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DESCRIPTIVE PHENOLOGY AND SEASONALITY OF A CANADIAN BROWN-WATER STREAM

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Abstract

A phenological-type synthesis was attempted for 10 years of limnological data of a brown-water stream of Alberta, Canada. The objectives were to predict the normal occurrence of seasonal events in the stream and to formulate indices upon which to base general stream management strategies. The stream supports a diverse chironomid fauna (109 species); and four taxa, chironomids, ostracods and the ephemeropterans *Leptophlebia cupida* and *Baetis tricaudatus,* account for 61% of the total yearly fauna by numbers. There are two obvious major seasons: a 7 month ice-free season (ca 15 April-15 November) and a 5 month winter season. Based on numerical classification of physical and chemical parameters, the ice-free season is separated into spring (April and May), summer (June, July and August) and autumn (September and October) seasons; and these four seasons can serve as the basis for describing biological seasonality. There are few detectable periodic events during the long, 5-month winter season: flow and water temperature are relatively constant and at minimum values. There are no reproductive periods for species studied; no new generations appear; drift densities are at minimum values; and for most taxa, little growth takes place in winter. Some of the important phenological events of the three ice-free seasons include: (1) a total emergence, hence reproductive, period of 6 months (April-September) for aquatic insects studied, with the largest number of taxa reproducing in late June and early July; (2) a 3½ month period (late April-early August) when water temperatures are on the rise (log phase of total degree days curve), with maximum rate increase in May, maximum rate decrease in October, and maximum water temperature values in early August; (3) a completely green (trees and marsh grasses) watershed of less than 2 months (late June-early August); (4) a leaf-drop period of 1½ months (September-mid October), with maximum litter-fall rate in early September; (5) maximum discharge in April; (6) minimum standing crop by numbers in April and maximum numbers in September; (7) maximum daily drift and drift densities (all taxa) in August; (8) maximum impounding effect of beaver dams in September; (9) maximum aquatic macrophyte standing crop in September; and (10) maximum 'potential' food resources (detritus of aquatic macrophyte and terrestrial leaf origin) in mid October.

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Introduction

Canadian boreal forest regions exhibit large numbers of slow-moving streams that meander through poorly drained, muskeg-type terrain. A common feature of these streams is the brown color of the water; this is due to humic and fluvic substances. Since 1966, I have been studying limnological features of one brown-water stream, the Bigoray River, located in west-central Alberta. The initial goal was simply to gain a perspective of the stream's invertebrate fauna in regards to stream faunas of other climatic regions. I used a life cycle approach, working out the cycles of abundant species and documenting relative changes in their numbers and biomasses throughout the year (Clifford, 1969). Subsequently, there have been several additional studies (see Methods). The final phase will be to manipulate experimentally the stream. Prior to conducting the manipulatory phase, it would be advantageous to attempt a synthesis of the numerous premanipulatory studies. These data encompass about a decade and were generated from a variety of biological studies, by several workers, using techniques and equipment that differed according to the objective of the specific study. There was no single structural or functional theme. But there is a unifying feature for the Bigoray River's studies in that with few exceptions each study encompassed at least one entire calendar year, and seasonally varying environmental parameters were measured in each study.

The synthesis approach I used can be described as a phenological approach. According to the US/IBP Phenological Committe 'Phenology is the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species'. An important aspect of phenological studies is to establish seasonality by predictable phenological events instead of astronomic calendar dates (Lieth, 1974). It is now known that in most streams the fauna's major energy source is allocthonously-derived organic matter (Hynes, 1970, 1975; Cummins *et al.*, 1972; Fisher & Likens, 1972; Sedell *et al.*, 1974). Terrestrial phenology itself should therefore be important in the study of stream events: the mechanisms that regulate seasonal events on land will greatly influence the recurring seasonal patterns in the stream per se. Cold temperate and subarctic regions would seem especially suited for establishing phenological relationships, because of the clear-cut rhythmic environment at these high latitudes.

For Bigoray River, information is available for a large number of seasonal events. The premise is that governing or at least some how associated with these events are a few major physical cycles, i.e. water temperature, flow, and light; and these driving variables are seasonally predictable. My main interest, therefore, was to detect recurring biological cycles in the Bigoray River and associate each cycle with the major physical cycles and also with other physical, chemical, and biological cycles. It was necessary to deal with indirect relationships and non-numerical correlation between specific biological phenophases. Although the correlation between two phenophases may not indicate a true relationship in the sense of cause and effect, the assumption is that either event is predictable from the other because both events are due to the same unmeasurable causes, i.e. the sum total of seasonal environmental variables.

My approach was to establish average yearly cycles for Bigoray River phenomena, make associations between average cycles on a seasonal basis, and finally determine seasonality by clustering techniques. With these data, it should be possible to predict, within limits, the normal occurrence of seasonal events in the stream and also how a natural catastrophy or manipulation by man might affect the cyclic events and hence the biology of the stream. The approach can also serve simply as one approach to describe the stream and hence fit in into the broad lotic system spectrum (Pennak, 1971).

Methods

Methods of some studies have been published; others are unpublished, and some are in preparation. Below is a coded list of these studies including the field years and a brief synopsis of biological sampling procedures as they pertain to this report. During each study, routine physical and chemical measurements were also made. With the exception of total alkalinity, hardness and turbidity (which were determined with a Model DR-EL Hach Kit), all constituents were determined via Standard Methods (A.P.H.A., 1971), either in the field or in the Water Laboratory, Department of Zoology, University of Alberta.

A. Clifford (1969): Stream invertebrates were collected with a dip net having a mesh size of 720 microns; during each date, the area both above and below the bridge (ca 40 m of stream) was sampled and the material was treated as one sample (1966-67).

B. Unpublished: As for A, except the dip net had a mesh size of 320 microns (1967-68).

C. Bond (1972): As for B, except aquatic invertebrates collected above bridge ('pool') were treated separately from organisms collected below bridge ('riffle') (1968-69).

D. Clifford (1972a): Two drift nets, one on top of the other, sampled a partial slice of the main stream's water column, including the surface water. Each net had a 9 cm^2 aperature and a 320-micron mesh. Seven sampling intervals of 1 hour duration were evenly spaced over each 24-hour day (1970-71).

E. Clifford (1972d): A wide-mouthed plankton net (mesh size 76 microns), placed beneath a waterfall, filtered the entire flow of tributary. Seven sampling intervals of 20 minutes were evenly spaced over each 24-hour day (1970-71).

F. Clifford (1972b): Benthos was collected during the day (1600 hours) and at night (2300 hours) using a modified Neil-square-box sampler having a mesh of 320 microns; the sampler enclosed an area of 844 cm^2; four samples were taken during each sampling date. Volume biomass was determined by water displacement using a microburette (1970-71).

G. Unpublished: Benthos was collected using a coring device that sampled 70 cm^2 of substrate to a depth of ca 20 cm; a stratified random design was used, and 10 cores (1974) or 5 cores (1975) were taken during each sampling date (1974-75).

H. Boerger & Clifford (1975): Sixteen floating box traps, each 0.1 m^2, were arranged in four transects across the stream; the traps were operated continuously from 25 April to 23 October (1973).

I. Boerger, H. ('Community structure of Chironomidae inhabiting a brown-water stream,' in prep.): Litter-fall rate was measured using 18 litter boxes (each 1 m^2) distributed in stream via stratified random design; litter was collected at ca 5-day intervals in autumn 1973 and dried at 70°C. Total macrophyte, *Sparganium*, and filamentous algae biomass was determined by removing all plant material from 22 randomly chosen 0.1 m^2 quadrants for each sampling date of summer and autumn 1973.

J. Hamilton, H. ('Food habits of ephemeropterans from three Alberta, Canada, streams,' in prep.): Diatom standing crop was estimated from five rocks collected (below bridge) during each of 14 sampling dates. After brushing, sedimentation, and clearing, counts were made on two subsamples for each date and equated to calculated exposed surface area of rocks (1975-76).

Other published Bigoray River studies include: Clifford (1970a, 1970b, 1972c, 1976), Clifford, Robertson & Zelt (1973), Clifford & Boerger (1974), Hayden (1971), and Hayden & Clifford (1974).

Necessary information about data treatment is found in the figures and tables' captions or where such data are presented in the text. However Figures 5 and 8 require further explanation.

Figure 5

Except for terrestrial phenologies and litter-fall rate, data were ultimately collated into the following nine sampling intervals, with the midpoint of each interval taken as the average sampling date: (1) January-February-March, (2) April, (3) May, (4) June, (5) July, (6) August, (7) September, (8) October, and (9) November-December.

Terrestrial. Air temperature and precipitation data were from Edson, Alberta, (Atmospheric Service, Environment Canada). Day lengths were calculated from Edmonton (latitude 53° 33'), Alberta, sunrise-sunset data. Day length times water degree days graph was constructed by taking day length values of the average sampling date for each of the nine sampling intervals (e.g. 15 February equals 9.86 hrs.) and then multiplying this by total degree days (main stream) of preceding 5 days (e.g. 11-15 February equals 5.5; hence 9.86 times 5.5 equals 54.2 for 15 February). Marsh grasses and *Salix-Populus* phenologies were compiled from routine observations in 1975 and 1976 and from scattered field notes, 1966-1974. Data for litter-fall rate were from study I.

