THE SYNECOLOGY OF PHYCO-PERIPHYTON IN OLIGOTROPHIC LAKES

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TABLE OF CONTENTS

Chapter

LIST OF TABLES

LIST OF ILLUSTRATIONS

Figure Page

CHAPTER I

INTRODUCTION[1]

Most limnological literature over the last century has been concerned with primary productivity--cause and effect. This previous research elucidates many important concepts in the productivity of freshwaters, and generalizes the resultant concepts for overall use. However, in a lentic body of water sufficient in size to promote a reasonable standing crop of fish, there exists numerous biocoenoses which have not been fruitfully and fairly considered in an appraisal of lentic biopotential, and which may eventually have solvency in the problem of fish population dynamics. All possible productive biocoenoses should be investigated to demonstrate their effect on the entire lentic community.

Through decomposition, run-off, and direct precipitation vital nutrients are released into a lake so that life processes may continue. The utilization of these nutrients is the basis of Juday's (19) pyramid of numbers which is revised and depicted in Figure 1.

Figure 1 represents the idea that the primary producers are the important and necessary link in the chain of food production for the

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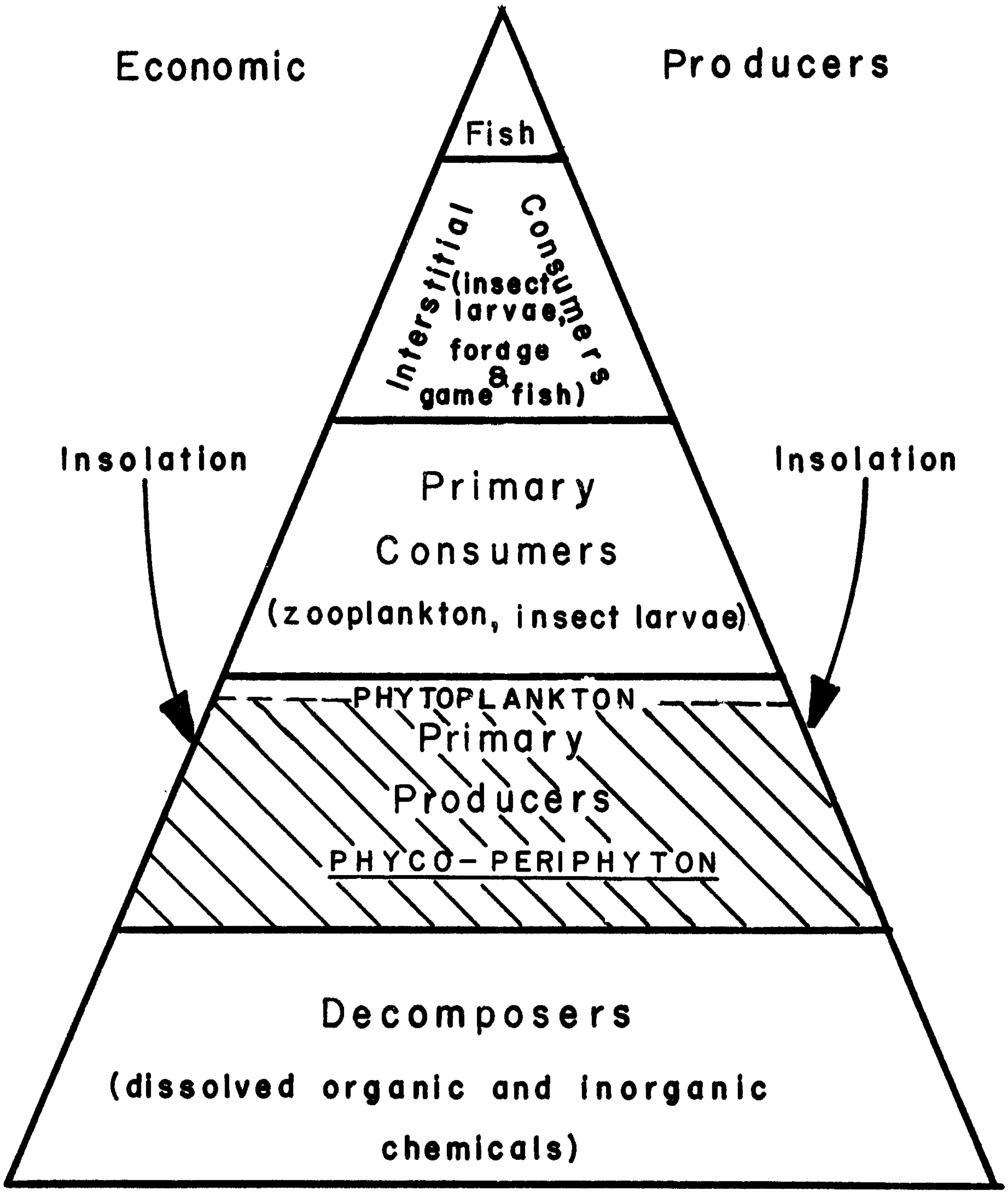

Fig. 1--Schematic Demonstration of the Juday Pyramid of numbers showing the primary production area of the pyramid to be 90 percent formed by the phyco-periphyton.

consumers. Andrews and Hasler (1) have stressed the importance of the primary producers in supplying the five pounds of food necessary to produce one pound of fish. Where does this primary production come from? What is the most important niche of the lake that produces it? What biocoenosis contributes most to this production?

The above questions are just a few of the many questions involved in this synecology study. Of major interest in this paper is the quantitative research of the littoral zone, the nutrients, and the various phyco-synusiae of the phyco-periphyton biocoenosis. This work is based on the hypothesis that the majority of lakes throughout the world are greatly influenced by the littoral area where fish spawn, and where the greatest variety of benthic insects are found. Also, algal production per unit area is greater in the littoral ecosystem, than elsewhere. The high standing crop and production of phyco-periphytes (the basis of aquatic food chain) and a demonstration of their tropic-dynamic effect on the lakes' synthesis are shown.

It is impossible in any natural situation to single out factors or study unit parts of the ecosystem. Dice (10) described an ecosystem in relation to productivity as, ". . . governed by the total effective solar energy falling annually on the area, by the efficiency with which the plants are able to transform this energy into organic components, and by those physical factors of the environment which affect the rate of photosynthesis." The importance of the littoral biocoenosis termed phyco-periphyton in the pulse of an aquatic microcosm, cannot be overemphasized.

Productivity encompasses a multitude of definitions to the aquatic biologist. In this study the term productivity will be used in two ways. First, it will be used to refer to primary production of algae developed in a space-time continuum; and will be recorded as weights and numbers per time period. The second usage of the word productivity will encompass its economical aspect and will be stated as kilograms of fish produced per area measure.

The periphyton in this study will be prefixed by the work phyco, and will refer only to those assemblages of algae found on live and dead aquatic plant material. It is believed that this usage will prevent the confusion often associated with the synonomous terms periphyton and aufwuchs which include assemblages of animals along with the plant communities.

Purpose

Although primary productivity has been studied by many investigators over the past 100 years, only recently has periphyton dynamics been considered (5, 8, 14, 16, 22, 23, 25, 27, 33, 35, 40, 41, 42). Waterworks engineers have become interested in periphyton from the standpoint of water quality, especially taste and odor problems. Sanitation engineers (14, 20, 21) are concerned with periphyton and its destructive and productive ability under the stress of sewage effluent.

Fish culturalists (26, 27) are studying periphyton because many food and forage fish derive nutrient from gleaning algae from the aquatic substratum. Phycologists (15, 40, 41, 42) may see in these organisms a key to algal succession, and an answer to the origin of phytoplankton.

This preliminary study is designed to (a) demonstrate the highly productive nature of the littoral area as compared to the pelagic region, (b) the possible importance of phyco-periphyton in the diets of fish, (c) the effects of meteorological conditions on distribution of phytoplankton, and (d) a demonstration of the invalidity of using artifical substrates as a universal means of measuring productivity.

To undertake a study of this nature, it was necessary to eliminate as much as possible all extraneous factors which are man-made and unnatural to the aquatic biocoenosis. Having only natural conditions influencing the data, it is easier to comprehend pollutional effects where ever man has established himself on a body of water. This study was conducted on nine Canadian lakes which follow both the geologic and biologic criteria for oligotrophy, and are pristine. In this study the concept of synecology will be applied to the phyco-periphyton biocoenosis.

History

Since limnology was founded less than a hundred years ago little work has been accomplished on the productivity of the littoral zone and periphyton dynamics. The majority of the studies on phyco-periphyton have been floristic in nature, concerned with descriptive terminology, and some with ecology while a few have attempted recently to demonstrate quantitative data (5, 16, 22, 23, 25, 35).

Fassett (13) has stated, "Aquatic plants may support algae or small animals which are directly or indirectly food for game fish." In 1939, Roll (33) published an attempt to clarify periphyton terminology and established consistency in this area of research. He decided to use the term periphyton, and described it as those assemblages of organisms growing on live and dead plant matter, and stones. He excluded benthic forms. Also, included in his work was a complete citation of all previous work concerned with phytosociology and terminology in Germany.

The best basic source of periphyton information was published by Young in 1942 (42). The term periphyton has been found in the literature of Newcombe (22, 23), Welch (39), and Grezenda and Brehmer (16). In Ruttner's book (34), a reintroduction of the term aufwuchs, used by workers preceding Roll (33), was noted, and it is accepted in the latest limnology text by Reid (30), as well as in the work of Whitford (40, 41). Other terms have been used to a limited extent. In the work of Fritch (15) the terms epilithic (on stones) and epiphytic (on plants) are used. Later work by Prowse (27) adopts the term epiphyte. Butcher's (4) classic work on rivers includes a particular reference to sessile algae, and Fjerdingstad (14) uses the term benthic algae to refer to periphyton type communities in a river. Finally, Castenholz (5) reports his work using the term attached algae.

As for other studies of the unique biocoenosis, Tarka (37) and Lowe (18) have just listed algae found in the periphyton communities.

Roll (33) reports Hentschell in 1917 made the first studies of periphyton using glass slides, and this method has been used lately by Newcombe (22, 23), Patrick (25), Cooke (8), Castenholz (5), Grezenda and Brehmer (16), Whitford (40, 41) and Sladecek and Sladecov (35) with a new modification by Anita, et al. (2) using a large volume plastic sphere.

Cholokny (6) pioneered the ecology of epiphytes. Young (42) reports Nauman in 1936 was the first to investigate periphyton for waterworks engineers. Fjeringstand's (14) work concerned the ecological studies of river pollution and benthic algae.

Brehmer and Ruttner (3) made the first real investigation of the littoral zone ecology and demonstrated nutrient depletion in a zone around the substratum. Young (42) relates that Hentschell and Vischer have been active in studies of ship bottom fouling by periphyton. Newcombe (22, 23), Castenholz (5), Young (42), and Whitford (40, 41) have done the most extensive work to date on the subject of periphyton. Ruttner (34) and Whitford (41) have demonstrated further that current is necessary in nutrient replenishment. Fritch (15) demonstrates with reference to German workers, the effect of natural substratum on population and growth.

Fritch (15), Young (42), Welch (39), Prowse (26, 27), Edmundson (12), and Reid (31) have recognized the importance of a knowledge of the littoral zone and its periphyton in admitting to a deficiency of information in this area.

Geomorphology

The parameters of this experiment called for the initial investigation of phyco-periphyton to be performed on a pristine oligotrophic lake. Lakes answering this description, and that are easily accessible, are nonexistent in the United States generally.

Through the courtesy and support of the Ontario Department of Lands and Forests, approximately 3,000 lakes in the Haliburton District, Algonquin Provincial Park of North Eastern Ontario, were made available for study. Research was conducted on the following lakes: Brewer (44 hectares), Bridle (21.3 hectares), Clarke (13.6 hectares), Costello (24.0 hectares), Galairey (586 hectares), Gordon (19.2 hectares), Kearney (20.2 hectares), Little McCauley (14.5 hectares), and the control lake, Opeongo (5,600 hectares). They were accessible by logging roads and short canoe portages.

These lakes are scattered over 150 square kilometers of boreal woodland, 388 to 438 meters above sea level. They lie at the headwaters of one tributary of the Ottawa River, the Madawaska. The soil surrounding the lakes is predominantly peat with some humus. According to Clark (7) this type of country is geologically characterized

