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Title: ON RECONCILING LAKE CLASSIFICATION WITH THE EVOLUTION OF FOUR OLIGOTROPHIC LAKES IN OREGON

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Limnological data were collected from studies of four Oregon lakes that are classified as oligotrophic--Crater, Odell, Waldo, and Woahink. Phytoplankton primary production was estimated periodically using a standard carbon-14 *in situ* method. Bioassay experiments were conducted to determine whether water samples, treated with various kinds and concentrations of inorganic nutrients, might stimulate carbon uptake by phytoplankton. Chlorophyll *a* measurements complemented production estimates made with carbon-14.

In comparing the lakes, differences were noted concerning lake origin, watershed features, basin morphometry, surface elevation, optical and thermal properties, and water chemistry. More notable, however, was the significant difference in phytoplankton primary production and biomass among the four lakes. During July and August, 1969, productivity averaged 253.1 (Crater), 1533.2 (Odell), 35.5 (Waldo), and 301.1 (Woahink) mgC/m^{2}day. For the same period,

concentrations of chlorophyll a averaged 34.4 (Crater), 99.03 (Odell), 4.7 (Waldo), and 24.7 (Woahink) mg/m^2. This resulted from the different uses each lake received. It is suggested that, on the basis of productivity, lakes are unique environments and are evolving at different rates in response to natural and artificial (cultural use) enrichment.

The need for an adaptable classification system that would take into account the continuous process of lake evolution was emphasized. Such a system, based on the relationship between phytoplankton primary productivity (mg $C/m^2/hr$) and light energy absorbed by phytoplankton for photosynthesis (coefficient $\overline{K}_b$ which represents the ratio of production to radiation at any depth; Platt, 1969), was proposed. The system will serve to diagnose, to a degree, the causes of lake eutrophication, will continue to provide an instantaneous assessment of lake productivity, and will have predictive power in determining lake evolution.

On Reconciling Lake Classification with the Evolution of Four Oligotrophic Lakes in Oregon

by

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ON RECONCILING LAKE CLASSIFICATION WITH THE EVOLUTION OF FOUR OLIGOTROPHIC LAKES IN OREGON

INTRODUCTION

Lakes which are classified as oligotrophic possess, in theory, the attributes summarized by Welch (1952). Lakes of this type are relatively deep with an orthograde oxygen curve and low hypolimnetic temperatures. The volume of the hypolimnion is generally larger than that of the epilimnion. Although limited in quantity, the plankton is represented by a diversity in species. Phytoplankton biomass rarely attains "bloom" proportions. Aquatic vascular plants are not abundant. A paucity of inorganic nutrients, the chief criterion for classifying a lake as oligotrophic, restricts biological productivity. As a result, the load of organic materials is considerably less than that developed in enriched lakes.

Several lakes in Oregon, including Crater, Odell, Waldo and Woahink lakes, have been regarded by investigators as being oligotrophic (Kemmerer, et al., 1924; Pettit, 1936; Griffiths and Yeoman, 1938; Newcomb, 1941; McGie and Breuser, 1962; Averett, 1966; Carter et al., 1966; Nelson, 1967; Hoffman, 1969; Larson and Donaldson, in press). Several of the forenamed authors, while not expressing the term "oligotrophy," alluded to the oligotrophic qualities of the particular lakes which they examined (Kemmerer, et al., 1924;

Pettit, 1936; Griffiths and Yeoman, 1938; Hasler, 1938; McGie and Breuser, 1962; Nelson, 1967; Hoffman, 1969). These views concerning the classification of the four lakes are supported, in part, by limnological data collected during the course of this study.

Crater, Odell, Waldo, and Woahink lakes are used differently. The excellent water quality of Crater Lake (National Park) is maintained by regulations that prohibit certain uses. Conversely, Odell and Woahink lakes are used intensively for recreation by various interest groups. Few, if any, regulations exist which might restrict the type and amount of use that either lake receives. Waldo Lake was, until recently, somewhat remote. Now, a newly-constructed highway makes this near-pristine environment easily accessible.

Man uses lakes for various purposes, all of which provide the algae with a source of essential primary nutrients. Unlimited use entails increased nutrient enrichment which in turn accelerates lake eutrophication. Thus, a lake that is used unconditionally will undergo an artificial enrichment that will shift it gradually (or perhaps abruptly) to a higher level of trophy. Ohle (1953, 1955) described the artificial (man-induced) process of lake evolution as "racing aging" or "racing eutrophication" which contrasts with the slower-paced, natural course of eutrophication.

Realizing the use to which each of the four lakes is being put, one becomes less inclined to group these lakes into an identical trophic category merely because they feature all the characteristics that describe an oligotrophic lake. It is most important to be able to provide an accurate, instantaneous assessment of individual lake productivity without being bound to the restrictive categories of a traditional classification system. Since lakes undergo continuous change in trophy in response to natural and artificial enrichment, the need arises for an adaptable classification system that will take into account the continuous process of lake evolution or aging. This, then is the purpose of the study.

Specific objectives are: (1) to evaluate the classification "oligotrophy" assigned to the four lakes, (2) to determine to what extent each lake has evolved in response to morphometric-edaphic-climatic-cultural interactions, (3) to determine the factor or factors that are restraining or accelerating the rate of eutrophication in each lake, and (4) to consider the value and reliability of traditional lake classification and to propose, as an alternative, an adaptable system that is more diagnostic than it is taxonomic.

Eutrophication: A Process of Lake Evolution

Simply stated, a lake exists in nature as an inland topographic depression which retains water and is influenced by an environment that determines the rate at which the lake will evolve from youth to maturity to old age to extinction. The evolution of a lake, commonly referred to as eutrophication, follows a continuous and irreversible course. Lake basins, sharing the fate of all geomorphic features, are subdued by gradational processes which tend to level the surface of the earth. Rock and soil materials, gathered from the watershed by erosional agents, are conveyed to the lake and deposited as sediments. Ultimately, a lacustrine plain, underlain by well-developed laminations of mostly silts and clays, becomes the site of an extinct lake.

Equally important in the filling and eventual "death" of a lake is the accumulation and sedimentation of organic materials. Dense growths of aquatic plants, developed as the result of optimal temperature, light and nutrient conditions, may accumulate to the point when open-water zones no longer exist. In lakes that are unusually high in carbonate alkalinity, pH and calcium concentration (Wetzel, 1965), heavy deposits of precipitated calcium carbonate or marl may occur. The settling of biological residue, particularly planktonic remains, adds further to the buildup of organic sediments.

Under abnormally arid conditions when the loss of water through evaporation is not balanced by periodic precipitation and surface-ground-water inflow, a lake may reach extinction without undergoing evolutionary succession. For most lakes, however, longevity is a function of basin aggradation by allochthonous materials as well as autochthonous organic accumulations.

Rawson (1939) and Mortimer (1942) suggested that increases in lake biological productivity and sedimentation are evolutionary tendencies, the rates of which are governed by specific edaphic, climatic and basin morphometric features. Climate and morphometry interact with the edaphic component by influencing the distribution and utilization of incoming primary nutrients (Rawson, 1939; Deevey, 1940). The relative importance of each factor (i.e., climate, morphometry, edaphics) depends mainly on the origin, location and use of the lake basin.

Climate relates to lake production and sedimentation in terms of (1) energy influx and distribution, (2) intra-lake circulation and thermal stratification, (3) biogeochemical cycles and (4) hydrological budgets. The morphometry of a lake (e.g., mean depth, mean slope, area, volume, shoreline development, shoreline length, etc.) may influence production by promoting (or impeding) the circulation of nutrients, heat energy and dissolved gases. Generally, shallow lakes having extensive shoal areas and irregular shorelines are considerably more productive than very deep lakes with reduced littoral zones. Edaphic features of the basin that contribute to the overall nutrient and sediment input include (1) drainage texture (drainage density, stream frequency), (2) surface-groundwater hydrology, (3) soil composition, (4) watershed vegetation, (5) mineral resources, and (6) human activities. The geochemistry of sediments determines, in part, the rate of return of soluble nutrients to the lake water.

Mortimer (1942) described three phases that chronicle the evolutionary process in most lakes. A slow increase in productivity marks the initial or primary phase. As production accelerates, reducing conditions are stimulated at the mud-water interface by the accumulation of organic debris. Soluble nutrients, released by the reduction of recent organic deposits, are recycled to the photic zone where they are utilized by a new generation of photosynthetic organisms. The cyclic exchange of primary nutrients continues until a second phase, expressed by a marked increase in production, is achieved. If reducing conditions become excessive, iron will be precipitated as insoluble ferrous sulfide. Thus, an essential nutrient (iron) is bound at the mud-water interface and is not available for production. Consequently, a sudden decline in production occurs and the lake enters a sterile tertiary phase. This "climax" situation is maintained as long as the nutrient supply (derived principally from drainage sources) is not sufficient to stimulate increased production. In lakes where low production persists, such as those that are extremely deep and/or geochemically oligotrophic, the second or third phases may be reached only after an extremely long period of time. Nevertheless, since all lakes are depositional environments, they will continue to evolve due to the accumulation of sediments.

Rodhe (1969) commended Mortimer on his visionary work, but criticized the view that a deep, oligotrophic lake may never progress to the secondary or tertiary phases. Even these lakes will respond to artificial enrichment and gradually become more productive.

Trophy: A Guideline for Lake Classification

Lake classification, the systematic grouping of lakes into distinct and rather artificial categories, is probably the most controversial topic in comparative limnology. Seemingly, many of the lake classification systems are sound and practical. But vain, sometimes costly attempts to fit a wide variety of lakes into an abstract system of restrictive categories have raised much criticism about the validity and practicality of lake classification (Larkin and Northcote, 1958).

Perhaps the most familiar classification was one proposed in a series of papers by Thienemann (1918, 1921, 1925, 1926, 1927) and Naumann (1917, 1919, 1921, 1925, 1926, 1929, 1931, 1932). Together, they adopted two rather indefinite categories (i. e., oligotrophy meaning "low" production; eutrophy indicating "high" production) as the basis of their classification. Both terms were contrived earlier by Weber (1907) to describe the vertical distribution of nutrients in a bog. He found the deepest layers of a typical bog to be rich (i. e., eutrophic) in basic plant nutrients whereas the uppermost levels were nutrient-impoverished (i. e., oligotrophic).