Tributary. Discharge data were from spot measurements, 1966-1976. Residue and organics data were from study G. Daily drift (numbers/day) and drift densities (numbers/m^3) data were from study E.

Physical-chemical (main stream). Data for physical and chemical parameter graphs were from all studies, except organic N and P, which were from data of study G.

Plant material. Leaf litter, macrophyte, and filamentous algae data were from study I and field observations, 1966-1976. Diatom standing crop graph was based on data of study J.

Drift. Data were from study D.

Emergence. Total Ephemeroptera data were from study H; total Chironomidae data were from study I, with methods of study H.

Species diversity. Data were from studies indicated on the graphs. The Shannon-Weaver function was used to estimate diversity, mean diversity $\bar{d}$ being calculated by the machine formula of Lloyd, Zar, and Karr (1968). Relative diversity (all studies) was determined by dividing total diversity of each study into each $\bar{d}$ value of that study; and then, after correcting for unequal number of sampling intervals of the various studies, calculating average relative diversity (converted to percentages) of all studies of each of the nine sampling intervals.

Quantitative. Standing crop by numbers and dry weight data were from study G; volume-biomass data from study F.

Populations. Within-taxon population curves of drifting statoblasts, ephippia, young-of-year suckers, and terrestrial insects were from data of study D; upstream-and downstream-trapped sucker data were from study C. All other populations curves were based on weighted averages (converted to percentages) of studies A, B, C, F, and G.

Figure 8

Physical and chemical parameters were water temperature, flow, turbidity, true color, nitrate, orthophosphate, total hardness, silica, pH, total alkalinity, total residue, and conductivity. Using nine interval data of Figure 5, I constructed a two-way table with 9 columns (sampling intervals) and 12 rows (the parameters); data were standardized by rows (proportions), and then dissimilarity measures were calculated using Euclidean distance squared. Clustering analysis was by sum of squares method (Ward, 1963; Orloci, 1967).

General description

The North Fork of the Bigoray River (53° 31′ N, 115° 26′ W), part of the Arctic Ocean drainage, is located on the dry continental side of the Canadian Rocky Mountains in west-central Alberta (Fig. 1). Climate is subarctic by the Koëppen classification. Average total precipitation is 45 cm per year; average annual air temperature is 4° C. Average frost-free period is about 70 days (Twardy & Lindsay, 1971).

Geology and Vegetation
The watershed's bedrock materials are composed of sandstone and soft shale and are of freshwater origin. During Wisconsin time, the area was completely glaciated by the Laurentide Ice Sheet advancing from the east. The ice sheet retreated about 10,000 years ago; resulting topography is plains of undulation ground moraine and hummocky moraine. About 45% of the surficial deposits is till.

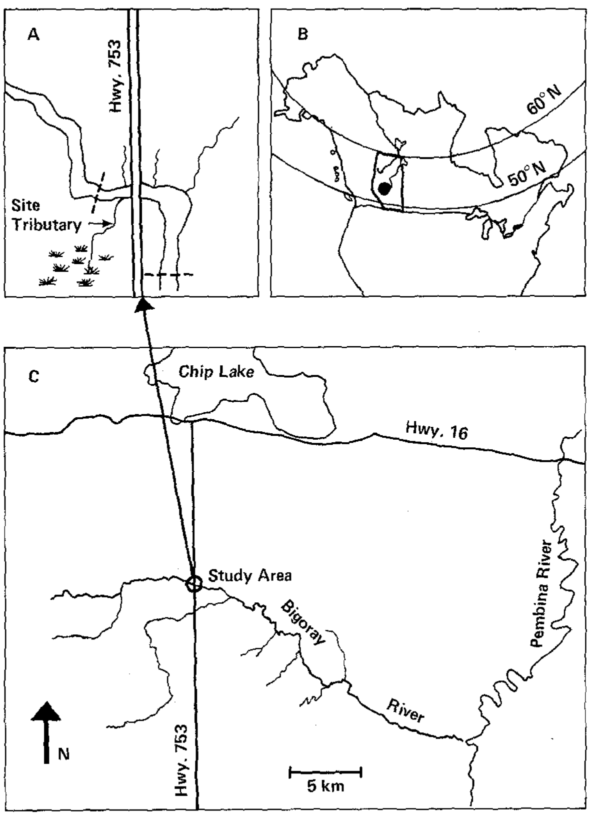


Fig. 1. Sampling site (A), latitudinal (B), and general area (C) maps of Bigoray River, Alberta.

Major soils are poorly drained organic soils. About 50% of the watershed upstream from the study site is of organic soils, and the stream valley upstream from the study site is entirely of organic soils until one reaches the headwater regions (Twardy & Lindsay, 1971). These organic soils are an intermingling of two types: one is a poorly drained organic soil of sedge peat; the other is a very poorly drained organic soil of *Sphagnum* and feather moss origin and is usually much deeper than sedge peat soils and has a higher acidity. Sedge peat soils are more abundant and apparently account for the water having a relatively low acidity when compared to the acid water of many peatland regions. The peatlands can generally be described as minerotrophic by Heinselman's (1970) classification. Humic substances from peat soils account for the water's characteristic brown color. Organic soils and their associated vegetative complex (a mixture of sedges, grasses, and mosses) form the muskeg terrain, characteristic of the stream's valley.

The watershed is uninhabited by man; and there apparently have been no attempts at cultivation, raising livestock, or lumbering in the watershed, at least since the inception of the study in 1966. The only all-weather road is a gravel road sunning north and south and crossing the east-flowing stream at the study site (Fig. 1). Flora is typical of boreal forest organic terrains, major trees being black spruce *Picea mariana* (Mill.), willows *Salix* spp., tamarack *Larix laricina* (DuRoi) and poplar *Populus* spp. Species lists of entire flora and fauna are available on request from the author.

Morphometric Features of Basin and Study Site
Total area of watershed is 455 km^2; area drained at study site is 87.3 km^2. The stream is a third-order stream at the study site (altitude 846 m). For entire watershed, there are three third-order streams and one fourth-order stream, which empties into Pembina River. Large numbers of small intermittent tributaries drain into the main stream from the muskeg terrain. For example, four (first order) tributaries drain into a 65 m stretch of the main stream in the vicinity of study area. The stream's total length from headwaters to mouth is 76 km; from headwaters to study site, total length is 32 km. Ratio of stream length to watershed area (at study site) is 0.37 km/km^2. Stream gradient to study site is 3.1 m/km. At the study site, about 80% of the stream's descent has been achieved.

Most studies were in an area encompassing 15 m of stream upstream of the bridge and 50 m of stream downstream of the bridge (the area enclosed by broken lines of

Table I. Quarterly and annual averages of physical and chemical constituents, in mg/l unless otherwise indicated.

	J-M	A-J	J-S	O-D	Annual Avg.
Day Lengths (hrs.)	9.9	15.5	14.7	8.6	12.1
Air Temperature (C°)	-10.0	7.8	12.5	-4.1	3.8
Water Temperature (C°)	1.1	7.5	13.0	2.6	6.1
Max. Daily Water Temp. Change	0	2	3	0.05	1.4
Percent Total Ice Cover	100	10	0	50	40
Flow (m^3/sec)	0.09	1.50	0.93	0.28	0.70
True Color (PCU)	48	196	180	128	138
Turbidity (JTU)	14	37	30	22	26
Total Dissolved Solids	321	135	208	236	225
Specific Conductance (micromhos)	533	196	236	359	331
Hydrogen Ion	7.5	7.5	7.9	7.5	7.6
Total Alkalinity	306	84	123	190	176
Total Hardness	266	95	125	166	163
Nitrate-Nitrogen	0.06	0.04	0.05	0.04	0.05
Orthophosphate	0.12	0.12	0.13	0.14	0.13
Organic Nitrogen	0.23	0.55	0.38	0.24	0.35
Organic Phosphorus	0.03	0.07	0.09	0.06	0.06
Silica	7.7	3.9	4.6	6.1	5.6
Dissolved Oxygen	7.2	7.1	6.2	7.3	7.0
Percent Saturation 0_2	55	64	66	57	61
Sulfate	10	6	3	2	5.3
Chloride	2.7	2.4	3.2	3.7	3.0
Iron	0.8	0.7	0.7	1.0	0.8
Total Precipitation (cm)	6.2	13.5	19.1	5.8	Total 44.6
Total Degree Days (water temp.)	51	529	1270	340	2190

Fig. 1A). Above bridge, average mid-summer current velocity is usually less than 1 cm/sec.; below bridge, mid-summer average is about 20 cm/sec. Substrate above bridge is mainly sand, some silt and very little rubble, average particle size being 0.19 mm. Below bridge, substrate is also predominately sand, with some silt and relatively more rubble than above bridge. Crude estimates of average particle size below bridge is 2 mm, but there are some rocks as large as 30 cm. Banks are almost perpendicular, having a height of about 1 m; inland from the banks the terrain is usually flat. Estimated average slide slope from waterline to 10 m inland is 10%. The entire study site is 100% open, there being no canopy.