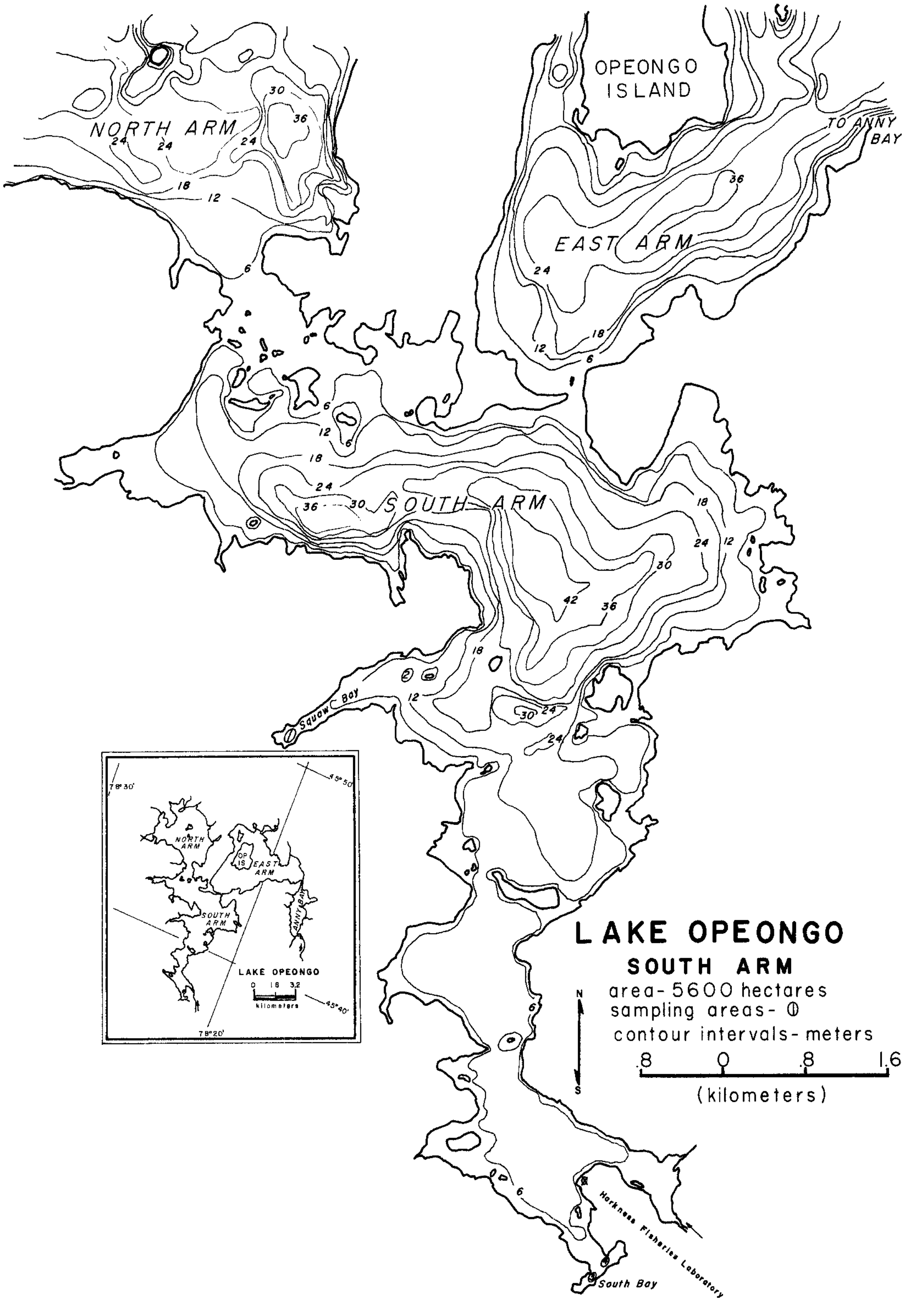

Fig. 2--Morphometric data for Lake Opeongo

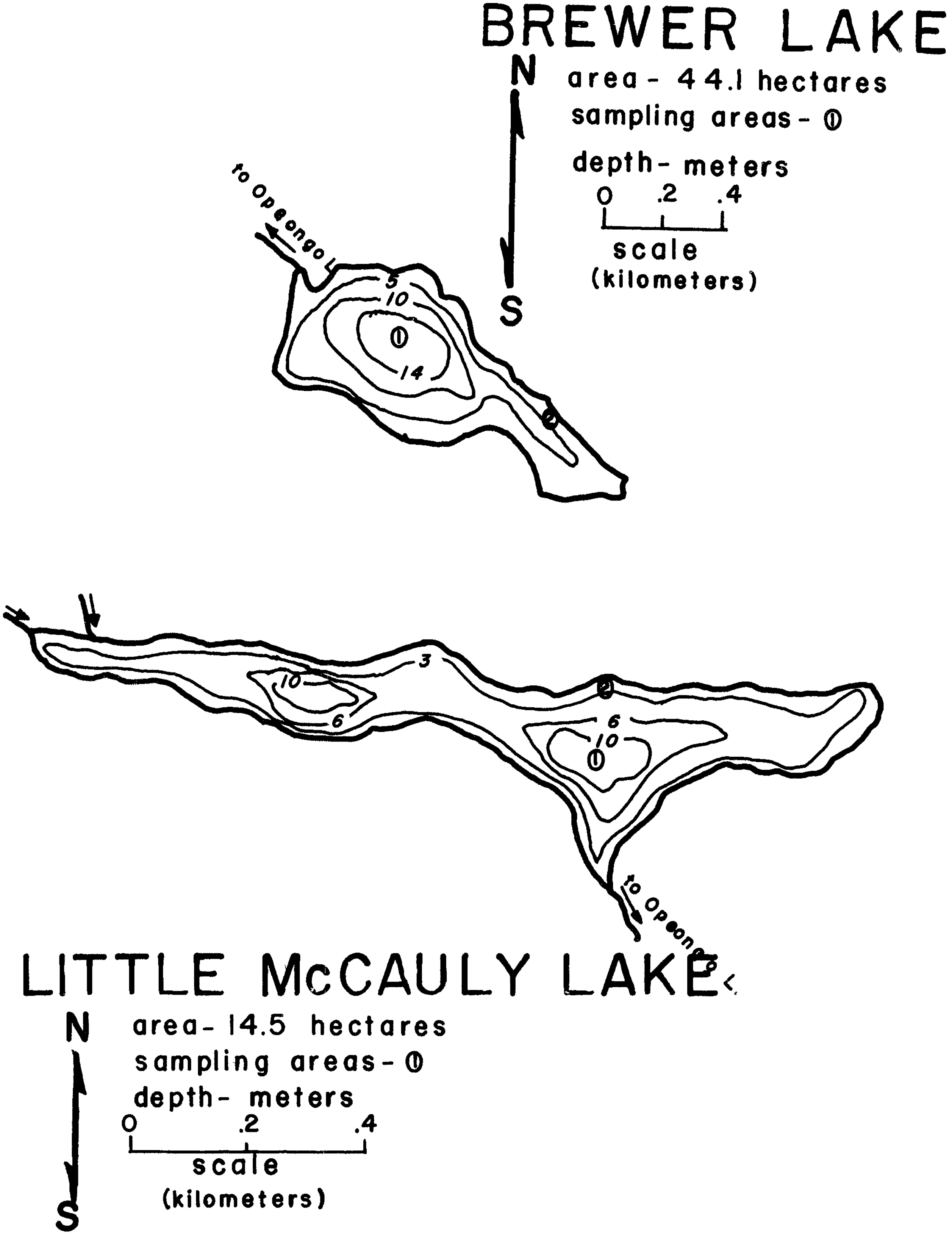

Fig. 3--Morphometric data for lakes Brewer and Little McCauly

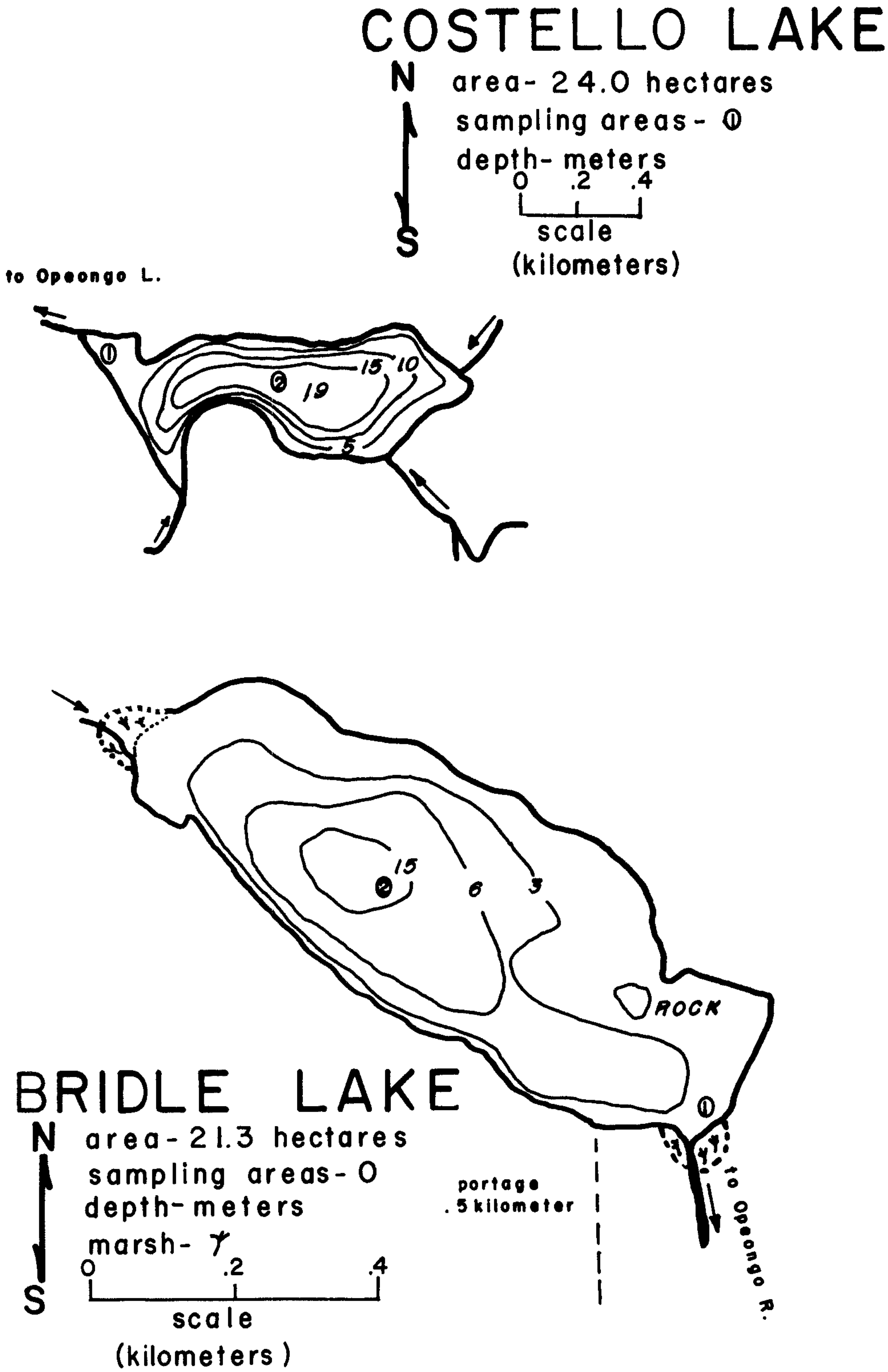

Fig. 4--Morphometric data for lakes Costello and Bridle

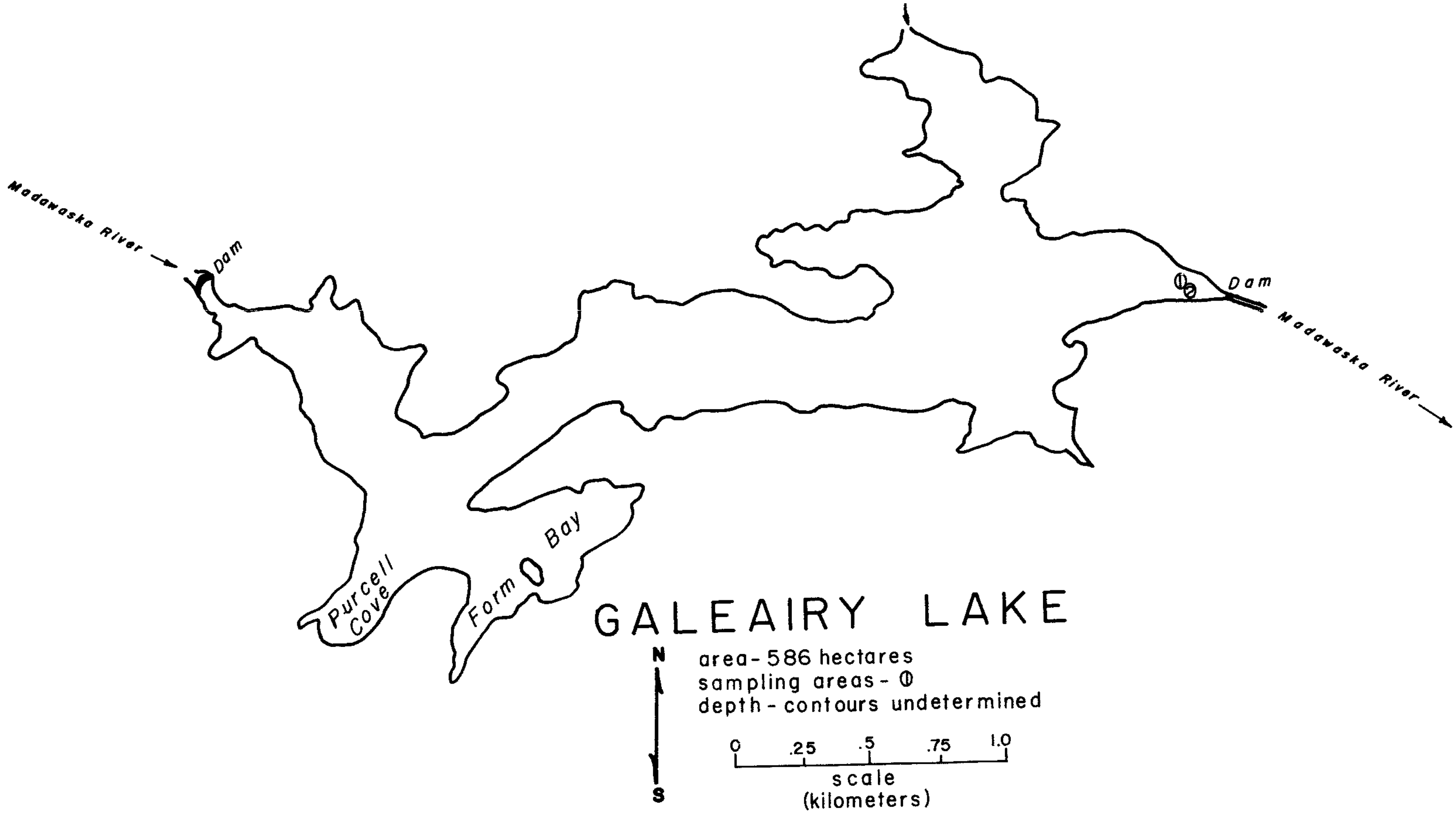

Fig. 5--Morphometric data for Galeairy Lake

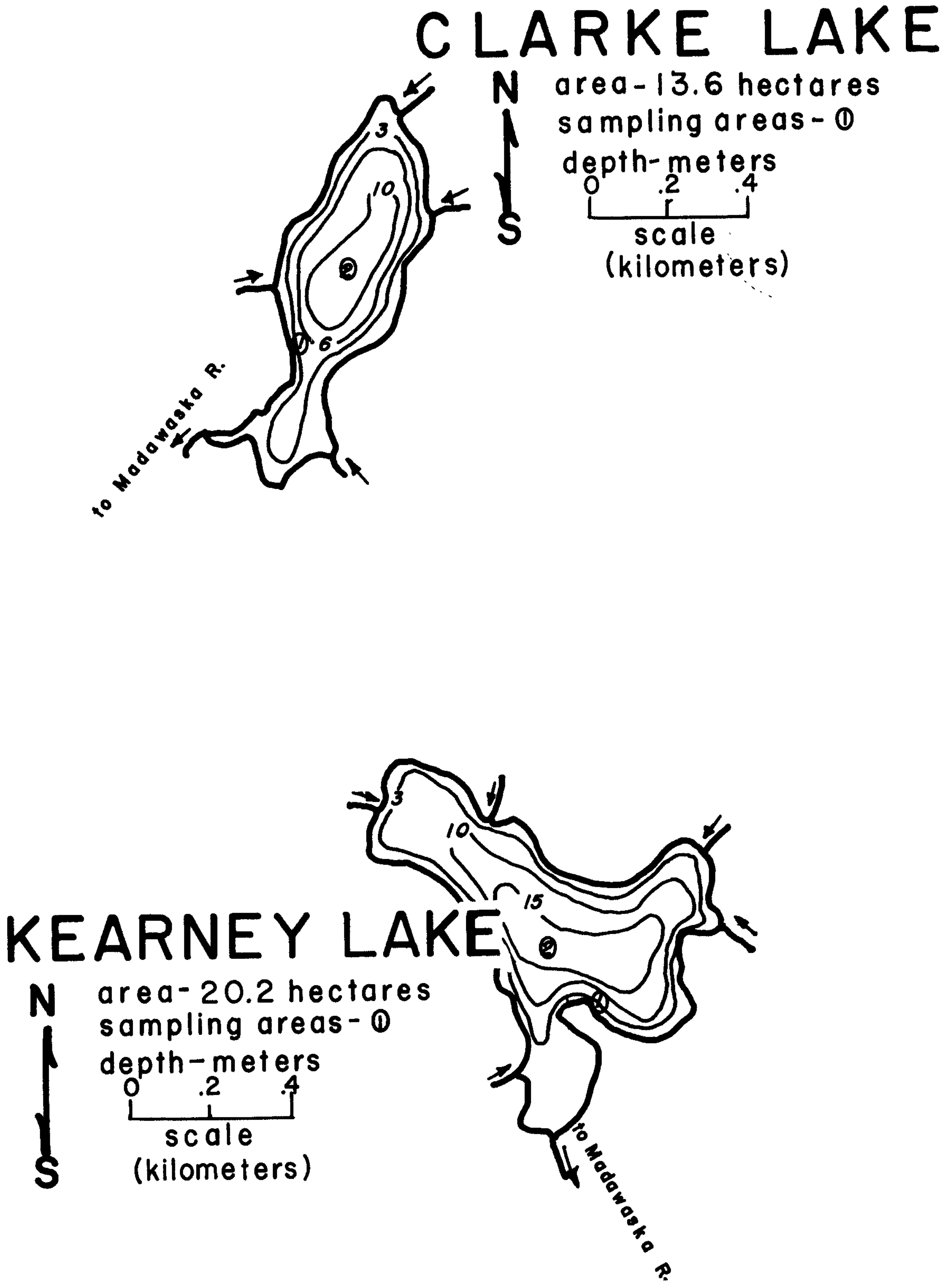

Fig. 6--Morphometric data for lakes Clarke and Kearney

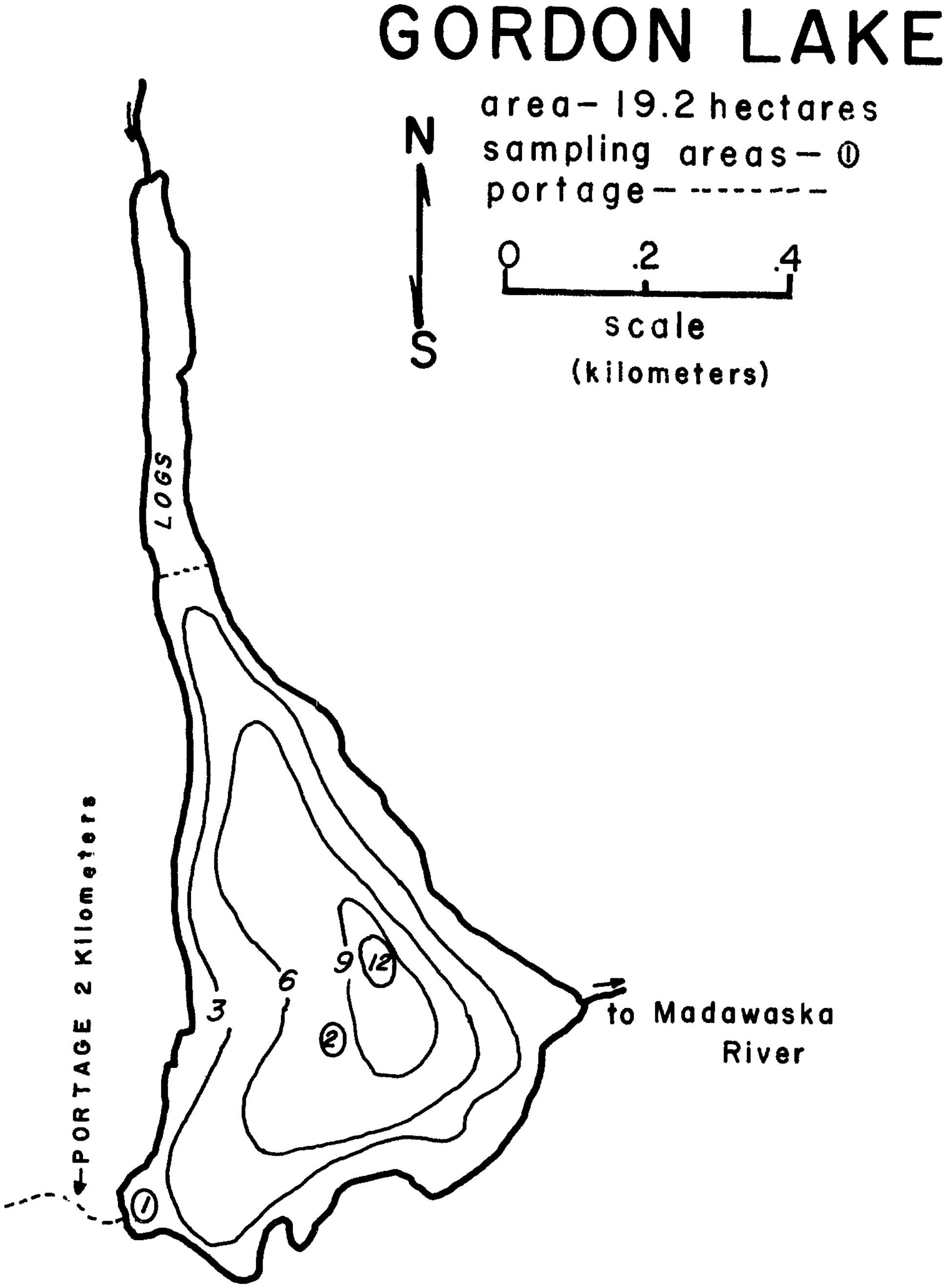

Fig. 7--Morphometric data for Gordon Lake

by the Precambian granite gneiss substratum which profusely outcrops. The entire park is situated on a geologic dome, which is characteristically referred to as the Grenville area of the Canadian Shield.

Dice (11) lists this area in the Canadian Biotic Province for it is typified by a Maple-Pine phytocoenosis, low relief, poorly drained depressions, and glacial topography. This is a slightly humid area as defined by the criteria of excess rainfall described in Thornthwaites' work (36). Precipitation averages twenty-four inches of rainfall a year with eighteen inches of evapotranspiration.

The area in which the lakes are located is where no human refuse enters the streams influent to the lakes. The lakes are geologically oligotrophic having a "U" shaped basin and a limited littoral zone. Bottom soils are predominantly pulpy and fibrous peat in the shallow areas and grade into gyttja (17) in deeper water.

Biomorphology

The lakes in this area are characterized by the adequate production of stenothermal Salmonidae and Coregonidae. The biologic productivity of primary producers is low compared to more fertile lakes. This idea is supported by using the Nygaard Index as described by Rawson in 1956 (29). In this demonstration, a profuse number of species in the denominator greater than the numerator demonstrates oligrotrophy. In lakes of high productivity (eutrophic), the number of species is low in the oligotrophic lake. In Table I, the lakes are listed in alphabetical order, demonstrating various morphological and productivity characteristics. Figures 2 through 7 demonstrate the hydrographic features of the nine study lakes. Comparing these figures to Table I the potential productivity shown by the shoreline development can be visualized, and the Nygaard Index for productivity demonstrated oligotrophy for all lakes concerned.

TABLE I
ALPHABETICAL LISTING OF THE MORPHOLOGICAL AND PRODUCTIVITY ASPECTS OF THE NINE LAKES STUDIED

Lake	Area (hectare)	Mean Depth (meters)	Maximum Effective Length (Kilometers)	Shore-line Devel.	Nygaard Index[1], [2]	Height Above Sea Level (meters)	Axis
Brewer	44.1	4.8	1.2	1.49	.75[1]	438	NW-SE
Bridle	21.3	5.0	.98	1.20	.17[2]	391	NW-SE
Clarke	13.6	5.2	.96	1.50	.20[2]	389	N-S
Costello	24.0	10.6	1.3	1.90	.20[2]	403	E-W
Galeairy	586.0	N.D.[3]	5.6	2.70	N.A.[4]	388	E-W
Gordon	19.2	6.05	1.6	1.30	.08[2]	389	N-S
Kearney	20.2	3.5	.96	1.90	N.A.[4]	391	NW-SE
Little McCauley	14.5	6.9	1.4	1.80	1.0[1]	436	NW-SE
Opeongo	5600.0	19.0 (South Arm)	6.4 (South Arm)	4.60	.71[1]	402	N-S

[1] $\frac{\text{Chlorococcalean species}}{\text{Desmidiaceae species}}$ = less than 1

[2] $\frac{\text{Centric Diatom Species}}{\text{Pennate Diatom Species}}$ = less than .2

[3] No Data

[4] Not Applicable

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CHAPTER II

MATERIAL AND METHODS

Chemical, physical, geographical, geological, meterological, floristic and faunistic data were collected. Of the nine test lakes investigated, Opeongo (Figure 3) was the major lake investigated. Chemical and physical samples were collected daily from two of the four stations (Figure 3). Phytoplankton and phyco-periphyton were collected bi-daily from each station for the first segment of the study and daily for the remaining segment. Once a week water was analyzed from the deepest portion of the lake in the South Arm.

In making plankton collections, a plankton net made of Number 25 silk bolting cloth and fitted with a collecting bottle designed after Foerster (7) was towed for approximately .2 kilometers through the top meter of water at both the pelagic and littoral stations. Care was taken in the weed beds not to disturb the plants mechanically.

A plankton net co-efficient was computed (21) and the data adjusted accordingly. Kemmerer water bottle samples were filtered in an attempt to determine significance of nannoplankton. Counts were made and added to the net co-efficient computation.

Phyco-periphyton was collected by the use of skin diving techniques. Small 135 milliliter screw top jars with chilled, filtered water were taken underwater. The water was filtered to remove any algae, alive or dead, and was chilled prior to leaving the laboratory for sampling so that the temperature would approximate that of the water and thus influx of lake water would be reduced to a negligible amount.

Once underwater, the cap of a jar was removed and the open end of the bottle was then placed slowly and gently over a plant leaf. After sufficient lengths of the plant leaf were placed inside the jar (this was done without touching any part of the leaf), the leaf was severed with a pair of scissors. Several leaves of young plants were studied. *Vallisneria americanum*, *Myriophyllum farwellii*, *Saggitaria sp.* (rosettes), *Potomogeton natans*, *Nymphaea odorata*, and *Nitella sp.* Submerged logs were also sampled qualitatively by breaking off pieces of wood under water. All phytoplankton and phyco-periphyton samples were filtered utilizing membrane filters of 0.45 micron porosity. The phyco-periphyton were liberated by violent shaking and repeated washings with a strong stream of water. A total of 250 samples were taken from all lakes. Random samples of all washed higher aquatics were checked for percent missed in washing. It was found that *V. americanum*, and *Saggitaria sp.* were essentially washed clean. Myriophyllum due to its large area and overlapping leaves retained 30 percent of the sample and data were adjusted accordingly.

