MONTANA STATE UNIVERSITY



Ecology of the diatom communities of the upper Madison River system, Yellowstone National Park
by Theodore Scott Roeder

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY in Botany
Montana State University
© Copyright by Theodore Scott Roeder (1966)

Abstract:
The rivers in Yellowstone National Park, receiving thermal discharges from geysers and hot springs, were investigated to determine the relationships between water chemistry and benthic diatom communities.

Examination of diatom collections revealed distinct differences in the floristics of some of the sampling stations. An ordination of the most abundant and frequently occurring species revealed the presence of two distinct communities of diatoms. One was found in the Gardner River where calcium was the dominant cation and the other occurred in the Madison River system where sodium was the dominant cation. Similar communities have been reported from European waters.

The construction of a matrix based on the percentage similarities of the most frequently occurring diatoms at each sampling station provided a method whereby further classification of these two communities was possible. In the Madison River system stations of low and high alkalinity were floristically different. Observed productivity was also greater at the stations with higher alkalinities.

Diversity indices prepared from the samples collected at each sampling station showed seasonal changes that were related to either changing physical parameters of the environment or to competition during the time when the environment was relatively constant.

ECOLOGY OF THE DIATOM COMMUNITIES OF THE UPPER MADISON RIVER SYSTEM, YELLOWSTONE NATIONAL PARK

by

THEODORE SCOTT ROEDER

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Botany

Approved:

Head, Major Department

Chairman, Examining Committee

Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

June , 1966

10987

ACKNOWLEDGMENTS

The author wishes to express his appreciation and gratitude to Dr. J. C. Wright for his helpful guidance, constructive criticism and conscientious attitude throughout the course of this study. Thanks are also due to Drs. J. H. Rumely and I. K. Mills for their counsel during the research period and time and effort spent in reviewing the manuscript.

Sincere thanks are also given to Drs. R. Patrick and C. W. Reimer of the Academy of Natural Sciences of Philadelphia for their assistance and helpful suggestions during the initial study of diatom taxonomy and their continued interest and encouragement during the remainder of the study. Thanks are also due to Dr. A. van der Werff, Netherlands, and Dr. W. R. Schmitz, Germany, for their suggestions and encouragement at the onset of this research program.

The cooperation and support of officials of the National Park Service in Yellowstone National Park was sincerely appreciated. Chief Park Naturalist, John Good, and Park Biologist, Robert Howe, were especially helpful and encouraging. Assistance of the Yellowstone Park Company in providing quarters and laboratory space is gratefully acknowledged.

This research was supported with funds from Public Health Service Research Grant WP-00125 and Training Grant 5T1-WP-1 from the division of Water Supply and Pollution Control. Funds for preliminary work during the summer of 1961 were provided by the Endowment and Research Foundation, Montana State University.

Finally, the author would like to thank his wife and family for their patience and understanding during the course of this study.

TABLE OF CONTENTS

	Page
VITA	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	v
LIST OF FIGURES	vi
ABSTRACT	viii
INTRODUCTION	1
DESCRIPTION OF THE STUDY AREA	6
METHOD	12
Water Chemistry	12
Diatom Studies	13
RESULTS	15
Water Chemistry	15
Temperature	20
Diatom Studies	22
Number of Genera and Species	22
Important Species	23
Diversity Measurements	36
Derived Measures	43
Indices of Similarity	43
Floristic Ordination	45
DISCUSSION	54
SUMMARY	65
APPENDIX	68
LITERATURE CITED	82

LIST OF TABLES

		Page
Table I.	Results of chemical analysis of water samples	16
Table II.	Number of species found at each station	22
Table III.	Matrix of percentage similarities of diatom community samples	44
Table IV.	Relative frequencies of the 6 most abundant diatoms from each sampling station.	46
Table V.	Matrix of percentage similarities between stations based on most frequently occurring diatoms.	47
Table VI.	Joint occurrance groups	49

LIST OF FIGURES

		Page
Figure 1.	Map of Yellowstone National Park, with location of sampling sites.	7
Figure 2.	Seasonal changes in chemical composition of the Firehole River	17
Figure 3.	Seasonal changes in chemical composition of the Gibbon River	18
Figure 4.	Seasonal changes in chemical composition of the Madison River.	19
Figure 5.	Seasonal changes in chemical composition of the Gardner River.	20
Figure 6.	Daily mean temperatures of the Madison River	21
Figure 7.	Seasonal changes of percentage composition of Achnanthes minutissima Kütz.	24
Figure 8.	Seasonal changes of percentage composition of Cocconeis placentula Ehr.	25
Figure 9.	Seasonal changes of percentage composition of Fragillaria construens (Ehr.) Grun.	27
Figure 10.	Seasonal changes of percentage composition of Achnanthes linearis (W. Sm.) Grun.	27
Figure 11.	Seasonal changes of percentage composition of Anemoneis variabilis (Ross) Reimer	29
Figure 12.	Seasonal changes of percentage composition of Cymbella affinis Kütz.	30
Figure 13.	Seasonal changes of percentage composition of Cymbella mexicana (Ehr.) Hust.	31
Figure 14.	Seasonal changes of percentage composition of Gomphonema parvulum (Kütz.) Grun.	32
Figure 15.	Seasonal changes of percentage composition of Fragillaria leptostauron	33

Page

Figure 16. Seasonal changes of percentage composition of Nitzschia frustulum (Kütz.) Grun. 34

Figure 17. Seasonal changes of percentage composition of Diatoma vulgare Bory 35

Figure 18. Seasonal changes of percentage composition of Navicula avenacea Breb. 35

Figure 19. Seasonal changes of diversity indices on the Madison River. 37

Figure 20. Seasonal changes of diversity indices on the Firehole River 39

Figure 21. Seasonal changes of diversity indices on the Gibbon River 41

Figure 22. Seasonal changes of diversity indices on the Gardner River. 43

Figure 23. Relative frequency of taxa plotted against the compositional index. 50

Figure 24. Average daily net photosynthesis at three stations, Madison River. 60

Figure 25. Relationships of water chemistry and diatom communities at the various sampling stations 64

ABSTRACT

The rivers in Yellowstone National Park, receiving thermal discharges from geysers and hot springs, were investigated to determine the relationships between water chemistry and benthic diatom communities.

Examination of diatom collections revealed distinct differences in the floristics of some of the sampling stations. An ordination of the most abundant and frequently occurring species revealed the presence of two distinct communities of diatoms. One was found in the Gardner River where calcium was the dominant cation and the other occurred in the Madison River system where sodium was the dominant cation. Similar communities have been reported from European waters.

The construction of a matrix based on the percentage similarities of the most frequently occurring diatoms at each sampling station provided a method whereby further classification of these two communities was possible. In the Madison River system stations of low and high alkalinity were floristically different. Observed productivity was also greater at the stations with higher alkalinities.

Diversity indices prepared from the samples collected at each sampling station showed seasonal changes that were related to either changing physical parameters of the environment or to competition during the time when the environment was relatively constant.

INTRODUCTION

The study of algal communities in flowing waters has been approached in two different ways. In the older traditional approach, the complex of different taxa, each considered to have definite ecological requirements, was taken as the basis of study. Community structure was described in terms of species frequency, numerical abundance and species per unit area. The more recent approach emphasizes biomass and productivity and is also concerned with the forces that introduce changes in the energy flow.

The species structure of communities of benthic diatoms has long been used to evaluate conditions in streams which receive various kinds and rates of pollution (Eddy, 1925; Butcher, 1932; Patrick, 1948; Fjerdingstadt, 1950; Foged, 1954; Patrick, Hohn, and Wallace, 1954; Blum, 1956; Hohn and Hellerman, 1963.). However, it has been impossible to compare directly the work of these various investigators due to the variety of methods and techniques used in obtaining and evaluating their data.

Eddy (1925) attempted to correlate successive algal communities with the age of the habitat, i.e., "young water, middle aged water, and old water," each of which was typified by particular groups of algal species.

Butcher (1932), utilizing the colonization of glass slides by benthic algae, evaluated these communities in relation to pollution in terms of floristics and relative species abundance. A modification of this technique was developed by Patrick, Hohn, and Wallace (1954) who used populations of benthic diatoms on glass slides to indicate the degree of pollution of natural waters. In relatively unpolluted waters, species diversity is generally high and usually several species share population

dominance. In polluted waters, the number of species is low and there is a great abundance of but one or a few species. The main objection to this type of study is the amount of time necessary to count and identify the large numbers of cells, a problem which precludes the consideration of more than just a few samples. In addition, recent work by Hohn and Hellerman (1963) shows that diatom growth on glass slides may not represent the natural diatom community when water temperatures are low.

According to Odum (1963), in summarizing the work of others, a characteristic feature of communities is that they contain few species which are common, (i.e., represented by large numbers of individuals), and large numbers of species which are rare at any given locus in time or space; however, the actual number of rare species is variable, so the total diversity is also variable. Both Patrick (1948) and Gaufin (1952) point out that either the absence or the presence in small numbers of some "rare" species may be more indicative of water quality than the abundance of more ubiquitous species. Recognition of the importance of these species which may be missing or present in very small numbers will depend largely on the experience of the investigator.

Other workers have used species diversity measurements but have treated the data in a different manner. Patten (1962) used the range of diversity of phytoplankton to indicate seasonal changes as related to nutrient (pollution) changes in Raritan Bay. Margalef (1956) proposed analysis of natural communities by methods derived from information theory, by which diversity can be calculated directly from a sample.

Species diversity is sometimes expressed in the form of an index, by which it is possible to compare species or community diversity directly in different ecosystems or in the same ecosystem at different times. Because diversity indices permit the integration of large amounts of information about numbers and kinds of organisms, such indices may provide a more reliable indication of organic, chemical or thermal pollution than the mere occurrence or absence of certain "indicator" species.

Fjerdingstad (1950) discussed the difficulty of using some of the more commonly encountered indicator species in different situations. In most rivers pollution is seldom of a single type, and diatoms which may be indicative of a certain type of pollution may not be important when pollution is of the composite type.

Several investigators have attempted to classify benthic diatoms according to their pollution tolerance, but there is no agreement as to the true status of many organisms because of local differences in species and environment (Gaufin, 1952). Margalef (1961) has shown that in the event of a sudden increase in nutrients certain species are led to take full advantage of their capacity for population increase. This will result in a decrease in diversity and one or a few species may attain great abundance. "Pure" water areas are usually characterized by large numbers of species, each with small numbers of individuals. Hence, if a river is subject to a number of different situations which affect the aquatic environment, the diversity of the aquatic community will be

changed as the situations change. If a stream is sampled at a number of stations progressing from "pure" water areas in the upper reaches of the stream through regions where chemical, organic or thermal enrichment takes place, there should be changes in the diversities of the communities sampled.

Yount (1956), working in the relatively constant, unpolluted environment of Silver Springs, Florida, considered a drop in diversity of benthic diatoms over a period of time to be the result of competition. This decrease in diversity corresponded to an increase in productivity of certain taxa at the expense of others. Thus the change in diversity at any one station over a period of time may be related both to successional changes caused by competition and to the effects of the changing environment.

Jurgenson (1935), Nowak (1940), Butcher (1932, 1940) and Patrick (1948) have stated that it is the attached forms (benthic organisms) which grow and reproduce in a given area that give the most reliable indication as to whether the environment of an area is suitable for aquatic life.

Up to this time no one has attempted to utilize the diversity index concept in describing changes in communities of benthic diatoms. Patten (1962) applied the diversity index concept to planktonic populations rather than to benthic forms. Williams (1961) used only the most abundant planktonic forms in small samples as indicators of water quality but did not utilize his data for calculating diversity.

The purpose of the present investigation was to determine if relationships existed between the diversity and species composition of the benthic diatoms and the water chemistry of rivers which receive thermal discharges from the geysers and hot springs in Yellowstone National Park.

DESCRIPTION OF THE STUDY AREA

Eleven sampling stations were established on the Madison River, its headwater streams the Firehole and Gibbon Rivers, and on the Gardner River. All are located in the western and northern parts of Yellowstone National Park in northwestern Wyoming and adjacent Montana and Idaho (Figure 1). This region is a high plateau, deeply dissected by rivers and surrounded by mountains. Within this area is the greatest concentration of hot springs and geysers in the world today.

At an elevation of 8,209 feet (2,500 m) the Firehole River originates at the outlet of Madison Lake and flows generally northward for 21.5 miles (34.6 km) until it joins the Gibbon River at Madison Junction. As it passes through the Upper Geyser Basin (Old Faithful area), Biscuit Basin, Midway Geyser Basin and the Lower Geyser Basin, this river receives the discharge of a great many geysers and hot springs. Allen and Day (1935) estimated that the total amount of thermal waters flowing into the Firehole River was 54.92 cu ft/sec (1.55 cu m/sec). Fisher (1960) reported an increase in the thermal discharge of about 10 percent following the earthquake activity of 1959.

In the upper reaches of the river (above the Old Faithful area), there is a negligible amount of thermal drainage. The river is small (3-8 m wide), turbulent in some areas and well aerated. Bedrock in this reach of the river is a relatively recent (Pleistocene) plateau flow of rhyolite (Boyd, 1961).

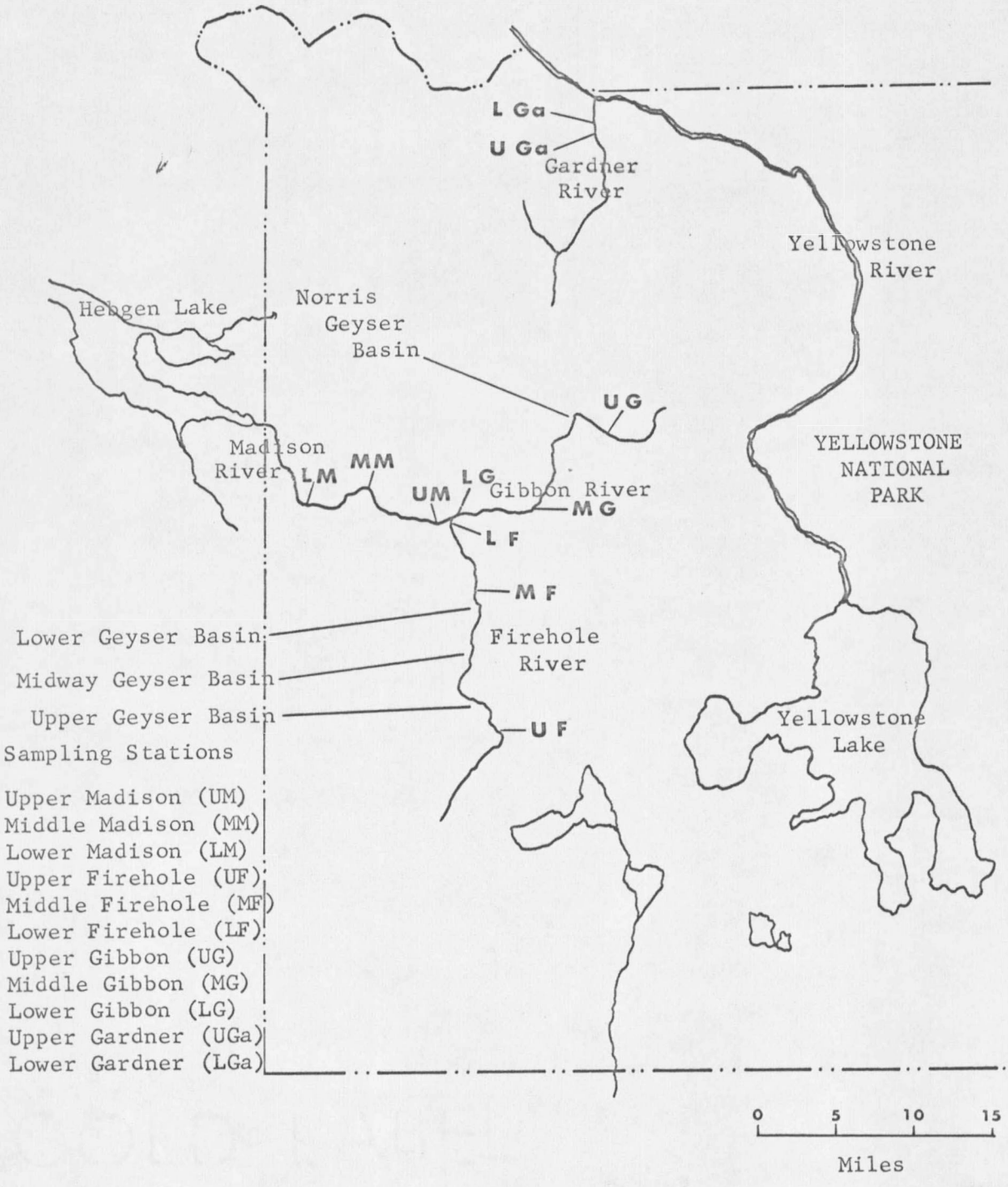

Figure 1. Map of Yellowstone National Park, with location of sampling sites.

The sampling station for the upper Firehole River was located at the bridge crossing the river on the Lone Star Geyser Road, 8.6 miles (13.8 km) downstream from Madison Lake and at an elevation of 7.606 feet (2,318 m). A short distance below this site (0.5 mi or 0.8 km), a diversion dam directs some of the stream into the water supply system for the Old Faithful area. The middle sampling station was located in the Lower Geyser Basin just above the confluence of the Firehole River and Nez Perce Creek. This site is 12.9 miles (20.8 km) downstream from the upper station and is accessible from the lower end of the Fountain Freight Road. The lower sampling station of the Firehole River was located at the north end of the Firehole Canyon, 0.5 miles (0.8 km) above the confluence of the Firehole and Gibbon Rivers at Madison Junction. This site is accessible from the Firehole Falls Loop Road and is just above the overflow discharge from the water supply chlorinator for the Madison Junction area. The chlorinator periodically adds chlorinated water to the Firehole River at this point. The elevation at this site is 6,812 feet (2,076 m) and the distance between this station and the upper station is 17.6 miles (28.7 km).

The Gibbon River starts at Grebe Lake on the Sulfatara Plateau northwest of Canyon Village. The river then passes through Wolf Lake and over Virginia Cascade before entering Norris Geyser Basin. The Gibbon receives its greatest amount of thermal waters from the hot springs and geysers in the Norris area. Downstream, the river continues to receive intermittent drainage of thermal water from a number of smaller thermal areas until just above its confluence with the Firehole River. The thermal discharge, according to Allen and Day (1935), is 6.85 cu ft/sec (0.19 cu m/sec).

The headwaters originate in an area of Pliocene rhyolite tuff and more recent Quaternary alluvial deposits (Boyd, 1961). Most of the area through which the river passes is composed of welded rhyolite tuff with the south side of the lower portion of the river bounded by plateau flows of undifferentiated rhyolite. The river bed is a mixture of bedrock, boulders, rubble, gravels, sand and silt with siliceous sinter from old thermal drainages found in localized areas.

Three sampling stations were located on the Gibbon River. The upper station was located at the bridge over the river at the Norris Canyon Cut-off Road, 0.5 miles (0.8 km) east from Norris Junction, at an elevation of 7,480 feet (2,281 m). This is above the major thermal discharge into the river. The middle station was located at the Mesa Road bridge, 11.5 miles (18.5 km) downstream from the upper station, and at an elevation of 6,950 feet (2,120 m). The lower station was located approximately 100 yards (91 m) above the confluence with the Firehole River at Madison Junction, 16.2 miles (26.1 km) downstream from the upper station and at an elevation of 6,806 feet (2,074 m).