Thienemann and Naumann, while proposing similar methods of classifying lakes, failed to agree entirely on a lake component that could provide a reliable index of production. Thienemann judged productivity with regard to benthic organisms (particularly chironomid larvae) and the concentration of dissolved oxygen in the hypolimnion. Naumann interpreted production from phytoplankton associations and lake sediments (Rodhe, 1969). An attempt by Thienemann (1925, 1926) to resolve the disagreement resulted in a bipartite system which differentiated between clear-water lakes (either oligotrophic or eutrophic) and lakes having brownish-colored waters. To the latter group of lakes, Thienemann applied the term dystrophy. Lake waters of this type, in addition to being stained by large quantities of organic and humic substances, were found to be moderately acidic and oxygen deficient. Dystrophic lakes, generally, were considered to be early seral stages in the successional development of a bog.

Naumann (1921), seeking a more explicit system, introduced a complex version that specified the composition of the sediments (in addition to indicating the trophy of the lake). Paratrophy could refer either to an oligotrophic or eutrophic lake which contained dy sediments. The sediments of an orthotrophic lake (likewise either oligotrophic or eutrophic) consisted largely of gyttja. Dy deposits, which incorporate sizeable amounts of humus materials, were observed in brown, acidic waters under anaerobic conditions. Gyttja, a reddish-gray, finely textured mud consisting mostly of biological residue and chemical precipitates (Reid, 1961), appeared to be the dominant sedimentary component in clear, more basic waters.

Because of their unusual physical or chemical features, many lakes were excluded from the Thienemann-Naumann systems of classification. As a group, these lakes constituted what Thienemann (1931) referred to as "disharmonious." Of special concern were lakes with extremely acid waters. In considering these, Thienemann (1931) introduced the category acidotrophic to include all dystrophic lakes having waters with pH values less than 5.5. Naumann elaborated further by recognizing siderotrophic, alkalitrophic, argillotrophic and 24 other anomalous types of lakes (Rodhe, 1969).

The criticisms and modifications that followed the ideas advanced by Thienemann and Naumann are numerous. Most of the controversy has centered on the classification of dystrophic lakes. Strøm (1928), besides restating Naumann's view that dystrophic lakes might also be oligotrophic or eutrophic, found that some eutrophic lakes were considerably rich in humus. These he re-classified as humic mud lakes. Earlier, Jarnefelt (1925) had encountered similar lakes. To these, he applied the term mixotrophic. Yoshimura (1933a) separated acidotrophic lakes into two types, one in which the acid originates from mineralogical sources and the other in which the acid is produced by biological processes. Later, Yoshimura (1933b) subdivided acidotrophic lakes into three groups (i.e., ortho-acidotrophic,

acidotrophic and siderotrophic). He considered minerals to be the chief source of acid for these. In addition, he established a second major category, that of dystrophy. It included only those lakes that derive acid exclusively from organic matter. Similarly, he divided it into three subtypes, ortho-dystrophic, dystrophic and siderotrophic, one of which was a term borrowed from Thienemann. Ohle (1936), aware of certain dystrophic lakes in which the acid originated from minerals as well as from biological accumulations, rejected the Yoshimura system. Prescott (1939) distinguished between bog lakes and lakes classified as dystrophic in a major revision of the Thienemann-Naumann classification. Berg (1955) and Berg and Petersen (1956) concluded from their studies of a humic, acid lake in Denmark that dystrophy was virtually indefinable. Lakes that tend to become dystrophic, should theoretically, accumulate large quantities of humus while evolving from a relatively low-acid, clear-water state. Therefore, to decide as to whether a lake is sufficiently rich in humus as to qualify it as dystrophic is completely arbitrary. Hansen (1959, 1961) expressed the opinion that much confusion and disagreement exists over the use of the term dystrophy. The term is misapplied when used to describe the nutrient status of a lake. Dystrophy, which means "rich in humus" should describe, rather, the extent of humic enrichment. Hansen proposed that the term dystrophy be replaced by a more appropriate nomenclature. For example, polyhumous could be used when referring to either an oligotrophic or eutrophic lake that contains dy or tyrfopel (sapropel) sediments. And, oligohumous could refer to only those lakes with gyttja deposits.

There was no general agreement concerning the oligotrophic and eutrophic categories. Lundbeck (1934) divided oligotrophic lakes into two groups--primary or edaphic oligotrophy which is caused by restricted nutrient input, and secondary or morphometric oligotrophy which results from great depth. Jarnefelt (1958) suggested that eutrophic lakes are either pleio-eutrophic or meio-eutrophic. In the former case, eutrophy is revealed by a distinctive vegetative coloring that reduces Secchi disc transparency. In a meio-eutrophic lake, "vegetation turbidity" is not manifest. Here then, it is necessary to assess eutrophy on the basis of a numerical relationship between organisms that indicate oligotrophic conditions and organisms that are commonly associated with eutrophy.

Hutchinson (1938) and Mortimer (1942) were of the opinion (as were many limnologists of that time) that lakes evolved or aged gradually on the way to becoming eutrophic. The natural transition was not as abrupt as the Thienemann-Naumann classification seemed to suggest. Both authors borrowed the term mesotrophy from earlier workers (e.g., Weber, 1907; Lundbeck, 1926, 1936; Lenz, 1925, 1927) to account for lakes that were neither oligotrophic nor eutrophic, but at an age somewhere in between. More recently, Brundin (1958) has devised a benthic faunistical lake type system that recognizes three primary categories (i. e., oligotrophic, mesotrophic, eutrophic), two of which diverge into five subgroups (i. e., ultra-oligotrophic, moderately oligotrophic, moderately eutrophic, stronger eutrophic and ultra-eutrophic). Certainly no less elaborate was a system proposed by Jarnefelt (1958):

I. "One-layer lakes (not stratified):

 A. Ortho-eutrophic

 B. Dyseutrophic:

  1. Oligo-dyseutrophic

  2. Meso-dyseutrophic

  3. Polyhumic

 C. Ortho-oligotrophic

 D. Dysoligotrophic:

  1. Oligo-dysoligotrophic

  2. Meso-dysoligotrophic

  3. Polyhumic

II. "Three-layer" lakes (stratified):

 A. Eutrophic:

  1. Epilimnion oligotrophic

  2. Hypolimnion eutrophic

B. Oligotrophic:

1. Epilimnion oligotrophic

2. Hypolimnion oligotrophic

METHODS

During 1968 and 1969, limnological data were collected from studies of Crater, Odell, Waldo, and Woahink lakes. Because of weather conditions, sampling on lakes in the Cascade Range was limited to a five-month period, from June to October. At Woahink Lake, regular monthly sampling was maintained from June, 1968 to September, 1969 (except for January and March, 1969).

Thermal profiles were determined periodically with a Whitney portable thermometer (model TC-5A) which has a meter scale calibrated in 0.1° C units. Temperatures were read at intervals of 0.6 m to a depth approximating the lower limit of the metalimnion. Deeper temperature readings were recorded every 50 m in Crater Lake, 10 m in Odell Lake, 10 m in Waldo Lake and 1 1/2 m in Woahink Lake.

Incident radiation was measured with a Belfort recording pyrheliometer. Continuous measurements were recorded during experiments which estimated photosynthetic rates by phytoplankton.

Light attenuation data were obtained with a Kahl submarine photometer (model 268 WA 310) which has a spectral range (in sunlight) of 400 - 640 mμ. Blue, green and red filters, having spectral ranges of 400 - 550 mμ, 460 - 660 mμ and 500 - 720 mμ, respectively, were used to determine the relative attenuations of these components of the visible spectrum. The maximum depth to which the photometer could be lowered was 105 m. Photometer readings were recorded for every meter to a depth of 10 m; thereafter, the recording intervals were lengthened to 5 m.

Light penetration was determined also with a standard-sized (20 cm diameter) Secchi disc. A larger-sized disc (1.0 m diameter) was tested at Crater and Waldo lakes, which have extraordinarily high Secchi disc transparencies.

Water samples for chemical analyses were collected at the surface and at several evenly-spaced sampling depths extending to 500 m in Crater Lake, 30 m in Odell Lake, 40 m in Waldo Lake and 18 m in Woahink Lake. Water analyses, except those for Na, K, Ca, Mg and Zn, were conducted in a mobile laboratory within 12 hours after the samples were collected. pH values were obtained with a Corning pH meter (model 7). Specific conductance was measured with a Beckman conductivity bridge (model RC-16B2). Total alkalinity was determined colorimetrically, using bromcresol green-methyl red indicator solution. Total hardness was determined by EDTA titration. The method for determining total dissolved solids (total residue) was derived from the Standard Methods handbook (APHA, 1965). An atomic absorption spectrophotometer (Perkin-Elmer model 303) analyzed samples for Na, K, Ca, Mg and Zn. The Winkler method (azide modification) was used to measure dissolved oxygen.

Vertical plankton tows with a no. 6 mesh net (intake diameter equaled 0.5 m) were taken periodically. Samples were fixed in 5% formalin for later analyses. Stomach contents of fish netted in Waldo Lake by the State of Oregon Game Commission were studied to determine the relative importance of limnetic zooplankton as a food resource in the lake.

Phytoplankton primary production was measured in situ with ^{14}C. The method used was a modification of a 1961 technique prepared by the Fisheries Research Institute, University of Washington, Seattle (F. R. I. field manual, section S6, carbon-14). Water samples were collected with a 2 1/2 liter plastic water bottle (Van Dorn type). Sampling depths were variable in each lake as will be indicated in later sections. A 125 ml-portion of water from each sampling depth was inoculated with 1 ml of a stock solution of $Na_2{}^{14}CO_3$ (5.0 μCi/ml) and returned to the depth from which it was drawn. Dark bottles accompanied light bottles at every other depth to determine non-photosynthetic uptake of ^{14}C. Occasionally, duplicate light bottles were added to assess experimental error. Following a four-hour incubation period (1000 - 1400 hrs), all samples were retrieved and filtered with a Millipore apparatus (47 mm-diameter AA Millipore filters) in the mobile laboratory. The uptake of ^{14}C was determined by liquid scintillation counting at Oregon State University. Net production rates (mgC/m^3/hr) were plotted against depth for each sampling date. The resulting curves were integrated and net production rates for the sampled water column were estimated for the incubation period ($mgC/m^2/hr$).