Physical and Chemical Features

At the study site the stream is small; average summer base flow is 0.80 m^3/sec and average winter base flow is 0.14 m^3/sec. Table I shows annual averages of physical and chemical constituents. Because of the organic terrain's high water-storage capacity, it takes heavy rains to influence flow appreciably. Average number of storms per year resulting in flow that is five times base flow is estimated as three. Beaver dams, especially in late summer and autumn, influence flow features. Crude estimates indicate an average of one dam per 0.6 km of stream in late summer. In a sense, they act as giant leaf packets and as barriers probably promote on-site processing of organic matter (Cummins, 1974). Many dams are partially destroyed during high water of spring.

The stream is completely ice-covered for about 5 months of the year, and water temperatures are near 0° C for about 6 months. Summer water temperatures have never exceeded 20°C, and daily fluctuations are small, 3° C being the largest observed. Average total degree days of water temperature per year is only 2,190, 58% being contributed in July, August, and September. The water's pH is always above 7.0 and only rarely exceeds 8.3. Color of the water is dark brown during the ice-free season, but in late winter the stream is quite clear. Dissolved oxygen values are never critically low, even in late winter, although average percent saturation values do not approach 100%.

Stream Flora

Aquatic macrophytes appear to be relatively more important in this slow-moving stream than in most lotic systems. At the study site above the bridge, the plants can extend from bank to bank by late summer. They serve as an important substrate for chironomids and also act as a screen, impeding the downstream movement of coarse particulate organic matter, especially masses of filamentous algae. In one study, terrestrial litter input, mainly *Salix* leaves, was calculated as 20 g dry wt./m^2/year compared to 120 g dry wt./m^2/year for total aquatic macrophytes (see Methods, study I). *Sparganium* and *Potamogeton* account for most of the macrophytes' biomass. The green alga *Microspora Loefgvenii* (Nordst.) is the most abundant filamentous alga. Two species of *Achnanthes* make up the major component of the diatoms community. In a 1-year study of epilithic diatoms, these two species collectively made up at least 55% of the diatom standing crop for each of the 14 sampling dates (see Methods, study J). Other abundant taxa were *Nitzchia* (three species), *Cocconeis placentula, Rhoicospenia curvata* and *Synedra* sp. Total yearly standing crop of diatoms in Bigoray River was about five times lower than found (using the same methods) in another Alberta stream.

Stream Fauna

Generally, one would expect streams of this and higher latitudes in North America to have a less diverse fauna than streams at lower latitudes (Stout & Vandermeer, 1975). And for most taxa, this statement holds for Bigoray River fauna. However the Chironomidae fauna is diverse, there being 109 species so far identified. This is a large number relative to species numbers of other major taxa of Bigoray River and even an impressive diversity when compared to chironomid diversity in more southerly streams. Of 8,025 larvae identified, 46% were Orthocladinae, 22% Tanyponinae, 18% Chironomini, and 14% Tanytarsini (study I). Species numbers within each of the seven major taxa of stream insects are: Chironomidae (109), Coleoptera (31), Ephemeroptera (19), Trichoptera (16), Hemiptera (6), Simuliidae (4), and Plecoptera (4). Unfortunately only the ephemeropterans, plecopterans, and non-limnephilid trichopterans can readily be identified to species in the immature form. Triclad flatworms are a major group of stream invertebrates that have not been found in Bigoray River. The fauna is composed mainly of eastern, or plains, species with a few cordilleran species, e.g. *Zapada cinctipes* and *Callibaetis coloradensis*.

Yearly average of mean species diversity $\bar{d}$ was 2.5 when all studies were considered. Average standing crop biomass was 0.86 g dry wt/m^2/year. Average standing crop of individuals as determined with a coring device (study G) was 20,489/m^2/year, which included large numbers of very small early instar chironomids and numerous entomostracans (ostracods, cladocerans, and copepods). These data would therefore indicate an invertebrate fauna exhibiting relatively less diversity and biomass than found in many unpolluted streams, but having a large number of very small individuals per unit area.

By numbers, the drift fauna is composed of 13 abundant taxa, making up 95% of the year's total drift fauna (Clifford, 1972a). Entomostracans make up a large part of the drift, collectively accounting for 50% or more of the total drift fauna for about three quarters of the yearly sampling dates. During most of the ice-free season, chironomid adults and pupae and *Baetis* nymphs make up a large part of the non-entomostracan drift component. In winter, cyclopoids and *Leptophlebia cupida* nymphs

Table II. Yearly percentage composition of Bigoray River fauna. Last column indicates the operational taxonomic units (OTUs) used in the phenological analysis. Percentages based on studies A, B, C, F, and G (see Methods).

Arthropoda (95.0)	Insecta (72.8)	Diptera (42.0)	Chironomidae	35.4
			Simuliidae	4.1
			Ceratopogonidae	1.7
			Dicranota (Tipulidae)	0.8
		Ephemeroptera (16.7)	*Leptophlebia cupida*	6.6
			Baetis tricaudatus	5.7
			Callibaetis coloradensis	1.8
			Caenis simulans	1.4
			Paraleptophlebia debilis	0.4
			Siphlonurus alternatus	0.4
			Siphloplecton basale	0.2
			Centroptilum sp. B	0.2
		Trichoptera (7.5)	*Cheumatopsyche analis*	3.8
			Hydropsyche spp.	2.8
			Limnephilidae	0.8
			Polycentropus cinereus	0.1
		Coleoptera (3.4)	Elmidae larvae	2.8
			Adult Coleoptera	0.6
		Plecoptera (1.9)	*Zapada cinctipes*	1.7
			Arcynopteryx sp.	0.2
		Hemiptera (0.8)	Corixidae	0.8
		Megaloptera (0.5)	*Sialis cornuta*	0.5
	Crustacea (21.6)	Ostracoda (13.4)		13.4
		Cladocera (4.1)		4.1
		Copepoda (3.2)		3.2
		Amphipoda (0.9)	*Hyalella azteca*	0.6
			Gammarus lacustris	0.3
	Hydracarina (0.6)			0.6
Mollusca (1.3)	Bivalvia (Sphaeriidae) (1.1)			1.1
	Gastropoda (0.2)			0.2
Annelida (Oligochaeta) (1.4)				1.4
Nematoda (0.4)				0.4
Others (1.9)				1.9

account for most of the drifting animals. Most of the drifting entomostracans originate in marshy areas, which drain into Bigoray River via small intermittent tributaries (Clifford, 1972d). But beaver dams and sluggish side arms of the main stream probably permit the maintenance of entomostracan populations in the main stream for much of summer and autumn. Also, ostracods and some cyclopoids maintain permanent populations in the main stream.

Life cycle data are available for 17 species of invertebrates (Clifford, 1969, 1976; Clifford, Robertson & Zelt, 1973). For Ephemeroptera, some taxa having been studies over several years, the major growth period for most species is autumn; there is little growth and for some species no growth during the long winter. In contrast, the plecopteran *Zapada cinctipes* continues to grow throughout winter.

The stream supports very sparse resident fish populations. Only one specimen each of lake chub *Couesius plumbeus,* arctic grayling *Thymallus articus,* burbot