For microscopic analysis, a phase microscope having up to 2000 magnifications was used. Slides of one quarter of each membrane filter were made according to McNabb (14). Counts of the algae and *Keratella cochealaris* (4), the zooplankton indicator chosen for this study, were made using oil immersion, and the statistical method outlined by McNabb (14). Random selection of adjacent and cross-filter quadrants were also made to determine random distribution. It was found that no significant difference in quadrants existed, and when a comparison of the statistical counts to the actual counts were made the product approached unity and fell within the range McNabb (14) lists for correct significance.

A square meter frame was constructed of wood and weighted with rocks. It was used to count numbers of individual plant species and Pelecypoda per square meter in both weed beds. Means of these counts were then computed to ascertain productivity in the weed beds themselves.

Chemical tests for oxygen, carbon dioxide, ortho-phosphates, sulfates, nitrates, ferric iron, chlorides, total hardness, carbonates, and biocarbonates were run according to the methods outlined in Standard Methods, tenth edition (1). Phosphates, nitrates and sulfates were determined on a portable colorimeter, and the other tests were run titrametrically.

A modified Kemmerer water bottle was used for water sample collections along with a device designed for more careful sampling of water. This water sampler, known as the Foerster Sub-surface Water Sampler (8), was used in the weed beds to sample water directly in close proximity to the vegetation.

The pH was determined using a portable electric pH meter, temperature by a thermister thermometer, water color with a cobolt disc comparator, wind speed by a portable anemometer and underwater photographs were made with a Makoshark submersible camera and a Rolliflex camera in a water telescope. Current speed was calculated theoretically from the wind speed read on the anemometer held .5 meters off the water surface (Figure 21).

Chemical-physical data were checked against simultaneous work performed by the Ontario Department of Lands and Forest, and that analyzed by the Ontario Water Resources Commission. Checks for pollution were made at intervals over the summer using the Mohr chloride test and the portable membrane filter coliform method as outlined by Standard Methods (1).

Fish were collected using six lengths of alternated one-half and three-fourths-inch mesh, twenty-five meter, monofilament gill netting, and small mesh minnow traps. Nets were left in the weed bed areas for twenty-four hours. Traps were left in continuously and checked daily. Seining was also used in sampling. Fish scales were aged and stomach analyses were made for possible ingested phyco-periphyton.

A control constructed of aluminum wire screen was placed over Vallisneria americanum plants at Station 3. Samples were taken periodically to check the possibility of graze rates and current effects. Deep (Station 3) and shallow (Station 1) weed beds were chosen for comparative purposes (Figure 2). They were chosen close to the laboratory so that all chemical work could be completed the same day. Eight other lakes were sampled for comparison to Lake Opeongo. Samples were collected simultaneously with collections at Opeongo.

Phyo-periphyton was collected using glass lantern slides 10 by 12.5 centimeters to be checked against natural attached material. Air dry weights of organic matter on the filters were calculated to give an idea of the organic productivity in milligrams per hectare.

All algal taxonomy (Table 2) was checked against several sources: Prescott (16), Tiffany and Britton (18), Smith (17), Desichachary (2), Tilden (19), Irene-Marie (12), Huber-Pestalozzi (10), Elmer (5), Lowe (13), and Druet and Daily (3). Fish fauna (Table 5) were checked against Hubbs and Lagler (9) and Trautman (20). Higher aquatic plants were keyed according to Fassett (6) and Meuncher (15).

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CHAPTER III

RESULTS

Qualitative

Table II lists the genera and species encountered in this study. These data are so placed as to demonstrate the various synusiae of the phytoplankton and phyco-periphyton biocoenoses.

Vallisneria americana, Sagittaria sp. (rosettes), and Myriophyllum farwellii show close association in phyco-periphyton genera. V. americana has more genera represented, but it will be shown later there is less quantity. Table II also illustrates that Potamogenton natans and Nymphaea odorata lack the inhabitation as noted in all the other higher aquatic plants studied. They are of a similar morphological construction having tubular stems with partially emergent, floating leaves. Whether these two plants have a morphology nonconducive to inhabitation, or secrete substances inhibiting growth of the phyco-periphtes is not known. Let it be sufficient for this study to note that these two emergent plants are not highly productive in numbers of genera inhabiting their surface.

