easily recognizable diatoms in the lake effluent. Since these diatoms were purely of lacustrine origin, it was possible to use them as index particles in evaluating losses below station B. It is apparent that losses described only by selected cellular components represent isolated cases. But it is believed that such cases, with due consideration, can be extended to the evaluation of losses of other microseston components.

Trophic utilization

The trophic uptake of suspended particles was closely related to the presence of simuliid larvae, which were the most abundant and singularly important seston feeders in Laurel Creek. Nonselective food intake of these larvae has been established both by literature consensus and by examination of digestive tracts of Laurel Creek simuliids. Figure 9 shows the composite contents of several larval digestive tracts selected randomly

FIG. 10. Gross appearance of simuliid digestive tracts from three different stream locations indicating nonselective feeding upon available microseston. White particles are bleached algal cells, dark particles are humified detritus. Compare with sampling locations and compositions of the simuliid digestive tracts in Figure 9.

without regard to speciation. Actually, nonselective feeding was apparent even from the gross appearance of the larval guts taken from different locations (Fig. 10). Preservatives had bleached or leached the pigments from algal cells but had not altered the brown color of organic debris. In the vicinity of station B, digestive tracts were white because the microseston was nearly all cellular material. At station D, they were light brown owing to an admixture of cellular and detrital particles. The digestive tracts at station H were dark brown because they contained mainly humified detritus.

The centric diatom, *Stephanodiscus,* was selected as an indicator of trophic uptake because of its robustness and abundance in lake effluent water throughout the study period. *Stephanodiscus* cells, which were probably alive in the stream, could be distinguished from the empty frustules by the presence of intact, organized protoplasm. Empty frustules were assumed to have resulted primarily from consumer ingestion. That these diatoms were affected by simuliid digestive processes was indicated by the disorganization of protoplasm in all such cells dissected from the larval guts. Ratio counts were made of intact cells to total frustules (intact and empty) on all samples from station B downstream, yielding an independent estimate of intact cell percentages for each location. The patterns of progressive downstream loss of intact *Stephanodiscus* cells for each sampling date are plotted in Figure 11. Loss curves are supplemented by bar graphs showing the magnitude of each interstation decrease. In July, when runoff was high, cell concentrations low, and fly populations moderate, a small but progressive downstream decrease of intact cells occurred. This loss totaled less than 20% at station H. The decrease in section B-C at that time was slight (3%). Cumulative decrease in August was more than 90%, 60% of which occurred in section B-C, where extremely dense populations of simuliid larvae were noted. Significant losses of *Stephanodiscus* cells also were sustained in sections E-F and F-G. October's cumulative decrease was 42%; none of this loss appeared in section B-C, from which simuliid larvae had disappeared. Larvae were still abundant in the lower part of the stream, where cell losses remained high. Nearly all of the cells leaving the lake (station B) were intact in July and August, but only 84% were intact in October. This difference suggests that the lake population of this algal species was approaching senescence on the latter date.

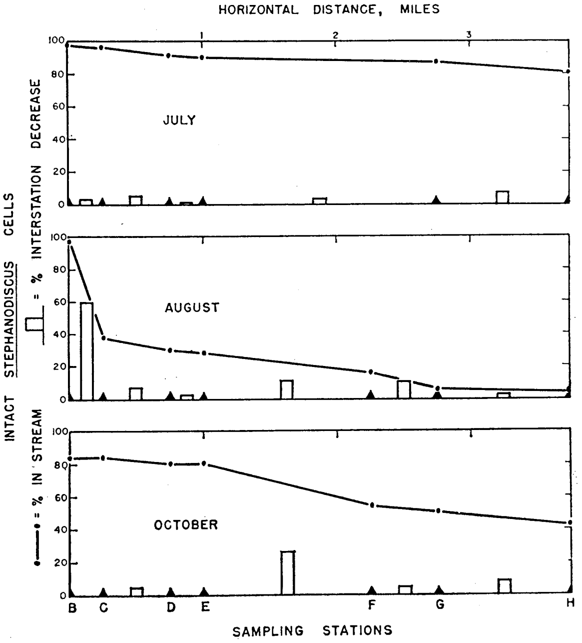

FIG. 11. The percentages of intact *Stephanodiscus* cells in Laurel Creek on the three sampling dates, showing changing trends in downstream decrease. Included are bars indicating the magnitudes of individual interstation decreases.