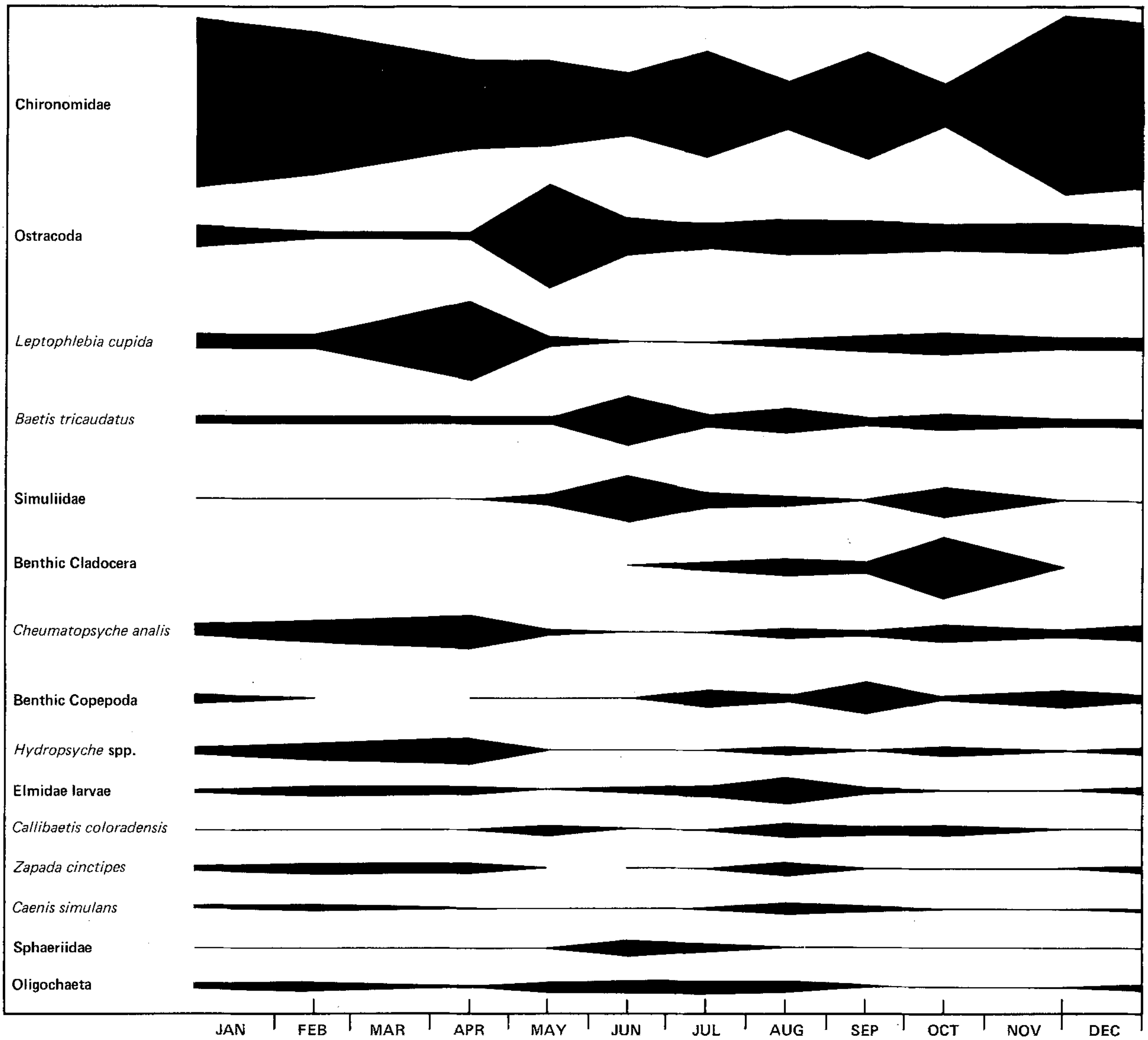


Fig. 2. Seasonal percentage composition of OTUs making up 1.0% or more of total yearly fauna by numbers. Based on data of studies A, B, C, F, and G and collated into nine sampling intervals. Width of spindle is proportional to numbers of animals for each of the sampling intervals.

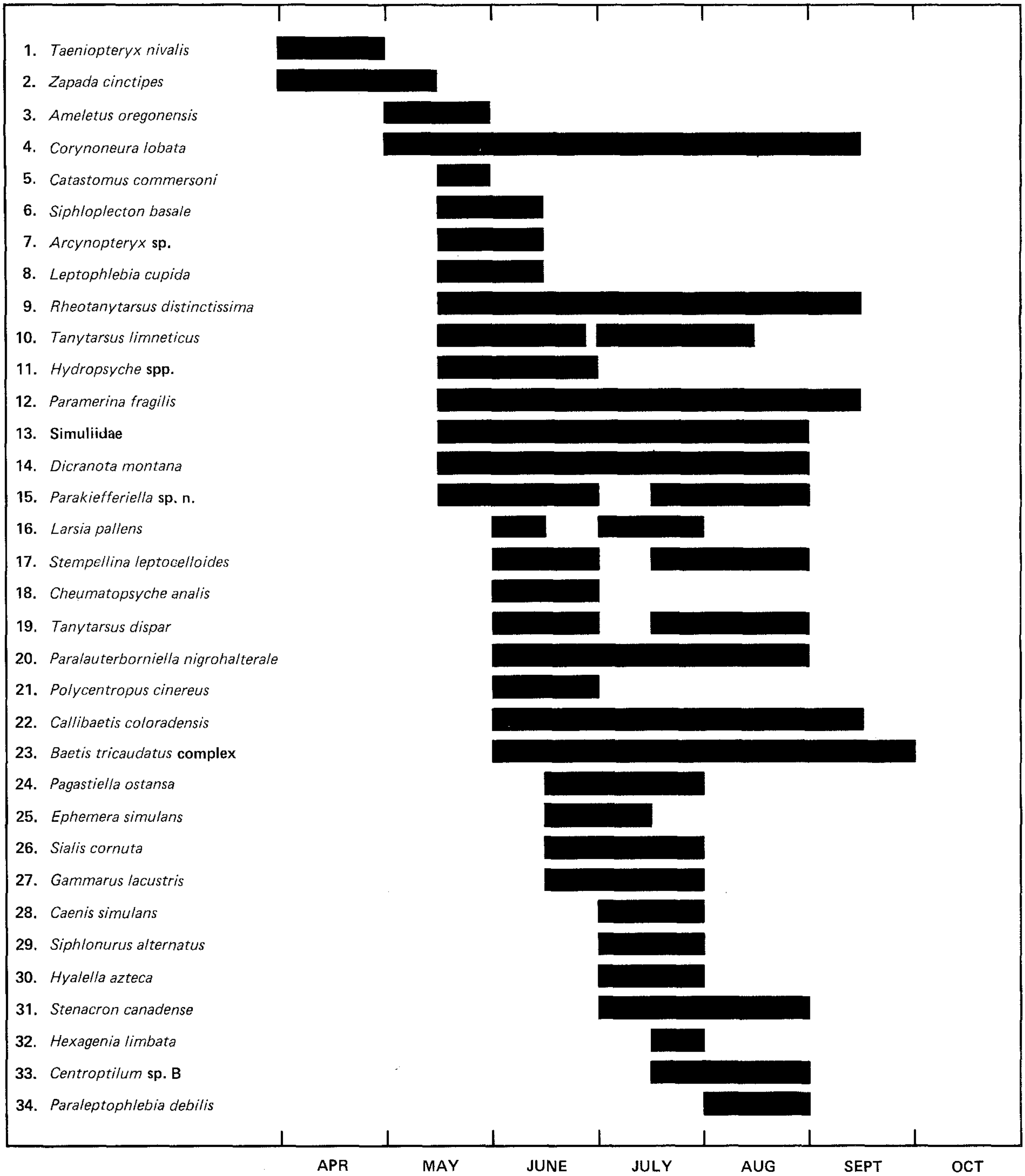


Fig. 3. Reproductive periods of Bigoray River animals, based on 15-day intervals. Data for chironomid species from Boerger (in prep.); all others from Clifford (1969), Boerger & Clifford (1975), and field observations of all studies.

Lota lota, Rocky Mountain whitefish *Prosopium williamsoni,* and spoonhead sculpin *Cottus ricei* has been collected. Resident fish are mainly white suckers *Catostomus commersoni* and northern pike *Esox lucius.* However, shortly after the ice goes out in the spring, large numbers of white suckers migrate into Bigoray River from Pembina River. The migration involves only mature fish between age 6 to 13 years (Bond, 1972). Afger spawning, adult fish descend the stream. Eggs hatch about 15 days after spawning and then the young-of-year also move downstream, almost exclusively at night (Clifford, 1972c).

Phenology

Community Composition

Table II shows the fauna's yearly percentage composition; the last column indicates the operational taxonomic units (OTUs) used in all subsequent analyses. Stream invertebrates are mainly arthropods (95%). In terms of OTUs, Bigoray River can be described as a chironomid-ostracod type stream (49%), but the ephemeropterans *Leptophlebia cupida* and *Baetis tricaudatus* complex are abundant; these four taxa collectively account for 61% of the total yearly fauna. Ten OTUs (the four above and Simuliidae, Cladocera, *Cheumatopsyche analis,* Copepoda, *Hydropsyche* spp., and Elmidae larvae) make up 82% of the fauna, the other 23 taxa accounting for only 18% of the total yearly fauna.

Seasonal percentage composition of taxa also reflect the relative importance of chironomids, ostracods, *L. cupida,* and *B. tricaudatus* (Fig. 2). Chironomids are the dominant taxon for all sampling intervals except May, when ostracods are relatively more abundant, and October, when cladocerans are dominant. Relative community structure changes little in winter (November-March), at which time chironomids continuously account for at least 60% of the total fauna. Relative changes taking place