The log samples and Nitella sp. demonstrate an abundance of Bascillariophyceae. Lake Opeongo is much more productive than the other eight lakes studied although qualitatively the phyco-periphyton

TABLE II

DISTRIBUTION OF THE GENERA FOUND AS PHYCO-PERIPHYTON AND PHYTOPLANKTON IN THE NINE TEST LAKES

Plants	M	Ni	Ny	P	S	V	L	Sl	Pd	Ps	C	O		B		Br		Cl		Co		Ga		Go		K		LM	
												pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py
CYANOPHYTA																													
Anabaena sp.	X					X	X		X	X		X	X					X	X			X	X					X	X
Aphanocapsa sp.									X	X		X																	
Aphanotheca sp.	X				X	X							X																
Chroococcus giganteus turgidus	X		X	X	X	X	X		X	X		X	X	X	X	X	X							X	X				
Coelospaerium sp.				X					X	X		X	X			X	X	X	X										
Merismopedia sp.					X	X				X		X	X						X										
Microcystis aeruginosa rupestris	X	X		X	X	X	X		X	X		X	X	X	X	X	X												
Rhabdoserma sp.									X	X		X																X	X
Rivularia borealis (?) (after Tilden)	X												X																
Lyngbya sp.							X						X																
CHLOROPHYTA																													
Ankistodesmus sp.									X			X																	
Arthrodesmus quadridens						X			X	X		X	X																
Bulbocheate sp.	X				X	X							X		X														X
Chlorella-like	X			X				X	X	X		X	X		X	X	X												
Chlorococcum sp.					X	X	X	X	X	X		X	X		X	X	X									X	X		

TABLE II — Continued

Plants	M	Ni	Ny	P	S	V	L	Sl	Pd	Ps	C	O		B		Br		Cl		Co		Ga		Go		K		LM	
												pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py
Closterium	X			X			X	X	X	X		X	X																
turgidum																													
Cosmarium	X	X	X		X		X	X	X	X		X	X	X	X			X	X				X	X	X	X			
bipunctatum																													
quasillus																													
quinarium																													
subtumidium																													
Cylindrospermum						X							X																
sp.																													
Desmidium	X	X	X		X	X	X		X	X		X	X		X			X	X			X	X	X	X	X	X		
aptogonum																													
spp.																													
Euastrum	X				X				X	X		X	X																
affine									X	X																			
Eudorina									X	X		X																	
sp.																													
Gloeocystis sp.									X			X																	
Gymnozyga sp.	X								X	X		X	X																
Hyalotheca	X		X		X	X	X		X	X		X	X											X	X			X	X
dissiliens																													
neglecta																													
Micrasterias sp.							X		X	X		X	X																
Pandorina sp.					X	X			X	X		X	X																
Pediastrum									X	X		X																	
duplex																													
Pleurotanium sp.	X									X			X			X	X												
Scenedesmus	X		X			X			X	X		X	X																
obliquus (?)										X		X	X																
Sphaerella			X							X		X	X																
lacustris																													
Sphaerozosma										X		X																	
granulatum																													
Staurastrum	X									X		X	X											X	X				
megacanthum																													
gracile																													

TABLE II — Continued

Plants	M	Ni	Ny	P	S	V	L	Sl	Pd	Ps	C	O		B		Br		Cl		Co		Ga		Go		K		LM	
												pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py
Stichococcus			X							X		X	X																
bacillaris (?)																													
Stipitococcus sp.					X					X		X	X																
Tetrahedron sp.										X		X																	
Trentopohlia										X		X																	
aurea (?)																													
Ulothrix sp.			X			X	X						X															X	X
Volvox sp.	X					X				X		X	X																
Westella									X	X		X																	
linearis (?)																													
Dictyosphaerium sp.						X							X																
Heamatococcus						X							X																
lacustris	X	X	X	X	X	X	X	X	X	X	X	X	X																
Oedogonium sp.	X				X	X							X																
EUGLENOPHYTA																													
Euglena sp.									X	X		X																	
Mallomonas						X			X	X		X	X																
caudata																													
elliptica																													
Phacus sp.										X		X																	
Trachelomonas									X	X		X																	
charkowiensis																													
Chrysosphaerella	X													X															
longispina																													
PYRROPHYTA																													
Ceratium									X	X		X				X													
hirunidella																										X			
Dinobyron	X	X			X				X	X		X	X																
cylindricum																													
Peridinium sp.									X	X		X																	

TABLE II — Continued

Plants	M	Ni	Ny	P	S	V	L	Sl	Pd	Ps	C	O		B		Br		Cl		Co		Ga		Go		K		LM	
												pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py
Synura		X	X	X					X	X		X	X			X	X							X	X				
uvella																													
CHRYSOPHYTA																													
(Bascillariophyceae)																													
Achnanthes sp.		X					X	X		X		X	X					X	X										
Amphora	X	X			X	X	X	X					X	X					X	X	X	X							
ovalis																													
Asterionella	X	X		X	X	X	X	X	X	X		X	X	X	X								X	X					
formosa																													
gracillima																													
Cyclotella	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
melosiroides																													
Cocconesis sp.	X				X	X					X		X																
Cymbella prostrata	X						X	X	X	X	X	X	X																
Diatoma	X	X			X			X					X																
anceps																													
Denticula	X	X			X	X							X						X		X		X		X		X		
ellegans																													
Eunotia	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X		
lunaris																													
pectinalis																													
robusta																													
Epithemia spp.			X		X	X	X			X	X	X	X	X	X							X	X						
Fragillaria	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
construens																													
crotonesis																													
pinnata																													
virescens																													
Frustulia			X			X							X						X				X		X				
rhomboides																													
Gomphonema	X	X			X	X	X	X	X	X	X	X	X	X	X				X		X		X				X		X
acuminatum																													
constrictum																													
montanum																													

TABLE II — Continued

Plants	M	Ni	Ny	P	S	V	L	Sl	Pd	Ps	C	O		B		Br		Cl		Co		Ga		Go		K		LM	
												pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py	pl	py
Gyrosigma	X		X		X	X	X	X					X																
acuminatum																													
attenuatum																													
Hantschia		X					X						X																
amphioxys																													
Melosira	X		X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
crenulata																													
distans																													
Meridion		X				X		X					X																
circulare																													
Navicula spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Nitzschia spp.	X	X			X	X	X			X	X	X	X	X	X					X	X	X	X			X	X	X	X
Pinnularia	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X							X	X	X	X
braunii																													
cardinalis																													
mesolepta																													
termes																													
Suriella	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X										
ovalis																													
Stauronesis						X		X			X																	X	X
anceps																													
acuta																													
phyllodes																													
Synedra	X	X	X	X	X	X	X		X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
ulna																													
radians																													
Tabellaria	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
fenestra																													
flocculosa																													

M—*Myriophyllum,* Ni—*Nitella,* Ny—*Nymphaea,* P—*Potamogeton,* S—*Saggitaria,* V—*Vallisneria,* L—Log, Sl—Slides, Pd—Plankton Deep, Ps—Plankton Shallow, C—Control, pl—Plankton, py—Periphyton, O—Opeongo, B—Brewer, Br—Bridle, Cl—Clarke, Co—Costello, Ga—Galeairy, Go—Gordon, K—Kearney, LM—Little McCauley.

and phytoplankton are similar. This same idea holds true for the East and North Arms of Lake Opeongo where *V. americana* was sampled and found to show no significant difference in phyco-periphyton populations.

Depth of the water in the weed beds in Lake Opeongo (Stations 1 and 3) seemed to affect the qualitative numbers of genera to no significant degree when the same leaf surfaces, e.g., at the same depth, are compared. Differences were noted in relation to depth. Looking at Figure 19, it is seen that the middle of a *V. americana* plant is much higher in genera found than the top or the bottom of the plant. The top of the plant is inhabited mostly by the algae which are adapted to current buffeting, e.g., *Gomphonema geminatum*. At the base of the plant, Pyrrophytes are found entangled and are included as phyco-periphyton. Higher yields of genera and numbers of population were then noted on the middle portion of the plant. The middle portion of the plant was that which was sampled most regularly, for this reason and because minnows were seen to feed in this area of the plant most frequently.

Sagittaria sp. and *M. farwellii* show no significant differences in habitation since they exist in a small volume of water, and do not extend over such a considerable length as do *V. americana* leaves.

Figure 8 is a schematic drawing depicting the phyco-periphyton synusia on a *M. farwellii* leaflet. This drawing is a composite from collections taken over a week of sampling during peak production. Note the attachments and entanglements of genera.

TABLE III

HIGHER AQUATIC PLANT SPECIES FOUND AT STATIONS 1 AND 3

Family	Station 1 1 meter	Station 3 2 meters
Allismaceae	*Saggitaria, sp.* (rosettes)	....
Haloragidaceae	*Myriophyllum farwellii*	*Myriophyllum farwellii*
Hydrocharitaceae	*Vallisneria americana*	*Vallisneria americana*
Lentibulariaceae	*Utricularia geminiscapsa*	*Utricularia geminiscapsa*
Nymphaeaceae	*Nuphar advenum*	*Nuphar advenum*
Potamogetonaceae	*Potamogeton natans*	....
	Potamogeton spp. (filamentous forms)	*Potamogeton spp.* (filamentous forms)
	....	*Potamogeton robbinsii*
Characeae (Algae)	....	*Nitella sp.*

The relative difference in genera and quantity for the three main test plants is shown in Figure 17. The data are depicted dimensionally to represent the relative shape of each species' leaf. The phyco-periphyton synusia on V. americana, Sagittaria sp., and M. farwellii is Tabellaria-Bulbocheate-Microcystis; the log is Tabellaria-Ulothrix-Microcystis, and Nitella sp. is Tabellaria-Gonphonema-Microcystis.

While the above mentioned plants were studied most, many other plants made up the particular weed beds. Table III lists the species of plants that made up the weed beds studied. Species seem to have a definite depth orientation, and they were distributed in definite patches. The three genera studied most extensively in this study, V. americana, Sagittaria sp. and M. farwellii, were the most evenly distributed throughout the entire weed beds, and were found at both stations.

Quantitative

Quantitative work on the phytoplankton and the phyco-periphyton are depicted in two ways, density and air dry weights.

In Figures 9 and 10, phytoplankton and phyco-periphyton are plotted, reading from the bottom in density of cells per liter of water. Cubing the density diameter will give actual numbers per liter. Between the phytoplankton and phyco-periphyton curves are plotted the chemical-physical data. For comparison of the production in a unit area, the phyco-periphyton curves may be read from the top down for the density is listed in square centimeters.

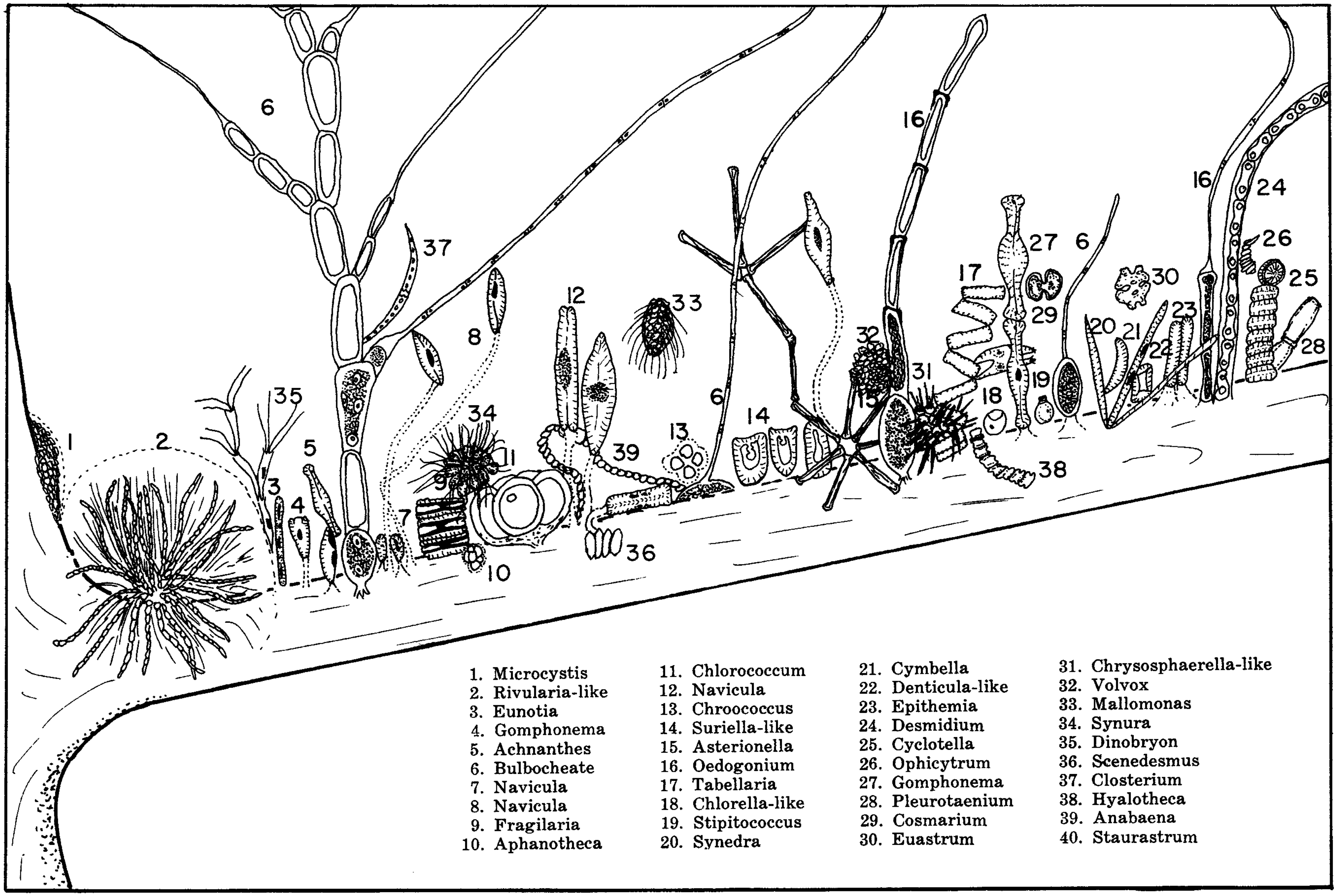

Fig. 8--Schematic representation of a portion of a Myriophyllum farwellii leaflet. Only the top portion of the leaflet is represented.

Figure 9 depicts Station 1. The phytoplankton trend is a normal undulating curve showing little definite tendency to peak. This is characteristic of plankton trends prior to the late summer maximum. The phyco-periphyton trends demonstrate a decrease in July corresponding to the chemical conditions. The late August maximum in phyco-periphyton holds with the available nutrients. After the phosphate nitrate rise, the phyco-periphyton begins a peak. It appears from the data depicted here that the higher quantity of organisms even in the lull period between peaks utilizes the available nutrients to a far higher degree than do the weed bed phytoplankton, thus demonstrating that if only the phytoplankton was sampled no true indication of the organic production would be obtained. The production and utilization of carbon dioxide, dissolved oxygen and bi-carbonates also demonstrate unity.

The lag in population density on August 23 appears to be a result of meteorological conditions induced from a four-day steady current, and a 10/10 total cloud cover as shown in Figure 21. The slight corresponding rise in phytoplankton on the same date is also indicative.

The data at Station 1 are erratic at times as is expected since the water depth is only one meter. This would of course subjugate this more shallow area to more stresses by currents, evaporation, light and temperature fluctuations. However, the general trend is demonstrated. "Students" T test calculations were run on the productivity peak at Station 1 and Station 3. The significance of this obvious peak lies at the

.001 percent level when comparison of organic weights and numbers are made.

Station 3 (Figure 10) shows similar data as was demonstrated at Station 1. In this particular set of data, the curves are much smoother due to the depth of the water and its limiting influence on fluctuations. Further, this weed bed lying at two meters in depth was in a more sheltered position at the southern end of the lake, and the effect of the wind fetch was reduced. Again chemical-physical data demonstrated a unity trend as explained for Station 1. The same density curve is expressed at this station and compares similarly to the phytoplankton. Again, meteorological conditions may be influential here and will be explained later under a section devoted to meteorological conditions.

Note that the curves, plotted for density of phyco-periphyton and phytoplankton vary considerably if population density numbers are compared.

When the numbers of phytoplankton and phyco-periphyton are checked simultaneously, it is obvious that there is a significant difference in numbers per liter of production.

Comparison of standing crop at peak productivity as well as at the lull periods (Figure 18), shows a 100:1 ratio of production by the phyco-periphyton over the phytoplankton. At the apex of each bar on the graph is the theoretical yield of fish flesh for this particular biocoenosis. The graph demonstrates the limited yields of the phytoplankton at the period graphed in comparison to the phyco-periphyton.

