1973

The ecology of submerged aquatic macrophytes of Red Rock Lakes National Wildlife Refuge Montana

David Gregory Paullin
The University of Montana

Recommended Citation

Paullin, David Gregory, "The ecology of submerged aquatic macrophytes of Red Rock Lakes National Wildlife Refuge Montana" (1973). *Graduate Student Theses, Dissertations, & Professional Papers*. 6713.
https://scholarworks.umt.edu/etd/6713

THE ECOLOGY OF SUBMERGED AQUATIC MACROPHYTES OF RED ROCK LAKES NATIONAL WILDLIFE REFUGE, MONTANA

By

David G. Paullin

B.S., Humboldt State College, 1971

Presented in partial fulfillment of the requirements for the degree of

Master of Science in Wildlife Biology

UNIVERSITY OF MONTANA

1973

Approved by:

S Preece

Chairman, Board of Examiners

John M. Stewart

Dean, Graduate School

June 15, 1973

Date

-18-73

ACKNOWLEDGMENTS

The writer wishes to express his appreciation for the financial support provided by the Montana Cooperative Wildlife Research Unit and the U. S. Bureau of Sport Fisheries and Wildlife. Also, appreciation is expressed to Refuge Manager Gene Stroops for the equipment and living quarters that were provided during this investigation.

I wish to extend a special note of thanks to my committee chairman, Dr. Sherman J. Preece, and to committee members Dr. Bart W. O'Gara and Dr. James R. Habeck for their helpful suggestions and criticism of this manuscript and their guidance and assistance throughout all phases of this study.

My appreciation is extended to Roger Page, Chris Yde, and Bernie Hildebrand for their assistance in collecting field data. I wish to thank Assistant Refuge Manager Ron Papike for his assistance in plant identification and collection and for his helpful suggestions throughout the course of this investigation. I am indebted to Bureau Biologist Larry Napier who devised the plant sampling procedure used in this study.

My thanks are extended to Stephanie Fleischer and Virginia Johnston who assisted in the preparation of the final manuscript.

I am particularly grateful to my fiancee, Cathy Maurer, and my parents for their continuous help and encouragement throughout the study.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

LIST OF FIGURES

Chapter I

INTRODUCTION

This study originated as a consequence of the Wilderness Act of September 3, 1964 (Public Law 88-577). This act, in part, requires the Secretary of the Interior to review every roadless area of 5,000 contiguous acres or more and every roadless island within the National Wildlife Refuge System and, within 10 years after the effective date of the act, report to the President of the United States his recommendations concerning the suitability or nonsuitability of each such area or island as wilderness.

As announced in the Federal Register (Gottschalk 1970), the Red Rock Lakes National Wildlife Refuge, where this study was conducted, contains potential wilderness resources that meet the basic criteria described in the Wilderness Act of 1964.

The Red Rock Lakes Refuge is administered by the Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service. Although the Refuge is managed under a multiple use concept that includes hunting, fishing, grazing, and the observation and enjoyment of all local flora and fauna by the general public, the primary Refuge objective involves the protection and preservation of the nesting and resting habitat of the trumpeter swan (Olor buccinator).

In an effort to better understand the trumpeter swan and its habitat requirements and interactions, as well as the possible benefits or disadvantages that a wilderness status would have upon future management options, the U. S. Bureau of Sport Fisheries and Wildlife in conjunction with the Cooperative Wildlife Research Unit at the University of Montana initiated, in 1971, a study of the "Ecology of the Trumpeter Swan."

This study was conducted in two segments. The first segment pertaining directly to the ecology of the swans was carried out by University of Montana doctoral candidate Roger Page. The second segment, herein, deals with the ecology of the submerged macrophytes found within the Refuge lakes.

This thesis summarizes the soil, water, and aquatic macrophyte research that has been conducted to date on the Refuge. The specific objectives of this research were:

1. To determine what chemical factors inherent in the lake bottom soils and surrounding watershed of the Refuge might contribute to the productivity of submergent vegetation or which might limit plant growth by deficiencies or by the toxic effects of inordinately high concentrations.

2. To describe water dynamics of the Red Rock Lakes marsh by measuring stream discharge into the marsh and outflow

from the marsh.

3. To characterize the waters of the lakes and ponds by chemically analyzing water samples and to determine what factors in the water affect the distribution, abundance, and productivity of aquatic macrophytes.

4. To identify and map the submerged macrophytes of the major lakes and ponds and to record both distribution and abundance.

5. To describe the general habitat requirements of the submerged macrophytes.

6. To characterize the phenology of the major species of submerged macrophytes.

7. To characterize plant successional patterns with the use of past Refuge records and to predict possible future trends and changes.

8. To determine or predict the effects of different management practices upon the aquatic macrophytes.

Plant, soil, and water research was conducted on the seven major lakes and ponds lying within the Refuge boundaries (Table 1). Plant field work was restricted to submerged macrophytes in these open water areas and did not include emergent species such as Typha, Scirpus, Juncus, and Carex which cover approximately 8,600 acres. The importance of emergent plants to the trumpeter swan in terms of nesting habitat, escape cover, and food sources should not be overlooked nor underrated, but logistics, time, and work loads with the submerged plants did not warrant any intensive work with these plant communities.

Table 1

Lakes and Ponds Within the Study Area

Area	Acres
Upper Lake	2,880
Lower Lake	1,540
River Marsh	570
Swan Lake	415
Widgeon Pond	132
Culver Pond	27
MacDonald Pond	12
Total	5,576

In pursuing the objectives of this study over the past 2 years, many insights into the ecology of the submerged macrophytes of the Refuge were gained. In some cases, no doubt, more work is needed before the dynamics of the system can be fully understood.

Chapter II

DESCRIPTION OF THE STUDY AREA

Location

The Red Rock Lakes National Wildlife Refuge was established in 1935 to protect and preserve one of the last remaining breeding areas of the trumpeter swan in the contiguous 48 states. The Refuge contains approximately 40,000 acres of open water, marsh, dry sagebrush uplands, fertile hay meadows, forested slopes, and portions of the rugged Centennial Mountains which form part of the Continental Divide.

Situated at an elevation of 6,600 feet, the Refuge lies at the eastern end of the Centennial Valley in Beaverhead County, Montana (44° 37' latitude, 111° 45' longitude). The Valley is approximately 40 miles long and 7 miles wide and is bordered on the north by the low, rolling Gravelly Range and on the south by the rugged Centennial Mountains. Development of the Refuge (roads, ditches, dams, etc.) is minimal and concentrated at the east end of the Refuge so that much of the marsh still lies in its undisturbed near-pristine condition.

Climate

The Centennial Valley is characterized by long cold winters and short cool summers. The average annual precipitation is 20 inches (1961-1972). This precipitation is quite evenly distributed throughout the year with the exception of June which is usually the wettest month (Fig. 1).

Average snowfall during the long winter months is 150 inches. Snowfall during every month of the year is not uncommon.

The mean annual temperature is 34.9°F. During extreme cold periods, air temperatures commonly drop to the -30°F to -40°F range. The summer maximum temperature rarely exceeds 90°F.

Although frost occasionally occurs during every month of the year, the average length of the frost-free season is about 51 days. This season extends from mid-June to mid-August, the latter period corresponding to the general termination of the growing season for most of the submerged macrophytes.

Geology

The geologic formations of the Refuge area were well mapped (Fig. 2) and described by Egbert (1960). The structure and stratigraphy of these formations are treated in great detail by Mann (1960), Egbert (1960), Hanson (1960), Strickland (1960), Kummel (1960), Moritz (1960), and Honkala (1967).

The Refuge is bounded on the north by the low rolling hills of

Figure 1. Annual precipitation pattern of the study area.

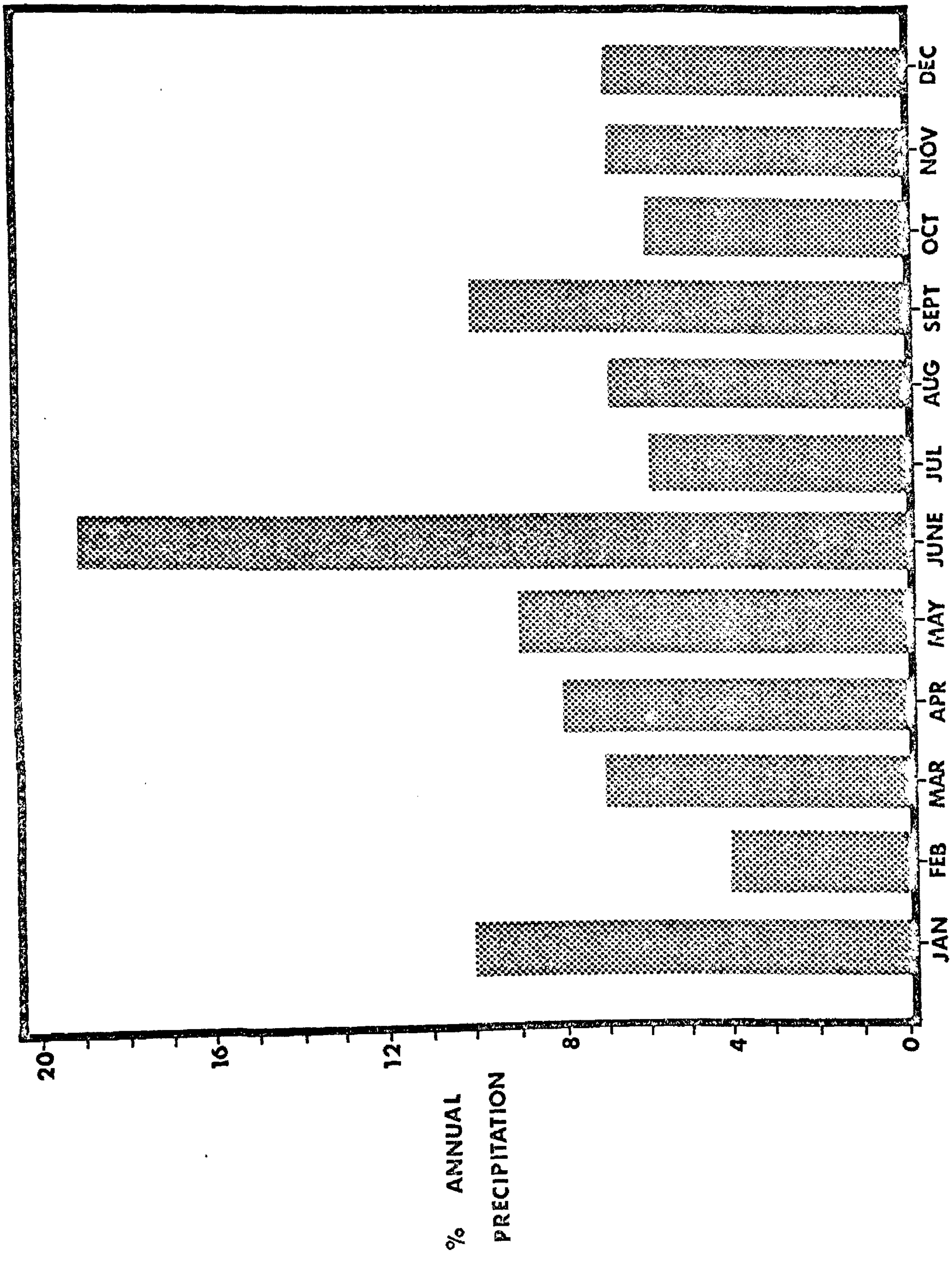
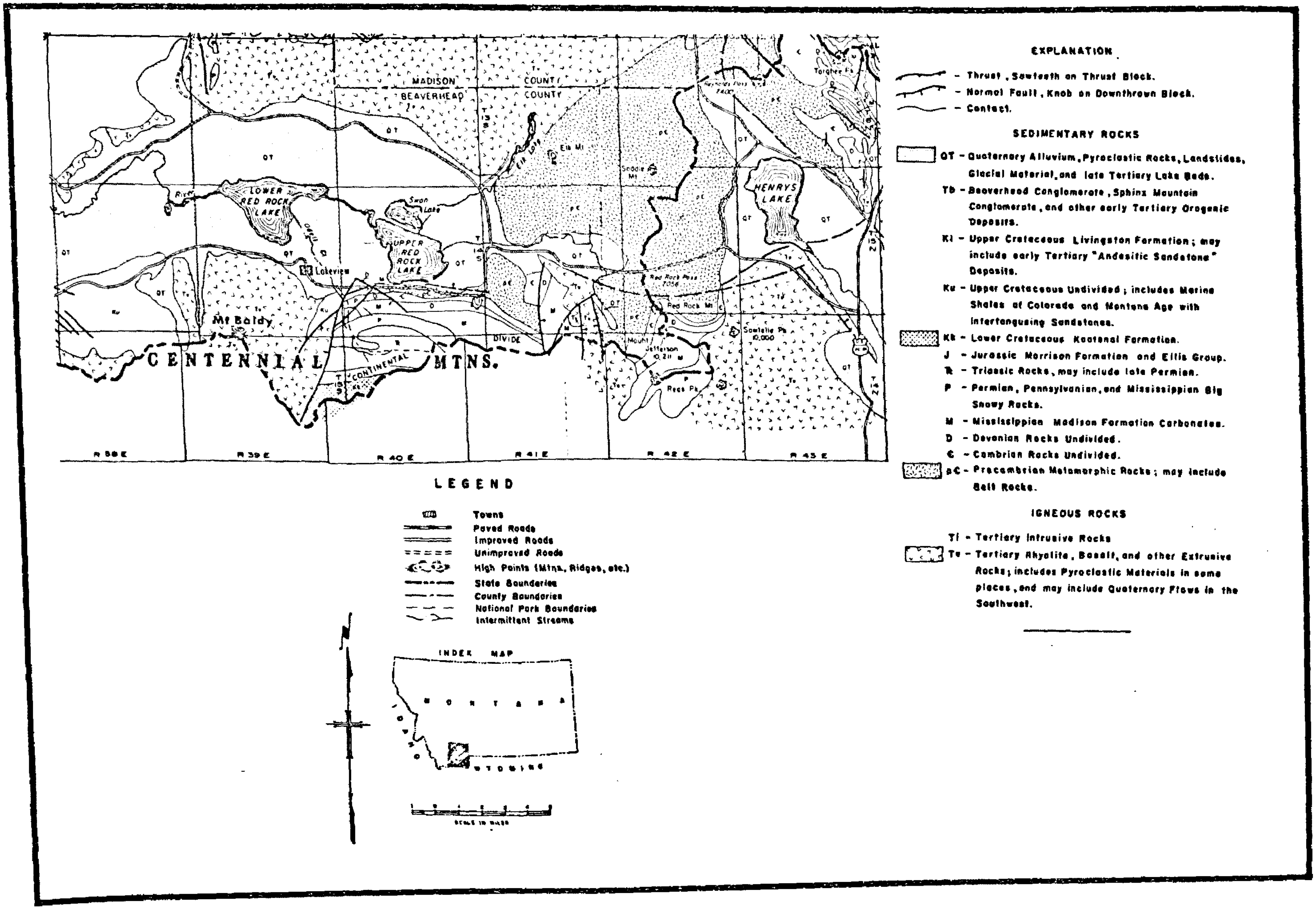

% ANNUAL PRECIPITATION
0
4
8
12
16
20
JAN
FEB
MAR
APR
MAY
JUNE
JUL
AUG
SEPT
OCT
NOV
DEC

Figure 2. Geologic map of the study area (Egbert 1960).

MADISON COUNTY
BEAVERHEAD COUNTY
Elk Mt
Saddle Mt
HENRYS LAKE
Targhee Pk
7400
Swan Lake
LOWER RED ROCK LAKE
UPPER RED ROCK LAKE
River
Odell
Lakeview
Mt Baldy
CENTENNIAL MTNS.
CONTINENTAL DIVIDE
Red Rock Pass 7056
Red Rock Mt
Sawtelle Pk 10,000
Mount Jefferson 10,211
Reas Pk
T 13 S
T 14 S
T 15 S
T 15 N
T 14 N
R 38 E
R 39 E
R 40 E
R 41 E
R 42 E
R 43 E
QT
Tb
Kl
Ku
Kk
J
Ꞧ
P
M
D
Ꞓ
pC
Ti
Tv
EXPLANATION
Thrust, Sawteeth on Thrust Block.
Normal Fault, Knob on Downthrown Block.
Contact.
SEDIMENTARY ROCKS
QT - Quaternary Alluvium, Pyroclastic Rocks, Landslides, Glacial Material, and late Tertiary Lake Beds.
Tb - Beaverhead Conglomerate, Sphinx Mountain Conglomerate, and other early Tertiary Orogenic Deposits.
Kl - Upper Cretaceous Livingston Formation; may include early Tertiary "Andesitic Sandstone" Deposits.
Ku - Upper Cretaceous Undivided; includes Marine Shales of Colorado and Montana Age with intertonguing Sandstones.
Kk - Lower Cretaceous Kootenai Formation.
J - Jurassic Morrison Formation and Ellis Group.
Ꞧ - Triassic Rocks, may include late Permian.
P - Permian, Pennsylvanian, and Mississippian Big Snowy Rocks.
M - Mississippian Madison Formation Carbonates.
D - Devonian Rocks Undivided.
Ꞓ - Cambrian Rocks Undivided.
pC - Precambrian Metamorphic Rocks; may include Belt Rocks.
IGNEOUS ROCKS
Ti - Tertiary Intrusive Rocks
Tv - Tertiary Rhyolite, Basalt, and other Extrusive Rocks; includes Pyroclastic Materials in some places, and may include Quaternary Flows in the Southwest.
LEGEND
Towns
Paved Roads
Improved Roads
Unimproved Roads
High Points (Mtns, Ridges, etc.)
State Boundaries
County Boundaries
National Park Boundaries
Intermittent Streams
INDEX MAP
MONTANA
IDAHO
WYOMING
SCALE IN MILES

the Gravelly Range. These hills are comprised of Tertiary extrusive rocks primarily of rhyolite and basalt.

The Centennial Mountains immediately adjacent to the south boundary of the Refuge belong to the Laramide orogeny system and are included in the broader category of "Central Rockies" (Eardley 1951). The Centennial Mountains are oriented approximately in an east-west direction and extend their range for 40 miles from Monida Pass, Montana to Henry's Fork of the Snake River in Idaho. Mount Jefferson, east of the Refuge, is the highest point in the entire range, reaching an elevation of 10,211 feet. Because of the great length of the Centennial Range, discussion is limited to that segment of the Centennials within the watershed of the Refuge, i.e., from Mount Baldy adjacent to the Refuge's western boundary; east, along the Continental Divide to the headwaters of Red Rock Creek and the area also known as Alaska Basin.

The Centennial Mountains, immediately adjacent to the Refuge, are tectonic in origin, arising from the prominent "Centennial Fault"; a fault block of east-west orientation that runs along the foot slope of the mountains near the Refuge's southern boundary. The Centennial Mountains to the south of the fault are the uplifted range-block and the Centennial Valley to the north is the down-thrown basin block. The uplift of the Centennial Range began in Lower Cretaceous time, which marked the advent of the Laramide orogeny, and continued to early, lower Eocene time (Honkala 1960). The fault front of the Centennial Mountains is a precipitous 3,000 foot scarp of impressive beauty.

The Centennial escarpment was further modified by glaciation. Small terminal moraines at the foot slope of the mountains are common as are small north-south trending glacial valleys and cirques. More recently, the scarp was modified by tremendous avalanches and landslides which scar the lower, forested, mountain sides.

The rocks comprising the Centennial Mountains are divisible into: (1) Precambrian metamorphics; (2) Paleozoic, Mesozoic, and Cenozoic sediments; and (3) Cenozoic volcanics. The watershed to the east of the Refuge, including most of the Alaska Basin area and the Tom Creek drainage, is comprised almost entirely of Precambrian metamorphosed carbonates. These carbonates represent the oldest rocks found in the Refuge watershed.

Above the Precambrian metamorphics, at the headwaters of Red Rock Creek and Tom Creek, sedimentary rocks prevail. Represented in these high altitude rocks are Cambrian rocks which are progressively overlain by sedimentaries of Devonian Jefferson Limestone or Three Forks Formation; Mississippian Madison Formation limestone; Permian Phosphoria Formation; Pennsylvanian Amsden and Quadrant Formation; and finally, in some areas, Tertiary volcanics (Egbert 1960, Mann 1960). With the exception of the Phosphoria Formation which contains cherts, shales, and phosphorite (Cressman and Swanson 1960), the above strata are primarily composed of limestone, dolomite, and sandstones (Mann 1960).

The Centennial escarpment running contiguous with the south Refuge boundary is similar geologically to the headwater regions of Red Rock Creek but more complex due to the presence of additional sedimentary strata. Among the geologically younger sedimentary strata found in this region are rocks of the Triassic (Dinwoody Formation), Jurassic (Morrison Formation and Ellis Group), and finally lower Cretaceous (Kootenai Formation) (Egbert 1960, Mann 1960). These strata are primarily limestone, sandstone, siltstone, and dolomite (Mann 1960).

The continuity of the Centennial Mountains near the Refuge is disrupted by a north-south trending fault through the Odell Creek drainage. Honkala (1960) theorized that this is a high-angle normal fault. The geologic parent material east of the Odell Creek fault (just discussed) is quite different than the rocks found west of the drainage. The area west of Odell Creek is dominated by Mount Baldy (elevation 9889 ft.) and its surrounding foothills. Unlike the previous portions of the Centennials, Mount Baldy is almost exclusively comprised of Tertiary volcanics.

The geologic composition of the Valley floor is Quaternary alluvium which resulted from the erosional breakdown of the surrounding mountains.

Soils

The mapping, classification, and description of upland Refuge soils has been well documented (Nielson and Farnsworth 1966). Their survey revealed that there are eight orders of soils found on the Refuge which are further classified into 30 different soil series. Refuge soils can be classified under the broader category of soil associations, of which 11 are found on the Refuge (Fig. 3).

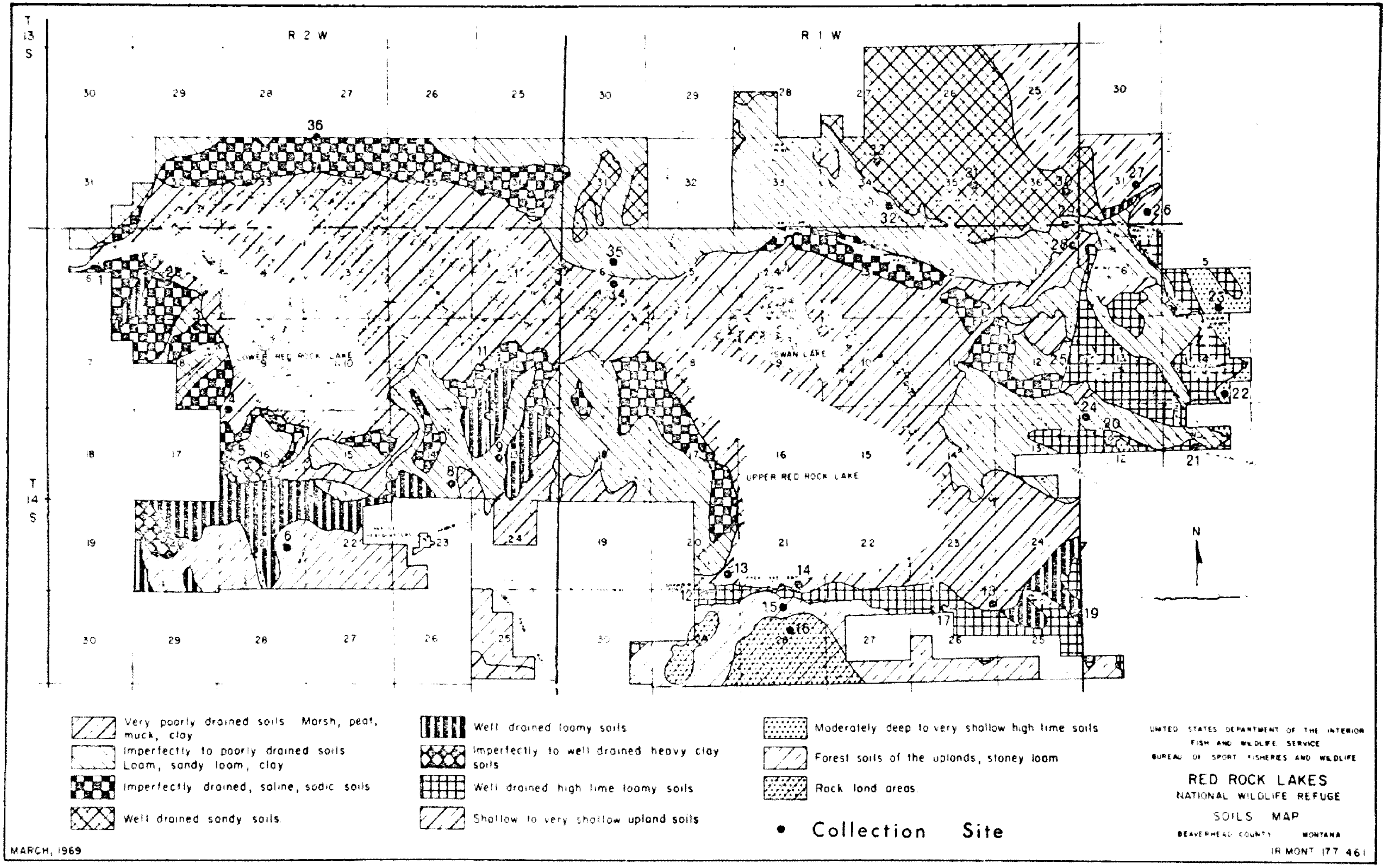
Despite this great diversity of soil types, only a few of the 30 soil series are common and widespread on the Refuge. Sixty percent of the Refuge's upland soils are accounted for by the Ching, Bug, Raynesford, and Breca series and the Arvada-Beckton, Arvada-Ching, and peat-muck complexes.

Watershed

The watershed of the Refuge is bounded on the south by the Centennial Mountains, on the east by the Alaska Basin and its adjacent hills, and on the north by the Gravelly Range. The Refuge watershed is open to the west where lake water exits via the Red Rock River.

The southern extent of the watershed is drained by Tom, Lone Willow, and Odell creeks. During periods of peak runoff in early summer, Duff, Collins, Humphrey, Shambow, and Hackett

Figure 3. Soil association map of the study area.


R 2 W
R I W
T 13 S
T 14 S
LOWER RED ROCK LAKE
SWAN LAKE
UPPER RED ROCK LAKE
N
Very poorly drained soils. Marsh, peat, muck, clay
Imperfectly to poorly drained soils Loam, sandy loam, clay
Imperfectly drained, saline, sodic soils
Well drained sandy soils.
Well drained loamy soils
Imperfectly to well drained heavy clay soils
Well drained high lime loamy soils
Shallow to very shallow upland soils
Moderately deep to very shallow high lime soils
Forest soils of the uplands, stoney loam
Rock land areas.
● Collection Site
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF SPORT FISHERIES AND WILDLIFE
RED ROCK LAKES
NATIONAL WILDLIFE REFUGE
SOILS MAP
BEAVERHEAD COUNTY MONTANA
IR MONT 177 461
MARCH, 1969

creeks also carry considerable amounts of water. Springs from this area feed Cole, Nye, East Shambow, Grayling, and East Nye creeks throughout the summer months.

The Alaska Basin area to the east of the Refuge is drained primarily by Red Rock Creek. Warm springs play an important role in this eastern portion of the Refuge. Culver Springs is the primary water source for Culver Pond, and Elk Springs is the primary water source of MacDonald Pond. Warm water from these two springs are responsible for maintaining ice-free areas during the winter where resident trumpeter swans congregate and are artificially fed.

The Gravelly Range to the north of the Refuge contributes very little water to the marsh lakes. Teepee Creek is the main stream that enters the Refuge from the north and its flow is limited to a few weeks in early summer.

Lake Origin

The marsh proper, i. e., Upper, Lower and Swan lakes and River Marsh, is tectonic in origin, being formed from the downthrown basin block of the Centennial fault. During the recent geologic past this basin block was inundated by a glacial lake. Brower (1897) estimated that the lake extended from the Alaska Basin west to Lima Reservoir and covered approximately 300 square miles. The large Red Rock Lakes and surrounding marshland are all that remain of the ancient lake today.

The spring-fed Refuge ponds are all man-made or in some way artificially altered. MacDonald Pond resulted from the impoundment of Elk Creek Springs and the effluent from Elk Lake. The earthen dam and control structure were constructed in 1953. Culver Pond was created by the impoundment of Culver Springs in 1959. Both the MacDonald and Culver impoundments were built to expand the preexisting ponds which were impounded by the original settlers of the area. Widgeon Pond, created in 1964, represents the newest of the Refuge ponds and was formed by the impoundment of Picnic Creek.

Chapter III

METHODS AND PROCEDURES

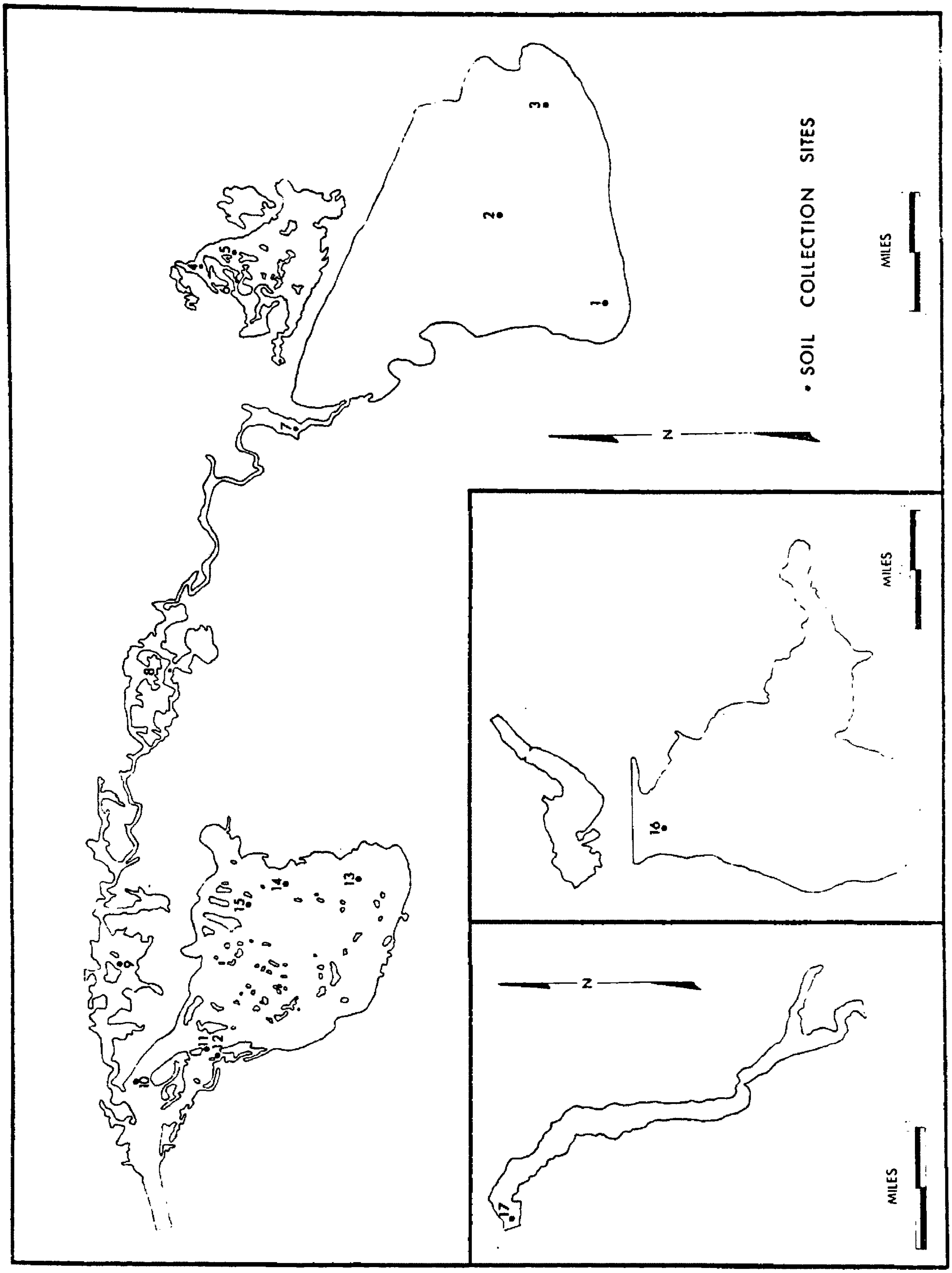
Soils

In June, 1971, 36 upland soil samples were collected at the sites indicated in Figure 3. These sites were selectively chosen to represent each of the 11 soil associations present on the Refuge. In addition, 17 soil samples were collected from the lake bottoms of the Refuge at the sites indicated in Figure 4. Chemical and textural analyses of upland and lake-bottom soils were conducted by the Plant and Soil Science Laboratory of Montana State University, Bozeman.

Available soil calcium, magnesium, potassium, and sodium were determined using the standard 1 N ammonium acetate (NH_4OAc) extraction procedure at pH 7.0. Available iron and manganese were determined by the DTPA-TEA (Diethylene triamine pentaacetic acid, Triethanolamine) extraction method. Measurements for these six elements were made on the Perkins-Elmer model 290-B atomic absorption spectrophotometer.

Available phosphorus was determined using the ammonium fluoride (NH_4F)-hydrochloric acid (HCl) extraction procedure. Percent organic matter was determined using the 1 N potassium

Figure 4. Soil collection sites.



• SOIL COLLECTION SITES
MILES
N
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
MILES
16
N
MILES
17

dichromate ($K_2Cr_2O_7$) oxidation method. Both of these parameters were measured on the Spectronic 20 colorimeter.

Soil pH was measured with the Beckman-Zeromatic II pH meter. Salinity was measured by a Beckman salinity meter.

Mechanical analysis of the soil was conducted using the Bouyoucos method. Textural classes for the soil samples were derived from the standard textural triangles for soils (Buckman and Brady 1960).

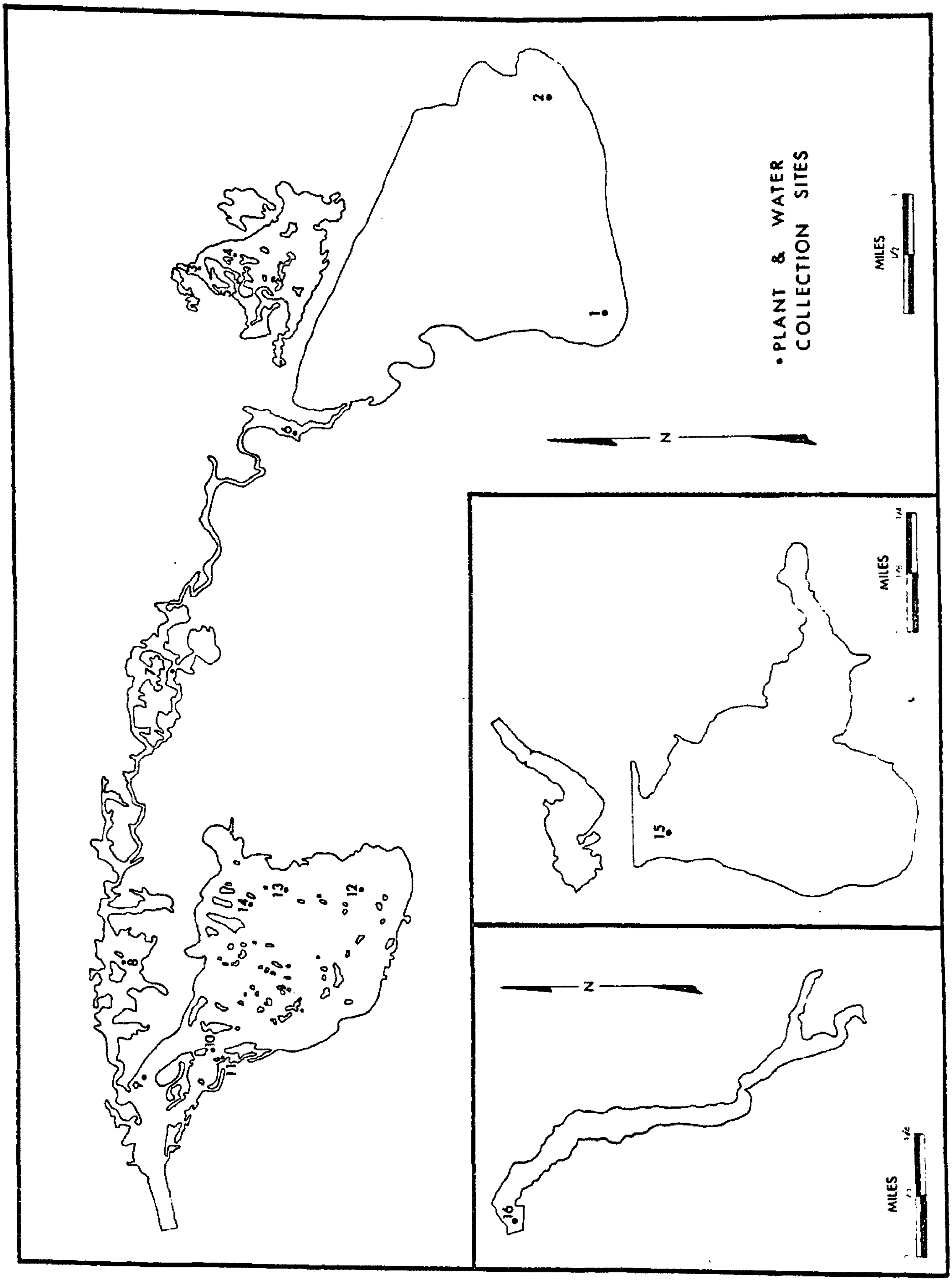
Water

Chemistry. Much of the field work conducted during the 1972 season centered around the collection and analysis of water samples. Sixteen collection sites (Fig. 5) were selectively chosen in the seven major water bodies of the Refuge. These sites correspond to those areas where lake bottom soil samples were collected and where plant growth of selected macrophyte species was monitored.

Water collections were made on a biweekly basis from late May to early September. An additional collection was made in October to determine the affects of autumnal circulation on the water chemistry of the Refuge lakes.

Collections were made at approximately the same time each day to minimize variation due to diel fluctuations. There is no doubt

Figure 5. Plant and water collection sites.


• PLANT & WATER
COLLECTION SITES
MILES
1/2
MILES
1/4
MILES
1/4
N
N
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

that some variation is attributable to daily changes in cloud cover and the incidence of the sun, especially in the dissolved gases.

Ten parameters of water chemistry were selectively chosen on the basis of their importance to general biological processes. Alkalinity, pH, dissolved oxygen, and carbon dioxide determinations were made immediately after collection and the remainder of the measurements were made within 36 hours of collection time.

Hydrogen ion concentrations were determined with a Beckman pH meter. All other measurements were made with the Hach Model DR-EL portable water analysis laboratory.

Alkalinity was determined by the standard sulfuric acid titration method using brom cresol green-methyl red indicator solution for bicarbonate ions and phenolphthalein indicator solution for carbonate ions. Calcium and total hardness concentrations were determined by the EDTA method. Dissolved oxygen was determined by a modified Azide-Winkler method with PAO solution being used in the drop count titration procedure. The 1, 10-phenanthroline method was used to determine soluble iron and the turbidimetric method was used to determine sulfate concentrations. Phosphate was determined using the ammonium molybdate reagent method. A modified diazotization (1-naphthylamine-sulfanilic acid) method was used to determine inorganic nitrogen. Finally, carbon dioxide was determined by titration with sodium hydroxide with phenolphthalein solution as the indicator.

Streamflow. The precipitation pattern for the Refuge was highlighted in Figure 1. In an effort to quantify the relationship between precipitation patterns and water receipts into the marsh, influent rates during the 1971 season were monitored on 19 feeder streams, and effluent was monitored at the control structure at the west Refuge boundary.

Stream discharge was measured as cubic feet per second (cfs) where discharge equals stream velocity times the cross-sectional area of the stream. The velocity was determined by a Price Current Meter and the depth and width of the stream determined by a yardstick (depth) and a 50-foot measuring tape (width).

Lakes

Morphometry. Morphometric measurements of the Refuge lakes follow the procedures outlined by Reid (1961) and Hutchinson (1957). Lake area was determined by planimetry from aerial photographs of the Refuge. Lake length, defined as the shortest distance through the water or on the water surface between the most distant points on the lake shore (Hutchinson 1957), was determined by direct measurement from Refuge maps. Lake breadth is defined as the length of a line from shore to shore cutting the line delineating lake length at right angles at any point, and was measured directly from Refuge maps.

Length of shoreline was determined by means of a rotometer. Shoreline development was derived as the ratio of the shoreline length to the circumference of a circle having the same area as the lake (Reid 1961). Average and maximum depths were determined from 1,126 measurements taken on the Refuge during 1971 when the submerged macrophytes were being mapped.

Optical properties. Water color was measured using the standard U.S. Geological Survey platinum-cobalt units, determined by the Hach Model DR-EL portable water analysis laboratory. Due to the extreme clarity and shallowness of the lakes, the standard Secchi-disc, transparency-measurement could not be taken.

Turbidity measured in Jackson Turbidity Units (JTU's) was determined by spectrophotometric methods using a formazin standard. The Hach laboratory was used in this determination.

Fluctuation. Steel posts were permanently fixed in each lake to act as lake level reference points. Changes in each lake level were measured directly from the reference posts where baseline levels were clearly marked in early spring.

Vegetation

Geography. Materials used in the mapping of submerged macrophytes included an airthrust boat, 10 1-gallon plastic jugs used as floating markers, stopwatch, maps, a surveyor's rod to measure water depth and a line-of-sight compass.

A total of 1,126 mapping plots were taken on the Refuge. The number of sample plots taken in each lake ranged from 20 to 290, depending on its size.

Transect lines were randomly located on maps using a baseline triangulation method with a line-of-sight compass, using known landmarks as reference points. Ten samples were taken on each transect. Due to the complexity of islands and bays in the River Marsh, Swan Lake and parts of Lower Lake, this technique was not feasible. In those areas, sample plots were selectively chosen from aerial photographs to give the best possible coverage of the lakes.

The airthrust boat was driven along a transect line while the engine was operating at a constant R.P.M. Plastic jugs with anchors were tossed over the side of the boat at 15 second intervals, marking each sample site.

A sample plot consisted of 1 square meter adjacent to the floating marker. The portion of the sample that contained vegetation was ocularly estimated to the nearest 5 percent. This estimation is synonymous with the term "cover" as described by Shimwell (1971) and represents the percentage of the lake bottom within the 1 square meter plot that is obscured by vegetation.

Where visibility was obscured by turbid waters, plants were dredged up with a pair of sampling tongs. Adjustments were made to equate the two sampling procedures.

Species composition within each sample was ocularly estimated to the nearest 5 percent and recorded on species index cards. Species which comprised less than 5 percent of the vegetation within the sample plot were recorded as a "trace" on the index cards.

The location of sample plots in the field were marked on enlarged aerial photo maps and used as master maps from which species distribution maps were made.

Zonation. Lake depth was recorded at each of the 1,126 mapping plots. The zonation of each species according to lake depth was determined by averaging depths for all the sample plots in which a particular plant species occured. The minimum and maximum recorded depths for each plant species constituted zonational range.

Spatial distribution. The classification of the submerged macrophytes of the Refuge according to their horizontal distribution or "pattern" follows the scheme devised by Shimwell (1971). General field observations on the growth habits of each species were used to place each plant in its proper category.

Classification of submerged macrophytes by stratification (vertical distribution) was determined by measuring plant height with a metal surveyor's rod. Plant height was measured on mature plants to avoid discrepancies caused by short, immature plants.

Coverage. The percent coverage of each plant species within the 1,126 mapping plots was ocularly estimated to the nearest 5 percent with records being kept for trace species. From these values, plant frequency, species composition, percentage of the lake bottom vegetated, and acreage cover/species were computed.

