1966

A study of the littoral invertebrates of three mountain lakes in Glacier National Park Montana

Dennis M. Lehmkuhl
The University of Montana

A STUDY OF THE LITTORAL INVERTEBRATES

OF THREE MOUNTAIN LAKES IN

GLACIER NATIONAL PARK, MONTANA

by

DENNIS LEHMKUHL

B.A. University of Montana, 1964

Presented in partial fulfillment of the requirements for the degree of

Master of Arts

UNIVERSITY OF MONTANA

1966

Approved by:

Royal Bruce Brunson
Chairman, Board of Examiners

Fred S Honkala
Dean, Graduate School

MAR 1 6 1966
Date

ACKNOWLEDGEMENTS

Many people were responsible for the completion of this project and I would like to take this opportunity to express my appreciation to those who were involved.

Most of all, I should like to thank Dr. Royal Brunson who suggested this study and who provided much encouragement and assistance in the course of the work. Dr. William Rowan of the University of Montana and Dr. Arden Gaufin of the University of Utah gave invaluable assistance and suggestions on field methods and manuscript preparation.

I am grateful to the staff of the United States National Museum for help with identification of specimens. Without the assistance of Dr. Richard Froeschner, taxonomic lists would have been much more incomplete. The cooperation of Dr. Oliver Flint and others at the museum enabled me to list generic and specific names in many groups in which the taxonomy is difficult and incomplete.

I should like to thank Mr. Francis Elmore for a collecting permit and for permission to work in Glacier National Park. While the field work was in progress, Dr. Richard Solberg, Director of the University of Montana Biological Station, provided laboratory space and equipment at the station. The cooperation of Dr. Gerald Prescott of Michigan State University (visiting professor at the Biological Station) in the identification of plants is appreciated. In addition, I wish to thank Dr. Richard Allen, Richard Russell, Alan Nebeker, and many other friends and students who have given assistance or encouragement in this study.

I should also like to express my appreciation to my wife, Bundy, for her assistance in typing and in construction of tables and graphs.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES AND FIGURE

INTRODUCTION

General

Very few glacial fed lakes remain in the United States at the present time. Recently glaciers have been receding rapidly, and, although a number of large mountain glaciers remain in the Canadian Rockies and Alaska, Glacier National Park is one of the last remaining areas having true glaciers on the mainland of the United States. Lakes associated with glaciers have many unique qualities.

The action of moving ice in glaciers grinds the substrate into fine particles referred to as rock flour and these fine particles of rock are then carried to streams and lakes as the glacier melts. At the edge of the glacier the water is often very milky in color because of its heavy load of suspended material, but as the milky water from the glacier becomes diluted in its course downstream, and as some of the suspended material settles out, the water becomes the blue-green turquoise color characteristic of lakes and streams originating from glaciers. Lakes of this type have been studied very little in the United States, especially with regard to invertebrate communities and community species composition.

In the summers of 1964 and 1965 periodic collections of invertebrates were taken and certain limnological observations were made on Grinnel, Josephine and Swiftcurrent lakes in Glacier Park, Montana (Figure 1). Attempts were made to determine species present, community composition, changes in structure of communities through the summer, and physical and chemical differences from one lake to another.

The presence or absence of organisms in water is in part regulated by the physical and chemical characteristics of the water. In the lakes studied, organisms are subjected to a number of unique conditions. The water is poor in dissolved mineral content because it comes almost directly from snow and rain and has not been in contact with soil long enough to pick up many essential minerals. In addition the rock strata of the area is mostly sedimentary and, while it is rich in some minerals, it is poor in many others. Cold water temperatures result from the altitude of the lakes and from the source of the water. Water from the snow fields contains many dissolved gases and is usually saturated with dissolved oxygen, giving the lakes certain characteristics associated with streams. Long periods of freezing and heavy snow cover reduce solar insulation to the lakes.

General Literature Review

Several relevant studies have been done in this country, notably those of D. S. Rawson and Robert Pennak. Rawson (1942) compared some large alpine lakes in Western Canada. His paper covered the climate and surroundings of the lakes and gave a fairly complete mineral analysis of the lake water. Comparative morphometry, physical and chemical conditions, periods of ice cover, and comparisons of selected physical and biological data were also given. Taxonomic information on the fauna was determined only to the ordinal and familial level. Plankton and other organisms were tabulated for each lake as being rich, poor, or fair. The paper contained explanations for mineral content in relation to the surrounding rock strata.

Rawson (1953) also studied a high alpine lake near Jasper in

Alberta. He described the lake basin, the chemical and physical conditions in the lake and the planktonic and bottom fauna. The bottom organisms and plankton were identified to species in many cases. Invertebrate fauna was collected with a small Ekman dredge or specimens were obtained from the stomachs of fish.

Pennak (1941a, 1941b, 1945a, 1945b, and 1955) reported on the limnology of mountain lakes in northern Colorado. These papers are almost entirely limnological in content and little mention is made of the invertebrates. Brunson and Nelson (1952) reported on three lakes in northwestern Montana, one of which is of comparable altitude and of value in comparison with the lakes discussed in this study.

A previous study on the lakes dealt with in this paper was carried out by R. O. Megard (1958) and was concerned only with the microcrustacea. It described the geography and geology of these lakes, the vegetation of the area, and gave results of the microcrustacean study.

While the general features of North American mountain lakes are known from a limited number of studies that have been done, much information is available from studies on European alpine lakes. Pesta (1929) devoted one volume of Die Binnengewässer to alpine lakes. Other studies include Steiböck (1934, 1938) and Strøm (1938).

The flora and fauna of mountain lakes have not been extensively investigated and no detailed report is available on the bottom invertebrates. Dodds and Hisaw (1925) reported on the distribution of Ephemeroptera, Plecoptera, and Trichoptera in relation to altitude in Colorado. Cushing (1964) studied plankton productivity and water chemistry in the Montreal river-lake-stream system and his paper discusses the relationship between animal numbers and available nutrients from upstream to downstream. Judd (1964) studied bottom insects emerging as adults in a pond in Ontario.

No information is yet available relating to the time of emergence of insects under the special environmental conditions of alpine lakes as compared to the same species under different conditions, the species composition of invertebrate bottom communities, population density and dynamics within alpine lakes, and the structure of food chains. Macan (1963) lamented our lack of knowledge of aquatic communities and their regulation, not only in alpine lakes, but in the aquatic habitat in general.

Description of Study Area

The study area lies just below the east side of the Continental Divide in Glacier National Park in northwestern Montana. It is located in the Grinnell Valley of the Lewis Range. The approximate position of the lakes is 48°48' north and 113°40' west. The Continental Divide, with a high point in this area of 9541 feet, is an arête lying directly west of the study area. The Grinnell Valley is about three miles long and one mile wide and has an average elevation of 5000 feet. In this area, the mountains ride abruptly from the prairie a few miles to the east as a result of the Lewis overthrust. The mountains of the park were heavily glaciated in the Pleistocene and the valleys are wide-bottomed and "U" shaped. Grinnell Valley has a broad, even floor and the walls rise steeply. The beds of the lakes in the valley were gouged out by glaciers but terminal and lateral moraines also help to confine the lakes. Hutchinson (1957) discussed in detail the formation of various types of mountain lakes.

The rocks of the park are predominantly sedimentary and belong to a unit called the Belt series. Metamorphosis of this sediment has resulted in large amounts of dolomites, argellites, and quartzite. The mountains of the park, including those in the study area, are made of rock layers of various colors which allow identification of the strata. These layers are composed of limestone, shale, and sandstone, and their metamorphosed products.

Dyson (1960) described the six layers of the Belt series found in Glacier Park. The Atlyn formation forms the base of the layers and it is composed of sandy dolomites which weather to a light buff and are resistant to weathering and erosion. In the Swiftcurrent Valley, it forms the dam which holds Swiftcurrent Lake and creates Swiftcurrent Falls.

The Appekunny formation forms a 300 foot layer on the top of the Atlyn formation. It is composed mainly of greenish shales and argellites, the latter being metamorphosed and crystallized shales. Part of the bed of Swiftcurrent Lake and all of the bed of Josephine Lake is in the Appekunny formation or in moraine material resting on this formation.

The Grinnell formation is formed predominantly of red argellites, the color resulting from the presence of iron oxide. The formation also contains a layer of white quartzite, a former sandstone.