It is also noted that the yields in comparing the weed beds show that the more shallow weed bed produces a higher organic load, and comparing this graph to Figure 16, there are larger numbers produced at Station 1 than at the deeper Station 3. Comparison of the differences of densities and dry weights produced at Stations 1 and 3 for the over-all peak production is significant below the 1 percent level. This indicates that the depth of the water is a limiting factor on production, and that the more shallow weed bed is much higher in productivity. In Figure 22 a composite of the weights of the phytoplankton organic production shows a general downward trend from the previous month. In this graph, the mean of all stations compared to the most shallow station shows the general trends in the phytoplankton. Slight increases in numbers which are not too evident in the weights are noted. Comparing the weights and numbers in Figure 16 shows a slight upward trend of organic weight at the end of August. This small rise was accompanied by a rise in detritus formation on the *M. farwellii* leaves.

Keratella cochlearis (3) (Figure 11) was chosen as an indicator of zooplankton for graze rates. Generally, this species appeared while zooplankton increased over the peak of phyco-periphyton productivity. The reason here for the *K. cochlearis* trend is due to its known preference for feeding on periphyton (2). It was also evident that a peak was occurring since the filtering rates of the zooplankton did not keep pace with the subsequent algal production, and no over-all flattening of the peak is noted as would be expected if the zooplankton would and could have kept pace.

In Figure 11 the chemical data keeps unity with the algal production as in the phyco-periphyton.

An attempt to control graze rates verified an assumption that currents effect an exchange of waste bi-products from photosynthesis and respiration. Figure 14 shows the control in place over _V. americana_ at Station 3. The aluminum control screen was placed on at the beginning of sampling in July. It was left in place over a two-week period and samples were taken beginning on the fifth of August. It is evident in looking at the curve in Figure 14 and comparing it to Figures 9 and 10 that a significant reduction in total density production is evident. Checking with Table II, it is noted that there was an accompanying significant drop in numbers of genera. Columns II, III, and IV of Figure 14 show the only constantly recurring genera, and the very significant reduction in numbers when they are compared to noncovered plants in Figure 12. Columns V and VI of Figure 14 demonstrate the over-all reduction in further comparison to noncontrolled synusiae.

The conclusion drawn from this control segment of the study is the necessity of nutrient-waste exchange and the uselessness of trying to control grazing.

Figure 12 demonstrates the productivity of the more significant genera that appeared consistently in all phyco-periphyton collections, including phytoplankton.

Momentary peaks in the phytoplankton may be indicative of current effects as will be explained later.

The last segment of quantitative analysis is based on the use of artificial bare areas (glass slides). The data expressed in Figure 20 is expressed in two types of representations. In the spherical curve, plots of the density per square centimeter are made. This datum is a composite of the samples from both Stations 1 and 3. To compare this curve with the naturally collected samples it is necessary to note that at the top of each phyco-periphyton curve at Stations 1 and 3, density per square centimeter is plotted.

In comparing the artificial bare area data with the natural data, many factors are evident. First, a peak in phyco-periphyton on the slides occurs before the peak found on the plants. It is believed that this curve is just an indication of a colonization of an artificial bare area with the available nutrients. However, the ability to maintain the peak does not exist over the period dominated by the natural trend on the plants. These slides were placed directly in among the type plants used in this study. The second feature to be noted is that the data shown in Part 2 of Figure 20 show a large production of certain diatoms (Table II), and very few Chlorophytes or Cyanophytes. In comparison to the natural substratum (Figures 17-19), there is a very significant lack of many diatoms as well as Chlorophyta and Cyanophyta genera. In all, the artificial bare area gave a false indication of the true productivity trends and did not indicate many of the significant genera. This is especially true when compared to log and plant samples collected (Table II).

Finally, quantitative data were computed for a mean sized plant of the three plants extensively studied. These data are computed so as to demonstrate the number of plants necessary to yield a hectare of surface area, and how small an area of lake surface this takes up (Table IV). M. farwellii would take up the least water surface area to contribute the highest production. Efficiency, or the ability of the plants to produce a higher standing crop, is computed mathematically to arrive at a theoretical efficiency, and a computation from actual data yields an actual efficiency. Theoretical efficiency for V. americana and M. farwellii is 93 percent. This is the efficiency of the phyco-periphyton in producing organic matter over the open water and weed bed phytoplankton. The actual efficiency as shown by the data is 99 percent.

Chemical-Physical

Mean data are plotted in Figure 13. Each circumference of an individual circle represents 100 percent. Data for each particular day for each lake and station were averaged. This average was performed for each individual ion analyzed, and the graph represents the over-all

TABLE IV

THEORETICAL PRODUCTIVITY OF PLANT SURFACES COMPARABLE TO A HECTARE OF OPEN WATER[1]

Plants	Mean Surface Area	No. Plants/ Hectare Needed	No./M^2	No. M^2 Needed	Productivity Ratio	Theoretical	Actual
						Efficiency	
Vallisneria americana	1 M^2 per plant	10×10^3	15	665 M^2	15:1	93%	99%
Myriophyllum farwellii	.25 M^2 per branch	40×10^3	55	727 M^2	14:1	93%	99%
Saggitaria sp. (rosettes)	.05 M^2 per plant	200×10^3	50	4000 M^2	2.5:1	60%	...

[1] This theoretical analysis is based on organic yield in air dry weights and actual plant counts.

average over the entire summer for the ionic constituents measured. What is represented is not a milligram per liter notation, but a percent of the total a particular ion represents at any given time and sample.

For definite measurements in mg./l., reference should be made to Figures 9, 10, and 11. With the graphs depicting percent of the constituents at any given moment, a comparison of constituents can readily be made. The four lakes listed for the Opeongo River system in three cases (Brewer, Costello, Kearney) feed water into Lake Opeongo through an influent river located in the bay north of the Fisheries Station (Figure 2) known as Costello Creek. These lakes are at higher elevations, and have less influxing nutrients excepting run-off and a few tiny rivulets. Further, their shore-line development (Table 1) indicates little conduciveness for inhabitation and production of nutrients by the biota. Bridle Lake (Figure 4) flows into the effluent Opeongo River at a lower elevation, but it is somewhat isolated and is under similar stresses as seen for the previous three. This same idea holds true for the lakes Gordon, Kearney and Clarke of the Madawaska System. They are influent into the river and receive water as the previous lakes did. It is noted that the nutrients are higher in Galeairy and Opeongo. In both lakes, biological productivity is higher. This is evident as shown in the productivity data in Figure 15. Figure 15 represents a comparison of mean standing crop of phyco-periphyton in the other lakes and compared to Opeongo. In this presentation, the smaller and more isolated lakes show a low comparative production. This is in accordance with the chemical data.

Further evidence in the basic growth nutrients of orthophosphate and nitrate signify the collecting of nutrients, and the higher productivity is also related to the higher shore-line development.

The center figure for Lake Opeongo shows an interesting comparison to Galeairy Lake which receives much more influent water, and has a chance of receiving more nutrients.

In the Opeongo figure, the center circle is a mean of five stations. The next circle going out from the center is the open water, deep station samples taken from the 42 meter area in the South Arm of the lake. Here a reduction of the growth nutrients, especially evident in the nitrates, is significant. Circles three and five correspond to stations one and three in the weed beds. They show a much better balance of nutrients when compared to the deep station and to circles four and six which represent the deeper areas of the bays in which the weed beds are located.

Generally, when comparing the two weed beds they show a more advantageous chemical composition over-all in nutrients measured. Ferric iron and chlorides were analyzed and no trace was determined with the methods used. Carbonates were also absent as would be expected when compared to the pH data (Figures 9, 10, and 11). The water color index was 35 and green, secchi disk reading was 4 meters and turbidity was less than 1.

Temperatures show a typical decrease over the period of the sampling as would be expected for this time of year (Figures 9, 10, and 11).

Comparing the chemical-physical data in Figures 9, 10, and 11, it is evident the weed beds are more conducive to organic production. This is evident since this region of the water is shallow and would be under a better influence of the aerobic decomposers that recycle the nutrients faster than in deeper water.

Meteorological Data

Figure 21 represents the meteorological data for the month of August. Overcast days correspond well with the increase of respiration by-products such as carbon dioxide, and the decrease of photosynthesis by-products such as oxygen (Figures 9 and 10).

Comparing the small upsurge of phytoplankton (Figures 9, 10, and 11) and the corresponding genera in the phyco-periphyton samples with the theoretical current speed over the period of August 19 to 21 an upsurge in the selected phytoplankton genera is evident (Figure 12). This corresponds to a theoretical current speed of 1200 cm./sec. maximum, and westerly winds continuing over a period of five days. "Students" T analyses for this upsurge over these dates were run on the plankton as a whole. The result showed statistical significance in the region of the 5 percent level. This would seem to indicate a current effect since the phytoplankton did not respond to the nutrients in the weed bed, and the small rise in density drops off after the wind changes direction and intensity. It seems that in the weed bed at Station 1, westerly winds have the greatest effect, and if persistent over a period of time have the effect of loosening the phyco-periphyton from the plant surface and adding these organisms to the plankton. A decrease in the corresponding genera in the phyco-periphyton is noted. The genera in Figure 12 are noted as not being as tenaciously held to the substratum as other genera of the phyco-periphyton. Comparison of the phyco-periphyton genera to corresponding genera from the phytoplankton demonstrated a slight drop in the phyco-periphyton genera, and a corresponding increase in the phytoplankton. Comparisons on the fifth of August also seemed to show a similar correlation. The period from August 12 to 15 likewise shows a correlation with the type genera listed for August 21.

The lull in the phyco-periphyton peak at Station 1 (Figure 9) on August 23 seems to correspond to the total overcast, and this is supported by the data recorded in the type genera reported in Figure 12.

Correlation of meteorological conditions to the productivity data is often obscured by many interwoven factors. However, some of the data are comparable.

Consumption of Phyco-periphyton

Fish stomachs were analyzed, and underwater observations of fish feeding habits were made. Table V yields information as to the ingestion of algae by four species of fish investigated in this study. Each of the algae noted are found in the phyco-periphyton (Table II) while some of the algae such as Chlorellalike cells, Tabellaria and Melosira are found also in the phytoplankton.

Underwater observations in the weed beds for long periods of time have yielded some insight into the feeding habits of young Perca flavescens (first and second summer), Pimephales notatus (first summer), Pimephales promelas (first summer), and Notropus heterolepis (first summer). The latter three fish were seen to actually glean material from the three test plants. These fish swam up to a plant and proceeded with a chewing motion of the mouth to ascend along the plant leaf. Perca flavescens darted rapidly this way and that, and appeared to be chasing something, which they probably were, as indicated by the micro-crustacean fragments in their stomachs. Ten fish from each species were selected at random to check ingestion.

In other consumption data Keratella cochlearis is a noted periphyton feeder, and was discussed previously. Other rotifers and planktonic crustaceans were also noted to have ingested algae. Diatoms were quite prevalent in their diet and there were broken diatom frustules in their digestive tracts.

Snails (Valvata sp.) were noted on the increase at the end of August. There were six snails per ten centimeters of Vallisneria americana leaf. It is known that they ingest the cases of the Tendipedid larvae which are made of algal cells cemented together (1). The

TABLE V

INGESTION DATA FOR FOUR SPECIES OF WEED BED FISH

Fish	Plant Matter	Animal Matter
Perca flavescens	Melosira, Chlorella-like cells	Crustaceans
Notropis heterolepis	Bulbocheate, Oedogonium Tabellaria, Chlorella-like cells	Tendipedids Crustaceans
Pimephales notatus	Mallomonas, Chroococcus, Chlorella-like cells, Synedra	....
Pimephales promelas	Chlorella-like cells, Bluegreen filaments, *Tabellaria fenestra,* Stauronesis, Gomphonema, Cosmarium, Nitzchia, Navicula, Closterium, coccoid bluegreen, *Tabellaria flocculosa*	Amphipods Crustaceans Tendipedids

Tendipedids were also on the increase at this time. Tendipedids are known to ingest algae (1, 4, 5), and finding them on these plants would indicate their preference for a good food source.

Another organism *Palmetohydra* was prevalent on the plants found during the lull period in early August. Hydra are known to prefer low algal concentrations, and this is proof of a decrease in phyco-periphyton production. When the phyco-periphyton increased the hydra disappeared.