During the summer of 1969, an attempt was made to determine the relative effects of various nutrients (P, Fe, NO_3, NH_3) on rates of photosynthesis by phytoplankton. Four nutrient stock solutions (KH_2PO_4, $NaNO_3$, NH_4Cl and $FeCl_3$) were prepared using analytical grade reagents. Every effort was made to avoid contamination and to insure sterile nutrient media. Glassware was rinsed repeatedly with concentrated HCl. Other precautions recommended by Drs. Goldman and Shapiro (personal comm.) for the preparation and utilization of nutrient media were followed. Each stock solution was diluted to an initial concentration and dispensed into 20 ml glass ampules. The ampules were sealed by flame, autoclaved and placed in refrigerated storage. During bioassay experiments, the nutrient media were transferred from the ampules to 125 ml culture bottles using disposable hypodermic syringes. Three 2 1/2 liter water samples, drawn from a predetermined depth in the photic zone (i.e., 70 m in Crater Lake, 6 m in Odell Lake, 24 m in Waldo Lake and 4 m in Woahink Lake), were apportioned into 40 125 ml culture bottles. Each subsample (and a duplicate) was treated with a different concentration of one or more nutrient salts and 1 ml of the stock solutuion of $Na_2{}^{14}CO_3$. For comparative purposes, two additional subsamples (controls) received the $Na_2{}^{14}CO_3$ solution only. All culture bottles (subsamples) were suspended from the same rack and lowered to the depth from which they were drawn. After four hours (usually during 1100 - 1500 hrs), the samples were recovered and filtered using the materials described earlier.

Detectable concentrations of chlorophyll a provided a partial estimate of phytoplankton biomass (Strickland, 1960). Water samples for pigment analyses were obtained between 1100 and 1130 hrs at the surface and at five evenly-spaced sampling depths extending to 200 m in Crater Lake, 30 m in Odell Lake, 40 m in Waldo Lake and 18 m in Woahink Lake. The samples were treated immediately with saturated $MgCO_3$ to neutralize the acid produced by algal decomposition (Strickland and Parsons, 1965). Within a period of less than six hours, a specific volume of each sample was filtered with the Millipore unit (filter pore size equaled 0.8 μ). The filters were placed in a desiccator and stored in a freezer compartment held at -25.0° C. Pigments were extracted by grinding the filter and rinsing it into a centrifuge tube containing 10 ml of 90% distilled reagent grade acetone. Each tube was stoppered, shaken vigorously and stored in a refrigerator for 1-2 hrs. Later, the tubes were centrifuged for 10 minutes at 15,000 rpm. The supernatant liquid from each tube was decanted into a 1 cm-path-length spectrophotometer cell. Immediately, the optical density of each solution was measured photometrically at wavelengths of 750 mμ, 665 mμ, 645 mμ and 630 mμ. Measurements were corrected against a blank cell containing 90% acetone only. The concentrations of chlorophyll a were calculated in accordance with the Strickland and Parsons equation (1965).

All sampling proceeded from a single index station in each lake. When establishing a permanent station, it was hoped that the site would be convenient, practical and representative of lake conditions. Normally, Station 9 was the sampling site at Waldo Lake. Rough surface conditions created by strong northwesterly winds made it necessary, however, to use Station 5 on October 3. At Odell and Woahink lakes, sampling was conducted at stations 1 and 3, respectively.

THE BASIN ENVIRONMENTS

Reeves (1968) defined a lake basin as a depression, formed in response to various geologic processes, in which water accumulated. The body of water that eventually occupied the basin became a lake environment (Reid, 1961; Reeves, 1968).

This chapter will serve to introduce the four lakes that were studied. In addition, the edaphic (geochemical), climatic and morphologic factors that existed in the basins and ultimately acted upon the lake environments will be compared and discussed. Relative locations, sizes and shapes of the four study lakes are illustrated in Figures 1 and 2.

Geography and Geology

Crater Lake

Crater Lake is the deepest lake in the United States and the seventh deepest in the world (Edmondson, 1966) (Figure 3). The lake is located in the southwestern quarter of Oregon, approximately 104 km north of the Oregon-California border, and 193 km inland from the Pacific Ocean (Phillips and Van Denburgh, 1968). The lake occupies the collapse caldera of volcanic Mt. Mazama (Nelson, 1967). Radiocarbon dating studies by Rubin and Alexander (1960) and Fryxell (1965)

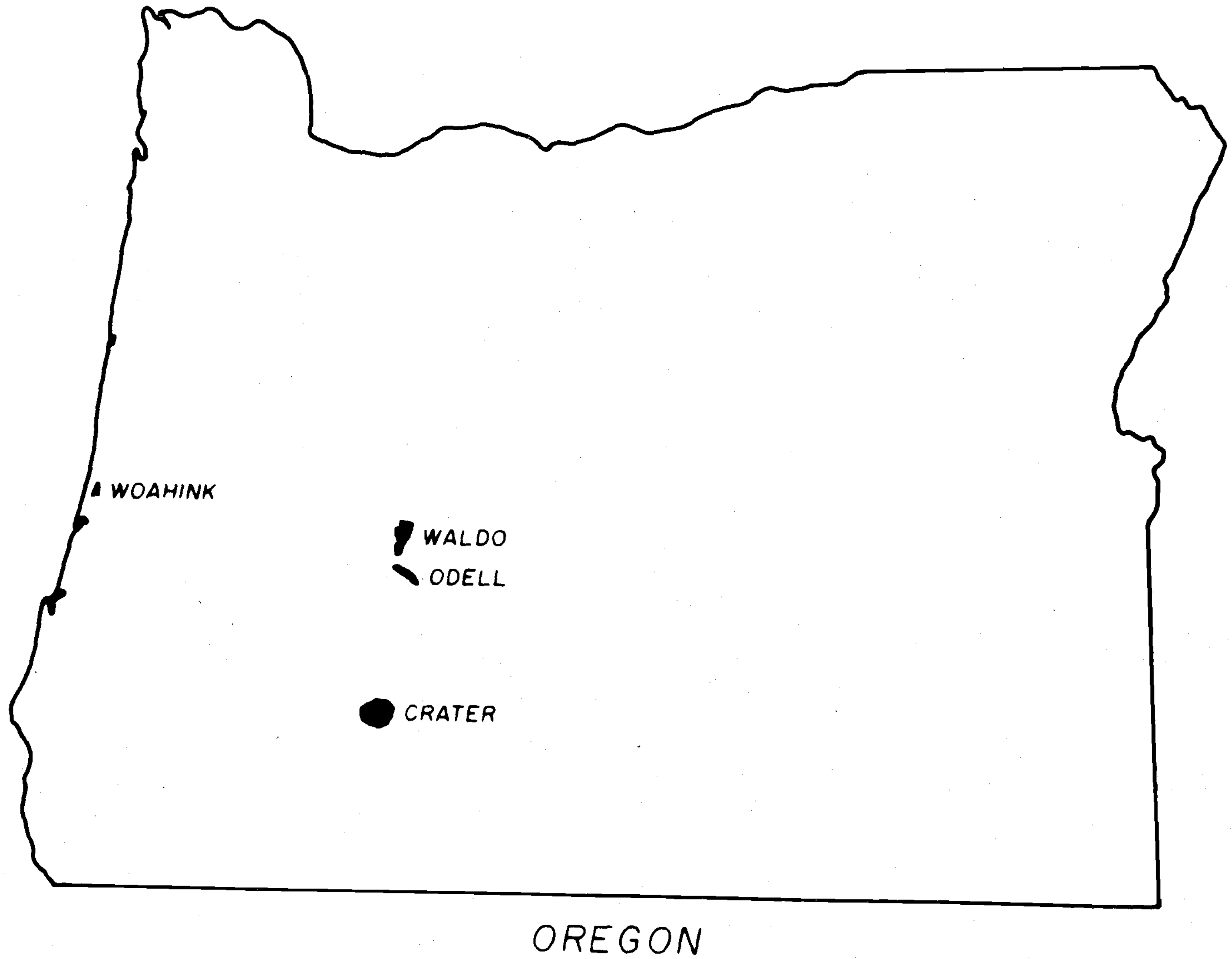


Figure 1. Relative locations of the four study lakes in Oregon.