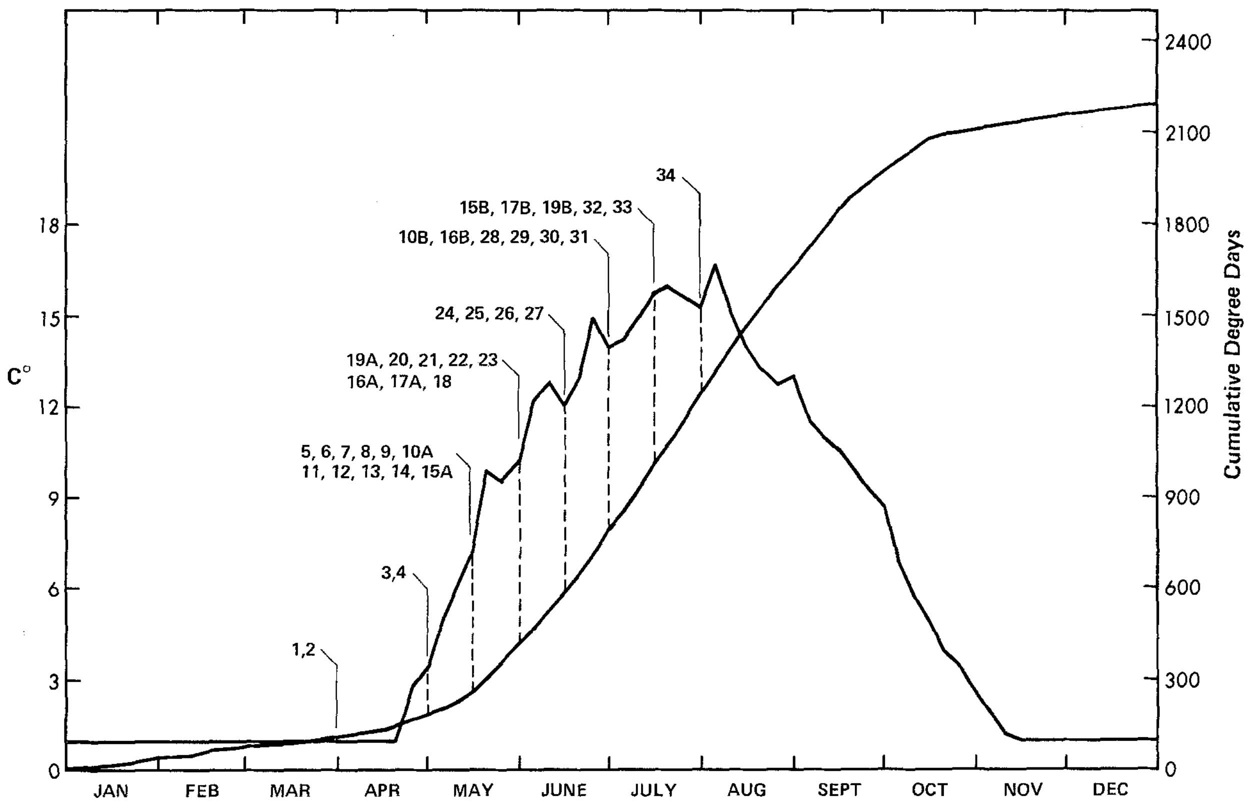


Fig. 4. Beginning of reproductive periods for Figure 3 species as related to average 5-day water temperatures and cumulative water degree days. Degree days based on mean daily water temperature. A and B represent the first and second generations respectively of bivoltine species.

during the ice-free season are mainly due to seasonal disappearances (emergence) and appearances (new generations) of aquatic insects and the build up of entomostracan populations in autumn.

Reproductive Periods
The 'reproductive periods' of most taxa of Fig. 3 are based on emergence or flight periods. For univoltine ephemeropterans and other short-lived (as adults) amphibiotic insects, these periods accurately reflect the taxa's reproductive periods. For others, the bars probably indicate reproductive periods more extensive than take place. Also, the few late emerging *B. tricaudatus* specimens of September might not reproduce. And for some multivoltine taxa, the long, continuous reproductive period actually consists of a number of short and sometimes overlapping reproductive periods.

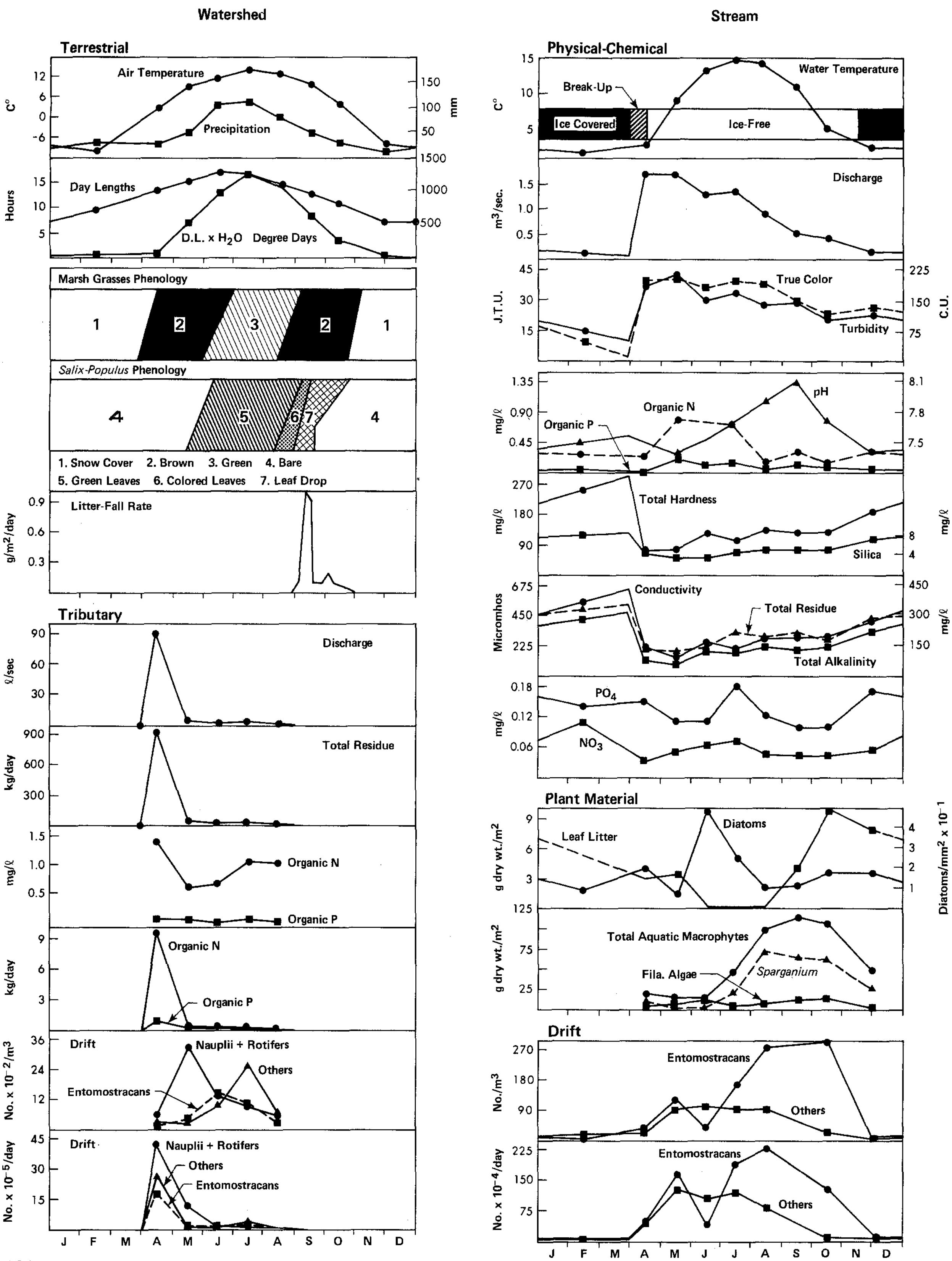
The total reproductive period extends from 1 April to 1 October, about a 6 month reproductive period for the taxa studied. October is the only ice-free month when little or no reproduction takes place. The plecopterans *Taeniopteryx nivalis* and *Zapata cinctipes* usually emerge as soon as the ice goes out; but *Z. cinctipes* nymphs sometimes emerge under the ice. Figure 3 also illustrates correlations between seemingly unrelated phenophases. For example *S. basale* nymphs invariably emerge at the same time that white suckers are spawning. Both phenophases are conspicuous and field observations have repeatedly confirmed this relationship.

The reproductive period starts when water temperatures are constant at 1°C and total degrees days (based on calendar year) are only 110 (Fig. 4). Reproduction stops when water temperatures are about 9°C and declining rapidly. The entire reproductive period encompasses about 1850 degree days. All taxa have finished reproducing or are reproducing when water temperatures start declining in early August. The total degree days curve is sigmoidal, and the start of all taxa's reproductive periods is essentially a log-phase phenomenon.

Phenophases in General
Figure 5 portrays seasonal cycles in Bigoray River, and Fig. 6 shows some of the cycles' more prominent phenophases. Most cycles represent what has happened on-the-average over several years, and in this respect they are static events. However data for each parameter did indicate a seasonally recurring cycle in the sense of the relative humps and hollows of each cycle occurring at about the same time year after year. A possible exception is the suggested cyclic nature of invertebrate species diveristy. Yearly trends in absolute $\bar{d}$ values varied considerably depending on the sampling device, the stream area, and the year of the study. The trend, however, is for maximum diversity to occur in autumn, and relative diversity of all studies combined gives some indication of a seasonal cycle in species diversity. But the trend is not as pronounced as was found by Slobodchikoff & Parrott (1977) for aquatic insect communities of an Arizona, USA, stream.

The taxa's population cycles, i.e. within-species population percentage densities of Fig. 5, are arranged seasonally in respect to maximum population densities. Maximum population densities might be due to large number of small, new generation individuals, in which case the subsequent decline in population density will represent a type of field survivorship curve. However other phenomena, especially delayed hatching, overlapping generations, and the seasonal congregation of individuals of certain species at times when there is limited inhabitable substrate, will influence the population cycles. And of course several OTUs encompass more than one species, in some cases a large number of species. All taxa of Figure 5 are cyclic in respect to population density, except chironomids and ostracods (as is to be expected considering the number of species included in each of these OTUs). These two taxa were included because of their dominance in the fauna. Also consistent seasonal population density trends could not be detected for the following: *Stenacron, Callibaetis, Arcynopteryx, Polycentropus, Dicranota, Sialis* Hydracarina, Oligochaeta, Nematoda, Limnephilidae, and Elmidae larvae.