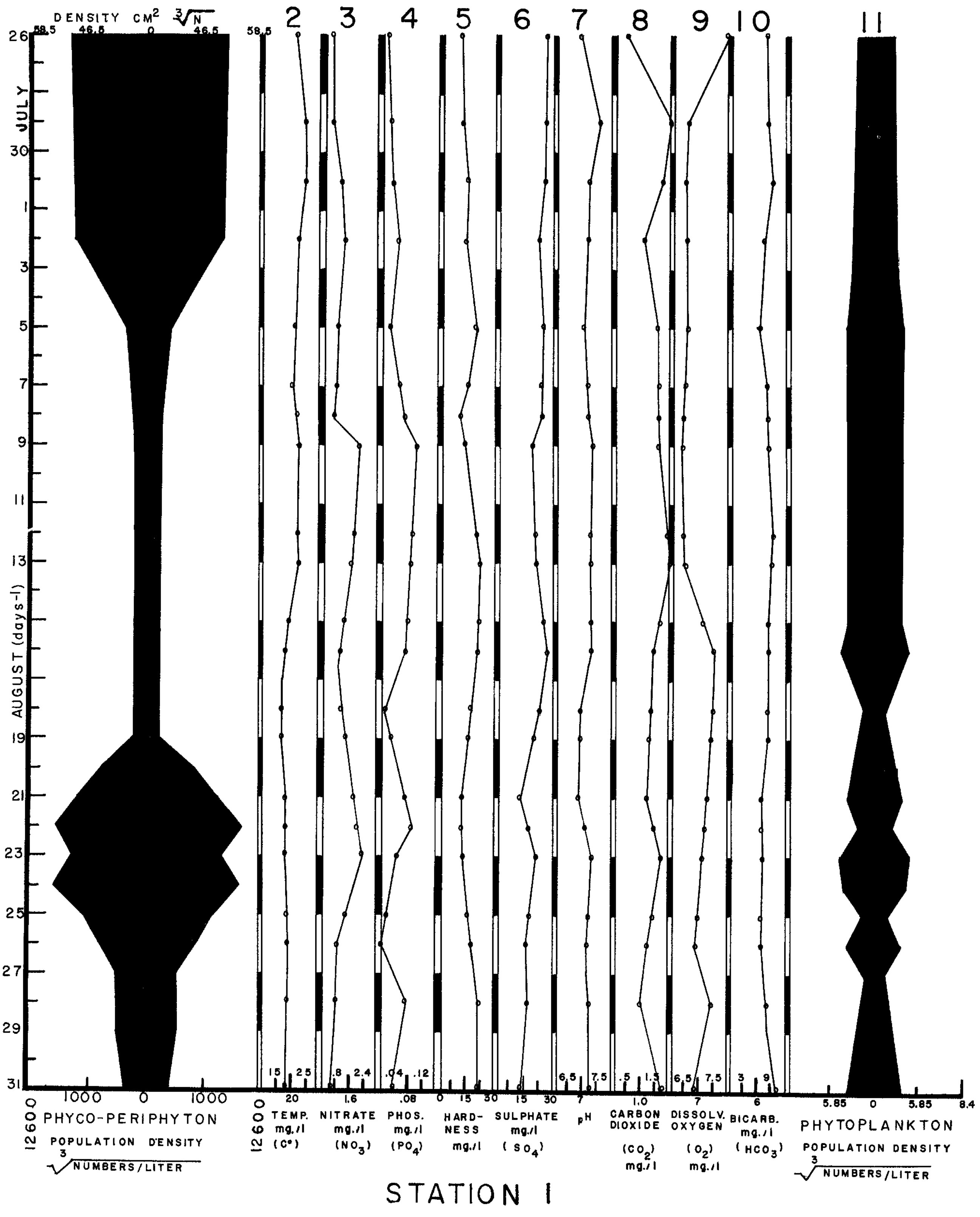

Fig. 9--Synopsis of Productivity Data for Station 1

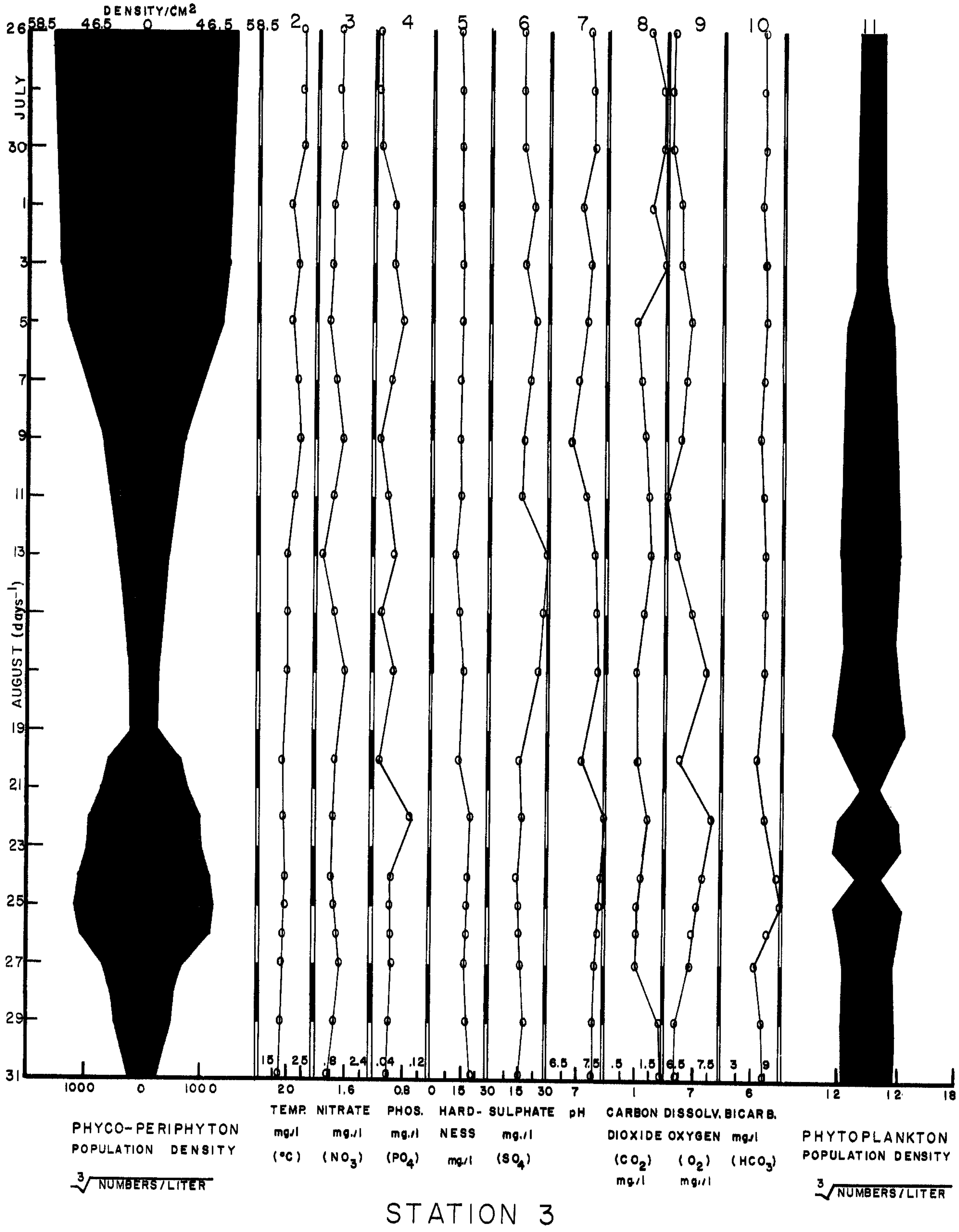

Fig. 10--Synopsis of productivity data for Station 3

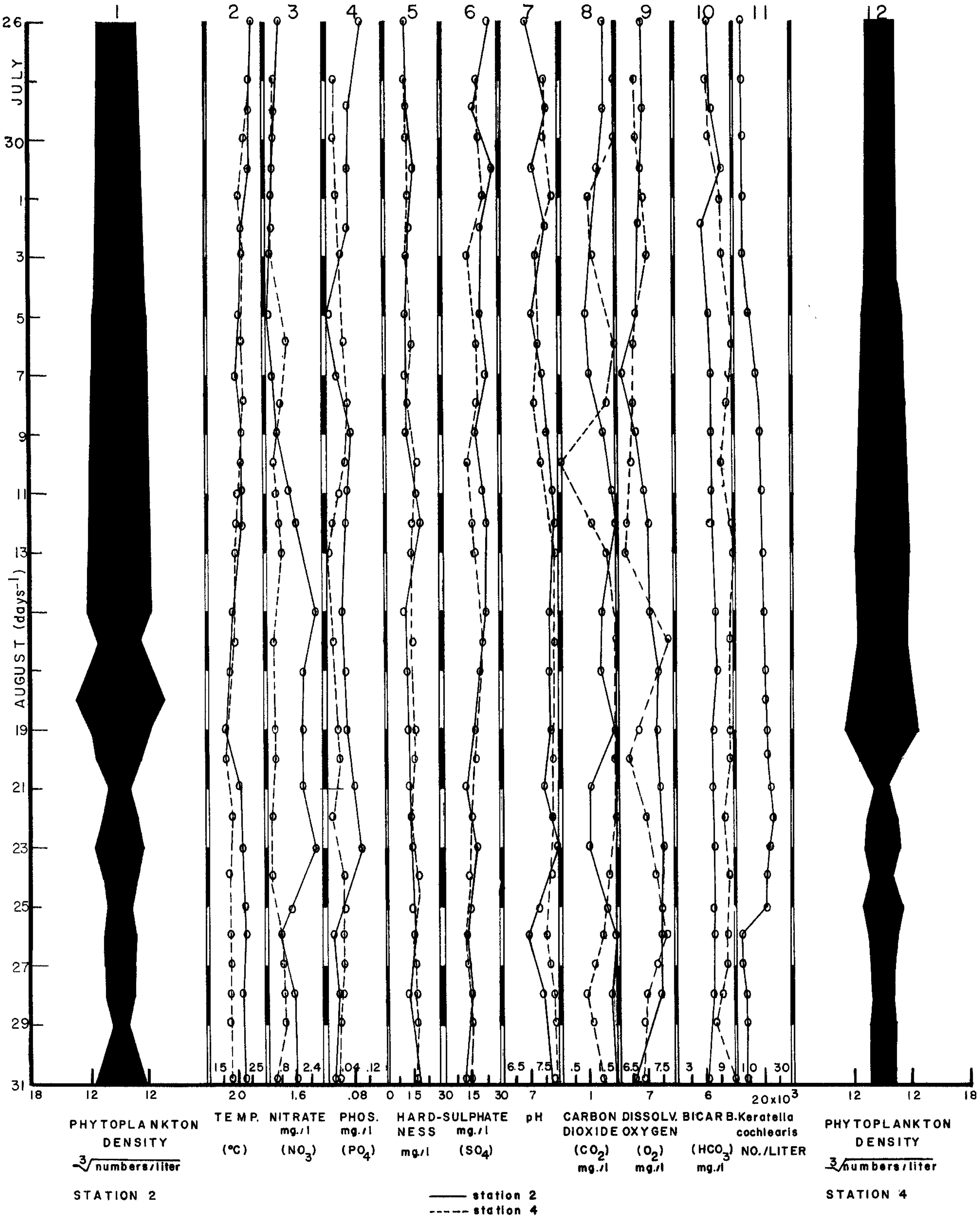

Fig. 11--Synopsis of productivity data for Stations 2 and 4

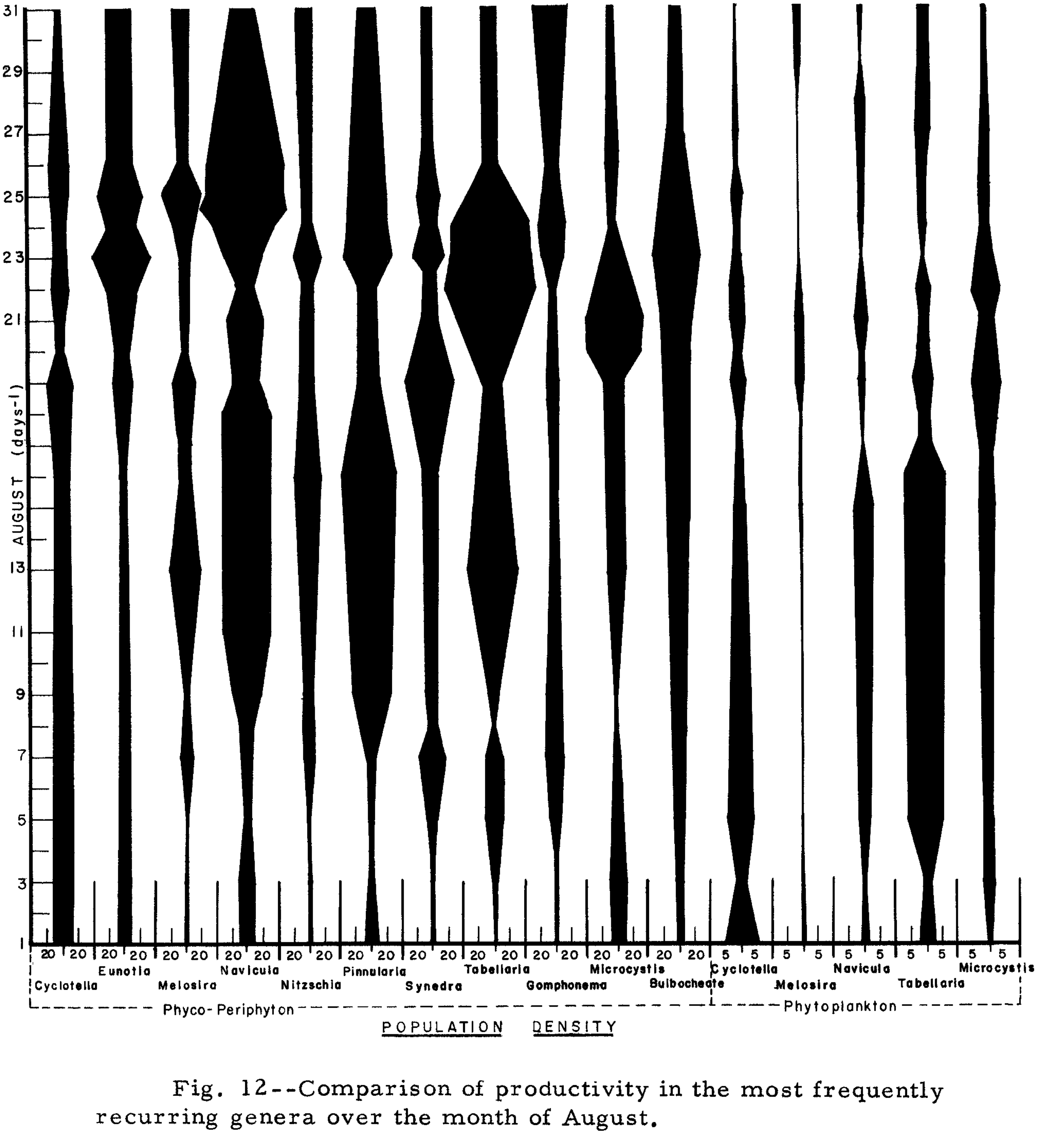

Fig. 12--Comparison of productivity in the most frequently recurring genera over the month of August.