Frequency represents the percentage of the samples in which a species occurred.

$$\text{Frequency} = \frac{\text{no. samples containing spp.}}{\text{total no. samples in lake}} \times 100$$

Species composition was based on coverage estimates in each observation.

$$\%\ \text{Spp. Comp.} = \frac{\text{sum of \% coverage of 1 spp. in lake}}{\text{sum of \% coverage of all spp. in lake}} \times 100$$

The percentage of the lake bottom vegetated was computed by the following formula:

$$\%\ \text{Bottom Veg.} = \frac{\text{sum of \% coverage of all samples}}{\text{total no. of samples in lake}} \times 100$$

Acreage cover/species was determined as follows:

$$\text{Acreage cover/spp.} = \%\ \text{bottom veg.} \times \%\ \text{species comp.}$$

Association. Species composition data collected in the 1,126 mapping plots were used to determine the submerged macrophyte sociology. Indices of joint species occurrence were calculated using the method described by Swindale and Curtis (1957). The joint index is equal to the number of quadrats of occurrence of the less common species. The occurrence of the less common species was used in order to avoid a low joint occurrence index for two species merely because one occurred infrequently (Swindale and Curtis 1957).

Axis construction and ordination procedures follow the outline presented by Bray and Curtis (1957).

Environmental analysis. Environmental data for each plant species and each lake were averaged following Beals (1968), and differences among the species and lakes were determined by statistical analysis using the U test (Mann and Whitney 1947). Tests were conducted at significance levels of .10, .05 and .01.

Nutritional analysis. Nutrient analyses of submerged macrophytes were conducted by the Chemistry Station at Montana State University, Bozeman. Analytical procedures follow the Official Methods of Analysis of the Association of Official Analytical Chemists (1965).

Crude fat was determined by the anhydrous ether extraction method. Percent moisture was determined by oven drying plant matter at 95-100°C for 5 hours at pressures not over 100 mm Hg. Crude fiber was measured as the loss in biomass following ignition of dried plant residue after digestion of the original sample with 1.25% H_2SO_4 and 1.25% NaOH. Plant protein was determined by the Kjeldahl method. Phosphorus was determined by the photometric-ammonium molybdate-hydroquinone-sodium sulfite method. Calcium was determined by ignition of plant matter at 500-550°C, precipitation with $(NH_4)_2C_2O_4$ and titration with 0.05 N $KMnO_4$.

Growth rates and phenology. Because of the large number of submerged macrophyte species on the Refuge and other time-consuming field commitments, growth rates and phenology were monitored on only eight species. These species were selectively chosen because of their general Refuge-wide abundance. Monitoring sites were synonymous with the water and soil collection sites in Figure 4.

Growth rates were determined by monitoring changes in wet weight biomass throughout the growing season. Plants exhibiting a closed or matted growth form were sampled by 1 $ft.^2$ sampling tongs as described by Webster (1965). Dispersed plants were randomly harvested by clipping at the substrate level. Biomass was determined by a 1,000 gram dietetic scale. Plant phenology was determined by direct field observation.

Since Refuge personnel have been involved annually in the estimation of aquatic plant production on a per acre standing crop basis, productivity estimates were not determined in this investigation to avoid redundancy of field work. No attempts were made to place the monitored stands in enclosures so herbivory by waterfowl affected biomass determinations.

Chapter IV

RESULTS AND DISCUSSION

Geology

The importance of parent geologic material to plant communities is obvious. In aquatic macrophyte communities this importance is twofold. First, the surrounding geologic strata determine, to a great extent, the chemical and physical properties of the soils upon which the plants grow. Second, the parent geologic material manifests many direct chemical and physical influences on the water in which these plants grow.

In terms of stream flow and geologic strata, the watershed of the Refuge is roughly divisible into three areas. First, Culver, Widgeon and MacDonald ponds and Swan Lake derive their water from springs flowing from Precambrian metamorphosed limestones. The carbonate nature of these metamorphics plays an important role in maintaining the high levels of total water hardness and bicarbonate ion alkalinity in these waters. The ground-water filtering properties of this limestone aquifer account for the remarkable clarity of these spring-fed bodies of water.

Second, Upper Lake derives its water from streams originating in Alaska Basin and the Centennial escarpment which are dominated in the area of their headwaters by sedimentary limestones, siltstones, and sandstones. Since the bulk of the influent into this lake is surface run-off, Upper Lake receives large silt loads each year from the easily decomposed sedimentary strata.

Third, Lower Lake receives its water from the Mt. Baldy drainage which is dominated by Tertiary volcanic rocks. Since igneous rocks are generally more resistant to weathering than sedimentary rocks, the influent into Lower Lake carries less silt and consequently the lake is much clearer than Upper Lake where siltation rates are high.

Soils

Soil genesis is dependent upon the interactions of parent material, vegetational and biological influences, climate, topography, and time. As would be expected, the upland soils of the Refuge reflect, to a great extent, the chemical and physical nature of the geologic strata in the nearby Centennial Mountains.

The chemical analyses of the lake-bottom sediments of the Refuge are summarized in Appendix II. A closer look at the chemical nature of these soils will shed light on possible mechanisms regulating the distribution and abundance of aquatic macrophytes.

Classification.

The lake bottom soils belong to the soil order Histosol, i.e., those soils which are high in organic matter. These soils are also loosely known as hydrosoils due to their predominating aquatic environment.

Due to the herbaceous nature of the organic matter in the lake soils, and therefore a lack of woody tissue, these Histosols are more specifically known as muck soils. Muck soils are characterized by the fact that the original plant tissue in the organic matter fraction is indistinguishable.

Texture. Soil texture ranged from silty clay loam to sandy clay loam but most of the lake soils are clays or clay loams. Samples collected from the ponds were noticeably lower in percentage of silt than soils from the marsh proper. The high percentage of silt in the soils of the marsh proper is attributable to the fact that most of the influent entering the marsh is silt-laden runoff water, whereas the ponds are spring fed.

Organic matter. By convention, soils that have an organic matter fraction in excess of 20 percent are termed muck. Several of the analyzed samples fall within or very close to this category. Soils containing 10-15 percent organic matter have their textural classification prefixed by the term "mucky," e.g., mucky loam, mucky clay. Only samples taken in Culver Pond and Upper Lake are excluded from this broad classification.

The high amounts of organic matter found in the lake-bottom soils are associated with the anaerobic conditions which persist there. Under such conditions, annual detritus accumulation usually exceeds the decomposition rates of anaerobic bacteria.

Organic matter imparts many important chemical and physical properties to the lake-bottom soils. The cation exchange capacity of organic matter is quite high (200-400 milliequivalents/ 100 grams of soil) (Hausenbuiller 1972). Since the organic matter holds a large number of ions in available form, Refuge soils are protected from drastic changes in pH; i.e., they are strongly buffered.

Organic matter aids greatly in maintaining and enhancing soil fertility. Organic matter contains 95 percent of total soil nitrogen, 60 percent soil phosphorus, and 80 percent soil sulphur in most soils (Hausenbuiller 1972). Organic matter also serves as a chelating agent for micronutrients thus making them more available in the soil and less likely to leach away.

Finally, organic matter aids in maintaining stable soil structure. Organic colloids act as foci for the flocculation of dispersed soil particles. Thus, the organic nature of the lake-bottom soils is a beneficial characteristic so long as the percentage of organic matter does not reach levels high enough to make the water acid and thus alter the integrity of the submerged macrophyte communities.

Phosphorus. With the close proximity of the phosphate-rich Phosphoria formation in the Centennial Mountains, the Refuge lies in a phosphate-rich watershed. Yet, chemical analysis reveals a paucity of exchangeable phosphorus in the Refuge soils.

The scarcity of available phosphorus is due to its strong tendency to form insoluble compounds with calcium under alkaline conditions. Under the high calcium regime of the Refuge, most phosphorus entering the system from the surrounding watershed is tied up in insoluble mono-, di-, tri-, and octacalcium phosphates, thus making them unavailable to aquatic macrophytes for metabolic processes.

These phosphates will become available only after a reduction in soil pH to a range of 6.0-7.0 where phosphorus availability is maximum. This is unlikely, however, due to the highly buffered conditions of the Refuge soils.

At the pH range of the Refuge soils soluble inorganic phosphorus occurs in two ionic forms: $H_2PO_4^-$ (20 percent of the total P) and $HPO_4^=$ (80 percent of total P) (Hausenbuiller 1972). This soluble phosphorus rarely exceeds concentrations of 1 ppm due to fixation by calcium. Both ionic forms can be utilized by plants.

It is interesting to note that the highest phosphate concentration measured on the Refuge was from a sample collected at the mouth of Odell Creek, which drains the area of the now defunct J. R. Simplot, open-pit phosphate mine. In all likelihood, phosphates are entering the Lower Lake from the area of the mine.

Phosphorus is probably a limiting factor for submerged macrophyte growth. In fact, next to nitrogen, phosphorus is the most widely deficient nutrient in most plant communities (Hausenbuiller 1972).

Calcium. All of the lake soils analyzed are highly calcareous. This high calcium content is associated with the extensive formation of marl ($CaCO_3$) in all the Refuge lakes. In the Centennial Valley most of the calcium is derived from secondary minerals such as calcite and dolomite which are prevalent in the limestones of the Centennial Mountains.

Calcium is an excellent soil buffer. At high calcium levels, the soil pH is held at intermediate levels (7.0-8.2). This situation is desirable due to the fact that other nutrients are usually more available at these intermediate ranges.

Calcium is beneficial in the maintenance of stable soil structure. The presence of calcium enhances the colloidal flocculation of dispersed soil particles, thus reducing turbidity hazards.

In calcareous soils, calcium is abundantly available due to the ease with which lime dissolves in the acidic region of the plant root. Therefore, calcium can not be considered a deficient plant nutrient in the Refuge lakes.

Magnesium. The analyzed lake-bottom soils are high in exchangeable magnesium. The average concentration exceeds 1000 ppm. The large proportion of exchangeable magnesium is due primarily to the large cation exchange capacity of organic soils. The secondary mineral dolomite, which is prevalent in the local limestones, is probably a primary source of magnesium.

Magnesium is less easily leached from the soil than calcium and therefore presents less of a problem to plant nutrition. Since magnesium availability is highest between pH ranges of 6.0-8.5 (Buckman and Brady 1968), this nutrient presents no drastic problem to aquatic macrophytes in terms of deficiencies. Like calcium, magnesium is important in soil flocculation.

Potassium. Potassium is most abundant in minerals such as micas, feldspars, and illite; the latter is common in marine deposits such as those found in the Centennial Mountains. Potassium occurs in lesser concentrations than calcium and magnesium, but is used in greater amounts by plants so it is therefore an important plant nutrient. It is next to nitrogen and phosphorus in being the most commonly deficient soil nutrient.

Lake soils are rich in potassium in comparison to most upland mineral soils. Using the figure of 1.7 percent for the total potassium content of mineral soils (Buckman and Brady 1968), and availability of 1 percent, the average available potassium concentration for mineral soils is 170 ppm. All Refuge soils exceeded this concentration and many contained twice this average amount.

The high amounts of potassium in the lake soils appear to be due to three phenomena. First, since 90 percent of the available potassium is associated with soil colloids, it appears that these high concentrations can be attributable to the high colloidal fraction of muck soils. Second, lime is capable of fixing potassium, thereby reducing leaching losses. Third, potassium is most available at pH regimes greater than 6.0, which would include all of the Refuge lake bottoms. The high concentrations of potassium in the lake soils would indicate that this nutrient is not limiting or deficient.

Iron. Iron is the most abundant micronutrient found in soils with total concentrations often reaching 5 percent of the soil content. As with other nutrients, availability is the critical factor regarding soil iron.

Iron in the soil occurs in two valence states, the oxidized ferric ion (Fe^{+++}) and the reduced ferrous ion (Fe^{++}); the latter is the more soluble of the two. Under well oxidized conditions, the ferric ion is prevalent in the soils and lends the typical red, yellow, or reddish-brown color to the soil. Conversely, under a waterlogged and anaerobic regime, the reduced ferrous ion prevails and lends a blue or grayish color to the soil. Both the oxidized and reduced conditions were found in the soils of the Refuge lakes.

Under conditions of high organic matter, such as those found in the muck soils of the Refuge lakes, much of the available soil iron becomes chelated, i. e., attached to organic anions. Chelated iron remains in solution at higher pH than do inorganic ionic forms and are therefore held in available form for plant nutrition.

Data presented by Bear (1964) and Cook and Powers (1958) indicate that extractable iron from freely-drained, upland, surface-soils occurs in the range of 20-50 ppm. In every case, iron concentrations in lake soils of the Refuge exceeded the magnitude of these figures by as much as three times. The high iron concentration of the lakes can be explained by two interacting phenomena, prevalent iron chelation in muck soils, and the reduction of iron to the soluble ferrous state under the waterlogged, anaerobic environment of the lake bottom. These phenomena are supported by data collected by Cook and Powers (1958) who showed that available iron concentrations in upland soils increased as much as six times after being inundated by man-made reservoirs and stock ponds.

Manganese. Manganese occurs as the oxidized and insoluble manganic ion (Mn^{+4}) or the reduced and soluble manganous ion (Mn^{+2}). The amount of available manganese in the soil is dependent upon several interacting phenomena.

As pH increases, manganese availability decreases, especially when pH exceeds 7.0. Under these alkaline conditions, the manganic ion prevails and is readily precipitated as highly insoluble MnO_2. Manganese deficiencies would be expected under the alkaline conditions of the lake soils; however, manganese is strongly chelated to organic matter and it is therefore held in available form rather than being precipitated in unavailable forms.

It is therefore not surprising that the lake soils are not deficient in manganese. Manganese concentrations of lake soils (26-27 ppm) fall exactly within the range which Bear (1964) describes as an average figure for "healthy" soils.

Salinity. Lake soils ranged in salinity from 1.5 to 4.0 mmhos which would classify them as only moderately salty. Since the lake soils are not exceedingly salty and due to the abundance of diluting water, salinity is not a critical factor in the lake soils and is not of sufficient magnitude to be detrimental to the aquatic plant communities.

Sodium. The lake soils are low in sodium with most of the samples falling below 1.0 milliequivalent (230 ppm). Under such conditions, sodium is not critical in terms of limiting plant distribution.

General characteristics. The analyzed lake soils belong to the soil order Histosol which are typically high in organic matter. Specifically, they are muck soils, i.e., soils in which the original plant tissue in the organic matter fraction is indistinguishable. Soil texture ranges from silty clay loam to sandy clay loam but most of the lake soils are clays or clay loams.

Lake soils are highly calcareous and moderately alkaline. These soils are surprisingly rich in magnesium, potassium, iron, and calcium. Available phosphorus is quite deficient in these soils, but this phenomenon is not unique to the Refuge area. Nitrogen availability was not measured, but due to the high organic fraction in the soil, its high concentration can be predicted. Manganese is neither deficient nor overly abundant but well within the range of "healthy" soils. Finally, lake soils are moderately saline and low in sodium, neither of which present any drastic problems in limiting aquatic plant species.

Watershed

Despite the remoteness of the Centennial Valley and its isolation from large population centers, the Refuge watershed is not undisturbed.

Dirt roads have been cut in the Valley floor along the north, south, and east sides of the Refuge. A single east-west road bisects the floor of Alaska Basin.

The only recent, large-scale mining activity in the area was conducted in the Odell Creek drainage (Section 33, R1W, T14S) by the J. R. Simplot Company of Idaho. In 1958, the Simplot Company began mining phosphate rock from the Permian Phosphoria formation by open-pit methods (Cressman and Swanson 1960). The operation was not continued in 1959.

Clear-cut logging and the numerous skid trails and logging roads associated with them occur in Sections 19 and 20 (R2W, T14S) south of Lower Lake. Clear cuts also occur in Sections 21, 22, 28, and 29 (R1E, T14S) in the Alaska Basin drainage. In addition to these man-made disturbances, natural catastrophes, in the form of massive rock slides and avalanches, are frequent in Sections 25, 26, 27, 28, and 29 (R1W, T14S) south of Upper Lake. The effect of all these disturbances on stream flow and the physical and chemical properties of Refuge waters is unknown, but certainly in some areas they have contributed to the siltation of local streams.

The possibility of future disturbance in the Centennial Valley is uncertain, however, Scholten (1967) surmised that the area could conceivably have a potential for oil development.

Stream Flow

Appendix III summarizes the stream discharge data for the 1971 season. The general pattern is a decline in total influent and effluent during the summer months from the June maximum (Fig. 6). This is to be expected considering the fact that June is the wettest month of the year and that the snow fields in the adjacent mountains are constantly diminishing throughout the summer months.

A plethora of problems is encountered in trying to accurately quantify the magnitude of influent and effluent on the Refuge. Springs in the area are extremely abundant and many of these are inaccessible for measurement. In addition, there are undoubtedly submerged springs that feed the lakes directly and are unmeasurable. Direct rainfall onto the lakes, accelerated evaporation rates during the summer, and ground water movement off the Refuge also add to the problems in deriving accurate estimates. Other field commitments during the 1972 season preempted the collection of additional stream-flow data.

Lakes

Morphology. The relative age of a lake can be determined by its average depth and shoreline development (Table 2). As a lake ages, sediments from the surrounding watershed begin to settle in the deeper portions of the lake and fill the lake basin. As the lake

Figure 6. Streamflow patterns of the study area.

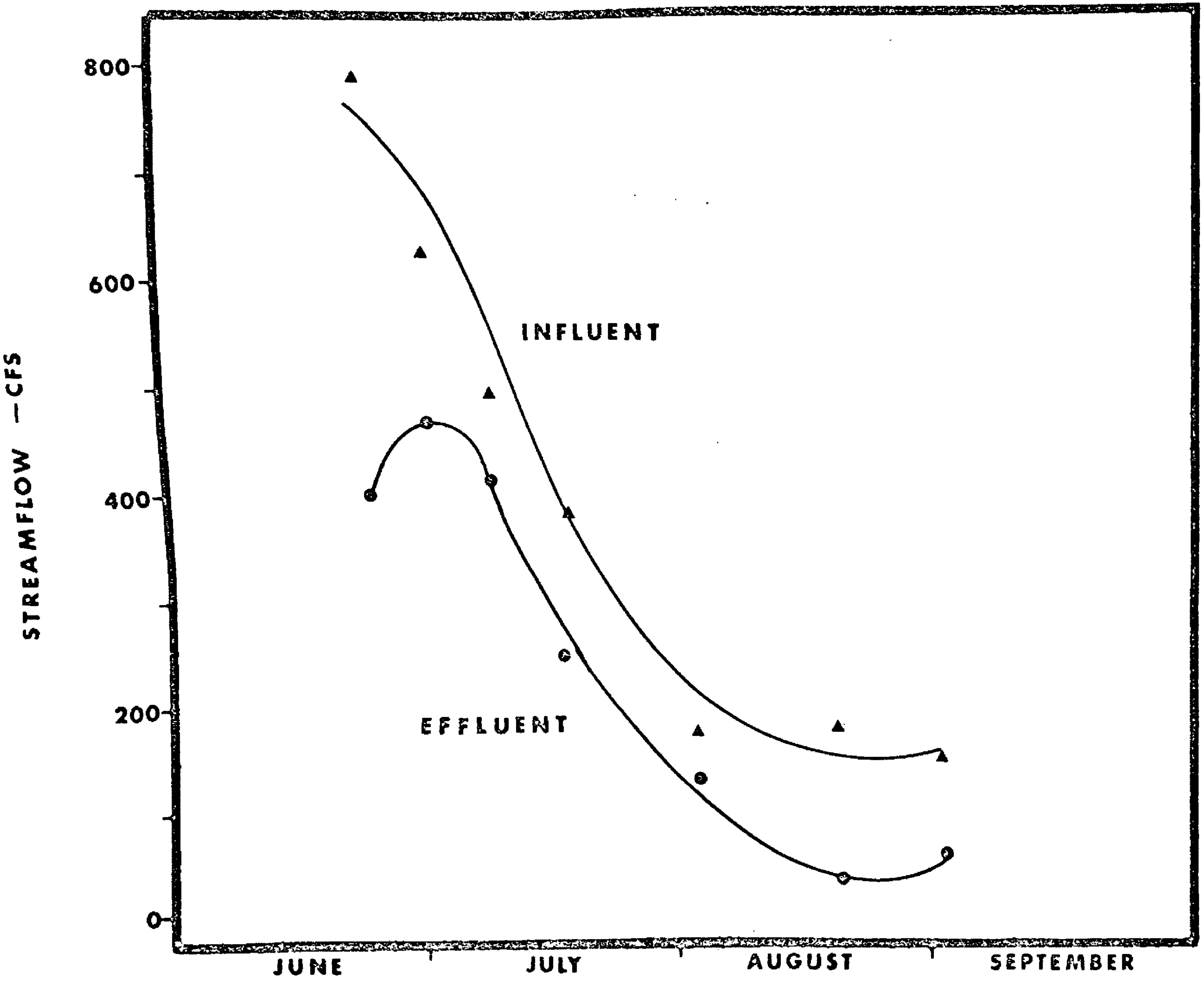

INFLUENT
EFFLUENT
STREAMFLOW —CFS
800
600
400
200
0
JUNE
JULY
AUGUST
SEPTEMBER

Table 2

Lake Morphology

Area	Miles			Depth (Ft.)		Shoreline Development
	Length	Width	Shoreline	Average	Maximum	
River Marsh	8.75	.25	79.7	2.2	8.1	34.5
Swan Lake	1.50	.94	25.6	2.1	2.8	9.1
Lower Lake	3.44	1.89	36.9	3.2	5.6	6.7
Culver Pond	.93	.04	2.4	2.7	5.0	3.3
MacDonald Pond	.40	.13	2.7	2.7	4.8	2.3
Widgeon Pond	.78	.63	2.7	5.2	8.8	1.7
Upper Lake	3.69	2.25	12.2	4.7	7.1	1.6

becomes shallower, islands of emergent vegetation (Scirpus and Typha) begin to appear and encroach from the shoreline. These combined forces of island formation and shoreline encroachment act simultaneously to increase the shoreline development of the lake. Thus, shallow depths and highly developed shorelines are indicators of lake age.

The extensive shoreline development in the River Marsh is due to the meandering nature of the Red Rock River. Drainages characterized by extensive meanders represent very old and mature systems (Hutchinson 1957). Succession is much further advanced in the River Marsh than the other lakes in the marsh proper.

Swan and Lower lakes represent intermediate stages in lake succession. Here shoreline development is moderate, islands abundant, and lake depth shallow.

Upper Lake represents the successionally youngest lake in the marsh proper. Here islands are nonexistent, shoreline development is minimal, and lake waters deep. The reason for the lag of Upper Lake is due to the fact that this area was probably the lowest point in the basin block depression since it is nearest the Centennial fault, thus making it the deepest part of the ancient glacial lake.

Brower (1897) presents evidence to support this theory by recording depth readings for Upper Lake of 10, 15, 20, and 25 feet. This information clearly indicates that Upper Lake is rapidly filling in, at least 18 feet in the last 75 years in some areas. As the Upper Lake basin continues to fill in, its slope will become more gradual and the rate of filling should decline.

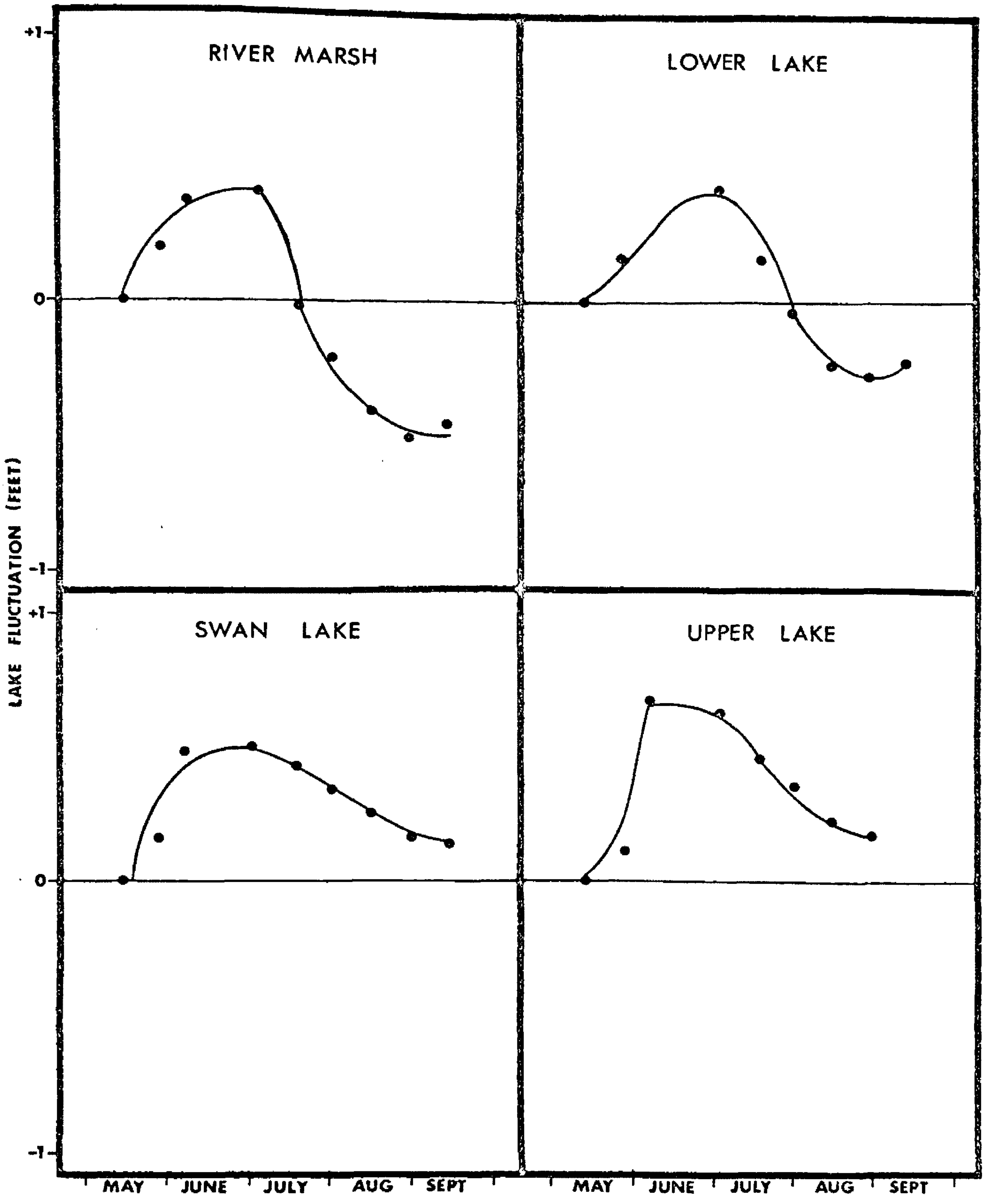
It is interesting to note that the maximum depth recorded by Brower (1897) for Lower Lake was 6 feet, yet 75 years later the maximum depth recorded was still 5.6 feet. These differences in filling rates are probably attributable to differences in the geological material of the respective watersheds of Upper and Lower Lake.

It is not surprising that the successional development of the ponds is relatively young. The minimal shoreline development and deep waters are to be expected in light of their recent construction.

Fluctuation. The magnitude of fluctuation varied from lake-to-lake depending, to a great extent, on the proximity of feeder streams and the general shape of the lake basin (Fig. 7). Fluctuation in the ponds was not as extensive as in the marsh proper and, due to the interference of artificial control structures, measurements were discontinued.

The water level in the marsh proper rises from May to July and begins to recede thereafter. Considering the precipitation pattern of the Refuge (Fig. 1) this would be expected. Upper Lake exhibited the greatest fluctuation, probably due to the many streams that feed directly into it.

Figure 7. Lake level fluctuations, 1972.


RIVER MARSH
LOWER LAKE
SWAN LAKE
UPPER LAKE
LAKE FLUCTUATION (FEET)
+1
0
-1
+1
0
-1
MAY
JUNE
JULY
AUG
SEPT
MAY
JUNE
JULY
AUG
SEPT

Thermal properties. Measurements of thermal stratification beyond a brief preliminary survey were not taken. Perhaps this was an oversight, but other field commitments did not warrant extensive investigation in this area.

The Refuge lakes are dimictic, i. e., they exhibit a vernal and autumnal turnover or "mixis." In view of the fact that the Refuge lakes are relatively shallow, some skepticism might arise regarding the probability of summer stratification; however, Cook and Powers (1958) demonstrated that summer stratification in shallow waters is a real phenomenon and occurred in waters less than 3 feet deep.

The formation of summer stratification resulted in the depletion of dissolved oxygen reserves in the deeper areas of the marsh, thus resulting in a reducing environment. This phenomenon was evidenced by extensive areas of blue-black soils indicating that iron was present in its reduced ferrous state. In the shallow shoreline areas water was isothermal and lake bottoms oxidized.

Water

Light transmission. Light transmission in the water was not measured. Since submerged macrophytes grew in even the deepest areas of the lakes, the entire marsh system can be considered a euphotic zone, i. e., light effective in photosynthesis reaches all depths.

Color. Refuge waters are remarkably clear and there were no instances where the view of the entire lake bottom was obscured due to discoloration. Water color ranged from 0 (perfectly clear and uncolored) in the Refuge ponds to a maximum of 240 units in Swan Lake.

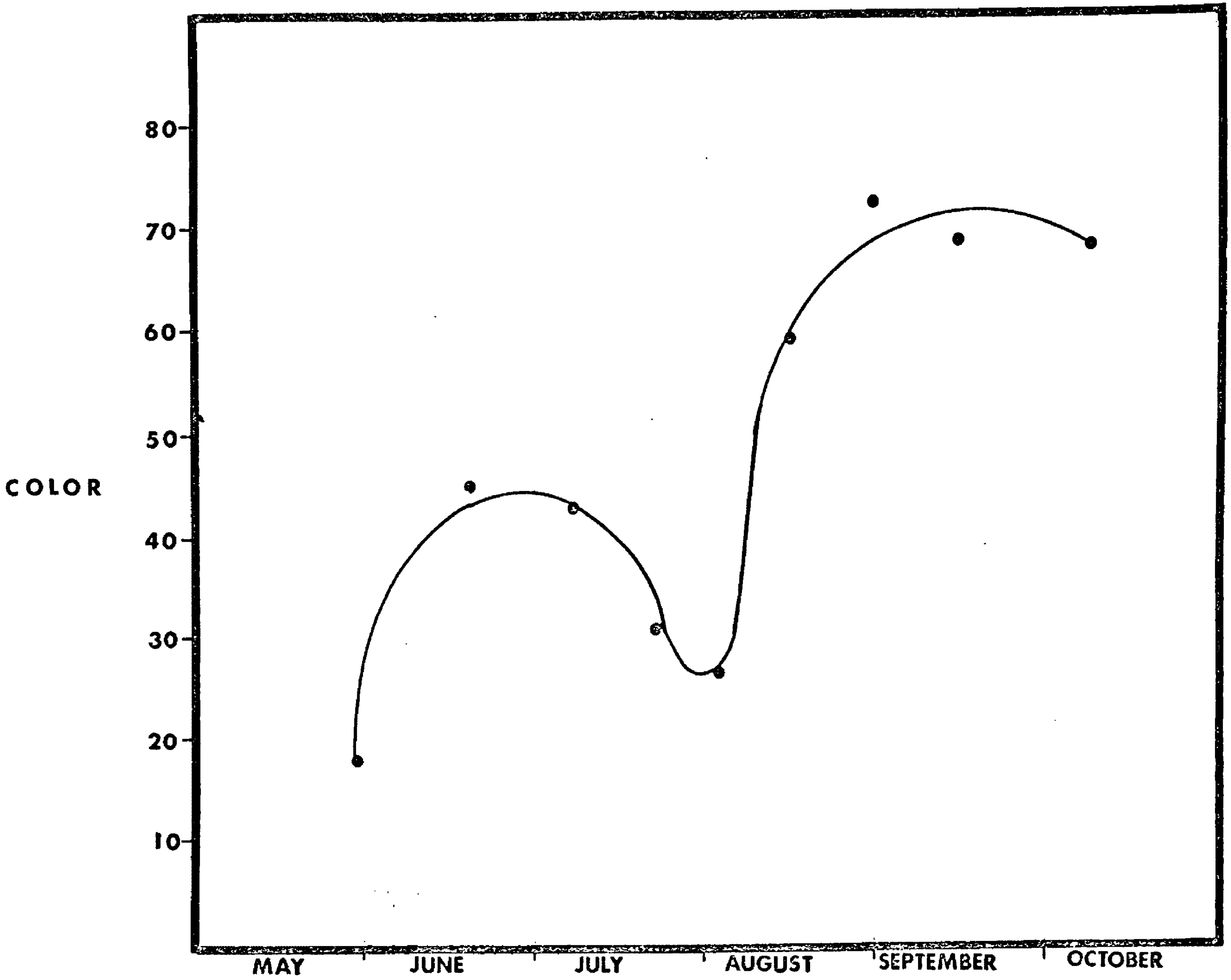
There was a general decline in water color during the growing season (May to August) followed by a rapid increase (Fig. 8). Since dissolved organic matter is the prime determinant of water color (Hutchinson 1957), it is suspected that the decline during the growing season is due to the bacterial breakdown and assimilation of the organic matter that accumulated during the winter months. With the termination of the growing season in August, wide-scale decomposition of plant and animal biomass occurs, resulting in the increased discoloration of the water in late summer.

In general, lake water became yellow or tea-brown in late season. This phenomenon was evident throughout the marsh proper, and especially so in Swan Lake.

Discoloration of lake water was greatest in the small sheltered bays that were little disturbed by wave action and currents. These bays are usually surrounded on three sides by Carex stands and their associated peat soils. Organic extracts from these peat soils stain the water.

The yellow color of the water can possibly be due to two factors. Hutchinson (1957) notes that increased populations of diatoms

Figure 8. Seasonal variation in water color.


COLOR
80
70
60
50
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

can impart a yellow color to lake waters. On the other hand, Shapiro (1957) attributes yellow color to carboxylic acids in solution. The latter theory seems more probable due to the fact that the yellow waters were most commonly found adjacent to Carex stands, a likely source of these acids following the decomposition of peat.

Turbidity. Turbidity of Refuge lakes was directly related to the size of the water body. Large water bodies such as Upper Lake, where windsweep and wave action are intense, were always more turbid than the smaller ponds and bays of the marsh that were largely protected from wind and wave disturbance. Without exception, on windy days Upper Lake was the most turbid water body on the Refuge, often becoming milky white.

Turbidity increased throughout the summer season (Fig. 9). The duration and intensity of wind in the Centennial Valley generally increases throughout the summer, with August and September being notably windy months. Thus, increased wind disturbance and its associated wave action, added to the disturbance caused by increasing populations of feeding waterfowl during fall migration, probably accounts for the late season increase in turbidity.

Hydrogen. The pH of lake waters increased from late spring to early August and then declined in late summer (Fig. 10). This pulse is caused by the photosynthetic activities of the marsh vegetation.

Figure 9. Seasonal variation in water turbidity.

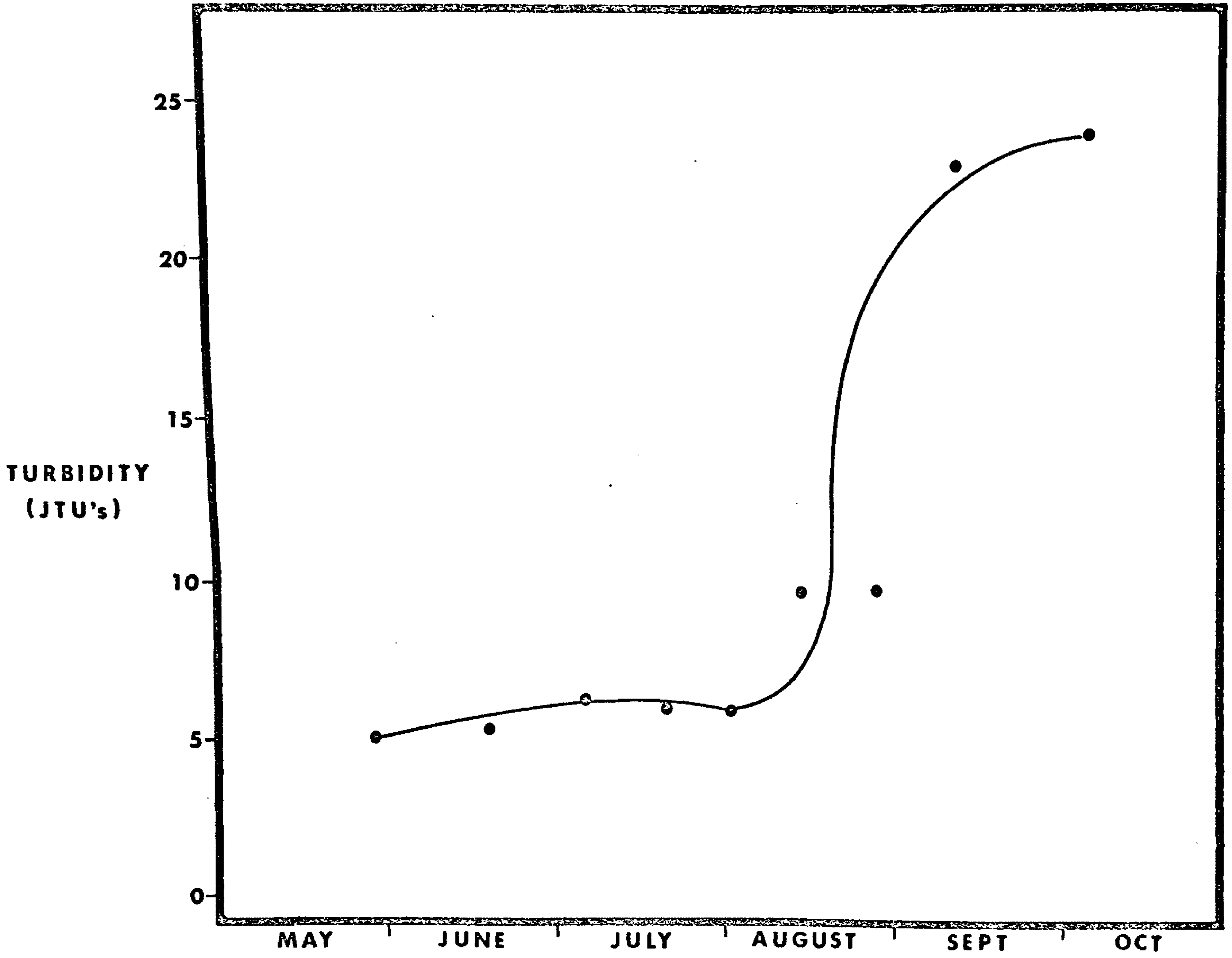
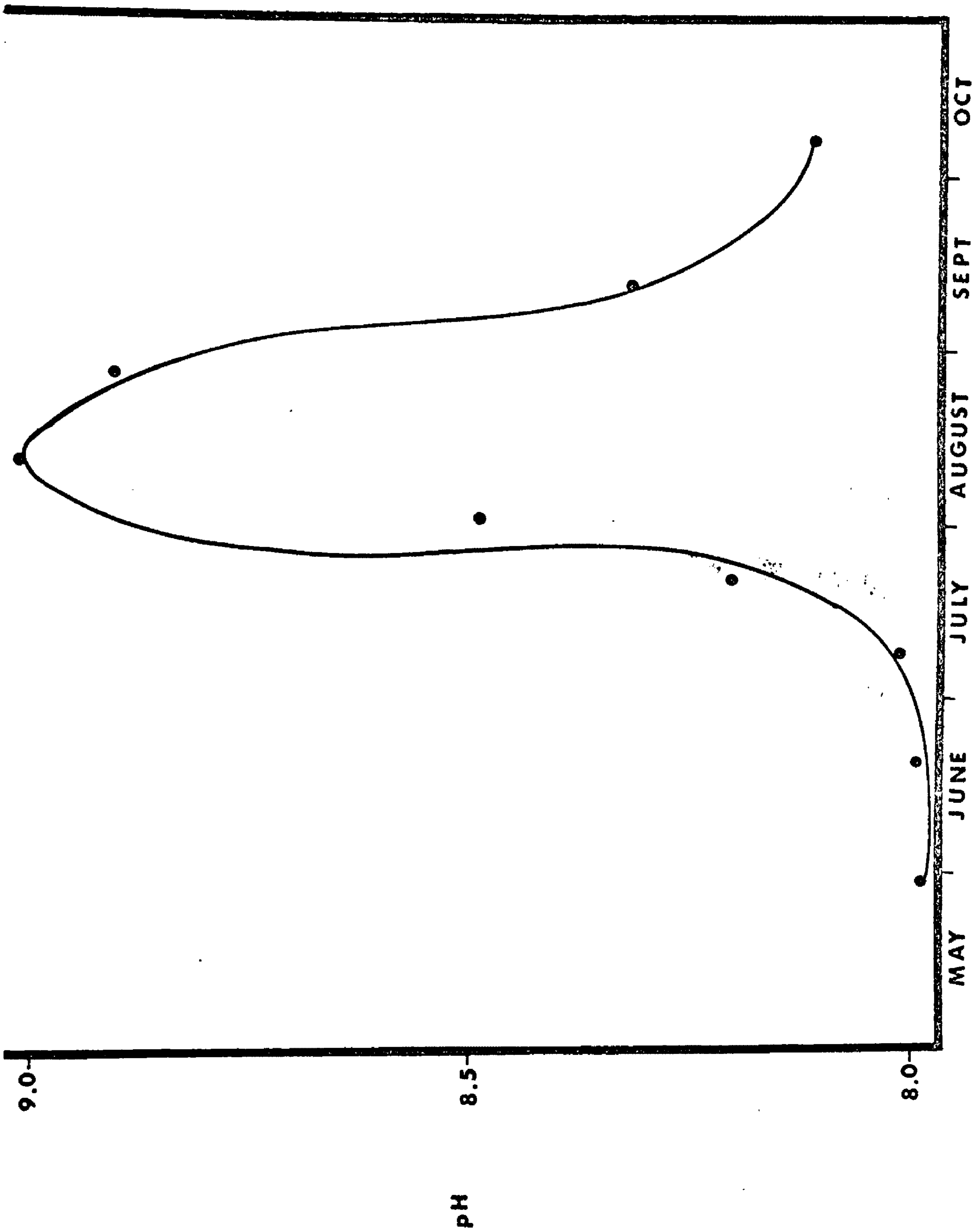

TURBIDITY
(JTU's)
25
20
15
10
5
0
MAY
JUNE
JULY
AUGUST
SEPT
OCT

Figure 10. Seasonal variation in water pH.


pH
9.0
8.5
8.0
MAY
JUNE
JULY
AUGUST
SEPT
OCT

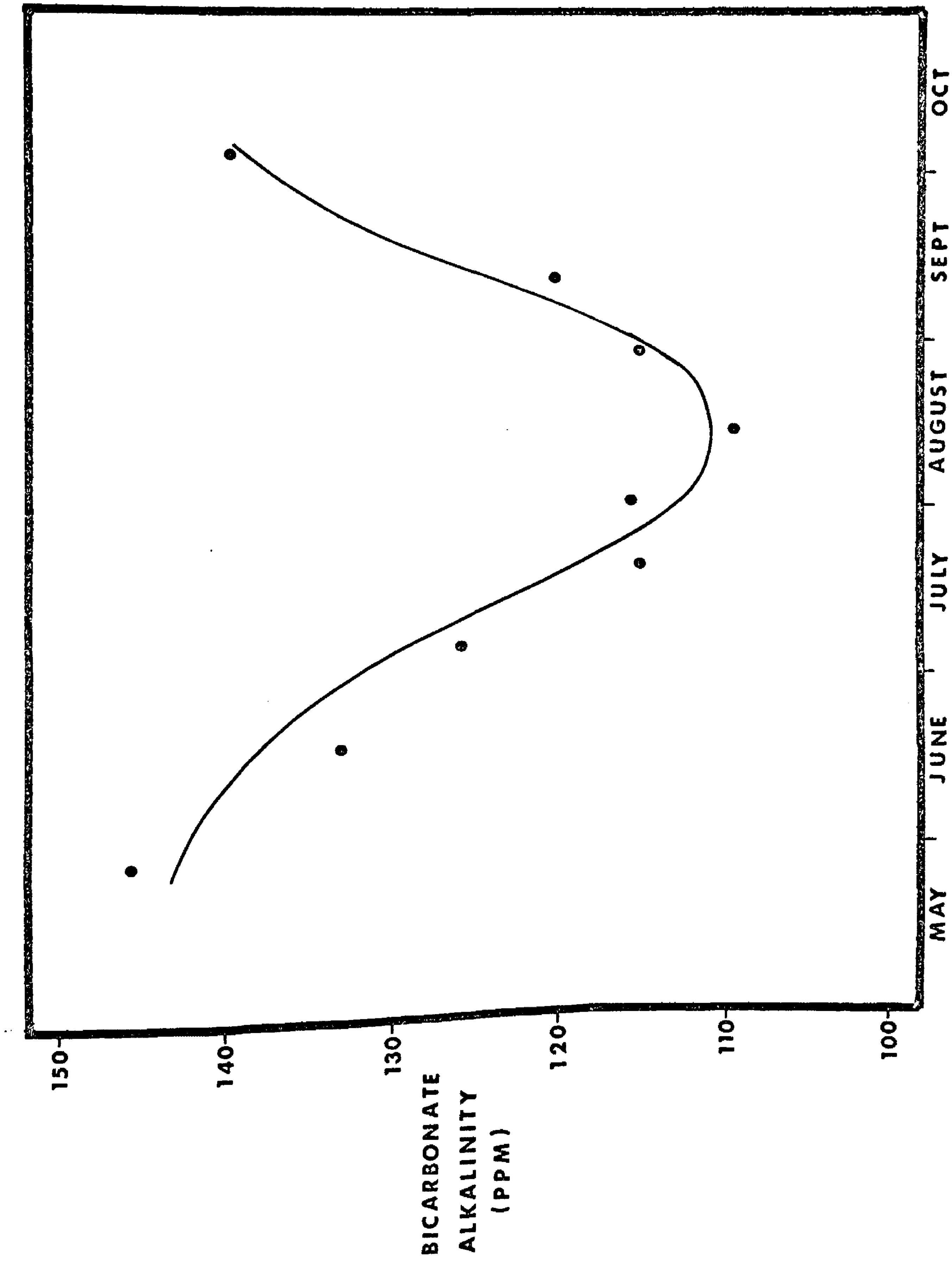
Photosynthetic rates increase from early spring to midsummer in proportion to the increase in plant biomass (Sculthrope 1967). During the photosynthetic process, marsh vegetation removes dissolved CO_2 from the water, causing an increase in pH. When the general growing season ends in August, photosynthesis shuts down and the dissolved CO_2 concentration in the water increases, thus driving the pH of the water down.