Seasonality
Lietch (1974) defines seasonality as 'the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar, calendar) year.' For the Bigoray River analysis, the four temperate calendar seasons were disregarded, although their notations, i.e. spring, summer, etc., were retained. Subjectively, based on the nine yearly sampling intervals, there are two obvious major seasons: a 7 month ice-free season (ca 15 April-15 November) and a 5 month winter season. Using numerical classification techniques, I attempted a numerical estimate of seasonality by clustering the nine sampling intervals using physical and chemical data (Fig. 8). The two major seasons, ice-free and winter, are separated after the first operation. Four clusters are recognizable after two additional operations,


Watershed
Stream
Terrestrial
Air Temperature
Precipitation
C°
mm
Day Lengths
D.L. x H_2O Degree Days
Hours
Marsh Grasses Phenology
Salix-Populus Phenology
1. Snow Cover 2. Brown 3. Green 4. Bare
5. Green Leaves 6. Colored Leaves 7. Leaf Drop
Litter-Fall Rate
g/m²/day
Tributary
Discharge
ℓ/sec
Total Residue
kg/day
Organic N
Organic P
mg/ℓ
Drift
Nauplii + Rotifers
Others
Entomostracans
No. x 10^{-2}/m³
No. x 10^{-5}/day
Physical-Chemical
Water Temperature
Break-Up
Ice Covered
Ice-Free
m³/sec.
True Color
Turbidity
J.T.U.
C.U.
pH
Total Hardness
Silica
Conductivity
Total Residue
Total Alkalinity
Micromhos
PO_4
NO_3
Plant Material
Leaf Litter
Diatoms
g dry wt./m²
Diatoms/mm² x 10^{-1}
Total Aquatic Macrophytes
Fila. Algae
Sparganium
No./m³
No. x 10^{-4}/day
J F M A M J J A S O N D

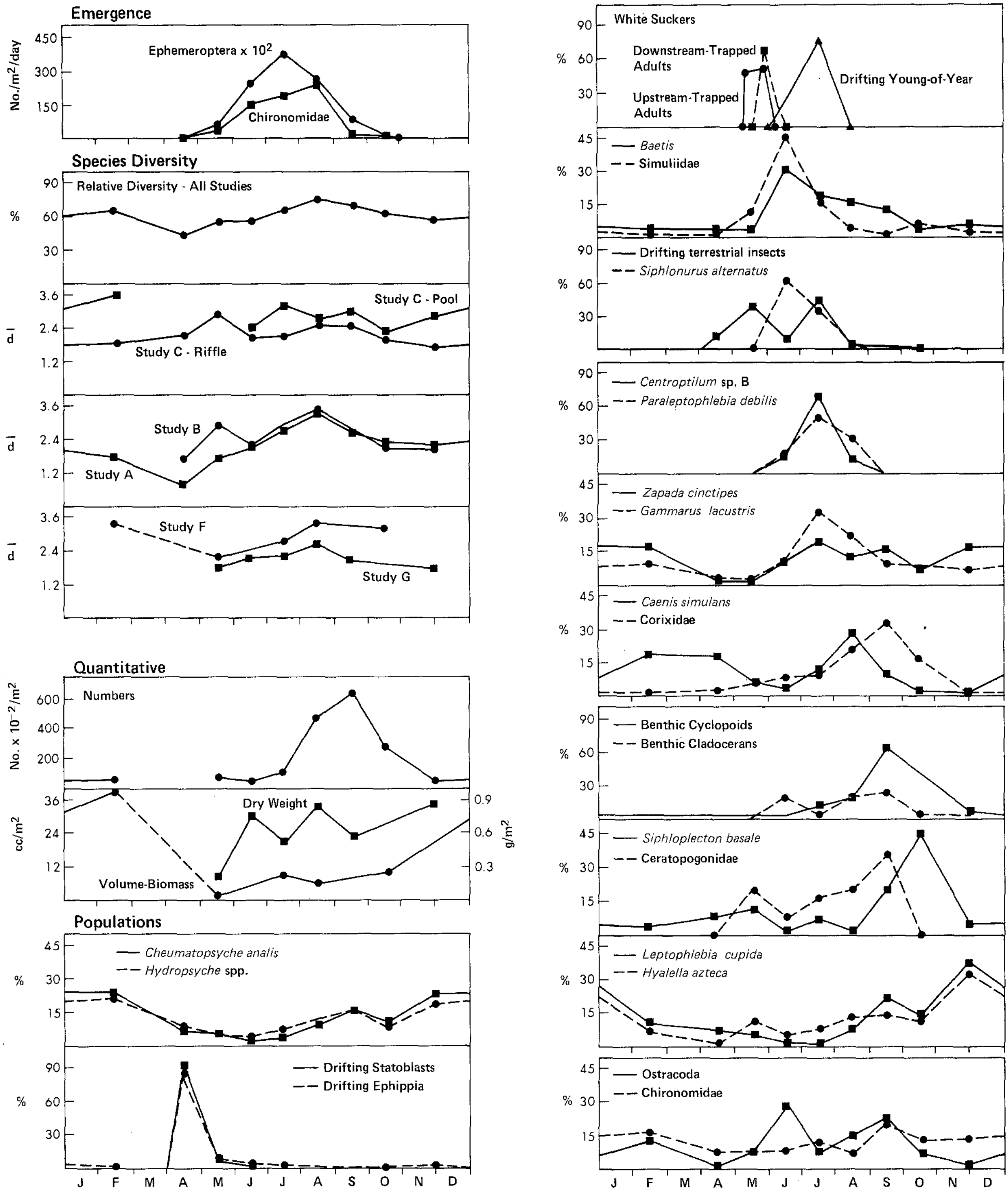


Fig. 5. Seasonal cycles in Bigoray River and its watershed. See Methods and Phenophase in General Sections for further explanation.

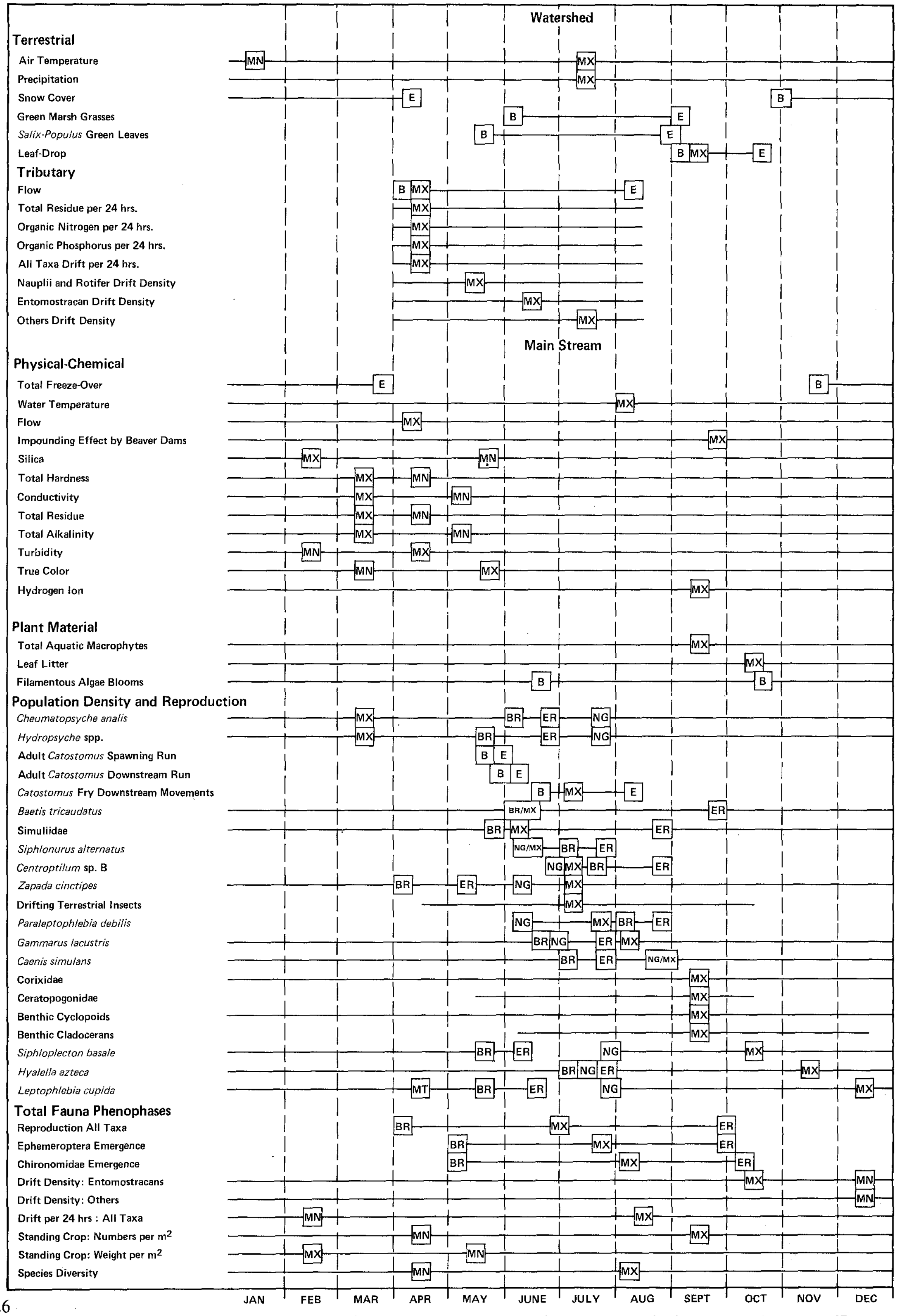


Fig. 6. Selected phenophases. Symbols: Mx = maximum, Mn = minimum, B = beginning, E = end, BR or ER = begin or end of reproductive period, NG = first appearance of new generation, MT = begin *L. cupida* migration. Mx and Mn markers are centered over the phenophase dates; all others start or end at the beginning or end of phenophase intervals.