The Madison River starts at Madison Junction at the confluence of the Firehole and Gibbon Rivers. The river flows in a westerly direction until it enters Hebgen Lake. The upper six miles (9.6 km) of the river are faced on the north by cliffs and hills of welded tuff. On the south side of the river are the more rugged cliffs and talus slopes (rhyolite flows) of the Madison Plateau. Downstream from the plateau the river passes through an area of decomposed rhyolite and tuff. The river bottom is variable, the

river flows over boulders, rubble, large and small gravels, sand and silt with a partially cemented surface layer resting on a cemented base.

Three sampling stations were selected on the Madison River: The upper station was located 1.18 miles (1.9 km) below the confluence of the Firehole and Gibbon Rivers (N.P.S. pullout designation, "Wild Animals at Home") at an elevation of 6,800 feet (2,072 m). At this site the river meanders between the cliffs of the Madison Plateau which lie to the south and large hills of tuff which lie to the north of the westward flowing river.

The middle station was located about 50 yards (45 m) below the 7 Mile Bridge, 5.7 miles (9.1 km) downstream from the upper station. At this point the river flows at the base of the tuff cliffs which lie to the north. They are considerably lower in elevation than at the upper station. To the south the plateau flow of rhyolite is also much lower in elevation. The river at this point flows over bedrock covered lightly with sands, gravels and rubble.

The lower station was located at the site of the old Riverside Ranger Station, 6.3 miles (10.2 km) downstream from the middle station and at an elevation of 6,640 feet (2,024 m). The sampling area is near the lower end of a long riffle area (approximately 5 miles or 8 km) where the river bottom varies from cemented materials to sand, gravel and rubble.

The sampling stations on the Gardner River were located north of Mammoth Hot Springs along the North Entrance Road. The upper station was located about 50 yards (45 m) above the inflow of the Hot River at an elevation of 5,760 feet (1,756 m). The Hot River arises about 50 yards (45 m)

from the Gardner River and provides the drainage for the Mammoth Hot Springs terrace area. The lower sampling station was located 0.5 miles (0.8 km) below the upper station, just downstream from the upper bridge over the Gardner River. The river bottom at both stations is composed of rubble, large and small gravels, sand and silt.

The main runoff from the heavy snows which cover this mountainous area in winter occurs during late May and June. Following extremely severe winters, the runoff will continue into July. During this high water period, it is impossible to collect benthic diatom samples from several of the stations. In general, the heaviest rainfall coincides with the time of the greatest snow melt. Usually the streams start to recede in late June and by middle July have reached a relatively constant level (Surface Water Records of Montana, 1963, 1964).

METHODS

Water Chemistry:

Water samples were collected from the river stations at varying intervals during the Fall, Spring and Summer, 1963-1964. The samples were obtained in one-liter "Polypropylene" plastic screw-cap bottles which had been washed, rinsed once with distilled water and three times with river water from the sampling station before being filled with the water sample. Immediately after collection, the samples were placed in an ice-chest and refrigerated until time for analysis. Hydrogen-ion concentration (pH) measurements were taken with a Beckman Model G pH Meter in the field and were repeated at Bozeman as part of the analysis of the samples. Upon return to Bozeman, all samples were filtered through a medium-porosity sintered-glass filter to remove particulate matter. Analyses were generally completed less than 48 hours after the samples had been collected.

Determinations were made of the following: sodium, potassium, calcium, magnesium, chloride, silicate, pH, conductivity and total alkalinity. Sulfate, phosphate and nitrate were also determined in some of the samples.

Sodium, potassium, calcium and magnesium determinations were made with a Beckman Model DU Flame Spectrophotometer, following the procedures given in the Beckman Instruction Manual #334-A. Total alkalinity, chloride, phosphate, silicate and sulfate determinations were made as described in Standard Methods for the Examination of Water and Wastewater, 11th Edition (1960). Nitrate determinations followed the chromotropic acid method of

West and Lyles (1960) but were successful only in showing that nitrate levels in these waters were too low (less than 0.0016 meq/l) for accurate determination by this method.

Diatom Studies:

Approximately 25 ml of diatom material were collected at each station at about monthly intervals. The collections were taken from the rocks, sticks and macrophytes found at the sampling sites. Such procedure provided a composite collection from each site. A description of the materials sampled was made on a collection data sheet at the time of sampling. Upon return to the laboratory at Bozeman, Montana, all samples were examined with a compound microscope to ascertain the relative numbers of living and non-living diatoms; this ratio (the number of living to non-living cells) was noted on the collection data sheet so a proportional correction could be made of the diatom counts. All samples were preserved by the addition of sufficient formalin to produce a 3-5% formalin solution in the sample bottles.

To make a detailed evaluation of the diatom populations, the diatoms were first "cleaned," using the boiling nitric acid - potassium dichromate technique described by Hohn and Hellerman (1963). Then permanent microscope slides were prepared for study.

The slides were examined for two purposes: First, the slides were scanned to determine if any differences in floristics could be easily observed when comparing slides from the different sampling stations. A

species list prepared early in the study indicated there were conspicuous differences between the upper and lower sampling stations on all the rivers studied. These data were used to determine community types on the basis of floristics of the sampling stations. This method was used to provide an index of relationship for every possible combination of sampling stations, based on the formula by Kulczynski (1927):

$$I = \frac{2c}{a + b}$$

where c is the number of species found in common at two stations, and a and b represent the total numbers of species at each of stations a and b. Using the techniques described by MacFadyen (1957) and Whittaker and Fairbanks (1958), a trellis diagram was constructed to show the similarities in species structure of the various sampling stations.

Finally, a more detailed examination of each slide was made whereby a number of fields were observed. Starting at one edge of the coverslip, every diatom observed was identified to species and tabulated until approximately 300 cells were counted on each slide and tabulated as to number of cells per species. From this tabulation, the community diversity was calculated for each collection, using the following equation (Margalef, 1951):

$$d = \frac{m - 1}{\ln N}$$

where m represents the number of species and N the number of diatom cells counted. This index of diversity is derived from the supposed linear relationship between species number and logarithm of total individuals. Diversity indices from the various stations were compared.

The data tabulated in the detailed counts were also used to provide abundance and frequency information of the species at each station.

RESULTS

Water Chemistry:

Results of the chemical analyses of water samples are given in Table I. Ranges of concentrations and mean values are recorded. Sodium was the most abundant cation in the Madison River system and was found in highest concentrations below the major thermal drainages along the Firehole River (middle and lower sampling stations). The rhyolite bedrock in this area is a feldspar of sodium and potassium alumino-silicates. The thermal waters passing through this rock tend to leach out the sodium which remains in solution. Although the same process takes place with regard to potassium, its rate of solubilization is much slower and other processes tend to return it to the solid phase (Boyd, 1961).

Calcium and magnesium were found only in small amounts in this river system. There are few calcium-bearing rocks in this area, hence only small amounts of calcium could be expected from these waters.

Both the Firehole River and the Gibbon River showed marked differences in water chemistry between the upper sampling station and the middle or lower sampling stations. Both upper stations were above major thermal discharges and had similar rates of flow. Both upper stations had a similar water chemistry.

Higher ion concentrations were found at the middle and lower stations of the Firehole and Gibbon Rivers than at the upper stations. Sulfate concentrations were highest in the middle and lower Gibbon River due to the sulfate water inflow from several drainages along the lower part of the river. The pH was also lower below these acid drainages along the middle

Table I. Results of chemical analysis of water samples.

		Conductivity $K_{25} \times 10^6$	Alkalinity meq/l	Calcium meq/l	Magnesium meq/l	Potassium meq/l	Sodium meq/l	Chloride meq/l	Sulfate meq/l	Phosphate meq/l	Silicate meq/l	pH
Upper Madison	Range	274-527	1.25-2.40	0.10-0.52	0.00-0.18	0.12-0.30	2.10-5.00	1.64-2.20	0.42-0.49	0.004-0.019	2.00-2.63	7.18-7.72
	Mean	429	2.04	0.20	0.09	0.25	3.61	1.69	0.46	0.013	2.39	7.42
Middle Madison	Range	274-488	1.25-2.50	0.09-0.21	0.00-0.10	0.12-0.28	2.10-4.80	0.89-1.83	0.41-0.46	0.006-0.017	2.02-2.65	7.30-7.89
	Mean	424	2.13	0.14	0.04	0.28	3.82	1.58	0.44	0.013	2.42	7.60
Lower Madison	Range	274-484	1.25-2.30	0.10-0.70	0.00-0.11	0.12-0.28	2.10-4.40	0.94-1.75	0.40	0.005-0.022	2.02-2.50	7.80-8.39
	Mean	404	1.96	0.26	0.03	0.22	3.68	1.52	0.40	0.015	2.33	8.14
Upper Firehole	Range	54-128	0.20-0.52	0.05-0.48	0.00-0.10	0.03-0.10	0.22-0.82	0.19-0.56	0.10	0.008	1.52-1.85	7.00-7.69
	Mean	92	0.39	0.16	0.07	0.08	0.59	0.41	0.10	0.008	1.61	7.42
Middle Firehole	Range	330-581	1.25-2.60	0.10-0.50	0.00-0.08	0.12-0.27	2.70-5.20	0.33-2.40	0.14-0.17	0.009-0.025	2.18-2.76	8.30-8.63
	Mean	423	1.95	0.18	0.03	0.21	4.30	1.73	0.16	0.017	2.53	8.46
Lower Firehole	Range	274-640	2.20-2.90	0.08-0.50	0.00-0.12	0.11-0.27	2.25-5.15	1.03-2.26	0.34-0.45	0.006-0.027	2.04-2.71	8.10-8.65
	Mean	459	2.46	0.17	0.05	0.21	4.19	1.96	0.38	0.018	2.49	8.33
Upper Gibbon	Range	62-127	0.40-0.70	0.10-0.50	0.00-0.12	0.04-0.13	0.25-0.80	0.05-0.19	0.30-0.78	0.004	1.54-2.86	6.97-7.54
	Mean	108	0.62	0.20	0.06	0.10	0.54	0.14	0.54	0.004	1.99	7.36
Middle Gibbon	Range	169-329	0.65-1.40	0.10-0.60	0.00-0.21	0.10-0.30	1.00-3.25	0.66-1.55	0.67-0.93	0.002-0.013	1.78-2.89	7.71-7.75
	Mean	283	1.11	0.22	0.09	0.22	2.15	1.16	0.80	0.007	2.21	7.65
Lower Gibbon	Range	194-433	0.90-2.00	0.14-0.73	0.00-0.13	0.11-0.29	1.25-3.90	0.56-1.69	0.65-0.96	0.002-0.014	1.78-2.89	7.10-7.40
	Mean	353	1.71	0.25	0.09	0.25	2.95	1.22	0.77	0.009	2.27	7.23
Upper Gardner	Range	161-261	1.30-2.20	0.85-1.60	0.33-0.82	0.02-0.09	0.15-0.60	0.14-0.28	0.50-0.62	0.001-0.005	1.01-1.29	8.09-8.35
	Mean	231	1.83	1.15	0.63	0.06	0.43	0.22	0.56	0.003	1.14	8.22
Lower Gardner	Range	234-640	1.55-3.10	1.10-3.25	0.65-2.26	0.04-0.86	0.25-1.65	0.23-1.08	2.15-2.89	0.005-0.011	1.06-1.29	7.68
	Mean	493	2.61	2.31	1.48	0.35	1.09	0.74	2.52	0.008	1.18	7.68

and lower Gibbon River, as compared to the Firehole River. Figures 2 and 3 illustrate some of the seasonal changes in water chemistry found in these rivers. The wide variations in concentrations were largely related to dilution of the rivers by the spring rains and melting snow.

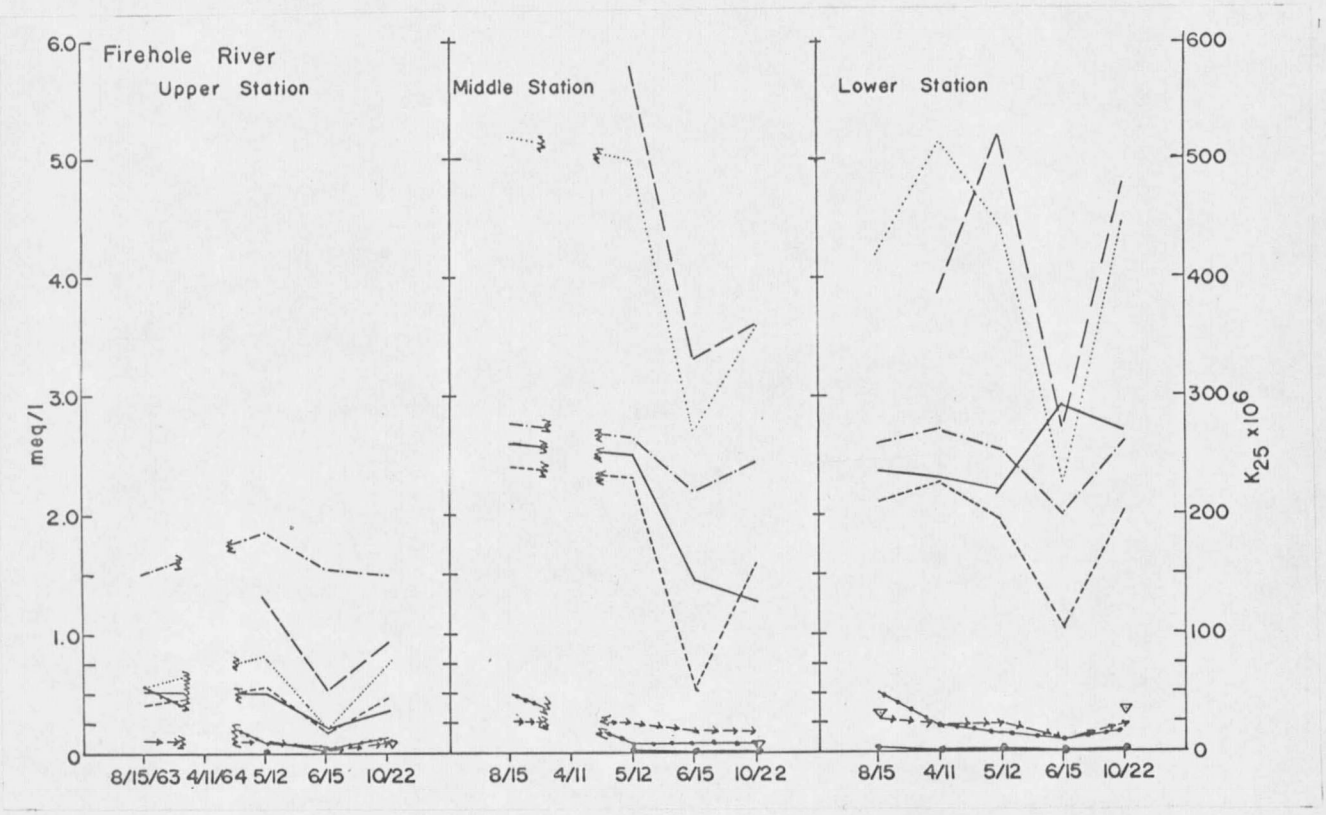

Figure 2. Seasonal changes in chemical composition of the Firehole River. Conductivity———, Alkalinity———, Sodium·····, Potassium→→→→, Calcium and Magnesium •••••, Chloride - - - - -, Sulfate ▽, Phosphate •——•, and Silicate —·—·—.

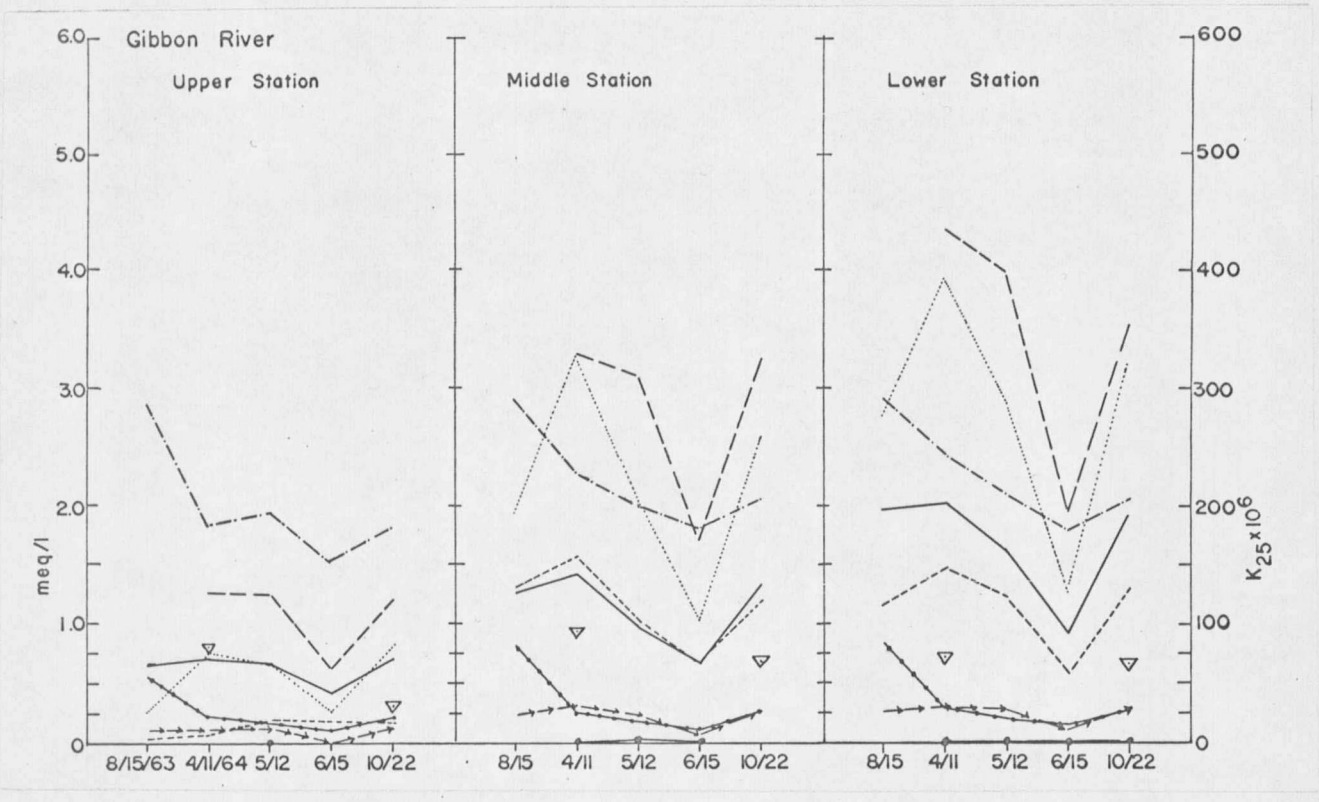

Figure 3. Seasonal changes in chemical composition of the Gibbon River. Conductivity———, Alkalinity ——— , Sodium·····, Potassium→→→ , Calcium and Magnesium•••••; Chloride-----, Sulfate ▽ ▽ , Phosphate •——• , and Silicate—·—·—.

The water chemistry of the Madison River was similar to that of the lower Firehole River. Concentrations of the various ions remained quite constant at all three sampling stations. Seasonal changes are illustrated in Figure 4. Sodium was the dominant cation and bicarbonate the dominant anion. Chloride concentrations remained fairly high at all stations

(0.95 - 2.00 meq/1). Silicate concentrations remained close to the saturation level of the water (approximately 100 ppm at 25 C).