Refuge lakes can be classified as slightly alkaline to strongly alkaline depending upon the location and time of year. In no instances were acid waters detected; however, water samples taken in sheltered bays that were closely associated with the acidic peat soils of the _Carex_ communities were circum-neutral (pH 7.1-7.2). The macrophytic alga _Nitella flexilis_ predominated in these areas.

Alkalinity. Using the scheme described by Moyle and Hotchkiss (1945), the Refuge lakes are classified as having hard carbonate waters (alkalinity 40-200 ppm). Within the pH regime of the Refuge waters (7.0-9.0), the bulk of the alkalinity is attributable to bicarbonate ions in solution (Reid 1961).

Photosynthetic demands of the marsh vegetation depleted free dissolved CO_2 reserves in the water during the summer, thus increasing the pH of the water. As pH increased above 8.0, bicarbonate concentrations began to decline (Fig. 11) due to the

Figure 11. Seasonal variation in bicarbonate alkalinity.


BICARBONATE
ALKALINITY
(PPM)
150
140
130
120
110
100
MAY
JUNE
JULY
AUGUST
SEPT
OCT

dissociation of these ions to carbonate and hydrogen ions.

The frequency of carbonate alkalinity measurements during the season varied with changes in the pH regime (Fig. 12). Carbonate ion concentrations were barely detectable in the pH range of 8.4-8.6 and reached a maximum concentration of 50 ppm in areas where pH ranged from 9.6-9.8.

Following the termination of the growing season in August, free CO_2 concentrations increased and pH declined. This change is reflected by the decline in carbonate ion concentrations in late summer (Fig. 12) and an increase in bicarbonate ion concentrations (Fig. 11).

Free CO_2 varied widely from station-to-station but in general, concentrations were undetectable when pH exceeded 8.0. Under these conditions photosynthesizing plants split off CO_2 from bicarbonate ions which brings about the precipitation of calcium carbonate ($CaCO_3$).

Calcium. Calcium concentrations declined until early August and then increased in late summer (Fig. 13). This phenomenon can be explained in terms of photosynthetic activity of the submerged macrophytes and the subsequent pH changes.

Late spring is characterized by a flourish of macrophyte growth and increased photosynthetic rates. In the photosynthetic process, macrophytes remove dissolved CO_2 from the water thus

Figure 12. Frequency histogram of carbonate alkalinity.

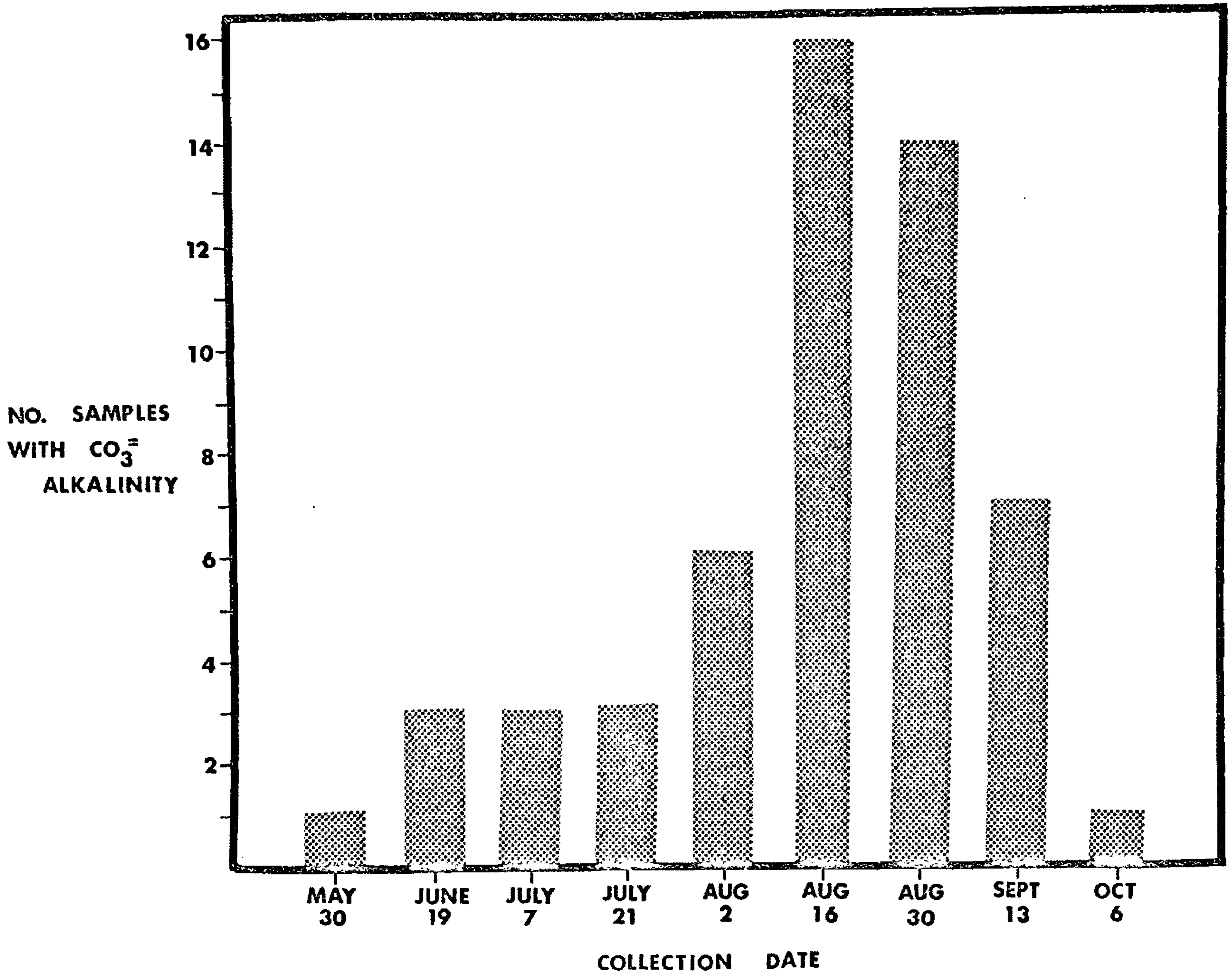

NO. SAMPLES WITH $CO_3^=$ ALKALINITY
16
14
12
10
8
6
4
2
MAY 30
JUNE 19
JULY 7
JULY 21
AUG 2
AUG 16
AUG 30
SEPT 13
OCT 6
COLLECTION DATE

Figure 13. Seasonal variation in soluble calcium.

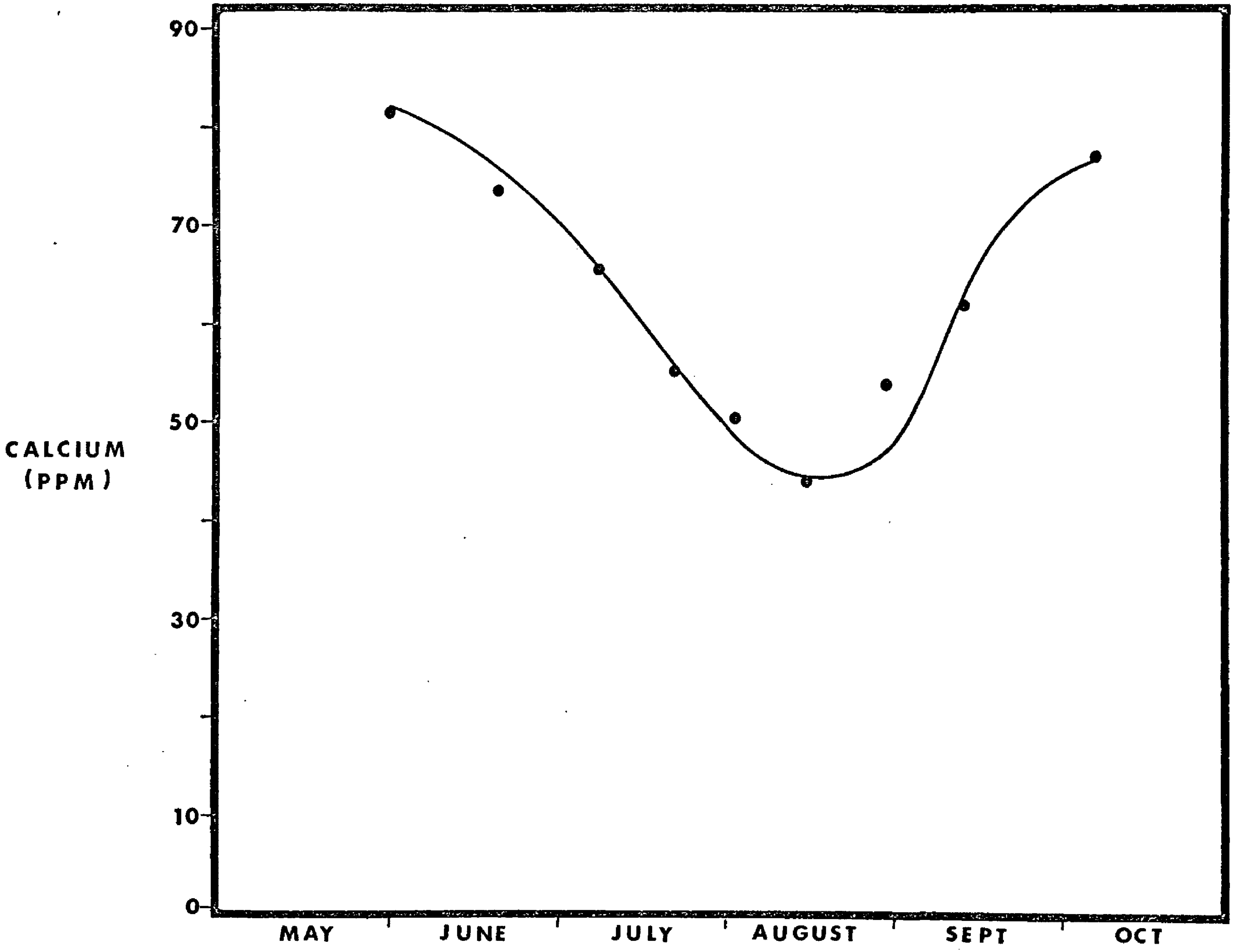
increasing the pH. In some cases where vegetation was abundant and photosynthetic rates were high, pH approached 10.0. Following the removal of free CO_2 from the system, photosynthesizing plants split off CO_2 from bicarbonate ions which brought about the precipitation of calcium carbonate ($CaCO_3$).

In fresh water systems, calcium carbonate precipitate is commonly known as marl or bog lime. This process is quite common in the Refuge lakes and ponds and evidence for its widespread occurrence can be found on such plants as <u>Elodea canadensis</u>, <u>Chara vulgaris</u>, <u>Potamogeton praelongus</u>, and <u>P. richardsonii</u> where marl appears as a white crust on the leaves. The net effect of this process is the removal of soluble calcium from the water during the growing season (Fig. 13).

In early August, the growing season is near completion and rates of photosynthesis begin to decline. Subsequently, CO_2 diffuses into the system from the atmosphere at a greater rate than it is removed by photosynthesis. The addition of CO_2 serves to produce carbonic acid which dissociates and lowers the pH. As the concentration of dissolved CO_2 increases, the solubility of $CaCO_3$ increases. The net effect is that in late summer, as pH drops, calcium that was formerly tied up in marl is released into solution, accounting for the increase in late summer.

Refuge lakes and ponds can be classified as "rich" (Ohle 1934)

Figure 13. Seasonal variation in soluble calcium.


CALCIUM
(PPM)
90
70
50
30
10
0
MAY
JUNE
JULY
AUGUST
SEPT
OCT

in calcium. This is not surprising, in view of the amount of calcium-rich limestone in the watershed.

Total hardness. The total hardness of the lake waters declined from spring to midsummer and then increased in late summer (Fig. 14). Since this parameter is a measure of calcium and magnesium hardness, the mechanisms involved in the seasonal fluctuation of total hardness are the same as those described for soluble calcium (Fig. 13).

Dissolved oxygen. Dissolved oxygen concentrations were highest in late spring and early fall (Fig. 15). The increased solubility of oxygen with lower temperatures accounts for these higher concentrations in the cooler waters of spring and fall. Since late summer and early fall are characterized by increased wind activities, accelerated wave actions on the lakes could also account for increases in dissolved oxygen concentrations.

The midsummer months showed a decline in total dissolved oxygen. This decline is due to decreased oxygen solubility with warmer temperatures and an increase in the biological demand for oxygen for respiration.

Percentage of oxygen saturations were lowest in midsummer (75-85 percent) and highest in the spring and fall (90-100 percent). Corrections factors for the Refuge's high altitude were taken into

Figure 14. Seasonal variation in total water hardness.

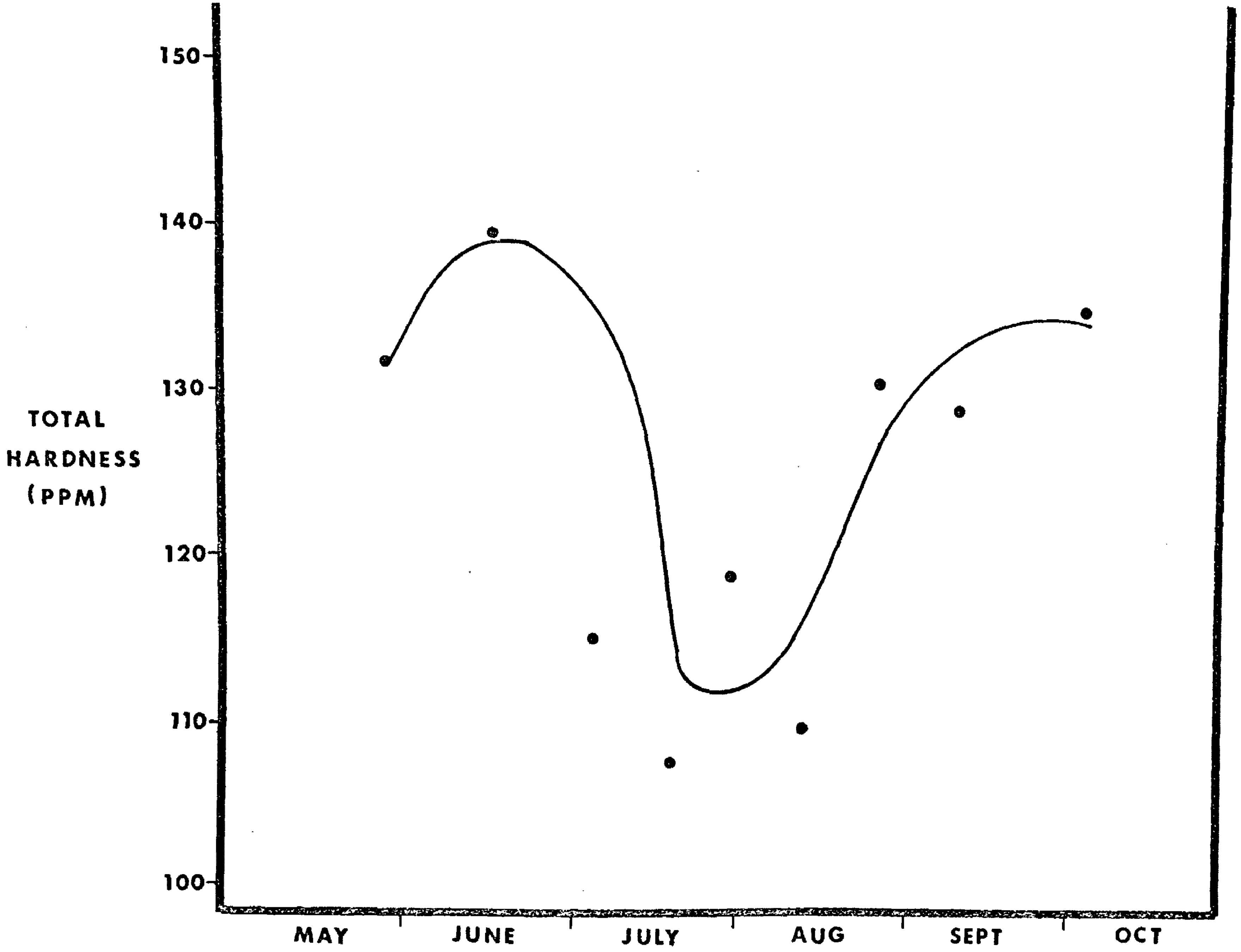
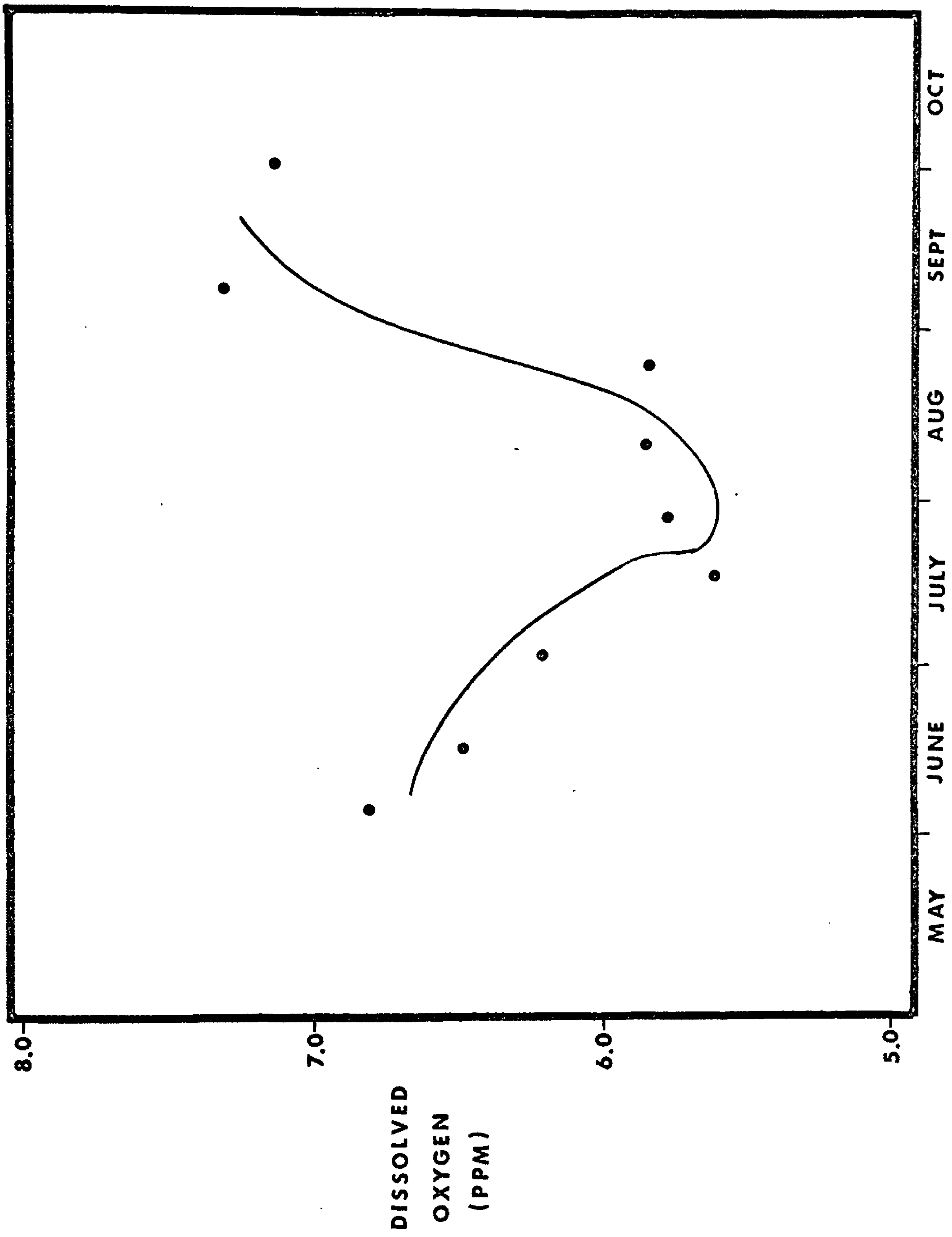

TOTAL
HARDNESS
(PPM)
150
140
130
120
110
100
MAY
JUNE
JULY
AUG
SEPT
OCT

Figure 15. Seasonal variation in dissolved oxygen.


8.0
7.0
6.0
5.0
DISSOLVED
OXYGEN
(PPM)
MAY
JUNE
JULY
AUG
SEPT
OCT

consideration when calculating percentage of saturation (Rawson 1944).

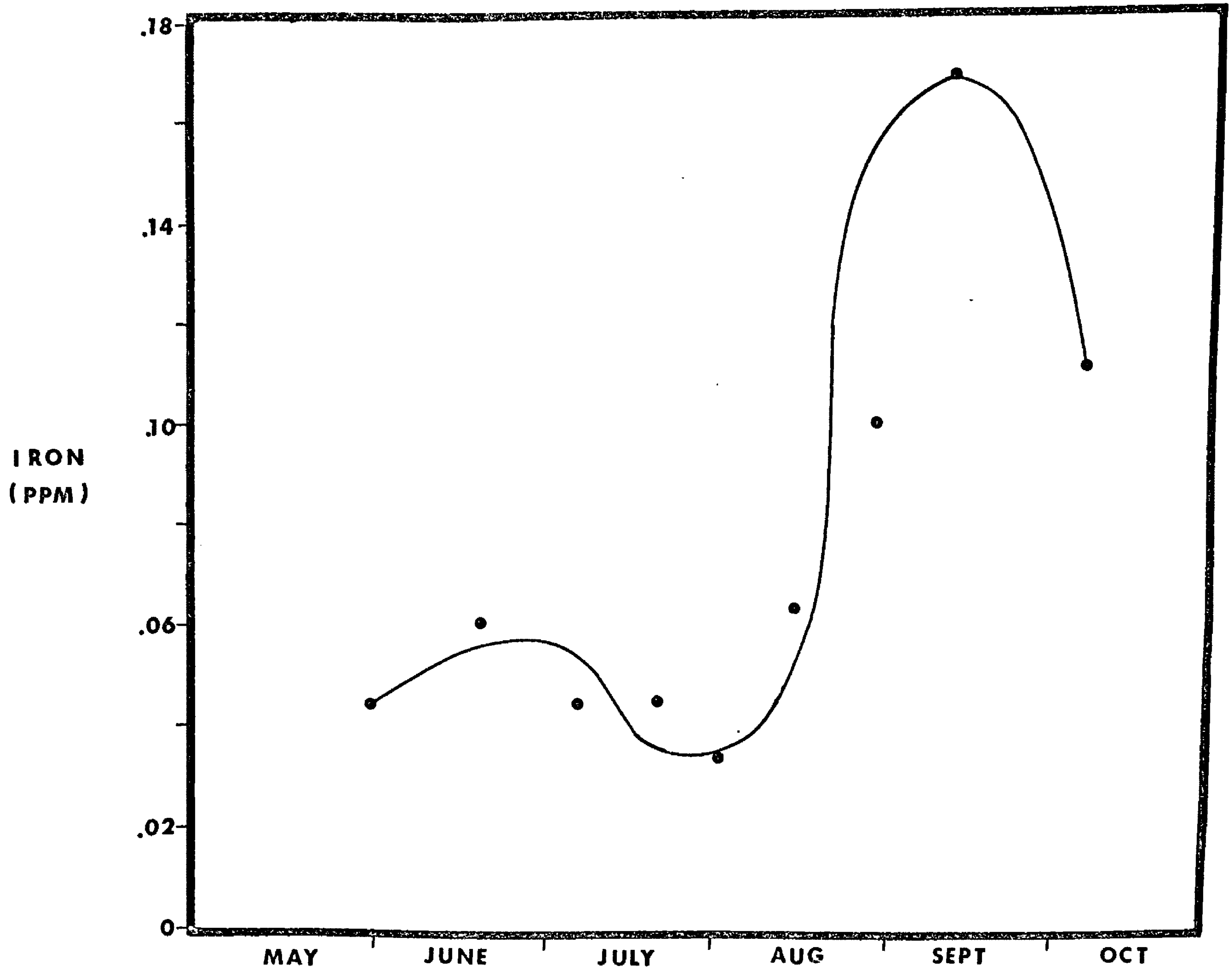
Iron. Soluble iron decreased slightly from late spring to midsummer and then increased in late summer (Fig. 16). Two possible mechanisms are responsible for this phenomenon.

As summer progresses, the deeper regions of the lakes become depleted of oxygen due to increased biological demand and thermal stratification (summer stagnation). In the presence of CO_2 from bacterial decomposition, organic matter in the muck soils serves as a reducing agent and the relatively insoluble ferric (Fe^{+3}) ions are reduced to the more soluble ferrous (Fe^{+2}) ions, thus increasing total soluble iron (Hutchinson 1957).

In early October the lake waters overturn during the period of autumnal circulation and subsequently the oxygen supply is restored. Ferrous iron is then oxidized to the insoluble ferric iron, and the total soluble iron concentration decreases.

An alternate mechanism for the increase of iron over the summer months was described by Hutchinson (1957) in which soluble iron increases with increased staining of the water due to dissolved organic matter. As the total amount of decomposition products increases in the water (Fig. 8), greater amounts of iron will be adsorbed to these colloidal fragments, thus accounting for the

Figure 16. Seasonal variation in soluble iron.


IRON
(PPM)
.18
.14
.10
.06
.02
0
MAY
JUNE
JULY
AUG
SEPT
OCT

increase in iron that was evidenced.

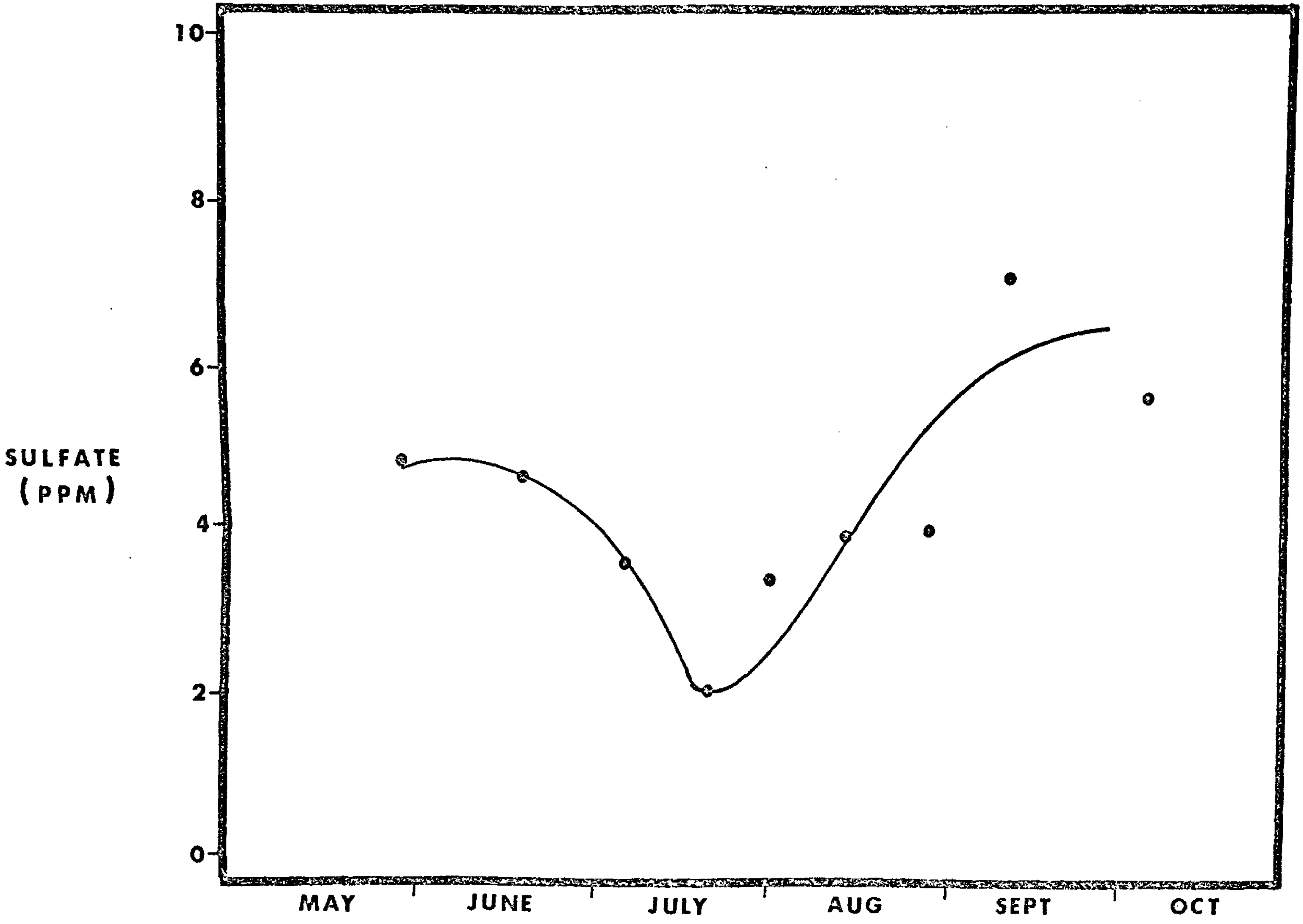
The increase in iron over the summer months is probably due to the combined interactions of the two processes above. Field evidence tends to support this dual theory. In the deep waters such as Upper Lake, the microzone is definitely reduced as evidenced by the blue-black color. This phenomenon meets the criterion of the first mechanism. The increased staining of lake waters during the summer months has been substantiated (Fig. 8), thus fulfilling the criterion for the second mechanism.

Most fresh-water lakes of the temperate region have soluble iron concentrations less than 0.20 ppm (Reid 1961). Since iron measurements of the Refuge lake water fall within this category and do not exceed this figure, it is concluded that the lakes are not exceedingly toxic nor deficient in soluble iron.

Sulfate. Sulfate concentrations declined from late spring to midsummer and then increased in late summer (Fig. 17). This pattern was also seen in the iron concentrations of the Refuge and the mechanisms involved in both cases are quite similar.

As summer progresses, increased biological demands deplete oxygen supplies in the lake waters. As anaerobic conditions are approached, sulfate bacteria chemosynthetically reduce sulfate to hydrogen sulfide gas. This pungent gas, commonly known as "swamp

Figure 17. Seasonal variation in soluble sulfates.


SULFATE
(PPM)
10
8
6
4
2
0
MAY
JUNE
JULY
AUG
SEPT
OCT

gas," is quite noticeable in late summer, especially when the muck soils of the lake bottom are disturbed.

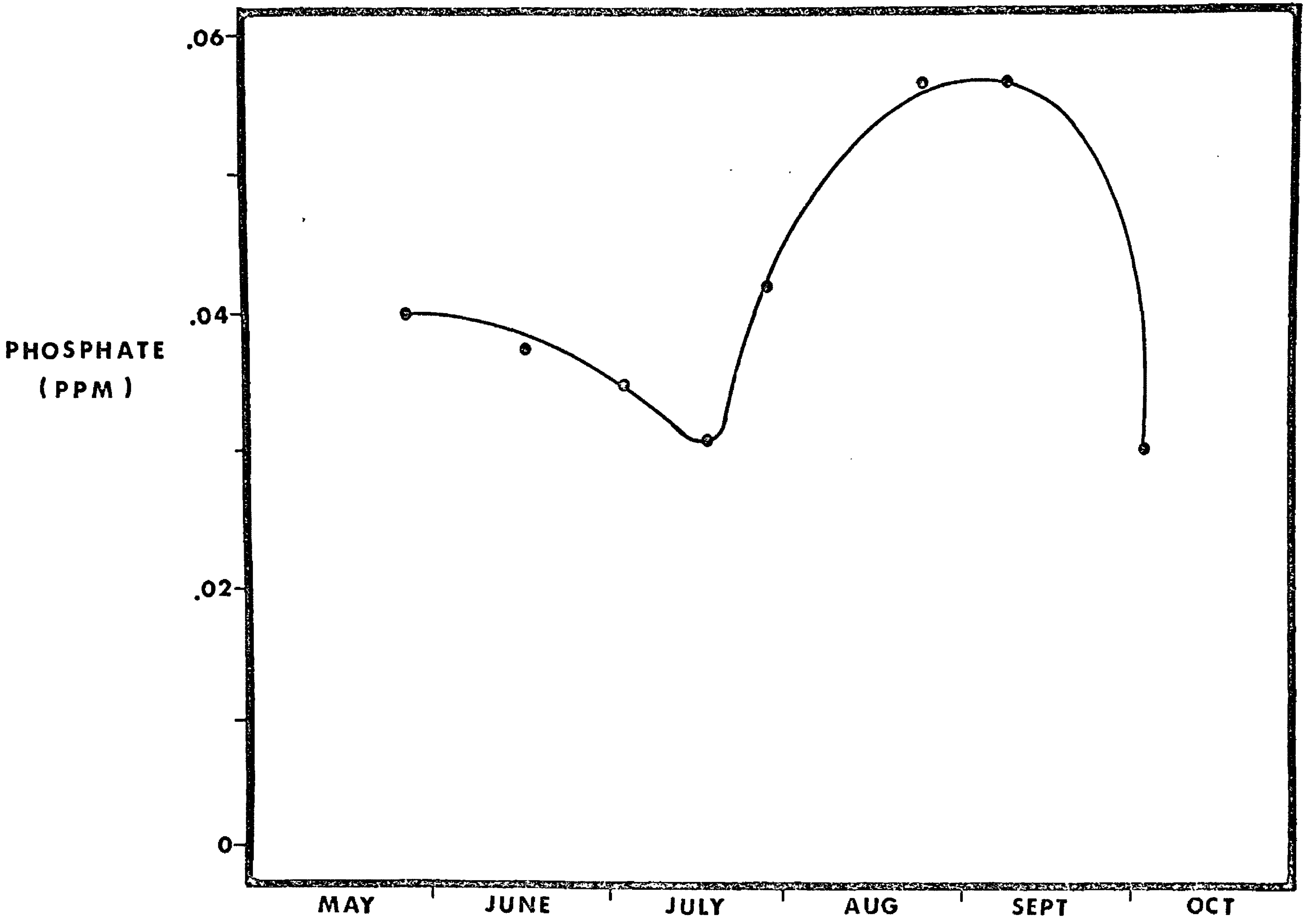
Sulfate reduction takes place at the mud surface (microzone) and the hydrogen sulfide in conjunction with methane often appears as a thin black coating, known as sapropel, on the mud surface (Reid 1961). Due to the alkaline nature of the lake waters, hydrogen sulfide is precipitated as iron sulfide (FeS), thus causing sulfate concentrations to decline.

By early August, the growing season is near termination, thus reducing the total biological oxygen demand. This, coupled with increased wave action during the windy season of late summer, and the autumnal mixis act together to increase the oxygen concentration of the lakes. As the lake microzones become oxidized, sulfur compounds are oxydized in the mud and lost to the water as soluble sulfate. This process explains the increase in sulfate concentrations that were witnessed in late summer and early autumn.

Phosphate. Phosphate declined until the end of the growing season (Fig. 18). This decline is probably due to the high biological demand for this essential nutrient by rapidly growing bacteria, plankton, and macrophytes.

The increase in phosphate concentrations in late summer seems to be related to the termination of the growing season and the

Figure 18. Seasonal variation in soluble phosphates.


PHOSPHATE
(PPM)
.06
.04
.02
0
MAY
JUNE
JULY
AUG
SEPT
OCT

decompositional breakdown of plant and animal biomass. Despite the fact that most of the phosphorus released from decompositional breakdown is organically bound, some phosphate goes into solution and this could account for the increase that was noted.

This theory is supported by the findings of Ohle (1934) who found that soluble inorganic phosphate was directly related to the amount of staining in the water. Water color of the Refuge lakes varied in the same manner as the phosphate concentrations, thus lending more credence to the theory.

The decline in phosphate in the fall also corresponds with a decrease and leveling off of water color. This decline is most likely attributable to the oxidation of organic matter following the autumnal circulation and precipitation of orthophosphate by calcium and iron.

Despite the close proximity of the phosphate-rich Phosphoria formation in the Centennial Mountains, phosphate concentrations in the Refuge lakes are not excessive. The lack of abundant orthophosphate is attributable to its high biological demand and to the rapid rate at which phosphates are tied up in insoluble compounds such as calcium and ferric phosphates. The average orthophosphate concentration in temperate region lakes is 0.01-0.03 ppm (Reid 1961) which would classify the Refuge lakes as being slightly above average.

Nitrate. Nitrates increased throughout the summer months and sharply declined in early fall (Fig. 19). An adequate explanation of this increase is difficult to resolve in view of the fact that much of the data presented in the literature (Hutchinson 1957, Domogally et al., 1925) indicates that nitrates usually decline during the summer months. Arenson (1969) however, working at Quake Lake, Montana, just north of the Refuge, found that nitrates increased from June to September followed by a decline, similar to that of the Refuge waters.

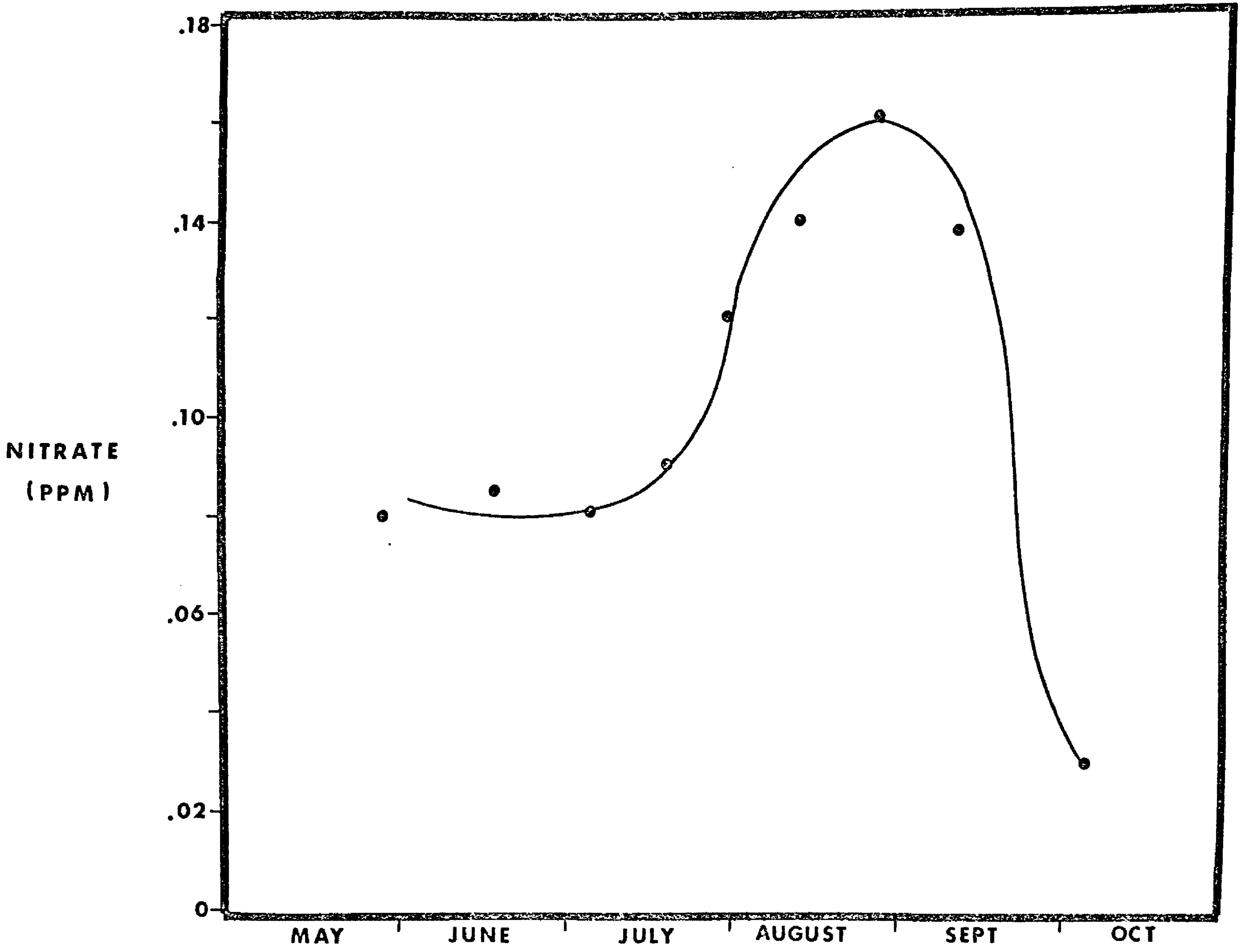
Nitrates usually enter the water as a by-product of bacterial nitrification. Rates of nitrification are dependent upon the concentrations of ammonia which are derived from the decomposition of proteins and the deamination of amino acids (Hutchinson 1957).

Ohle (1934) found that ammonia concentrations were higher in stained waters due to dissolved organic matter. Water color generally increased during the summer months which would imply that ammonia concentrations also increased. Since nitrification rates are dependent upon ammonia concentrations, it seems plausible that this mechanism could increase nitrate concentrations during the summer.

Rain water contains, on the average, 0.5 ppm ammonia and 0.2 ppm nitrate (Hutchinson 1957). Since the summer months in the Centennial Valley are marked by frequent rain showers, nitrates could possibly enter the system by this means.

Nitrogen compounds derived from the soil can also enter the

Figure 19. Seasonal variation in soluble nitrates.