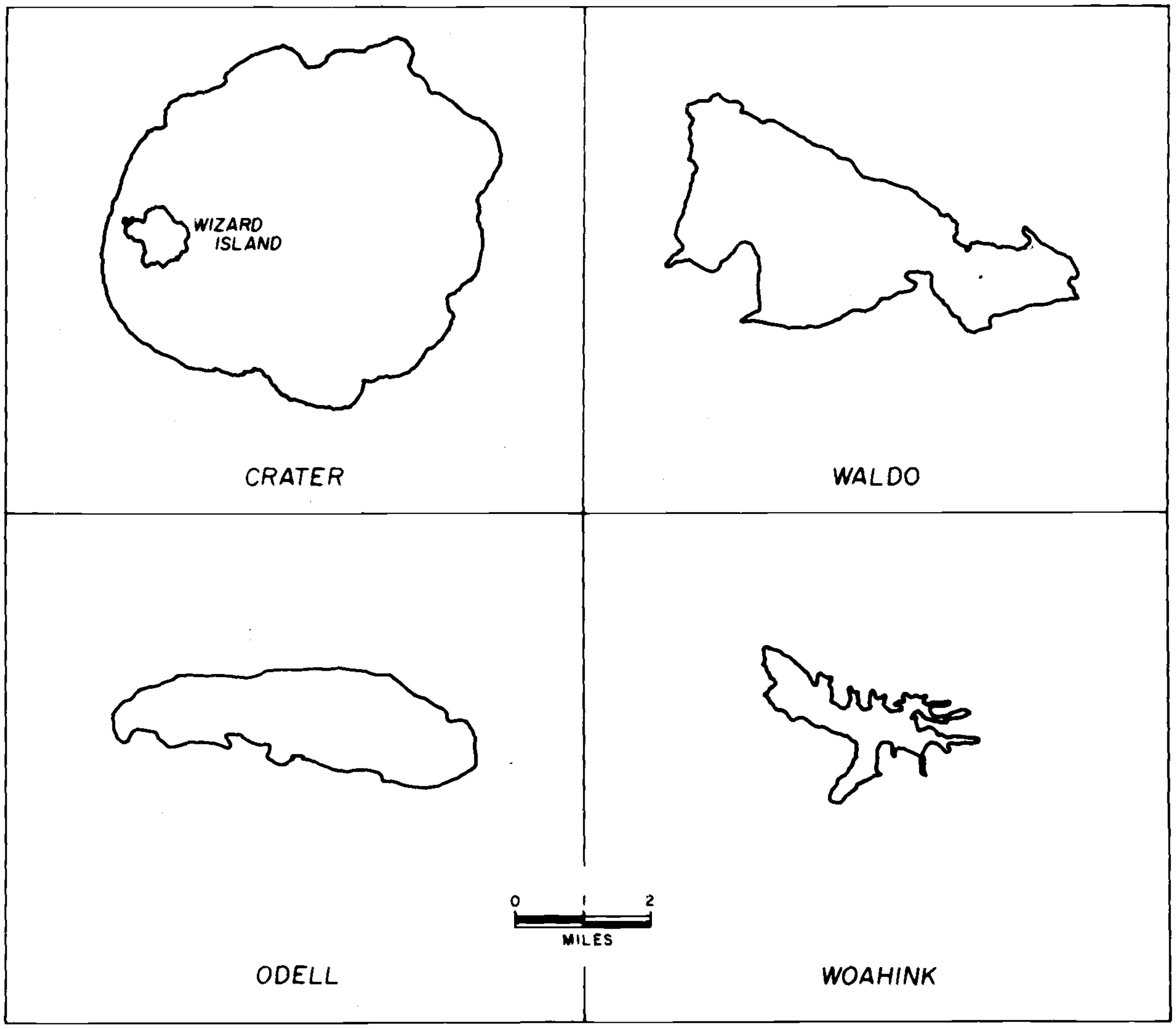
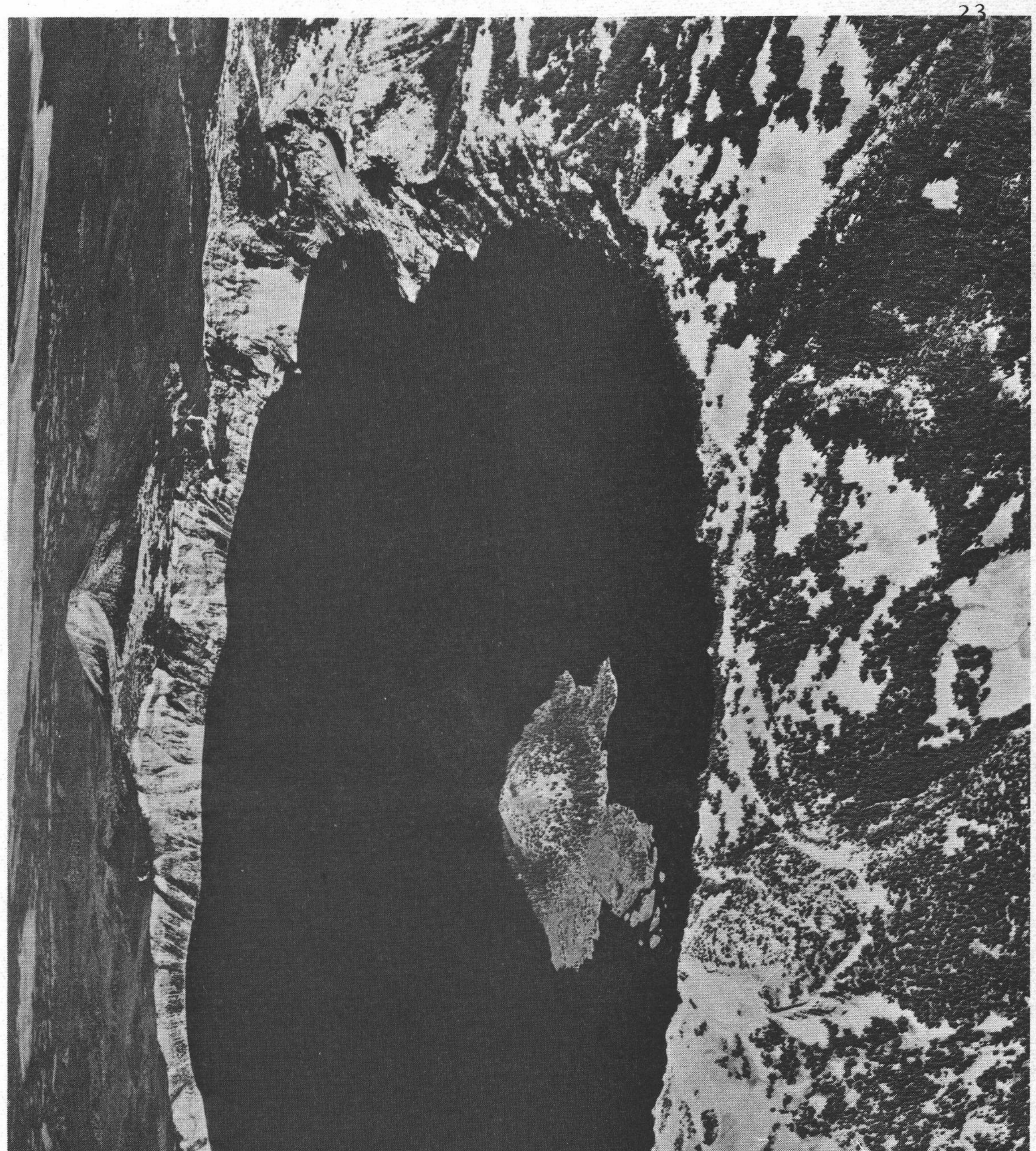


Figure 2. Size and shape relationships among the four study lakes.

Figure 3. Aerial view of Crater Lake, Oregon (Delano Photographics)



place the approximate age of the lake at 6600 years. Probably, water began to collect in the basin soon after the collapse. But the major accumulation of water has occurred within the last 700 to 1,000 years (Nelson, 1967). The re-occurrence of volcanic activity produced an emergent secondary cone (Wizard Island) and two submerged domes on the floor of the basin (Nelson, 1967).

Crater Lake is a closed basin, having no known outlets (Nelson, 1967). Water is lost through seepage (perhaps 20 - 30% of the total loss, J. R. Donaldson, personal comm.) and evaporation (Phillips and Van Denburgh, 1968). Of the total amount of water the lake receives, over 78% is precipitation falling directly on the lake surface (Phillips and Van Denburgh, 1968). The remaining water input comes from surface runoff (snowslides, sheetwash, meltwater tributaries) and groundwater inflows. No permanent streams enter the lake.

Crater Lake is enclosed by steep caldera walls that ascend from 150 to 610 meters above the surface of the lake (Nelson, 1967). In places, the walls rise vertically to the crater rim. Where landslides (including debris slides and debris falls) have reached the shoreline, deltaic "beaches" have formed.

The regolith of the basin is, for the most part, very coarse and permeable. The major constituents include andesite, dacite and dacitic pumiceous ash and lapilli (J. S. Cahoon, personal comm.). Rock debris is generated by the processes of weathering and mass-wasting along the caldera wall. The soils are immature and lack a distinctive horizonation. Only the upper few inches of the soil profile is darkened by organic matter. Large sections of topsoil are removed periodically by landslides and avalanches (Phillips and Van Denburgh, 1968). Generally, the rates of rock weathering, soil formation and organic accumulation are impeded considerably by low annual mean temperature and the immaturity of the basin regolith (J.S. Cahoon, personal comm.).

The surface area of the walls surrounding the lake represents the entire drainage area for the basin. Thus, the area of the watershed is much less than the surface area of the lake (1/3 to 1/4 the area of the lake), a feature that is usually reversed in other lake environments. This, in addition to the low fertility and organic content of the basin soils (and because nearly 80% of the annual precipitation is received directly by the lake) suggests that the peripheral watershed is contributing relatively little to the nutrient supply in the lake.