The Siyeh formation is a layer that rests on the Grinnell formation and is a buff color when weathered. This layer is composed

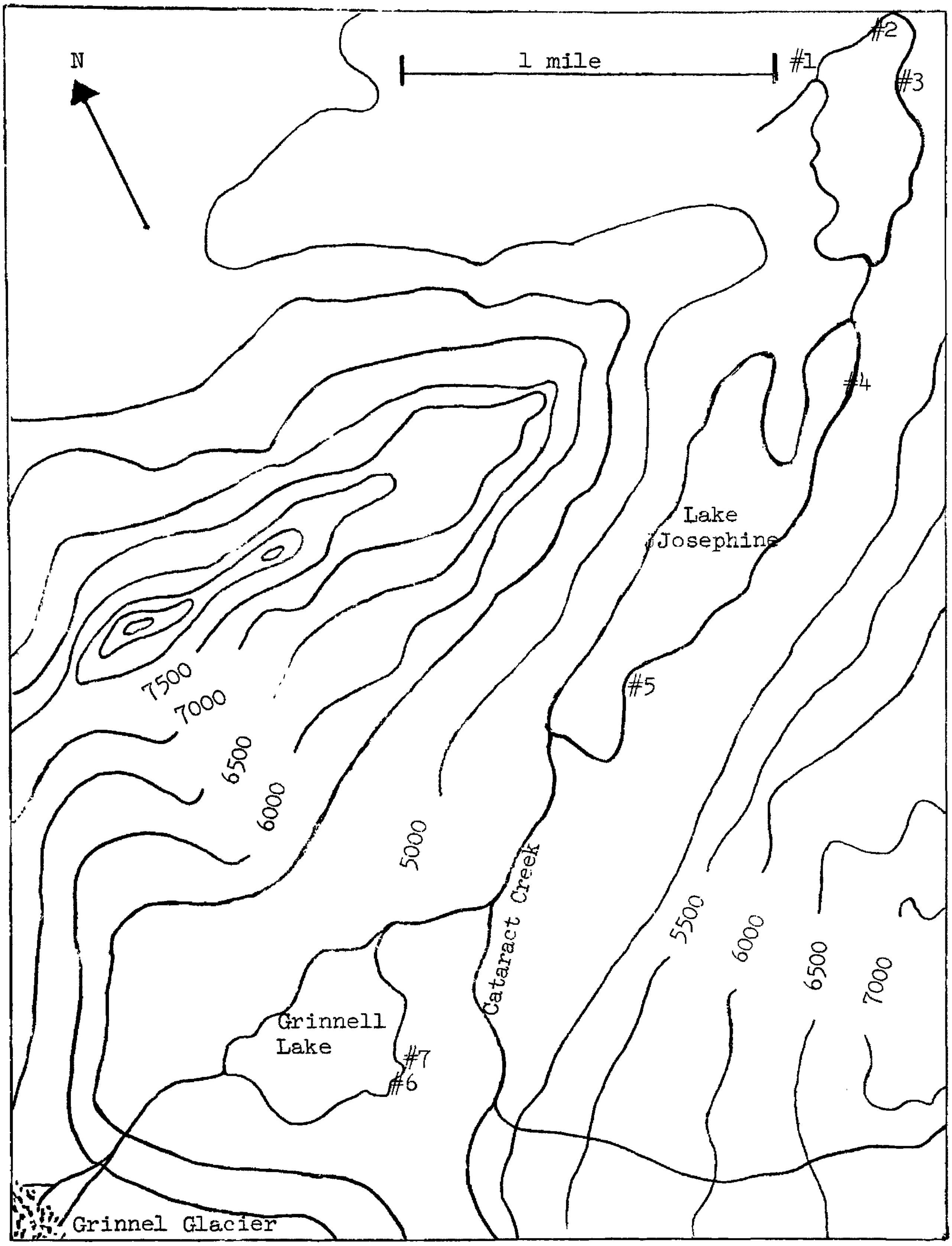


Figure 1. Map of Study Area Showing Collecting Stations

of limestone and it caps the Garden Wall or ridge to the west of the study area along which the Continental Divide runs.

The next two layers, Shepard and Kintla, are not as important in the study area. The limey beds of the Shepard formation cap the summit of Swiftcurrent Mountain at the head of the Swiftcurrent Valley, but the Kintla formation is not found near the study area (Dyson, 1960).

Climate

The east slope of the Continental Divide where the study area is located has a distinctly continental climate and it is little affected by air currents from the ocean as is the area of the park on the west side of the Divide. The east slope is subjected to high wind velocities and wide extremes in temperature.

In the park, the Continental Divide averages about 8000 feet in elevation and timberline ranges from 7000 to 8000 feet. Timberline in this area appears to be edaphic and climatic timberline is probably much higher. At this elevation, snow may fall at any time of the year.

Climatic conditions at Babb, located a few miles east of the study area, are indicative of local conditions. These may be summarized as follows: (Aller, 1960)

Averages	Annual	Apr.	June	July	Aug.	Sept.	Nov.	Dec.
Precip.	19.45	1.74	3.06	2.21	1.92	2.24	.85	.88
Ave. Temp	38.6	37.9	53.9	60.0	58.4	50.4	30.7	20.2
Extremes Low Temp.		-8	22	28	21	-30	-31	-48
High Temp.		84	95	95	96	89	68	80

Babb is east of the study area and conditions are not as severe there as in the study area. At Grinnell Lake, snow is present until the middle of July.

The vegetation in the valley is an Engelmann spruce and balsam fir community and is described by Edwards (1957).

METHODS

Collecting Stations

Seven collecting stations were set up in the lakes with an attempt to include all major habitat and bottom types, three in Swiftcurrent Lake, two in Josephine Lake, and two in Grinnell Lake.

Station No. 1 was located on Swiftcurrent Lake near the entrance of a stream from the Swiftcurrent Valley. This station was located on a mud delta covered with willows which I have identified as *Salix bebbiana*. It was on the northwest side of Swiftcurrent Lake and had more vegetation than any of the other sites. Its muddy bottom supported the only truly submerged aquatic vegetation of any of the collecting stations. Soft mud was found on this shore and submerged plants included *Potamogeton richardsonii*, *Potamegaton pusillus*, and a species of *Myriophyllum*, probably *M. spicatum*. Also found growing on the bottom at this station was a small grass-like, sterile plant which appeared to be an *Eleocharis*, but which may have been *Juncus marginatus*. Fruiting plants of *J. marginatus* grew on the adjacent shore and are known to have a sterile form similar to the specimens found (Fassett, 1957). Plants growing on the immediately adjacent shore included *Carex rostrata*, *C. straminea*, *C. flava*, *Prunella vulgaris*, *Habenaris* dilatata, and Juncus marginatus. These may be submerged at certain times of the year. The bottom drops gradually at this point.

Station No. 2 in Swiftcurrent Lake, located near the exit of Swiftcurrent Creek, had a wave-washed gravel bottom made of 1 or 2 inch gravel with many scattered 8 to 10 inch rocks. It had no vegetation other than algae, most of which were sessile diatoms.

Station No. 3 is along the east shore of Swiftcurrent Lake where the bottom is made up of gravel, mud, and rocks. Vegetation here included Carex flava, C. aquatalis, C. rostrata, and Habenaria dilatata. Carex rostrata was found growing in several inches of water, but the other plants were not submerged. No truly aquatic submergent vegetation grew here except algae.

Station No. 4 was a mud and gravel shore on the lower end of Josephine Lake near the stream exit. The bottom drops very gradually from the shore, and the rocks often have a slight covering of silt from glacial rock flour. Except for diatoms and algae, no vegetation is established on the bottom at this point.

Station No. 5 was located on a gravel point on the upper end of Josephine near a boat dock. During high water, the shore line was of gravel, but as the water level dropped in July and August, the gravel was above the water level and the bottom at the edge of the water was of mud and silty clay. The bottom dropped fairly rapidly at this point. There was no rooted vegetation where samples were taken.

Station No. 6 was a wave-washed, gravel-covered shore on the east side of Grinnell Lake. The rocks and gravel had a heavy layer of silt covering them as a result of the settling of suspended glacial rock flour. No vegetation was present except algae. The bottom had a very gradual slope, and the water was no more than one meter deep 50 feet from shore.

Station No. 7 was a grassy inlet with a mud bottom about 200 yards north of Station No. 6. *Carex aquatalis* grew along the shore and into 6 to 8 inches of water. Scattered individuals of *Ranunculus sceleratus*, dense beds of *Equisetum litorale* and *Carex straminea* grew along the edge of the water. The bottom in Grinnell is covered by a silt layer derived from the settling out of rock flour. This silt is found to a lesser extent in Josephine Lake and is absent in any quantity from Swiftcurrent Lake.

Collecting Techniques

Most samples of invertebrates were taken in water with a depth of from six to thirty inches. A boat was not available and only locations accessible with hip waders were sampled.

A hand screen, constructed from a piece of window screen with 18 wires per inch and about 3 feet by 3 feet in size with handles nailed to two parallel sides, was used to make most collections. Samples were taken by holding the screen at an angle away from the user while the bottom of the net and the handles were anchored in the substrate. The water and the bottom were then kicked vigorously until a current of water went through the screen. The hand screen proved to be a very effective method for obtaining a complete sample of the larger invertebrates.

Chemical Tests

Tests were made for the quantity of dissolved oxygen, dissolved carbon dioxide, carbonates, bicarbonates, pH, phenolphthalein alkalinity, and methyl orange alkalinity. A standard field kit with the necessary reagents and indicators was used to make these tests. A Helige colorimeter was used to test for calcium and magnesium.