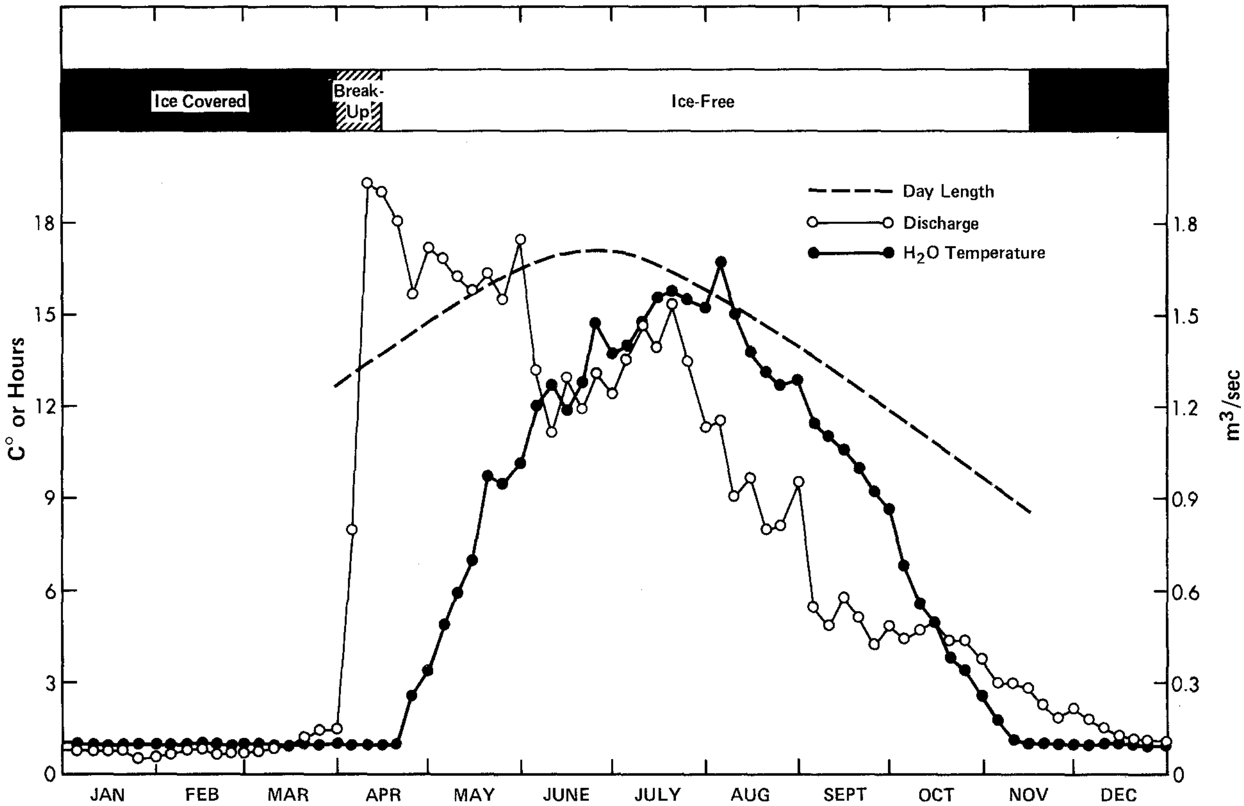


Fig. 7. Average 5-day water temperature, flow, and effective day length values.

and these three operations were arbitratily considered significant. Physical and chemical cyles of Bigoray River can therefore be separated into four seasons: a long winter (November through March), a short spring (April and May), summer (June, July and August) and a short autumn (September and October). Most biological cycles can be related to one of the two (so designated) driving variables, water temperature and flow. And analysis indicated these two parameters were most important in determining the clusters. Therefore these four seasons, based on physical and chemical cycles, were also used as the basis for describing biological seasonality.

Synopsis of Seasonal Events

By referring to Figs. 3-7, it is now possible to give a descriptive phenological account of the brown-water stream. In keeping with the premise that calendar seasons should be disregarded, it would seem best to start the 'new year' at the beginning of one of the two major seasons, instead of at the beginning of the calendar year. Since both water temperature and flow are rapidly approaching base values in early November, the beginning of the winter season, 1 November, is considered the start of the new year.

Winter

November-December (yeardays 1-61, degree days = 95). Air temperatures are declining rapidly in November, but level off (ca -9°C) in mid December. By mid November, minimum and constant water temperature values are first achieved, and the entire stream becomes completely ice-covered, hence ending effective day lengths. Only 4% of total yearly degree days are achieved in November and December. Flow is in the autumn-decline stage through November; but in early December, the relatively constant winter-base-flow stage is achieved. *Hyalella* and *Leptophlebia* populations are at maximum densities in November and December respectively. Drift densities for both entomostracans and the 'other' component are minimum in December. 'Benthic' (i.e. collected in substrate samples as opposed to drift samples) cladocerans disappear in December.

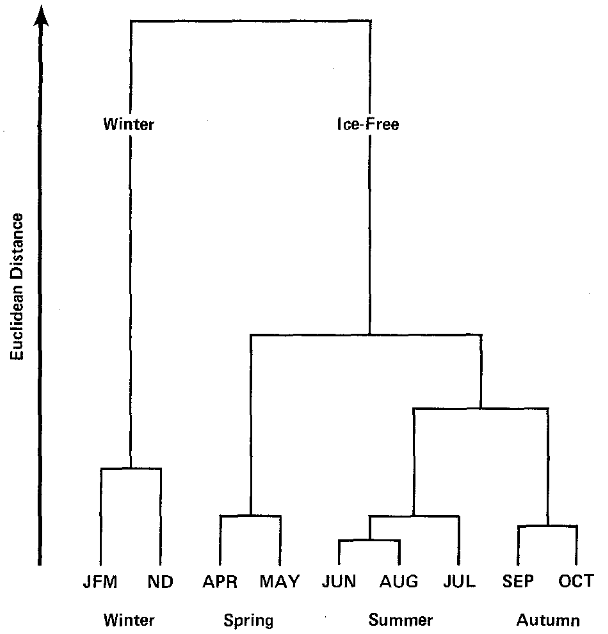


Fig. 8. Fusion pattern of the nine sampling intervals using physical and chemical data. See Methods section for further explanation.

January-February-March (yearday 62-161, degree days = 105). Minimum air temperature occurs in January. Flow continues to be in winter-base-flow stage, and water temperatures are near 0°C and constant. In February and March, those chemical constituents that vary inversely with flow, i.e. silica, hardness, conductivity, residue, and total alkalinity, are at maximum concentrations; whereas turbidity and true color are at minimum concentrations. In February, total daily drift is lowest; and standing crop biomass, due to limited inhabitable substrate for large organisms, is highest. *Cheumatopsyche analis* and *Hydropsyche* spp. larvae are at maximum population densities. Patches of bare ground appear in late March. By the end of winter season total degree days represent 9% of total yearly degree days.

Spring

April (yeardays 152-181, degree days = 85). Snow cover completely disappears in mid April. Ice break-up and hence effective day lengths start 1 April; the stream is ice-free in mid April. Water temperatures remain near 0°C until late April, then start rising rapidly. Maximum discharge (spring-flood stage) occurs shortly after break-up. By early May, most chemical constituents varying inversely with flow are at minimum values; whereas turbidity is maximum in mid April. Standing crop by numbers and probably species diversity are lowest in April. Emergence and hence reproduction starts *(Zapada* and *Taeniopteryx)* at the beginning of April. First terrestrial insects appear in main stream drift. The tributary starts to flow and achieves maximum discharge, contributing maximum amounts of materials to main stream, e.g. ca 9 kg organic nitrogen and 900 kg total residue per day. *Leptophlebia* nymphs start moving from main stream into tributaries and then into marshes. Spring run-off accounts for flushing action of the marshes, resulting in maximum dispersal rate of ephippia and statoblasts, although these devices appear mainly non-viable. This phenophase correlates with tributary flow, and it is likely that most ephippia and statoblasts originate in marshes drained by tributaries. At end of month, total degree days to date represent 13% of total yearly degree days.