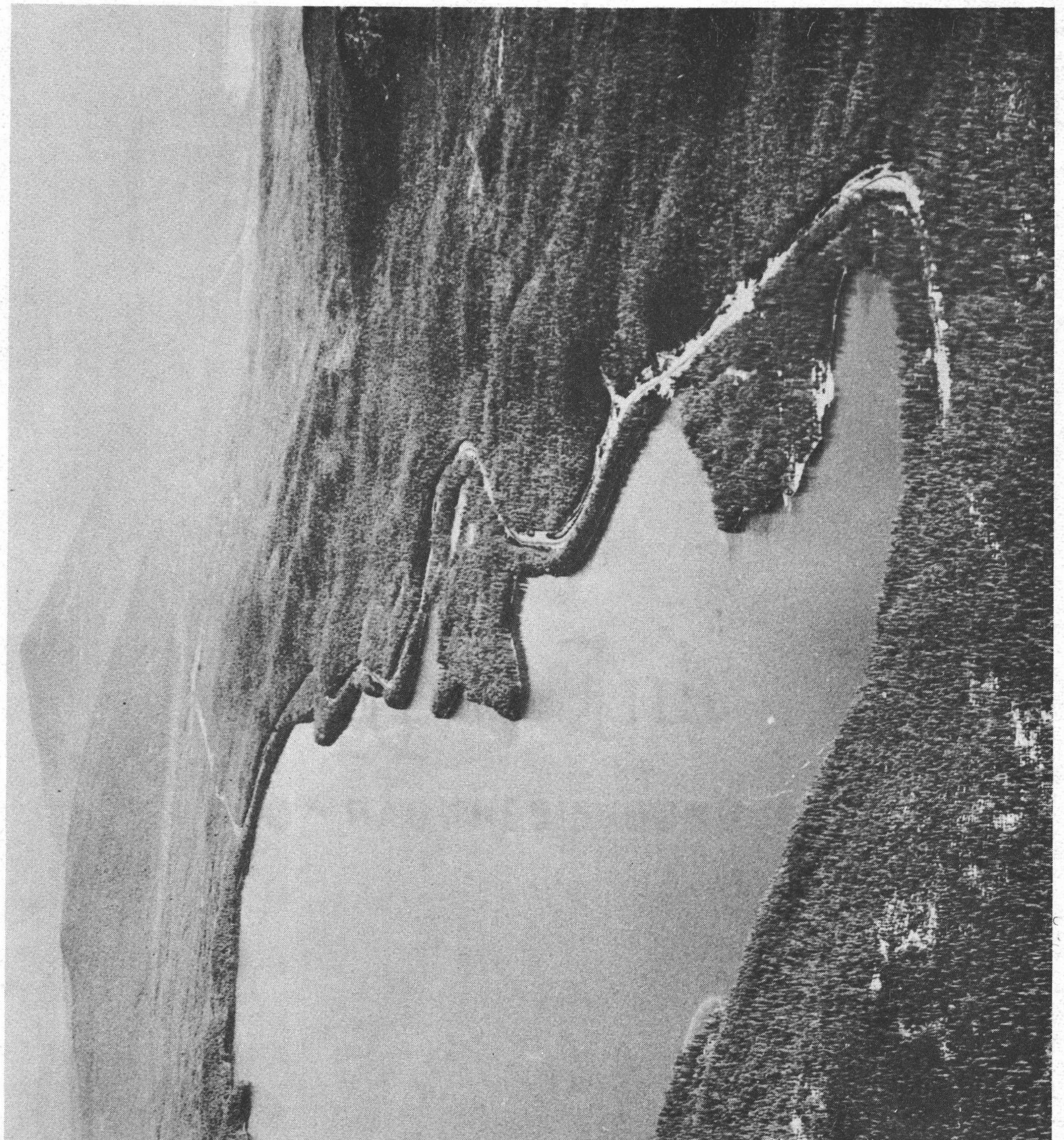
Phillips and Van Denburgh (1968) listed three possible means whereby dissolved solids are introduced into Crater Lake: (1) subaerially, from springs and surface runoff, (2) underwater, from the dissolution of soluble materials along the caldera walls, and (3) underwater, from fumaroles and thermal springs. The relatively high concentrations of sulfate, chloride, sodium, silica, and calcium arise chiefly from the second and third sources. The tendency for dissolved solids to increase in the lake is checked, however, by the loss of solutes through seepage. Phillips and Van Denburgh (1968) estimated the loss at 7000 tons per year and suggested that it may exceed the annual input. This, they believe, has a slight freshening effect on the lake.

Odell Lake

Odell Lake, situated at the summit of the Cascade Range in the Deschutes National Forest, is 65 km directly north of Crater Lake (Figure 4). The basin is thought to be a glacial trough closed at the eastern end by a terminal moraine. The age of the basin is estimated at 10,000 to 12,000 years (E. Taylor, personal comm.).

During the eruptions of Mt. Mazama, volcanic ash was carried northward where it showered onto the loamy soils and andesitic lava in the Odell Lake basin. In time, a mantle of pumiceous ash and lapilli covered the basin to a thickness ranging from 35 to 150 cm. The mantle is coarsely textured and, therefore, is extremely permeable. Of the total volume of pumiceous material, 20% to more than 50% is comprised of pebbles or "granules" (Wentworth, 1922) larger than 2 mm in diameter. The upper few inches is darkened by organic accumulation. In places, particularly on high angle slopes, the mantle has been removed by weathering and mass-wasting to expose pre-existing soils and rock. Because of the texture of the

Figure 4. Odell Lake, Oregon, viewed from the west.



surface layer, sheetwash runoff is very slow or nonexistent. Subsurface percolation of water through pumiceous and loamy materials is very rapid, thereby facilitating the passage of dissolved nutrients into the lake.

Odell Lake is fed by two large, permanent tributaries (i.e., Trapper and Crystal creeks) (Averett and Espinosa, 1968). Both supply the lake with meltwater drained from higher elevations. On a map of Odell Lake, Newcomb (1941) indicated an additional 30 to 35 smaller tributaries. Most of these are shown to enter the lake from the north. The major outlet tributary is Odell Creek which flows eastward for 13 miles until it discharges into Davis Lake (Averett and Espinosa, 1968). Groundwater springs are known to exist along the south shoreline (Averett and Espinosa, 1968).

Waldo Lake

Waldo Lake is located in the Willamette National Forest, approximately 89 km southeast of Eugene, Oregon, and 14 to 16 km north of Odell Lake (Figure 5). The lake basin, estimated to be 10,000 to 12,000 years old, is a glaciated depression enclosed by end and lateral moraines (E. Taylor, personal comm.).

The regolith of the basin consists mostly of light colored pumice and rounded rock boulders up to 1 1/2 m in diameter. The materials are well-drained and are rapidly permeable. The

Figure 5. Aerial view of Waldo Lake, Oregon, looking northward toward the Three Sisters peaks.

composition of the bedrock is mainly fractured hard basalts. Depth to bedrock is no greater than 2 m. Bedrock is exposed in many places, especially at the north end of the lake. There, pumice material contains 60 to 70 percent by volume of boulders (L. D. Evans, personal comm.). As expected, the soils have a very low organic content and are relatively barren.

The lake receives no permanent surface drainage. During the spring, however, snowmelt runoff enters the lake through countless temporary streams. Carter et al. (1966) suggested that spring seepages may exist on the lake floor. At the north end, the lake discharges into the North Fork of the Willamette River.

Woahink Lake

Woahink Lake is situated on the central coast of Oregon, approximately 165 km west-northwest of Waldo Lake (Figure 6). The lake basin, typical of nearly all the coastal lakes in the state, is a former stream valley obstructed at its mouth by alluviation and sand dune encroachment (Baldwin, 1964). The movement of sand is generally in an easterly-northeasterly direction. In places along the west shoreline, the lake is adjoined by dune complexes.

The soil of the Woahink basin consists mostly of sand or sandy loam. The soil west of the lake is described as pure sand (Griffiths and Yeoman, 1938). Further inland, between the east shore of the

Figure 6. Aerial view of Woahink Lake, Oregon, looking northeastward toward the Coast Range.

lake and the Coast Range, the sand grades laterally into a weakly-developed sandy loam (Griffiths and Yeoman, 1938). Permeability is extremely rapid; soil fertility is very low (D. W. Brackett, personal comm.).

Woahink Lake is fed by three tributaries that enter from the north and east (McGie and Breuser, 1962). The longest is about 5 km in length. Together, they drain an area of 14.2 km^2. The lake empties southward into adjacent Siltcoos Lake through the Woahink Creek outlet (McGie and Breuser, 1962; D. W. Brackett, personal comm.).

The surface level of Woahink Lake fluctuates very little throughout the year (D. W. Brackett, personal comm.). McGie and Breuser (1962) reported the seasonal fluctuation to be 1/2 m or less. Nothing can be found in the literature, however, concerning the rate of flushing in the lake. Flushing may be an important factor in limiting production, particularly during the late fall and winter months.

Climate

Crater Lake

Phillips and Van Denburgh (1968) reported climatic data compiled during a 32-year period (1930-1962) at the Crater Lake Weather Station. Annual temperature and precipitation averaged 3.9° C and

171.2 cm, respectively, with most of the precipitation occurring as snowfall. A 10-year (1951-1960) climatic summary of the United States (U. S. Weather Bureau, 1965) contains slightly different values for Crater Lake (i. e., the annual mean temperature and precipitation were 3.5° C and 177.8 cm, respectively).

During the wettest year (1950-1951), total precipitation amounted to 236.4 cm (Phillips and Van Denburgh, 1968), causing the level of the lake to raise 76.2 cm. Usually though, the annual water budget (i. e., water income-water loss) is nearly balanced (Phillips and Van Denburgh, 1968).

Incident radiation averaged 227.7 and 239.7 g cal/cm^2/4 hrs (1000 - 1400 hrs) during the summers of 1968 and 1969, respectively.

Odell Lake

Climatic data for the Odell Lake region was obtained from the U. S. Weather Bureau (1965), and Phillips and Van Denburgh (1968). For the period 1951 - 1960 (U. S. Weather Bureau, 1965), annual mean temperature was 5.0° C. Total annual precipitation, including 8 1/3 meters of snowfall (yearly mean), averaged 152.4 cm (U. S. Weather Bureau, 1965). Phillips and Van Denburgh (1968) reported an annual mean precipitation of 156.1 cm in the period 1950 - 1964.

During 1968 (June - September), incident radiation averaged 241.1 g cal/cm^2/4 hrs (1000 - 1400 hrs). For the same period in

1969, the value was slightly less (i.e., 236.6 g cal/cm^2/4 hrs).

Waldo Lake

Climatic records were not available for Waldo Lake. One can assume, however, that the climatic features of the Odell and Waldo basins are reasonably similar, considering that they are within 16 km of one another.

Incident radiation was measured periodically at Waldo Lake during the summer of 1969. The average value obtained was 266.1 g cal/cm^2/4 hrs (1000 - 1400 hrs).