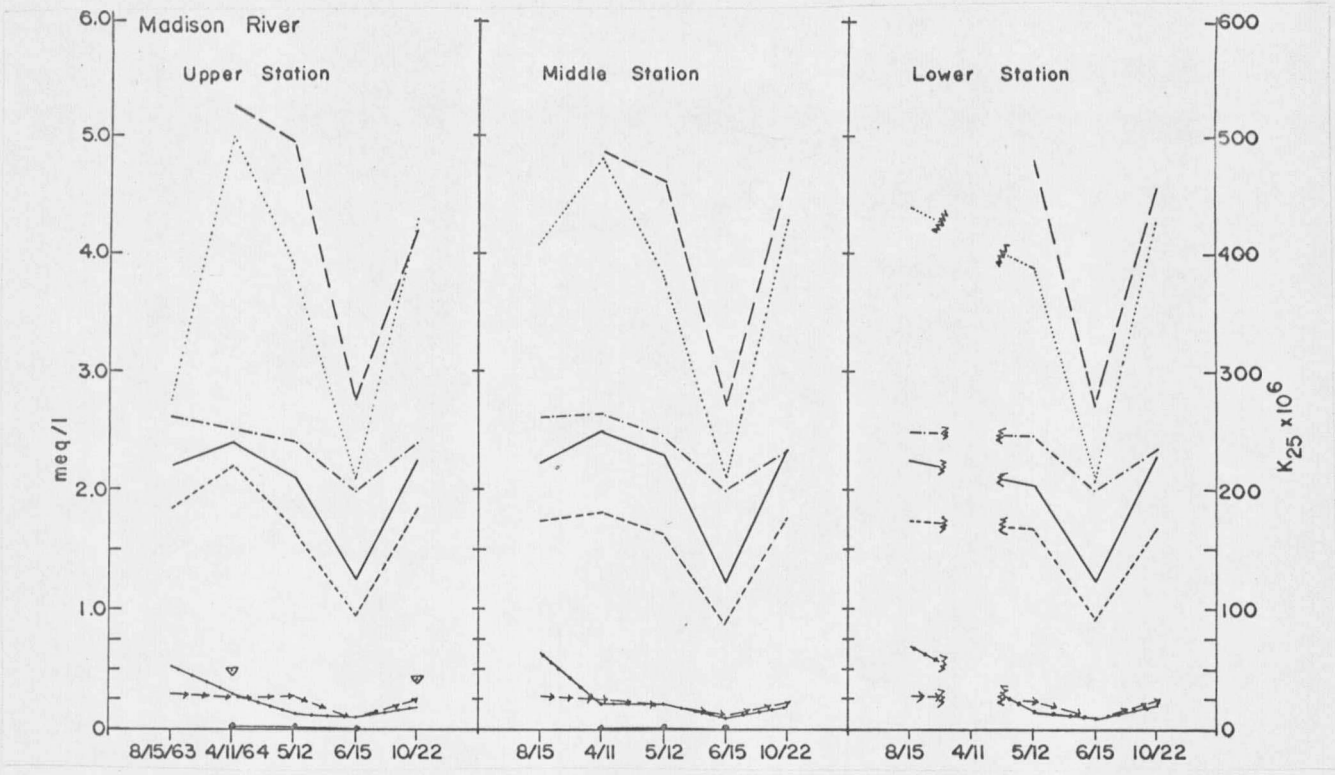

Figure 4. Seasonal changes in chemical composition of the Madison River. Conductivity———, Alkalinity———, Sodium·····, Potassium→→→, Calcium and Magnesium•••••, Chloride-----, Sulfate▽ ▽, Phosphate•——•, and Silicate—·—·—.

The waters of the Gardner River differed noticeably from those of the Madison and its tributaries. Calcium and magnesium concentrations were greater in the Gardner due to the presence of shales and sandstones in the headwater areas, as well as small drainages from old travertine deposits. The discharge of the Hot River caused a marked increase in concentrations of calcium, magnesium, bicarbonate and sulfate at the lower station (Figure 5).

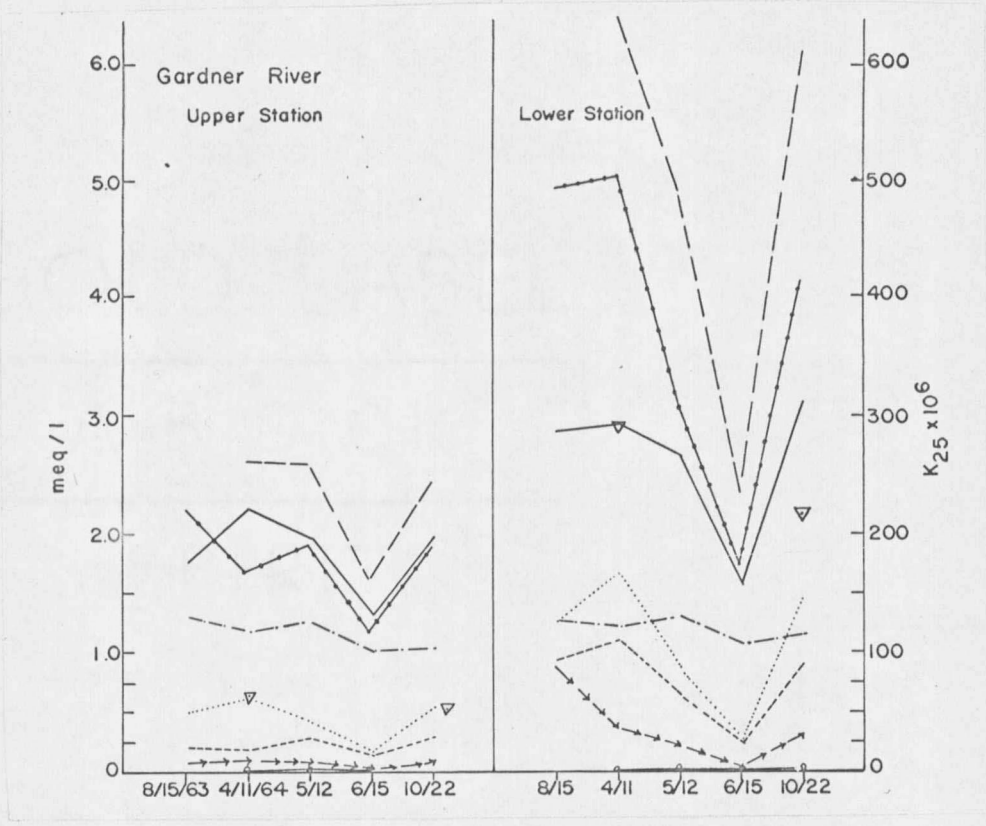

Figure 5. Seasonal changes in chemical composition of the Gardner River. Conductivity———, Alkalinity———, Sodium·····, Potassium→→→, Calcium and Magnesium•-•-•, Chloride-----, Sulfate ▽▽, Phosphate•——•, and Silicate—·—·—.

Temperature Studies:

Temperatures were recorded at the sampling stations on the Madison River by means of submersible temperature recording devices. During any one day, the variation in mean temperatures between the three stations was less than 2 C from April 10 to October 2. Daily mean temperatures fluctuated rather widely (approximately 8 C) until late June. At this time the spring runoff ended and water temperatures rose rapidly to about 20 C and remained at a high level until mid-August. Highest mean temperatures were

recorded in late July. In late August two snowstorms and a period of low ambient temperatures were reflected in temporarily lowered mean water temperatures and in September rather wide variations were recorded, depending largely on the local weather patterns (Figure 6).

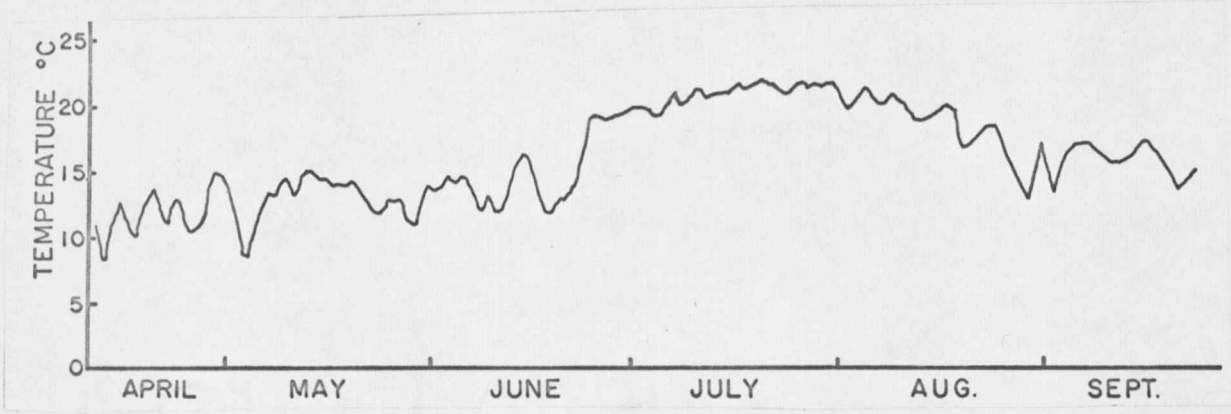

Figure 6. Daily mean temperatures of the Madison River, April 10 - September 22, 1964.

Temperatures in the Firehole and Gibbon Rivers were measured at periodic intervals with maximum-minimum thermometers and standard laboratory thermometers. At the lower stations the general temperature pattern was similar to that in the Madison River. At the upper stations temperatures were considerably lower. During the winter the upper stations were ice and snow covered. The lower station on the Gibbon River was ice-covered only during the most extreme cold weather, whereas no ice has been reported at the lower station on the Firehole River. The water temperature during the winter months at this station was 4.25 C at a time when the air temperature was about -67 C. The highest temperature recorded at the lower Firehole River station was 26.5 C on July 10, 1964.

The water temperatures at all the stations were within the range generally reported as suitable for diatom growth.

Diatom Studies:

Number of Genera and Species:

A total of 311 species and varieties of diatoms was found in the rivers studied (see Appendix A for species and distribution lists). 181 species and varieties were found in the Firehole River, 162 in the Gibbon River, 194 in the Madison River and 108 in the Gardner River. Table II gives the numbers of species and varieties at each sampling station.

Table II

Number of Species Found at Each Station

Firehole River			Gibbon River			Madison River			Gardner River	
U	M	L	U	M	L	U	M	L	U	L
125	94	96	105	96	105	131	117	91	71	91

Of the total number, only 19 species were found at all eleven stations during the 1964 season, with an additional eight species found at all the stations in the Madison, Firehole and Gibbon Rivers. These are species with a broad ecological amplitude, and are generally widely distributed in North America. Undoubtedly, other widely distributed species would be found if sufficient material were examined from the collections.

The genera represented by the greatest numbers of species were Navicula (47), Achnanthes (39), Nitzschia (30), Cymbella (24), Pinnularia (23), Fragillaria (18), Gomphonema (15), Eunotia (13) and Synedra (13). All other genera were represented by less than nine species or varieties. 121 species were found at only one station and generally represented less than one per cent of the sample in which they were found.

The diatom flora from the Madison River and its tributaries in Yellowstone Park seems to be closely allied to that of more northern regions in Alaska, Denmark, Sweden, Norway and Finland. The flora is different from that found in the eastern United States, and some of the species seem to be restricted to the Yellowstone Park region. As more diatom collections are made in the Pacific Northwest and northern Rocky Mountain areas some of these species will undoubtedly be found to be more widespread. However, as pointed out by Hustedt (1937) and Patrick (1948), the typically rheophilic diatoms of a region contain the most characteristic or endemic species of a region.

Important Species:

The following is a discussion of the ecology and distribution of diatom species which either occurred most frequently in the diatom samples or had a unique distribution in the area sampled.

Achnanthes minutissima Kützing (Figure 7)

Achnanthes minutissima was one of the five most abundant species and was present in all the samples collected. Williams (1961) reported it as occurring in the plankton of well-aerated rivers. Hustedt (1930) stated that it was common in most waters in central Europe over a wide range of temperature and where the pH ranged from 6.20 - 7.00. In the Madison River system it was most prominent at the lower station on the Gibbon River. The lowest pH values of the eleven stations were generally found here. The species was plentiful at the upper Firehole sampling station which also had a lower pH than the stations downstream. Although common in the Madison River, no distribution pattern was discernable at the stations sampled. The species was very abundant at the lower Gardner sampling station.

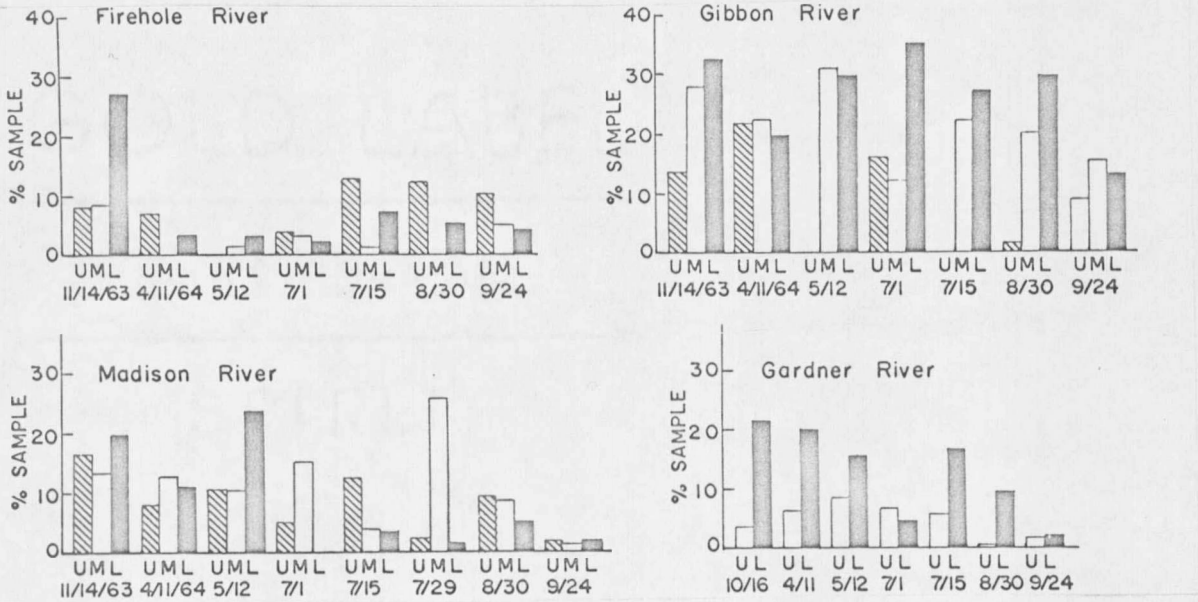

Figure 7. Seasonal changes of percentage composition of Achnanthes minutissima Kütz.. U, M and L represent the upper, middle and lower stations, respectively.

Cocconeis placentula Ehr. (Figure 8)

Cocconeis placentula was one of the most abundant and in several collections accounted for over 50% of the diatoms counted in one sample. Hustedt (1942) reported it to be a temperature-independent, cosmopolitan, freshwater species. Foged (1954) said it was an alkaliphilic, current-indifferent species. Butcher (1940) used it as an indicator species since it disappeared where organic enrichment occurred and reappeared further downstream where the water was again "clean." According to Foged (1954) the species occurs in the heavily polluted portions of several streams in Denmark, but he did not report its abundance in the polluted areas. It is apparent that there is a great deal of conflicting information as to the usage of this species as an indicator of pollution.

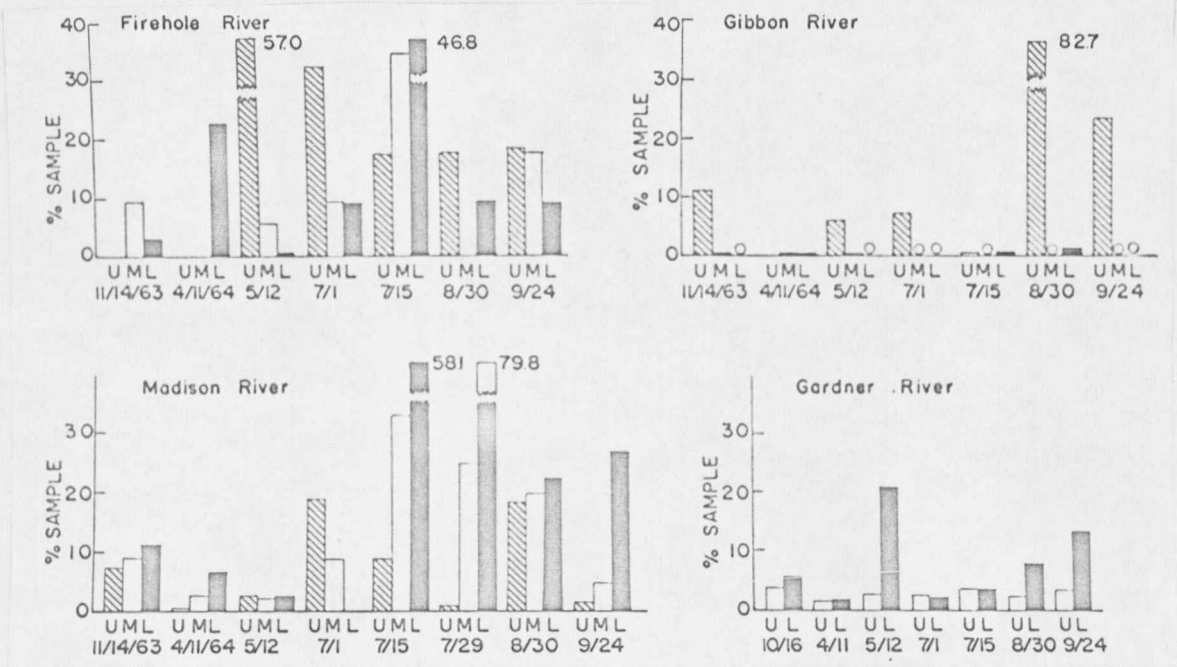

Figure 8. Seasonal changes of percentage composition of Cocconeis placentula Ehr.. U, M and L represent the upper, middle and lower stations, respectively.

The species is frequently the first to colonize "bare" areas and is often found coating the leaves and stems of submerged macrophytes as well as the filaments of green algae, particularly Cladophora sp. Cocconeis placentula was very abundant at the upper station on the Firehole River, above the source of any artificial pollution. It was commonly found at the other stations on the Firehole River, but generally less abundantly. It was also plentiful at times at the upper Gibbon River sampling station, but infrequent at the lower sampling stations (1% or less/sample). The species increased noticeably at the lower stations on the Madison River.

The stations where this diatom was most abundant were those which were removed from possible sources of organic enrichment. The importance of the species as an indicator of pollution may be dependent upon its abundance rather than its presence.

Fragillaria construens (Ehr.) Grun. (Figure 9)

Fragillaria construens was found at all the sampling stations. Foged (1954) lists it as a current-indifferent alkaliphil. Hustedt (1942) considered it to be temperature indifferent. Kolkwitz and Marsson (1908) stated that it was an oligosaprobe, in contrast to Cleve-Euler (1951) who reported that it occurred in severely polluted waters. The diatom seemed to grow well at all stations, which suggests that it had a broad ecological amplitude.