Identification of Organisms Collected

Attempts were made to identify the organisms with the available literature. For general identification and information, Edmondson (1959), Pennak (1953), and Usinger (1963) were used. Fassett (1957) was used for plant identifications. Dr. Gerald Prescott checked some of the plants but the author assumes full responsibility for incorrect determinations.

Specialized monographs and papers were consulted whenever available for invertebrate groups. These included: Ross (1944), Betten (1934), Ross (1937), Needham, Traver and Hsu (1935), Burks (1953), Moore(1912), Mann (1963), Frison (1936 and 1942), Needham and Claassen (1939), Jewett (1959), Henderson (1924), and Herrington (1962).

People verifying identifications included Richard Russell, University of Montana, Mollusca; Oliver Flint, U. S. National Museum, Trichoptera and Sialidae; G. Steyskal, U. S. Department of Agriculture, Syrphidae, Tabanidae, Empididae, Dolichopodidae, and Muscidae (Diptera); C. W. Sabrosky, U. S. Department of Agriculture, Lauxonmiidae; A. Stone, U. S. National Museum, Tipulidae; W. W. Wirth, U. S. National Museum, Tendipedidae; and A. Gaufin, University of Utah, Plecoptera and Ephemeroptera. Hirudinea were identified by the author.

RESULTS

Specimens Collected

In the summer of 1964 over 1500 specimens were collected from the three lakes. This included approximately 75 Tipulidae, 250 Ephemeroptera, 85 Mollusca, 125 Plecoptera, 40 Sialidae, 325 Trichoptera, 60 Hirudinea, and a great number of Diptera, Coleoptera, Annelida and other groups.

In addition to this, several hundred specimens were collected in the summer of 1965. The total number of specimens collected was well over 2000.

A list of species and the date and location of collection is given in Table 3. In all, over 50 species or genera were identified. At least 50 additional species were collected, but these were annelids, tendipedids, or members of other groups in which the taxonomy is difficult or incompletely worked out, or groups in which specimens were not properly preserved for identification.

A few facts about the life history of certain species can be determined from the data collected. Table 4 gives the dates of collection of mature and immature forms of certain species, the dates of the emergence of adults, and the period during which leeches were brooding young.

Comparison of temperatures and chemical data for the three lakes can be made from Tables 1 and 2.

Ice Cover

One factor which appears to be important in the productivity and distribution of invertebrates in the lakes studied is that of ice cover. On November 22, 1964, Swiftcurrent Lake had one and one half inches of ice plus a light snow cover. The upper lakes were not visited on this date because of stormy weather and the long hike involved, but it is assumed that they also had an ice and snow cover and that they had frozen over much earlier than had Swiftcurrent. On May 22, 1965, Swiftcurrent was free of ice but there were snow drifts several feet in depth around the shores of the lake. Josephine Lake had floating ice and a heavy snow cover around the edges on May 22. On this date, Grinnell Lake had drifts of snow cover ten feet deep around the shores and the body of the lake was completely covered by a heavy layer of ice and snow. From this, it appears that the lakes have an ice and snow cover for over six months, and probably a much longer period in the upper lakes.

No test holes were dug in the ice during the winter, but the heavy snow cover on the ice probably provides enough insulation to prevent the ice from becoming exceedingly thick.

Depth of Lakes

National Park Service soundings report that the maximum depths of the lakes are: Grinnell, 75 feet; Josephine, 42 feet; and Swiftcurrent, 28 feet (Park Headquarters Personal Communication).

Table 1. Water Temperatures, Summer, 1964

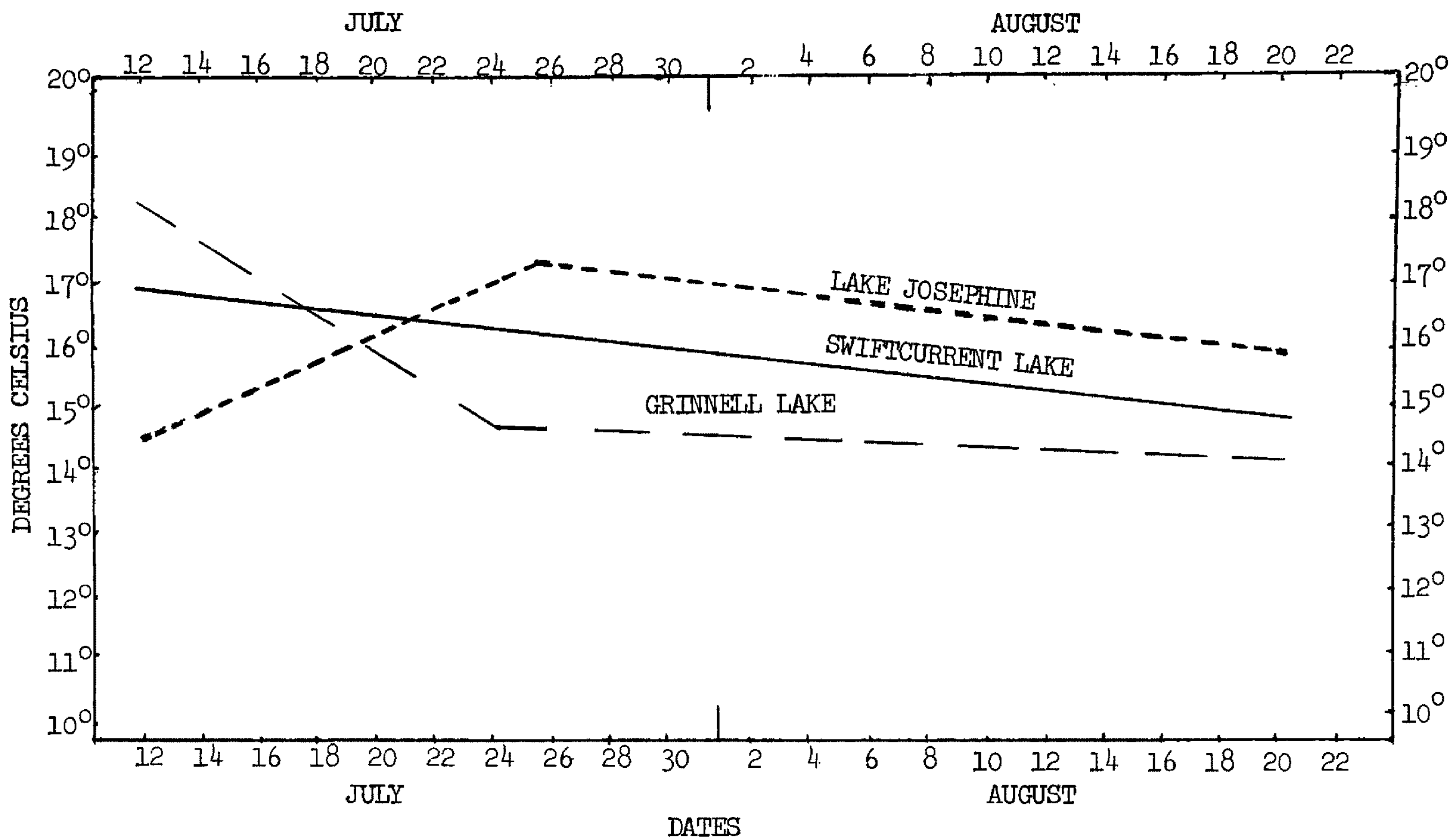


Table 2. Results of Tests for Selected Chemicals in Swiftcurrent, Josephine, and Grinnell Lakes in the Summers of 1964 and 1965

	July 12 1964	July 26 1964	Aug. 10 1964	Aug. 20 1964	Aug. 7 1965
Norm. Carb.					
Swiftcurrent	None	None	None	None	----
Josephine	None	None	None	None	----
Grinnell	None	None	None	None	----
Carbon Dioxide					
Swiftcurrent	1	1	0.5	----	----
Josephine	1	1	1	2	----
Grinnell	2	1	0.5	1	----
Bicarbonate					
Swiftcurrent	58	47	52	----	----
Josephine	52	39	39	46	----
Grinnell	37	39	29	36	----
pH					
Swiftcurrent	7.5	----	----	----	----
Josephine	7.3	----	----	----	----
Grinnell	7.4	----	----	----	----
O_2					
Swiftcurrent	9.5	8.1	9.8	----	----
Josephine	9.8	7.2	13.1*	7.4	----
Grinnell	9.1	9.1	7.9	8.3	----
Calcium					
Swiftcurrent	----	----	----	----	11.4
Josephine	----	----	----	----	15.7
Grinnell	----	----	----	----	14.3
Magnesium					
Swiftcurrent	----	----	----	----	11.6
Josephine	----	----	----	----	14.5
Grinnell	----	----	----	----	7.9

All readings in parts per million
*Possibly due to contaminated glassware
----Indicates no reading taken.

Table 3. Location and date of collection for invertebrates. Unless otherwise specified, all dates are in 1964.

Collecting Stations:

1 - Willow-covered shore in Swiftcurrent Lake,

2 - Gravel-covered shore of Swiftcurrent Lake,

3 - Southeast shore of Swiftcurrent Lake,

4 - Shore at lower end of Josephine Lake,

5 - Shore at upper end of Josephine Lake,

6 - Gravel-covered shore on Grinnell Lake,

7 - Grassy shore in Grinnell Lake.