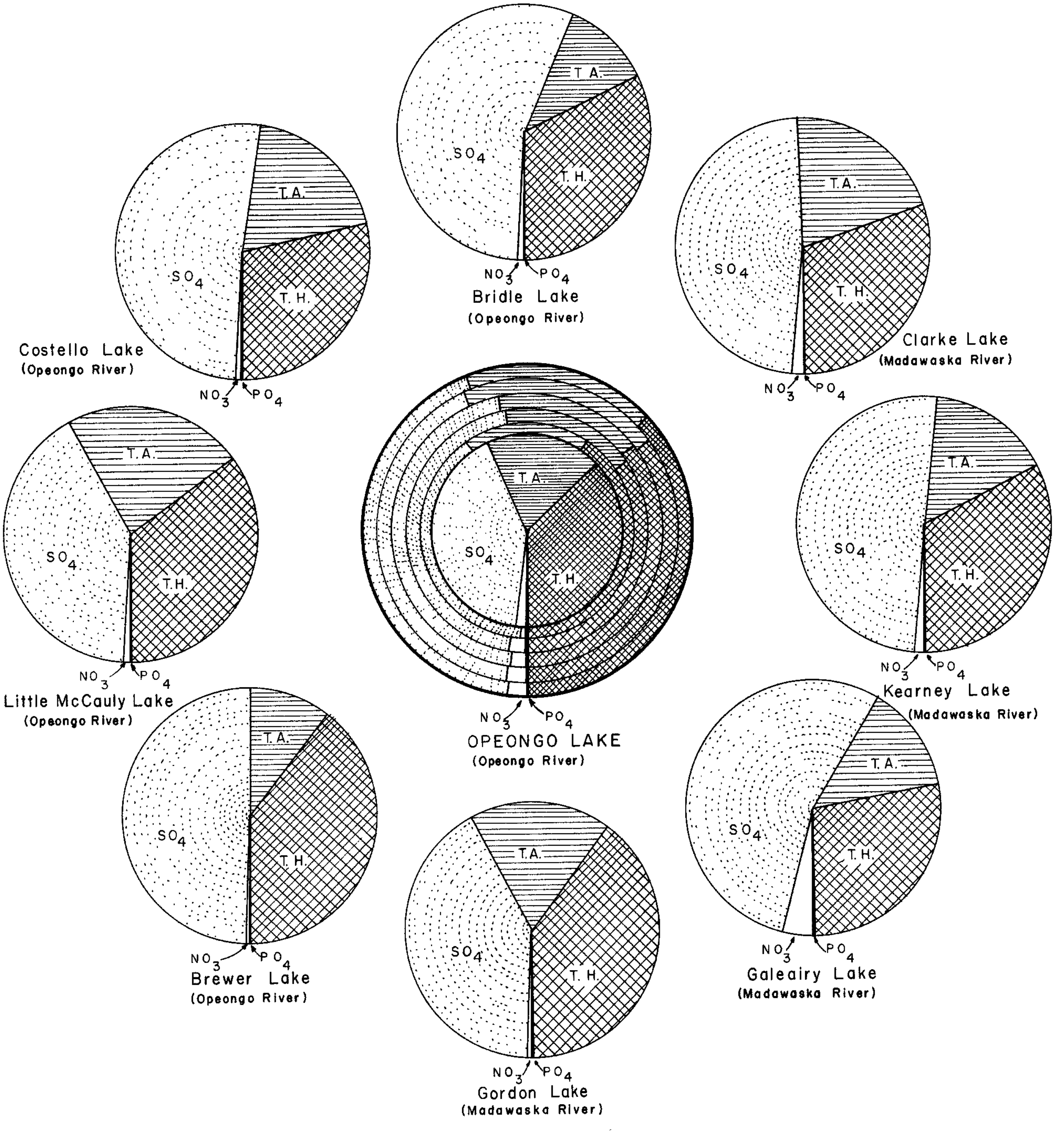

Fig. 13--Comparative chemical data for the nine lakes studied

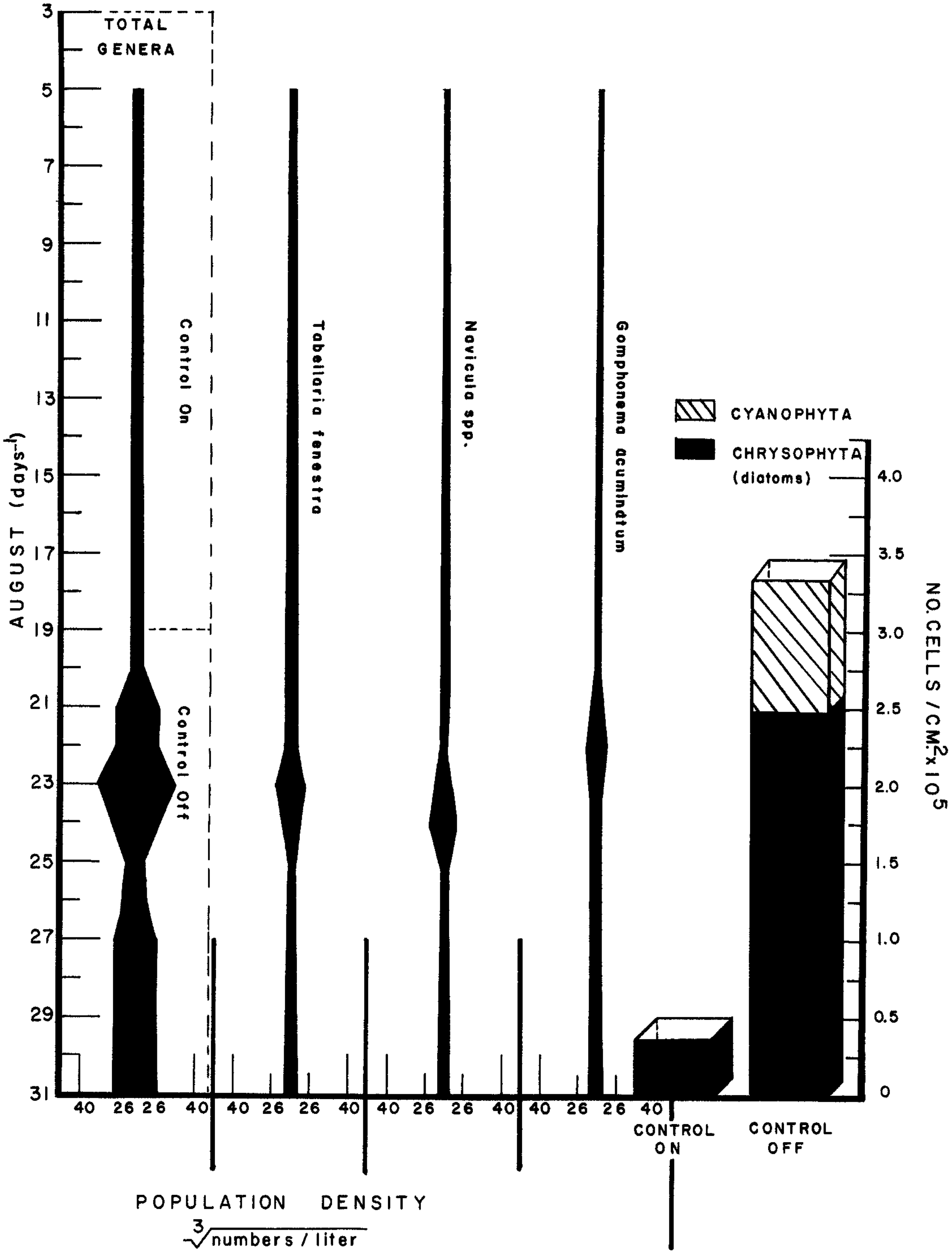

Fig. 14--Population data from the aluminum screen control

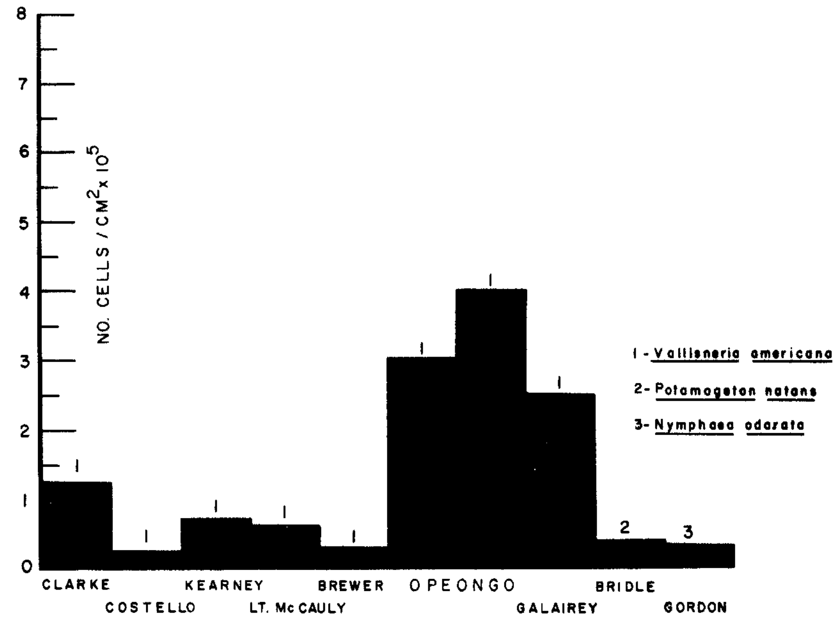

Fig. 15--Mean standing crop comparison of the nine study lakes

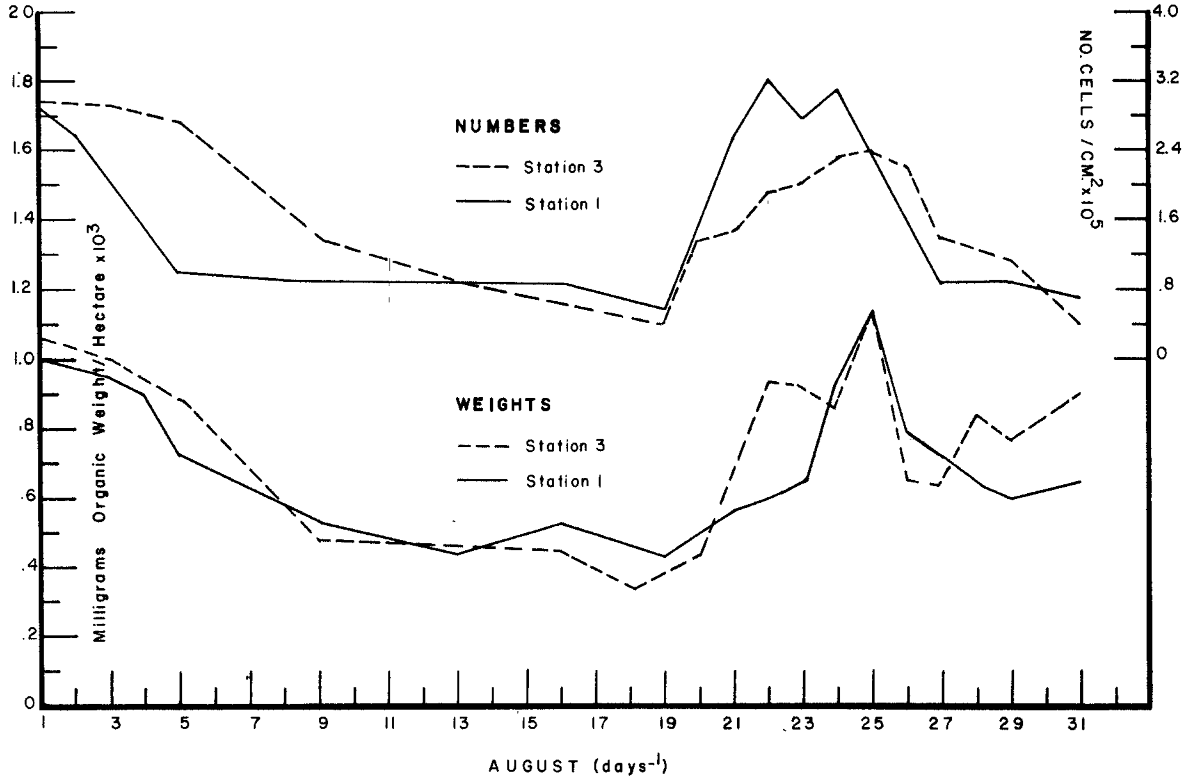

Fig. 16--Comparison of the organic weight and numbers of population during August in Lake Opeongo.

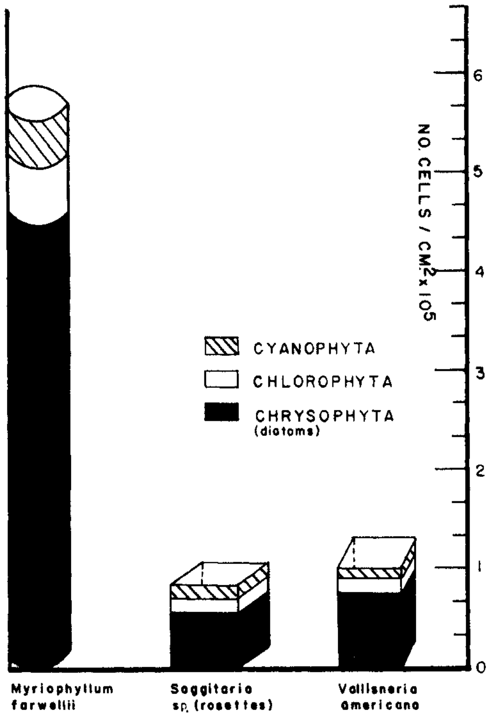

Fig. 17—Comparison of the standing crop of the three principal plants studied. The three plants are depicted schematically to show relative shape of the leaves.

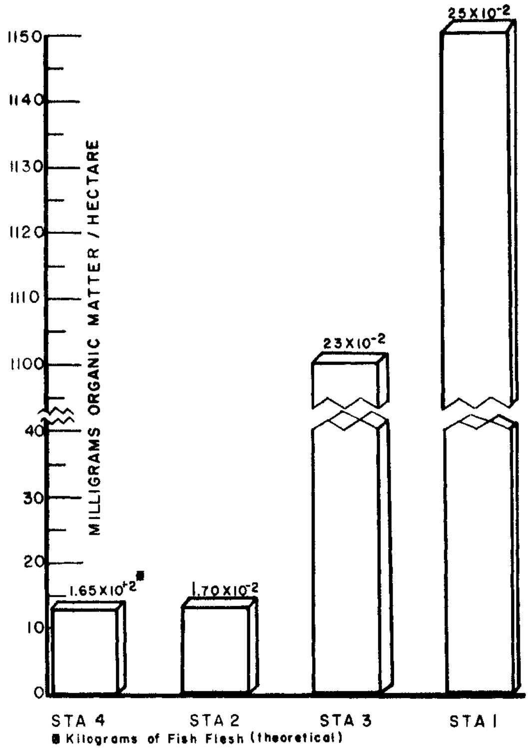

Fig. 18—Comparison of the organic weights during peak productivity of the phyco-periphyton in Lake Opeongo. At the apex of each bar is a representation of the theoretical yield of fish flesh.

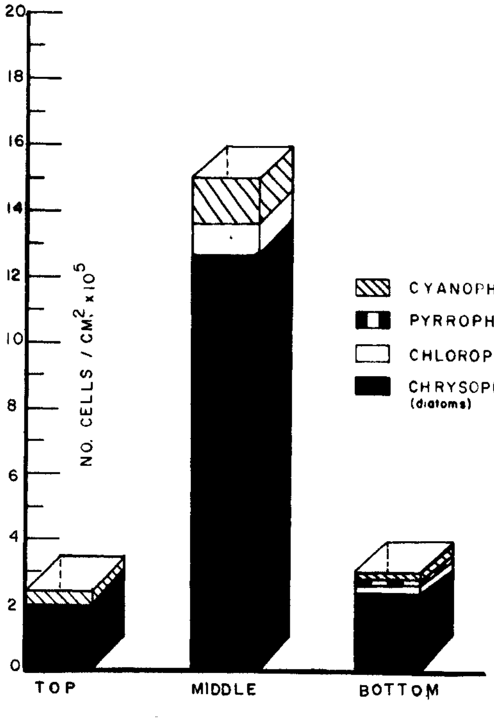

Fig. 19—Demonstration of the most highly productive portion of *Vallisneria americana.*

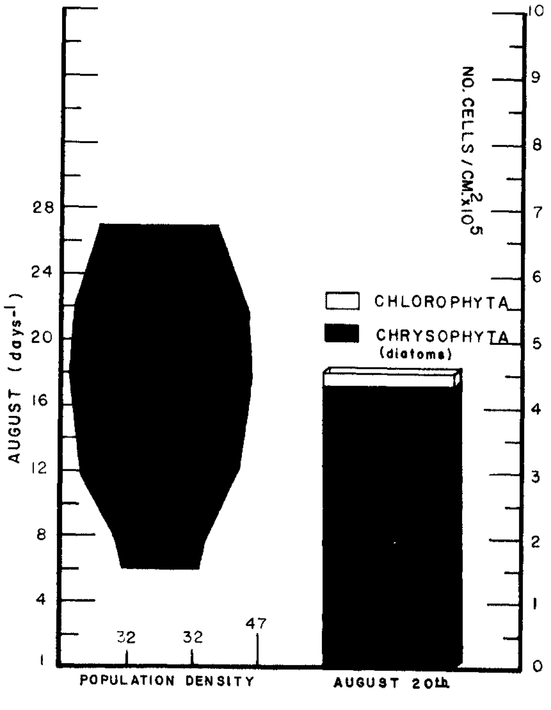

Fig. 20—Production data for the artificial bare areas. The bar shows the relative numbers of the Algal Divisions found on the slides.