At the time of maximum consumer influence (section B-C, August) intact *Stephanodiscus* cells decreased by 60% within a 400-m (¼-mile) stretch of stream. This loss rate was unusually large, as was the density of simuliid larvae at that time and location. Below station C in August, cells decreased at the rate of about 10% per 1.6 km (1 mile). A similar loss rate occurred in October downstream from station E. In both instances, simuliid larvae were present, but not in exceptionally large numbers. A loss rate of 10% per mile, therefore, would appear to represent the normal stream situation.

Physical damage

The *Stephanodiscus* cells described above appeared morphologically robust and thus resistant to breakage during turbulent downstream passage. However, small losses were observed (Fig. 11) on all dates in section C-D and G-H, and two factors suggest that these losses might be due mainly to mechanical damage. First, trophic uptake varied among the sampling dates, especially above station D, and can be discounted as a continuous cause. Second, these two sections have the steepest gradients (22% and 18%; c.f. Fig. 3) and therefore the greatest turbulence. If *Stephanodiscus* is resistant to damage by such turbulence, the effect should be more apparent upon a more delicate algal form. *Asterionella* was selected as the index for this evaluation. Like *Stephanodiscus,* it is an obligate limnoplanktonic diatom. It is, however, very different morphologically, being elongate (pennate), and occurring in fragile radial colonies. It was abundant in the stream only in July, when flow volume was maximal and *Stephanodiscus* losses were minimal.

Asterionella ratio counts were made for each station, both of the number of isolated frustules (i.e., not in colonies) relative to the total number of all frustules, and of the number of intact frustules relative to the total number of frustule pieces (entire and fragmented). Although these two counts gave similar results, the colony count was considered less reliable because of low numbers toward the terminal end of the study area. Moreover, it seems possible that colony disruption could have resulted from digestive processes but rather unlikely that passage through an invertebrate alimentary tract would cause individual frustule breakage.

Results of these counts are given in Figure 12, as percentages of intact frustules present (solid curve) and as interstation losses (bars). The stream profile curve (dashed) is included to show the relationship between gradient and cell loss. Cumulative loss through the study area totaled nearly 60%, or about 9%/km. Highest interstation losses were in C-D (24%) and G-H (19%) where gradients were 22% and 18% respectively. In the relatively flat (8% gradient) section E-G, the loss rate was only 2.5%/km. The close, direct relationship of *Asterionella* loss to stream gradient supports the contention that water turbulence caused the observed frustule breakage.

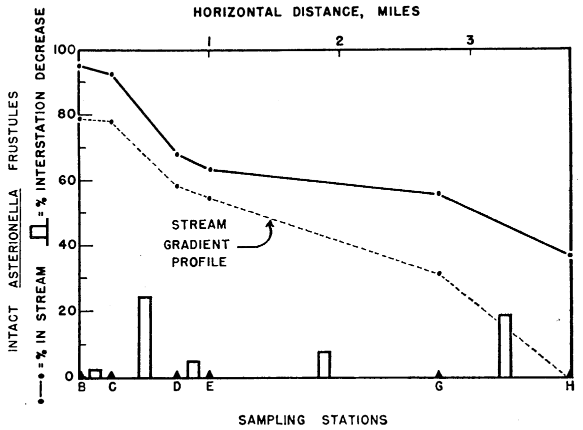

FIG. 12. The percentages of intact *Asterionella* frustules along the study area in July. The stream profile is included for comparison with downstream decreases.

Sedimentation

The significance of sedimentation as a loss factor rests in part on empirical evidence. In a turbulent, steep-gradient stream such as Laurel Creek, a minimum amount of sedimentation would be expected to occur. Throughout the study area, there were neither obvious extensive accumulations of low-density particles (viz., organic), large or small, nor of fine inorganic material such as silt. Thus, scouring rather than accumulation appears the dominant influence.

The morphology of Laurel Creek suggests but one location where sedimentation of microseston might have occurred in measurable magnitude: the pond area occupying about a third of the length of section B-C. The low mean gradient of this section (3%; cf., Fig. 3) is due largely to the pond's presence. When trophic losses from simuliid filtration were minimal, in July and especially in October, the concentrations of total microseston (Fig. 7) decreased in section B-C by 5.5% and 10%, respectively. Since there was little apparent gain in flow volume within this section and therefore no dilution of the observed concentrations, it is believed that these decreases represented sedimentation losses. The fact that runoff and turbulence were much higher in July when the decrease in microseston was lower, and vice versa, reinforces this premise. Even in a location so conducive to sedimentation as B-C, the observed losses were small. This suggests that, in the entire stream, sedimentation was relatively unimportant.