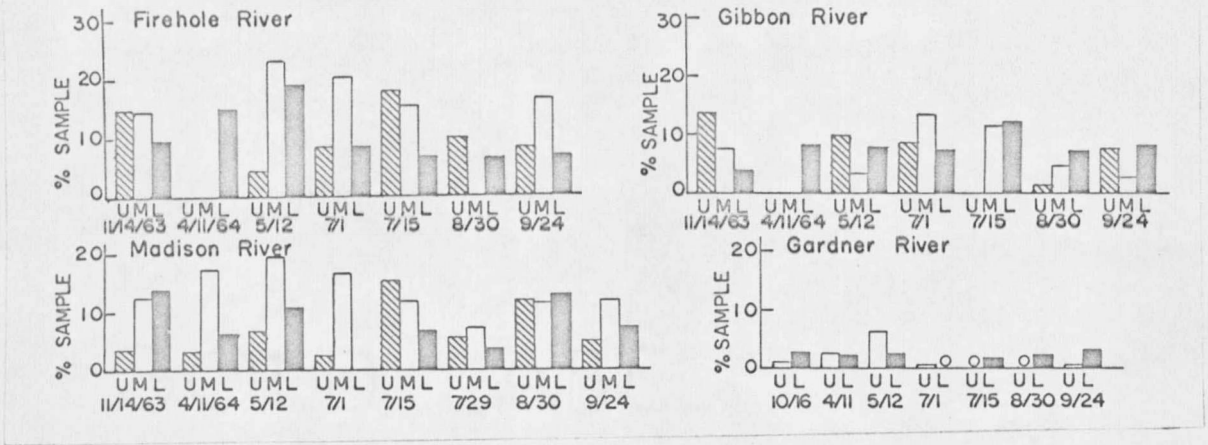

Figure 9. Seasonal changes of percentage composition of Fragillaria construens (Ehr.) Grun.. U, M and L represent the upper, middle and lower stations, respectively.

Achnanthes linearis (W. Sm.) Grun. (Figure 10)

Although not as abundant as were the preceeding species, Achnanthes linearis had a more unusual distribution. Patrick and Freese (1960) found it abundant in the Arctic on a number of different substrates. Hustedt (1930) listed it as being plentiful in mountain streams over a broad pH range (6.00 - 9.50). It was temperature and current indifferent, although common only where the temperature was less than 15.5 C.

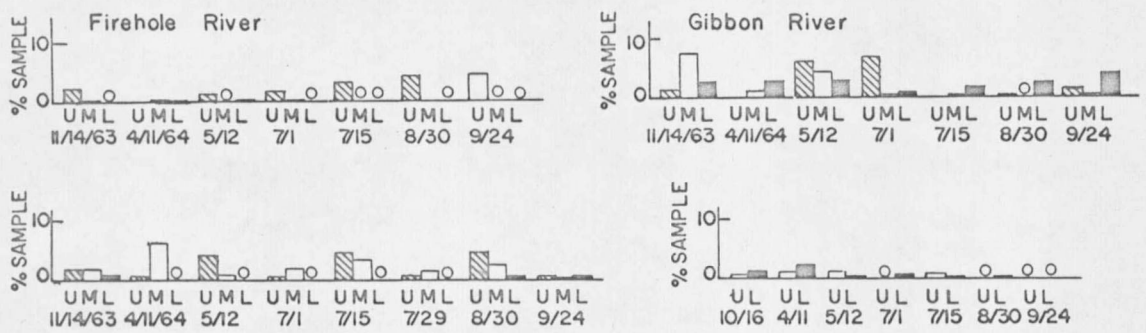

Figure 10. Seasonal changes of percentage composition of Achnanthes linearis (W. Sm.) Grun.. U, M and L represent the upper, middle and lower stations, respectively.

The species was found at the upper stations on the Firehole and Gibbon Rivers, whereas it was seldom found in the warmer waters of the lower Firehole River. It did occur at the lower Gibbon River station but was most abundant early and late in the season when water temperatures were low (under 15.0 C). It was more prominent at the upper and middle stations on the Madison River and was frequently missing from samples collected at the lower station.

Anemoneis variabilis (Ross) Reimer (Figure 11)

The taxonomy of Anemoneis variabilis has been reviewed recently by Reimer (1961), but information on its ecology seems to be somewhat conflicting. This may be due to taxonomic errors by some of the earlier writers. Foged (1954) considered it to be current- and pH-indifferent and reported its collection from acid localities. Manguin (1962) described it as occurring in the littoral zone of oligotrophic or eutrophic alkaline waters. Hustedt (1942) found it to be pH- and temperature-indifferent. Reimer (personal communication) considers it to be an alkaliphil which is tolerant of wide ecological variations.

The species was found to be abundant at the lower station on the Gibbon River and almost completely lacking from the upper stations. It was also rarely found in the Firehole River. It occurred in varying proportions at the Madison River stations, but no pattern of distribution was discernible.

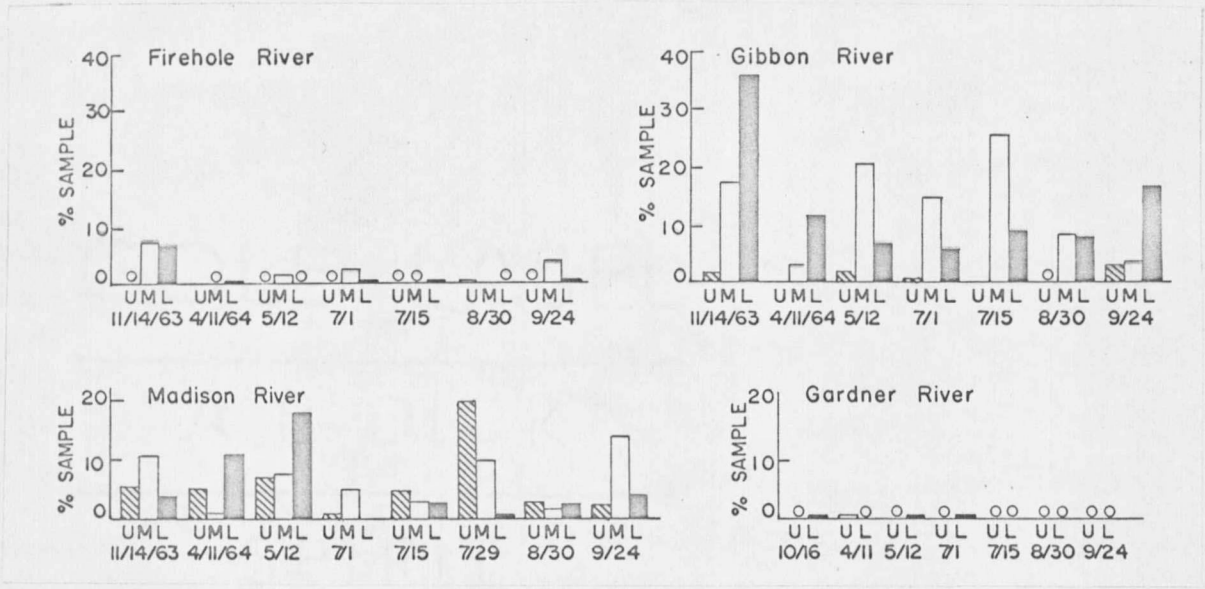

Figure 11. Seasonal changes of percentage composition of Anemoneis variabilis (Ross) Reimer. U, M and L represent the upper, middle and lower stations, respectively.

Cymbella affinis Kützz. (Figure 12)

There is some question as to the correct nomenclature for Cymbella affinis since it is a variable species. In shape and striae count, the forms from Yellowstone Park were identical to C. affinis Kutz. However, the number of central punctae were variable from one to four; most specimens had two or three. Hustedt (1937) placed the forms with more than one central punctum in C. sumatrensis Hust., which was described as an endemic form from mountain streams in Sumatra. Reimer (personal communication) considers the two species to be identical on the basis of the published descriptions, and the present author agrees. Therefore, until slides of C. sumatrensis are available for examination, the species will be considered as C. affinis. Foged (1954) considered C. affinis to be a current-indifferent, alkalibiontic form. Patrick and Freese (1960) described it

as being widely distributed in fresh water. Hustedt (1930) discussed the extremely variable nature of the species, but mentioned that its best development was in warm waters. However, in his Abisko paper (1942) he gave a temperature range for this species of 10.2 - 12.0 C. It was found to occur abundantly at much higher temperatures in several areas in Yellowstone National Park.

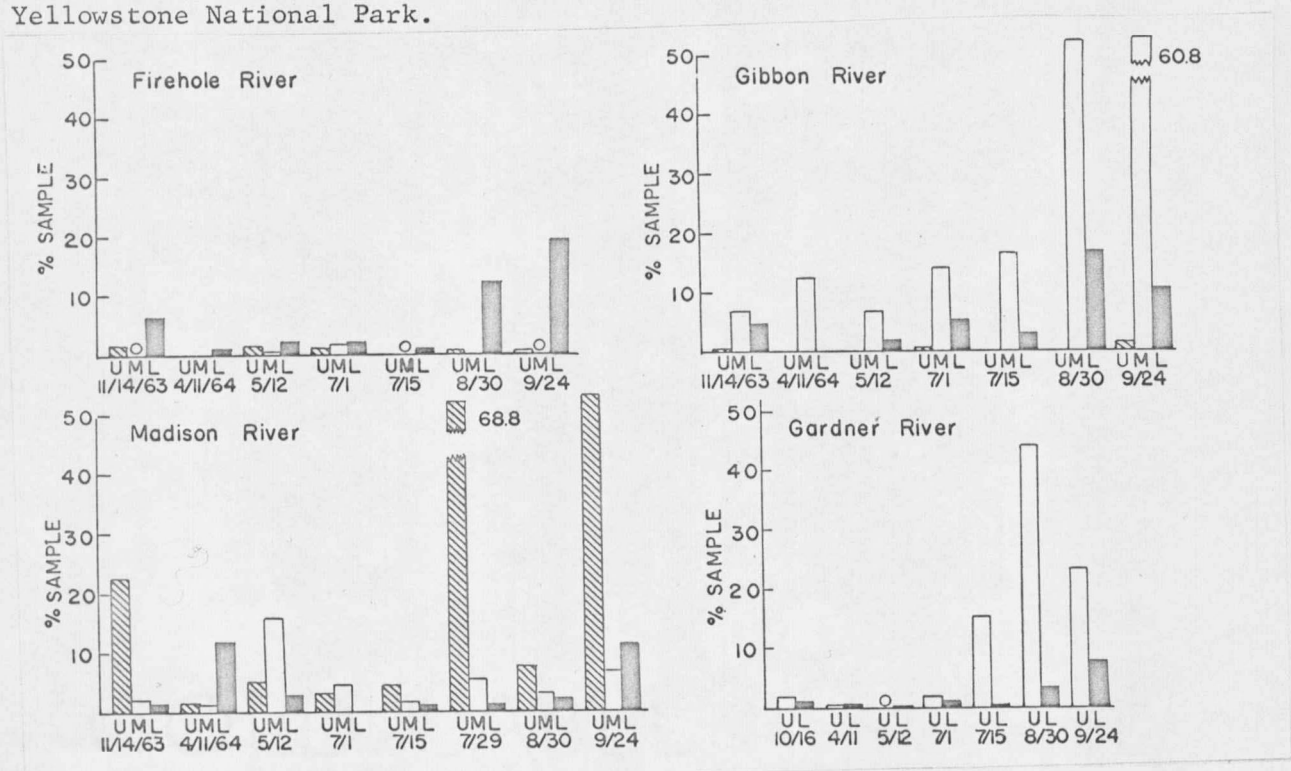

Figure 12. Seasonal changes of percentage composition of Cymbella affinis Kützz.. U, M and L represent the upper, middle, and lower stations, respectively.

The distribution of the species was somewhat unusual in the study area. At the upper stations in the Firehole and Gibbon Rivers it was absent or found in small numbers (0 to less than 2% of a sample). At the lower stations it was more abundant, particularly in late August and September comprising from 10.5% to 19.5% of the samples. C. affinis was most

important at the upper station on the Madison River in late July and late September. At these times a diatom bloom was observed, and diversity measurements at this station indicated the lowest diversity of the 1964 season.

Cymbella mexicana (Ehr.) Cleve (Figure 13)

Cymbella mexicana has an unusual distribution in North America, generally being found only west of the Mississippi River. Stoermer (unpublished) found it in Lake Okiboji, Iowa, growing at depths of 20 to 40 feet. Manguin (1961) reported the species from Lake Karluk, Kodiak Island, Alaska. Reimer (personal communication) considered it to be an alkalibiont, generally found among the benthic diatoms of alkaline lakes.

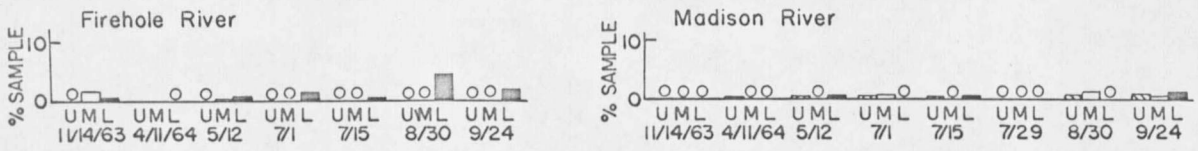

Figure 13. Seasonal changes of percentage composition of Cymbella mexicana (Ehr) Cleve. U, M and L represent the upper, middle and lower stations, respectively.

The diatom was not found in any samples from the Gibbon River but did occur at the middle and lower stations on the Firehole River. Its presence in the Madison River samples was largely limited to collections taken in August and September. Although the species was not abundant in any of the samples (less than four per cent by number), it was one of the largest diatoms encountered in this study. The volume of this species may be greater than that provided by all the other cells in a sample in which it occurred.

Gomphonema parvulum (Kützing) Grun. (Figure 14)

Gomphonema parvulum has been used as a pollution indicator by a number of authors (Fjerdingstad, 1950). However, in the Yellowstone Park waters sampled it did not become abundant enough at any station to be considered an indicator species. Fjerdingstad (1950) reported it as occurring in the alpha-mesosaprobic zone; but he cautioned that a number of the species found in this zone are among the most tolerant forms and may also be common under oligotrophic conditions. Foged (1954) considered the species to be pH-indifferent and associated with running water. Hustedt (1930) described it as occurring "especially in standing waters." It was commonly found in the Madison River at all three stations; but it was most frequent at the middle station during the period of low diversity in late July. It comprised less than one per cent of any sample collected at the upper Firehole River station; but it was always present in greater abundance at the two lower stations on the Firehole River and at all three stations on the Gibbon River.

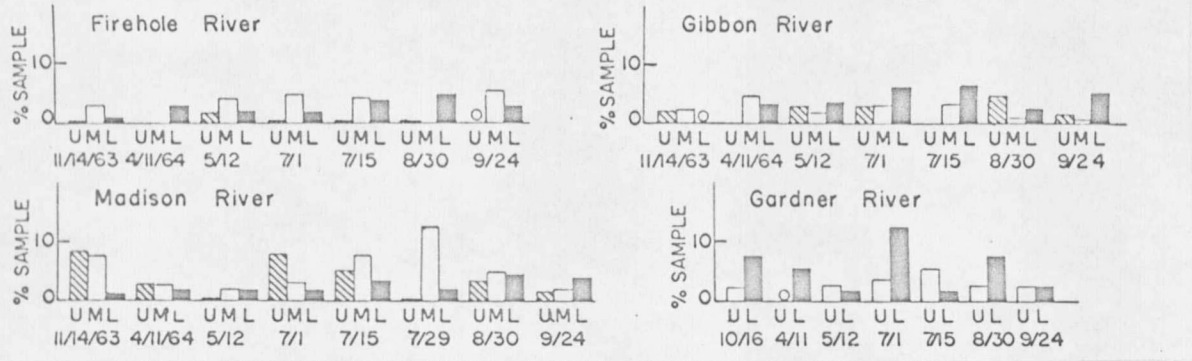

Figure 14. Seasonal changes of percentage composition of Gomphonema parvulum (Kützing) Grun.. U, M and L represent the upper, middle and lower stations, respectively.

Fragillaria leptostauron (Ehr.) Hust. (Figure 15)

Fragillaria leptostauron was frequently one of the dominant forms in the Firehole River; but it occurred less abundantly in the Gibbon and Madison Rivers. Foged (1954) listed the species as having its optimum development in stagnant waters. Hustedt (1930) stated that it occurred on silty substrates in slowly moving waters. Patrick and Freese (1960) reported its occurrence at the edge of silt-bottomed streams in Alaska. Fjerdingstad (1950) listed it as occurring in the alpha-mesosaprobic zone. In the Yellowstone area its abundance on the Firehole River indicates that it may be tolerant of conditions other than those described in the literature. Here the water is definitely not stagnant, and there is little or no silt deposition at the sampling stations.

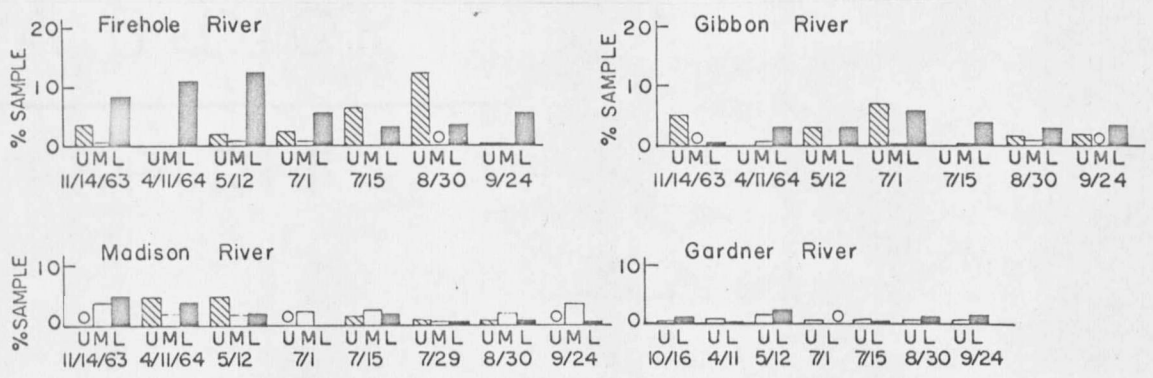

Figure 15. Seasonal changes of percentage composition of Fragillaria leptostauron (Ehr.) Hust.. U, M and L represent the upper, middle and lower stations, respectively.

Nitzschia frustulum (Kützing) Grun. (Figure 16)

Nitzschia frustulum was most abundant (5.0 - 8.0%) at the lower station on the Gibbon River and rarely occurred at the other stations. Foged (1954) listed the diatom as being pH-indifferent, occurring in

stagnant waters and tolerating brackish conditions. Patrick and Freese (1960) described it as occurring with algae in tundra pools and in algal film (neuston) from a silt bottomed pool. Hustedt (1930) said that it occurred in brackish waters as well as fresh water. Reimer (1954) found the species in both fresh and brackish water.