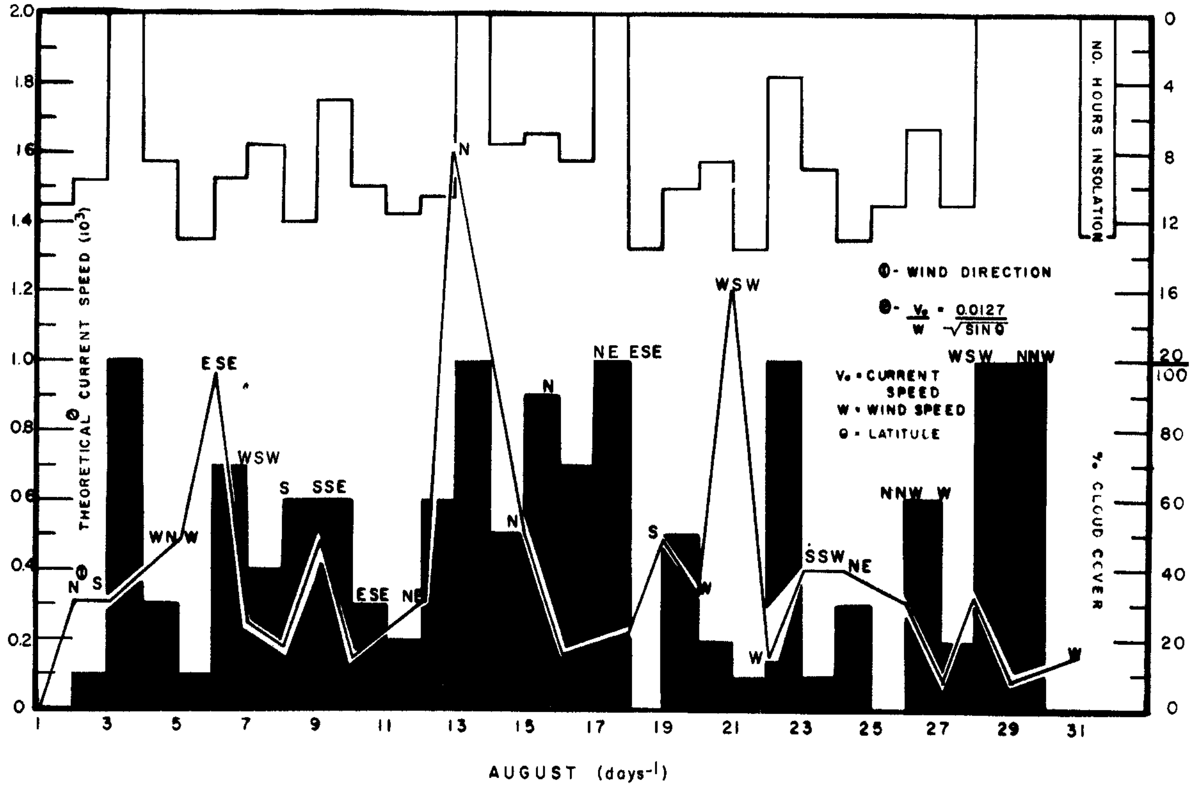

Fig. 21--Meteorological data for August

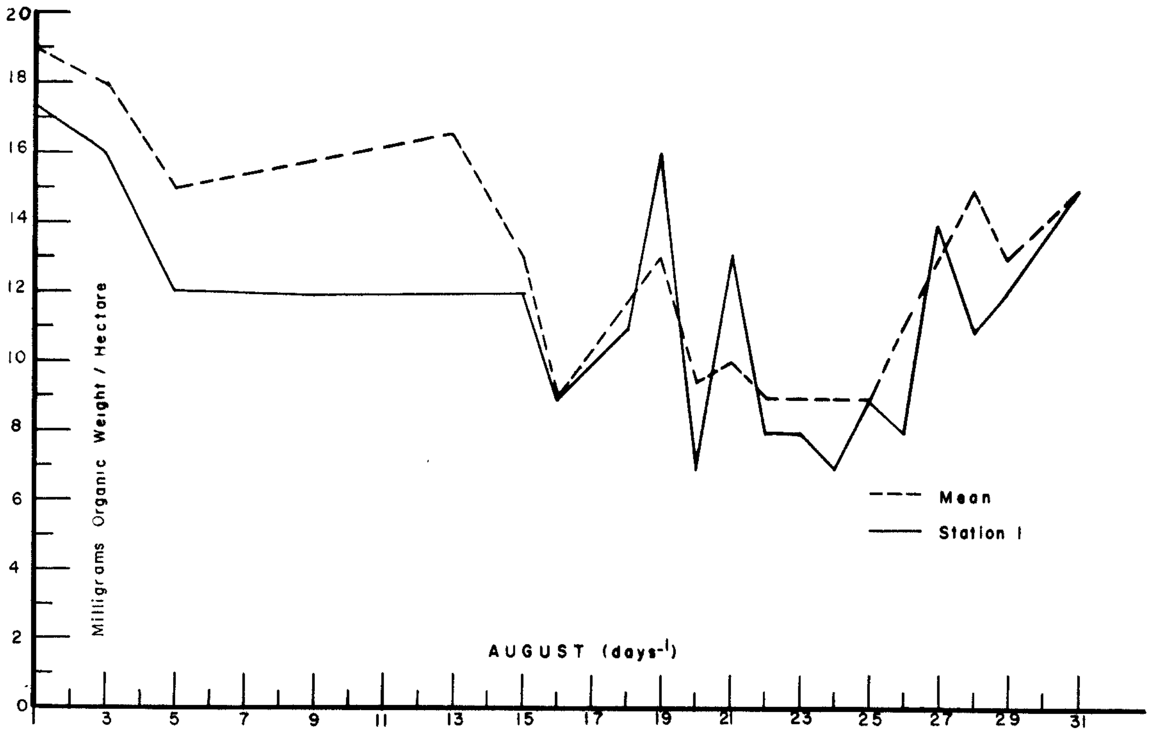

Fig. 22--Mean phytoplankton trends compared to Station 1 for the month of August.

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CHAPTER IV

DISCUSSION

"No fixed object living or nonliving, submersed in natural water is devoid of aufwuchs" (25).

The channels of energy through a biocoenosis are difficult to delineate due to overlapping of significant factors and interaction of biotic potentials. Only the first portion of energy utilization in the ecosystem is a relatively easily defined commodity. In this first step insolation energy is fixed as photosynthetic products and stored for utilization in respiration.

It is this area of primary bioproduction that has been of such great interest in Limnology: for here we have cause and effect relationships. But where is the most highly productive portion of a lentic community? Is it a random distribution, or is primary productivity ecotype oriented?

In the data just presented these questions are answered. The most highly productive area, hectare for hectare, comparing a weed bed to the pelagic is the weed bed. There is a definite ecotype orientation even in the weed bed. Ebling and others (5) have noted ecotyped habitation in their work also. In the weed bed, Vallisneria, Saggitaria, and Myriophyllum have an ecotype referred to here as the Tabellaria-

Bulbocheate-*Microcystis* synusia. While the log has a *Tabellaria*-*Ulothrix*-*Microcystis* synusia, and Nitella has *Tabellaria*-*Gomphonema*-*Microcystis*.

The general picture evoked by the graphs in Figures 9, 10, 11, and 12 demonstrates the high comparative productivity of the littoral zone. Inspection of these graphs also shows the chemical constituents to keep pace with the peaks of production.

Meteorological conditions seemed to have a definite effect on production (Figures 9, 12, and 21). The wind also had a definite influence with continuing direction and a strong water current speed which would account for a rise in the phytoplankton genera from those genera found in great quantities on the plants. The chemical data when compared to that of the open water showed no indication for the peaking of the phyco-periphyton, and thus current effects were shown to be significant. This would agree with the work by Coulter (4) and Samll (27).

Data collected by placing glass slides in the water disagreed with the concepts expressed by Patrick (20), Newcombe (18, 19), Castenholz (2), and Greaenda and Brehmer (6). In this study the actual colonization rate was noted. The rate was indicative of the lack of competition by a natural substratum. It is suggested that in fish culturing, slides could be suspended to allow algal colonization and eventual feeding utilization by the fish. Further the slides could be used to measure the effects of sewage pollution by noting the effects produced on the various synusiae from the sewage effluent. These data could then be compared to a natural substratum to note any differences in effects by synergistic or antagonistic relations in the natural environment.

The grazing studies showed quite well the utilization of phyco-periphyton which agreed with the data expressed by Cavanaugh and Tilden (3), Johannsen (10), and Mallock (15). Especially in Cavanaugh and Tilden's work (3) where actual observations were made of Tendipedid larvae ingesting phyco-periphyton and utilizing it for the construction of their cases. Snails were seen to actually ingest the cases directly off the insect larvae. This was very important when the same situation manifested itself in late August. The Tendipedid larvae increased on the plant leaves, and not long after the snail population increased. It is known that both of these organisms are utilized by fish as food. Whitefish and Cisco use snails and Tendipedids for food, and the data presented in Table V show Tendipedids used by the Flathead Minnow. Algae were found in the stomachs of weed-bed inhabiting fish. Table V depicts various algae found in the stomachs of the fish studied. Few identifiable traces of algae were found in the excrement of the study fish.

It should be noted that the genera and species reported were at their optimum growth for the temperatures listed (Figures 9, 10, and 11). These data are verified by the work of Whitford and Schumacher (31) in the work on stream periphyton in North Carolina.

Anabaena sp. was observed to be deteriorating to some degree as the temperature dropped, and as it dropped over the summer towards autumn, Microcystis spp. also became less abundant (Figure 12). Meridion circulare only became noticeable in the samples as the temperature dropped toward fifteen degrees centigrade. It should be noted that very important factors such as the water quality and nutrients also show a definite influence in modifying temperature effects (Figures 9, 10, and 11).

The chemical data demonstrated a more conducive habitat in the weed bed biocoenosis for plant growth and reflected a better utilization of the available nutrients by the phyco-periphyton than did the phytoplankton. This would account for such ideas as expressed by Hassler and Jones (9), Penfound (21), and Welch (29).

To add weight to the preliminary stomach analyses, Thomson (28) reported eight herbivorous fish from Australia fed upon filamentous algae and diatoms. Prowse (23, 24) related that species of Talaipia fed extensively on periphyton. Prescott (22) noted the Bluntnose Minnow fed almost solely on phytoplankton. Reighard (26) viewed suckers utilizing periphyton while Griffith and Voorhees (7) found Melosira from the periphyton in several species of shinners. Kraatz (11) reports a long list of suckers, shinners, and perch as algal ingestors. Lagler (13, 14) listed Black Mollies as periphyton feeders, and eluded to algal usage by young fish in his book on fishery biology.

While algae are ingested by fish in some lakes, they may not be universally ingested in every situation. Fish will feed on the available nutrient most conducive to their life history. This fact accounts in part for the many races in a particular species of fish such as the Lake Trout. Martin (16) reported Lake Trout in one lake in Algonquin Park, Ontario, fed on plankton since there was an absence of the usual prey, the Whitefish. These fish were stunted to some degree in comparison to more favourably raised fish. He also related (17) that when transplants were made of the stunted generations of Lake Trout from the poor lake to Opeongo (a much better lake and one that has Whitefish), they developed as the other fish in the lake.

"There is some evidence that dense stands of submersed rooted aquatic plants may bind up nutrient materials throughout the growing season, so that they are not available for the production of phytoplankton and the organisms that feed upon phytoplankton," stated Bennett (1). Bennett further feels this loss of nutrients may be reflected in the fish population through the eventual reduction of the food supply. If this is true, algae and higher aquatic plants are in direct competition for available dissolved nutrients. However, higher aquatic plants are for the most part rooted in the benthic substratum. In the benthic substratum, composed of organic soils undergoing aerobic and anaerobic decomposition, it would seem most logical that if the higher aquatic plants have farily well developed root systems, adapted as they are for absorption and transport, that the main supply of nutrients would come from the aquatic soils. The higher aquatic plants, therefore, are not the primary utilizers of the dissolved nutrients (Figures 9, 10, 11, and 13). These data depict the high incidence of standing crop and algal production during the study period.

If a careful program of higher aquatic plant management (fertilization and cropping) were to be instituted, it is believed that this will foster a more bountiful community. However, it should be noted that the specific fish with which culturing is being instigated is the limiting factor. To have a balanced habitat where cover and food are in significant abundance for the predated and thus in abundance for the predator is an important factor for the fisheries biologist to consider.

In further disagreement with Bennett (1) who believes higher aquatic plants are detrimental in the aquatic habitat, this study along with the work of Prowse (24) has definitely demonstrated that if for no other reason than the additional substratum, the higher aquatic plants are important. As mentioned previously, the glass slides might be useful in replacing the higher aquatic plants, but the non-universality in species inhabiting their surface and loss of cover would limit their use.

It is recommended from this work that fisheries biologists and limnologists not overlook the significant feature in productivity that higher aquatic plants hold in the metabolism of a lentic community. As was shown in this study, it is not actually the higher aquatic plant, but the phyco-periphyton growth which seemed to limit the nutrients of a weed bed, and only by foresight planning in stocking fish and invertebrates who crop this growth and utilize it can this nutritive source be put to proper use.

"Are we to regard as plankton only those forms which are found in the middle of deep lakes?" asks Prowse (23). This statement is perhaps a haunting querie to aquatic biologists. In the work of Prowse (23) he also lists phytoplankton species found as periphyton and vice versa, as this study demonstrated. This also is the case with the work done on Florida springs by Whitford (31). In his work, he demonstrated the role of sessile algae in affecting release or adherence of algae on the substatum in running water.

According to Young (32), Lunbeck in 1925 stated that weed beds support a higher gram for gram relationship in production per square meter than open water. This research has shown a 100:1 ratio of the standing crops of the phyco-periphyton to the phytoplankton at peaks of production. This is very evident when the same period of productivity in the weed beds is compared to the open water.

Griffiths (8) has shown the importance of nutrients in the weed beds, while Krecker (12) has demonstrated the idea of leaf type limiting the amount of production on the plant surface to the animal population. This supports the data collected here. Numerous investigators have expressed the importance of the littoral biocoenosis, but only three (2, 4, 27) have given quantitative data.

This has been a pilot study on pristine waters intended to give insight into the possible effects domestic and industrial sewage may have on a lake. It is hoped that this work will be a guide to future work in this highly important field.

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CHAPTER V

SUMMARY AND CONCLUSIONS

1. Generally, this study has shown that the weed bed biocoenosis is much more productive than previously believed.

2. Chemical nutrients in the weed beds are much more conducive for over-all growth than in the deeper areas.

3. Lake Opeongo was much higher in bio-production than any of the other lakes studied.

4. Grazing of the phyco-periphyton by primary consumers was shown to exist, but to be negligible in causing any tempering of the over-all production curves.

5. Chemical and physical data all showed unity in being responsible for the phyco-periphyton peak at the end of August.

6. Meteorological conditions showed a tendency to influence members of the phyco-periphyton biocoenosis and these were shaken off the higher aquatic plant substratum into the phytoplankton.

7. Fish species sampled in the weed beds show ingestion of algal constituents common to the phyco-periphyton.

8. The weed beds supported a much higher yield of fish than the open water where comparisons were made.

9. In a plant for plant comparison, the Myriophyllum supported a much higher algal production in the phyco-periphyton biocoenosis than any of the other plants sampled.

10. In a hectare to hectare surface area comparison, a small number of higher aquatic plants having a surface area of one hectare take up considerably less than one hectare of water surface, and produce 100 times more standing crop of organic weight than the hectare of open water in the deeper areas of the lake.

11. Phyco-periphyton utilization by organisms other than fish was noted.

12. Production in a low nutrient habitat in the absence of sewage was found to be very significant. It is hoped further production studies of this biocoenosis in regards to sewage pollution will have definitely comparable results since this study has conclusively demonstrated that the phyco-periphyton biocoenosis is the greatest primary producer in the entire lentic system when considered area for area.

13. Sampling of the phytoplankton will not indicate the productivity peaks in the lentic community, and further the quantification of phytoplankton does not demonstrate the diatom pulse accompanied by the other green and blue-green algal forms in the phyco-periphyton.

14. This tremendous production of the phyco-periphyton in the weed beds tends to temper any attempt of the phytoplankton to peak with the available nutrients, and may demonstrate an antagonism by the

weed bed to phytoplankton production in that area. However, it is noted that the phytoplankton production is of little significance in the littoral area when compared to the phyco-periphyton production.

15. This bio-production is based on only three species of plants, and many other plants also exist in this biocoenosis, as well as logs and rocks which have their own characteristic phyco-periphyton; these then would possibly boost the primary production of the phyco-periphyton possibly another hundred fold.

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