May (yeardays 182-212, degree days = 230). Marsh grasses, i.e. conspicuous low vegetation of muskeg region, mainly sedges and grasses, remain brown throughout May, but *Salix* and *Populus* trees start leafing out. Discharge remains high (spring-high stage), and water temperatures exhibit the largest rate increase for any month. The stream exhibits maximum color and minimum silica values in late May. White suckers move up from Pembina River and spawn; by the end of month, some adult suckers are moving back downstream. Thirty eight percent of the aquatic insects studied start their reproductive period in May (see Figs. 3 and 4), including the mayflies *Ameletus* in early May and *Siphloplecton* and *Leptophlebia* in late May. Standing crop biomass is lowest in May, due mainly to emergence of species having large individuals and also the prior movements of many large *L. cupida* nymphs into tributaries. Tributary flow is much lower and the tributary's rotifer-nauplii (all copepods) drift component exhibits maximum densities. By end of May, total degree days to date represent 23% of total yearly degree days.

Summer

June (yeardays 213-242, degree days = 380). Average last spring frost is 15 June. Marsh grasses start turning green in early June. *Salix* and *Populus* are in full-leaf by mid June. Flow decreases but is still in spring-high stage. Water temperatures continue to rise. Total degree days at end of month represent 41% of total yearly degree days.

The previous year's leaf litter has almost completely disappeared, but the first filamentous algae bloom occurs. Also, standing crop of epilithic diatoms is greatest in June, but this is based on only a 1-year study without corroborative field notes of other years. The last of the non-residence adult suckers have moved downstream. Sucker eggs start hatching and shortly thereafter the young-of-year start moving downstream. About 70% of all OTUs are reproducing in June and about 70% are also reproducing in July; therefore the last week of June and first week of July will be considered the period of maximum reproduction for arthropods of this brown-water stream. Pertaining to mayflies, *Baetis, Callibaetis*, and *Ephemera* start their reproductive period. Nymphs of the summer mayflies *Siphlonurus, Paraleptophlebia*, and *Centroptilum* first appear, as do the new generations of *Zapada* and *Gammarus. Baetis, Siphlonurus*, and Simuliidae are at maximum population densities in June. 'Benthic' cladocerans first appear in samples. Tributary continues to flow, and its entomostracan component is at maximum drift densities.

July (yeardays 243-273, degree days = 450). This is the only month that both the marsh grasses and trees are green for the entire month. Average air temperatures and precipitation are maximum in July. Water temperatures continue to rise, although more slowly than in May or June. The total degree days curve is about in the middle of the log phase. At end of July, total degree days to date represent 61% of total yearly degree days. Flow remains high until late July, at which time the summer-decline stage starts. Density of aquatic macrophytes is increasing rapidly. Maximum downstream movement of sucker young-of-year take place. As indicated, about 70% of all OTUs are reproducing in July. The summer mayflies *Siphlonurus* and *Centroptilum* start reproducing, as do *Caenis, Stenacron* and *Hexagenia*. Total mayfly emergence density is greatest in July. By the end of July, 56% of all OTUs have completed their reproductive period. New generations of *Hyalella, Cheumatopsyche, Hydropsyche, Siphloplecton*, and *Leptophlebia* first appear. *Paraleptophlebia, Zapada*, and drifting terrestrial insects are at maximum population densities. Tributary continues to flow and its 'other' component (mainly chironomid larvae and nematodes) is at maximum drift density.

August (yeardays 274-304, degree days = 400). First average autumn frost occurs on 22 August. By end of August, marsh grasses are again brown, and most of *Salix* and *Populus* leaves are colored. Water temperatures reach average maximum values (16.6°C) in early August and start declining rapidly, ending log phase of total degree days curve. By the end of August, total degree days represent 79% of total yearly degree days. Flow's summer-decline stage continues throughout August. *Sparganium* is at maximum population density. Last of young-of-year suckers move downstream in early August. *Paraleptophlebia* is the only univoltine OTU that starts reproducing in August. By end of August, the reproductive periods of 85% of OTUs are over. The new generation of *Caenis* first appears and is at maximum population density; *Gammarus* population is also at maximum density. Total chironomid emergence density is greatest in early August. (The emergence cycles of total Ephemeroptera and total Chironomidae generally follow the water temperature cycle and resembles even more closely the day length times water degree days cycle.) Total (all taxa) daily drift is greatest in August, due mainly to the large entomostracan component. Standing crop by numbers is increasing rapidly, due to large numbers of new generation individuals and the build-up of 'benthic' cladocerans and cyclopoids. There are indications that maximum species diversity occurs in August. The tributary ceases flowing in mid August.

Autumn

September (yeardays 305-334, degree days = 310). Leaf-drop starts at beginning of September and by month's end, *Salix* and *Populus* trees have lost ca 75% of their leaves. Maximum litter-fall date is 12 September. Water continues to cool rapidly; at end of September, total degree days represent 93% of total yearly degree days. Flow continues to decrease rapidly in early September, but levels off in mid September when autumn base-flow stage begins. At this time, water velocity has decreased considerably, due in part to the impounding effect of beaver dams, this phenophase being maximum in September. Total aquatic macrophytes are at maximum density, and this also assists in reducing water velocity. Also, the combination of numerous beaver dams and the dense stand of macrophytes appears to impede the downstream movement of leaf litter; thus promoting on-site processing of organic matter at a time when there is maximum input of litter to the stream. The water's pH is highest in September. No OTU starts its reproductive period in September, and only 15% of the OTUs are on-the-wing and presumably could still be reproducing, including the mayflies *Baetis* and *Callibaetis*. By the end of September, when water temperature is ca 9°C and falling rapidly, all OTUs have completed their reproductive periods. No new generations appear in September. Corixids, ceratopogonids, and benthic cyclopoids and cladocerans are at maximum population densities. And standing crop by numbers is greatest in September.

October (yeardays 335-365, degree days = 145). Average daily air temperature drops rapidly and by end of month is 0°C, at which time the watershed is almost completely snow-covered. *Salix* and *Populus* trees have lost all their leaves by end of month. Water temperatures exhibit the largest rate decrease for any month. Ice along stream edges first appears in mid October. Total degree days for October represent 7% of total yearly degree days. Flow is relatively constant, in autumn-base-flow stage, until late October, when autumn-decline stage starts. Values for chemical constituents that vary inversely with flow start increasing rapidly. The substrate's leaf litter is at maximum concentration; the second major filamentous algae bloom occurs, and aquatic macrophytes are dying off rapidly. In short, October appears to be the time of maximum food resources for most taxa. After mid October, no terrestrial insects are found in the drift. Entomostracan drift densities are greatest in October, as is Siphloplecton's population density. No new generations of OTUs appear in October and there is no reproduction by OTUs. However a few adults of some other chironomid species are occasionally seen in early October, and rarely a few adult *Baetis* are collected in early October. It is not known whethere these very late emerging insects reproduce.

Concluding remarks

In a comprehensive phenological study of a watershed, one should be able to note the phenological state of certain key terrestrial plants and then predict fairly accurately what is taking place in the stream at that time. The Bigoray River study was not designed as a watershed phenology study, and the few terrestrial phenological observations are rudimentary. Unfortunately the Bigoray River area is remote, and there is no permanent station at the study site, from which one could obtain the necessary daily or weekly observations. Workers wishing to pursue further this type approach to studying streams, e.g. to mathematically model seasonality, would find it profitable to include data sets on terrestrial plants.

There are sufficient phenological data available for Bigoray River to obtain a comprehensive descriptive picture of the stream–subjectively fitting it into the broad lotic system spectrum. Also these data can be used as indices upon which to base general stream management strategies. Some of the important phenological events that characterize Bigoray River include: (1) an ice-free season of 7 months (April-November); (2) a total emergence, hence reproductive, period of 6 months (April-September) for aquatic insects studied, with the largest number of taxa reproducing in late June and early July; (3) a 3½ month period (late April to early August) when water temperatures are on the rise (log phase of total degree day curve), with maximum rate increase in May, maximum rate decrease in October, and maximum water temperature values in early August; (4) a completely green (trees and marsh grasses) watershed period of less than 2 months (late June to mid August); (5) a leaf-drop period of 1½ months (September to mid October), with maximum litter-fall rate in early September; (6) maximum discharge in April; (7) minimum standing crop by numbers in April and maximum numbers in September; (8) maximum daily drift and drift densities (all taxa) in August; (9) maximum impounding effect of beaver dams in September; (10) maximum aquatic macrophyte standing crop in September, and (11) maximum 'potential' food resources (detritus of aquatic macrophyte and terrestrial leaf origin) in mid October.

Finally, there is the seemingly arhythmic nature of the environment during the long, 5-month winter season. I suggested (Introduction) that streams at this and higher latitudes would seem especially suited for phenological studies because of clear-cut rhythmic environment at these latitudes. It therefore seems paradoxical that for almost half the year there are few detectable periodic events. Water temperature and flow are at minimum values and relatively constant. Dirft densities are at minimum values. There are no reproductive periods for species studied; no new generations appear; and for most taxa, e.g. the thoroughly studied mayflies, little growth takes place in the winter.

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