NITRATE
(PPM)
.18
.14
.10
.06
.02
0
MAY
JUNE
JULY
AUGUST
SEPT
OCT

lakes by the influents of streams and springs. This phenomenon occurred in one instance where nitrate concentrations in Elk Creek Springs were measured at 0.77 ppm. This concentration is several times greater than any measurement made on the Refuge and represents a readily available source of nitrates for macrophytes. From the great abundance of springs in the area, it seems possible that other springs are contributing nitrogen compounds to the water and could conceivably account for the summer nitrate increase.

Plants

In its contemporary usage, the term "aquatic macrophyte" has no precise taxonomic meaning, but is used to refer to the larger submerged aquatic plants to distinguish them from microscopic plankton, periphyton, and small algae. The *Characeae* was included in the study because of their local abundance and their known value to waterfowl as a food source (Martin and Uhler 1939). The term "aquatic macrophyte" as used in this investigation is synonymous with the term "hydrophyte" as used by other authors (Den Hartog and Segal 1964, Raunkiaer 1934).

History. The exact nature of the native submerged macrophytes of the Refuge is obscure. During the 1930's and 1940's, Refuge personnel undertook an extensive program of introducing non-native species throughout the marsh proper and the adjacent ponds. The problem of discerning native species from those introduced is complicated by the fact that many past Refuge records used the common plant names or only the generic name.

Seven species of submerged macrophytes were recorded as introduced on the Refuge. Of those seven only Potamogeton pectinatus, and Najas flexilis are now present in the marsh. Since western Montana is within the natural distribution area for these species (Hitchcock et al., 1969) it is accepted that they are members of the original flora. Thus, the net effect of the plantings, in terms of submerged species, has been nil.

The submerged macrophytes of the marsh were intermittently surveyed over the years by Refuge personnel. Beed (1955, 1956) conducted the initial aquatic macrophyte survey of the marsh proper using a point transect method. Refuge records from 1956-1966 lack quantitative surveys and are limited to brief narrations based on visual estimates.

In 1966 and 1968-1972, quantitative surveys were conducted. Recent surveys employed a harvest method devised by Webster (1965) and were conducted to estimate the biomass of standing crops of macrophytes, an index to the food plants available to the trumpeter swan and other waterfowl.

Taxonomy. The taxonomic nomenclature of this investigation (Appendix IV) follows Hitchcock et al. (1969) and Prescott (1962). Voucher specimens are deposited at the University of Montana Herbarium.

Growth forms. Several life form classification schemes for aquatic plants have been presented (Sculthrope 1967, Den Hartog and Segal 1964, Penfound 1952, and Luther 1949). Table 3 summarizes the growth forms of aquatic macrophytes found on the Refuge.. The classification scheme and terminology used in this table is a composite of Sculthrope (1967) and Luther (1949).

The difficulty in accurately describing the life forms of aquatic macrophytes arises from the great variation in aquatic habitats. Evidence of this variation in growth forms is evident in the lakes of the Refuge. For example, Ceratophyllum demersum growing in the shallow water of Lower Lake is attached to the lake substrate and is somewhat dwarfed in size; whereas, plants of the same species growing in the deep waters of Widgeon Pond are free floating and much larger. Likewise, Sagittaria cuneata growing in Lower Lake is comprised of a basal rosette of submerged linear leaves, yet the same plant in Upper Lake often will have sagittate leaves floating on the lake surface.

Despite the partial overlap that occurs in such a scheme, growth form classification provides an insight into the ecology of

Table 3

Growth Forms of Submerged Macrophytes

- I. Hydrophyte basal parts penetrate substrate (Rhizophytes)
  - A. Leaves floating
    - *Polygonum amphibium*
    - *Sagittaria cuneata* (occasionally)
  - B. Leaves submerged; reproductive organs floating, aerial, or submerged
    - 1. Rosette plants
      - *Sagittaria cuneata*
      - *Isoetes spp.*
    - 2. Caulescent plants
      - *Elodea canadensis*
      - *Najas flexilis*
      - *Zannichellia palustris*
      - *Potamogeton pectinatus*
      - *P. friesii*
      - *P. richardsonii*
      - *P. praelongus*
      - *P. foliosus*
      - *P. zosteriformis*
      - *P. pusillus*
      - *Chara vulgaris*
      - *Nitella flexilis*
      - *Ceratophyllum demersum* (occasionally)
      - *Ranunculus aquatilis*
      - *Myriophyllum spicatum*
      - *Callitriche hermaphroditica*
      - *Hippuris vulgaris*
- II. Free-floating macroscopic hydrophytes (Pleustophytes)
  - A. Hydrophytes which lie freely on the lake bottom (Benthopleustophytes)
    - *Lemna trisulca*
  - B. Hydrophytes that float freely between the bottom and the lake surface (Mesopleustophytes)
    - *Ceratophyllum demersum*
    - *Utricularia vulgaris*

submerged macrophytes, which will be apparent in later paragraphs.

Geography. Distribution maps of each submerged species are included in Appendix V. Because of the complex mosaic of vegetational growth patterns, no attempt was made to show relative abundance on the maps.

Species distributional maps reveal that some distinct patterns do occur on the Refuge. Species such as Elodea canadensis, Zannichellia palustris, and Callitriche hermaphroditica are generally limited to the pond region in the eastern portion of the Refuge. Lemna trisulca is found almost exclusively in Lower Lake while Potamogeton praelongus is limited to the larger water bodies of the marsh proper. Explanation of these and other distributional phenomena appear in later paragraphs.

Pattern. The classification scheme devised by Shimwell (1971) was used to classify the Refuge macrophytes according to their horizontal distribution or pattern (Table 4).

Plant pattern in the marsh is clearly a direct function of reproductive mechanisms. Plants which reproduce vegetatively by means of rhizomes, tubers, or winter buds (Appendix VIII) generally exhibited a closed pattern. Within these species, aggregation into large clumps or the formation of extensive mats was common.

Plant species such as Najas flexilis, Isoetes spp.,

Table 4

Horizontal Plant Distribution

A. CLOSED: plants spaced so as to form continuous lateral contact

Elodea canadensis
Chara vulgaris
Hippuris vulgaris
Myriophyllum spicatum
Lemna trisulca

B. LOCALLY CLOSED TO OPEN

Potamogeton pusillus
Potamogeton pectinatus
Potamogeton richardsonii
Potamogeton foliosus
Potamogeton zosteriformis
Nitella flexilis

C. OPEN: horizontal space between individuals not more than twice the diameter of the plant species

Ranunculus aquatilis
Potamogeton friesii
Najas flexilis

D. SPARSE: horizontal space between individuals greater than twice the plant diameter

Ceratophyllum demersum
Utricularia vulgaris
Polygonum amphibium
Sagittaria cuneata
Isoetes spp.
Callitriche hermaphroditica

Callitriche hermaphroditica, Zannichellia palustris, and Polygonum amphibium which generally reproduce sexually exhibited a much more open pattern. Also included in this category are the free-floating species Ceratophyllum demersum and Utricularia vulgaris; however, their open pattern is more likely a function of their free-floating mobility rather than their reproductive mechanisms.

Plants which were known to reproduce both sexually and vegetatively exhibited horizontal patterns intermediate to the two above groups. Included in this group are Potamogeton pectinatus, Potamogeton richardsonii, and Potamogeton praelongus.

Stratification. Plant distribution in vertical space (Table 5) was found to be a direct function of water depth (Fig. 20). Ground plants of low stature were generally limited to the shallow water of the shoreline areas. The exception in this case is Lemna trisulca which was found in the deeper waters of Lower Lake.

Tall submerged macrophytes were generally found in the deeper lake waters. It is a well-established fact that deeper water produces taller plants (Sculthrope 1967, Fernald 1932); however, since tall plants growing in shallow water were taller than low stature ground plants, it is assumed that these plants represent a true canopy among the submerged macrophytes rather than just a response to increasing lake depth.

Table 5

Stratification of Submerged Macrophytes

A. GROUND PLANTS: vertical height less than 1 foot

- Chara vulgaris
- Lemna trisulca
- Isoetes spp.
- Sagittaria cuneata
- Najas flexilis
- Nitella flexilis
- Callitriche hermaphroditica
- Utricularia vulgaris
- Hippuris vulgaris

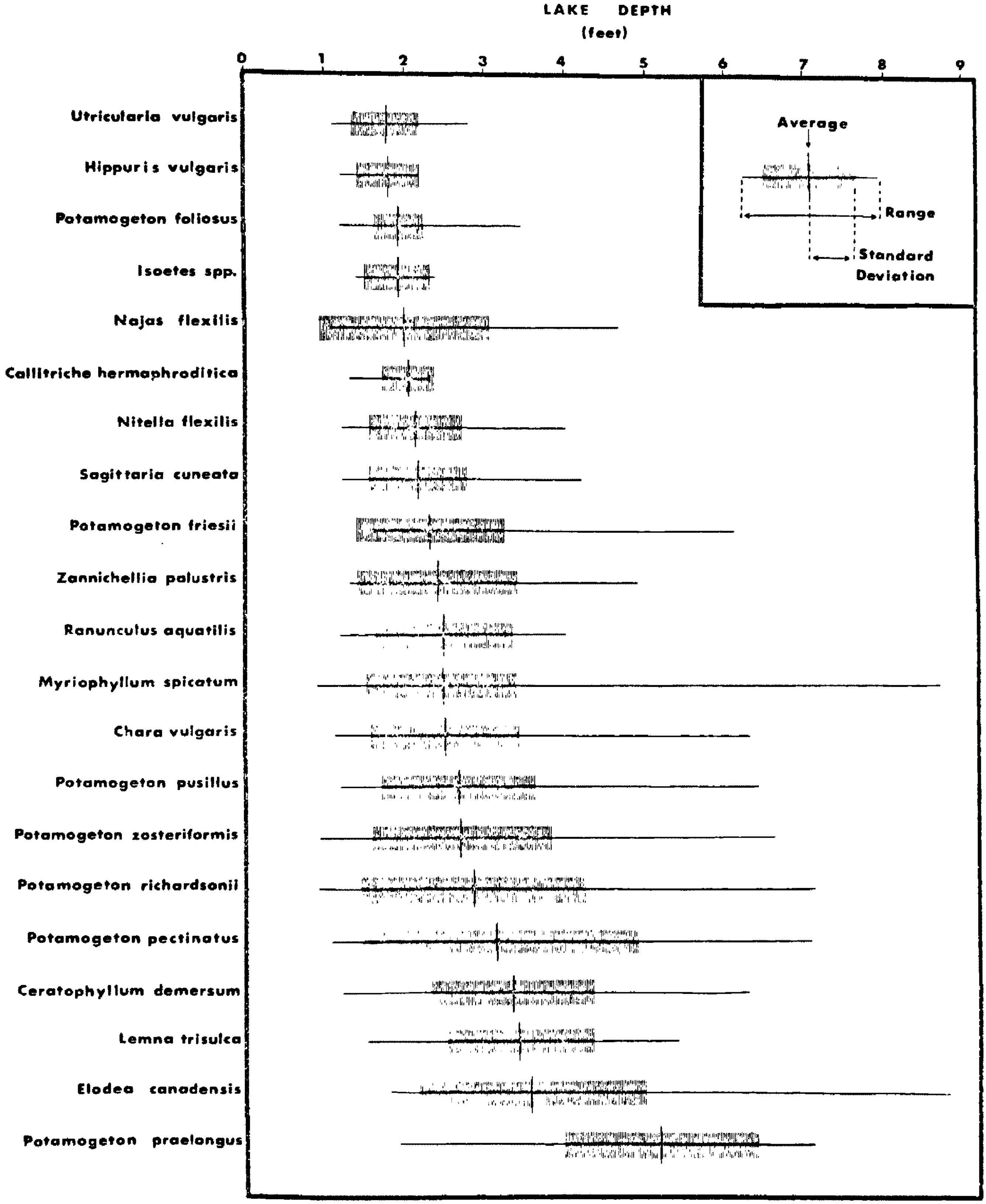
B. INTERMEDIATE PLANTS: vertical height 1-3 feet

- Myriophyllum spicatum
- Potamogeton foliosus
- Potamogeton friesii
- Potamogeton pusillus
- Potamogeton zosteriformis
- Ranunculus aquatilis
- Zannichellia palustris

C. TALL PLANTS: vertical height greater than 3 feet

- Potamogeton pectinatus
- Potamogeton richardsonii
- Potamogeton praelongus
- Elodea canadensis
- Ceratophyllum demersum
- Polygonum amphibium

Figure 20. Plant zonation by lake depth.


LAKE DEPTH
(feet)
0
1
2
3
4
5
6
7
8
9
Utricularia vulgaris
Hippuris vulgaris
Potamogeton foliosus
Isoetes spp.
Najas flexilis
Callitriche hermaphroditica
Nitella flexilis
Sagittaria cuneata
Potamogeton friesii
Zannichellia palustris
Ranunculus aquatilis
Myriophyllum spicatum
Chara vulgaris
Potamogeton pusillus
Potamogeton zosteriformis
Potamogeton richardsonii
Potamogeton pectinatus
Ceratophyllum demersum
Lemna trisulca
Elodea canadensis
Potamogeton praelongus
Average
Range
Standard Deviation

Utricularia vulgaris and *Ceratophyllum demersum* note special mention in regard to their stratification. Due to their long length, both species are technically tall plants; however, *Utricularia vulgaris* because of its free-floating growth form is usually oriented in a horizontal manner, so that its vertical spatial component was minimal and not unlike a ground plant. *Ceratophyllum demersum*, on the other hand, usually floats vertically so that it was classified as a tall plant.

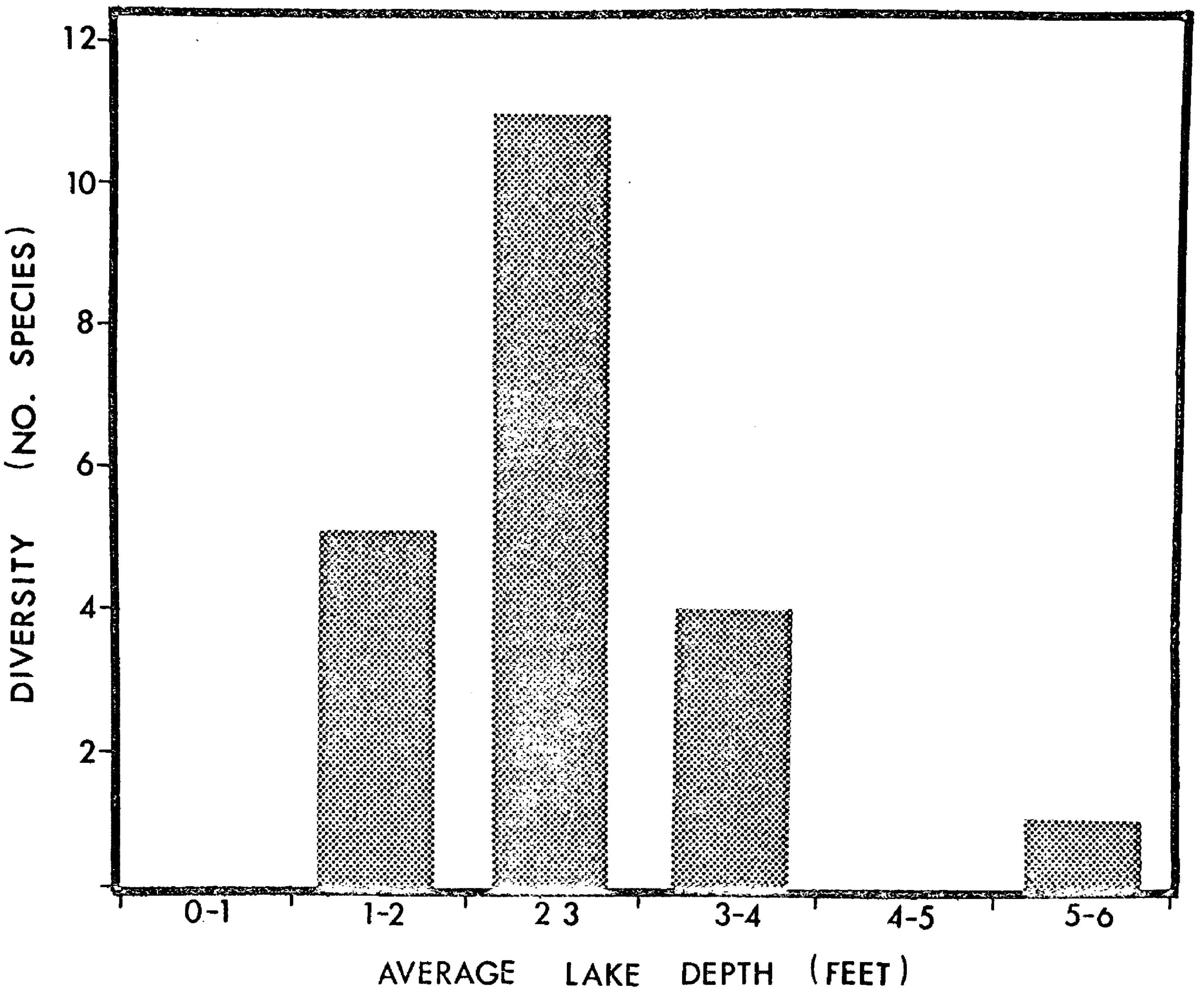
Zonation. Submerged macrophytes of the Refuge exhibited zonational responses to increasing lake depths (Fig. 20). The greatest effect of water depth is upon species diversity (Fig. 21).

In shallow depths species diversity was limited primarily to ground plants and in the deeper lake regions diversity was limited to tall plants. Species diversity was greatest in intermediate depths from 2-3 feet.

The high species diversity at the intermediate depths is generally attributable to the plants which comprise the intermediate height class; however, another factor, not readily apparent in Fig. 21, is responsible for increased species diversity at intermediate depths.

The depth ranges for each species in Figure 20 indicate a great overlap of species zonation at intermediate depths (2-3 feet). Not only do the ground plants grade into the intermediate depths from

Figure 21. Variation in species diversity with changing lake depth.


12
10
8
6
4
2
DIVERSITY (NO. SPECIES)
0-1
1-2
2 3
3-4
4-5
5-6
AVERAGE LAKE DEPTH (FEET)

the shoreline areas, but the tall plants also grade into the intermediate depths from the deep lake centers. This phenomenon was observed repeatedly during the mapping work when as many as 11 species of plants were recorded within a square meter plot at depths from 2-3 feet. These plants included species from all height classes.

Conversely, sample plots taken in depths less than 1.5 feet or in regions greater than 5.0 feet usually contained less than three species within a square meter plot.

Coverage. Because previous aquatic plant surveys were concerned primarily with determining production of waterfowl food plants, plant abundance was usually measured in terms of standing crop biomass and expressed as the total tonnage of wet plants on a per lake basis. While tonnage estimates are useful for food studies, in terms of phytogeography and succession their meaning is often obscure and the numbers bulky.

For this reason, total acreage cover of each species (Appendix VI), was selected to express plant abundance in the hope that acreage would be more meaningful in determining future compositional changes. In order of decreasing magnitude, Potamogeton richardsonii, P. pectinatus, and Myriophyllum exalbescens are the three most abundant species occurring in the Refuge lakes.

Polygonum amphibium did not occur in any of the 1,126 sample plots and therefore is deleted from Appendix VI. Due to the sparse occurrence of this plant it is assumed that its overall Refuge abundance is less than that of Callitriche hermaphroditica, the least abundant species sampled.

Overall plant coverage in each lake, expressed as the percent of lake bottom vegetated, was found to be strongly correlated with the average lake depth (Fig. 22). This is not surprising in light of previous findings pertaining to plant diversity and water depth (Fig. 21).

Shallow water bodies such as Swan Lake and River Marsh represent successionally old lakes where plant growth is abundant. Deeper water bodies, either natural or man-made, are successionally younger and plant growth is less abundant due to either decreased light at deeper depths, or increased disturbance (greater wave action or recent construction activities).

Growth curves and phenology. Elodea canadensis showed steadily increasing growth from early June until mid-August (Fig. 23). Decline in standing crop biomass during late August coincides with the rapid influx of trumpeter swans from the marsh proper following the completion of the summer molt, and the congregation of large flocks of migrating waterfowl. Since Elodea canadensis does not die off during the winter (Appendix VIII), the difference between the high standing crop biomass in August and the low standing crop in the

Figure 22. Changes in the percent of lake bottom vegetated with changes in lake depth.

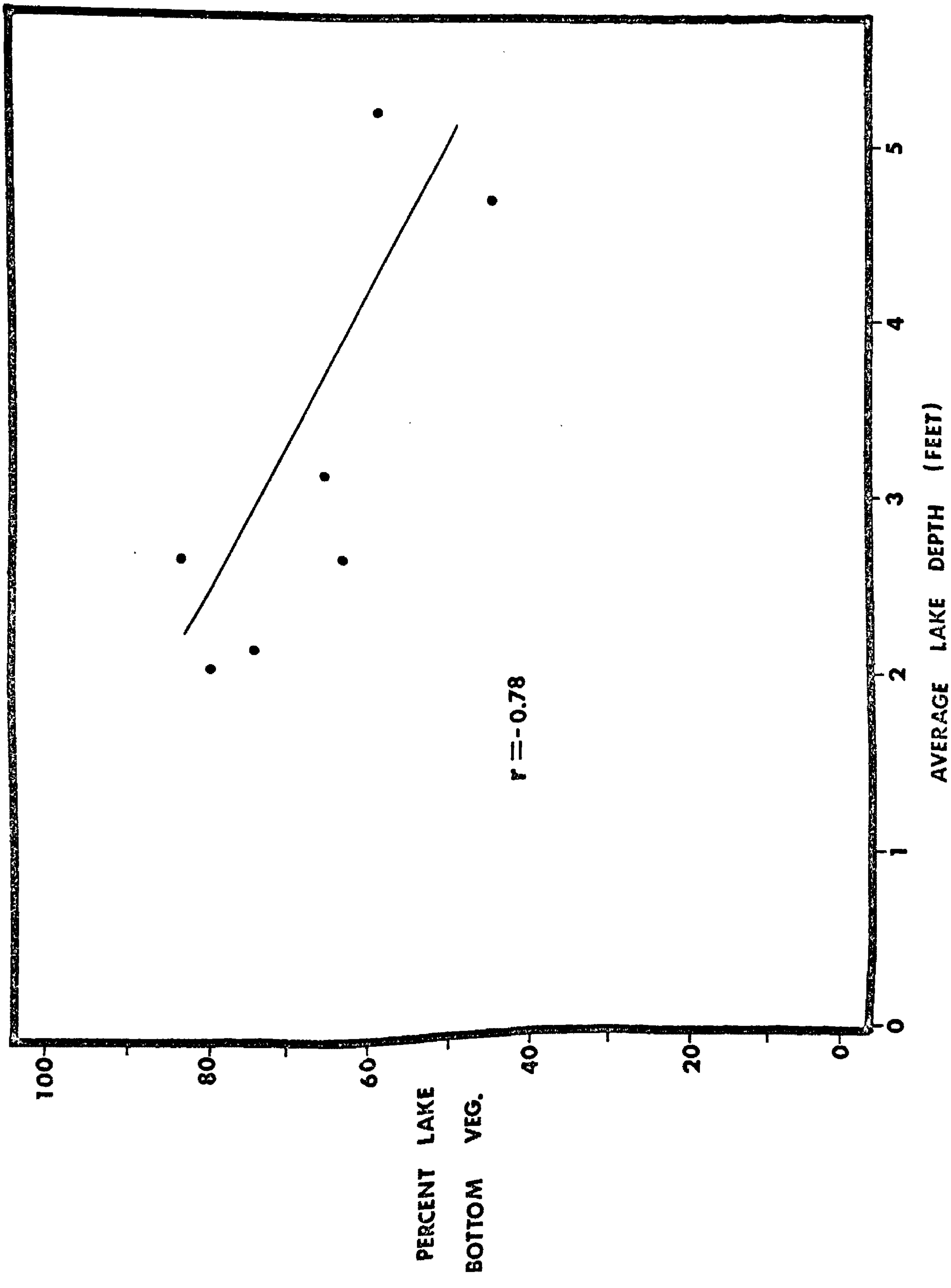
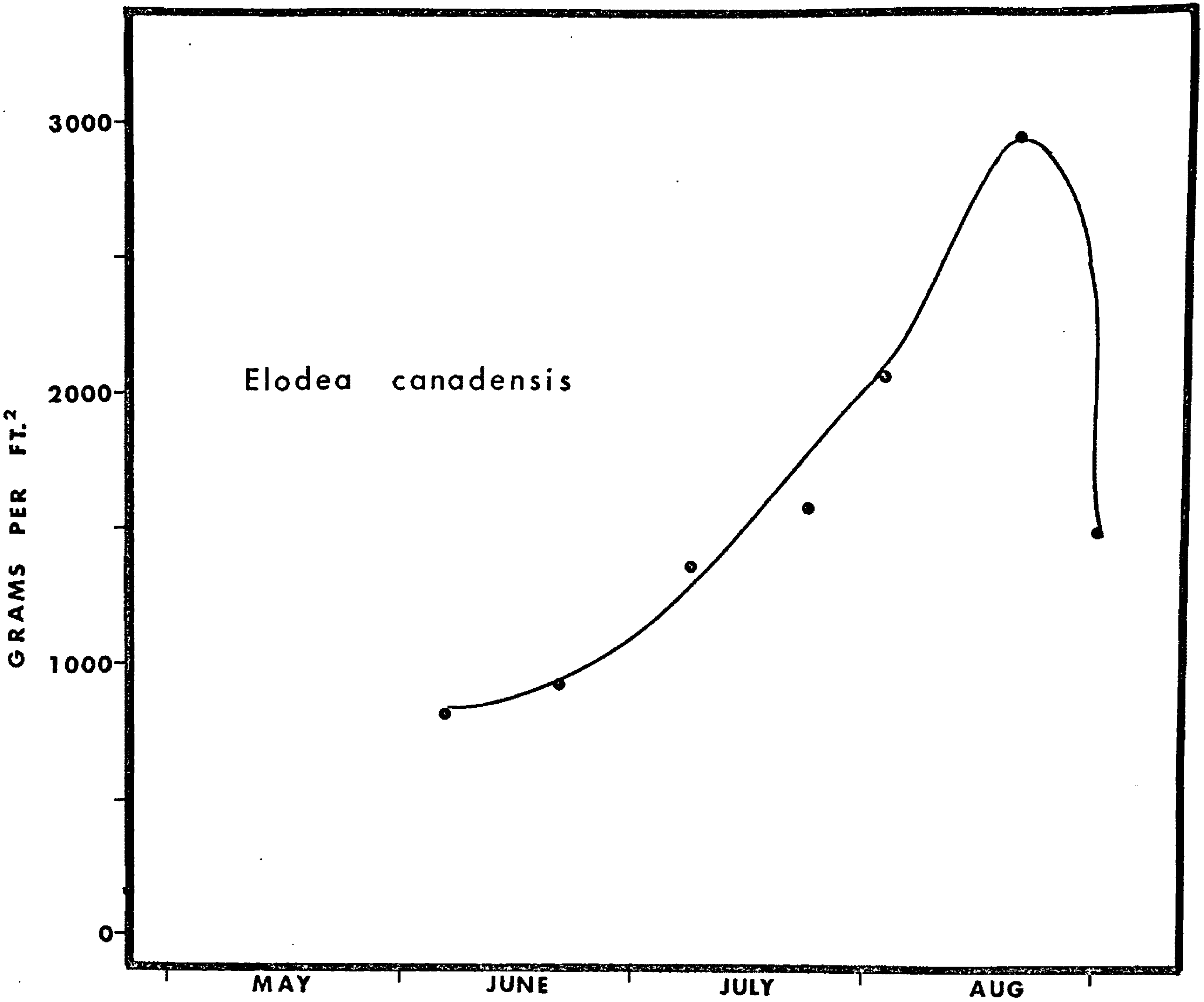

r = -0.78
PERCENT LAKE BOTTOM VEG.
100
80
60
40
20
0
AVERAGE LAKE DEPTH (FEET)
0
1
2
3
4
5

Figure 23. Seasonal changes in Elodea canadensis biomass.


Elodea canadensis
GRAMS PER FT.^{2}
3000
2000
1000
0
MAY
JUNE
JULY
AUG

spring probably represents the extensive herbivory that occurs in Widgeon and Culver ponds during the fall. At that time waterfowl populations are high due to migratory influxes and hunting pressures in other areas of the Refuge.

Elodea canadensis reproduces almost exclusively by vegetative means (Sculthrope 1967). A few minute inflorescenses were noted in Culver Pond in mid-July and were still present in early August but no fruits were observed. Dormant apices were noted in early May and October of 1972.

Potamogeton zosteriformis generally ceased growth by the first of August (Fig. 24). On 7 July approximately 90 percent of the plants were flowering but no fruits were seen during the growing season. Fernald (1932) considers the flowers of *Potamogeton zosteriformis* to be infertile. Winter bud formation was extensive during August and was so advanced by 30 August that harvesting was prevented due to the advanced state of decomposition.

Initiation of growth in *Sagittaria cuneata* (Fig. 25) seems to be delayed in comparison to the other observed species. This delayed growth habit is probably responsible for the fact that *Sagittaria cuneata* was still growing when harvesting was terminated at the end of August. No flowers were observed on this plant since it perennates almost exclusively by stem tubers (Sculthrope 1967). Underground vegetative structures of *Sagittaria cuneata* are eaten

Figure 24. Seasonal changes in Potamogeton zosteriformis biomass.

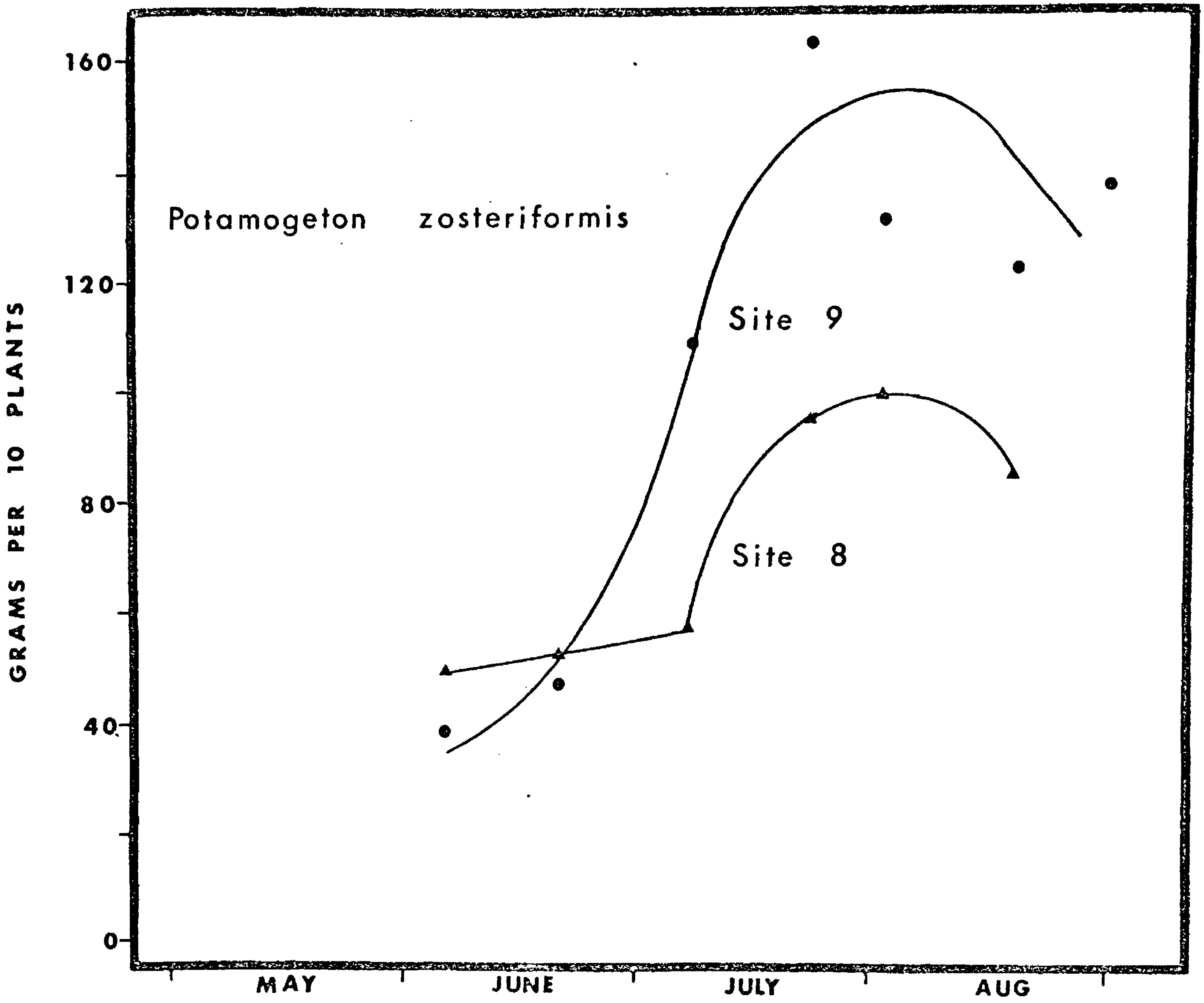
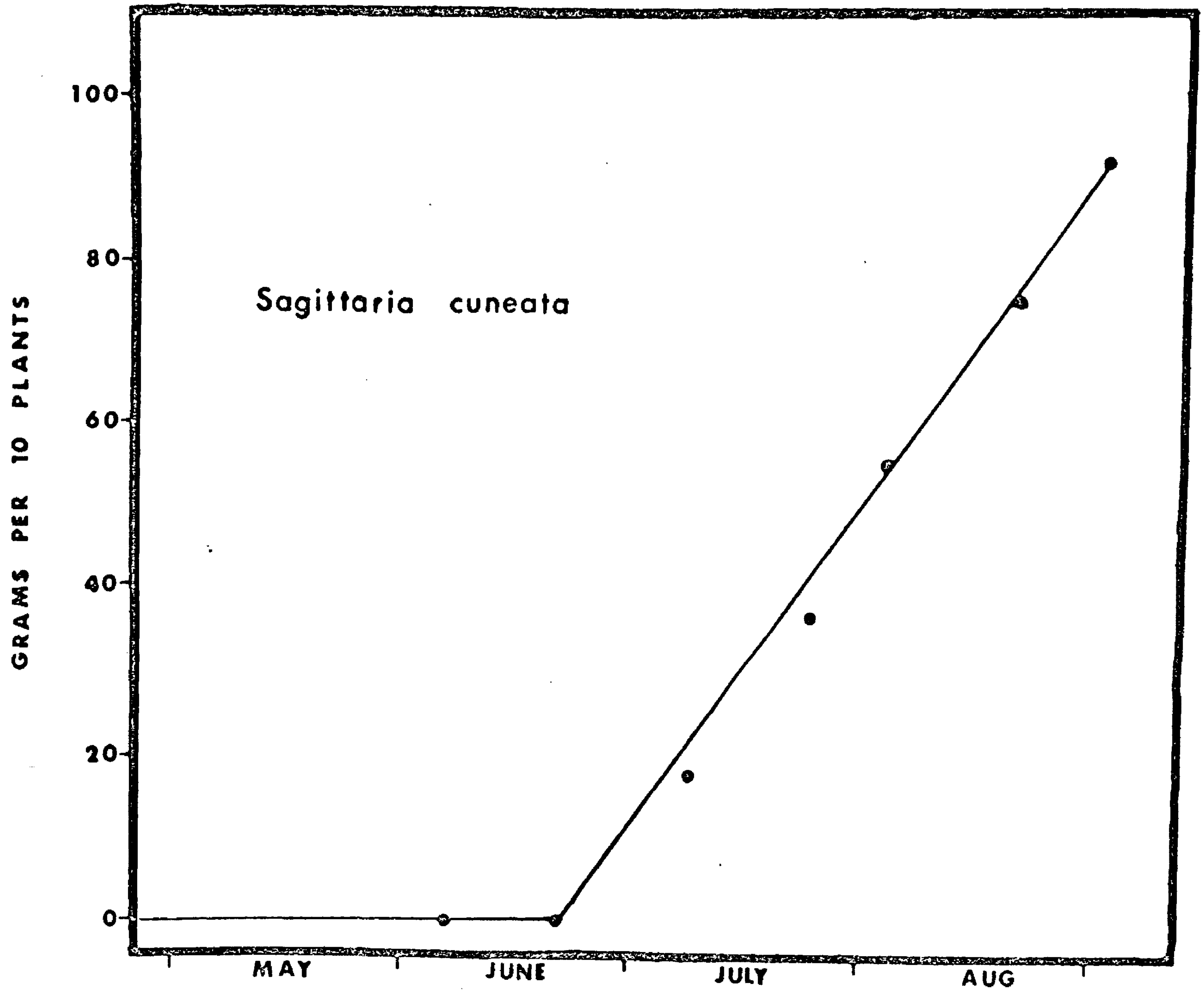

Potamogeton zosteriformis
Site 9
Site 8
GRAMS PER 10 PLANTS
160
120
80
40
0
MAY
JUNE
JULY
AUG

Figure 25. Seasonal changes in *Sagittaria cuneata* biomass.


Sagittaria cuneata
GRAMS PER 10 PLANTS
100
80
60
40
20
0
MAY
JUNE
JULY
AUG

by the trumpeter swan and other waterfowl with great relish, and as early as 30 July practically all of the plants were uprooted by feeding birds. Above-ground stems and leaves are virtually untouched by waterfowl.

Growth of Potamogeton richardsonii commenced in late May and terminated in early August (Fig. 26). It was observed that roughly 40 percent of these plants flowered; the remainder reproduced vegetatively by rhizomes. By 7 July, 60 percent of the flowering plants were in full bloom, 20 percent still had green unopened flower buds, and 20 percent were already pollinated with minute green fruits being evident. By 2 August all plants were fully fruited with large green seed heads. By 30 August nearly 100 percent of the seeds had been eaten by waterfowl.

By extrapolating the growth curve of Chara vulgaris to 24 April 1972 when ice on the Refuge lakes broke up (Stroops, pers. comm.) and the growing season began, it can be seen that this macrophytic alga exhibited a very rapid growth in early spring (Fig. 27). Indeed, it was observed that large concentrations of trumpeter swans were actively feeding on Chara vulgaris in early May, when many of the other submerged macrophytes had not yet emerged from the lake substrate. Whether the decline in biomass in late June is due to the termination of the growing season or increased herbivory is unknown. Extensive oogonial development was noted in late June. This indicates

Figure 26. Seasonal changes in Potamogeton richardsonii biomass.

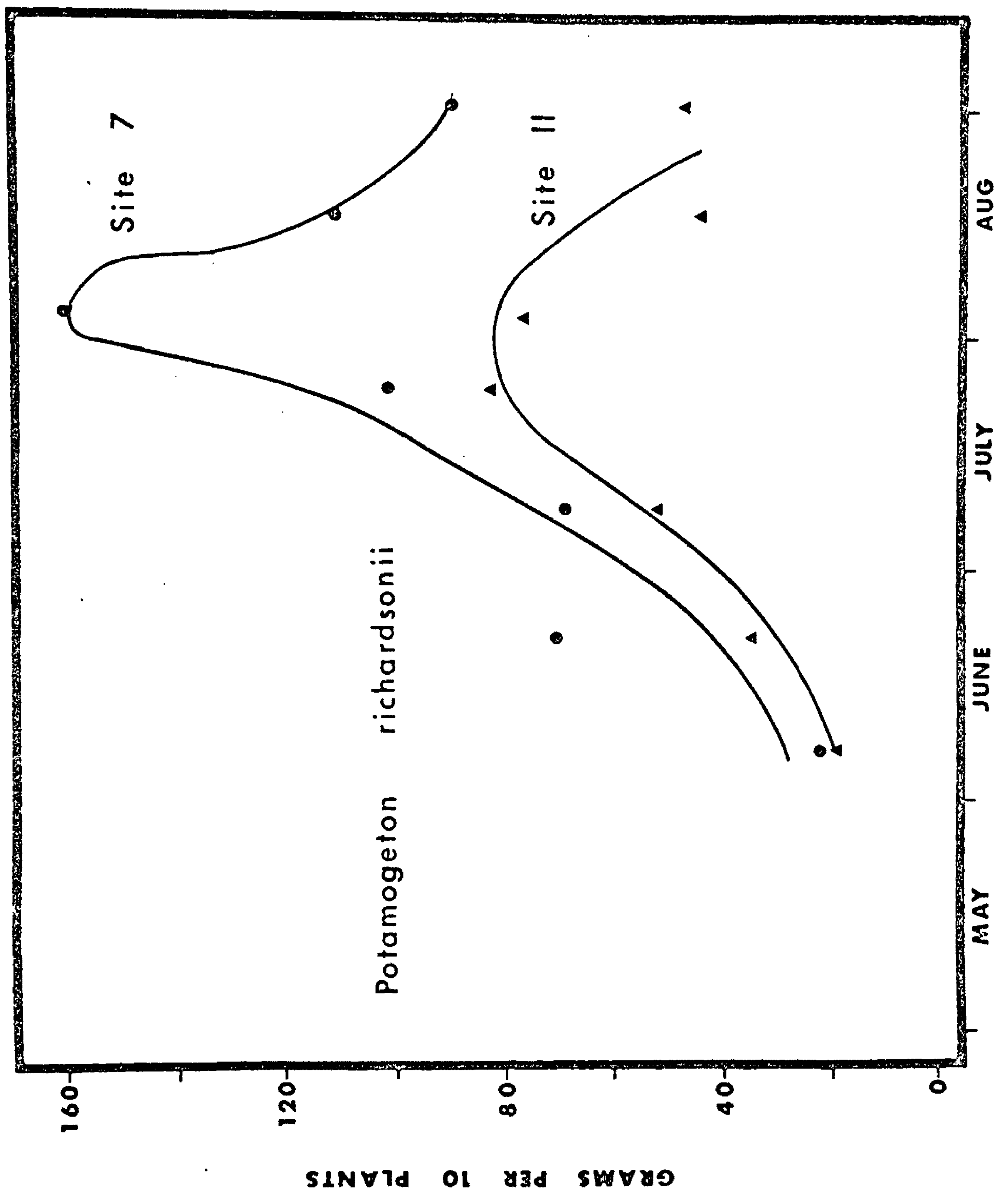
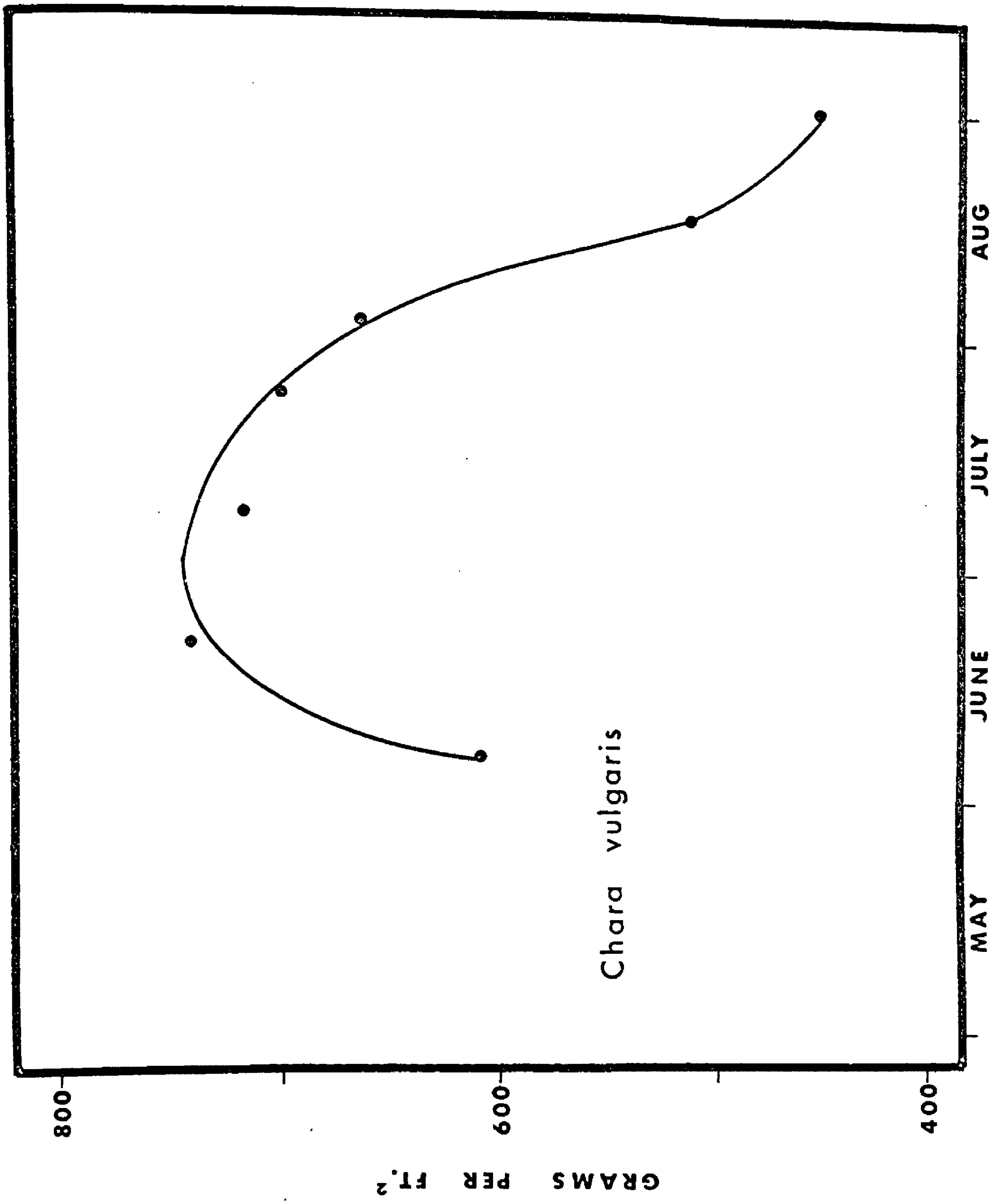

Potamogeton richardsonii
Site 7
Site 11
GRAMS PER 10 PLANTS
0
40
80
120
160
MAY
JUNE
JULY
AUG

Figure 27. Seasonal changes in *Chara vulgaris* biomass.