Woahink Lake

The climate for Woahink Lake differs considerably from the other three study lakes. In the period 1951 - 1960, annual mean temperature was 11.2° C; annual precipitation during the same period averaged 217.2 cm (U. S. Weather Bureau, 1965). These data were obtained from the nearest recording station, located about 5 km to the east of Woahink Lake (Canary, Oregon). Additional information concerning wind velocity and direction was provided by the U. S. Coast Guard, Siuslaw River Station, Florence, Oregon. Incident radiation during the summers (June - September) of 1968 and 1969 averaged 221.4 and 200.2 g cal/cm^2/4 hrs (1000 - 1400 hrs), respectively.

Morphometry

Crater Lake

Byrne (1965) computed morphometric data for Crater Lake (Table 1). Supplementary information was provided in detailed geological surveys by Nelson (1961, 1967) and Phillips and Van Denburgh (1968). The contour map of Crater Lake (Figure 7) is modified from a bathymetric chart constructed by Byrne (1962).

Table 1. Lake morphology.

	Crater*	Odell	Waldo	Woahink**
Elevation, surface (m)	1882	1459	1650	12
Area (km^2)	48.0	14.4	25.1	3.2
Volume (km^3)	16.0	0.59	0.95	0.04
Depth, maximum (m)	589	86	128	21
Depth, mean (m)	325	41	38	10.5
Shoreline length (km)	31.0	21.5	40.0	22.3
Shoreline development	1.27	1.59	2.25	3.50
Relative depth (%)	7.52	2.01	2.26	1.18
Mean depth: max depth	0.55	0.48	0.30	0.50
Max depth: surface	0.085	0.023	0.026	0.012

*Byrne (1965)

**McGie and Breuser (1962)

The subaerial walls of the Crater Lake caldera are steeply sloped at an angle of about 45° (Nelson, 1967). Below the surface of

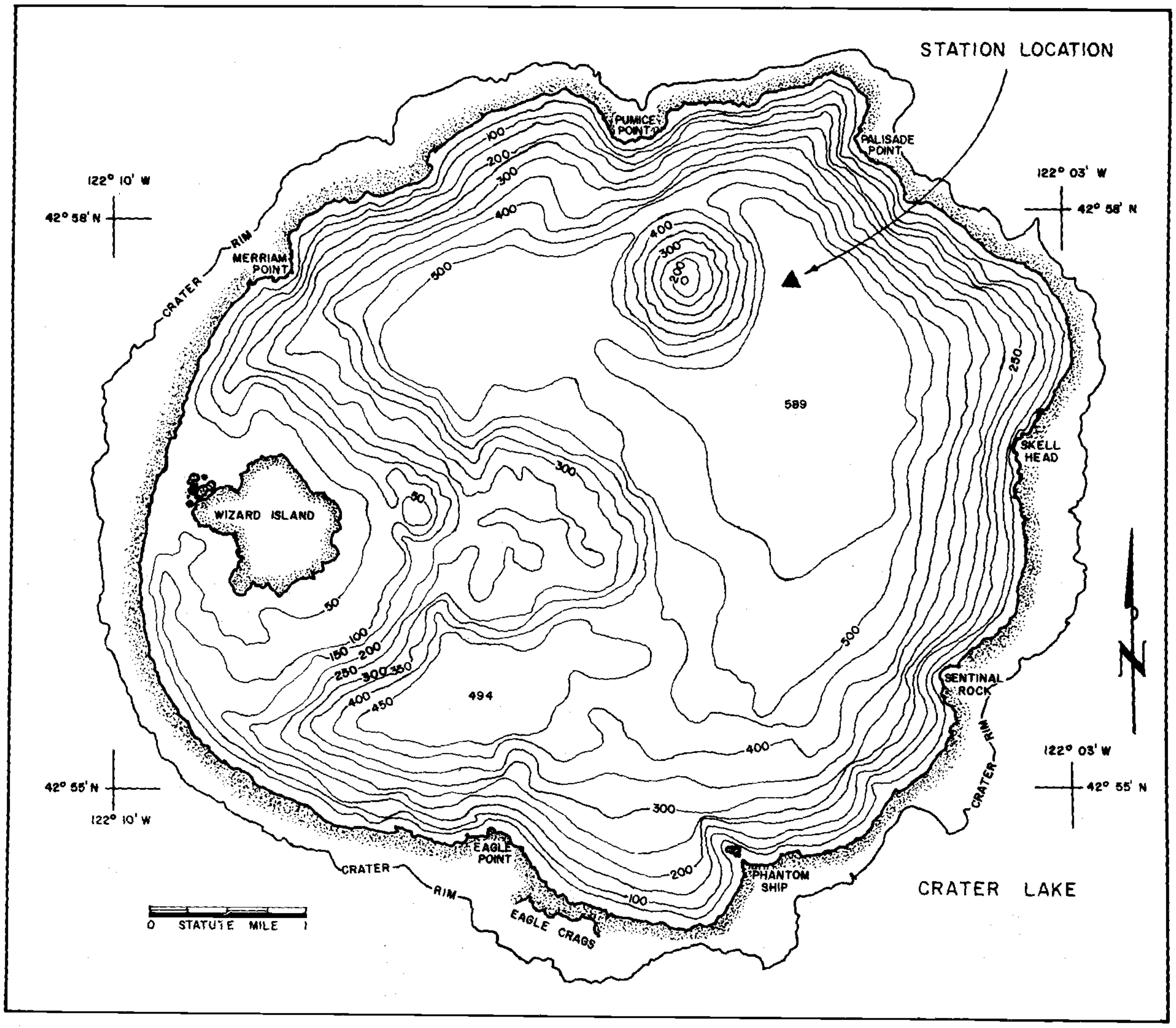


Figure 7. Bathymetric chart of Crater Lake, Oregon, showing sampling station locations. Contours based on USC and GS Hydro Survey No. 8498; contour interval, 50 m (Byrne, 1965).

the lake, the angle of decline is considerably less (i. e., about 30°). The walls of the caldera continue to descend at this angle until they intersect with the basin floor at depths ranging between 460 and 550 meters (Nelson, 1967; Phillips and Van Denburgh, 1968). Approximately one-half of the basin floor is sloped at an angle of less than 1°. In the eastern portion of the lake, the floor is completely flat over an area of about 1.3 km^2 (Nelson, 1967).

Crater Lake yields the very low shoreline development of 1.27 (Byrne, 1965). An index of 1.0 represents the configuration of a perfect circle.

Crater Lake attains its maximum depth over an area of 2.6 km^2 (Phillips and Van Denburgh, 1968). Nearly one-half of the lake floor is covered by water that reaches to a depth of more than 325 m (mean depth) (Byrne, 1965). Near the site of the sampling station (Figure 7), a submerged dome (Merriam Cone) rises to a height of approximately 390 meters above the basin floor.

Odell Lake

Morphometric data for Odell Lake are presented in Table 1. All values were computed from contour map no. 1274, State of Oregon Game Commission, Portland, Oregon (Figure 8). As shown, the basin is moderately elongated with a U-shaped cross profile (features that identify the basin as a glacial trough). Maximum depth occurs at

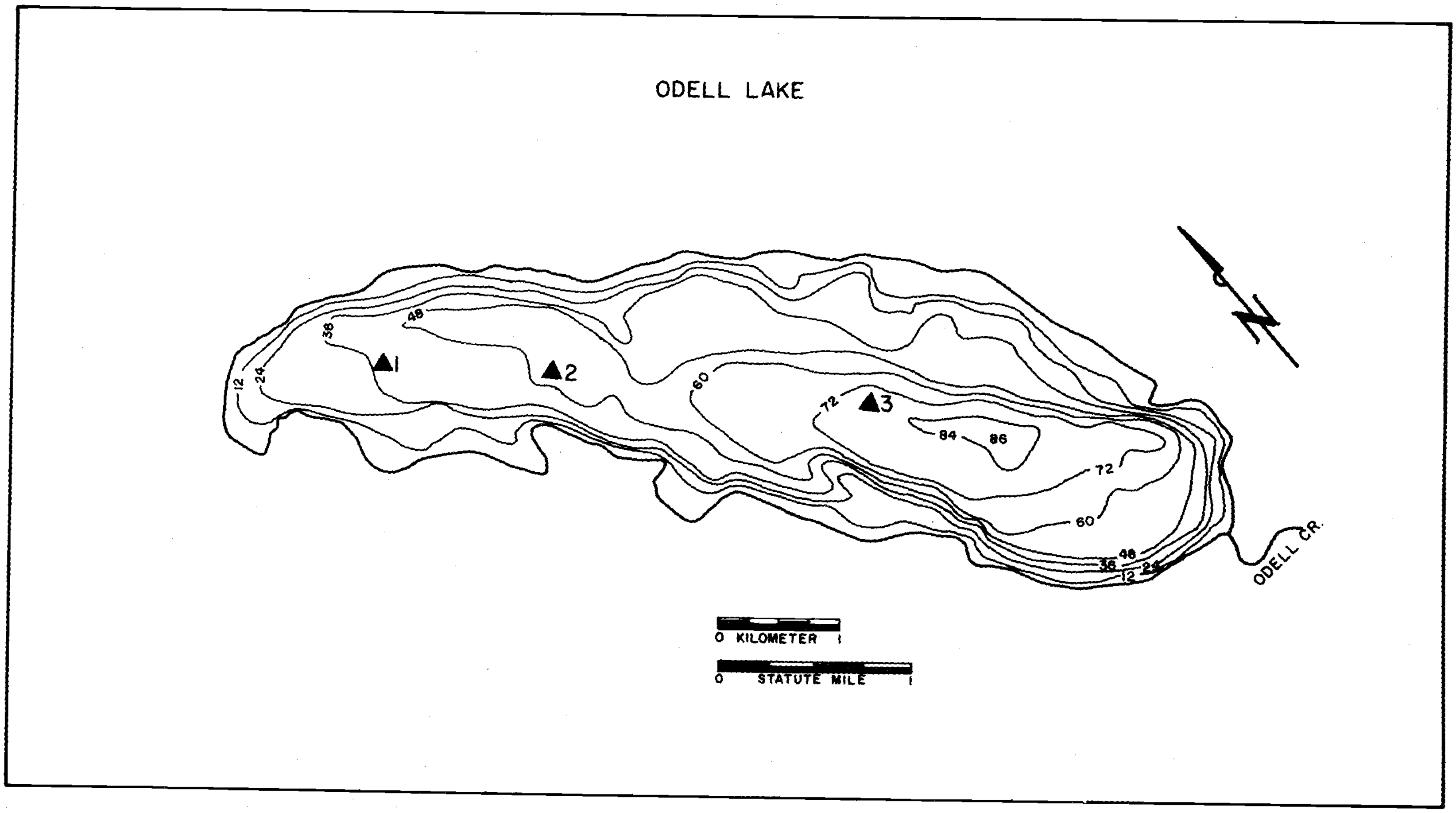


Figure 8. Bathymetric chart of Odell Lake, Oregon, showing sample station locations. Contours based on 1964 survey by the State of Oregon Game Commission, Portland, Oregon (map no. 1274); contour interval, 12 meters.

the eastern end of the lake where the slope of the basin wall is abrupt. The lake has a relatively low shoreline development of 1.59.