DISCUSSION AND CONCLUSIONS

Precise evaluation of the quantity of microseston in Laurel Creek is difficult because of the temporal and spatial fluctuations in flow volume, and because significant additions or losses of particulate matter can occur within a short length of stream. Two measures of abundance have been considered: relative abundance as concentration, and absolute abundance as discharge. Microseston concentration, which can be readily measured with considerable accuracy, is useful in describing the quantity occurring at a specific time and place, and therefore in making general comparisons within or between streams. It provides a useful characterization of the trophic status of suspended matter whose uptake is related either to filtration of certain water volumes, or to contact of water with substrate. However, with changing flow conditions, a critical description of the dynamic state of microseston can be made only on the basis of an absolute abundance such as discharge. The difficulty in making flow measurements precluded accurate discharge determinations, necessitating the description of temporal and spatial microseston variations by an appraisal of supply and removal factors.

Sources of microseston were not studied directly, but can be deduced from the data in Figure 9. These sources were analyzed in previous work (Maciolek 1966). They may be considered as local or diffuse, cellular or detrital, and autochthonous or allochthonous. Throughout the study area microseston was added either as cellular material dislodged from the substrate aufwuchs (autochthonous) or as organic debris primarily of terrestrial origin. Autochthonous stream material, however, was not considered important quantitatively, probably at maximum comprising no more than 10% of the total amount observed. Organic debris, associated mainly with streamside vegetation, may be added directly as microseston or indirectly via decomposition and fragmentation of the larger particles decomposing within the stream. Some of this detritus, however, originated through metabolic activity of stream fauna (e.g., fecal discharge, ecdysis). In the Laurel Creek system, lake production provided a highly localized supply of cellular material. Lacustrine discharge dominated the microseston for 3–4.5 km (2–3 miles) below the lake. Only in the terminal portion of the stream (stations G, H) did lacustrine influence diminish to the point where detritus assumed quantitative preponderance characteristic of the "true" stream environment (Cushing 1964; Maciolek 1966).

The loss of particulate matter is considered to result from three factors: trophic uptake, physical damage, and sedimentation. These operated continuously throughout the environment, but often in increments so small that assessment of their relative importance was difficult. Independent evaluation of a loss factor became possible only when localized and of sufficient magnitude to enable detection by the methods employed. In this study, specific index organisms were used to identify two of the loss factors. They are isolated instances of considerable magnitude, and therefore require some qualification and elaboration to place them properly in the overall pattern of seston removal.

One qualification in the use of diatom ratio counts applies to both trophic uptake and breakage. Intact *Stephanodiscus* frustules are composed of two halves which frequently separate when the cell is destroyed. These individual valves are not readily distinguishable from empty entire frustules, under cursory microscopic examination. Similarly, *Asterionella* frustules break into pieces recognizable by their single bulbous ends. The resulting increase in numbers of enumerable entities would thus serve to exaggerate the degree of digestion or breakage in the ratio counts. However, these exaggerations appeared to be partly, if not mostly, compensated by the tendency for some of the thin half-frustules or small fragments to pass unnoticed in field counts while intact units rarely were unobserved (judging from replicate counts of a single field).

Trophic utilization of microseston, described here by the loss of *Stephanodiscus* in the presence of a varying simuliid population, represents a much broader circumstance. On one hand, all particles appear to be ingested by passive feeders; on the other, microseston feeding is not limited to simuliids. Observation and inference indicate the presence of other passive feeders (e.g., other insects, ciliates, rotifers, pelecypods, oligochaetes) which, in total, have a broader but less dense temporal and spatial distribution. The simuliid utilization of microseston is imposed on a background of other trophic uptake, whereas the loss of *Stephanodiscus* can only be attributed primarily to simuliid feeding.

Digestibility of microseston is a second qualification, for ingestion alone does not represent permanent loss. Diatoms did appear to be digested by the simuliids in this study. Prowse (1964) stated, in connection with planktivorous fish, that "Diatoms are commonly digested, leaving empty frustules . . ." and further discussed the variable digestibility of other algal types. It is assumed that other diatoms of Laurel Creek would also have been digested. Since diatoms formed the bulk of cellular microseston, most of the cellular material enters the trophic cycle.