Chara vulgaris
GRAMS PER FT.²
800
600
400
MAY
JUNE
JULY
AUG

that herbivory accounted for the decline in biomass since it is known that the oogonia of the Characeae are choice waterfowl food (Martin et al., 1951).

Phenological observation of Potamogeton praelongus indicates that it is one of the earliest plant species to initiate growth (Fig. 28). Plants were in full flower by 19 June, and green fruits developed by 7 July. By 21 July, 90 percent of the seed heads were eaten by waterfowl and by 2 August no seeds were observed on the plants. During August extensive development of winter buds was noted even though Fernald (1932) notes that this is usually a rare occurrence in this species.

The termination of the growing season for Myriophyllum spicatum, based on the growth curves for the species is inconclusive (Fig. 29). Plants growing on site #5, which flowered extensively in mid-July and developed fruits in early August, exhibited a continually increasing biomass throughout the harvest season. Plants at collection site #6 did not flower and terminated growth in early August. The relationship between the mode of reproduction and duration of the growing season is unknown but there are indications that the sexually reproducing plants continued to grow longer than the plants that reproduced vegetatively. Extensive winter bud formation was noted at both sights.

Potamogeton pectinatus exhibited a steady increase in plant

Figure 28. Seasonal changes in Potamogeton praelongus biomass.

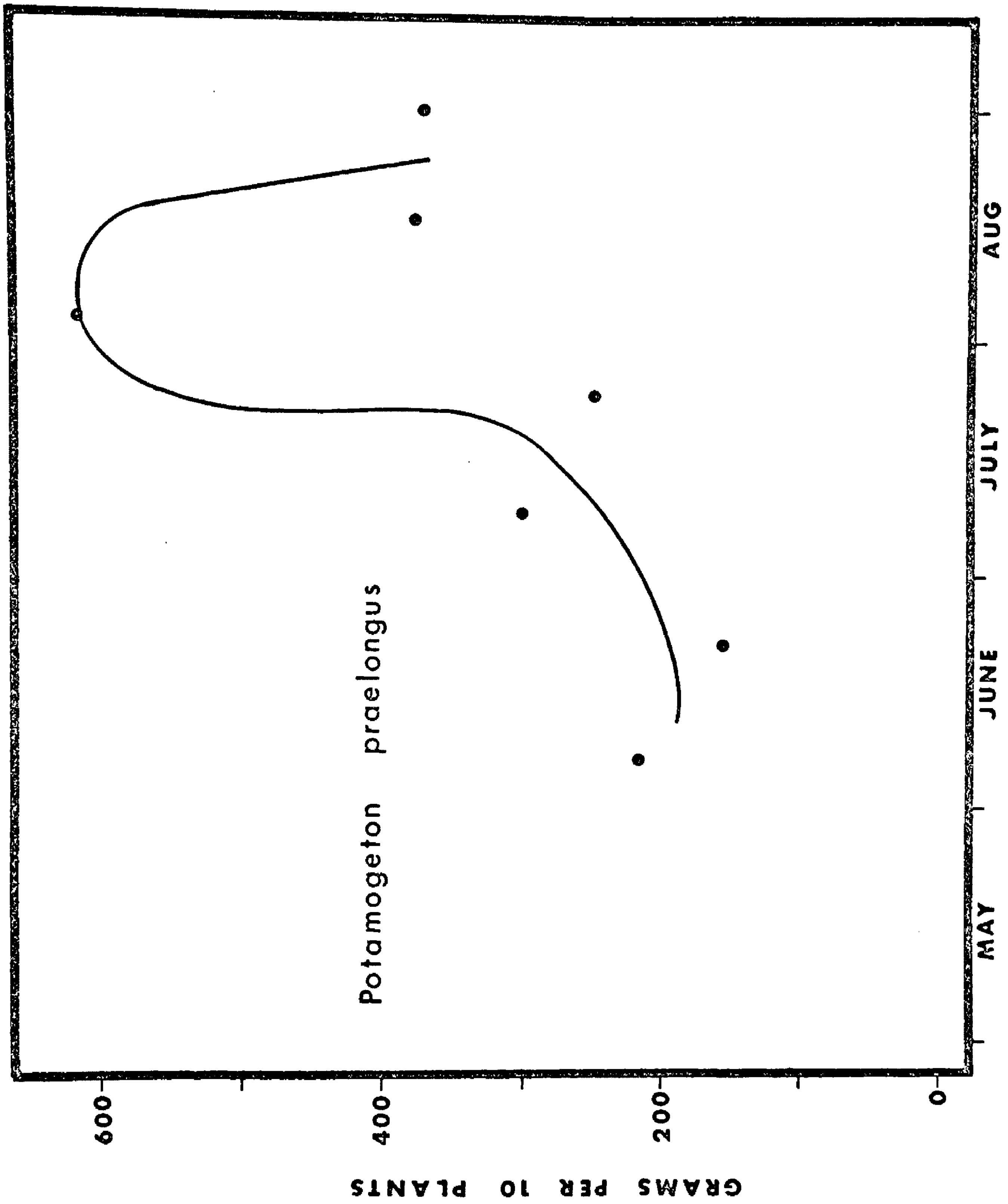
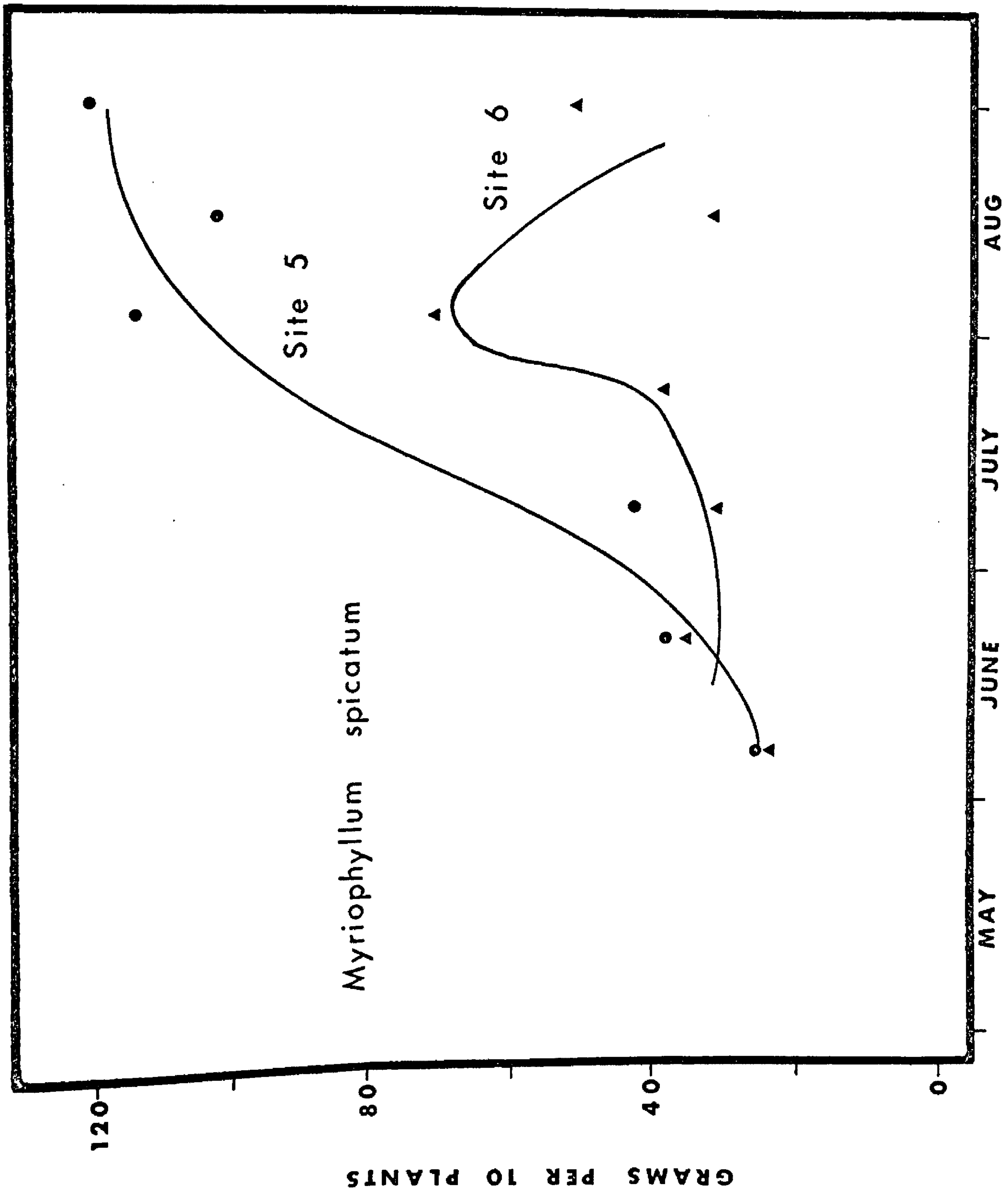

Potamogeton praelongus
GRAMS PER 10 PLANTS
600
400
200
0
MAY
JUNE
JULY
AUG

Figure 29. Seasonal changes in Myriophyllum spicatum biomass.


Myriophyllum spicatum
Site 5
Site 6
GRAMS PER 10 PLANTS
120
80
40
0
MAY
JUNE
JULY
AUG

biomass from late May to mid-August (Fig. 30). Seed production was extensive in all of the observed plants although depredation by waterfowl was light.

Ceratophyllum demersum exhibited a continual increase in biomass throughout the entire harvesting season (Fig. 31). Since this plant perennates by dormant apices much like Elodea canadensis (Sculthrope 1967), it appears that the growing season continues much longer than that of other submerged macrophytes which overwinter as winter buds, seeds, or underground tubers and rhizomes. Flowers were not observed on this species.

Thus, phenological observations of eight selected species indicate that the general growing season terminates by mid-August. Growth curves indicate some variations among the eight observed species. Chara vulgaris and Potamogeton praelongus appear to be early initiators of growth with Sagittaria cuneata being a late growth initiator.

Potamogeton pectinatus produced the most abundant seed crop while P. praelongus, P. richardsonii, and Myriophyllum spicatum produced only moderate seed crops. Ceratophyllum demersum, Elodea canadensis, and Potamogeton zosteriformis reproduced exclusively by vegetative means. Chara vulgaris produced extensive oogonia.

Figure 30. Seasonal changes in Potamogeton pectinatus biomass.

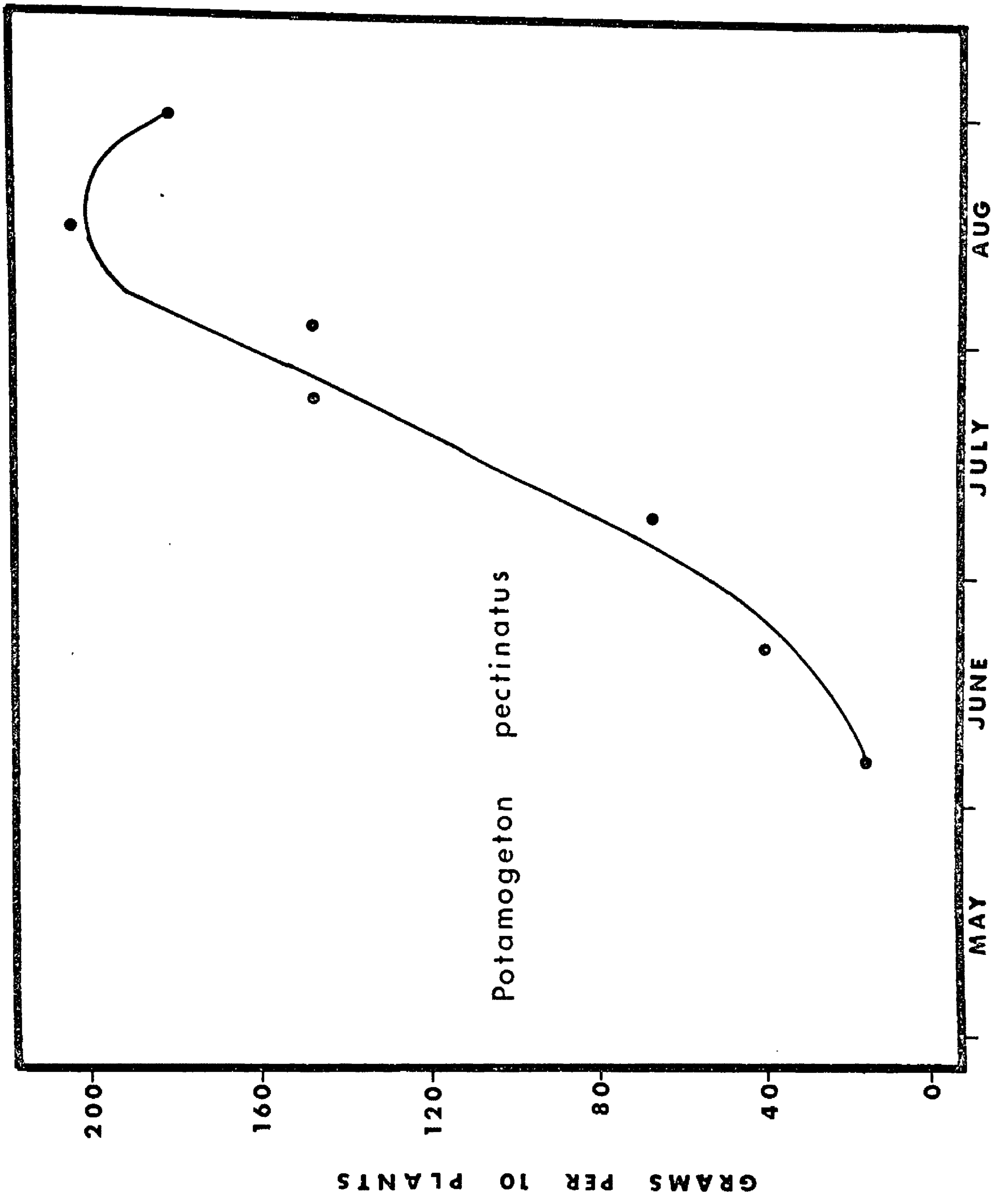
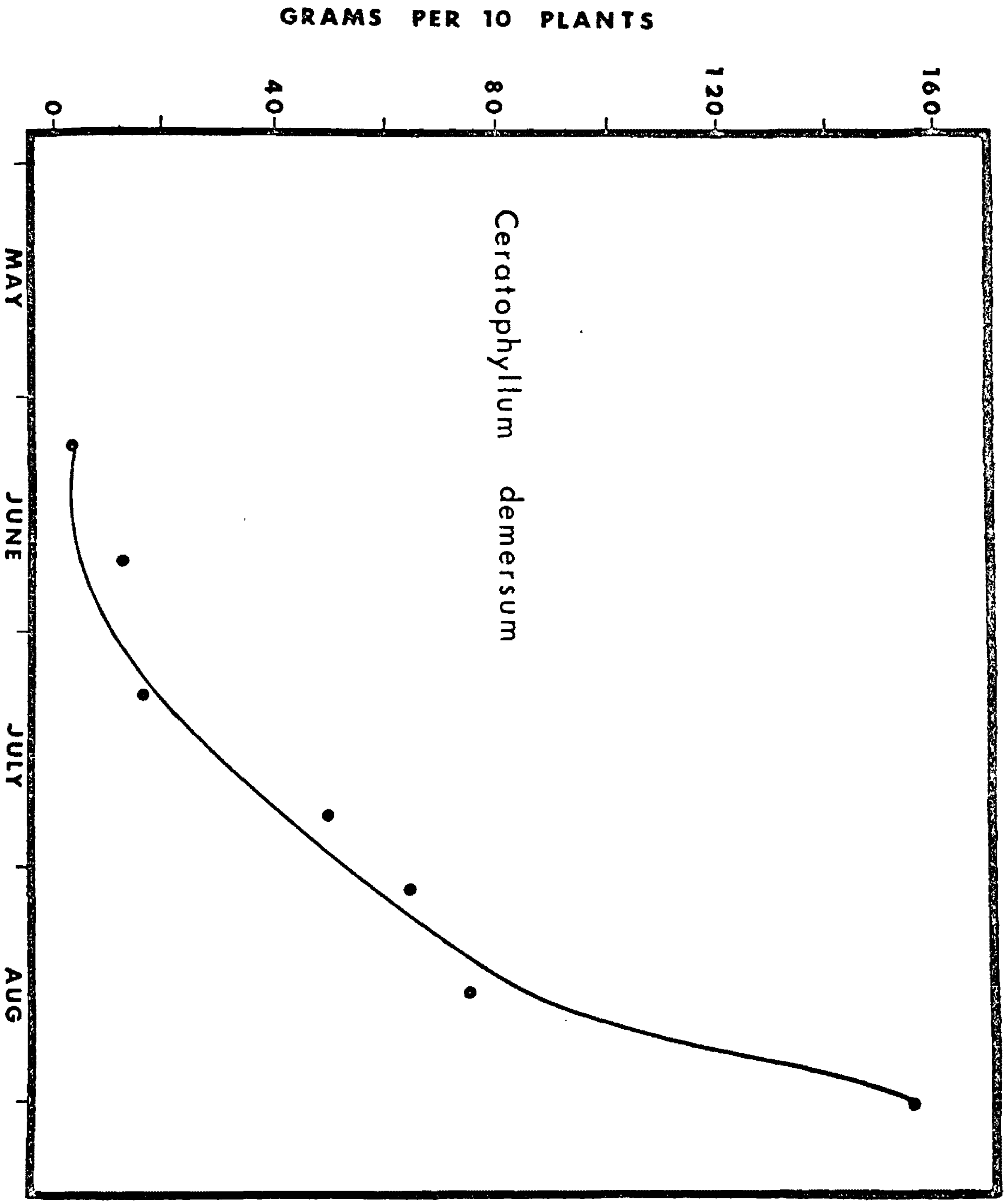

Potamogeton pectinatus
GRAMS PER 10 PLANTS
0
40
80
120
160
200
MAY
JUNE
JULY
AUG

Figure 31. Seasonal changes in Ceratophyllum demersum biomass.


GRAMS PER 10 PLANTS
0
40
80
120
160
MAY
JUNE
JULY
AUG
Ceratophyllum demersum

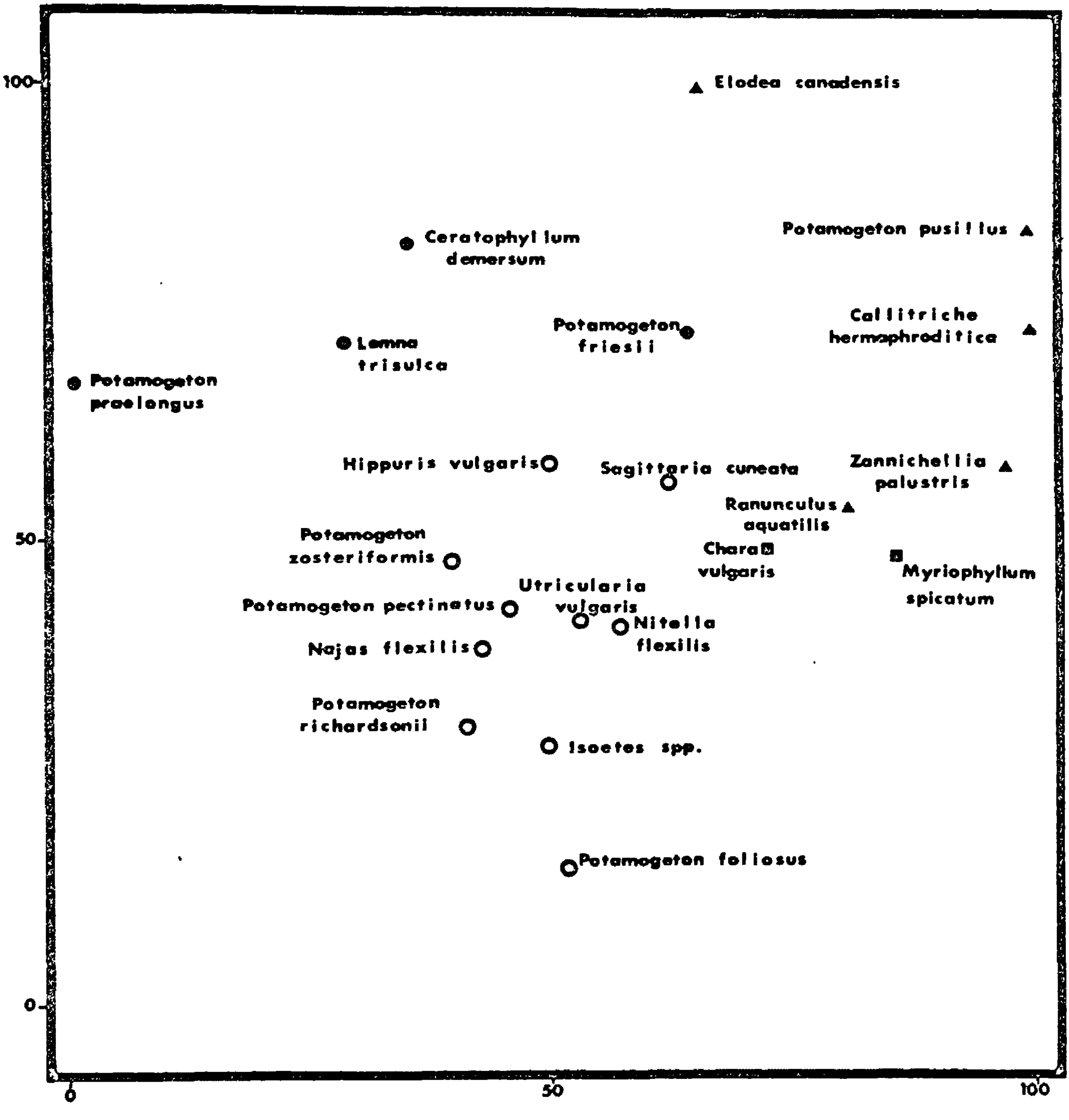
Association. Many phytosociologists have correlated plant distribution with certain environmental gradients (Beals 1968, Bray and Curtis 1957, Swindale and Curtis 1957, and Curtis and McIntosh 1951). The majority of these studies were conducted over large geographical areas where broad gradients in elevation, soils, climate, and aspect occurred. The difficulty of measuring environmental gradients in a limited area, such as the Refuge, where climate, aspect, and elevation are essentially constant, is obvious.

Because the aquatic plants on the Refuge respond to all environmental factors acting upon them, they can be used as indicators of the environment in which they live. By elucidating the phytosociological relationships of the plants to one another, a greater insight into the interaction between plant distribution and the environment can be gained. The initial phytosociological approach was directed at an ordination of individual plant species (Fig. 32) rather than plant communities or stands.

Spatial distance within the species ordination model is a direct reflection of plant association tendencies such that species close together are strongly associated and those separated by greater distances never or rarely occur together.

Each plant species has two numbers (X and Y) according to its location along the two axes of the ordination which Curtis and McIntosh (1951) refer to as adaptation numbers. The species

Figure 32. Ordination of submerged macrophyte species.


100
50
0
0
50
100
Elodea canadensis
Potamogeton pusillus
Ceratophyllum demersum
Potamogeton friesii
Callitriche hermaphroditica
Lemna trisulca
Potamogeton praelongus
Hippuris vulgaris
Sagittaria cuneata
Zannichellia palustris
Ranunculus aquatilis
Potamogeton zosteriformis
Chara vulgaris
Myriophyllum spicatum
Utricularia vulgaris
Potamogeton pectinatus
Nitella flexilis
Najas flexilis
Potamogeton richardsonii
Isoetes spp.
Potamogeton foliosus

distribution maps in Appendix V are arranged sequentially according to their "X" adaptation numbers so that the gradation in plant distribution is visually apparent. Species with high "X" adaptation values are generally most abundant in the Refuge ponds and species with low values are most abundant in Upper and Lower lakes. Intermediate species are found in Swan Lake and the River Marsh.

Each of the 21 species in the ordination model was placed within one of four groups based on their general tendency to aggregate in a particular portion of the ordination model. Species in group I are designated by dots, II by circles, III by squares, and IV by triangles. The four groups within the ordination of species coincide closely with the four groups found in the ordination of the lakes (Fig. 33) where the natural breaks in grouping are more evident. To avoid confusion, the symbols and numbers used in the species ordination are used simultaneously for the lake ordination model.

Environmental analysis. Some individual differences between ordination groups were noted for which no generalities could be formulated. However, statistical treatment of the 25 environmental parameters used in this analysis revealed some interesting trends and differences (Table 6). Among the 13 soil parameters tested, no significant differences in phosphorus, potassium, manganese, magnesium, sodium, and percentage of sand were found in

Figure 33. Ordination of the Refuge lakes and ponds.

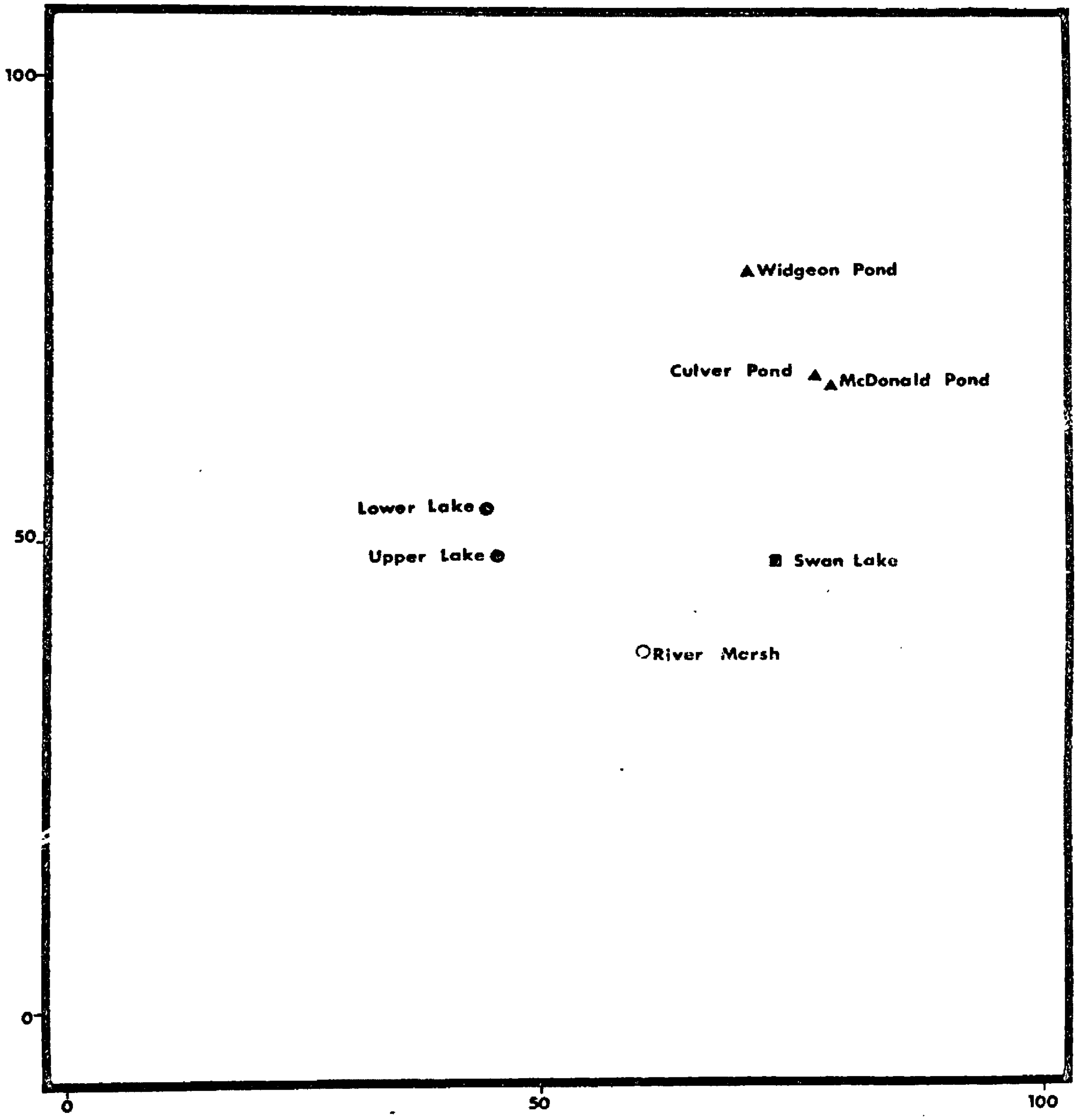

100
50
0
0
50
100
Widgeon Pond
Culver Pond
McDonald Pond
Lower Lake
Upper Lake
Swan Lake
River Marsh

Table 6

Environmental Analysis of Ordination Models (Significance levels of .01, .05, .10)

Species Ordination

Group I		Group IV	
Water	Soil	Water	Soil
Low Mg^{++} .10	High Fe^{++} .10	Low Color .10	Low Silt .10
	High Ca^{++} .10	Low Fe^{++} .10	High pH .10
		Low NO_3^- .10	Low Fe^{++} .10
		Low Turb. .10	
		Low $SO_4^=$ .10	
		High pH .10	
Group II		Group III	
Water	Soil	Water	Soil
	Low Clay .10	High pH .10	High pH .10
	High Organic Matter .10	Low Ca^{++} .10	
	High Ca^{++} .10		

Lake Ordination

I. Upper and Lower Lakes		IV. MacDonald, Widgeon and Culver Ponds	
Water	Soil	Water	Soil
Low Mg^{++} .05		High HCO_3^- .10	Low Silt .05
		High Total Hardness .10	High Clay .05
		Low Color .05	
		Low Fe^{++} .05	
		Low $SO_4^=$ .05	
		Low NO_3^- .05	
		Low Turb. .05	
II. River Marsh		III. Swan Lake	
Water	Soil	Water	Soil
Low $PO_4^=$ .05	Low Clay .05	High Color .05	High Fe^{++} .01
		High Total Hardness .05	High Salt .05
		High Fe^{++} .05	High Ca^{++} .01
		High pH .05	High Clay .05

either the lake or species ordination. Dissolved oxygen was the only water parameter that did not show any significant difference in either of the tested ordination models.

Within the lake ordination model the greatest differences noted were between the ponds and the marsh proper. Pond waters can be characterized as being extremely clear and almost sterile of many dissolved nutrients found in the marsh proper. The high bicarbonate alkalinity in the ponds is probably due to the close proximity of springs where bicarbonates from surrounding limestone deposits enter the ponds from ground water. The significantly small amounts of silt in the pond soils are to be expected, due to the lack of feeder streams which would normally carry silt loads into these ponds.

Environmental data collected in Swan Lake showed the greatest significant difference when compared to other lakes in the marsh proper. Characteristically, Swan Lake has the most highly colored water in the Refuge. In addition, Swan Lake water has the highest pH and iron concentrations. The large amounts of iron in the water are probably due to the large amounts of available iron in the lake substrate.

Swan Lake soils are significantly high in calcium and this is probably due to the extensive marl precipitation that takes place in this lake. The high clay fraction in the Swan Lake soils is probably due to the absence of any major, silt-laden, feeder-streams.

Waters of the River Marsh were significantly low in phosphates. Since the River Marsh is not fed directly by any major springs or streams, most phosphates entering the marsh from the surrounding watershed are probably assimilated or fixed before they reach the River Marsh.

It is readily apparent that the differences noted in the species ordination model are generally less statistically significant (Table 6) than the differences noted in the lake ordination model. This is probably due to the fact that the grouping in the species model overlapped lake boundaries.

Plant species on the left of the species ordination (Groups I and II) were significantly higher in soil calcium. This is probably due to the fact that these species grew in those portions of the marsh proper that received drainage water directly from the limestone-rich Centennial Mountains.

The right side of the species ordination (Groups III and IV) is characterized by high soil and water pH. This phenomenon is probably associated with the photosynthetic activity of large stands of closed vegetation such as Chara vulgaris, Myriophyllum spicatum, and Elodea canadensis. Other significant differences in the species ordination model follow those found in the lake ordination.

The impact of the tested environmental parameters upon plant distribution can be implied from these models, but the actual mechanisms, tolerances, and interactions of environmental parameters upon plant distribution are beyond the scope of this investigation.

Succession. The term "plant succession" as used in this investigation refers to changes in the structure and composition of vegetation with time (Shimwell 1971). Species composition and frequency data, collected from previous aquatic macrophyte surveys, serve as the basis for the plant successional discussion.

Unfortunately, there are no quantitative records of aquatic macrophyte communities prior to Beed's initial survey in 1955-56. Therefore, discussion of aquatic macrophyte succession is limited to the data collected over the 17-year-period 1955-1972 (Appendix VII).

Since no less than five different investigators participated in the aquatic macrophyte surveys during this period, some of the changes in species composition and frequency may reflect differences in sampling techniques and biases of the individual investigators. Despite these difficulties, some very evident successional trends can be discerned in the aquatic macrophytes of the Refuge.

Every surveyed lake or pond exhibited an increase in species diversity over the past 17 years. While this increase in the number of species recorded in each lake could be a reflection of an increased intensity of sampling, it is suspected that increases in diversity are attributable to the aging process occurring in each lake.

It has already been established (Fig. 21) that plant diversity increases with a decrease in water depth to a level of 2 feet. Thus, as lakes continually fill in with sediments from the surrounding watershed they become shallower and afford a more suitable habitat for a greater number of species. This theory is supported by the fact that plant species which were recently recorded in the lakes for the first time (Utricularia vulgaris, Hippuris vulgaris, Isoetes spp., Callitriche hermaphroditica, and Nitella flexilis) are all shallow water plants (Fig. 20).

Because of its relatively young age, Widgeon Pond lends much insight into this age-diversity phenomenon. Widgeon Pond was first surveyed in 1966 when the total lake diversity amounted to four species of aquatic macrophytes. Just five years later, total diversity was 12 species. Thus, it is felt that as lakes age, species diversity increases.

Fig. 20 reveals that, based on the average recorded lake depth for each plant species, diversity declines at depths less than 1 foot. This complication seems to pose some difficulties in generalizing the depth-diversity phenomenon. However, work conducted by Beed (1955-56) in Swan Lake reveals the probable involved mechanism.

By positioning steel fence posts around the periphery of emergent vegetation stands, Beed (1958) showed that Typha latifolia encroached 76 inches from the shoreline of Swan Lake where depths were less than 1 foot during the 3-year period (1955-1958).

In view of Beed's findings, it seems plausible to modify the diversity-depth generality to state that, as lake depth declines from very deep (6 to 9 feet) to moderately shallow (2 feet) diversity of submerged aquatic macrophytes increases. At shallow depths (less than 2 feet) submerged macrophyte diversity declines due to the encroachment of shoreline emergents.

The percentage of the lake bottoms covered by vegetation showed some interesting successional changes. In Beed's initial survey of Upper Lake in 1955-56, he calculated that the lake bottom was 88 percent vegetated and commented that, ". . . the very fertile bottom supports an almost unbelievably abundant and luxuriant plant growth." The 1971 survey revealed that Upper Lake was only 44 percent vegetated, and exhibited, especially in the deeper central lake regions, the greatest paucity of submerged macrophytes of any surveyed area. This dramatic change in Upper Lake seems to be attributable, at least in part, to a physical altering of the marsh environment.

In a follow-up study in 1958 Beed noted two remarkable changes in Upper Lake. First, lake depth measurements were approximately 12 inches deeper than the 1955-56 surveys. Secondly, due to the increased lake depth, wave action had reduced a once vertical 3-foot-high, soil bank on the Lake's north shore to a gentle sloping beach. A 100-yard wide strip of lake bottom adjacent to this shore was covered with a new layer of silt on which no submerged macrophytes grew.

The probable cause of this phenomenon was the construction of a water control structure in 1957 at the west boundary of the marsh. The net effect of this structure was the elevation of water levels by approximately 1 foot over much of the marsh. The increased shoreline erosion caused by the increased water depth resulted in drastic increases in the siltation of Upper Lake, which Beed (1958) noted probably retarded the normal flow of water in some parts of the marsh.

In 1958 Beed noted that increased siltation had completely plugged the outlet of Swan Lake. This condition was still prevalent in 1972; the outlet was almost completely occluded by silt. Blockage of the outlet is probably the reason why depth measurements for Swan Lake ranged from 1 to 11 inches in 1955-56 but averaged 2.1 feet in 1971.

The strong correlation between lake-bottom vegetation and lake depth (Fig. 22) suggests that the decline in the lake-bottom vegetation of Upper Lake after 1957 is, at least in part, due to the physical alteration of the marsh by the water control structure at the west marsh boundary. This theory is given additional support by the fact that Lower Lake was 81 percent vegetated in 1955-56 but only 64 percent vegetated in 1971. Vegetational data for the other lakes in the marsh proper are not available but it can be seen, at least in Upper and Lower lakes, that increased lake depths and siltation associated with the construction of the water control structure acted to set back the plant succession in these lakes.

Among the individual plant species, the greatest successional change since 1955 occurred in Elodea canadensis, which exhibited a marked decline throughout the entire Refuge. Beed (1956), in describing the growth of Elodea canadensis in Upper Lake, noted, "Elodea canadensis grows in pure stand over much of the area, especially in the deeper water." In 1971, Elodea canadensis was, for the most part, almost nonexistent in Upper Lake, especially in the deeper regions where most of the lake bottom was barren.

Statistical analysis of the species ordination model (Table 6) established the fact that the present distribution of Elodea canadensis is restricted to those waters of marked clarity where the lake bottoms are low in silt. Upper Lake, however, represents the antithesis of this condition, the silt content of the substrate and the turbidity of the water are high.

The impact of increased turbidity and siltation upon Elodea canadensis is unknown. It seems apparent from the early work of Beed (1956) that Upper Lake, prior to 1957, was very stable and supported a luxuriant bottom flora. Under those conditions, dense stands of *Elodea canadensis* probably stabilized the lake substrate and kept the turbidity, generally associated with strong afternoon winds, to a minimum.

Following the construction of the lower control structure in 1957, elevated lake levels and the concomitant wave action resulted in increased siltation and turbidity followed by a decline in *Elodea canadensis*. It was clearly evident in 1971-72 that the distrophic conditions following 1957 were still evident.

It is suspected that the deep water in the center of Upper Lake (5 to 7 feet) restricts the invasion of most submerged aquatics. At the time of this investigation, the only aquatic macrophytes which have reinvaded those areas in Upper Lake which previously supported *Elodea canadensis* are *Potamogeton praelongus*, *P. pectinatus*, and to a lesser degree *P. richardsonii*. Growth of these aquatics was sparse, and due to their open growth pattern, they have done very little to stabilize the distrophic conditions of Upper Lake.

The turbidity-siltation theory fails to account for the general decline in *Elodea canadensis* in the ponds and Lower Lake where turbidity and siltation are not a problem. A plausible explanation lies in the phenology of *Elodea canadensis* and the feeding habits of the trumpeter swan.

Appendix VIII reveals that of all the submerged macrophytes occurring on the Refuge, only Elodea canadensis, Ceratophyllum demersum, and Lemna trisulca remain dormant during the winter months when the lakes are frozen over. Consequently, Elodea canadensis represents one of the few available food plants for the trumpeter swan following spring breakup of the lakes.

Food studies conducted in 1971 by Refuge personnel revealed that Elodea canadensis is the preferred food plant of the trumpeter swan. Elodea canadensis is actively selected over other submerged aquatics.

Studies conducted by Page (1971, 1972) revealed that the trumpeter swan population of the Refuge peaked in 1954. Before that time Elodea canadensis was abundant throughout the Refuge (Beed 1956). During the 18-year period from 1954-1972, the resident swan population was maintained at an artificially high level by winter feeding programs conducted by Refuge personnel. During that period, the swans actually exceeded the natural carrying capacity of the range (Page, pers. comm.).

Since trumpeter swans have exceeded their carrying capacity for the past 18 years and they actively select Elodea canadensis, it seems plausible that the birds have overgrazed the plant and contributed to its decline. This theory is supported by observations made by Beed in 1960 who noted a marked change in the feeding patterns of the trumpeter swans on Upper Lake. In 1960, swans were observed feeding in areas where they never fed in 1955-56. Possibly this change in feeding sites was a direct response to declining Elodea canadensis stands following the 1957 disturbance.

The cause and affect relation between numbers of trumpeter swans and the abundance of Elodea canadensis is a matter of speculation. However, it is interesting to note that the decline of Elodea canadensis from 1955-1972 coincides with a decline in numbers of trumpeter swans during the same time period even though the present population (1972) still exceeds their natural carrying capacity.

Sculthrope (1967), in commenting on the spread of Elodea canadensis throughout the British Isles and western Europe, noted that after introduction, Elodea canadensis increased vigorously, and reached a maximum density after a few months to 4 years. The abundance phase persisted for as many as 5 years. Then, the plant began to wane, sometimes gradually and sometimes very quickly, occasionally to the point of complete extinction in local areas.

The overall conclusion implied by Sculthrope (1967) was that Elodea canadensis could not maintain a luxuriant and abundant growth over long periods of time. Thus, the decline in Elodea canadensis exhibited on the Refuge could be a natural course of events in the growth habit of the species.

Salisbury (1961) theorized that the decline of Elodea canadensis in Europe may be due to the fact, ". . . that some mineral nutrient or nutrients taken up by the plant becomes unduly depleted." Work conducted by Olsen (1954) indicates the possibility of iron as the limiting nutrient in the growth of Elodea canadensis.

Soil analysis data (Appendix II) indicate that available iron could be limiting Elodea canadensis growth on the Refuge. Historically, Swan Lake never contained Elodea canadensis beyond trace amounts primarily because of its shallow depths. Yet, Swan Lake soils have the highest (141-161 ppm) concentrations of available iron of any lake soils tested on the Refuge.