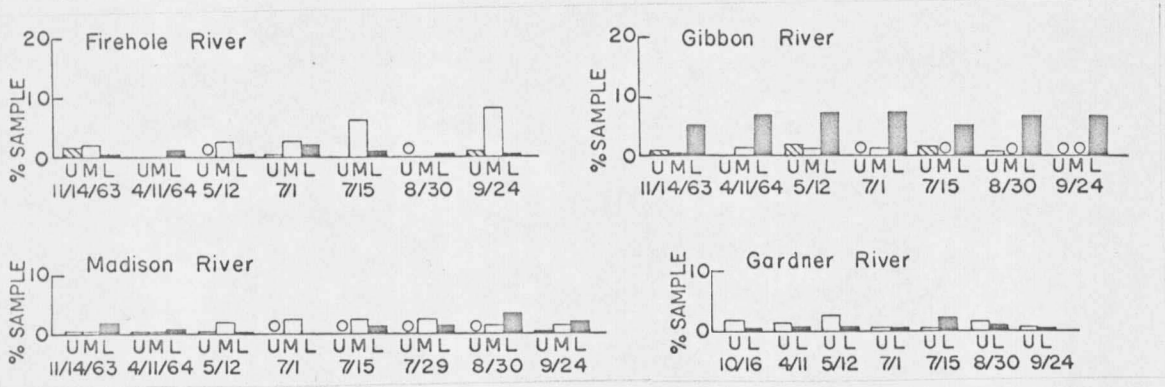

Figure 16. Seasonal changes of percentage composition of Nitzschia frustulum (Kütz.) Grun.. U, M and L represent the upper, middle and lower stations, respectively.

Diatoma vulgare Bory (Figure 17)

Diatoma vulgare was found only in samples from the Gardner River, occurring most abundantly at the upper station in August and September. Hustedt (1930) described D. vulgare as frequently occurring in standing water, but more commonly in flowing water, in both the planktonic and littoral zones. Cleve-Euler (1951) reported that it frequently occurs in both fresh and brackish waters. Patrick (1948) said the species was favored by a high percentage of nitrates in the water. Foged (1954) reported the species to be alkalibiontic, having its optimum development in running water. Other authors have stressed its occurrence in polluted

streams, although Fjerdingstad (1950) also found it in oligosaprobic waters (see discussion in Fjerdingstad, pp 94).

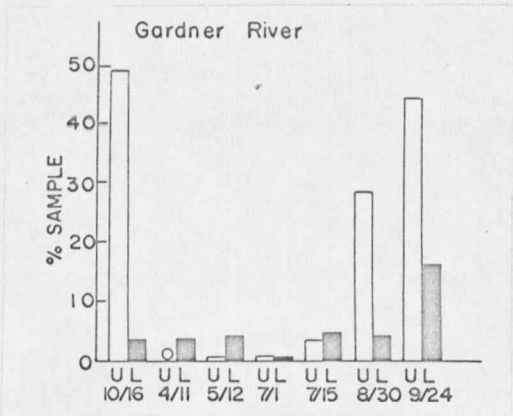

Figure 17. Seasonal changes of percentage composition of Diatoma vulgare Bory. U and L represent the upper and lower stations, respectively.

Navicula avenacea Breb. (Figure 18)

Navicula avenacea was found only in the Gardner River, occurring most abundantly at the upper sampling station in the early spring samples. This is the first reported occurrence of this species in North America.

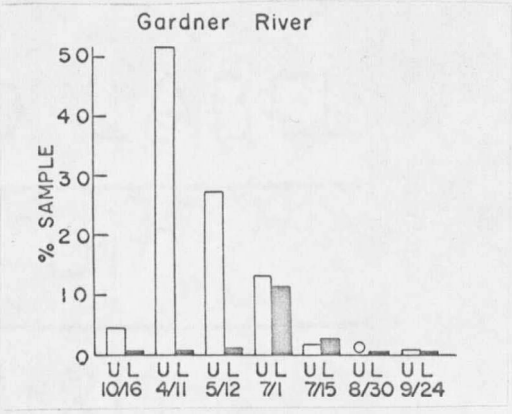

Figure 18. Seasonal changes of percentage composition of Navicula avenacea Breb.. U and L represent the upper and lower stations, respectively.

Diversity Measurements:

Madison River: When diversity indices were plotted for each station (Figure 19), it was apparent that some major changes in the diatom communities occurred during the 1964 growing season. Early in the year the diversity followed an expected and typical pattern. Community density was greatest at the upstream station, intermediate at the middle station, and least at the lower station. The situation changed noticeably in late July when the diversity dropped to a low level at all stations. Subsequently diversity increased at all stations in late August. The diversity indices at each station changed again during late September, with the upper station showing the lowest diversity. The last change seems to be the reverse of what one might expect. However, since the same change occurred the previous fall (1963), it may be related to some factor controlling growth at this station.

The samples from April through June exhibited a rather constant level of diversity despite the fact that this was the time of the spring runoff when there was a considerable dilution of the chemicals in the water. The change in diversity which took place during late July may have been related to several factors. At that time the water temperature was at its maximum for the year, approximately 25 C. This was above the temperature considered optimal for many diatoms. Hence, the thermal waters coming from the Firehole River may have acted as a limiting factor for the growth of some diatoms, and at the same time may have stimulated the growth of other species which were not depressed by higher temperatures. Another

factor operating at the same time was the effluent being added to the river from the Madison Junction sewage disposal plant. The major use of the campground occurred during July and early August, adding a considerable amount of effluent at this time which may have enriched the river sufficiently to affect the growth of diatoms and allow a few tolerant species to dominate the community. It was also observed during this period that the river contained large amounts of filamentous green and blue-green algae, which commonly occur in warm and enriched waters.

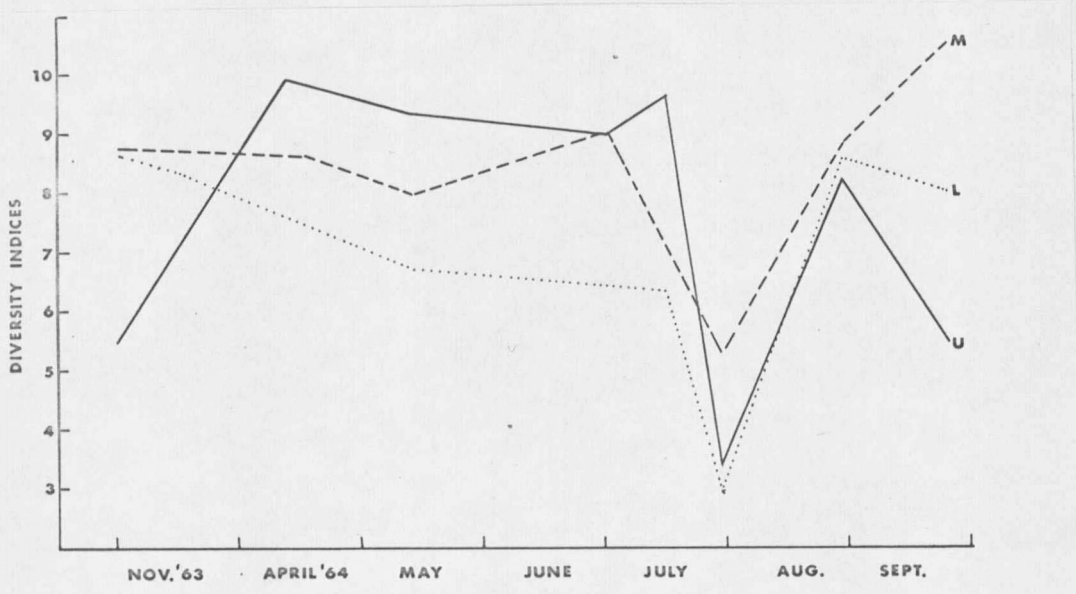

Figure 19. Seasonal changes of diversity indices on the Madison River. U, M and L refer to the upper, middle and lower stations, respectively.

Two periods of low diversity were found at the upper station on the Madison River in late July and late September. During both of these periods Cymbella affinis Kützz. comprised 50 per cent of the samples. This species was also dominant the previous fall (November 1963). The species composition of the entire community was quite similar at these three times.

This fact suggests that the environment was also similar at these times. However, considerable differences in water chemistry, temperature, light and rates of flow existed at these times, indicating that perhaps none of these parameters, by themselves, control or limit the populations of diatoms. Instead, it is highly probable that it is some combination of variable environmental conditions that is responsible for the diversity differences or similarities.

The middle and lower stations on the Madison River also exhibited a drop in diversity at the late July sampling period. However, the species of diatoms present at these stations differed noticeably from those at the upper station. Cocconeis placentula Ehr. became one of the most abundant species and C. affinis dropped to less than one per cent of the total sample. According to Butcher (1947), C. placentula normally appears abundant where a stream is recovering from organic pollution, an observation which supports the suggestion that organic enrichment may have been responsible for the drop in diversity at the upper station. The temperature factor may have been superimposed and important in the diversity drop at the lower stations.

It should not be assumed that the presence in great numbers of C. affinis at the upper station at these times, and its small numbers at the lower station, provide an indication of pollution. Rather, it might be assumed that C. affinis is an extremely variable species capable of growing and reproducing rapidly under a variety of conditions.

Firehole River: Diversity changes in the Firehole River were different from those in the Madison River (Figure 20). Early in the year the middle and lower stations maintained a fairly constant level of diversity that increased slightly during the spring run-off and then dropped during July and August. The decrease from mid-July to late August was not as prominent as in the Madison River samples. This was probably due to the misplacement of some of the samples from the July 30 sampling period. At the lower sampling station Cymbella affinis was the most abundant diatom during the last two periods, a situation similar to that which occurred in the upper Madison at the same time.

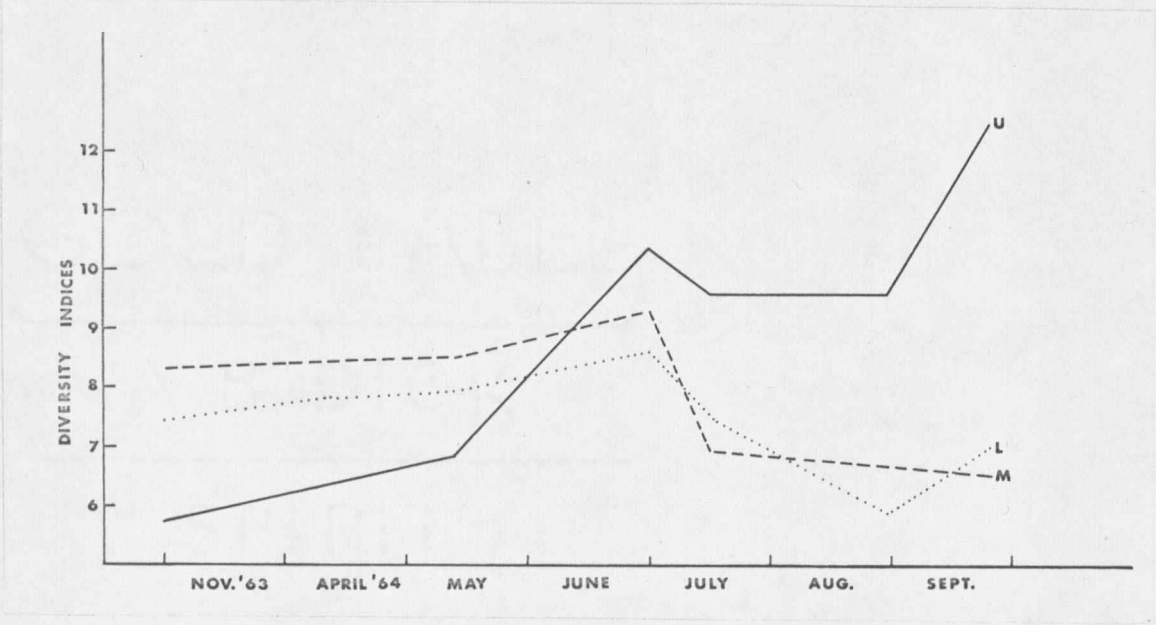

Figure 20. Seasonal changes of diversity indices on the Firehole River. U, M and L refer to the upper, middle and lower stations, respectively.

The diversity index at the upper station fluctuated more widely than at the lower station. The first collection taken in mid-May showed rather low diversity. Since the snow depth at that time was in excess of four feet and the ice-snow cover over the stream had recently collapsed, it may be that the algal growth was just getting started. Cocconeis placentula Ehr. was the most abundant species (60%). This species is frequently the first to populate newly exposed substrates. The same species was present in November 1963 at this station, although it accounted for only 30% of the sample; diversity at this time was also very low (5.77). This was probably due to the poor growing conditions in the late fall. Snow and ice were present in the stream and the water temperature was extremely low (2.0 - 5.0 C). In late September the highest diversity in the entire Madison river system was found at the upper Firehole River (12.5). Of a total of 318 cells counted, 73 species and varieties were found. 33.4% of the sample was composed of the five most dominant species, while 51 species were represented by only 1-2 frustules. The dominant species remained the same throughout most of the growing season at this station, in strong contrast to the downstream stations.

Gibbon River: The diversity indices of the Gibbon River (Figure 21) differed noticeably from those of the Firehole River. In early May, diversity at the upper station was rather low (7.5), probably due to the adverse environmental conditions similar to those found on the upper Firehole River at that time. The low level of diversity at the upper station in late August (3.9) seems to reflect the influence of some yet unknown factor

which did not noticeably affect diatoms at the lower stations. A number of the living diatoms collected in that sample exhibited a bright green color when examined under the microscope. According to van der Werff (personal communication), this color change frequently occurs in dying cells which have been affected by metal poisoning. The same situation had been noted in early September 1962. The factor which causes the color change in the diatoms is unknown. However, Smith and Kendall (1922) reported the presence of some "toxic" material coming from a small thermal drainage which is located about 6 miles upstream from the sampling station It may be that the material coming from this area remains toxic for varying distances downstream depending on the volume and rate of flow of the river. During late August and early September the flow was at a relatively low level, which increased slightly late in the fall. At the end of the season diversity at this station again increased to a maximum level (9.9).

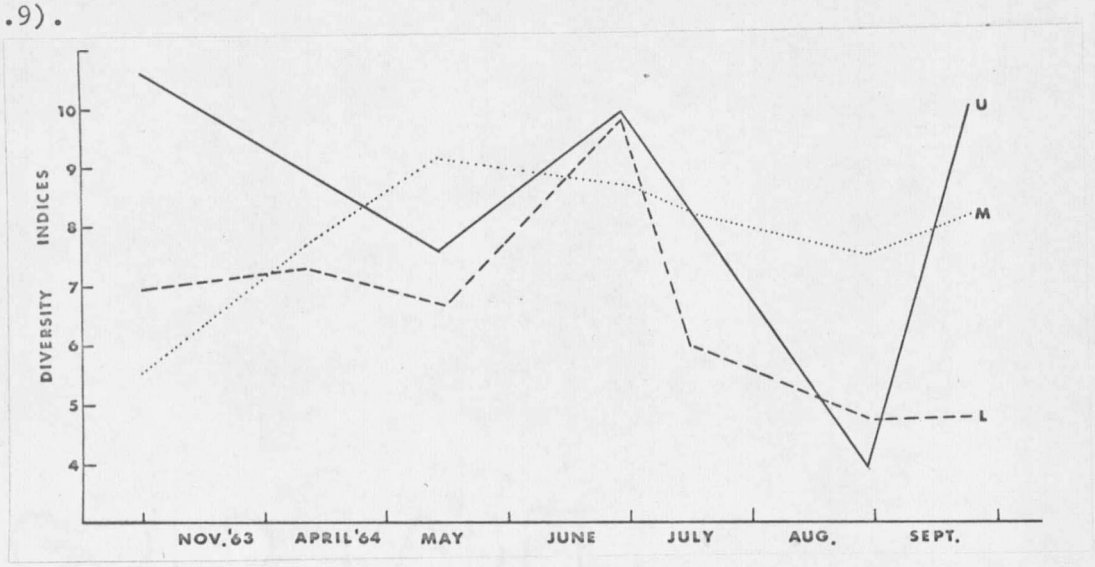

Figure 21. Seasonal changes of diversity indices on the Gibbon River. U, M and L refer to the upper, middle and lower stations, respectively.

During the early part of the season, the samples from the middle station had a pattern of diversity similar to the upper station. In July, the diversity dropped considerably and remained low throughout the remainder of the sampling period. During these sampling periods a diatom bloom was observed at this station. Anemoneis variabilis (Ross) Reimer, Cymbella affinis Kützz. and Achnanthes minutissima Kützz. were the most abundant species at this time.

The diversity indices at the lower station on the Gibbon River seemed to be more constant than at any of the other stations sampled during the 1964 season. This relative stability may be due to the small amplitude of pH changes reported at this station (pH range 6.9-7.5) during the growing season. Daily fluctuations in pH usually ranged between 6.9 and 7.1 pH units. According to Cholnoky (1960), the magnitude of pH change is of prime importance in determining diatom growth and species composition; and in a well buffered aquatic environment diversity changes may not be great.

Gardner River: Diversity indices of samples from the Gardner River were noticeably different from those of the Madison River system (Figure 22). Diversity was lowest at the upper station throughout the sampling period. This may be due to the constant influx of effluent from the Mammoth community. Diatom growth at both stations was poor during most of the growing season. However, at the lower station the yellow-green alga Vaucheria sp. and the green alga Enteromorpha intestinalis were extremely abundant during

most of the growing season. These two species of algae did not occur at the upper sampling station. The poor growth of diatoms in the calcium-rich waters of the lower station is unexplained at this time.

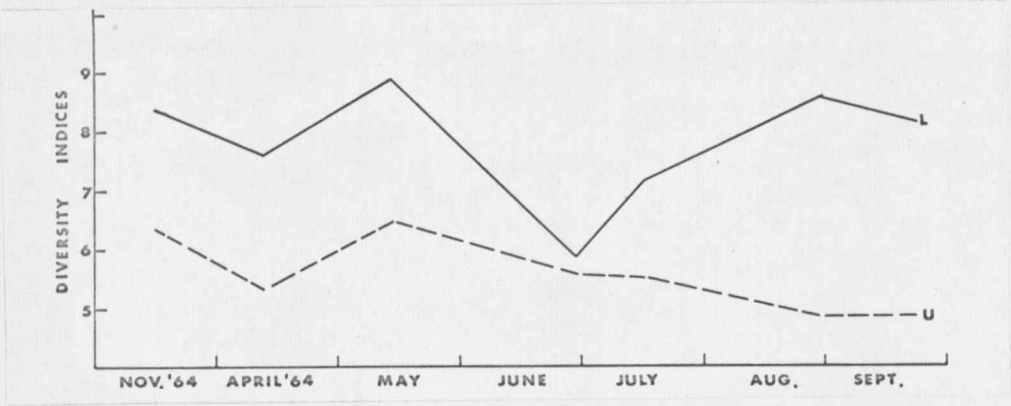

Figure 22. Seasonal changes of diversity indices on the Gardner River. U and L refer to the upper and lower stations, respectively.

Derived Measures:

Indices of Similarity: The indices of relationship for every combination of sampling sites, based on percentage floristic similarities of all possible combinations of the eleven sampling stations, were entered in a Kulczynski triangle or matrix (Table III). As shown in the table, the grouping provides a classification into two floristically similar groups (outlined with double lines on Table III). Group 1 included the stations on the Gardner River only, while group 2 included all the stations in the Madison River system. It is apparent that some of the stations were more closely related to each other than to the remainder; however, there was a high degree of interrelationship between all the stations sampled in each group.

Table III. Matrix of percentage similarities of diatom community samples, based on floristic similarities of eleven sampling stations. U, M and L refer to upper, middle and lower stations, respectively. The rivers are symbolized as: Gardner - Ga, Gibbon - G, Firehole - F, Madison - M.