The nonliving fraction of the microseston probably does not enter the trophic cycle to the same extent. Jones (1950) considered detritus nutritionally inferior to living algae. In Laurel Creek, organic debris seemed to consist largely of resistant material such as cellulose, lignin, and chitin. Much of this already had been exposed to humification or digestive processes of stream invertebrates. Although plankton-rich (lake-effluent) water is favored by passive-feeding insects (Illies 1956; Müller 1955), it cannot be assumed that organic detritus is without nutritional value. Many stream invertebrates are considered as detritus feeders (Jones 1950) and may reach greater numbers in association with detritus (Egglishaw 1964). Possibly, the microflora commonly associated with this detritus (Rodina 1963; Darnell 1964) is the actual nutritional source. It appears that much of the ingested detritus passes undigested back into the stream following excretion. The net effect on total microseston would thus be a disproportionately greater loss of cellular material following ingestion, a situation favoring the eventual predominance of detritus in the stream microseston.

The exceptionally high loss incidence of *Stephanodiscus* (15% per 100 m) we attribute to trophic uptake. Also attributable to this factor is the average loss of 3–6%/km of stream. This loss occurred in about 1 hr at average water velocities.

The breakage of diatom frustules relative to stream gradient was the criterion used to exemplify microseston removal by turbulent physicochemical influence. In a broad sense, physicochemical losses also would include dissolution and aerobic decomposition of labile organic particles in the oxygen-saturated water. But these effects could also promote fragmentation of larger debris particles into smaller ones, thereby contributing to the microseston. Thus, water turbulence is a factor which may operate to increase as well as diminish the amount of suspended organic matter.

In the relatively silt-free water of Laurel Creek, the main causal factor inducing fragmentation is believed to be the stress associated with turbulence (compression, decompression, and shearing), rather than the grinding described by Galtsoff (1924). *Asterionella* was considered susceptible to such destruction because of its shape. Larger elongate diatoms (e.g. *Synedra*) and filamentous algae would seem similarly vulnerable. Most sestonic algae of Laurel Creek were small unicellular forms that probably were influenced much less by turbulence. Degree of turbulence relates to the static factors of gradient and bottom roughness, and to variable flow volume (i.e. velocity). *Asterionella* losses averaging about 10%/km (15%/mile) (Fig. 12) were observed at the time of greatest flow volume and were proportional to the gradient. This combination of a susceptible organism and a time of greatest stream turbulence probably represents an instance where physicochemical loss in Laurel Creek was maximal.

The direct relationship between frustule breakage and stream gradient noted in Laurel Creek raises a question concerning the minimum gradient at which such breakage occurs. Barry (1962) found effluent limnoplankters generally undamaged after turbulent passage in a Colorado mountain stream. Observations on Convict Creek (Maciolek 1966) indicated that at time of maximum runoff, *Asterionella* survived transport through 5 km (3 miles) of 4%-gradient stream with little apparent damage. A small loss of *Asterionella* was noted in Laurel Creek where the gradient was only 3%. However, over one-third of this section is occupied by a pond; the remainder has a gradient of about 5%. Considered together, these observations suggest the existence of a critical gradient of at least 5% where cell breakage begins. It is obvious that the length of a stream section as well as its gradient must be considered, for even low-gradient streams have points of cascading turbulence. Apparently, a close succession of such places over a prolonged distance is necessary to produce measurable loss. The shortest stream sections considered here are 400 m (¼ mile). Therefore, the proposed "critical gradient" would not be expected to apply to stream sections much shorter than this.

Removal by sedimentation, in the present context, includes settling under gravitational influence as well as adhesion to stationary surfaces. These two factors accounted for nearly all plankton loss in Michigan streams reported by Chandler (1937). In his study, low water velocities and an abundance of aquatic vegetation, which provided vast surface area, were the principal causal conditions. Such conditions are absent in Laurel Creek, and the extent of sedimentation loss was difficult to assess. The single example, a loss of 10% of total microseston in section B-C in October, was probably due to settling of particles in the only large, quiescent area of the stream. It is likely, however, that some microseston must have adhered to the aufwuchs or precipitated in the niches beneath and between boulders and rubble. Although such material may be temporarily or permanently lost as microseston, it remains within the trophic structure of the environment. The extent of removal by sedimentation can be surmised as intermediate between direct trophic uptake and physicochemical losses.

The conditions of stream sedimentation described elsewhere (Maciolek 1966) also apply to Laurel Creek. For example, localized sedimentation is enhanced by decreasing flows or low steady-flow conditions, which occur in late fall and winter. Sedimentation has been observed for larger organic material (leaves, twigs, etc.); thereafter, sharply rising flows can resuspend most of this material, which has undergone partial decomposition during the quiescent interim. Thus, sedimented macrodebris when resuspended in turbulent water can fragment to increase the amount of detrital microseston at times of rising flow.