See pages 9 - 11 for detailed descriptions of collecting stations.

Table 3, No. 1

COLLECTION STATION	1	2	3	4	5	6	7
				DATES OF COLLECTION			
Diptera							
Certopogonidae					July 13*		
Dolichopodidae					July 13*		
Empididae							
Clinocerinae					July 13* July 26*		
Lauxaniidae							
Minettia sp.		July 12+					
Muscidae							
Lispocephala brevitarsis		July 12+					
Syrphidae						Aug. 10*	
Tabanidae							Aug. 20*
Tendipedidae	July 10* July 12* July 19*	July 12*	July 11+ July 23+ Aug. 9*	July 1* July 11* July 13+ July 26*		Aug. 10* Aug. 20* Aug. 25*	July 13* Aug. 20*
Tipulidae							
Dicranata sp.					July 13*		
Erioptera sp.	July 25+	July 25+			July 12+		
Hexatoma sp.					July 13*		
Limonia sp.			July 12+				
Limoniinae					July 13*	July 13* Aug. 25*	

* = IMMATURES
+ = ADULTS

Table 3, No. 2

COLLECTION STATION	1	2	3	4	5	6	7
	DATES OF COLLECTION						
Tipulidae (cont.)							
Pseudolimnophilia luteipennis	July 25+				July 26+	July 26+	
Tipula sp.	July 25*	July 12*+ Aug. 9*			July 13* July 26* Aug. 10*	July 13* July 26* Aug. 10* Aug. 20* Aug. 25*	Aug. 10* Aug. 20*
Ephemeroptera							
Baetidae							
Ameletus sp.	July 11* July 12*			July 11*	July 11* July 13*	July 13*	July 13*
Siphlonurus sp.	July 10* July 12*		July 25* Aug. 9*	July 1* July 13* July 26* Aug. 10* Aug. 21*		July 26*	Aug. 10* Aug. 20*
Ephemerellidae							
Ephemerella inermis	July 12* July 25* Aug. 9*				July 13*		
Heptageniidae							
Cynigmula mimus				July 12+			
Heptagena sp.		Aug. 9*		Aug. 21*			

* = IMMATURES
+ = ADULTS

Table 3, No. 3

COLLECTION STATION	1	2	3	4	5	6	7
				DATES OF COLLECTION			
Ephemeroptera (cont.)							
Leptophlebiidae							
Centroptilum sp.			Aug. 9*	Aug. 21+			
Paraleptophlebia sp.		Aug. 9* Aug. 19*	Aug. 9*	July 12+ Aug. 21* Aug. 25*	July 11* July 12+ July 13*	July 11* July 13* Aug. 25*	
Megaloptera							
Sialidae							
Sialis cornuta			July 11+		July 13+	July 26+	
Sialis hamata					July 11+	July 26+	
Sialis sp.						July 26* Aug. 10* Aug. 20*	
Plecoptera							
Capniidae							
Capnia sp.		Aug. 9* Aug. 19*		Aug. 21* Aug. 25*		Aug. 20* Aug. 25*	
Chloroperlidae							
Alloperla fidelis				July 11+ July 12+	July 26+		
Alloperla fusca					July 26+		
Alloperla lamba		Aug. 9+			July 26+		
Alloperla pallidula				Aug. 21+ Aug. 25+			

* = IMMATURES
+ = ADULTS

Table 3, No. 4

COLLECTION STATION	1	2	3	4	5	6	7
				DATES OF COLLECTION			
Chloroperlidae (cont.)							
Alloperla serrata						July 13+	
Alloperla sp.		July 12* July 25* Aug. 9* Aug. 19*	July 25*	July 13* July 26* Aug. 10* Aug. 21* Aug. 25*	Aug. 21*	Aug. 20* Aug. 25*	
Paraperla frontalis				July 13*+			
Utaperla soplodora					July 26+		
Perlodidae							
Isoperla fusca					July 26+		
Isoperla spp.		July 1* Aug 9* Aug. 19*		Aug. 10* Aug. 21* Aug. 25*	July 13*	Aug. 20* Aug. 25*	
Pteronarcella badia				July 12+			
Trichoptera							
Lepidostomatidae							
Lepidostoma sp.		July 12*					

* = IMMATURES
+ = ADULTS

Table 3, No. 5

COLLECTION STATION	1	2	3	4	5	6	7
	DATES OF COLLECTION						
Trichoptera (cont.)							
Limnephilidae							
Apatania shoshone		June 30* July 1*	July 11* June 25+	July 11*	July 11* July 13*	July 11+ July 13* July 26*+ Aug. 10+ Aug. 20+ Aug. 25+	July 1*
Clistoronia magnifica				July 17 1965+			
Dicosmoecus sp.	July 12* Aug. 9*		July 11*		July 26*	Aug. 24*	
Ecclisomyia maculosa		July 17 1965+	July 17 1965+				
Grammotaulius sp.	July 10* July 12*						
Hesperophylax sp.		July 1*					
Limnephilus harrimani				July 17 1965+			
Limnephilus n.s. near fumosa				July 12+			

* = IMMATURES
\+ = ADULTS

Table 3, No. 6

COLLECTION STATION	1	2	3	4	5	6	7
				DATES OF COLLECTION			
Limnephilidae (cont.)							
<u>Limnephilus</u> <u>sp</u>.	July 1* July 12* Aug. 9*	June 30* July 1*	July 11*	July 1* July 13*			July 1* July 11* July 13*
<u>Onocosmoecus</u> <u>unicolor</u>	July 10* July 12* Aug. 9*	June 30* July 1* July 25* Aug. 9*	July 1* July 10* July 11* July 25* Aug. 9*	July 1* July 11* July 26* Aug 25*	July 11* July 13*	July 26*	Aug. 10*
Psychomyiidae							
<u>Polycentropus</u> <u>sp</u>.		Aug. 19*					
Rhyacophilidae							
<u>Anagepetus</u> <u>debilis</u>		July 17 1965+					
Amphipoda							
Gammaridae							
<u>Gammarus</u> <u>limnaeus</u>			July 25				
Tolitridae							
<u>Hyalella</u> <u>azteca</u>	Aug. 9	July 12	July 25 Aug. 9				

* = IMMATURES
\+ = ADULTS

Table 3, No. 7

COLLECTION STATION	1	2	3	4	5	6	7
			DATES OF COLLECTION				
Hirudinea							
Erpobdellidae							
Erpobdella punctata		July 25	Aug. 19				
Glossiphoniidae							
Glossiphonia complanata	Aug. 9	July 12 Aug. 19		Aug. 25	Aug. 21		
Helobdella stagnalis	July 12 Aug. 9	July 1 Aug. 19	Aug. 9				
Mollusca							
Gastropoda							
Aplexa hypnorum	July 1 July 10 July 25						
Gyraulus parvis	Aug. 9						
Physa gyrina	July 25 Aug. 9	July 1	July 11	July 1 July 11 July 13 July 26 Aug. 10 Aug. 21 Aug. 25	July 13		

Table 3, No. 8

COLLECTION STATION	1	2	3	4	5	6	7
			DATES OF COLLECTION				
Gastropoda (cont.)							
Stagnicola palustris		Aug. 9 Aug. 19	July 25 Aug. 9			July 26	
Pelecypoda							
Pisidium caesertanum		Aug. 9	Aug. 25	July 13 Aug. 25		July 26 Aug. 10	Aug. 20
Pisidium variabile	July 12 Aug. 9						
Sphaerium nitidium		Aug. 19					