	LGa	UF	UM	UG	LG	MG	LF	LM	MF	MM	
#1	48.6	26.8	28.4	27.2	24.3	29.4	30.6	29.6	34.1	28.4	UGa
		29.4	31.0	28.4	28.2	33.3	36.6	32.6	36.8	31.0	LGa
			44.9	42.4	43.9	40.5	38.1	37.2	37.3	37.1	UF
				38.1	39.6	36.1	38.2	41.9	42.0	39.6	UM
					47.5	40.6	43.0	33.1	36.1	36.9	UG
#2						48.9	41.6	38.6	42.8	35.0	LG
							38.6	40.8	42.0	34.9	MG
								46.8	43.4	40.5	LF
									46.8	40.5	LM
										38.8	MF

In measuring relative similarity in terms of species composition, each species, whether rare or ubiquitous, had the same value. As a consequence, the rare species may be overvalued as compared to those occurring with high frequency and relative abundance. If the percentage frequency of the six species with the highest relative abundance in each sample is tabulated, the same breakdown into two floristically similar groups is evident (Table IV).

Further clarification of the floristic relationships indicated in Table IV results when indices of relationships are computed on the basis of these dominant species. Examination of the resulting matrix (Table V) clearly reveals a high degree of similarity of dominant species between the upper Gardner and lower Gardner and between the upper Firehole and upper Gibbon. Also evident, is a close relationship between all stations within the Madison River and between the Madison River and the middle and lower stations in the Firehole and Gibbon Rivers. The middle and lower stations within the Gibbon and Firehole Rivers, respectively, are also closely allied floristically. The resemblance between the upper Gibbon and Firehole River stations however, is much greater than that between the upper stations and the respective downstream stations on the two rivers.

Floristic Ordination: A total of 74 samples from the eleven sampling stations was used in compiling an index of joint occurrence between species pairs. A number of the species reported in the samples occurred rarely, or were found in only one sample. Since these species would not be reliable in the formation of this kind of classification system they were

Table IV. Relative frequencies of the 6 most abundant diatoms from each sampling station.

Species	UG	MG	LG	UF	MF	LF	UM	MM	LM	UGa	LGa
Fragillaria construens	100	86	100	100	100	100	75	100	100	29	14
Achnanthes minutissima	100	100	100	100	20	43	100	89	83	71	71
Cocconeis placentula	100	--	--	100	100	71	63	78	83	29	57
Synedra ulna	20	71	43	33	20	29	38	33	33	43	29
Anemoneis variabilis	--	86	100	--	20	14	75	66	50	--	--
Gomphonema parvulum	20	43	43	--	60	14	63	44	50	57	57
Cymbella affinis	--	86	71	17	--	43	75	55	17	43	14
Achnanthes linearis	40	29	14	33	--	--	38	11	--	--	--
Anemoneis serians	--	--	--	--	--	--	13	--	17	--	--
Achnanthes Kryophila	--	14	--	17	--	--	--	--	--	--	--
" lanceolata	20	--	--	--	--	--	--	--	--	--	29
" microcephala	--	--	--	--	--	--	--	11	--	--	--
Ceratoneis arcus	--	--	--	--	--	--	--	--	--	57	--
Cocconeis pediculus	--	--	--	--	--	--	13	11	--	29	29
Cyclotella compta	--	--	--	--	--	--	--	--	--	--	14
Cymbella microcephala	--	--	29	--	--	--	--	--	--	--	--
" ventricosa	20	--	--	17	--	--	--	11	--	43	14
Denticula tenuis	--	29	--	--	--	--	--	--	--	--	--
Diatoma vulgare	--	--	--	--	--	--	--	--	--	43	29
Epithemia argus	--	--	--	--	--	--	--	--	17	--	--
" turgida	--	--	--	--	40	--	--	11	33	--	--
" zebra	--	--	--	--	--	14	--	--	33	--	--
Eunotia arcus	20	14	--	17	--	--	--	--	--	--	--
" pectinalis var. minor	--	--	--	--	--	--	13	--	--	--	--
Fragillaria capucina	--	--	--	--	--	--	--	--	--	--	29
" crotonensis	--	--	--	--	--	--	--	--	33	--	--
" intermedia	20	--	--	--	20	--	--	--	--	--	--
" leptostauron	60	--	43	83	--	43	25	--	17	--	--
" pinnata	--	--	--	--	80	--	--	--	17	--	--
Gomphonema herculeanum	--	--	--	--	--	29	--	--	--	14	--
" intricatum	20	--	--	17	--	--	--	--	--	--	--
" olivaceum	--	--	--	--	--	--	--	--	--	43	43
Melosira fennoscandica	--	--	43	--	--	--	--	22	--	--	--
" sp. (Italica?)	40	--	--	67	--	29	--	--	--	--	--
Navicula avenacea	--	--	--	--	--	--	--	--	--	57	14
" cryptocephala	--	--	--	--	20	--	--	--	--	29	43
" gracilis	--	--	--	--	--	--	--	--	--	14	--
Nitzschia dissipata	--	--	--	--	--	29	--	--	--	--	--
" frustulum	--	--	--	--	40	100	--	--	--	--	--
" palea	--	--	--	--	--	--	--	11	--	--	--
Rhoicosphenia curvata	--	--	--	--	--	--	--	--	--	--	29
Rhopalodia gibba	--	--	--	--	--	--	13	33	17	--	--
Synedra mazamaensis	--	--	--	--	20	29	13	--	--	--	--
" pulchella	--	--	--	--	--	--	--	--	--	--	29
" tenera	--	29	--	--	--	--	--	--	--	--	--
" vaucheria	--	14	14	--	60	14	--	13	--	14	43

Table V. Matrix of percentage similarities between stations based on the most frequently occurring diatoms in Table IV. U, M and L refer to upper, middle and lower stations, respectively. The rivers are symbolized as: Gardner - Ga, Gibbon - G, Firehole - F, Madison - M.

LGa	UM	LM	MM	LF	MF	UF	UG	MG	LG	
.76	.60	.39	.40	.52	.48	.43	.34	.43	.44	UGa
	.56	.36	.38	.42	.45	.40	.45	.33	.41	LGa
		.68	**.71**	**.62**	.52	.54	.52	.54	.64	UM
			.68	.55	.57	.44	.43	.44	.54	LM
				.60	.59	.54	.52	**.62**	**.67**	MM
					.64	.37	.50	.52	**.62**	LF
						.32	.46	.48	.50	MF
							.72	.58	.52	UF
								.48	.50	UG
									.70	MG

omitted from the early part of the procedure (Swindale and Curtis, 1957). Consequently, all species which had a relative frequency of less than 1% of those counted in a sample and those which occurred in less than 10 samples were dropped from consideration. An index of joint occurrence was then calculated for the remaining 35 species of diatoms. The number of samples in which two species occurred is expressed as a percentage of the number of samples of occurrence of both species.

Species of pairs which did not occur jointly were placed at opposite ends of a list and species of pairs with high joint occurrence were placed near each other (Guinochet, 1955; from Swindale and Curtis, 1957). An order was thus obtained for the 35 species which was considered to be the species reaction to the complex of environmental factors. Then the species were divided into five groups in the order of their positions in the joint occurrence list (Table VI). For each sample, the relative frequency of a species was multiplied by the number of the joint occurrence group to which the species belonged. The products for each species considered were then summed to provide a compositional index for each sample.

The relative frequency of each species in each sample was then plotted against the compositional index of that sample, giving a family of curves (Curtis, 1959). When the curves of 14 species, some from each joint occurrence group, were plotted, the graph in Figure 23 resulted. The graph shows that when the samples were arranged according to the associative tendencies of their constituent species, the relative frequencies of the species form curves which overlap and whose peaks are distributed throughout the arrangement.

Table VI. Joint occurrence groups.

1.

Diatoma hiemale var. mesodon
Melosira fennoscandica
Epithemia zebra
Eunotia arcus
Fragillaria crotonensis
Gomphonema olivaceum
Nitzschia dissipata

2.

Cymbella ventricosa
Cocconeis pediculus
Nitzschia palea
Achnanthes lanceolata
Navicula cryptocephala
Nitzschia frustulum
Synedra ulna

3.

Cocconeis placentula
Gomphonema parvulum
Achnanthes minutissima
Fragillaria construens
Synedra vaucheria
Cymbella affinis
Fragillaria leptostauron

4.

Anemoneis variabilis
Melosira sp.
Achnanthes linearis
Fragillaria intermedia
Synedra rumpens
Rhopalodia gibba
Fragillaria pinnata

5.

Synedra mazamaensis
Ceratoneis arcus
Epithemia turgida
Achnanthes Kryophila
Achnanthes gibberula
Denticula thermalis
Synedra tenera

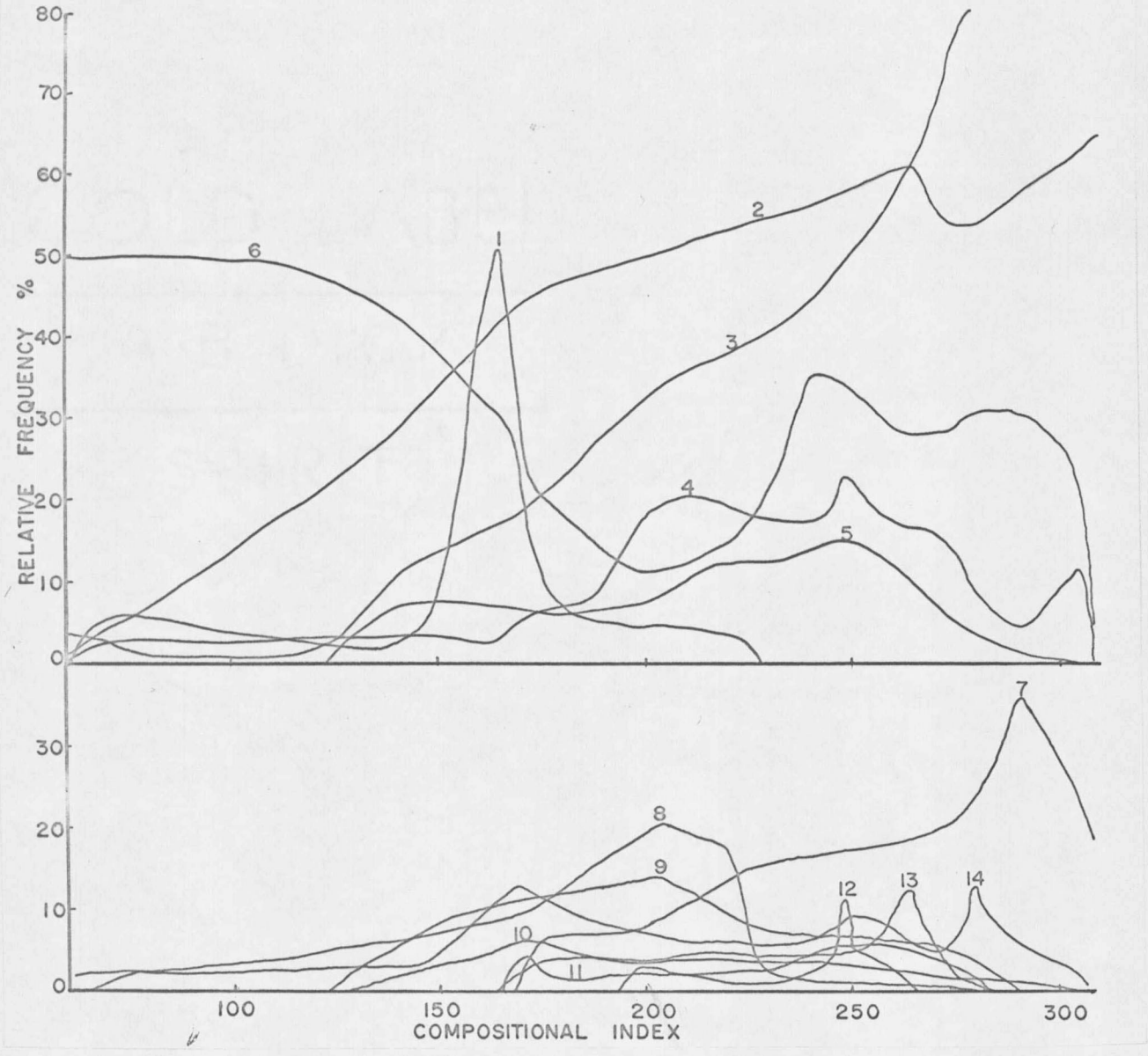

Figure 23. Relative frequency (smoothed curves) of taxa plotted against the compositional index.
1. Achnanthes minutissima, 2. Cymbella affinis, 3. Cocconeis placentula, 4. Fragillaria construens, 5. Synedra ulna, 6. Diatoma vulgare, 7. Anemoneis variabilis, 8. Ceratoneis arcus, 9. Cymbella ventricosa, 10. Navicula cryptocephala, 11. Fragillaria crotonensis, 12. Synedra mazamaensis, 13. Rhopalodia gibba, 14. Gomphonema parvulum.

However, the curves for the species Cymbella affinis Kützz., Achnanthes minutissima Kützz. and Fragillaria construens (Ehr.) Grun. completely cover the curves representing the other species found in the Madison River system. All of the samples collected from the Madison River and its tributaries had a compositional index greater than 120, and the abovementioned species seemed to cover this range of the compositional index and consequently could be used to indicate the community of diatoms found in the Madison River system. The other curves represent species whose presence was more sporadic, and as such were not as important in describing the diatom communities occurring here. The curve of Diatoma vulgare Bory., a species found only in the Gardner River, indicates the presence of a second major community of diatoms; although the Gardner contains some of the same ubiquitous species of the Madison River system, it is floristically different from that area.

Despite the variation in species abundance and frequency noted in the different samples, the presence of the most ubiquitous species Achnanthes minutissima Kützz., Cocconeis placentula Ehr. and Fragillaria construens (Ehr.) Grun. in almost all the samples collected from the Madison River system indicates that there is only one somewhat variable community of benthic diatoms in that area. Butcher (1947) described a similar community as one of two distinct communities occurring in English rivers, particularly from slightly eutrophic areas. It should be realized that these species may not always be abundant or even present in all samples, but that they generally do occur abundantly throughout the year.

In the calcium-rich waters of the Gardner River, a second community of diatoms was found which was characterized by the presence of Diatoma vulgare Bory, Cocconeis pediculus Ehr., Navicula avenacea Breb. and a species of the filamentous Chrysophyte Vaucheria. This community has also been previously described as occurring in the Ardennes region of Belgium (Symoens, 1957; in Blum, 1960).

Thus there were two communities of benthic diatoms in the area under study, from rivers which differ in geological history, water chemistry, and diatom speciation. It must be realized that a number of variations occurred in the diatom populations, which might be related to changes in water chemistry. Such changes may determine the presence or absence of certain species. However, the ubiquitous species found in the area were still the best indicators of the community, as these are species able to grow and reproduce rapidly in the particular environment.

DISCUSSION

In the study of diatom populations, whereby an index of diversity is proposed in order to compare changes at different stations or at the same station over a time interval, it is well to clarify what is meant by diversity and how the diversity index can be used.

Patrick, Hohn and Wallace (1954) have shown that natural communities of benthic diatoms are composed of relatively large numbers of species (50 - 150). A few species are very common or very rare; and a great many species are common but not abundant. The distribution of all of the species that are present may be plotted as a lognormal curve. A curve calculated from a smaller sample from the same area will have the same general form, but will be decapitated since the rare species will be missing. Patrick uses this lognormal distribution as the basis for her studies on the effects of pollution on the benthic diatom flora. Changes in diversity are reflected by a change in the shape of the lognormal curve. There are a number of other methods for representing diversity of plant or animal communities, but in general all are based on some kind of mathematical progression which attempts to approximate the growth of the natural community. However, there is a regularity of distribution of individuals by species in any taxonomic grouping so that an empirical mathematical expression can be used to describe the distribution (Margalef, 1957). A parameter for each community which expresses the way individuals are distributed among species is called an index of diversity.

The diversity index represents the wealth of species in the community. While there have been a number of diversity indices proposed, the one used in this work $d = \frac{m - 1}{\ln N}$ is based on a presumed linear relationship between the number of species and the logarithm of the number of individuals. It should be realized that expressing diversity in this manner is not the same as the lognormal distribution used by Patrick (1954), which is biologically realistic in relation to natural growth; whereas the diversity index expressed above is not. The application of the diversity index concept in the present work was to provide a method by which changes in the structure of communities of benthic diatoms could be readily measured and comparisons could be made with other communities at different times and locations. The index is also indicative of the environment in which the diatoms are found. If an environment becomes restrictive, a reduction in diversity should occur, for species which cannot grow in that environment would drop out, and thus a low diversity index would result. An environment in which competition is intense should also have a low diversity index since only a few species would be successful in occupying the area. In such an environment, a decrease in diversity may be related to an increase in productivity. According to Yount (1956), productivity is one of the main factors determining the species variety of an area; and conversely, the species composition of an area may also determine the productivity.

The original hypothesis upon which this investigation was based was that changes in the water chemistry of rivers in Yellowstone National Park would be reflected by changes in the communities of benthic diatoms found

in these rivers. It was speculated that these changes would involve floristic differences as well as differences in biomass and productivity. From the results, it appears that there are only two communities of benthic diatoms present in the waters studied. One is found throughout the Madison, Firehole and Gibbon Rivers and the other in the Gardner River. If this interpretation is correct, the question arises as to why the diatom populations are so similar in this rather extensive area, despite some noticeable differences in the water chemistry of the rivers studied.

Boyd (1961) mapped the rhyolite lava flows (plateau flows) of Yellowstone Park. The Madison River system occurs almost completely within the area covered by the plateau flows of lava. As a result, it might be expected that the chemical composition of ground water arising from this area would be somewhat uniform. Examination of the water analyses from the upper Firehole and upper Gibbon Rivers shows that this is essentially correct. The diatom floras of the two areas were also similar in species composition, although a greater number of species were found in the upper Firehole River samples.

As the Firehole and Gibbon Rivers flow toward Madison Junction, they are enriched by the discharge of a number of geysers and hot springs. However, the thermal features which are found along the Gibbon River differ chemically from those found along the Firehole River (Allen and Day, 1935). Consequently, the middle and lower sampling stations on both rivers show noticeable differences in water chemistry. Concentrations of sodium and chloride ions are much higher in the Firehole River, while sulfate concentrations are much higher in the Gibbon River. According to Lund (1965)

sodium and chloride ions may determine the species present rather than the quantitative development of the community. Variation in the concentration of these ions may account for the restricted occurrence of species such as Cymbella microcephala Grun., Denticula tenuis Kütz. and Synedra tenera W. Sm. which were at times relatively abundant in the Gibbon River; and Epithemia turgida (Ehr.) Kütz., E. zebra (Ehr.) Kütz., Fragillaria pinnata Ehr., Gomphonema herculeanum Ehr., Nitzschia frustulum Kütz. and Synedra mazamaensis Sover which occurred most abundantly in the Firehole River only. However, these species comprised only a minor part of the diatom community, appearing as sporadic "blooms" at various times during the year, or in smaller numbers only at certain stations on these rivers.

Differences in pH and alkalinity were also evident, but these may be considered as indicative of the total chemical environment rather than determining species composition. Generally, a pH range from 5.50 - 9.00 is considered suitable for algal growth, although different species may be present in different pH ranges (Lund, 1965). The rivers in Yellowstone Park had a pH range of 6.97 - 8.63 which is well within the range considered suitable for diatom growth.