Waldo Lake

The morphometric data that are given for Waldo Lake in Table 1 were derived from contour map no. 1014, State of Oregon Game Commission, Portland, Oregon (Figure 9). Generally, the slope of the basin is gradual. In the west-central and southwestern bays, deep (i.e., to a depth of 128 meters), steep-sided potholes have been quarried from bedrock surfaces by glacial plucking and gouging (E. Taylor, personal comm.). The rocky knolls that are scattered over the basin floor are thought to be bedrock "highs" that resisted glacial scour (E. Taylor, personal comm.). Several of these are exposed along the shore of the lake.

Woahink Lake

The morphometry of Woahink Lake (Table 1; Figure 10) was reported by McGie and Breuser (1962). Woahink Lake is a steep-walled basin that extends below sea level. Almost 50% (9 m) of the maximum depth occupies a cryptodepression. The lake has a shoal area (i.e., that area of the lake which is less than 15 m in depth) of about 0.8 km^2. Most of this occurs in the three major arms that project to the north and east. The dendritic shape of the basin, which characterizes the coastal lakes of Oregon, yields a shoreline development index of 3.5. Although the area of Woahink Lake is about 22%

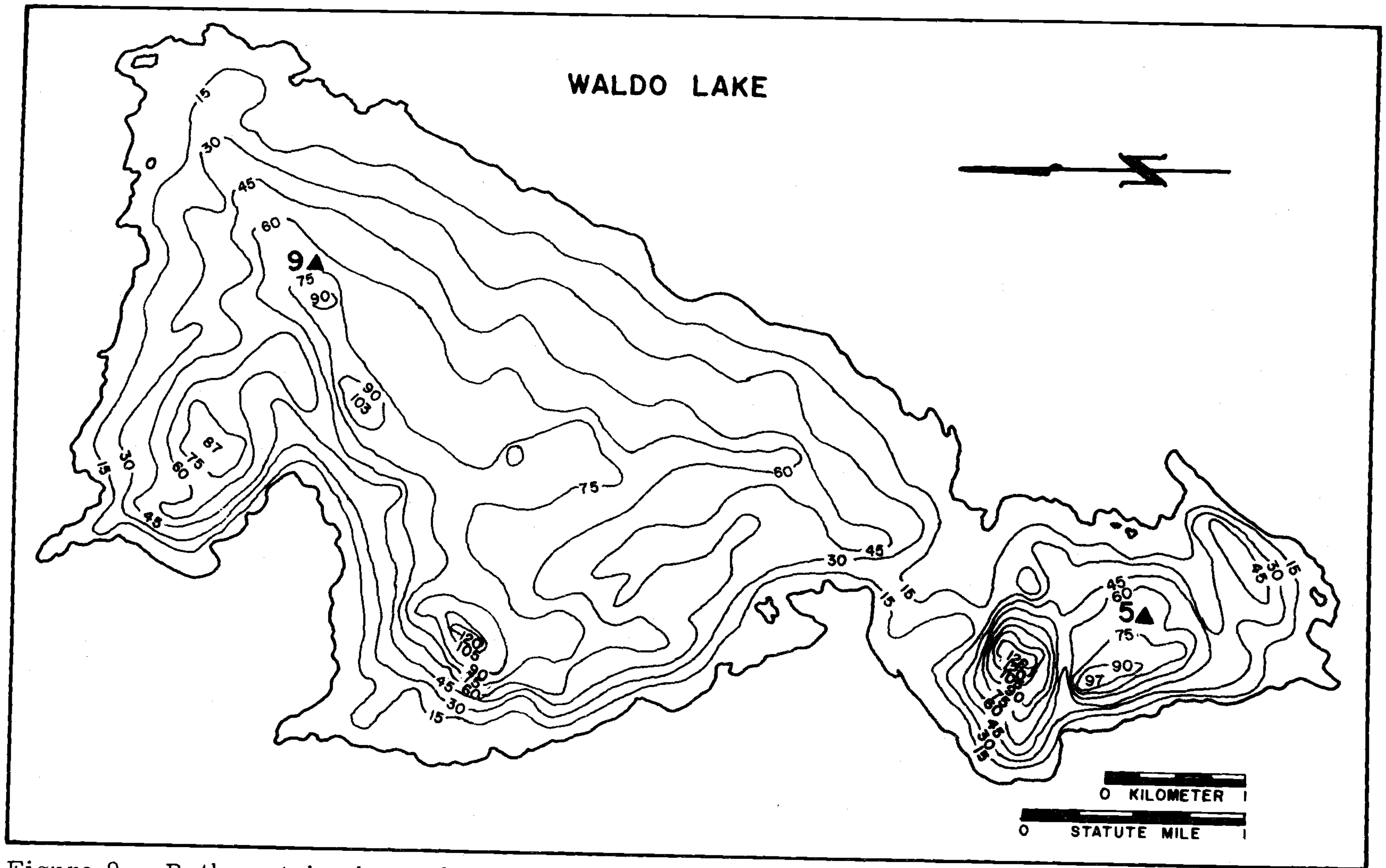


Figure 9. Bathymetric chart of Waldo Lake, Oregon, showing sample station locations. Contours based on 1958 survey by the State of Oregon Game Commission, Portland, Oregon (map no. 1014); contour interval, 15 meters.

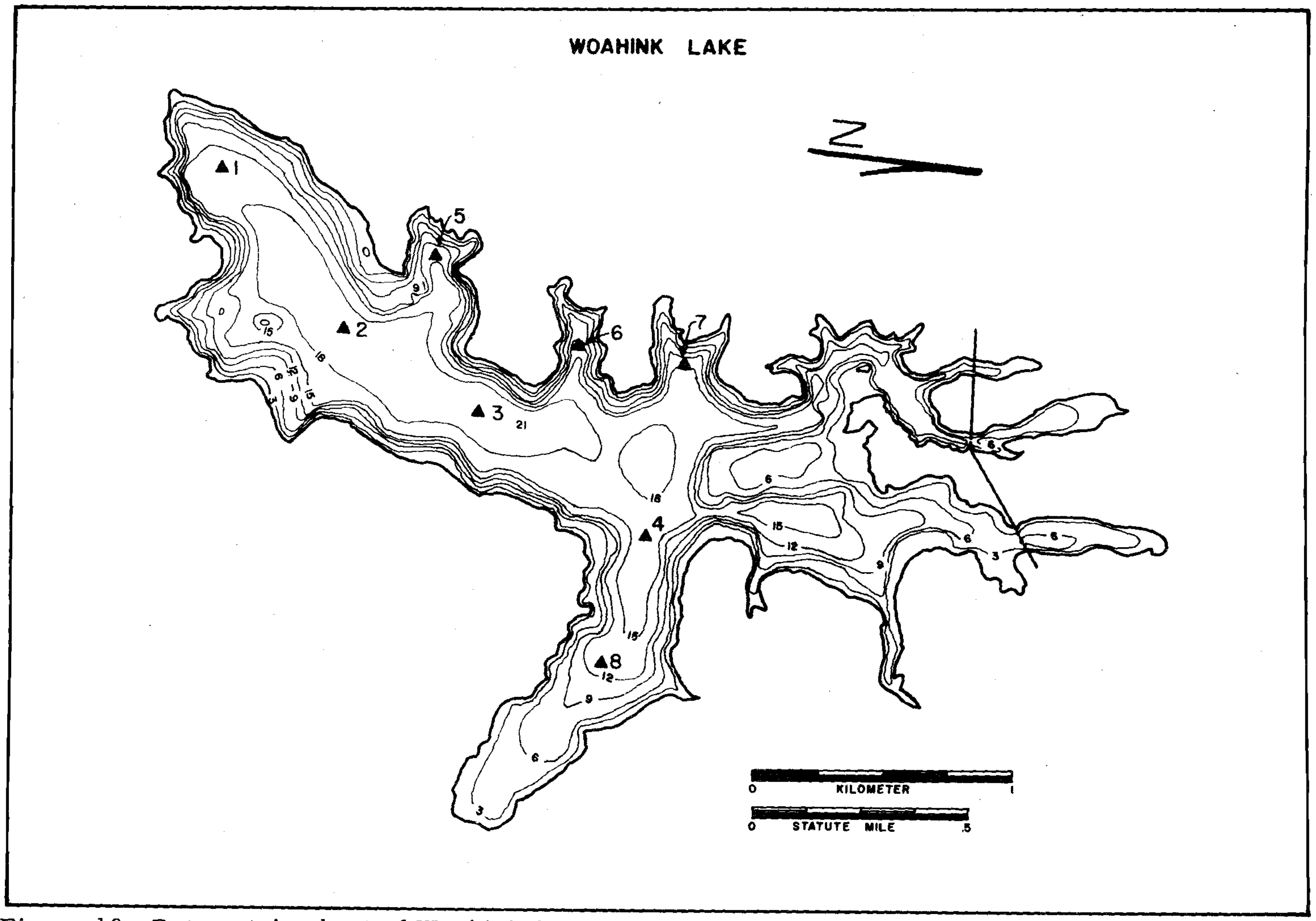


Figure 10. Batymetric chart of Woahink Lake, Oregon, showing sample station locations. Contours based on 1959 survey by the State of Oregon Game Commission, Portland, Oregon (map no. CL-61-6); contour interval, 3 meters.

of that of Odell Lake, the shorelines of the two basins are nearly equal in length.