TABLE 4 - LIFE HISTORY DATA

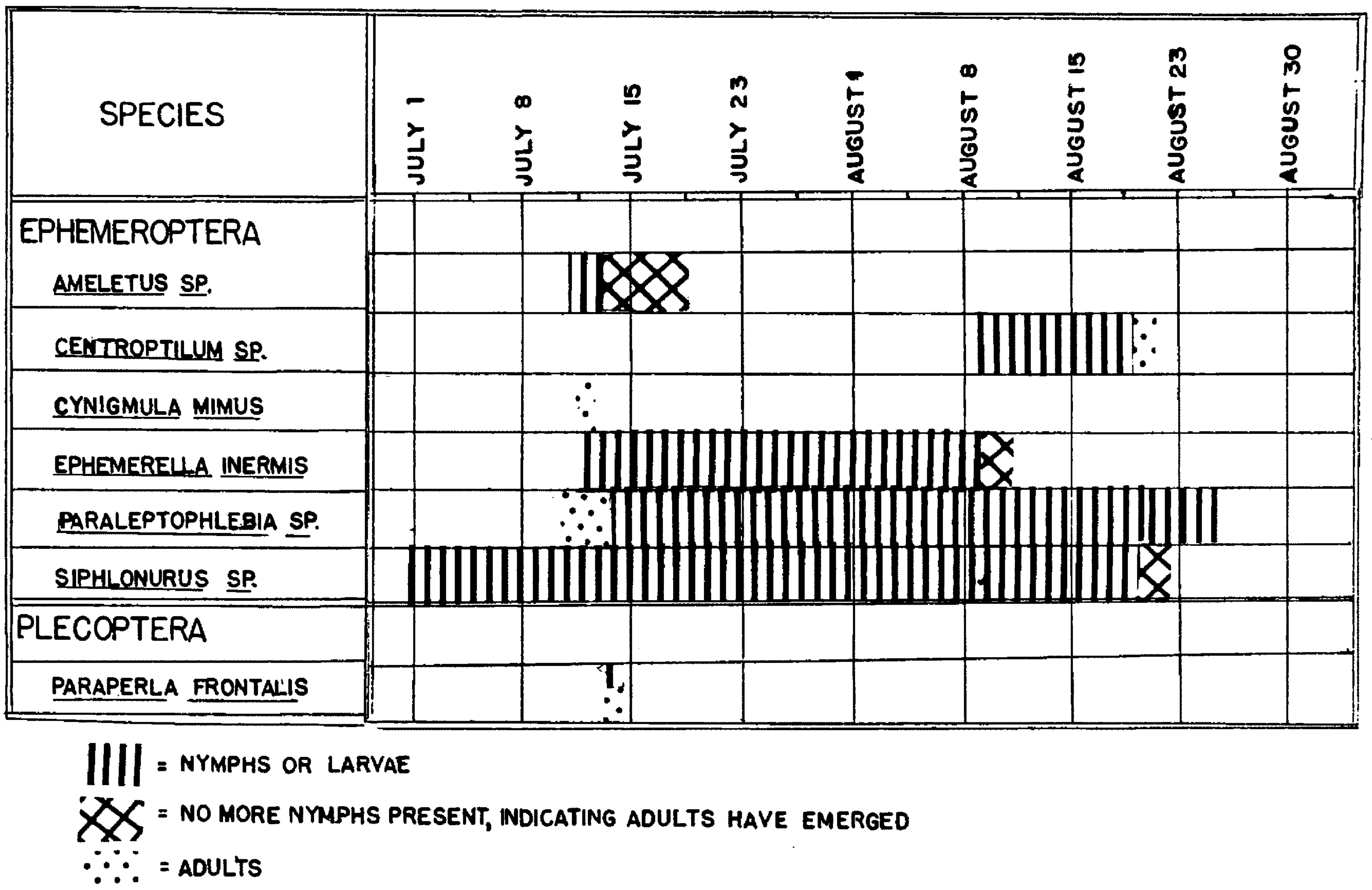
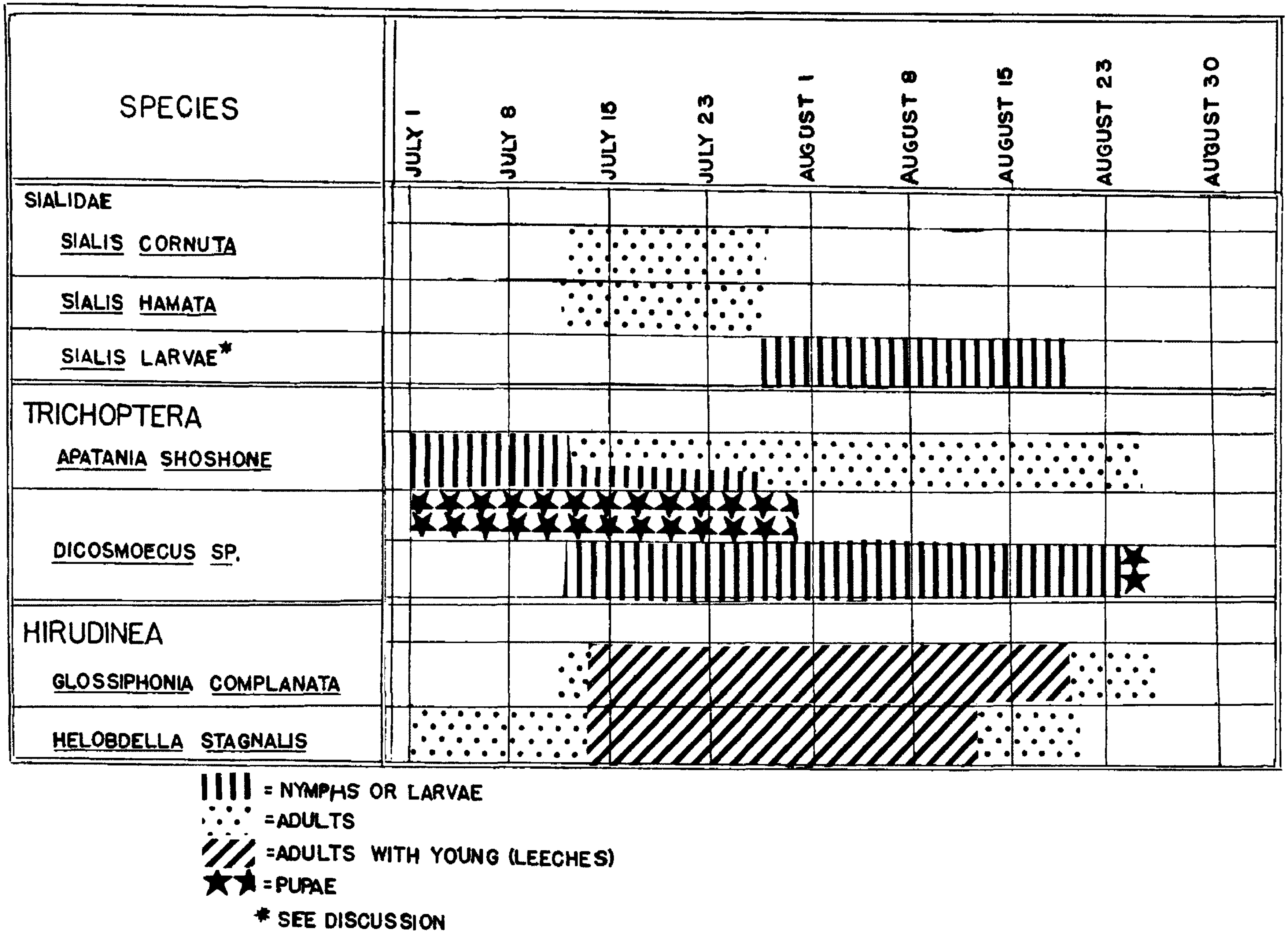


TABLE 4- CONTINUED



DISCUSSION

Physical Factors

Results of temperature readings in this study do not indicate any great change in water temperature during the summer (Table 1). The six degree temperature range found was from local variation in given areas and does not appear to represent a seasonal trend. During the period that readings were taken, the water temperature was not lower at higher altitudes; and, on a given date, temperatures were very similar from one lake to the next.

The constancy of water temperature is probably a result of mixing of the water by the wind. In addition, the lakes are in a series and all are connected by a stream. There is a constant replacement of water in the lower lakes and the water may not have time to become warm at this point in the stream system.

Megard (1958) found temperature readings slightly cooler than reported here, but his data were taken from bottom and surface readings some distance from the shore. The littoral area would be expected to be warmer due to solar radiation.

Bottom and surface temperatures (Megard, 1958) show no evidence of thermal stratification in any of the lakes. This is probably a result of mixing of water by winds, which are often heavy in this area.

As stated in the results, the lakes have a six month $\pm$ period of ice and snow cover. This greatly reduces solar insulation and the length of the growing season, especially in the upper lakes. The period of ice cover is probably a more important distributional limiting factor than the temperature of the water during the growing season.

Secchi disk readings for the determination of turbidity were 5.5 feet for Grinnell Lake, 15.5 feet for Josephine Lake, and 20 feet for Swiftcurrent Lake (Megard, 1958). The water in the upper lakes is made more turbid by the heavy load of sediments carried to the lakes from the glacier by streams. In addition to secchi disk readings, the larger amount of sediment in the upper lakes can be seen by observing the layer of silt on the lake bottoms and on the rocks. Grinnell Lake has a heavy silt layer on the rocks, whereas Swiftcurrent Lake has comparatively little. Silt is probably also a biological limiting factor and may account for the absence of many species in Grinnell Lake.

Chemical Factors

As would be expected from the surrounding rock strata and from the results of other works (Rawson, 1953), the lakes are poor in some dissolved minerals. Results of tests for calcium and magnesium in Table 2 show these elements to be present in very small amounts, but the amount was almost three times that found in Amethyst Lake by Rawson (1953). It should be pointed out that the samples tested for calcium and magnesium were allowed to stand several days before being tested, and that because of a lack of vacuum pump and other facilities, certain steps in the testing procedure had to be modified. Readings may not be accurate and should be accepted with caution. Measurements for calcium and magnesium were made with a Helige Colorimeter.