Although calcium was present in small amounts in the Madison River and its tributaries there was no evidence that it limited the growth of diatoms. Pearsall (1932), after working with the plankton in English Lakes, stated that a low monovalent-to-divalent cation ratio (M:D ratio) was necessary for abundant growth of diatoms. Droop (1958) concluded that tolerance to sodium ion might be the decisive parameter for diatom speciation, but that many species were indifferent to M:D or Ca:Mg ratios. This

tolerance to sodium may account for the noticeable similarity in the diatom flora of the Madison River system. Lund (1965) noted that the majority of algae can flourish over a wide range of M:D ratios. The M:D ratios in the Madison river complex ranged from 2.89 to 27.60, but there was no indication that diatom growth is inhibited by these high ratios.

Phosphate and nitrate have been considered the two major ions which could limit primary productivity. However, in the rivers investigated, phosphate was always present in the water samples, although at low levels during the spring runoff. There was an enrichment of phosphate by the thermal discharge which was not depleted sufficiently downstream so as to become limiting. Lund (1965) maintained that low phosphate levels may be important in stimulating diatom growth, while higher levels produced better growth of bluegreen algae.

Nitrate determinations were unsatisfactory due to the low sensitivity of the method of analysis, and nitrate levels never exceeded 0.10 mg/l. Nitrogen sources in the Madison River system would include ammonia from the thermal discharges, nitrogen compounds leached from the soils of the watershed and possibly nitrogen fixed by bluegreen algae that is subsequently released in organic form. Patrick (1948) has reported the utilization of organic nitrogen by diatoms. Both Patrick (1948) and Lund (1965) mentioned that although nitrogen determinations in unpolluted waters have been largely unsuccessful, these waters may still show abundant growths of diatoms. This may be the situation in Yellowstone Park waters, as diatom

growth was noticeably abundant much of the time. More work needs to be done on nitrogen availability and especially on the nitrogen requirements of the species of algae found in these waters.

There are a number of additional elements necessary for the growth and reproduction of diatoms, about which little is known at this time. It is possible that the differences in productivity observed at the various sampling stations are related to seasonal changes in the availability of some of these trace elements, several of which may be released in the thermal waters (Wright, 1964, unpublished).

If the seasonal changes in water chemistry (Figures 2 - 5) are compared with seasonal changes in diversity (Figures 19 - 22) it is noticeable that the lowest ionic concentrations preceded the decrease in diversity by over a month, suggesting that there was a rapid increase in diatom productivity in July due to the increase in mineral concentration of the water. Since the greatest influx of chemicals was due to the constant discharge of the geysers and hot springs (Allen and Day, 1935) it is apparent that more minerals will be available as the total volume of flow decreases. The period of high relative productivity (low diversity) continued in the lower Firehole and Gibbon Rivers until the end of August, but was modified in the Madison River slightly earlier in the season. At this time the discharge was approaching the lowest level for the summer, and concentrations of the various ions increased to the high levels which had been noted in the spring prior to the spring runoff.

Wright (1964, unpublished) determined net photosynthesis in the Madison River from changes in carbon dioxide concentrations associated with *in situ* changes of pH (Method of Beyers and Odum, 1959). Figure 24 shows the net photosynthesis for the three stations on the Madison River for July and August. It is apparent that two periods of high photosynthesis occurred, one reaching a maximum on July 14 and the other on August 10. The first maximum corresponded with a benthic diatom bloom which was noted during field observations on July 15. The diversity dropped slightly at the two lower stations at this time, but remained high at the upper station. At the end of July however, diversity indices at all stations dropped noticeably. This low diversity corresponded with either the low point between the two photosynthetic peaks or the beginning of the second increase in photosynthesis. It seems there was a lag period between the time when the diatom bloom was first observed (when photosynthesis was high) and the time when samples with low diversity were collected. This same time-lag was noted in the data presented by Yount (1956) whose sample with the highest productivity (as measured by chlorophyll content) showed greater diversity than succeeding samples which were slightly less productive. If a time-lag period is postulated for diatom growth whereby peak productivity may occur prior to the lowest diversity, it is apparent that the increase in diversity in late August on the Madison River (with lowered productivity of diatoms) should correspond to the second photosynthetic peak in Wright's data. This second increase in photosynthesis was correlated with a rapid growth rate of macrophytes (*Chara* and mosses) and a growth of filamentous algae (*Zygnema* and *Spirogyra*).

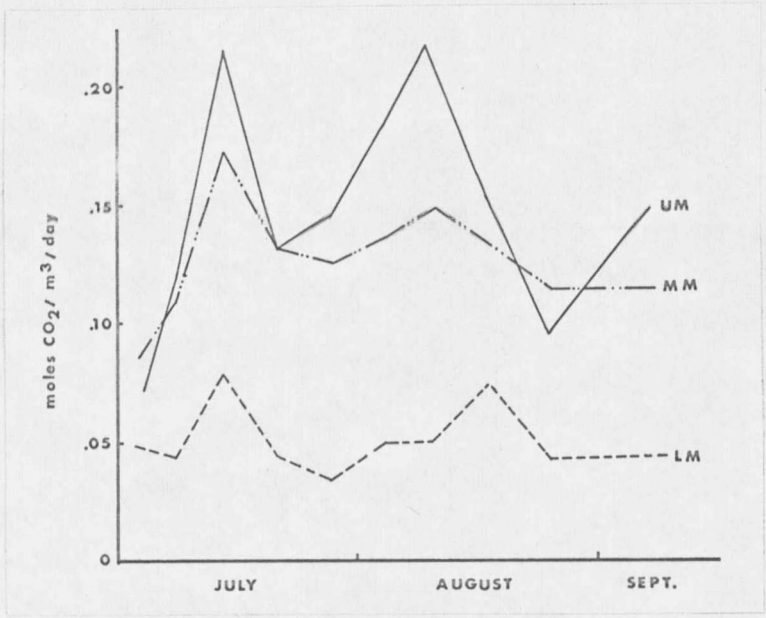

Figure 24. Average daily net photosynthesis at three stations, Madison River. U, M and L represent the upper, middle and lower stations, respectively. (Taken from Wright, 1964)

The diversity changes at stations on the Firehold and Gibbon Rivers were somewhat similar to those on the Madison River, except there was no increase in diversity (with a drop in productivity) noted in the samples collected at the end of August. These differences in the river may be due to several factors, although no data were collected to support these suggestions. During this time of the year the rates of flow of these streams were relatively constant. Influx of thermal waters was also constant, and as a result, major ions seemed to be present in amounts suitable for diatom growth. In this relatively stable environment it could be expected that the growth of diatom communities over a period of time would result in increased competition which in turn would result in a decrease in diversity.

This may be what happened in the Firehole and Gibbon Rivers until the environment was changed in September, when water temperatures dropped noticeably.

The situation on the Madison River may be somewhat different, due to the presence of a sewage treatment plant which discharged effluent into the river a short distance above the upper stampling station. The output from this treatment plant would be greatest during July and early August when visitation to the Madison Junction Campground was highest. In late August use of the campground decreased and, as a result, effluent discharge should also drop. Diatom growth during July should follow the expected pattern of increasing competition in a stable environment resulting in a decrease in diversity and increase in productivity. With a decrease in the amounts of nutrients entering the river in August those species which were able to grow best in the enriched environment may decrease and other species better able to grow in the "new" environment would appear. Diversity would temporarily increase until competition caused a few species to become diminant. It might be expected that the diatoms from the upper sampling station would be most affected due to the close proximity to the sewage discharge.

The diatom Cocconeis placentula Ehr. (See Figure 8), which occurred most abundantly in the sample collected early in July, showed a decrease in abundance from mid-July to late July, increase in late August and then decreased again in the September sample. This diatom species was used by

Butcher (1947) as an indicator of organic pollution, because it decreased noticeably in relative abundance when the streams he studied were organically enriched.

The Gardner River presents a completely different picture from the Madison River system in regard to water chemistry, diversity and productivity. The geology of the region drained by the Gardner river is considerably different from that drained by the Madison River, and the water chemistry is likewise different. The addition of calcium-rich water of the "Hot River" which drains Mammoth Hot Springs further intensified the differences between these two areas. In general, calcium, magnesium, potassium and sulfate were more abundant in the Gardner River; while sodium, chloride, silicate and phosphate were more abundant in the Madison River.

When the floras of the sampling stations were compared it was evident that the two sampling stations on the Gardner River were more similar to each other floristically than to any of the sampling stations in the Madison, Firehole and Gibbon Rivers. The ordination procedure further substantiated the floristic differences since the dominant species of the Gardner were generally found only in a restricted portion of the compositional index (0 - 120 compositional units). The dominant species of the Madison River system showed a much wider distribution along the compositional index. The influence of water chemistry was evident at both sampling stations in the Gardner River. The abundant diatom species: Diatoma vulgare Bory, Navicula avenacea Breb., Cocconeis pediculus Ehr. and the filamentous Chrysophyte Vaucheria have all been previously described as occurring in calcium-rich waters in Europe (Blum, 1960).

In the Gibbon, Firehole and Madison Rivers, it was observed that community diversity was generally highest at the upstream stations and less diverse at downstream stations. In the Gardner River, the reverse was found to occur. The upper station was consistently less diverse than the lower station. The lower station did show a decrease in diversity in late June, but there was no observable increase in diatom productivity at that time. Diatom growth was sparse at both stations until late August and September, when diatoms became more abundant. However, large masses of Vaucheria and Enteromorpha were present throughout the growing season at the lower station, indicative of a greater total productivity than occurred at the upper station. Vaucheria and Enteromorpha are both characteristic genera of calcium-rich waters (Blum, 1960). The scarcity of diatoms in this area seems to be quite unusual, and it would be well to examine this area in greater detail to see if any indications as to causality could be found.

The differences between diatom communities seem to be related to the high concentrations of calcium in the Gardner River or to the low concentrations of calcium with high concentrations of sodium found in the Madison River system. It was also apparent that there were differences within these two broad community categories. It was observed early in the study that there were considerable variations in the total amounts of plants growing in the streams at different sampling stations (including both algae and macrophytes). The middle and lower stations on the Firehole River, all three stations on the Madison River and the lower station on

the Gardner River had large quantities of plants growing in the water. The other stations frequently appeared to be almost devoid of all plants of the plants were scattered, and no large masses of algae were apparent. Greater plant growth occurred where the alkalinity or conductivity was greatest.

The eleven sampling stations can be arranged as shown in Figure 25 to illustrate the relationship of the diatom communities to the water chemistry. The arrangement is further supported by the presence and absence data of the various species which appear as the most abundant in the samples collected at all eleven stations (See Table 5).

	CALCIUM ALKALINITY	SODIUM ALKALINITY
LOW ALKALINITY LOW CONDUCTIVITY LOW PRODUCTIVITY	Upper Gardner River	Upper Gibbon River Middle Gibbon River Lower Gibbon River Upper Firehole River
HIGH ALKALINITY HIGH CONDUCTIVITY HIGH PRODUCTIVITY	Lower Gardner River	Middle Firehole River Lower Firehole River Upper Madison River Middle Madison River Lower Madison River

Figure 25. Relationships of water chemistry and diatom communities at the various sampling stations.

SUMMARY

Composite samples of diatoms were collected periodically from a series of sampling stations on the Madison River and its headwater streams, the Firehole and Gibbon Rivers, in Yellowstone National Park. Three sampling stations were located on each of the above-mentioned rivers. For purposes of comparison, two sampling stations were also established on the Gardner River. The upper stations on the Firehole and Gibbon Rivers were located above most of the thermal features; while the middle and lower stations were located further downstream, below the influx of waters from the geysers and hot springs. The upper station on the Gardner River was located above the discharge of the Hot River into the Gardner; while the lower station was located a sufficient distance downstream so that complete mixing had occurred.

Water samples were analyzed for conductivity, alkalinity, pH, sodium, potassium, calcium, magnesium, chloride, sulfate, phosphate, nitrate and silicate. Results of the analyses indicated that none of the ions could be considered to limit the growth of diatoms. Rather, the relatively high concentrations of some of the ions would tend to allow some species of diatoms to grow and reproduce better than others. Seasonal changes in water chemistry were noticeable; the lowest concentrations occurred during the spring runoff, and highest concentrations early in the spring and late in the fall.

Microscope slides were prepared from "cleaned" material from the diatom collections. Approximately 300 cells were identified to species from each slide. From these data a diversity index was calculated for

each sample. Diversity indices were relatively high early in the season, but dropped noticeably in late July. This decrease in diversity, as shown by the diversity indices, was related to a period of high primary productivity which had occurred two weeks earlier. A lag-period was postulated which would explain the low diversity following the period of greatest productivity. The low diversity and high productivity occurred when the aquatic environment was relatively constant. The constancy allowed competition to develop between the species present, with the result that some species were crowded out.

There were noticeable differences in the species of diatoms found at the different sampling stations. An ordination of the 35 most frequently appearing species showed distinct differences in species distribution between the stations in the Madison River system and the stations on the Gardner River. The distribution of the dominant species in the ordination indicated that two major communities of diatoms existed in the area studied. Similar communities had been described previously by European authors. A matrix based on floristic similarities between the eleven stations supported the above conclusions. Another matrix based on the frequency of occurrence of the six most abundant species in each sample was constructed. This matrix showed that a secondary breakdown of the two major communities could be made: The upper station on the Firehole River and all the stations on the Gibbon River were closely related, as were the middle and lower stations on the Firehole River, and all three stations on the Madison River.

When the results of the water analyses were correlated with the diatom distribution, it was apparent that the eleven sampling stations could be grouped into four categories depending upon whether calcium or sodium was dominant and whether alkalinity was low or high. The upper Gardner River was characterized by low calcium alkalinity and the lower station by high calcium alkalinity. The upper Firehole River stations and all stations on the Gibbon River had relatively low sodium alkalinity: whereas the middle and lower Firehole River stations and the stations on the Madison River had high sodium alkalinity. It was observed that the stations from which high alkalinities and conductivities had been reported also showed the greatest primary productivity. Evidence from this research conclusively demonstrates that the distribution of diatom communities is related to water chemistry.

APPENDIX

Appendix A. Alphabetical list of diatom species identified from the sampling stations.

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Achnanthes	aapajärensis A. Cleve.			x	x							
	amphicephala Hust.				x							
	antigua nomina nuda								x			
	arcuata A. Cleve.								x			
	austriaca Hust.						x					
	Bergiani A. Cleve.	x	x	x		x	x		x			
	Biasolettiana (Kütz.) Grun.		x			x	x		x	x		
	bicapitata A. Cleve.									x		
	Clevei Grun.		x	x		x	x	x	x	x	x	x
	conspicua A. Mayer			x	x	x		x				x
	" v. brevistriata Hust.								x	x		
	curta (A. Cl.) A. Berg.					x	x			x		x
	delicatula Kütz.	x										
	dicephala nomina nuda			x								
	didyma Cleve.	x		x	x							
	diversa A. Cleve.						x					
	exigua Grun.	x	x	x	x	x	x	x	x			x
	" v. lanceolata nomina nuda							x				
	exilis Kütz.								x			
	gibberula Grun.	x		x	x		x	x	x	x		
	Hawkiana Grun.					x				x		
	Kolbei Hust.		x									
	Kriegeri nomina nuda					x						
	Kryophila B. Pet.	x	x	x	x	x	x	x	x	x	x	x
	lacunarum Hust.									x		
	lanceolata Breb.	x	x	x	x	x	x	x	x	x	x	x
	" v. elliptica Schulz.	x	x					x				

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Achnanthes	laterostrata Hust.				x				x			
	Lemmermanni Hust.							x				
	linearis W. Smith	x	x	x	x	x	x	x	x	x	x	x
	marginulata Grun.			x	x	x	x					
	microcephala Kütz.									x		
	minutissima Kütz.	x	x	x	x	x	x	x	x	x	x	x
	montana Krasske	x										
	plönensis Hust.									x		
	praerupta nomina nuda		x									
	saxonica Krasske	x							x			
	scutellum nomina nuda								x			
	sp.										x	
Amphipleura	pellucida Kütz.							x	x	x		x
Amphora	delicatissima Krasske							x				
	Normanni Rabh.	x		x	x		x	x	x	x		
	ovalis Kütz.	x	x	x		x		x	x	x	x	x
	" v. pediculus Kütz.	x	x	x	x	x	x	x	x	x	x	x
	veneta (Kütz.)	x	x	x	x	x	x	x	x	x		x
	sp.							x	x			
Anemoneis	serians (Breb.) Cleve.							x				
	" v. brachysira Hust.	x	x			x	x	x	x	x		
	spharophora (Kütz.)									x		
	variabilis (Ross) Reimer	x	x	x	x	x	x	x	x	x	x	x
Caloneis	bacillum (Grun.) Meresch.			x	x							
	silicula (Ehr.) Cleve.										x	

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Ceratoneis	arcus Kütz.	x	x	x	x		x	x	x	x	x	x
Coeconeis	Cholnokyana A. Cleve		x	x								
	diminuta Pant.	x		x				x	x	x		x
	disculsus Schum.		x	x	x		x			x		x
	Hustedtii Krasske								x			
	pediculus Ehr.		x	x	x			x	x	x	x	x
	placentula Ehr.	x	x	x	x	x	x	x	x	x	x	x
	scutellum Ehr.							x	x			
	Thumensis A. Mayer				x							
Cyclotella	compta (Ehr.) Kütz.											x
	Kutzingiana Thwaites								x			x
	stelligera Cl. u. Grun.				x				x			
	sp.	x	x	x	x	x		x	x			
Cymatopleura	solea (Breb.) W. Sm.											x
Cymbella	aequalis Smith				x							
	affinis Kütz.	x	x	x	x	x	x	x	x	x	x	x
	alpina Grun.								x			
	capitata Grun.								x			
	Cesati (Rabh.) Grun.				x	x	x		x			
	cistula (Hempt.) Grun.	x				x		x			x	x
	cuspidata Kütz.	x										
	cymbiformis (Kütz.) v.Heurck						x	x	x			x
	delicatula Kütz.	x					x					
	gracilis (Rabh.) Cleve.				x				x			
	hybrida Grun.								x			
	laevis Naegeli		x				x					

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Epithemia	argus Kütz.	x	x	x		x		x	x	x		x
	Muelleri Fricke										x	
	Reicheltii Fricke								x			
	sorex Kütz.			x								
	turgida (Ehr.) Kütz.	x	x	x	x	x	x	x	x	x	x	x
	zebra (Ehr.) Kütz.	x	x	x	x	x	x	x	x	x		
Eucocconeis	lapponica Hust.	x						x				
Eunotia	alpina (Naeg.) Hust.	x										
	arcus Ehr.	x	x		x	x	x	x	x			
	diodon Ehr.	x										
	exigua (Breb.) Grun.	x	x	x	x	x	x	x				
	faba (Ehr.) Grun.	x				x						
	gracilis (Ehr.) Rabh.	x		x		x						
	incisa W. Smith	x			x	x	x	x				
	lunaris (Ehr.) Grun.	x	x	x	x	x	x	x	x	x		
	monodon (Ehr.)	x			x	x	x			x		
	pectinalis v. minor (Kütz.) Rabh.	x		x	x	x	x	x	x	x	x	
	polydentula (Brun.) A. Berg	x			x		x					
	septentrionalis Oestrup		x		x		x		x	x		
	suecica A. Cleve	x										
Fragillaria	aequalis Heib.								x	x		
	alpestris Krasske	x										
	amphicephala nomina nuda							x				
	brevistriata Grun.			x								
	capucina Desm.	x	x	x		x	x		x		x	x