Lakes which presently support abundant stands of Elodea canadensis have the lowest available iron concentrations (Widgeon Pond, 62 ppm and Culver Pond, 75 ppm). Upper and Lower lakes, which both recently supported abundant stands of Elodea canadensis, are likewise low in available iron (93 ppm and 77 ppm, respectively). Statistical tests comparing available iron with the percent species composition of Elodea canadensis for each lake reveal a correlation coefficient of -0.63.

Thus, preliminary results indicate that the iron depletion phenomenon described by Sculthrope (1967) and Olsen (1954) could be acting within the Refuge lakes to limit growth of Elodea canadensis. More detailed field studies are needed before any concrete conclusions can be drawn.

The decline of Elodea canadensis over the past 17 years is well documented. As with most ecological phenomena the cause of the decline is probably due to several interrelated factors, the most likely being increased siltation and turbidity in localized Refuge lakes, overgrazing by trumpeter swans, and micronutrient depletion (iron).

The lack of constancy in the changes of the other submerged macrophytes prohibits advancing generalizations regarding their succession. The recent appearance and local abundance of *Lemna trisulca* and *Ceratophyllum demersum* warrant further mention.

Prior to 1971, *Lemna trisulca* was an uncommon plant in Lower Lake, yet in 1971 it comprised almost 34 percent of the vegetation sampled in that lake. Personal communication with Refuge personnel (Papike, pers. comm.) indicates that, in 1971-72, *Lemna trisulca* was occupying those areas of Lower Lake that once supported stands of *Elodea canadensis*. Indeed, statistical analysis of species composition data from previous surveys indicates that the correlation between the decline of *Elodea canadensis* and the increase of *Lemna trisulca* in Lower Lake is remarkably significant ($r = -0.99$).

Several features of the physiology and phenology of *Lemna trisulca* are unique among the Refuge aquatic flora, and quite possibly can account for the increase of this plant. Appendix VIII reveals that *Lemna trisulca* is one of the few submerged aquatic macrophytes on the Refuge that lies in a dormant state during the winter months. Thus in early spring, mats of *Lemna trisulca* can begin new growth without much competition from other submerged macrophytes.

In commenting on the growth habit of the closely related species *Lemna minor*, Sculthrope (1967), notes that *Lemna* growth is greatly enhanced by increased amounts of sunlight. It thus seems plausible that, as the lake bottom began to open up with the decline of *Elodea canadensis*, *Lemna trisulca* could increase its abundance and range by the increased amounts of sunlight reaching the bottom of Lower Lake. In addition, Sculthrope (1967) mentions that *Lemna* thalli usually increase exponentially so that *Lemna trisulca* could conceivably invade newly opened areas faster than other species of submerged macrophytes.

The dense, closed pattern of *Lemna trisulca* mats occur almost to the complete exclusion of all other submerged macrophytes. They thus appear to be very affective competitors for the nutrients and light in local areas of Lower Lake. The lack of *Lemna trisulca* in Upper Lake where *Elodea canadensis* has also drastically declined is probably due to deeper water and increased turbidity which both act to limit the amount of sunlight that is crucial for the growth of *Lemna trisulca*.

Appendix VIII reveals that *Ceratophyllum demersum*, like *Lemna trisulca*, overwinters by dormancy. Thus, by lying dormant rather than decomposing, the parent plants of *Ceratophyllum demersum* have limited competition for the available nutrients immediately following spring breakup of ice on the lakes. The most significant increases in *Ceratophyllum demersum* occurred in Lower Lake and Widgeon Pond, both areas where *Elodea canadensis* has declined. Like *Lemna trisulca*, *Ceratophyllum demersum* appears to be invading areas that were once vegetated by *Elodea canadensis*.

Nutritional analysis. Preliminary nutritional analyses (Appendix IX) of the above-ground vegetative structures of 11 selected plant species, indicate that the submerged macrophytes of the Refuge compare favorably with agriculturally important forage plants and seeds. Samples of the wheat (*Triticum aestivum*) which is fed to the trumpeter swans during winter was also analyzed for comparative purposes.

The calcium content of the plants examined exceeds the normal range of 1.0-1.5 percent for legumes (Hausenbuiller 1972) in every case. High calcium concentrations are especially noticeable in *Chara vulgaris*, *Potamogeton zosteriformis*, *P. pectinatus*, and *P. praelongus*. The high calcium concentration of the Refuge macrophytes is attributable to the calcareous nature of the lake waters and the extensive formation of marl ($CaCO_3$) which precipitates as a white crust on the leaves of these plants.

The phosphorus content of the macrophytes falls within the normal range for most plants (Hausenbuiller 1972). The above-average phosphorus concentration in Sagittaria cuneata is attributable to its late growth habit (Fig. 25), since phosphorus content is usually high in actively growing plants (Hausenbuiller 1972). The high phosphorus content in wheat is normal for seeds (Hausenbuiller 1972).

The analyzed plants are favorably high in protein. The average protein content of the macrophytes examined exceeds that of buckwheat and corn (McAtee 1939), oats (Martin et al., 1951), polished rice, pearled barley, and cracked wheat (Martin and Uhler 1939).

The crude fat content of the examined plants falls below the level of most of the cereal grains mentioned above. This phenomenon seems to be inherent in aquatic plants (McAtee 1939, Gortner 1934).

Crude fiber contents are higher than that of cereal grains; this is to be expected considering the differences in the plant parts which were sampled. The high moisture content in comparison to that of terrestrial plants is also to be expected considering the internal plant anatomy and the aquatic environment in which these plants grow.

Thus, it can be seen that nutritional analyses of selected species of submerged macrophytes indicates that these plants are very nutritious food sources. The selectivity of feeding waterfowl was noted (Table 7). A more detailed analysis of selected plant parts (tubers, rhizomes, seeds) at different times of the year should reveal a more conclusive picture of the nutritional value of submerged macrophytes.

Food plant preference. The primary management objective of Red Rock Lakes Refuge is the preservation of the nesting and resting habitat of the trumpeter swan. Thus, any marsh manipulation directed towards the submerged macrophytes should center around enhancing the abundance of those plant species preferred by trumpeter swans.

The relative importance of submerged macrophytes as a food source for waterfowl is well documented (Martin et al. 1951, Moyle and Hotchkiss 1945, Martin and Uhler 1939, McAtee 1939). Table 7 summarizes the importance of the submerged macrophytes of the Refuge as food sources for waterfowl (primarily ducks) based on the findings of these authors.

Unfortunately, there is a dearth of information on the food habits and preferences of the trumpeter swan. Martin et al. (1951) established the fact, based on six stomach analyses of trumpeter swans collected in British Columbia and Montana, that Potamogeton pectinatus seeds and vegetative structures comprised the bulk (60 percent) of the food present in the stomachs. Vegetative structures of Ranunculus, Sagittaria, and Scirpus were present in lesser (2 - 10 percent) amounts.

Table 7

Submerged Food Plant Ratings for Waterfowl

Rating	Species	Parts Consumed
Excellent	*Potamogeton pectinatus	seeds and tubers
	*Chara vulgaris	entire plant
Good	*Sagittaria cuneata	tubers
	Potamogeton richardsonii	seeds
	Potamogeton friesii	seeds
	Potamogeton foliosus	seeds and leaves
	Najas flexilis	entire plant
	Zannichellia palustris	seeds
	Polygonum amphibium	seeds
	Lemna trisulca	entire plant
Fair	*Elodea canadensis	stems and leaves
	Potamogeton praelongus	seeds
	Potamogeton zosteriformis	seeds
	Potamogeton pusillus	seeds
	Ceratophyllum demersum	seeds and leaves
	Ranunculus aquatilis	seeds
	Hippuris vulgaris	seeds
Poor	Myriophyllum spicatum	seeds

*Important food sources of trumpeter swans.

Banko (1960), commenting on observations made in Yellowstone Park, documents the use of Potamogeton filiformis, Carex rostrata, Elodea canadensis, Lemna trisulca, Sagittaria cuneata, Chara spp., Myriophyllum spp., Scirpus spp., Nuphar polysepalum, and Sparganium augustifolia as food sources of the trumpeter swan.

Examination of two trumpeter swan stomachs in 1938 (Banko 1960) revealed 443 and 597 tubers of Potamogeton pectinatus in the samples. Leaf material from Ceratophyllum demersum and seeds from Carex spp., Hippuris vulgaris, Scirpus acutus, Sparganium spp., and Zannichellia palustris were also recorded.

Thus, preliminary food-habit studies reveal that the trumpeter swan is a highly opportunistic feeder, taking a wide variety of submerged and emerged plant matter. However, based on previous studies and observations during 1971-1972, several plant species appear to be of primary importance to adult swans.

Vegetative plant parts of Elodea canadensis are actively eaten by the swans whenever available. This plant probably constitutes the most important submerged food source because of its prolonged availability and its notable preference by the swans. Chara vulgaris is extensively fed upon in early spring by large concentrations of swans. This phenomenon seems to be related to the early availability of this macrophytic alga (Fig. 27). Tubers of Sagittaria cuneata are relished perhaps even more than Elodea canadensis, but the limited abundance and availability of this species tends to limit its importance. Tubers of Potamogeton pectinatus are also actively eaten by the swans.

In addition to the submerged species, seeds of the emergent sedges (Carex spp.) appear to be a primary food source for swans. The great abundance of Carex stands on the Refuge represent an almost inexhaustible food source; however, availability of the sedges is greatly hampered by the dense growth which makes most of the plants inaccessible to feeding swans.

Chapter V

SUMMARY AND CONCLUSIONS

A study of the submerged macrophytes of Red Rock Lakes National Wildlife Refuge in southwestern Montana was conducted from June 1971 to October 1972. The study area encompassed the 5, 600 acres comprising the seven major lakes and ponds of the Refuge. The primary objectives of this study were to determine the distribution, abundance, phenology, and successional trends of the submerged macrophytes, and to determine what chemical and physical factors in the soils and waters of the Refuge lakes are important in regulating the distribution and productivity of these plants.

Lake-bottom soils were very fertile with high concentrations of available calcium, magnesium, potassium, iron and organic matter. The soils were slightly alkaline, nonsaline, and low in available sodium and phosphorus.

Refuge lakes and ponds were remarkably clear with the entire marsh being a euphotic zone. The analyzed waters were alkaline, calcareous, and hard. Turbidity of the waters varied directly with lake size and color varied with proximity to acid peat soils of emergent Carex communities. The biological and physical processes of photosynthesis, decomposition, and summer stagnation caused fluctuations in soluble iron, sulfates, nitrates, phosphates, and dissolved oxygen during the summer months.

Refuge lakes were dimictic with stratification and stagnation occurring during summer. Average depth and shoreline development were indicators of the successional age of the lakes. Stream discharge measurements revealed that influent and effluent rates declined throughout the summer with lake levels fluctuating accordingly; the magnitude varied with proximity of feeder streams and shape of the lake basin.

Plant pattern was a function of the reproductive mechanism exhibited by individual species. Plants reproducing vegetatively exhibited a closed pattern, and sexually-reproducing plants showed a more open pattern. Stratification of macrophytes was directly related to water depths, with low stature ground plants limited to shallow shoreline areas and tall plants most abundant in the deeper regions of the lakes.

Zonation responses to increasing lake depths were demonstrated among the macrophytes. *Utricularia vulgaris* and *Hippuris vulgaris* occurred in the shallowest lake regions, and *Elodea canadensis* and *Potamogeton praelongus* were restricted to the deepest regions.

Species diversity increased with decreasing lake levels to a depth of 2 feet. Encroachment of emergent vegetation at depths less than 2 feet decreased submerged macrophyte diversity. Total plant abundance expressed as the percentage of the lake bottom vegetated, was strongly correlated with decreasing lake depths.

Observations of eight selected macrophyte species indicate that the general growing season terminated by mid-August. Chara vulgaris and Potamogeton praelongus were early initiators of growth, and Sagittaria cuneata was a late initiator.

Ordination models and statistical tests showed that waters of Widgeon, Culver, and MacDonald ponds were significantly high in bicarbonate alkalinity and total hardness, and low in water color, iron, sulfates, nitrates, and turbidity. The pond soils were significantly low in percentage of silt. Species distribution maps revealed that Elodea canadensis, Zannichellia palustris, Callitriche hermaphroditica, and Ranunculus aquatilis were most abundant in these ponds.

Lemna trisulca, Potamogeton praelongus, P. friesii, P. zosteriformis, Najas flexilis, Nitella flexilis, Hippuris vulgaris, Sagittaria cuneata, Isoetes spp., and Utricularia vulgaris were restricted to the marsh proper where nutrient levels in the soil and water were higher than in Refuge ponds.

The greatest successional change exhibited by the Refuge macrophytes during the 17-year period, 1955-1972, was that of

Elodea canadensis, which declined throughout all of its former range. The decline was attributable to physical distrubance, overgrazing by trumpeter swans, and micronutrient depletion. The recent increase in Lemna trisulca was strongly correlated to the decline in Elodea canadensis.

Nutritional analysis of selected plant species revealed that submerged macrophytes are nutritious food sources and compared favorably with cereal grains.

LITERATURE CITED

Anonymous. 1939-1972. Annual Narratives, Red Rock Lakes National Wildlife Refuge.

Arneson, R. D. 1969. Primary productivity studies in Quake Lake Montana. Unpubl. thesis (M. S.). Montana State University, Bozeman. 97 pp.

Banko, W. E. 1960. The trumpeter swan. N. Am. Fauna No. 63. U. S. Fish and Wildl. Serv., Washington, D. C. 214 pp.

Beals, E. W. 1969. Vegetation of the Erer-Gota Plain, Ethiopia. J. Ecol. 57:655-667.

Bear, F. E. 1964. Chemistry of the soil. 2nd ed. Reinhold Publ. Co., New York. 515 pp.

Beed, Watson E. 1957. Red Rock Lakes aquatic survey. U.S. Fish and Wildl. Serv. Report. 15 pp. Mimeo.

_________. 1958. Memorandum, Red Rock Lakes Refuge. 2 pp. Mimeo.

_________. 1960. Range, aquatic plants and water depth check--Red Rock Lakes. U.S. Fish and Wildl. Serv. Report. 3 pp. Mimeo.

Bray, R. J., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Mono. 27: 325-349.

Brower, J. V. 1897. The Missouri River. Pioneer Press, St. Paul, Minnesota. 206 pp.

Buckman, H. O., and N. C. Brady. 1960. The nature and properties of soils. 6th ed. The MacMillan Co., New York. 567 pp.

_________. 1969. The nature and properties of soils. 7th ed. The MacMillan Co., New York. 653 pp.

Cook, A. H., and C. F. Powers. 1958. Early biochemical changes in the soils and waters of artificially created marshes in New York. N.Y. Fish and Game Jour. 5:9-65.

Cressman, E. R., and R. W. Swanson. 1960. Permian rocks in the Madison, Gravelly, and Centennial Ranges, Montana. Billings Geol. So., 11th Ann. Field Conf. Guidebook. pp. 226-232.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecol. 32:476-496.

Den Hartog, C., and S. Segal. 1964. A new classification of the water plant communities. Acta. Bot. Neerl. 13:367-393.

Domogalla, B. P., C. Juday, and W. H. Peterson. 1925. The forms of nitrogen found in certain lake waters. J. Biol. Chem. 63:269-285.

Eardley, A. J. 1951. Structural geology of North America. Harper Bros., New York. 624 pp.

Egbert, R. L. 1960. Geologic map of the Madison Valley-Hebgen Lake, southwestern Montana. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook (pocket).

Fernald, M. L. 1932. Linear-leaved North American species of Potamogeton. Mem. Gray Herb. III. (Mem. Am. Acad. Arts and Sci.). XVII:1-183.

Gortner, R. A. 1934. Lake vegetation as a possible source of forage. Sci. 80:531-533.

Gottschalk, J. S. 1970. Second annual status report on wilderness review within National Wildlife Refuge system. Fed. Reg. 35: 6597-6598.

Hanson, A. M. 1960. Cambrian of the Madison River Valley area. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 207-212.

Hausenbuiller, R. L. 1972. Soil science (principles and practices). Wm. C. Brown Co. Publ., Dubuque, Iowa. 504 pp.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompsen. 1969. Vascular plants of the Pacific Northwest. Univ. Wash. Press, Seattle. Vol. I-IV.

Honkala, F. S. 1960. Structure of the Centennial Mountains and vicinity, Beaverhead County, Montana. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 107-113.

________. 1967. The Phosphoria Formation in Montana. Mont. Geol. Soc., 18th Ann. Field Conf. Guidebook. pp. 7-17.

Horowitz, Wm. (ed.). 1965. Official methods of analysis of the Association of Official Analytical Chemists. George Banta Co. Inc., Menasha, Wisconsin. 957 pp.

Hutchinson, G. E. 1957. A treatise on limnology. I. Geography, physics, and chemistry. John Wiley & Sons, Inc., New York. 1115 pp.

Kummel, B. 1960. The Triassic of southwestern Montana. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 233-238.

Luther, H. 1949. Vorschlag zu einer okologischen Grundeinteilung der Hydrophyten. Acta bot. Fenn. 44:1-15, cited by C. D. Sculthrope, The biology of aquatic vascular plants. St. Martin's Press, New York, 1967. p. 7.

Mann, H. B., and D. R. Whitney. 1947. On a test of whether one of two random variables is stochastically larger than the other. Am. Math. Statist. 18:50-69.

Mann, J. A. 1954. Geology of part of the Gravelly Range Montana. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 114-127.

Martin, A. C., and F. M. Uhler. 1939. Food of game ducks in the United States and Canada. U.S. Dept. Agr. Tech. Bull. No. 634. 156 pp.

________, H. S. Zim, and A. L. Nelson. 1951. American wildlife plants: a guide to wildlife food habits. Dover Publ. Inc., New York. 500 pp.

McAtee, W. L. 1939. Wildfowl food plants. Collegiate Press, Inc., Ames, Iowa. 141 pp.

Moritz, C. A. 1960. Summary of the Jurassic stratigraphy of southwestern Montana. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 239-243.

Moyle, J. B., and N. Hotchkiss. 1945. The aquatic and marsh vegetation of Minnesota and its value to waterfowl. Minn. Dept. of Cons. Tech. Bull. 3. 122 pp.

Nielson, E. C., and D. H. Farnsworth. 1965. Soil survey handbook for Red Rock Lakes Migratory Waterfowl Refuge. U.S. Dept. of Agr., Soil Cons. Serv. 175 pp.

Ogden, E. C. The broad-leaved species of Potamogeton of North America north of Mexico. Rhodora 45:57-105, 119-163, 171-214.

Ohle, W. 1934. Chemische und physikalische Untersuchungen norddeutscher. Seen. Arch. Hydrobiol. 26:386-464, cited by G. Evelyn Hutchinson, A treatise on limnology. I. Geography, physics, and chemistry. John Wiley & Sons, Inc., New York. pp. 729, 850.

Olsen, H. 1954. Hvilke betingelser ma vaere opfyldte for at Helodea canadensis kan opna den optimale udvickling, der er arsag til dens massevise optraeden i naturen? Bot. Tidssky. 51:263-273, cited by C. D. Sculthrope, The biology of aquatic vascular plants. St. Martin's Press, New York, 1967. p. 364.

Page, R. D. 1971. First Annual Report--The ecology of the trumpeter swan on Red Rock Lakes Refuge, Montana. Ph.D. Progress Report. 33 pp. Mimeo.

_________. 1972. Second Annual Report--The ecology of the trumpeter swan on Red Rock Lakes Refuge, Montana. Ph.D. Progress Report. 39 pp. Mimeo.

Penfound, W. T. 1952. An outline for ecological life histories of herbaceous vascular hydrophytes. Ecol. 33:123-28.

Prescott, G. W. 1962. Algae of the western Great Lakes. Wm. C. Brown Co., Dubuque, Iowa. 977 pp.

Raunkier, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford. 632 pp.

Rawson, D. S. 1944. The calculation of oxygen saturation values and their correction for altitude. Limnol. Soc. Am. Spec. Publ. No. 15, cited by G. K. Reid. Ecology of inland waters and estuaries. Van Nostrand Co., New York. pp. 147.

Reid, G. K. 1961. Ecology of inland waters and estuaries. Van Nostrand Reinhold Co., New York. 375 pp.

Salisbury, E. J. 1961. Weeds and aliens. Collins, London, cited by C. D. Sculthrope. The biology of aquatic vascular plants. St. Martin's Press, New York, 1967. p. 364.

Scholten, R. 1967. Structural framework and oil potential of extreme southwestern Montana. Mont. Geol. Soc., 18th Ann. Field Conf. Guidebook. pp. 7-17.

Sculthrope, C. D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York. 610 pp.

Shapiro, J. 1957. Chemical and biological studies on the yellow organic acids of lake water. Limnol. and Oceanog., Vol. 2, 161-179.

Shimwell, D. W. 1971. The description and classification of vegetation. Univ. Wash. Press, Seattle. 322 pp.

Strickland, J. W. 1960. Summary of Mississippian stratigraphy, western Wyoming and vicinity. Billings Geol. Soc., 11th Ann. Field Conf. Guidebook. pp. 217-225.

Swindale, D. N., and J. T. Curtis. 1957. Phytosociology of the larger submerged plants in Wisconsin lakes. Ecol. 37:397-406.

Webster, C. 1965. Habitat inventory techniques. Region I, U. S. Bureau of Sport Fisheries and Wildl. Report. 10 pp. Mimeo.

Appendix I

Upland Soil Analysis, Red Rock Lakes Refuge
June, 1971

Site No.	pH	% Organic Matter	Parts Per Million			
			Phosphorus	Potassium	Nitrate	Manganese
1	9.4	3.1	>123 h	>2000 h	0.0	9.34
2	8.9	3.4	66 m	>2000 h	0.0	13.50
3	7.9	>5.7	25 vl	1596 h	2.5	>20.
4	8.4	>5.7	48 l	>2000 h	1.0	>20.
5	6.9	>5.7	103 h	1706 h	0.0	16.26
6	6.7	>5.7	40 l	1490 h	1.0	18.20
7	6.9	>5.7	100 h	1510 h	0.0	12.04
8	7.5	>5.7	>123 h	>2000 h	2.5	>20
9	6.2	>5.7	48 l	1360 h	0.5	>20
10	6.9	>5.7	75 h	1294 h	0.5	>20
11	7.3	>5.7	25 vl	1426 h	1.5	>20
12	7.4	>5.7	43 l	1102 h	4.3	>20
13	7.5	>5.7	3 vl	844 h	2.0	>20
14	6.7	>5.7	>123 h	1080 h	1.5	>20
15	7.5	>5.7	60 m	622 h	0.5	14.54
16	7.0	>5.7	123 h	1040 h	3.3	>20
17	7.2	>5.7	79 h	844 h	0.0	>20
18	7.6	>5.7	34 l	270 h	0.0	>20
19	7.5	>5.7	>123 h	1040 h	1.5	>20
20	7.6	5.6	69 m	1230 h	0.5	12.86
21	6.8	>5.7	48 l	1618 h	0.0	11.60
22	6.6	>5.7	123 h	826 h	0.5	>20
23	6.7	>5.3	>123 h	788 h	0.0	>20
24	8.1	>5.7	15 vl	714 h	1.0	12.04
25	8.1	>5.7	40 l	980 h	1.0	17.78
26	6.5	>5.7	93 h	1338 h	0.5	>20
27	6.5	>5.7	107 h	960 h	0.0	>20
28	7.9	>5.7	23 vl	344 h	0.0	>20
29	8.7	2.8	5 vl	806 h	0.0	14.54
30	6.4	>5.7	103 h	586 h	0.0	>20
31	7.1	2.4	75 h	494 h	0.0	9.16
32	8.0	1.7	48 l	476 h	0.0	16.46
33	8.3	.25	43 l	176 m	0.0	6.84
34	7.7	>5.7	14 vl	324 h	4.3	>20
35	8.6	>5.7	3 vl	>2000 h	9.0	>20
36	8.9	>5.7	34 l	>2000 h	3.8	>20

Legend

vl - very low
l - low
m - medium
h - high
> - more than
< - less than

Appendix I (continued)

Site	meq/100g Soil			Parts Per Million		
No.	Calcium	Magnesium	Sodium	Zinc	Iron	Copper
1	>14.00	>9.87	>15.7	.45	6.2	1.9
2	>14.00	4.80	8.49	.82	8.6	.8
3	>14.00	>9.87	.96	.89	7.1	.9
4	>14.00	>9.87	>15.7	1.64	>30.0	5.1
5	>14.00	>9.87	.73	3.28	>30.0	1.7
6	>14.00	>9.87	.73	>4.0	>30.0	1.8
7	>14.00	>9.87	.61	1.01	>30.0	1.2
8	>14.00	>9.87	1.57	>4.0	>30.0	1.3
9	>14.00	>9.87	.73	>4.0	>30.0	3.3
10	>14.00	8.06	.61	>4.0	>30.0	1.1
11	>14.00	>9.87	1.32	>4.0	>30.0	4.3
12	>14.00	>9.87	.61	>4.0	>30.0	1.5
13	>14.00	>9.87	1.32	>4.0	>30.0	2.6
14	>14.00	>9.87	.61	>4.0	>30.0	1.6
15	>14.00	8.49	.47	>4.0	>30.0	1.2
16	>14.00	>9.87	.47	>4.0	>30.0	1.5
17	>14.00	>9.87	.47	>4.0	>30.0	2.3
18	>14.00	>9.87	.61	>4.0	>30.0	8.0
19	>14.00	>9.87	.47	>4.0	>30.0	1.4
20	>14.00	7.70	.47	1.72	19.7	1.1
21	>14.00	>9.87	.47	1.44	>30.0	2.4
22	>14.00	>9.87	.47	>4.0	>30.0	1.7
23	>14.00	>9.87	.47	3.89	>30.0	1.6
24	>14.00	>9.87	.73	1.92	11.6	2.2
25	>14.00	>9.87	.61	1.72	29.4	1.3
26	>14.00	8.06	.47	>4.0	>30.0	1.3
27	>14.00	5.53	.47	2.99	>30.0	1.1
28	>14.00	>9.87	.73	2.58	>30.0	1.4
29	>14.00	>9.87	1.69	.38	12.2	.5
30	>14.00	3.09	.47	>4.0	>30.0	.9
31	8.00	3.09	.47	1.24	22.5	.5
32	11.36	2.24	.61	.67	>30.0	.7
33	>14.00	1.02	.47	.38	7.1	.3
34	>14.00	>9.87	1.44	>4.0	>30.0	4.6
35	>14.00	>9.87	8.49	.97	10.4	1.0
36	>14.00	>9.87	>15.7	2.33	22.2	.9

Appendix I (continued)

Site No.	Salt Hazard (mmhos)	Soil Texture
1	15.4 strongly salty	clay
2	2.0 slightly salty	loam
3	1.8 ok	loam
4	2.9 slightly salty	loam
5	0.8 ok	loam
6	0.8 ok	loam
7	0.8 ok	loam
8	2.0 slightly salty	loam
9	1.1 ok	loam
10	0.8 ok	loam
11	1.5 ok	loam
12	1.0 ok	loam
13	2.2 slightly salty	loam
14	2.4 slightly salty	sandy loam
15	1.0 ok	loam
16	1.1 ok	loam
17	0.6 ok	loam
18	1.0 ok	loam
19	1.0 ok	loam
20	0.8 ok	loam
21	0.8 ok	loam
22	0.6 ok	loam
23	0.4 ok	loam
24	0.4 ok	loam
25	0.9 ok	sandy loam
26	0.7 ok	loam
27	0.5 ok	loam
28	1.3 ok	loam
29	1.3 ok	sandy loam
30	0.4 ok	sandy loam
31	0.3 ok	sandy loam
32	0.5 ok	sandy loam
33	0.3 ok	sandy loam
34	3.0 slightly salty	loam
35	4.6 moderately salty	loam
36	4.6 moderately salty	loam

Appendix II

Lake Sediment Analysis

Sample No.	pH	Parts Per Million							Salinity (mmhos)	Percent				Texture
		P	K	Fe	Mn	Ca	Mg	Na		Organic Matter	Sand	Silt	Clay	
1	7.7	1	256	72	32	8,400	634	131	3.0	8.0	21.92	43.36	34.72	Clay Loam
2	8.0	1	208	72	42	7,600	720	150	1.5	4.4	10.0	33.28	56.72	Clay
3	7.8	1	272	85.5	39	9,600	805	150	3.2	9.2	20.72	39.2	40.08	Silty Clay Loam
4	7.7	1	320	142.5	30	12,400	1,554	239	3.7	21.6	32.80	19.12	48.08	Clay
5	7.8	1	208	157.5	32	12,000	1,229	179	3.3	18.8	22.0	21.28	56.72	Clay
6	7.7	1	304	160.5	33	12,400	1,642	239	4.0	21.6	20.0	29.36	50.64	Clay
7	7.9	1	256	82.5	26	9,600	677	150	1.5	8.0	32.88	24.2	42.92	Clay
8	7.7	1	416	117.0	40	12,000	1,403	331	2.2	19.6	24.16	42.64	33.20	Clay Loam
9	7.7	1	288	109.5	43	12,000	989	161	3.0	19.6	26.16	32.56	41.28	Clay
10	7.7	1	368	102	43	11,600	1,530	161	3.7	19.2	50.68	22.56	26.76	Sandy Clay Loam
11	7.8	1	320	121.5	48	11,600	1,692	200	3.0	19.2	42.88	22.48	34.64	Clay Loam
12	7.6	40	416	73.5	36	12,400	1,754	200	3.0	28.0	28.72	35.56	36.72	Clay Loam
13	7.8	13	272	87	50	9,600	711	131	2.5	10.8	22.32	26.56	51.12	Clay

Appendix II (continued)

Sample No.	pH	Parts Per Million							Salinity (mmhos)	Percent				Texture
		P	K	Fe	Mn	Ca	Mg	Na		Organic Matter	Sand	Silt	Clay	
14	7.6	1	336	117	50	10,000	805	150	4.0	11.6	38.32	17.76	43.92	Clay
15	7.8	1	320	96	42	10,400	1,003	131	3.3	12.0	40.88	17.12	42.00	Clay
16	8.1	15	464	61.5	57	8,800	2,081	179	1.8	18.0	29.60	13.84	56.56	Clay
17	7.8	1	352	75	27	8,800	581	150	2.5	6.4	40.32	11.64	48.04	Clay

Appendix III

Stream Discharge, Red Rock Lakes Refuge
June 24 to September 1, 1971

	Stream Discharge (cubic ft./sec.)						
Gauging Station	June 24	July 2	July 9	July 17	Aug. 2	Aug. 19	Sept. 1
Duff Cr.	1.45	1.62	1.39	1.06	.76	.58	.58
Collins Cr.	3.74	3.74	2.24	1.28	.58	.24	.20
Humphrey Cr.	8.86	3.75	2.77	1.62	.60	.60	.38
Odell Cr.	184.65	204.30	125.15	95.00	--	43.00	38.30
Shambow Cr.	28.30	19.00	18.90	13.90	6.65	4.40	2.21
Cole Cr.	17.00	16.70	16.70	9.10	8.95	7.00	4.93
Nye Cr.	24.80	19.00	19.00	12.00	8.35	6.00	3.45
East Shambow Cr.	7.85	7.50	7.40	4.30	5.52	5.00	4.44
Grayling Cr.	15.00	15.00	15.00	15.30	9.00	7.75	6.65
East Nye Cr.	4.70	3.00	3.00	3.00	3.00	--	--
Lone Willow Cr.	13.40	9.00	4.60	3.30	1.00	dry	dry
Hackett Cr.	4.00	5.40	2.24	2.17	dry	dry	dry
Tom Cr.	33.20	16.30	16.30	7.90	4.00	2.78	1.92
Battle Cr.	1.84	2.40	2.20	1.80	1.50	1.20	.94
Red Rock Cr.	357.10	219.50	184.80	141.00	72.60	49.70	45.70

Appendix III (continued)

Stream Discharge (cubic ft. /sec.)

Gauging Station	June 24	July 2	July 9	July 17	Aug. 2	Aug. 19	Sept. 1
Dead Horse Spr.	2.00	.84	.75	.60	.60	.50	.50
Elk Cr.	40.20	44.50	35.80	32.90	32.00	25.30	36.80
Mallard Canal	12.61	8.31	13.50	8.10	6.40	12.61	4.70
Harlequin Canal	18.00	17.20	16.00	13.70	10.51	10.17	10.17
Total Inflow	778.70	617.06	487.74	368.03	172.02	176.83	161.87
Lower Structure (total outflow)	405.20	468.00	411.00	259.80	140.00	44.00	57.20

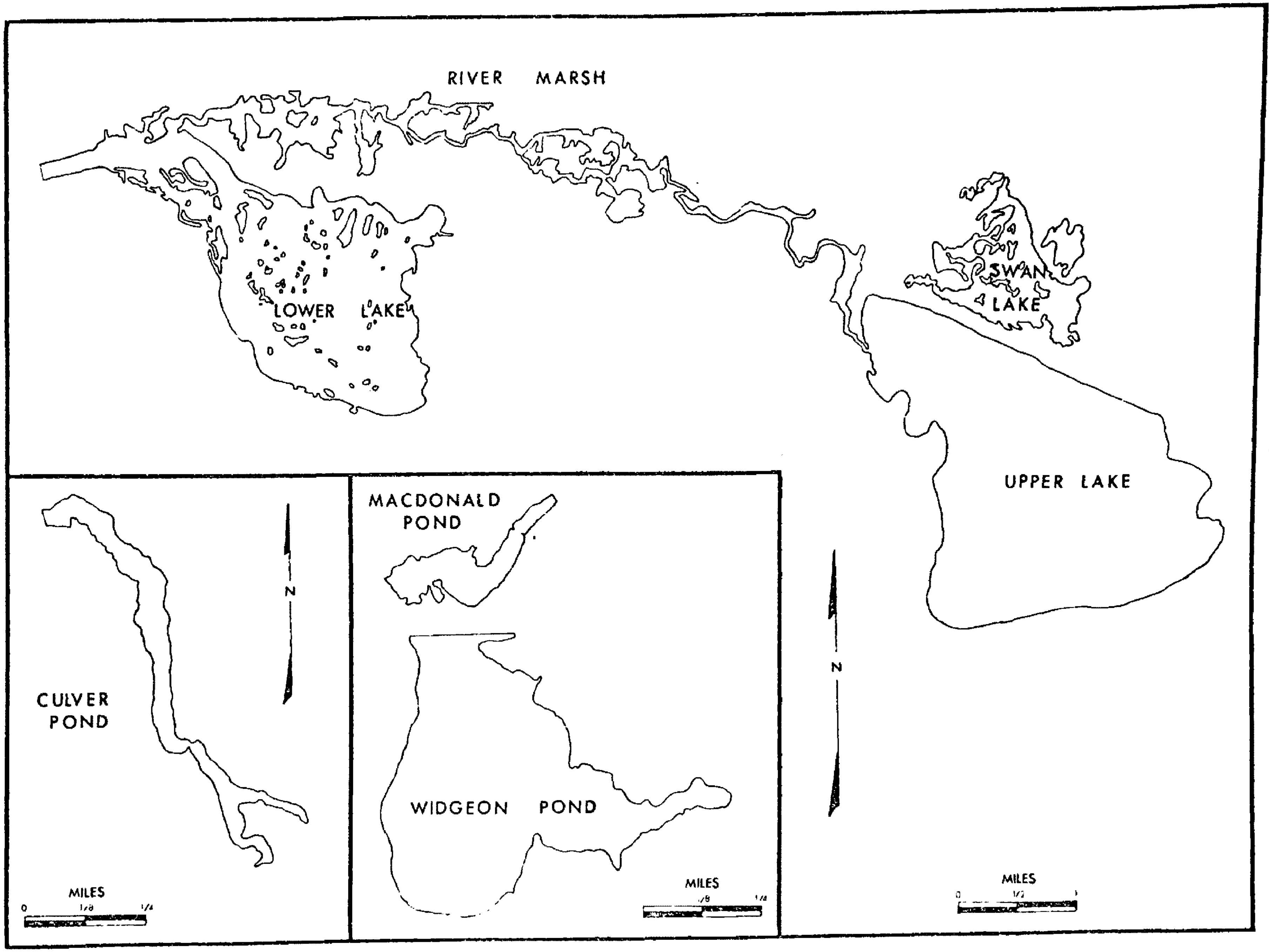
Appendix IV

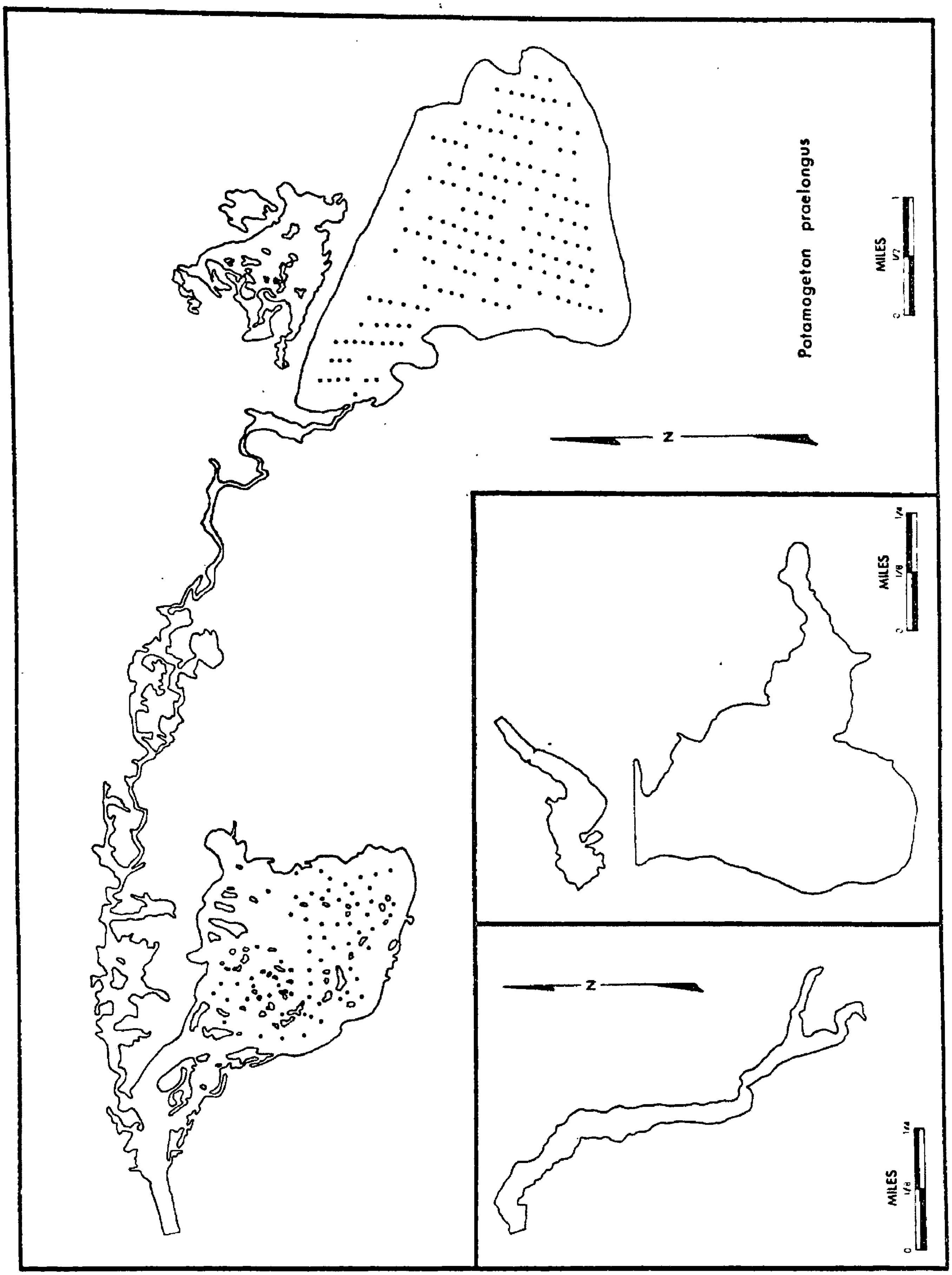
Submerged Macrophytes of Red Rock Lakes Refuge

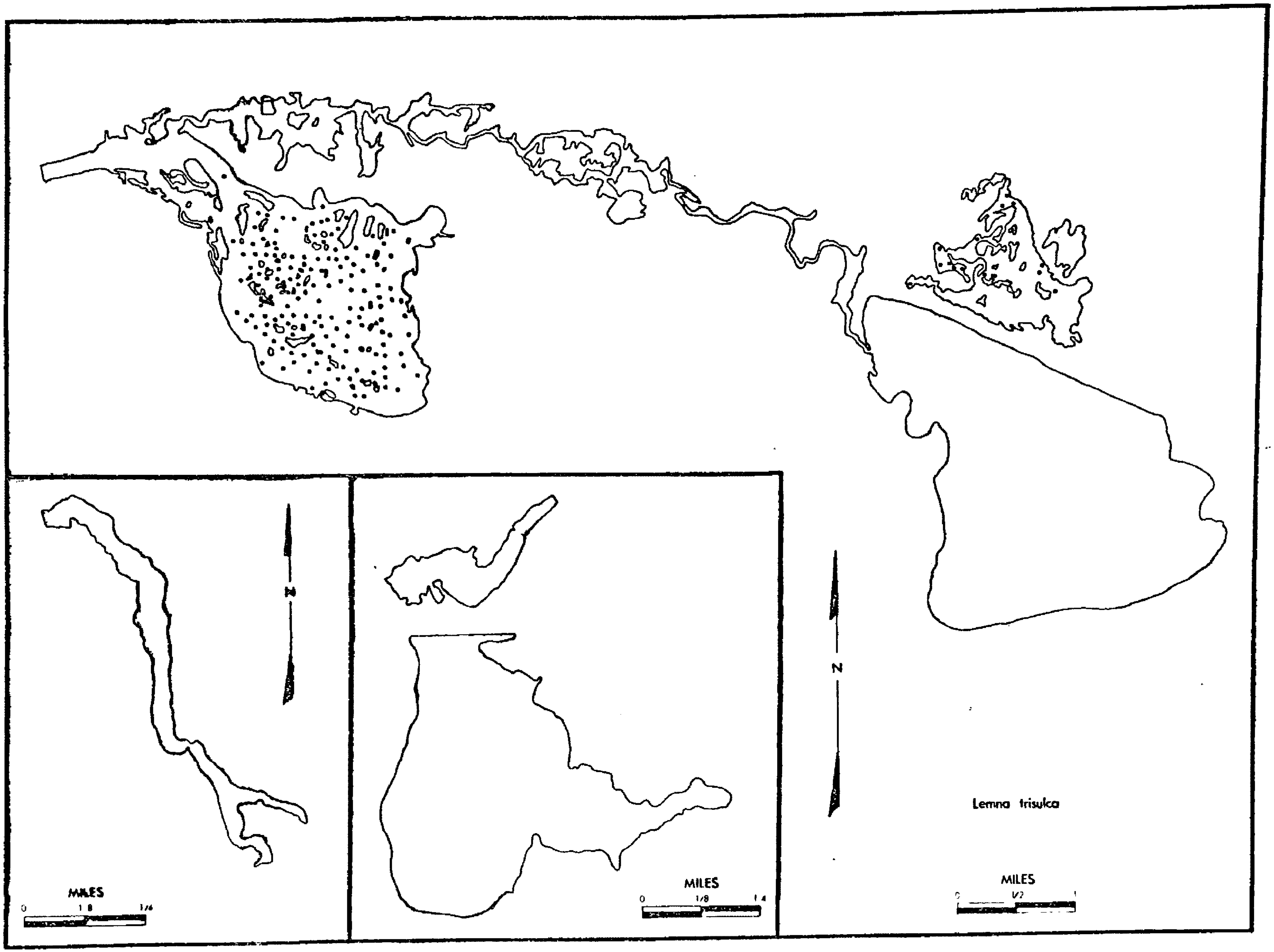
Scientific Name	Common Name
Potamogeton pectinatus	Sago Pondweed
Potamogeton richardsonii	Richardson's Pondweed
Potamogeton praelongus	Whitestem Pondweed
Potamogeton zosteriformis	Flatstem Pondweed
Potamogeton foliosus	Leafy Pondweed
Potamogeton friesii	Fries Pondweed
Potamogeton pusillus	Slender Pondweed
Chara vulgaris	Muskgrass
Isoetes spp.	Quillwort
Najas flexilis	Slender Naiad
Zannichellia palustris	Horned Pondweed
Elodea canadensis	Waterweed
Lemna trisulca	Star Duckweed
Ranunculus aquatilis	Water Buttercup
Utricularia vulgaris	Bladderwort
Ceratophyllum demersum	Coontail
Hippuris vulgaris	Mare's Tail
Callitriche hermaphroditica	Water Starwort
Sagittaria cuneata	Wapato
Nitella flexilis	Stonewort
Myriophyllum spicatum	Milfoil
Polygonum amphibium	Smartweed