The results in the present study do not differ from Cushing (1964), who found that total dissolved solids and ions necessary for photosynthesis decrease as one goes downstream, and, the decrease is partly coincident with the downstream increase in plankton numbers. Readings for calcium and magnesium were taken only on one date in the lakes in Glacier Park; but there does not appear to be an increase in calcium and magnesium from upstream to downstream even though Cushing (1964) and others assume that nutrients are added to the system throughout its course. Results show that there are more invertebrates and aquatic plants present in Swiftcurrent than in Grinnell, and these probably use up the added nutrients. Data are not sufficient to determine significant increases or decreases in nutrients present.

After corrections were made for temperature and elevation, it was found that these lakes were nearly saturated with dissolved oxygen. Wave action caused by heavy winds in the area and the fall of the water from the glacier to Grinnell Lake are probably responsible for the heavy O_2 concentration in the water.

Dissolved carbon dioxide was found in each analysis in amounts from 0.5 ppm to 2 ppm. Bicarbonate ions, which were present from the reactions between H_2CO_3 and limestone, increased downstream but not enough data were obtained to note definite trends. PH was found to be slightly basic with readings from 7.3 to 7.5. Megard (1958) found a pH of 7.9 in all of the lakes.

A Comparison with Other Lakes in the Area

A comparison of the lakes in this study with three lakes which Brunson and Nelson (1952) reported on may be of interest. The three lakes are Howard Lake, elevation 4500 feet; Lake Rogers, elevation 3900 feet; and Red Meadow Lake, elevation 5500 feet. All are in northwestern Montana.

Howard Lake, which is at nearly the same elevation as Swiftcurrent Lake, had large beds of Potamogeton in the littoral areas, beds of Nuphar, and scattered Chara and Utricularia. Howard Lake was also inhabited by many colonies of freshwater sponges and large concentrations of the tadpole stages of Rana p. pretiosa and Bufo b. boreas. Of the above, small beds of Potamogeton were observed in Swiftcurrent Lake and Megard (1958) reported some beds of Chara. The remainder of the plants and animals mentioned were not found in any of the three lakes in Glacier Park.

Lake Rogers, which is about 1000 feet lower than any of the lakes studied in the Park, has a very abundant growth of aquatic vegetation, a secchi disk transparency of about 15.5 feet, and great numbers of the leech Haemopis grandis. The lakes in the Park show very little resemblance to Lake Rogers.

Red Meadow Lake, which is 450 feet higher than Grinnell Lake but which is not fed by a glacier, has a definite thermocline. This is probably a result of springs flowing into the lake and of protection from winds. It had a secchi disk reading of 25.5 feet and a pH of 8.2 at the surface. Gammarus, which were uncommon in the lakes in Glacier Park, were numerous in Red Meadow Lake. Chara and Potamogeton richardsonii were found in both Red Meadow Lake and Swiftcurrent Lake. Red Meadow Lake, however, bears little resemblance to Grinnell Lake.

Invertebrates

Diptera

Members of the order Diptera present some of the most difficult problems in taxonomy of any of the aquatic invertebrates. A number of species of Diptera were collected but most of these were larvae. The taxonomy of this group, especially that of the immature forms of western species, has received so little attention that many could not even be identified to genus. Diptera were often important members of the aquatic community, but in most cases they must be treated on the familial or generic level because of the difficulty in the identification of species.

Families collected included Tipulidae, Tendipedidae, Syrphidae, Ceratopogonidae, Tabanidae, Empididae, Dolichopodidae, and Muscidae: many of these were represented by only a few specimens. The most important families were Tendipedidae and Tipulidae.

Tendipedids were very numerous, especially at station No. 1 in Swiftcurrent Lake. The family was represented by a great number of species and most of these emerged as adults in July and early August. Numbers of larvae collected dropped sharply in mid-August.

Several species of Tipulidae were collected as larvae, and by far the most numerous of these was Tipula sp. These larvae, which were often over an inch in length, occurred on gravel covered shores such as are found at station No. 2 in Swiftcurrent and station No. 6 in Grinnell Lake.

Other groups of Diptera are listed in Table 3.

Ephemeroptera

Mayflies were important members of the aquatic community of many areas of the lakes. There appeared to be only one species of Siphlonurus present and this species was collected in great numbers in areas of still water and vegetation. It was especially abundant on the Potamogeton richardsonii at station No. 1 in Swiftcurrent Lake. No adults were found, but from consideration of the dates of the disappearance of the nymphs, the adults must emerge within a few days instead of gradually over a long period of time as is the case in some species (Gladhill, 1958) (Table 4). No key is available to identify these nymphs to species.

Ameletus also appeared to be represented by only one species. No adults were collected, thus specific determination could not be made. These nymphs occurred on shores with a hard gravel bottom. They were not numerous in the lakes but they were widespread.

Ephemerella inermis Eaton were collected as nymphs only, and they occurred in areas with muddy bottoms and abundant organic debris such as station No. 1 in Swiftcurrent Lake (Table 3).

A number of adults of Cynigmula mimus Eaton were observed in mating swarms at the lower end of Josephine on July 12, 1964 (Tables 3 and 4). No nymphs were taken in the lakes and it is probable that nymphs inhabit nearby streams.

The herbivorous nymphs of Heptagena usually occur under stones or in debris near the banks of streams and rivers (Banks, 1953). Small instars of this genus were collected in Swiftcurrent and Josephine Lakes in mid and late August.

Adults of Paraleptophlebia sp. were collected in early July, but specific identification was not obtained on this collection. Paraleptophlebia nymphs occurred at all stations except No. 1 in Swiftcurrent and station No. 7 in Grinnell. They were found in areas of gravel and solid bottom (Table 3). It is not known if the adults and nymphs mentioned above belong to the same species.

Adults and nymphs of Centroptilum sp. were collected in Swiftcurrent and Josephine Lake. These tiny mayflies are said to typically inhabit shallow, rapidly flowing water (Burks, 1953). As shown in Table 4, adults emerged in late August.

Megaloptera

Sialidae

Two species of adult Sialids were found in the study area. These two species, S. hamata Ross and S. cornuta Ross are known to be chiefly western in distribution (Ross, 1937).

Larvae, which could not be identified to species, were collected from July 26 to August 20. Although there was much variation in length, those taken July 26 were mostly 5-7 mm long, while those taken August 20 were up to 10 mm long. Larvae of some species are known to live for 2 or 3 years; therefore, a single collection of larvae may have represented individuals of different age groups and may have represented more than one species. Thus, in Table 3, larvae are listed under Sialis sp. and adults are listed separately.

Sialid larvae were found only in the grassy inlet in Grinnell Lake. The most favorable habitat appeared to be shores with little wave action, much sunlight, and much dead, submerged vegetation. In this case the vegetation was *Carex*. No larvae were collected on gravel covered shores or in areas devoid of vegetation.

The results shown in Table 4 are misleading for *Sialis*. By chance, larvae were found immediately after the last adults were collected. The larvae were not from eggs laid by these adults, but they were probably one or more years old as shown by the size of the larvae.

Plecoptera

Stoneflies are usually restricted to streams and running water in the immature stages. Most are sensitive and require moving, well aerated, unpolluted water for proper nymphal development. Nymphs are occasionally found in northern lakes with gravelly shores, as was the case in the lakes studied.

Stonefly nymphs were not only found in the lakes, but were present in large numbers and in a wide variety of species.

Isoperla and *Alloperla* were represented by at least three species each. At least eight species of stoneflies inhabit the lakes as immatures. In addition, *Pteronarcella badia* (Hagen) and *Utaperla sapladora* Riker adults were collected along the shores. These probably were from nearby streams inasmuch as no nymphs were found in the lakes studied.

Capnia sp. or *spp.* nymphs occurred in all of the lakes wherever there was a shore of gravel. In 1964, nymphs of *Capnia* were collected only in mid and late August. *Pteronarcella badia* were found only as adults and were probably from stream nymphs.

Several species of Isoperla were present, both as adults and as nymphs. This genus and Alloperla were the most abundant genera of stoneflies in the lakes. Adults of Isoperla fusca (Needham and Claassen) were collected along the lake shores and several species of Isoperla nymphs were taken along the edge of the water.

One adult and four nymphs of Paraperla frontalis (Banks) were found in Josephine Lake (Table 3). These were the only specimens found during both years of collecting.

An adult of Utaperla sapladora collected along Josephine Lake was probably from a stream nymph. The nymph of this genus is undescribed and the species is said to be rare (Jewett, 1959).

Several species of Alloperla nymphs were collected, but again it was not possible to determine the species of the nymphs. Adults of A. fidelis Banks, A. serrata Needham and Claassen, A. lamba Needham and I. fusca (Needham and Claassen) were taken along the shores, but there was no way of knowing if these came from nearby streams or if they are from lake inhabiting nymphs.

Trichoptera

Approximately 320 caddisflies were collected in the summer of 1964 and 100 additional specimens were taken at later times. Most of these were larvae but the adults of six species were also collected. A new species of Limnephilus was found and will be described by Oliver Flint at the United States National Museum. The collections represented four families and twelve genera, making this order the most abundant group in the number of species identified and second only to Tendipedidae in number of individuals of invertebrates found in the lakes. Species could not be determined from the larvae of many of these Trichoptera.