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Cymbella	mexicana (Ehr.) Cleve.		x	x				x	x	x		
	microcephala Grun.		x	x	x	x	x	x	x	x		x
	naviculiformes Auerswald	x			x		x					
	parva (W. Sm.) Cleve.							x				
	prostrata (Berk.) Cleve.										x	x
	rupicola Grun.							x				
	sinuata Gregory	x			x	x	x	x	x		x	x
	stuxbergei v. siberica (Grun.) Wisl.						x					
	tumida (Breb.) v. Heurck.								x			x
	turgida (Greg.) Cleve	x										
	ventricosa Kütz.	x	x	x	x	x	x	x	x	x	x	x
	" v. silesiacia (Bleisch.) Cleve								x		x	x
Denticula	elegans Kütz.	x	x					x	x	x	x	x
	tenuis Kütz.	x	x	x		x	x	x	x	x		x
	thermalis Kütz.	x	x	x	x	x	x	x	x	x		
Diatoma	anceps (Ehr.) Grun.	x			x		x					
	elongatum Agardh											x
	hiemale (Lynghye) Heib.	x	x	x	x		x	x				
	" v. mesodon (Ehr.) Grun.	x	x	x	x	x		x	x		x	x
	vulgare Bory										x	x
Diatomella	balfouriana Greville	x		x	x	x	x	x	x			
Diploneis	elliptica (Kütz.) Cleve							x				
	finnica (Ehr.) Cleve	x										
	ovalis (Hilse) Cleve	x	x	x			x			x		

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Fragillaria	construens (Ehr.) Grun.	x	x	x	x	x	x	x	x	x	x	x
	" v. exigua (W. Sm.) Schultz	x										
	" v. subsalina Hust.	x						x				
	" v. venter (Ehr.) Grun.	x						x				
	crotonensis Kitton	x		x	x	x	x	x	x	x	x	x
	intermedia Grun.	x	x	x	x	x	x	x	x	x		x
	lapponica Grun.								x	x		
	leptostauron (Ehr.) Hust.	x	x	x	x	x	x	x	x	x	x	x
	nitzschioides Grun.								x	x		
	Pantocsekii A. Cleve										x	
	pinnata Ehr.	x	x			x		x	x	x	x	x
	virescens Ralfs.				x	x	x	x				
	sp.										x	
Frustulia	rhomboides (Ehr.) de Toni	x			x	x		x		x		
	" v. crassenerva (Breb.) v. Heurck	x		x	x	x	x	x	x	x		
Gomphonema	acuminatum Ehr.								x			
	angustatum (Kütz.) Rabh.	x			x		x	x			x	
	bohemicum Reich. & Fricke		x				x			x		
	constrictum Ehr.							x				
	gracile Ehr.	x							x			x
	herculeanum Ehr.		x	x				x	x	x	x	x
	intricatum Kütz.	x	x					x	x			x
	lanceolatum Ehr.	x		x				x		x		
	longiceps Ehr.	x	x	x	x		x	x		x	x	x

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Gomphonema	olivaceum (Lyngbye) Kütz.	x	x	x	x	x		x	x	x	x	x
	" v. calcarea Cleve										x	x
	olivacioides Hust.			x								x
	parvulum Kütz.	x	x	x	x	x	x	x	x	x	x	x
	ventricosum Gregory			x					x			
	sp.					x						x
Hantzschia	amphioxys (Ehr.) Grun.	x						x		x		
Mastogloia	Braunii Grun.					x						
	Dansei Meist.							x				
	Grevillei W. Sm.					x	x					
	Smithii Thwaites	x		x	x	x	x	x		x		
Melosira	distans (Ehr.) Kütz.	x						x	x			
	fennoscandica A. Cleve		x	x	x		x	x	x	x		
	granulata (Ehr.) Ralts	x	x	x				x			x	
	italica (Ehr.) Kütz.	x			x			x	x			
	Jurgensii C. A. Ag.				x							
	undulata (Ehr.) Kütz.		x	x				x	x	x		
	sp.	x	x	x	x	x	x	x	x	x	x	x
Meridion	circulare Agardh	x			x		x					
Navicula	aboensis Cleve										x	
	atomus (Naeg.) Grun.				x							
	avenacea Breb.										x	x
	bacilliformes Grun.						x					
	bacillum Ehr.				x							
	befringens nomina nuda			x								

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Navicula	bicapitellata Hust.	x										
	bryophila B. Pet.				x							
	cari Ehr.		x			x	x			x	x	x
	cincta Grun.			x			x	x	x	x		
	cocconeiformis Greg.	x							x			
	contempta Krasske				x							
	cryptocephala Kütz.	x	x	x	x	x	x	x	x	x	x	x
	detenta Hust.								x			
	dicephala (Ehr.) W. Sm.	x		x	x		x					x
	falaisiensis Grun.										x	
	gracilioides A. Mayer					x						
	gracilis Ehr.		x			x					x	x
	gregaria Donk.					x						
	hassiaca Krasske								x			
	hungarica Grun.		x									
	Kotschyi Grun.											x
	longirostris Hust.						x		x			
	minima Grun.	x						x				
	" v. atomoides Cleve							x				
	minimoides Manguin								x			
	minisculus Schum.											x
	mollisima Hust.	x										
	muralis Grun.				x							
	mutica Kütz.					x	x	x	x			
	oblonga Kütz.							x				
	pelliculosa (Breb.) Hilse							x				
	pseudoscutiformis Hust.	x	x		x	x	x	x				
	pupula Kütz.	x	x	x	x	x	x	x	x	x		x
	radiosa Kütz.	x		x	x	x			x		x	
	rhynchocephala Kütz.	x	x	x	x		x	x	x		x	x
	Rotaena (Rabh.) Grun.	x						x	x			

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Navicula	subatomoides Hust.							x				
	salinarum Grun.										x	
	simplex Krasske											x
	tenelloides Hust.	x										
	tripunctata (Müll.) Bory							x				
	variostriata Krasske	x						x				
	verecunda Hust.											x
	viridula Kütz.							x			x	x
	vitrea (Oestrup) Hust.							x				
Neidium	affine (Ehr.) Cleve	x			x	x	x		x			
	bisulcatum A. Cleve								x			
	iridis v. amphigomphus (Ehr.) v. Heurck			x	x		x					
	" v. ampliata Ehr.						x					
	productum (W. Sm.) Cleve							x				
Nitzschia	acuta Hantzsch	x			x				x			x
	amphibia Grun.		x	x				x		x	x	
	amphioxoides Hust.		x									
	capitallata Hust.		x									
	communis Rabh.					x			x			
	denticula (Grun.) Hust.						x	x		x		
	dissipata (Kütz.) Grun.	x	x	x	x	x	x		x		x	x
	filiformis (W. Sm.) Hust.						x	x				
	fonticola Grun.	x	x	x	x	x	x	x				
	frustulum Kütz.	x	x	x	x	x	x	x	x	x	x	x
	" v. subsalina Hust.										x	
	gracilis Hantzsch		x					x				

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Nitzschia	Hantzschiana Rabh.	x					x	x				
	Heufleriana Grun.							x				
	ignorata Krasske	x	x			x	x	x		x	x	
	Kutzingiana Hilse									x		
	linearis W. Sm.	x	x								x	x
	microcephala Grun.		x	x	x	x		x	x	x		
	obtusa W. Sm.				x			x				
	ovalis Arnott		x		x		x				x	
	palea (Kütz.) W. Sm.	x	x	x	x	x	x	x	x	x	x	x
	paleacea Grun.			x	x		x	x	x		x	x
	recta Hantzsch								x			
	romana Grun.						x	x				
	sigma (Kütz.) W. Sm.				x			x				
	stagnorum Rabh.			x					x			
	sublinearis Hust.			x							x	x
	thermalis Kütz.											x
	tryblionella Hantzsch			x								
	vitreae Norman				x							
Opephora	Martyi Heribaud	x	x		x	x			x	x	x	x
Pinnularia	aestuari Cleve									x		
	appendiculata (Agardh) Cleve					x		x				
	Balfouriana Grun.					x					x	
	borealis Ehr.	x	x	x	x	x	x			x		
	Braunii v. amphicephala (A. Mayer) Hust.							x				
	divergentissima (Grun.) Cleve		x		x		x					

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Pinnularia	gibba Ehr.	x				x	x					
	intermedia (Lagst.) Cleve					x						
	interrupta W. Sm.					x	x					
	Lagerstedtii (Cl.) A. Cleve	x										
	leptosoma Grun.		x				x					
	mesolepta fo. augusta Cleve				x			x				x
	microstauron (Ehr.) Cleve	x	x	x	x	x	x		x	x		
	minutissima Hust.			x								
	molaris Grun.			x								
	nodosa Ehr.			x								
	pulchra Östrup				x							
	stauroptera Grun.									x		
	stomatophora Grun.		x									
	streptoraphe Cleve						x					
	subcapitata Greg.	x				x		x	x			
	viridis (Nitzsch.) Ehr.	x								x		
	sp.		x			x						
Rhoicosphenia	curvata (Kütz.) Grun.	x	x	x	x			x		x	x	x
Rhopalodia	gibba (Ehr.) O. Müller	x	x	x	x	x		x	x	x		
	gibberula (Ehr.) O. Müller	x	x	x	x	x	x	x	x	x		x
Stauroneis	anceps Ehr.					x	x					
	phoencenteron Ehr.	x					x					
	pygmaea Krieger			x								
	Smithii Grun.											x

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Stephanopyxis	sp.				x							
Surirella	angustata Kütz.	x										
	biseriata Breb.	x										
	delicatissima Lewis										x	
	linearis W. Sm.											x
	" v. constricta (Ehr.) Grun.								x			
	ovata Kütz.					x					x	x
	" v. pinnata (W. Sm.)										x	
	robusta v. splendida Ehr.				x							
	simplex A. Cleve	x										
Synedra	acus Kütz.		x			x			x			
	amphicephala Kütz.	x					x	x				
	mazamaensis Sover		x	x				x	x	x		
	minuscula Grun.								x			
	parasitica W. Sm.		x									
	pulchella Kütz.		x	x		x	x	x	x	x		x
	rumpens Kütz.	x	x	x	x	x	x	x	x	x	x	
	tenera W. Sm.		x		x	x	x					
	ulna (Nitzsch) Ehr.	x	x	x	x	x	x	x	x	x	x	x
	" v. danica (Kütz.) Grun.	x			x	x		x		x		
	" v. oxyrhunchus Kütz.	x			x						x	x
	" v. Ramesi (P.& H.) Hust.											x
	vaucheri Kütz.	x	x	x	x	x	x	x	x	x	x	x

Appendix A. (Continued)

Species		Firehole River			Gibbon River			Madison River			Gardner River	
		U	M	L	U	M	L	U	M	L	U	L
Tabellaria	fenestrata (Lyng.) Kütz.	x					x	x		x		
	flocculosa (Rabh.) Kütz.	x	x			x	x	x		x		x
Tetracyclus	lacustris Ralfs	x								x	x	
	rupestris (A. Br.) Grun.	x		x						x		

LITERATURE

Allen, E. T. and Day, A. L., 1935. Hot springs of the Yellowstone National Park. Carnegie Institute, Washington, D. C. Pub. No. 466, 525 pp.

American Public Health Association, 1960. Standard methods for the examination of water and waste water. A.P.H.A. 11th Ed., 626 pp.

Blum, J. L., 1956. The ecology of river algae. Bot. Rev. 22(5):291-341.

Blum, J. L., 1960. Algal populations in flowing water. In Pymatuning Special Publ. No. 2. The Ecology of Algae, pp. 11-21. Univ. of Pittsburgh.

Boyd, F. R., 1961. Welded tuffs and flows in the rhyolite plateau of Yellowstone Park, Wyoming. Geol. Soc. Am. Bull., 72:387-426.

Butcher, R. W., 1932. Studies in the ecology of rivers. The microflora of rivers with special reference to the algae on the river bed. Annal. Bot. 46:813-861.

Butcher, R. W., 1940. Studies in the ecology of rivers. Observations on the growth and distribution of sessile algae in the river Hull. Journ. Ecol. 28:210-223.

Butcher, R. W., 1946. Studies in the ecology of rivers. The algal growth in certain highly calcareous streams. Journ. Ecol. 33:268-281.

Butcher, R. W., 1947. Studies in the ecology of rivers. The algae of organically enriched waters. Journ. Ecol. 35:186-191.

Cholnoky, B. J., 1960. In Harrison, A. D., Keller, P. and Dimovic, D., Ecological studies on Olifantsvlei near Johannesburg: with notes on the diatoms by B. J. Cholnoky. Hydrobiologia 15(½):89-134.

Cleve-Euler, A., 1951. Die Diatomeen von Schweden und Finnland. K. Sv. Vet. Akad.. Fjarde seriens 1-5:961 pp.

Droop, M. R., 1958. Optimum relative and actual ionic concentrations for growth of some euryhaline algae. Verhandl. Intern. Ver. Limnol., 13:722-730.

Eddy, S., 1925. Fresh water algal succession. Trans. Amer. Microscop. Soc., 44:138-147.

Fisher, R. A., Corbet, A. S. and Williams, C. B., 1943. The relation between the number of species and the number of individuals in a random sample of the animal population. J. Anim. Ecol., 12:42-58.

Fjerdingstad, E., 1950. The microflora of the river Molleaa. Folia Limnol. Scand. No. 5:123 pp.

Foged, N., 1954. On the diatom flora of some Funen lakes. Folia Limnol. Scand. No. 6:82 pp.

Gaufin, A. R. and Tarzwell, 1952. Aquatic invertebrates as indicators of stream pollution. Public Health Rept. 67:57-67.

Gaufin, A. R. and McDonald, D. B., 1965. Factors influencing algal productivity in Deer Creek Reservoir, Utah. Trans. Am. Micro. Soc. 84(2):269-279.

Hohn, M. H. and Hellerman, J., 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Trans. Amer. Microsc. Soc. 82:250-329.

Hustedt, F., 1930. Baccillariophyta (Diatomeae). In Pascher, A. Die Süsswasser-Flora Mitteleuropas. Heft 10:1-466.

Hustedt, F., 1930. Die Kieselalgen, Deutschlands, Österreichs und der Schweiz. In Rabenhorst's Kryptogamen-Flora, Band VII, Parts 1-3. 2112 pp.

Hustedt, F., 1937. Systematische und Ökologische Untersuchungen uber die Diatomeen-Flora von Java, Bali und Sumatra. Arch. f. Hydrobiol. Suppl., 15(1):131-177: 15(2):187-295.

Hustedt, F., 1942. Diatomeen aus der Ungebung von Abisko in Schwedisch-Lappland. Arch. für Hydrobiol. 39:82-174.

Jurgenson, C., 1935. Die Mainalgen bei Würzburg. Archiv. für Hydrobiol. Bd. 28.

Kolkwitz, R. and Marsson, M., 1908. Ökologie der pflanzlichen Saprobien. Berichte der Deutsch. Bot. Gesellsch., Bd. 26a:505-519.

Kulczynski, S., 1927. Zespoly roslin w Pieninach. (Die Planzen associationen der Pieninen.) Bull. Intern. Polon. Acad. Sci. Lett., Cl. Sci. Math. et Nat. Ser. B. Suppl. II:57-203.

Lewin, J. C., 1963. Diatoms. Ann. Rev. Microbiol. 17:373-414.

Lund, J. W. G., 1965. The ecology of the freshwater phytoplankton. Biol. Rev. Camb. Phil. Soc. 40(2):231-293.

MacFadyen, A. 1957. Animal Ecology: aims and methods. London, Pitman 264 pp.

Manguin, E., 1961. Contribution a la Flore Diatomique de l'Alaska. Lac Karluk, Especes Critiques ou nouvelles. Revue Algologique Nouv. Ser. 5(4):266-294.

Manguin, E., 1962. Contribution a la connaissance de la Flore Diatomique de la Nouvelle-Caledonie., Mem. du Museums National, Serie B. 12(1): 56 pp.

Margalef, R., 1951. Diversidad de especies en las comunidades naturales. P. Inst. Biol., Apl. 9:5-27.

Margalef, R., 1956. Informacion y diversidad espiefica en las comunidades de organismos. Inv. Pesq. 3:99-106.

Margalef, R., 1961. Communication of structure in planktonic populations. Limnol. and Oceanog. 6:124-128.

Nowak, W., 1940. Über die Verunreinigung eines kleines Flusses in Mähren durch Abwasser von Weissgerbereien, Leder und leimfabriken und anderen Betrieben. Archiv. für Hydrobiologie, Bd. 36.

Odum, E. P., 1963. Ecology. Modern Biology Series, Holt, Rinehart and Winston. 152 pp.

Patrick, R., 1948. Factors effecting the distribution of diatoms. Bot. Rev., 14( ):473-524.

Patrick, R., 1957. Diatoms as indicators of changes in environmental conditions. In: C. M. Tarzwell (Ed.) Biol. Problems in Water Pollution. Robt. A. Taft. Sanitary Engineering Center, Cinn., Ohio. pp. 71-83.

Patrick, R., Hohn, M. H. and Wallace, J. H., 1954. A new method for determining the pattern of the diatom flora. Not. Nat. Acad. Nat. Sci. No. 259:1-12.

Patrick, R. and Freese, L. R., 1960. Diatoms (Bacillariophyceae) from Northern Alaska. Proc. Acad. Nat. Sci. 112(6):129-293.

Patten, B. C., 1962. Species diversity in net phytoplankton of Raritan Bay. Jour. Marine Res. 20:57-75.

Pearsall, W. H., 1932. Phytoplankton in the English Lakes II. The composition of the phytoplankton in relation to dissolved substances. Journ. Ecol. 20:241-262.

Preston, F. W., 1948. The commonness and rarity of species. Ecology 29(3):254-283.

Reimer, C. W., 1961. New and variable taxa of the diatom genera Anemoneis Pfitz. and Stauroneis Ehr. (Bacillariophyta) from the United States. Proc. Acad. Nat. Sci. 113(9):187-214.

Smith, H. M. and Kendall, W. E., 1921. Fishes of the Yellowstone National Park. Bureau of Fisheries Document No. 904. 30 pp.

Surface Water Records of Montana, 1963, 1964. U. S. Dept. Int., Geol. Survey.

Swindale, D. N. and Curtis, J. T., 1957. Phytosociology of the larger submerged plants in Wisconsin lakes. Ecol., 38(3):397-406.

Symoens, J. J., 1957. Les eaux douces de l'Ardenne et des regions voisines: Les milieux et leur vegetation algale. Bull. Soc. Roy. Bot. Belg. 89:111-314.

Van Heurch, H., 1896. A treatise on the diatomaceae. Translated by W. E. Baxter. 1962 reprint by Wheldon and Westley, Ltd. and Verlag. J. Cramer. 558 pp.

West, P. W. and Lyles, G. L., 1960. A new method for the determination of nitrates. Anal. Chim. Acta, 13:227-232.

Whittaker, R. H. and Fairbanks, C. W., 1958. A study of plankton copepod communities in the Columbia Basin, Southeastern Washington. Ecology 39:46-65.

Williams, L. G., 1961. Plankton population dynamics. Nat'l Water Quality Network -- Supplement 2. Public Health Service Publication 663. 90 pp.

Wright, J. C., 1964. Progress Report. The hydrobiology of the Madison River and its headwaters. (Unpublished) 34 pp.

Yount, J. L., 1956. Factors that control species numbers in Silver Springs, Florida. L. & O., 1(4):286-295.

MONTANA STATE UNIVERSITY LIBRARIES
3 1762 10011180 4

D378
R622
cop. 2