Appendix V

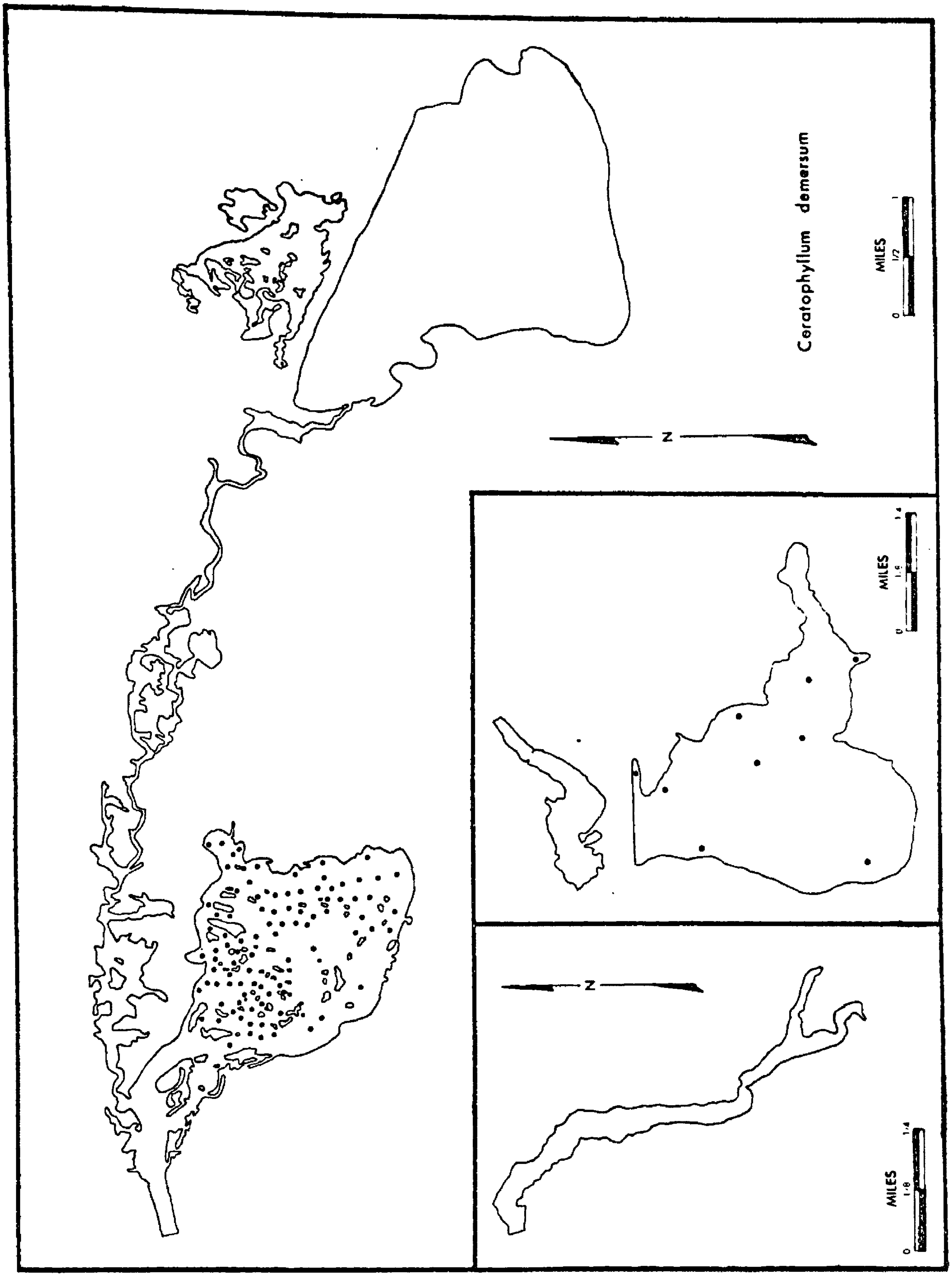
Species Distribution Maps


RIVER MARSH
LOWER LAKE
SWAN LAKE
UPPER LAKE
MACDONALD POND
CULVER POND
WIDGEON POND
N
N
MILES
0
1/8
1/4
MILES
1/8
1/4
MILES
0
1/2
1