Thus the changes in abundance and quality of Laurel Creek microseston resulted from dynamic conditions of the environment. The changing status of microseston is most readily explained by the agencies affecting its supply and removal. The sources in decreasing order of importance, were: 1) effluent limnoplankton, a localized contribution of diatom-rich phytoplankton, which provided a large and continuous supply of cellular material, and was the dominant microseston component in the upper two-thirds of the drainage; 2) terrestrial (especially streamside) vegetation, a diffuse source of organic debris, which became more important quantitatively at the lower end of the stream; 3) stream-produced (autochthonous) material, mostly algal cells from epilithic communities, which was supplied in small quantities throughout the water course.

Microseston losses resulted from the following factors, also listed in decreasing order of importance: 1) Trophic utilization by filter-feeding invertebrates, although a nonselective removal, favored ultimate permanent loss of cellular components because of their greater digestibility—it occurred throughout the stream but was locally pronounced according to the periodicity and distribution of exploiting consumers. 2) Sedimentation, including settling and adhesion, favored removal of larger, denser particles and showed seasonal variation in being more pronounced at low flow volumes. 3) Physicochemical decimation, including fragmentation and chemical degradation, was localized with turbulence (steepest gradients and highest runoffs) and was selective upon larger cellular material. All of the above loss factors favor an ultimate decrease of living cellular material and may be secondary causes of organic detrital gain thus acting to produce a detritus-dominant stream microseston.

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SOME FACTORS AFFECTING DRIFT RATES OF *BAETIS* AND SIMULIIDAE IN A LARGE RIVER

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(Accepted for publication October 17, 1967)

Abstract. Effects of eight factors on the drift rates of *Baetis* nymphs and Simuliidae larvae were tested with multiple regression analyses. Illumination, population density of all other organisms and temperature had significant influences on drift rates of both organisms. Turbidity and water-level fluctuations were related to changes in drift rates indirectly through influence upon light penetration and population density, respectively. Dissolved-oxygen concentration, calendar date, and depth of water at the sample site did not clearly affect drift rates of either organism. In areas where population densities were high, the eight factors tested accounted for 65% to 81% of the variability observed in drift rates. Maximum drift rates were 170 × 10^6 *Baetis* sp. nymphs (63.2 kg) and 10.9 × 10^6 Simuliidae larvae (5.4 kg) per day.

Introduction

Recent investigations have emphasized the magnitude of invertebrate drift in streams and its interaction with population density (Müller 1954; Waters 1961, 1966). Waters (1965) divided total observed drift into three classes: 1) "catastrophic" drift due to an unusually severe physical disturbance of the environment such as flooding, 2) "constant" drift due to ordinary accidental dislodgement, and 3) "behavioral" drift due to an active response by the individual organism. Behavioral drift is influenced by light intensity in several organisms (Tanaka 1960; Waters 1962; Müller 1963). Waters (1966) has also suggested that behavioral drift is directly related to production in excess of the carrying capacity of the stream bed.

Müller (1966) found that drift rates of *Gammarus* varied directly with temperature, and that drift rates of *Baetis* and Simuliidae increased following preemergence and prepupation activities, respectively.

The objectives of this study were: 1) to measure simultaneously the drift of two organisms, an unidentified species of *Baetis* (Ephemeroptera) and Simuliidae larvae (Diptera) and several environmental factors known or suspected to influence drift rates, and 2) to determine how much of the variability observed in the drift rates of these two organisms could be accounted for by the factors tested. It was necessary that we have an idea of how much of the variability could be accounted for to carry out effectively future drift-rate and production studies.

Methods

The study was conducted on the Green River, Utah and Colorado, immediately below Flaming Gorge Dam during the summers of 1964 and 1965. Sampling stations (I–IV) were established at Little Hole (11.7 km below Flaming Gorge Dam = 11.7 kmBD), Carr Ranch (68.7 kmBD), Echo Park (103.9 kmBD), and Island Park (125.5 kmBD; Fig. 1). This section of the Green River was a rather warm and turbid stream before installation of the dam in 1962. Since impoundment the first 50–60 km of river below the dam has become a clear, cold trout stream. With increasing distance from the dam, atmospheric influences and the addition of tributary waters combine to return the river toward a semblance of its preimpoundment state. The river environment was greatly altered at station I following impoundment. At station II the environment