The family Limnephilidae was by far the most numerous while Psychomyiidae and Lepidostomatidae were represented by one genus each and a total of four specimens for the two families.

The family Psychomiidae was represented only by the genus Polycentropus. The species of this specimen could not be determined, but the genus is known to favor streams and rivers, with some species having a tolerance for a wide range of habitat conditions, including lakes (Ross, 1944). Only two larvae were found and they were at station No. 2 in Swiftcurrent Lake.

Two larvae of Lepidostoma, family Lepidostomatidae, were found at the gravel covered shore in Swiftcurrent Lake. Ross (1944) states that species of this genus prefer streams or springs to lakes.

Several adults of Anagapetus debilis (Ross) were collected along the lake shores, but no larvae were found. The larvae of this species, in the family Rhyacophilidae, are probably from a stream.

The genera and species mentioned in the following discussion are all in the family Limnephilidae. Four larvae and one pupa of Dicosmoecus sp. were collected from station No. 1 in Swiftcurrent to station No. 6 in Grinnell. They were found in a variety of habitats but were not abundant (Table 3).

Onocosmoecus unicolor (Bks.) was the most widespread and abundant of the Trichoptera found in the lakes. Larvae occurred wherever there was bottom vegetation or heavy algal growth on the rocks. Only larvae were found and the time of adult emergence must have been after the last collections were made in the fall.

The arctic and sub-arctic species Apatania shoshone (Bks.) was moderately abundant in all of the lakes. Pupal stages were found in Swiftcurrent Lake when the first collections were made on July 1, 1964 and adults were found in the middle of July. At Grinnell Laek, larvae were collected until mid-July. From mid-July to the end of August only adults and empty larval cases were found. The time of emergence of this species in all three lakes appeared to be during the first week in July, but apparently a few days earlier in Swiftcurrent than in Grinnell (Table 4). The fact that the last larvae or pupae in Grinnell were observed on July 20, and that adults were present until the end of August indicated that adults may live over one month. No information is available on the feeding habits of the adults or larvae of this species.

Hesperophylax sp. was represented by a single specimen from station No. 2 in Swiftcurrent Lake. The genus Limnephilus was represented by at least four species of larvae. In one instance, four distinct types of larvae, each probably representing a different species, were taken in one sample with the hand screen in Josephine Lake. Limnephilus harrimani (Bks.) and one undescribed species were also found in the adult stage.

Species of Grammotaulius are all arctic and sub-arctic in distribution but little other information is available on them. The large larvae and stick cases of this group were found only in the sheltered areas of warm water and muddy bottom at station No. 1 in Swiftcurrent Lake.

Adults of Ecclisomyia maculosa (Bks.) and Clistoronia magnifica (Bks.) were collected but no larvae of these genera were found in the lakes. They may have been from streams. Denning (1951) states that E. maculosa is usually taken in July and August at elevations of about 10,000 feet in Wyoming.

Amphipoda

Two species of amphipods were found, both of which are very common and widespread in the United States. These were Hyalella azteca (Saussure) and Gammarus limnaeus (Smith). The most significant fact about this group was the small numbers of individuals present in the lakes. All were collected from Swiftcurrent Lake and only two specimens of G. limnaeus and seven specimens of H. azteca were collected in the entire summer of 1964. Very seldom are amphipods found in water depths of more than one meter (Pennak, 1953) and it is certain that the area they should have inhabited was well sampled.

Hirudinea

The leeches are one of the better known groups of aquatic invertebrates, probably because of the small number of species compared to other invertebrate groups, because many species are very widespread or even cosmopolitan, and because leeches are popular animals for physiological work. Good keys are available to this group, and I was able to identify the material collected without consulting a specialist.

Three species of leeches were found in the lakes and they were definitely more predominant in the lower lakes, being absent from the milky waters of Grinnell Lake. All three species were collected in Swiftcurrent Lake and only one species was collected in Josephine Lake.

Glossiphonia complanata (L.) an Asian, European, and American form was found in Swiftcurrent Lake and Josephine Lake. This was the most widespread species and was found in a variety of habitats. Glossiphonia complanata exhibits a large amount of parental care towards its young. It appears that brooding takes place from late July to near the end of August as determined from the specimens bearing young in 1964 (Table 4). Mann (1963) states that the entire process of caring for the eggs and young occupies about 24 days.

Helobdella stagnalis (L.) was found only in Swiftcurrent Lake, but it was widespread, being found at all stations in this lake. Mann (1963) states that this species is most abundant in hard waters, but it can occur in soft waters which do not contain excessive acid conditions. Helebdella stagnalis had young attached to its underside from July 12 to August 9 (Table 4).

Erpobdella punctata (Leidy) was collected only in Swiftcurrent Lake and it was not abundant.

These leeches are not of the blood sucking variety and most of them feed on invertebrates, especially molluscs. Some are in reality predators rather than parasites, since they kill the prey during the process of feeding. A lack of food organisms probably kept the leeches from inhabiting Grinnell Lake where snails and other prey species were not abundant.

Mollusca

Seven species of Mollusca, including three species of Pelecypoda and four species of Gastropoda, were found in the lakes, all showing very definite distributional and habitat preferences.

Physa gyrina (Say) was collected at all stations in Josephine and Swiftcurrent Lakes, but it was not found in Grinnell Lake. This species apparently could tolerate conditions in all locations of the lower lakes, but some factor, such as the long period of ice cover, lack of abundant plant growth, or the large amount of silt, made it impossible for the snail to thrive in Grinnell Lake.

Aplexa hypnorum (Linné) was collected only at station No. 1 on the muddy shore of Swiftcurrent Lake. In Montana, *A. hypnorum* is usually found only in ponds (R. B. Brunson, personal communication.)

Stagnicola palustris (Muller) inhabited the gravel covered shores and firm bottoms of Swiftcurrent Lake. The snail was not found on the muddy bottom of station No. 1 in Swiftcurrent nor was it found in either of the other two lakes. Some factor appears to limit its distribution in the higher lakes, as it was abundant in some locations in Swiftcurrent.

Sphaerium nitidum (Clessin) was collected only on the gravelly shore in Swiftcurrent Lake. It was not present in large numbers.

Gyraulus parvus (Say) was found only on the muddy bottom at station No. 1 in Swiftcurrent Lake.

The ecological separation of species in the genus *Pisidium* agrees with a recent revision of the group based on morphological shell characters (Herrington, 1962). *Pisidium variabile* (Prime) was found only on the muddy bottom at station No. 1 in Swiftcurrent Lake, while P. caesertanum (Poli) was found wherever the shore was of wave-washed gravel. Even the gravel covered shore in Grinnell, which often has a heavy covering of silt, was suitable for this species.

One of the problems met with in the study of aquatic invertebrates is that of taxonomy. Probably less than 20% of the aquatic insect larvae can be identified to species because they have not been correlated with the described adults. Because of this, the immature forms of Isoperla, Alloperla, Capnia, Siphlonurus, Ameletus, Paraleptophlebia, Hexagena, Tipula and other Dipteran genera, Sialis and all Trichopteran genera except Onocosmoecus and Apatania could not be identified to species on the basis of larval characters.

About seven species of Coleoptera, all of which were Haliplidae and Dytiscidae, were collected and tentatively identified by me; however, specific determinations have not been received on these specimens and they are not included in the table of species collected.

Other difficult groups were also found. Limnephilus (Trichoptera) Alloperla and Isoperla (Plecoptera) nymphs and larvae represented three or four species each but they had to be treated on the generic level in the discussion. Four species of adult Alloperla were collected, but it is not certain that their nymphs inhabit the lakes.

Tipulidae, Chironomidae, and other Diptera represented many species, but in most cases these had to be treated on the familial level.

Certain general trends in the number of species present and in the distribution of certain groups appear when the data are examined.

There is an increase in the number of species per lake from upstream to downstream. Numbers of species or genera identified per lake were: Swiftcurrent, 33; Josephine, 29; and Grinnell, 17. These numbers are approximate because many groups were not identified to species. One factor probably involved in this distribution is the period of the ice cover. As stated in the results, Grinnell Lake had a heavy ice cover and snow cover after the other lakes had thawed. Not enough observations were made to give exact dates and periods of ice cover, but observations that were made indicated that upstream lakes definitely had a much longer period of ice cover.

Water temperatures that were taken through a large portion of the growing season showed that there were not significant temperature differences from one lake to another. Temperature differences probably did not cause the variation in numbers of species.

Examination of the chemical data did not show significant differences between the lakes, although bicarbonates did increase somewhat as one went downstream. It is doubtful if chemical differences caused the differences in the number of species.

A factor that may decrease species numbers upstream is siltation. The water in Grinnell Lake was more turbid than were the lakes downstream. Rawson (1942) found a definite correlation between total suspended solids and plankton productivity in six alpine lakes studied in Canada.

A final factor that could result in fewer species upstream is the age of the lakes. As the ice of the glaciers retreated after the Pleistocene, Swiftcurrent Lake was the first to emerge. The ice continued to retreat, and, probably several thousand years after the appearance of Swiftcurrent Lake, Grinnell Lake was formed. The lower lakes have had more time to mature, soil has formed around the edges, and more organic debris has collected and decomposed, thus increasing the nutrients in the lower lakes. This would result in more species in the older lakes.