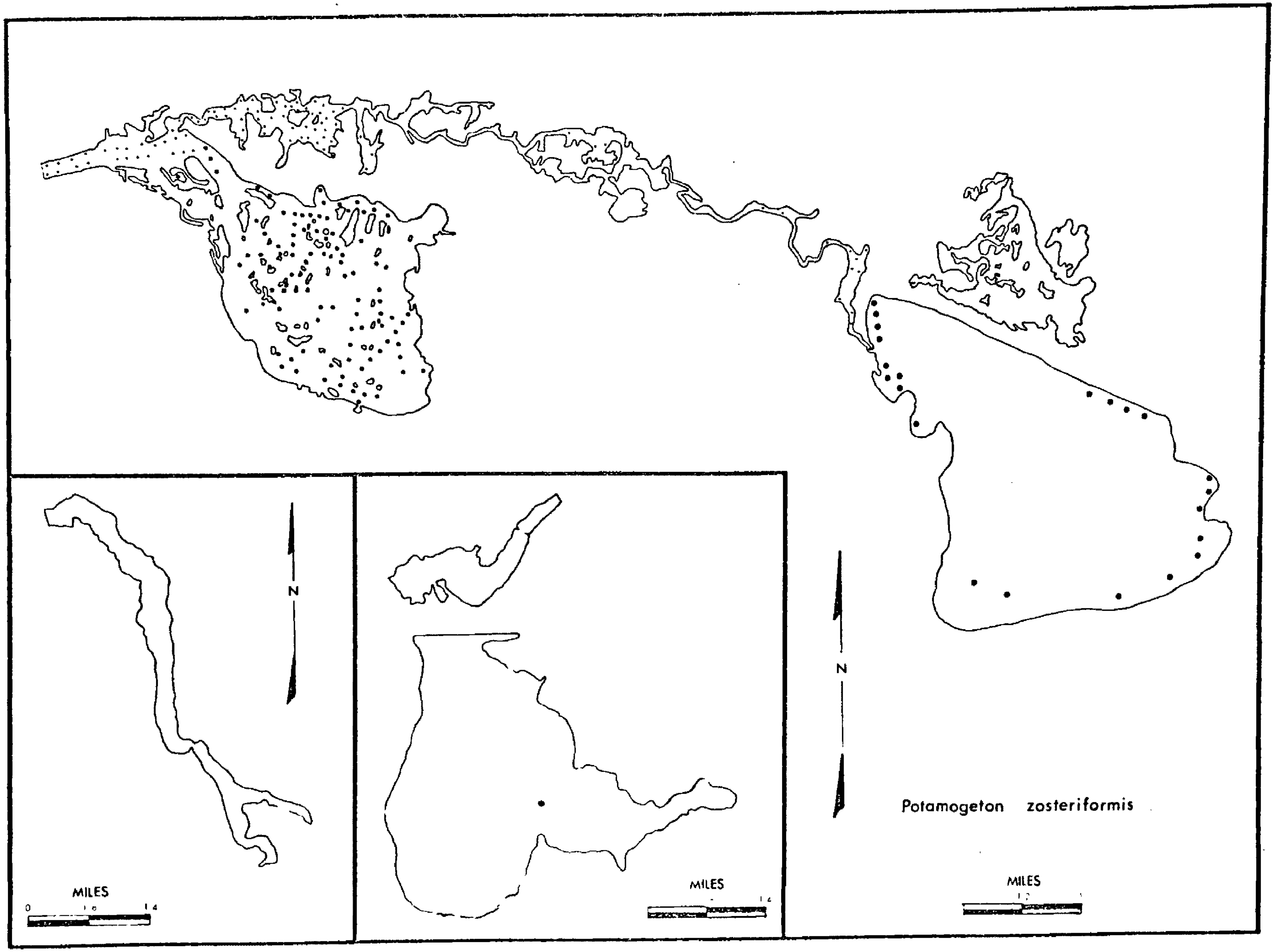

Potamogeton praelongus
MILES
0
1/2
1
N
MILES
0
1/8
1/4
N
MILES
0
1/8
1/4



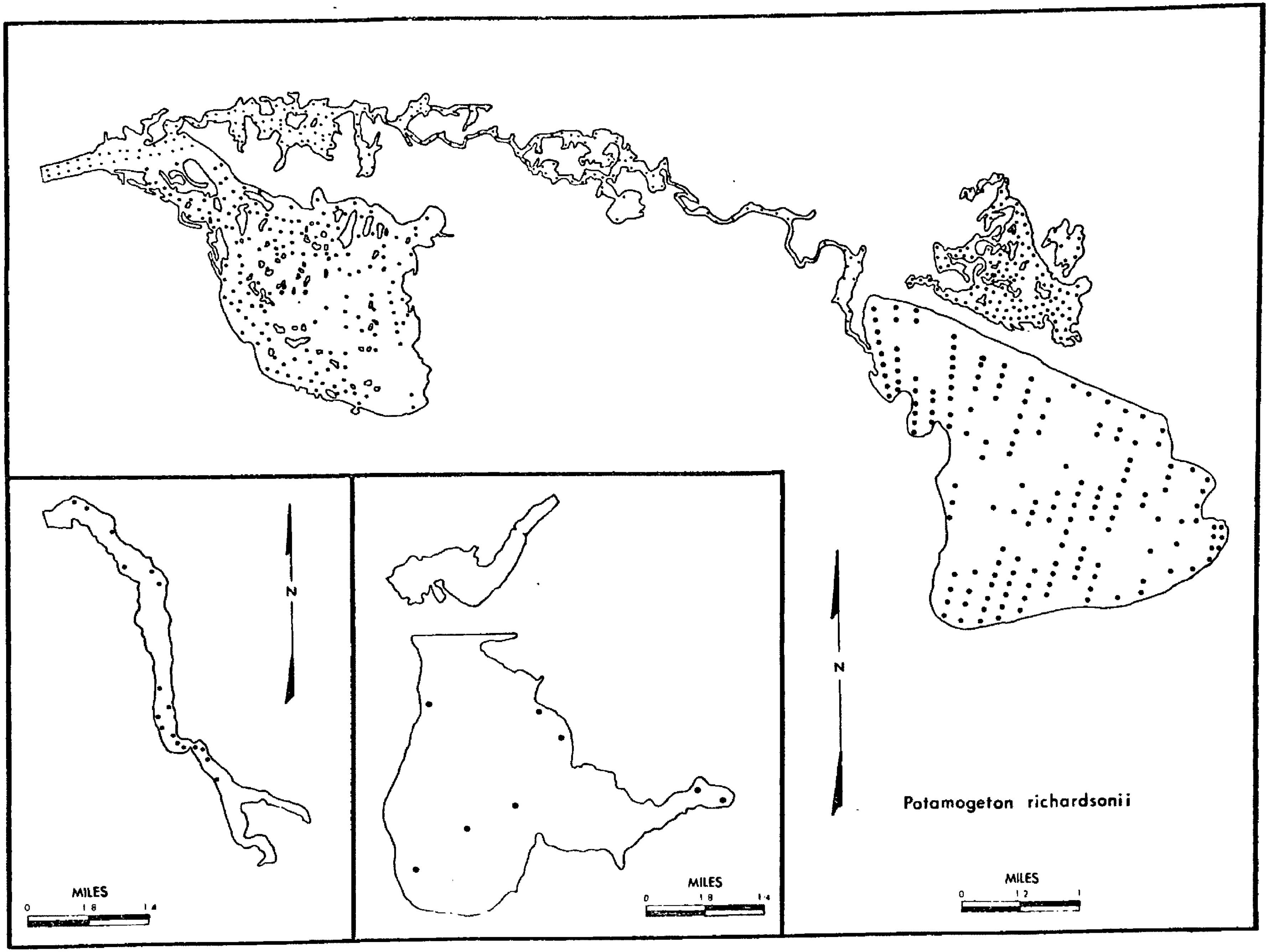
Lemna trisulca

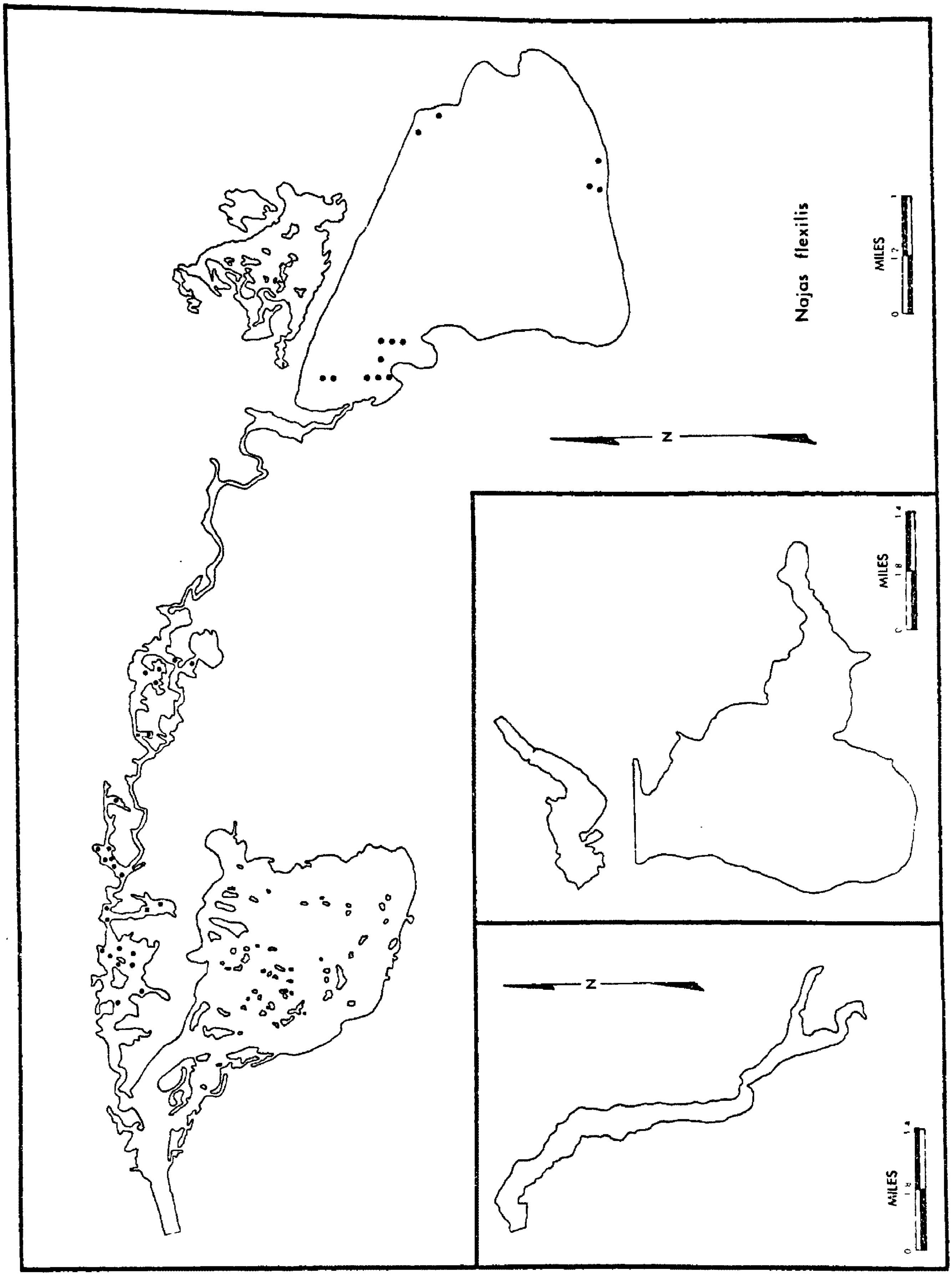


Ceratophyllum demersum

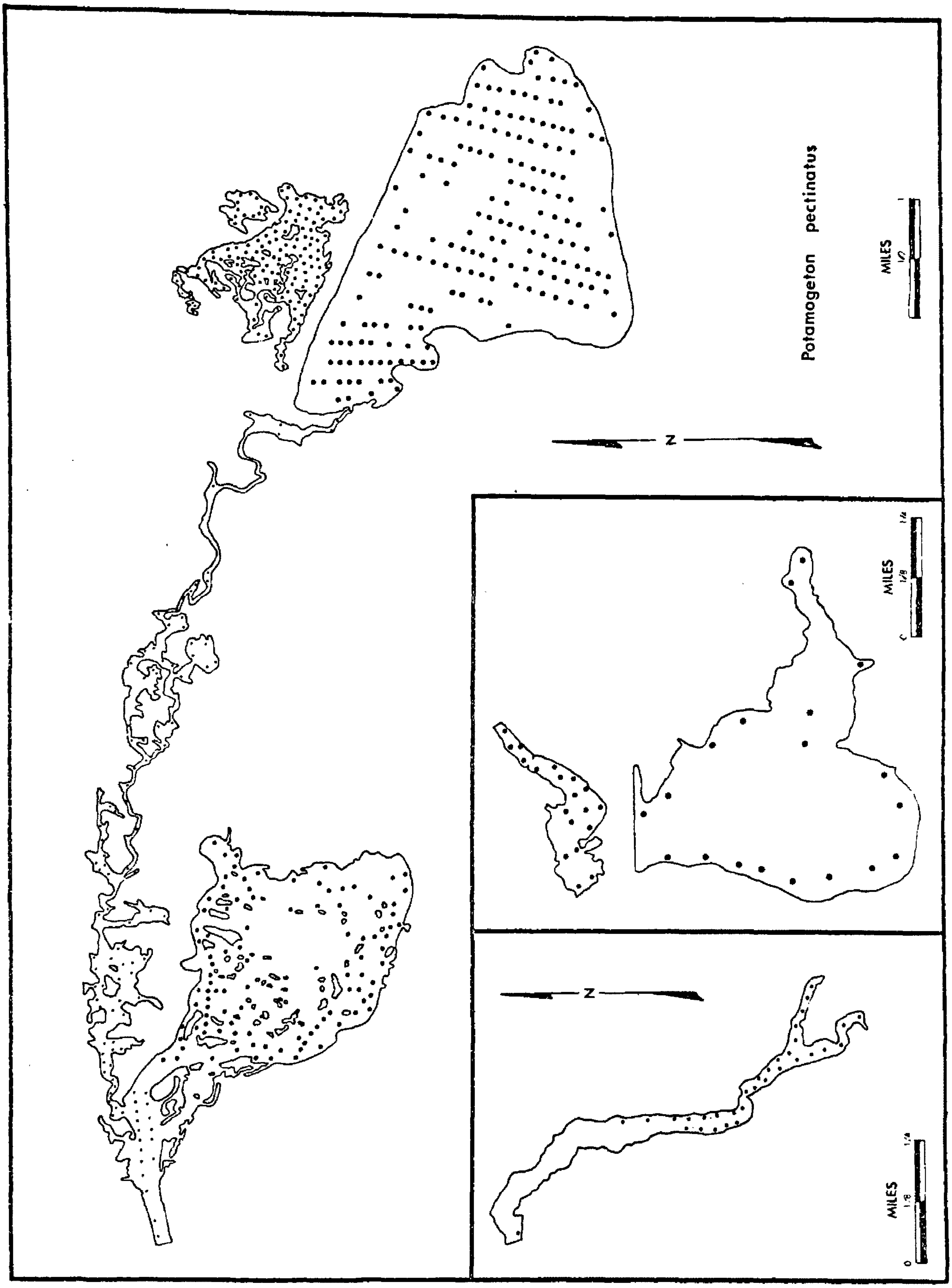


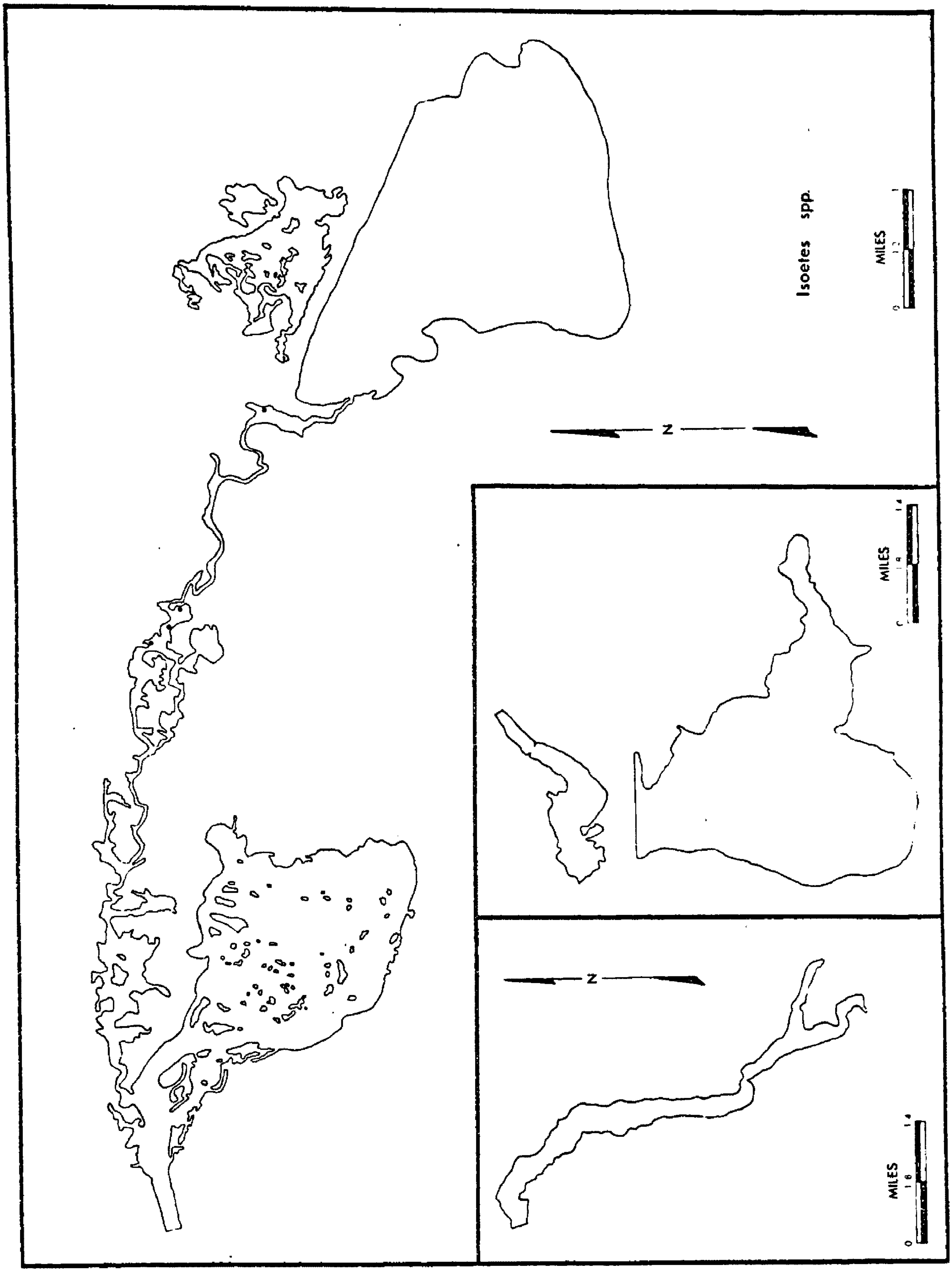
Potamogeton zosteriformis

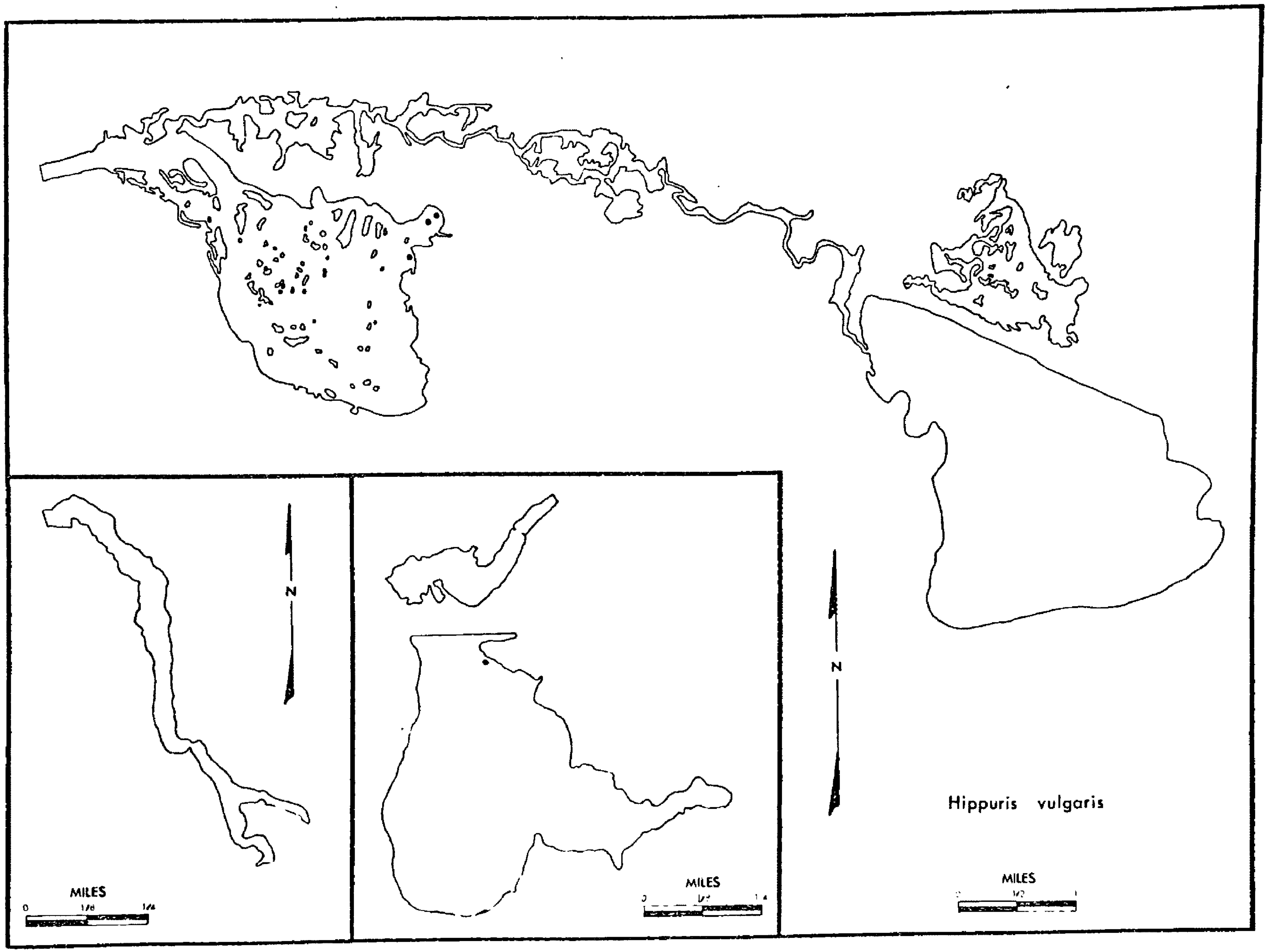

Potamogeton richardsonii
N
MILES
0 1/2 1
N
MILES
0 1/8 1/4
N
MILES
0 1/8 1/4



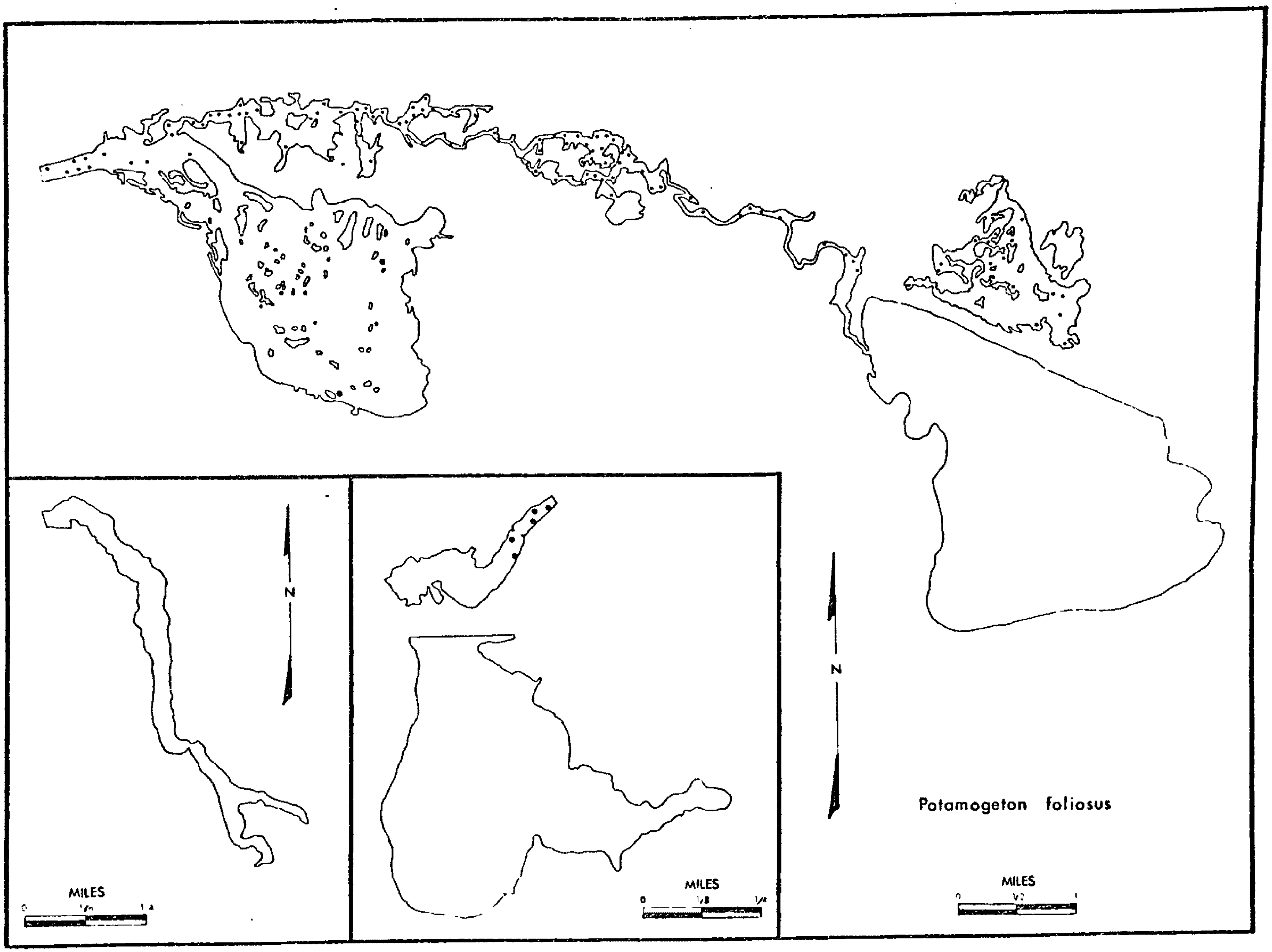
Najas flexilis


Potamogeton pectinatus
MILES
1/2
1
N
N
MILES
0
1/8
1/4
MILES
0
1/8
1/4

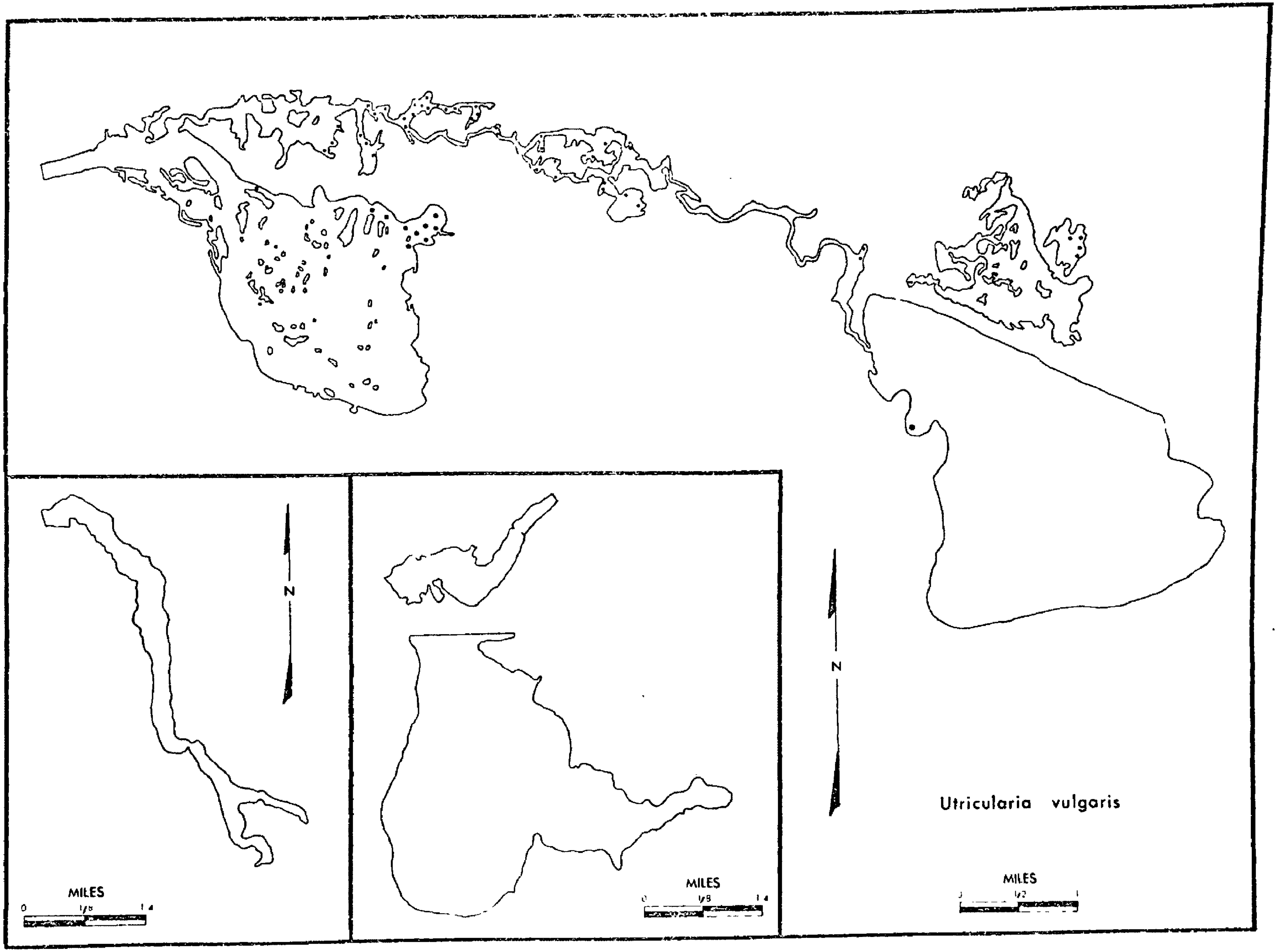

Isoetes spp.
MILES
0
1/2
1
N
MILES
0
1/8
1/4
N
MILES
0
1/8
1/4



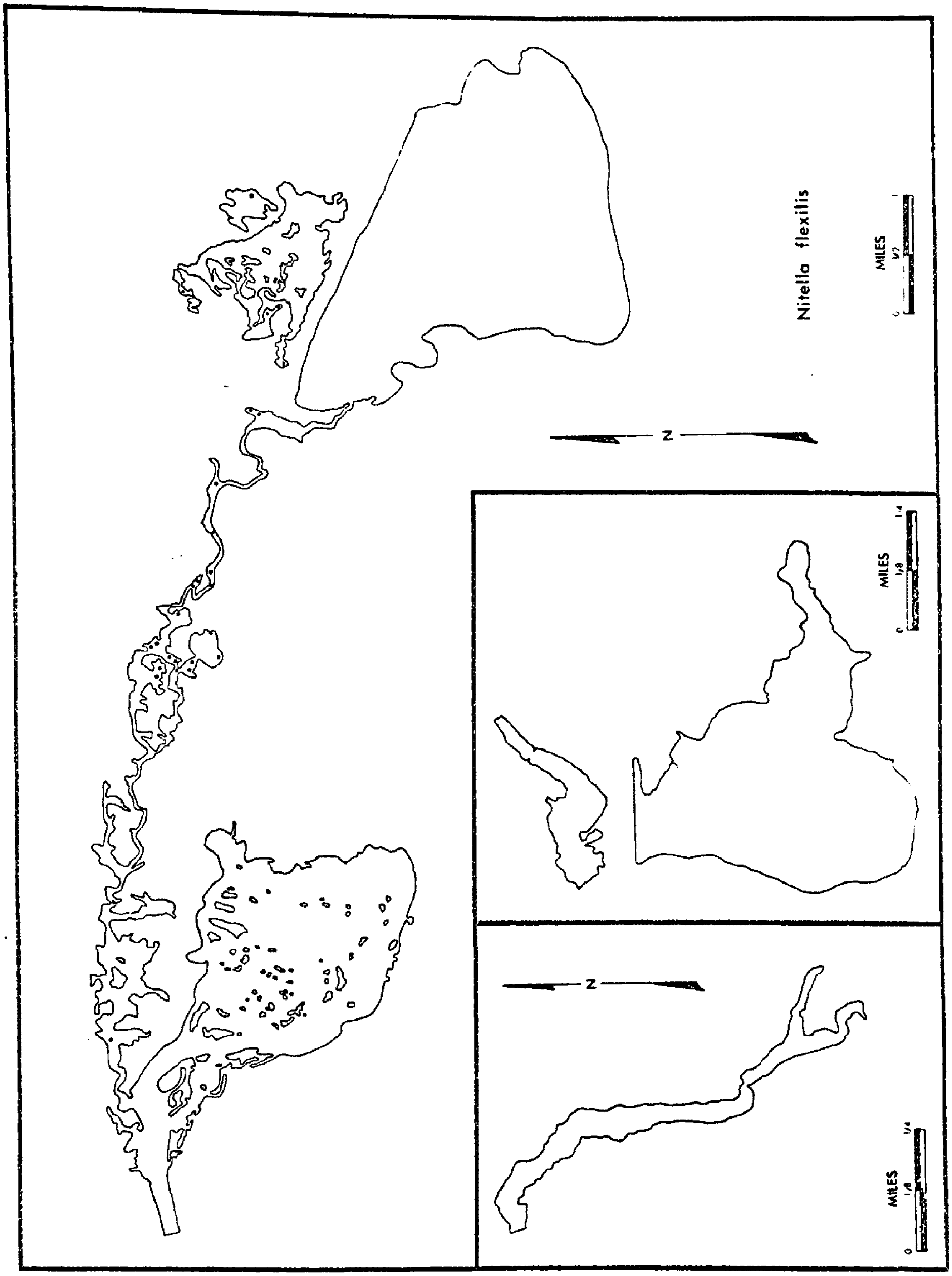
Hippuris vulgaris



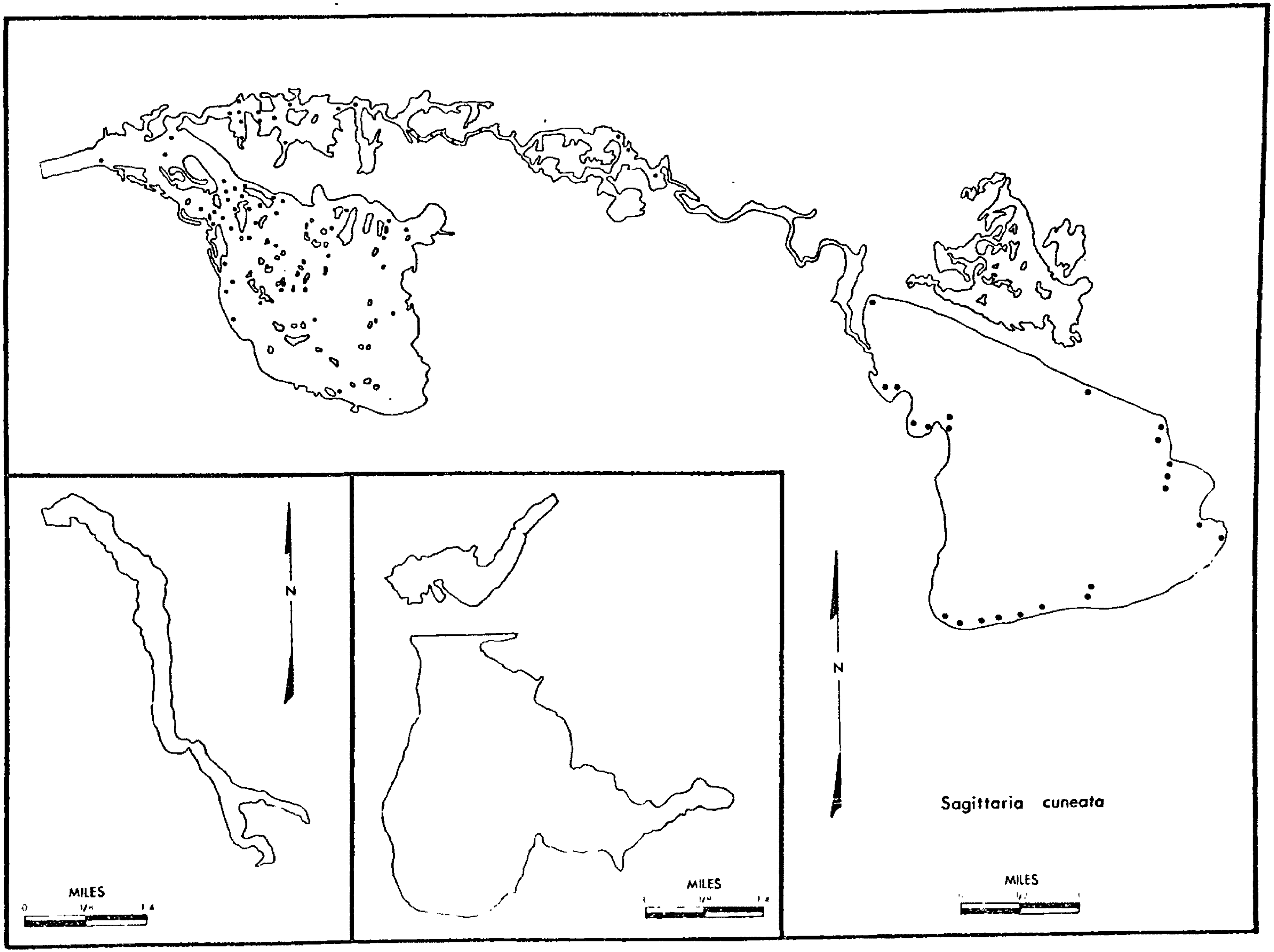
Potamogeton foliosus



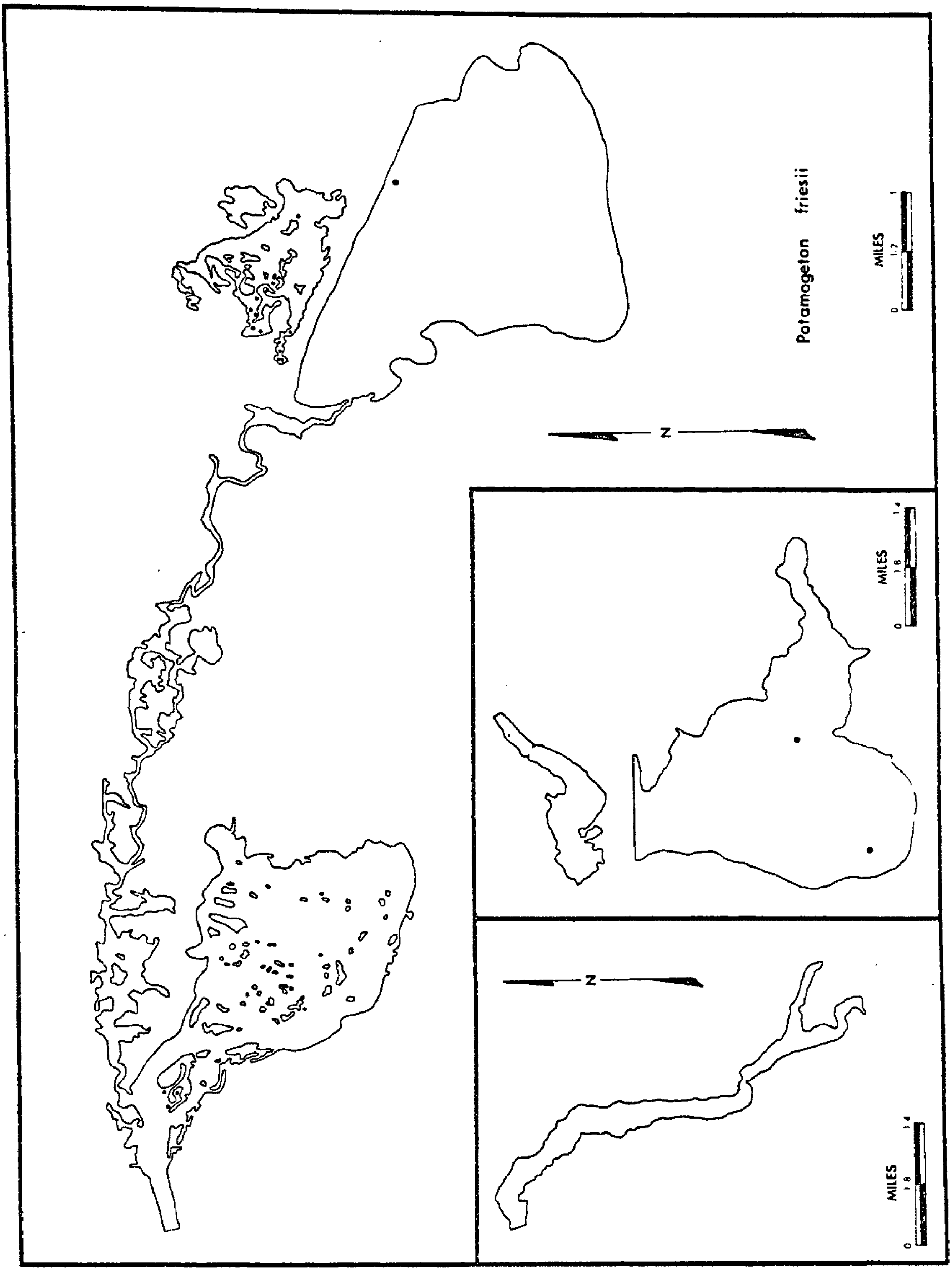
Utricularia vulgaris

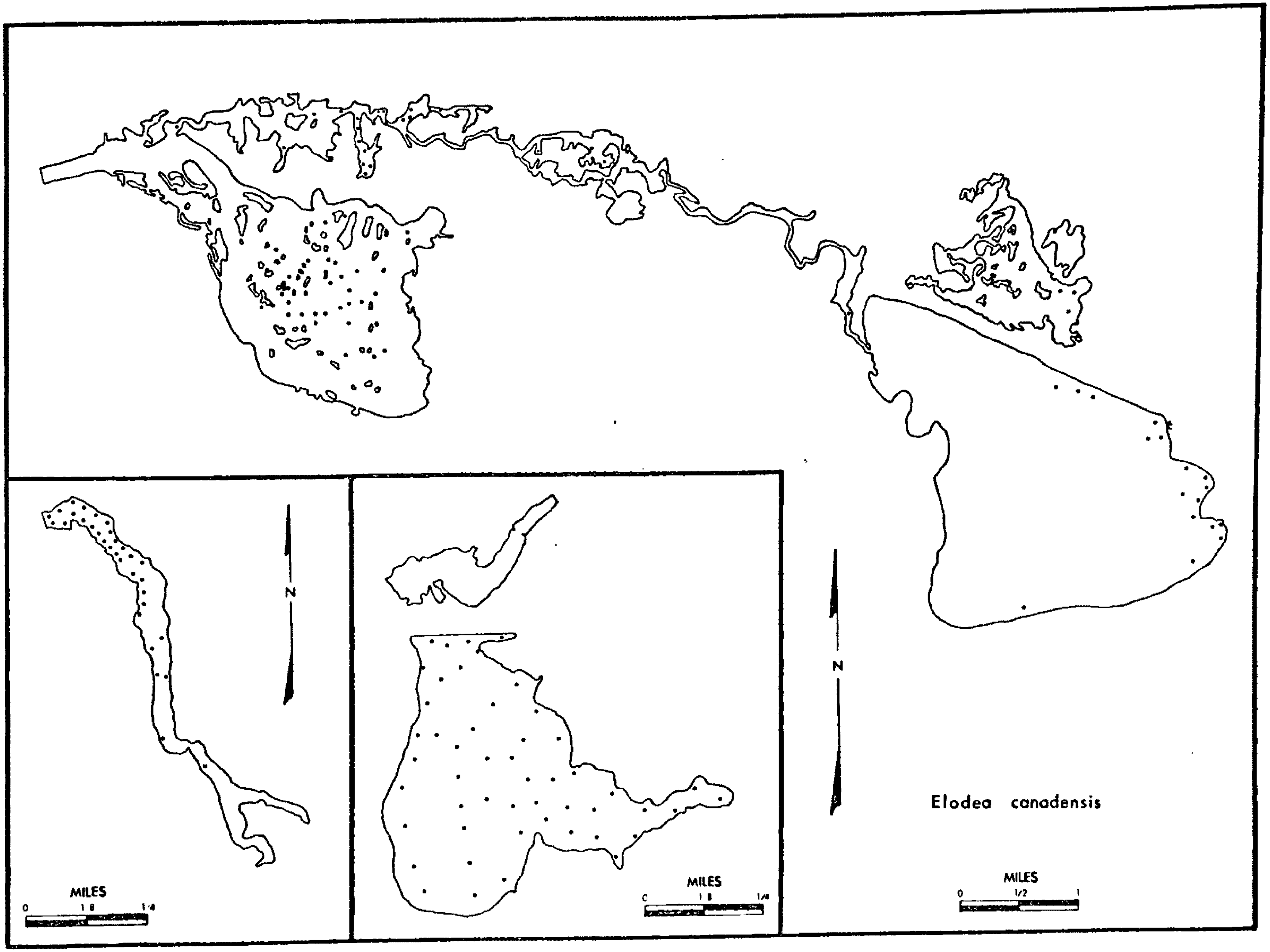


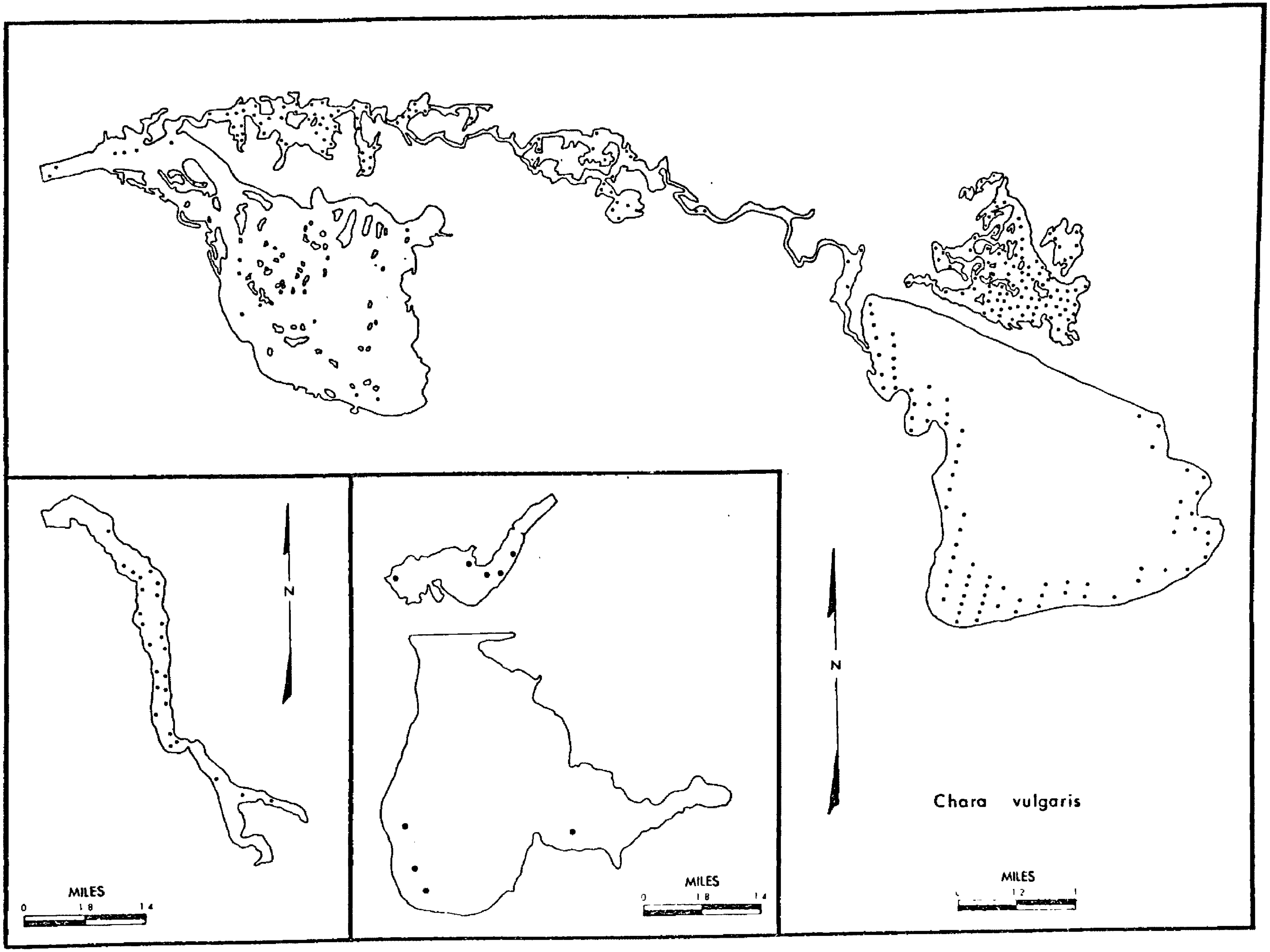
Nitella flexilis



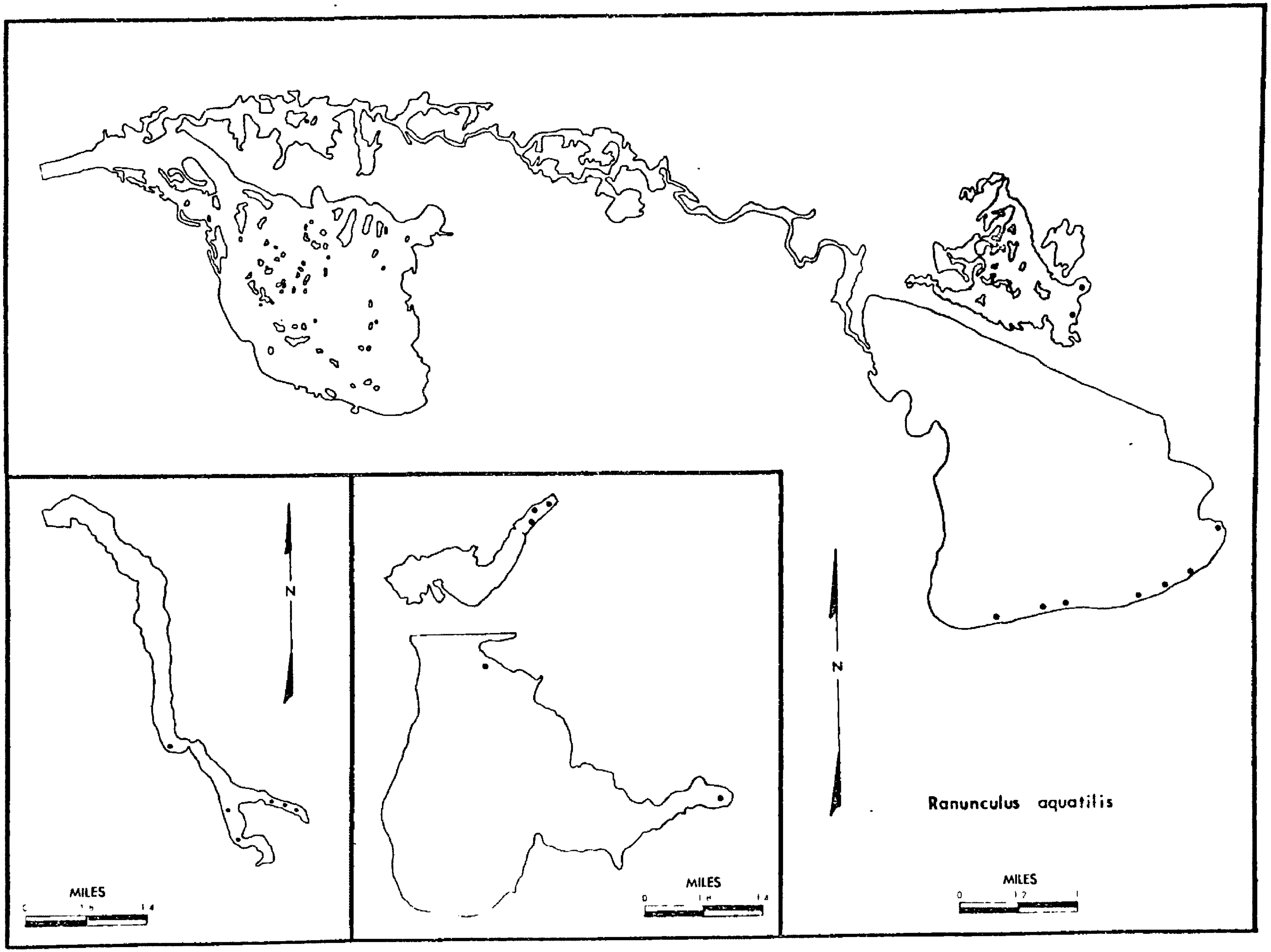
Sagittaria cuneata
N
MILES
N
MILES
MILES
0
1/8
1/4


Potamogeton friesii
MILES
0
1/2
1
N
MILES
0
1/8
1/4
N
MILES
0
1/8
1/4

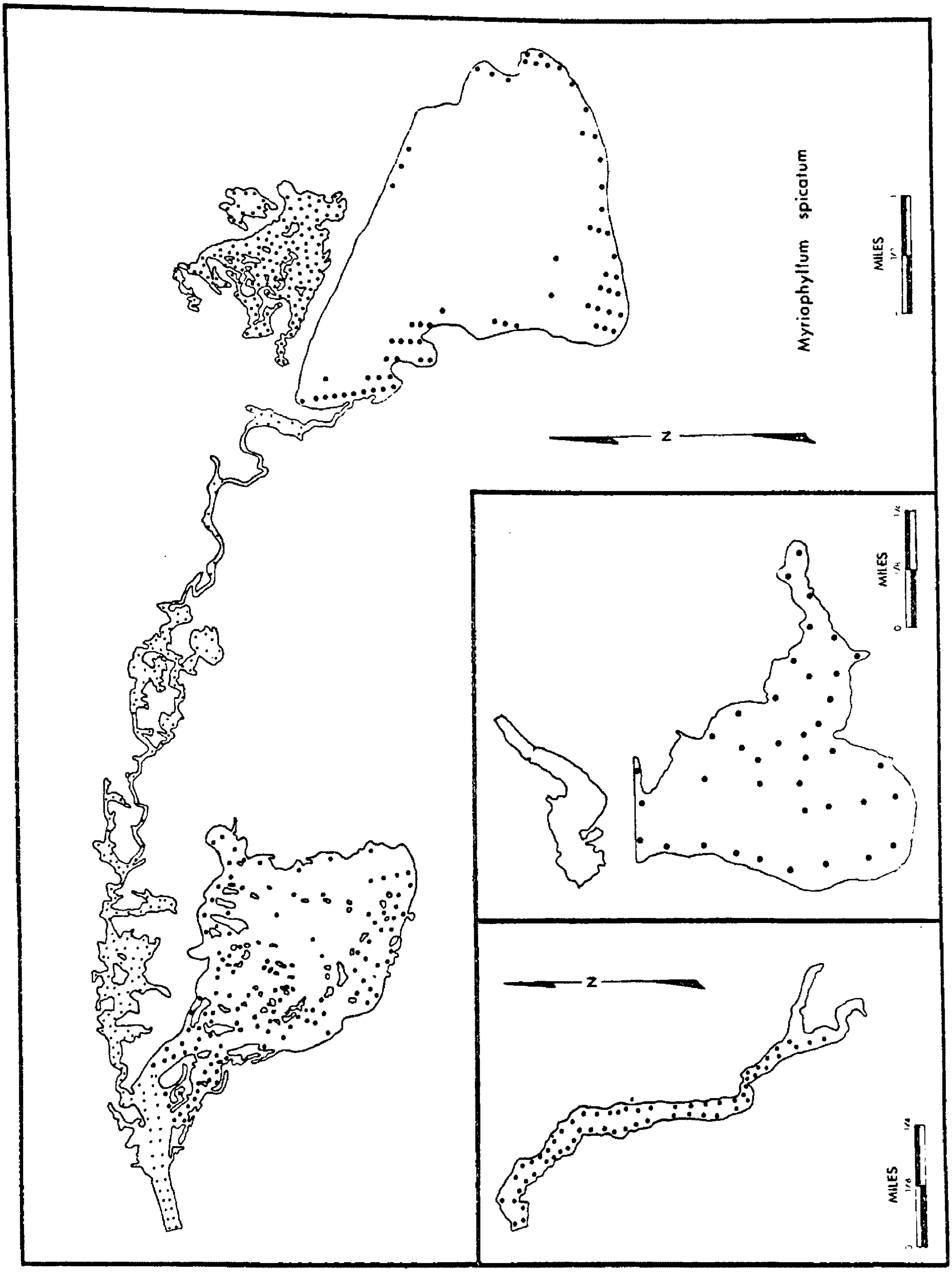

Elodea canadensis
N
MILES
0
1/2
1
N
MILES
0
1 8
1/4
MILES
0
1 8
1/4

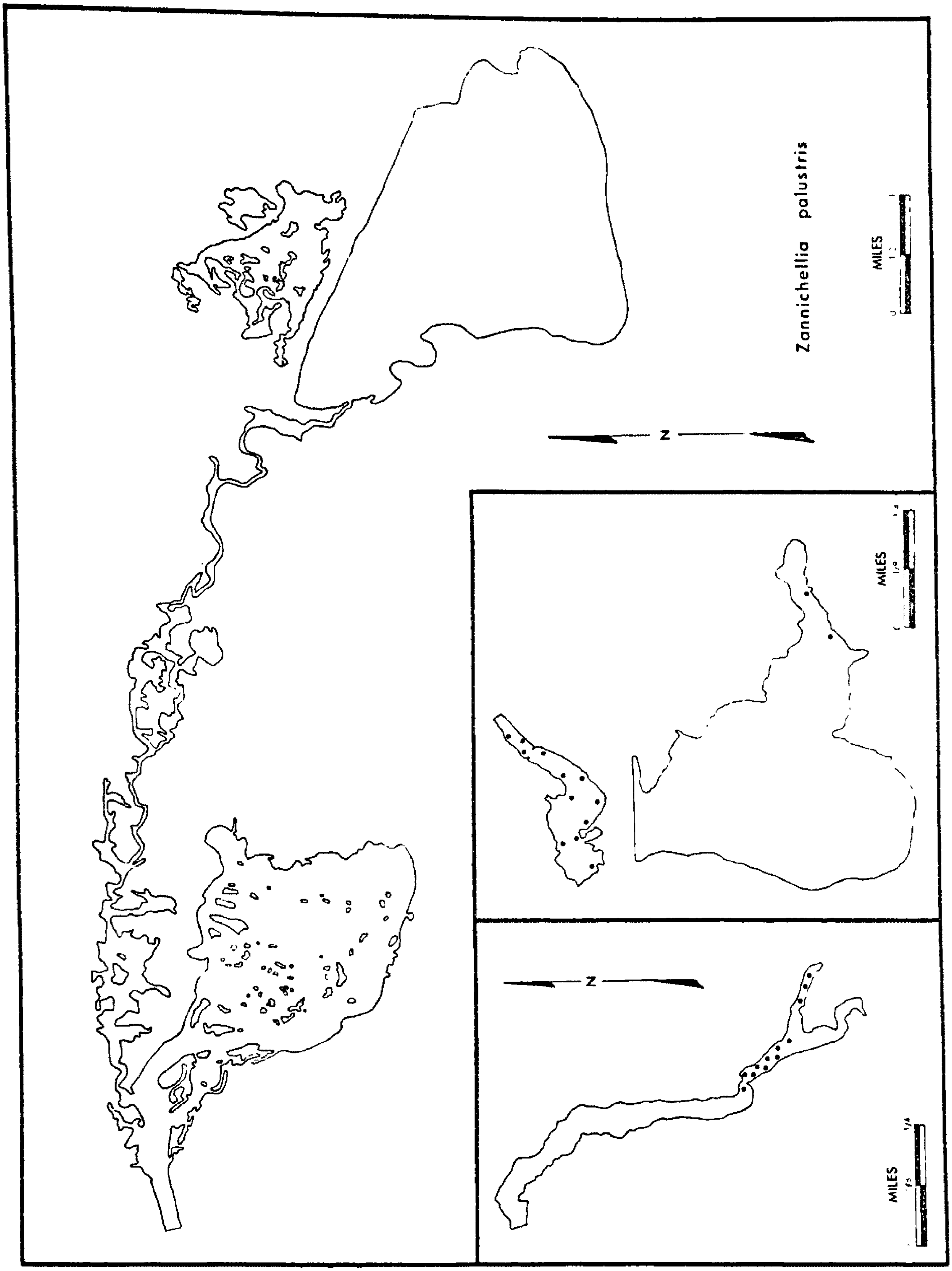


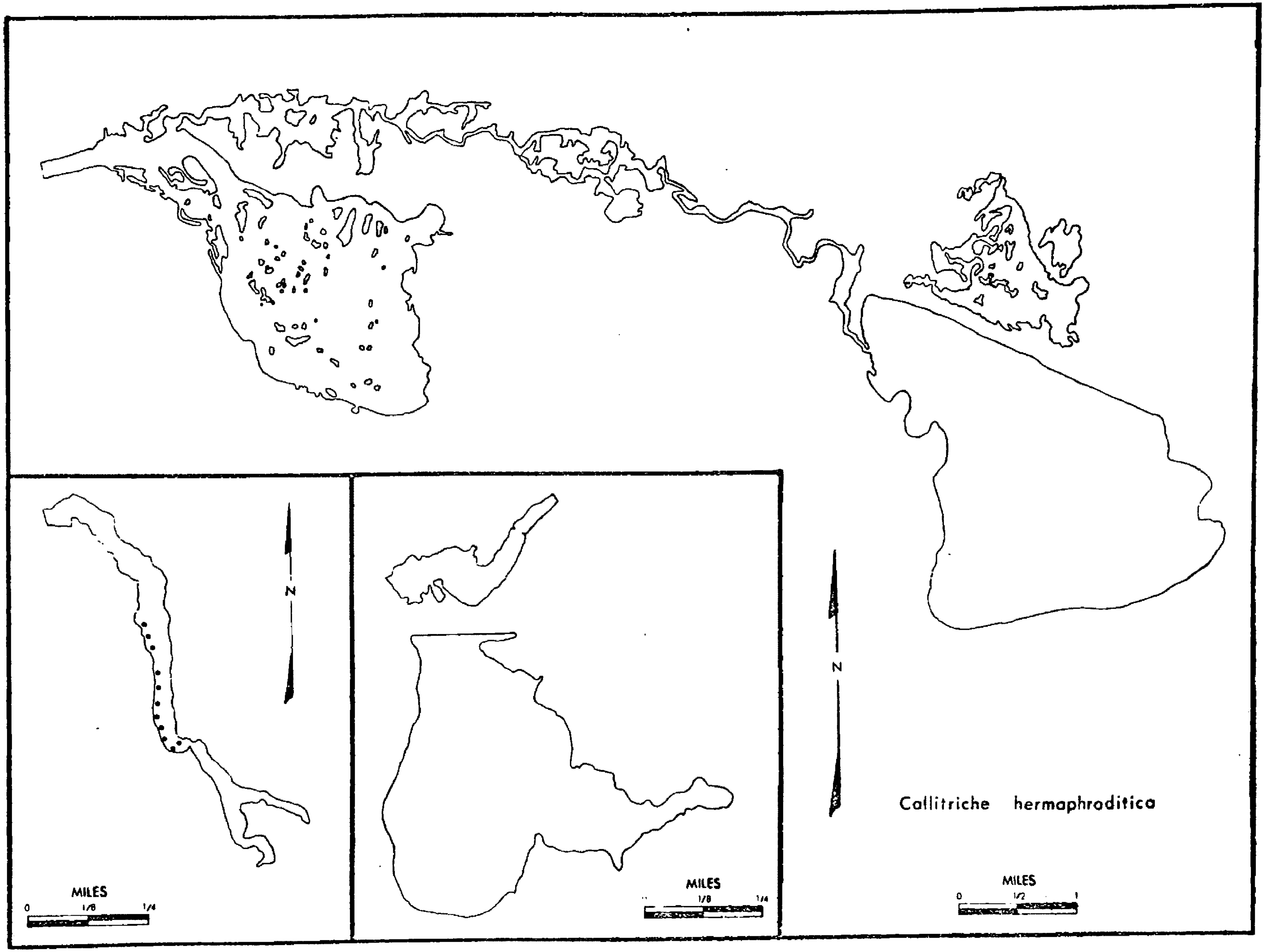
Chara vulgaris



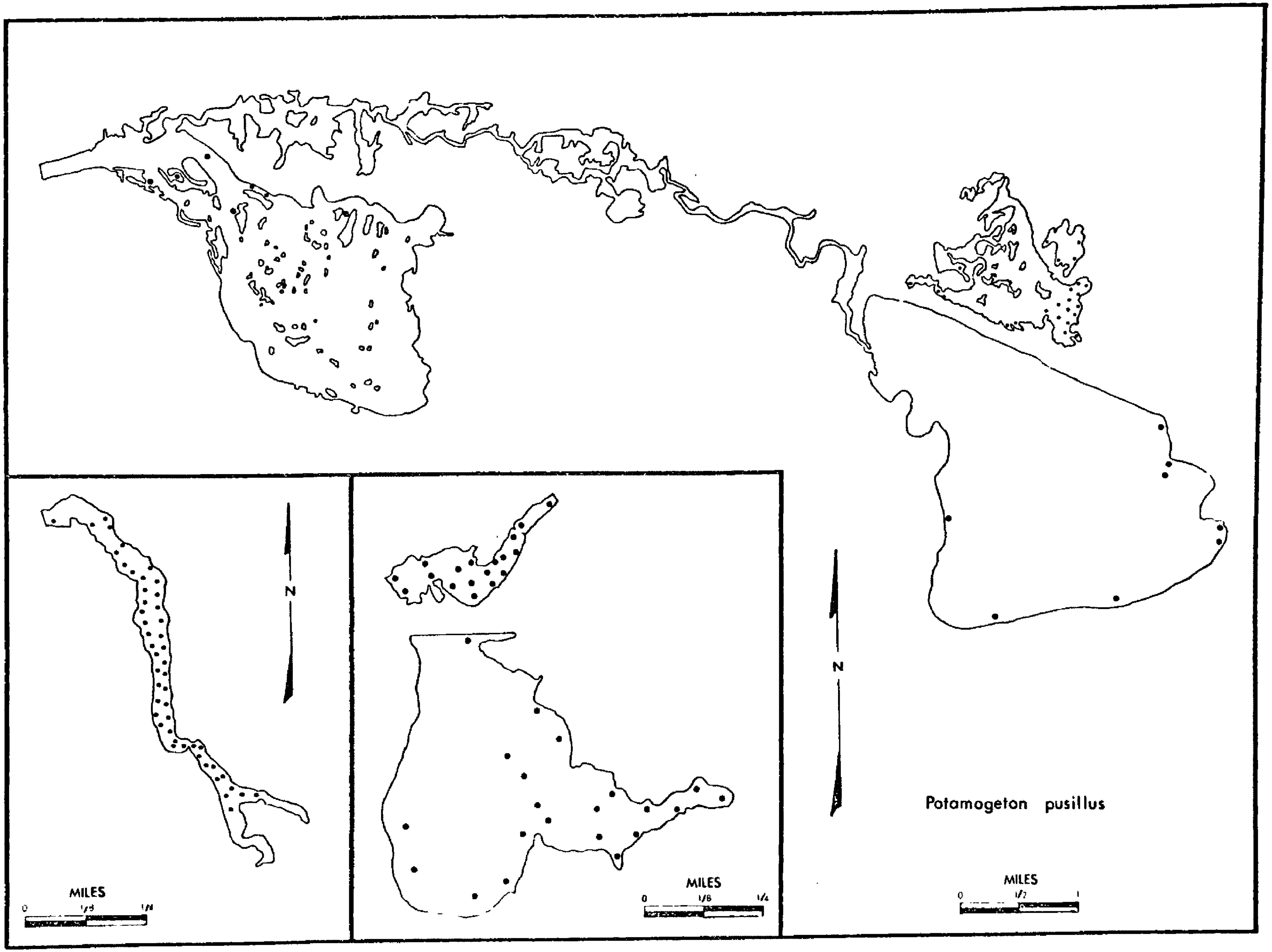
Ranunculus aquatilis


Myriophyllum spicatum
MILES
N
MILES
MILES
N


Zannichellia palustris



Callitriche hermaphroditica



Potamogeton pusillus

Appendix VI

Plant Abundance (acres)
1971

Species	Lower Lake	Upper Lake	River Marsh	Widgeon Pond	Swan Lake	Culver Pond	MacDonald Pond	Refuge Total
Potamogeton praelongus	47.0	325.3	--	--	--	--	--	371.3
Lemna trisulca	331.9	--	--	--	2.3	--	--	334.2
Ceratophyllum demersum	46.0	--	TR	.38	--	--	--	46.4
Potamogeton zosteriformis	37.2	10.7	29.4	.31	--	--	--	77.6
Potamogeton richardsonii	240.8	201.1	141.2	2.7	30.7	.47	--	617.0
Najas flexilis	--	11.5	2.5	--	--	--	--	14.0
Potamogeton pectinatus	82.2	341.7	34.4	7.2	51.0	3.12	3.9	523.5
Isoetes spp.	--	--	2.1	--	--	--	--	2.1
Hippuris vulgaris	5.0	--	--	.08	--	--	--	5.1
Potamogeton foliosus	1.0	--	28.2	--	1.6	--	.13	30.9
Utricularia vulgaris	10.8	TR	7.9	--	.33	--	--	19.0
Nitella flexilis	--	--	10.8	--	1.80	--	--	12.6
Sagittaria cuneata	12.7	6.5	.83	--	--	--	--	20.0
Potamogeton friesii	1.0	TR	--	TR	5.6	--	--	6.6

Appendix VI (continued)

Species	Lower Lake	Upper Lake	River Marsh	Widgeon Pond	Swan Lake	Culver Pond	MacDonald Pond	Refuge Total
Elodea canadensis	5.9	11.2	3.3	44.8	TR	4.18	--	69.4
Chara vulgaris	11.7	258.5	38.5	.08	84.7	.83	.34	394.7
Ranunculus aquatilis	--	18.8	TR	.23	TR	.10	TR	19.1
Myriophyllum spicatum	142.0	68.1	112.2	18.8	134.4	3.47	--	479.0
Zannichellia palustris	--	--	--	TR	--	.67	.96	1.6
Callitriche hermaphroditica	--	--	--	--	--	.17	TR	.20
Potamogeton pusillus	4.1	10.2	2.1	2.5	14.7	3.63	4.6	41.8
	979.3	1263.6	413.4	77.08	327.1	16.64	9.93	3087.
Acres Surveyed	1540	2880	570	132	415	27	12	5576
% Vegetation	63.6	43.8	72.7	58.3	78.8	61.7	82.0	55.0

Appendix VII

SWAN LAKE

Frequency of Occurrence of Vegetation Sampled

Species	1966	1969	1971
Myriophyllum spicatum	90	90	92
Chara vulgaris	43	47	51
Utricularia vulgaris	--	20	2
Potamogeton richardsonii	47	17	65
Lemna trisulca	3	17	7
Potamogeton pectinatus	26	13	76
Potamogeton pusillus	7	10	12
Zannichellia palustris	3	--	--
Potamogeton friesii	--	--	8
Elodea canadensis	--	--	2
Potamogeton foliosus	--	--	9
Ranunculus aquatilis	--	--	1
Nitella flexilis	--	--	2

Species Composition

Species	1956	1966	1969	1971
Myriophyllum spicatum	48.9	69.5	70.5	41.1
Chara vulgaris	2.2	24.3	19.9	25.9
Utricularia vulgaris	--	--	1.2	0.1
Potamogeton richardsonii	16.3	3.5	3.0	9.4
Lemna trisulca	--	0.1	0.2	0.7
Potamogeton pectinatus	17.4	2.2	4.2	15.6
Potamogeton pusillus	5.6	0.2	1.0	4.5
Zannichellia palustris	--	0.2	--	--
Potamogeton friesii	--	--	--	1.7
Elodea canadensis	--	--	--	TR
Potamogeton foliosus	9.7	--	--	0.5
Ranunculus aquatilis	0.4	--	--	TR
Nitella flexilis	--	--	--	0.5

Appendix VII (continued)

LOWER LAKE

Frequency of Occurrence of Vegetation Sampled

Species	1967	1969	1971
Elodea canadensis	72	52	11
Lemna trisulca	67	46	56
Potamogeton richardsonii	28	43	64
Myriophyllum spicatum	53	32	46
Ceratophyllum demersum	--	30	34
Potamogeton zosteriformis	19	16	34
Potamogeton pusillus	31	16	3
Potamogeton pectinatus	14	5	40
Chara vulgaris	11	5	3
Sagittaria cuneata	8	5	12
Potamogeton foliosus	--	5	TR
Potamogeton praelongus	11	5	20
Najas flexilis	6	3	--
Potamogeton friesii	--	--	1
Hippuris vulgaris	--	--	1
Utricularia vulgaris	--	--	4

Species Composition

Species	1956	1967	1969	1971
Elodea canadensis	60.5	44.1	53.8	0.6
Lemna trisulca	0.8	6.2	3.4	33.9
Potamogeton richardsonii	14.0	14.6	15.0	24.6
Myriophyllum spicatum	2.0	16.6	4.5	14.5
Ceratophyllum demersum	--	--	17.3	4.7
Potamogeton zosteriformis	2.9	4.4	1.3	3.8
Potamogeton pusillus	--	2.0	0.5	0.4
Potamogeton pectinatus	3.4	2.9	0.9	8.4
Chara vulgaris	0.9	2.9	0.7	1.2
Sagittaria cuneata	7.7	0.9	0.2	1.3
Potamogeton foliosus	3.1	--	--	0.1
Potamogeton praelongus	4.0	4.7	0.7	4.8
Najas flexilis	0.3	0.7	TR	--
Potamogeton friesii	--	--	--	0.1
Hippuris vulgaris	--	--	--	0.5
Utricularia vulgaris	--	--	--	1.1

Appendix VII (continued)

CULVER POND

Frequency of Occurrence of Vegetation Sampled

Species	1966	1968	1970	1971	1972
Elodea canadensis	57	65	71	43	36
Myriophyllum spicatum	67	35	54	79	34
Potamogeton pectinatus	33	35	39	43	43
Chara vulgaris	14	15	32	40	32
Potamogeton pusillus	10	--	22	69	50
Ranunculus aquatilis	38	20	20	8	24
Potamogeton richardsonii	--	5	7	24	16
Callitriche hermaphroditica	--	--	5	15	6
Zannichellia palustris	5	--	2	16	22

Species Composition

Species	1966	1968	1970	1971	1972
Elodea canadensis	54.0	67.2	63.9	25.1	33.2
Myriophyllum spicatum	22.8	3.6	6.1	20.8	13.6
Potamogeton pectinatus	1.6	10.0	8.9	18.7	8.7
Chara vulgaris	1.9	12.5	10.7	5.0	10.6
Potamogeton pusillus	0.5	--	4.1	21.8	19.4
Ranunculus aquatilis	18.5	6.0	5.2	0.6	9.3
Potamogeton richardsonii	--	0.4	0.1	2.8	2.5
Callitriche hermaphroditica	--	--	0.4	1.0	0.9
Zannichellia palustris	0.2	--	0.4	4.0	1.8

Appendix VII (continued)

WIDGEON POND

Frequency of Occurrence of Vegetation Sampled

Species	1966	1970	1971	1972
Elodea canadensis	90	100	96	90
Myriophyllum spicatum	6	30	78	33
Potamogeton pusillus	--	20	38	--
Ceratophyllum demersum	--	10	18	30
Potamogeton friesii	--	10	4	--
Chara vulgaris	--	7	8	3
Ranunculus aquatilis	6	7	4	--
Potamogeton pectinatus	--	3	38	7
Potamogeton filiformis	--	3	--	--
Potamogeton richardsonii	--	3	10	7
Lemna trisulca	3	--	--	--
Potamogeton zosteriformis	--	--	2	--
Zannichellia palustris	--	--	4	--
Hippuris vulgaris	--	--	2	--

Species Composition

Species	1966	1970	1971	1972
Elodea canadensis	98.9	89.5	58.3	46.9
Myriophyllum spicatum	0.2	1.7	24.4	4.8
Potamogeton pusillus	--	2.4	3.3	--
Ceratophyllum demersum	--	0.1	0.5	44.6
Potamogeton friesii	--	TR	TR	--
Chara vulgaris	--	0.2	0.1	2.4
Ranunculus aquatilis	0.8	0.8	0.3	--
Potamogeton pectinatus	--	0.3	9.4	1.0
Potamogeton filiformis	--	2.6	--	--
Potamogeton richardsonii	--	2.6	3.5	0.2
Lemna trisulca	0.1	--	--	--
Potamogeton zosteriformis	--	--	0.4	--
Zannichellia palustris	--	--	TR	--
Hippuris vulgaris	--	--	TR	--

Appendix VII (continued)

MAC DONALD'S POND

Frequency of Occurrence of Vegetation Sampled

Species	1967	1969	1971
Potamogeton pectinatus	42	58	95
Zannichellia palustris	79	58	60
Potamogeton foliosus	53	53	25
Chara vulgaris	68	5	25
Myriophyllum spicatum	11	--	--
Lemna trisulca	5	--	--
Potamogeton pusillus	--	--	90
Ranunculus aquatilis	--	--	15
Callitriche hermaphroditica	--	--	10

Species Composition

Species	1967	1969	1971
Potamogeton pectinatus	20.0	40.0	39.3
Zannichellia palustris	25.0	22.7	9.8
Potamogeton foliosus	25.3	35.8	1.3
Chara vulgaris	29.5	1.5	3.5
Myriophyllum spicatum	0.2	--	--
Lemna trisulca	TR	--	--
Potamogeton pusillus	--	--	46.3
Ranunculus aquatilis	--	--	TR
Callitriche hermaphroditica	--	--	TR

Appendix VII (continued)

UPPER LAKE

Frequency of Occurrence of Vegetation Sampled

Species	1966	1968	1970	1971	1972
Chara vulgaris	38	46	42	29	41
Potamogeton richardsonii	65	70	40	57	43
Myriophyllum spicatum	4	28	29	24	22
Potamogeton praelongus	15	12	21	52	17
Sagittaria cuneata	17	14	13	8	10
Potamogeton pectinatus	31	10	12	62	21
Najas flexilis	17	10	8	5	9
Elodea canadensis	31	10	5	6	1
Utricularia vulgaris	--	--	3	TR	--
Potamogeton filiformis	--	--	3	--	--
Potamogeton pusillus	--	--	2	3	1
Ranunculus aquatilis	2	--	1	2	1
Potamogeton zosteriformis	--	--	1	7	3
Potamogeton friesii	--	--	--	TR	--

Species Composition

Species	1956	1966	1968	1970	1971	1972
Chara vulgaris	25.3	24.0	33.2	58.9	20.5	56.7
Potamogeton richardsonii	3.3	43.1	36.8	13.2	16.0	16.5
Myriophyllum spicatum	0.2	0.7	14.5	9.7	5.4	9.8
Potamogeton praelongus	3.9	6.7	4.9	8.4	25.8	6.5
Sagittaria cuneata	2.8	1.8	4.1	1.2	0.5	1.2
Potamogeton pectinatus	4.8	8.7	4.7	4.3	27.1	4.2
Najas flexilis	4.0	0.4	1.0	0.3	0.9	0.5
Elodea canadensis	46.6	12.0	0.8	0.1	0.9	0.6
Utricularia vulgaris	--	--	--	0.3	TR	--
Potamogeton filiformis	--	--	--	3.0	--	--
Potamogeton pusillus	--	--	--	0.7	0.8	--
Ranunculus aquatilis	--	2.0	--	TR	1.5	1.5
Potamogeton zosteriformis	3.2	--	--	TR	0.8	2.5
Potamogeton friesii	--	--	--	--	TR	--
Potamogeton foliosus	5.7	--	--	--	--	--

Appendix VIII

Primary Over-Wintering Mechanisms of Submerged Macrophytes at Red Rock Lake Refuge

Species	Rhizome	Tuber	Winter Buds	Dormancy	Spores or Seeds
Isoetes spp.	X				X
Chara vulgaris					X
Nitella flexilis					X
Lemna trisulca				X	
Elodea canadensis				X	
Najas flexilis					X
Potamogeton pectinatus	X	X			X
Potamogeton friesii			X		infertile
Potamogeton richardsonii	X	X			X
Potamogeton praelongus	X	X	X		X
Potamogeton foliosus	X		X		X
Potamogeton zosteriformis			X		infertile
Potamogeton pusillus			X		infertile
Zannichellia palustris	X				X
Sagittaria cuneata	X	X			
Ceratophyllum demersum				X	
Ranunculus aquatilis	X				X
Hippuris vulgaris	X				X
Callitriche hermaphroditica					X
Utricularia vulgaris			X		
Polygonum amphibium	X				X
Myriophyllum spicatum			X		X

Appendix IX

Nutritional Analysis of Submerged Macrophytes

Species	Percent					
	Moisture	Protein	Crude Fat	Crude Fiber	Phosphorus	Calcium
Potamogeton richardsonii	88.2	14.9	1.08	21.4	.31	4.0
Potamogeton praelongus	86.0	10.5	1.52	17.2	.18	12.0
Ceratophyllum demersum	89.6	11.1	.77	14.5	.28	8.0
Potamogeton pectinatus	85.0	7.5	.50	11.6	.17	13.1
Utricularia vulgaris	95.1	10.4	1.12	12.0	.21	1.8
Lemna trisulca	87.0	13.3	1.22	11.5	.21	9.5
Potamogeton zosteriformis	80.6	9.8	.97	20.5	.17	16.1
Sagittaria cuneata	97.0	19.0	1.4	21.9	.58	2.7
Chara vulgaris	79.9	7.2	.62	6.9	.10	23.7
Myriophyllum spicatum	90.6	13.5	.74	12.5	.21	7.4
Triticum aestivum	9.6	11.6	1.57	3.0	.59	0.05
Elodea canadensis	89.9	10.4	1.22	11.5	.26	8.4