Josephine Lake had the largest number of Plecopteran species, probably because more cold water streams entered it than entered the other lakes. Many of the nymphs were collected in the vicinity of the entrances of streams. Grinnell may have been too silty for them and Swiftcurrent lacked the stream activity. Josephine also had the largest variety of Tipulids.

Swiftcurrent had the largest number of Trichopteran species. The wide variety of favorable Trichopteran habitats probably accounted for this. The habitat variations, especially those at stations No. 1 and 3, were rich in Trichoptera. Swiftcurrent also had the most molluscs and leeches and the only amphipods. Swiftcurrent and Josephine did not vary greatly in total number of species but the species composition was definitely different.

Grinnell Lake had the only Sialid larvae collected, but other species collected in Grinnell were generally those also found in the lower lakes.

SUMMARY

Over 2000 specimens of invertebrates were collected from Swiftcurrent, Josephine and Grinnell Lakes in Glacier National Park, Montana, in 1964 and 1965. These were taken from seven selected collecting stations in the littoral area which represented the major habitat types in each lake. The lakes are connected by streams and are fed by a mountain glacier.

Tests were made for calcium, magnesium, carbonate, and bicarbonate ions. Amounts of dissolved oxygen and dissolved carbon dioxide were measured and pH and temperature readings were taken during the growing season.

Dates of collection and identifications are given for all of the specimens which could be identified. Many groups could not be identified beyond genus because the taxonomy has been incompletely worked and some groups were not properly preserved for identification. The number of species or genera identified per lake were Swiftcurrent, 33; Josephine, 29; and Grinnell, 17.

Distributions and habitat preferences are discussed for each group for which data were sufficient. Chemical and physical factors in relation to the distribution of various groups are discussed. A table of life history data is given for species for which information was sufficient.

The number of species and the number of individuals increased downstream. Siltation from glacial rock flour and the period of ice cover appear to be the main limiting factors in the distribution of the

groups studied. Temperatures during the growing season vary little from lake to lake on a given date. Chemical data are not complete enough to correlate them to the distributions found.

LITERATURE CITED

Aller, Alvin R. 1960. The composition of the Lake McDonald forest, Glacier National Park. Ecology. 41:1.

Baker, Frank C 1911. The Lymnaeidae of North and Middle America. Chicago Academy of Sciences. Special Publ. No. 2. 539 p.

Betten, C. 1934. The caddisflies or Trichoptera of New York State. Bull. N. Y. State Museum. No. 292. 576 p.

Brunson, R. B. and H. E. Nelson. 1952. A limnological reconnaissance of three western Montana lakes. Proc. Mont. Acad. Sci. 12:45-61.

Burks, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bull. Illinois Nat. Hist. Surv. 26(1):1-216.

Castle, Gordon B. 1939. The Plecoptera of Western Montana. Canad. Entom. 71:208-211.

Claassen, Peter W. 1939. Plecoptera nymphs of America north of Mexico. Thomas Say Foundation of the Entom. Soc. Amer. Publ. No. 3. 199 p.

Cushing, Colbert E. 1964. Plankton and water chemistry in the Montreal river-lake-stream system, Saskatchewan. Ecology. 45:306-313.

Denning, Donald G. 1941. The Genus Grammotaulius in North America. Canad. Entom. 73:232-235.

__________. 1951. Records and descriptions of nearctic caddisflies, Part III. Jour. Kansas Entom. Soc. 24:4.

Dodds, G. S. and F. L. Hisaw. 1925. Altitudinal range and zonation of mayflies, stoneflies, and caddisflies in the Colorado Rockies. Ecology. 6:380-390.

Dyson, James L. 1962. Glaciers and glaciation in Glacier National Park. Special Bull. No. 2. Glacier Nat. Hist. Assoc., Inc. Kalispell, Montana. 26 p.

Edmondson, W. T. (ed.). 1959. Fresh-water biology, John Wiley and Sons, New York. 1248 p.

Edwards, J. Gordon. 1957. Some general observations on the ecology of Glacier National Park, Montana, with special reference to certain entomological aspects. Wasmann Jour. Biol. 15:123-151.

Fassett, Norman C. 1957. A manual of aquatic plants. Second Ed. University of Wisconsin Press, Madison. 405 p.

Frison, T. H. 1936. Plecoptera of Illinois. Bull. Illinois Nat. Hist. Surv. 20:281-471.

__________. 1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. Bull. Illinois Nat. Hist. Surv. 22:2.

Gledhill, T. 1958. The life history of Ameletus inopinatus (Siphlonuridae, Ephemeroptera). Hydrobiologica. 14(1):85-90.

Henderson, Junius. 1924. Mollusca of Colorado, Utah, Idaho, and Wyoming. The University of Colorado Studies. 13:2.

Herrington, H. B. 1962. A revision of the Sphaeriidae of North America. Misc. Publ. Museum Zool. University of Michigan, Ann Arbor. 74 p.

Hutchinson, G. Evelyn. 1957. A treatise on limnology. Vol. 1. John Wiley and Sons. 1015 p.

Jewett, Stanley G. 1959. The stoneflies (Plecoptera) of the Pacific Northwest. Studies in Entomology. No. 3. Oregon State Monograph, Corvallis.

Judd, W. W. 1964. A study of the population of insects emerging from Saunders Pond at London, Ontario. Amer. Midl. Nat. 71(2):402-414.

Macan, T. T. 1963. Freshwater ecology. John Wiley and Sons, New York. 338 p.

Mann, K. H. 1963. Leeches (Hirudinea) their structure, physiology, ecology and embryology. Pergamon Press, New York.

Megard, Robert O. 1958. Studies on the microcrustacea of three Montana Lakes in Glacier National Park, Montana. M.A. Thesis. The University of New Mexico. Albuquerque, New Mexico. 32 p.

Moore, J. P. 1912. Leeches of Minnesota. Geol. Nat. Hist. Surv. Zool. Ser. Part 3, No. 5.

Needham, J. G. and Peter W. Claassen. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. Thomas Say Found. of Entom. Soc. of Amer. Vol. 2. 397 p.

Needham, J.G., F. R. Traver, and Y. Hsu. 1935. The biology of mayflies. Constock, Ithaca, N. Y.

Pennak, R. W. 1941 a. An introduction to the limnology of northern Colorado. University Colorado Studies. Ser. D. 1:203-220.

__________. 1941b. A bibliography of high altitude limnological investigations in the western United States. University Colorado Studies. Ser. D. 1:225-229.

__________. 1945a. Hydrography and Morphometry of some northern Colorado lakes. University Colorado Studies. Ser. D. 2:245-262.

__________. 1945b. Some aspects of the regional limnology of northern Colorado. University Colorado Studies. Ser. D. 2:263-293.

__________. 1953. Fresh-water invertebrates of the United States. Ronald Press Co., New York. 769 p.

__________. 1955. Comparative limnology of eight Colorado mountain lakes. University of Colorado Studies in Biol. No. 2. 1-75.

__________. 1963. Ecological and radio carbon correlations in some Colorado mountain lakes and bog deposits. Ecology. 44(1):1-15.

Pesta, O. 1929. Der Hochgebirgssee der Alpen. Die Binnengewässer. 8. Stuttgart.

Rawson, D. S. 1942. A comparison of some large alpine lakes in Western Canada. Ecology. 23(2):143-161.

__________. 1953. The limnology of Amethyst Lake, a high alpine type near Jasper, Alberta. Canad. Jour. Zool. 31:193-210.

__________. 1960. A limnological comparison of twelve large lakes in Northern Saskatchewan. Limnology and Oceanography. 5(2): 195-211.

Reid, George K. 1961. Ecology of inland waters and estuaries. Reinhold, New York. 375 p.

Ross, Clyde P. 1959. Geology of Glacier National Park and the Flathead Region, Northwest Montana. Geological Survey, Professional Paper 296. U. S. Government Printing Office.

Ross, H. H. 1937. Nearctic alder flies of the Genus Sialis (Megaloptera, Sialidae). Bull. Illinois Nat. Hist. Surv. 21:57-78.

__________. 1944. The caddisflies, or Trichoptera, of Illinois. Bull Illinois Nat. Hist. Surv. 23:1. 326 p.

Ruttner, Franz. 1963. Fundamentals of limnology. Third Edition. (Transl. from German by Frey and Fry). University of Toronto Press, Toronto. 295 p.

Steinböck, O. 1934. Zur Frage der Sprungschicht in Hochgebirgsseen. Arch. Hydrobiol. 27:397-415.

__________. 1938. Arbeiten über die Limnologie der Hochgebirgewässer. Intern. Rev. Hydrobiol. Hydrog. 37:467-509.

Strøm, K. M. 1938. Norwegian mountain lakes. Arch. Hydrobiol. 33:82-92.

Usinger, R. L. 1963. Aquatic insects of California. University of California Press, Berkeley and Los Angeles. 508 p.