THE LAKE ENVIRONMENTS

The physical and chemical nature of the water that constitutes the lake environment is determined by the impinging components of the basin (i. e., geochemistry, climate and morphometry). The thermal, optical, and chemical properties that have resulted will now be considered.

Temperature and Dissolved Oxygen

Temperature and dissolved oxygen profiles are compared in Figure 11. Additional profiles representing conditions which existed in 1968 appear in Figures 12-15.

Crater Lake

In Crater Lake, thermal stratification developed during June and was maintained until late September. The depth of the epilimnion was relatively shallow (Hoffman, 1969). At times, thermal stratification (particularly the level of the thermocline) was not distinct (Figures 11, 12). Temperature data from Figure 11 were used to compute a heat income of 35,831 g cal/cm^2. This is somewhat higher than the value 30,010 g cal/cm^2 estimated for the summer of 1966 (Kibby, Donaldson and Bond, 1968). The summer heat budget for Crater Lake was comparatively high in view of the summer heat incomes for Lake

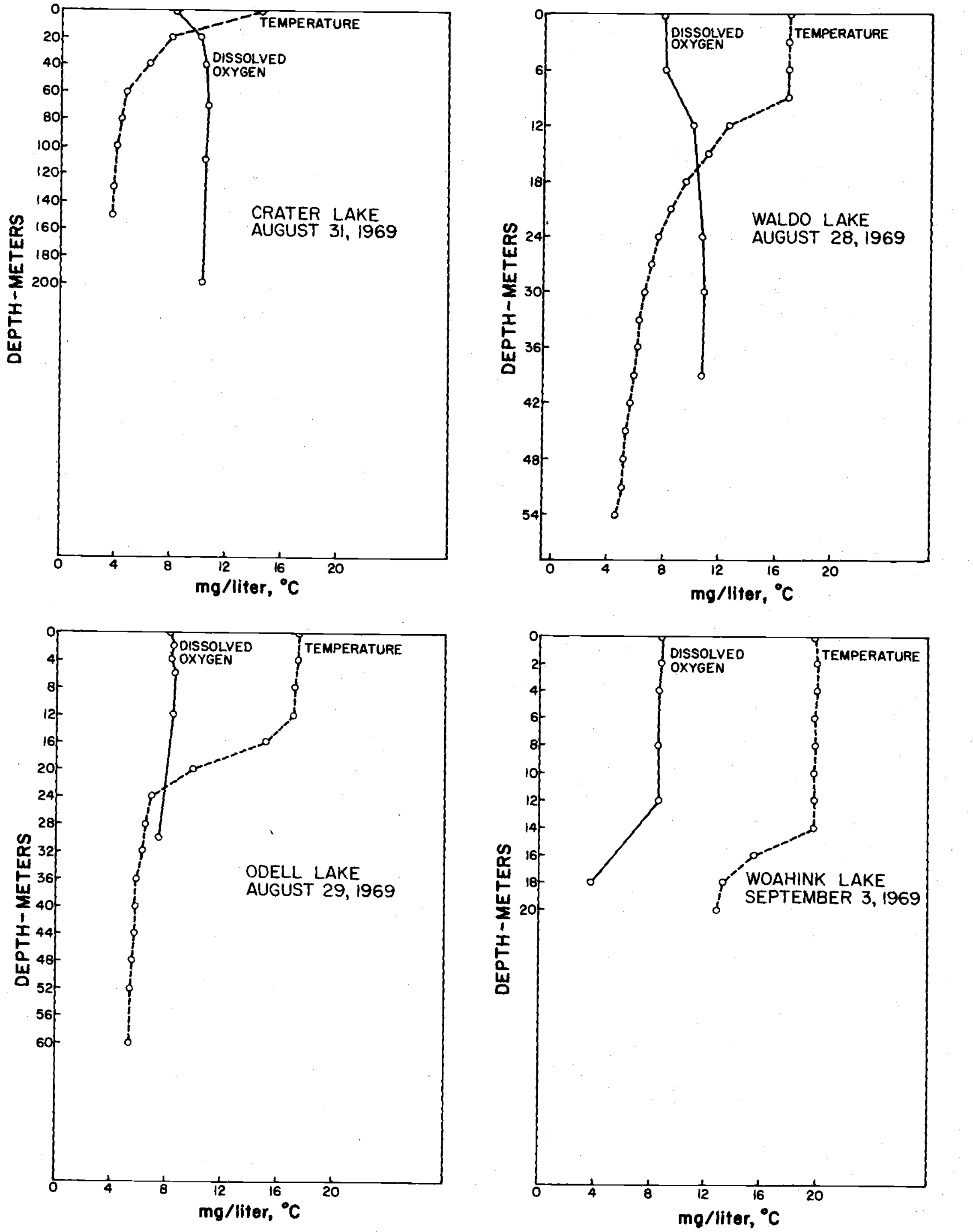


Figure 11. Temperature and dissolved oxygen profiles compared among the study lakes. In reference to the vertical relationship between temperature and oxygen, Crater, Odell, and Waldo lakes readily fit the description of an oligotrophic lake. In each of these, temperatures below the thermocline fall rapidly to nearly 4° C. The hypolimnion is well-oxygenated, even when thermal stratification is pronounced (as in Odell Lake). In Woahink Lake, however, the oxygen and thermal profiles tend to be parallel, a feature that one might interpret as eutrophic. A discussion of this will follow.

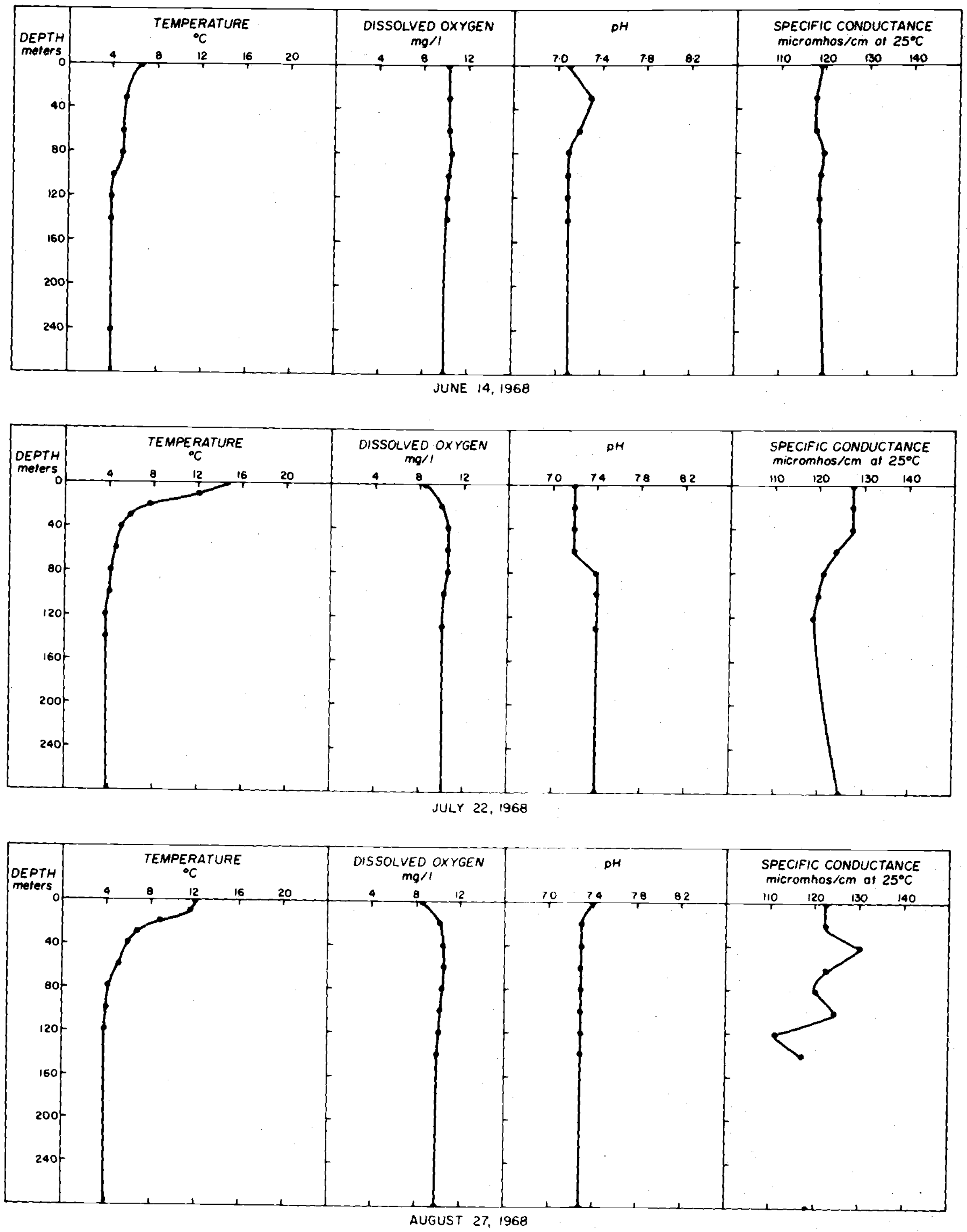


Figure 12. Temperature, oxygen, pH and conductivity profiles in Crater Lake, Oregon. June-August, 1968.

Michigan (40,800 g cal/cm^2) and Lake Baikal (42,300 g cal/cm^2) (Reid, 1961). For this reason and because wind action in the basin is very strong during the winter (Kibby et al., 1968), the lake seldom freezes over completely. The lake was covered by ice during the severe winter of 1897-98 and, again, for two days in 1924 (Waesche, 1934). More recently, in 1949, an ice layer varying in thickness from 5 to 30 cm covered the entire lake for three months (February to April) (Walker, 1949; Hoffman, 1969). Additional thermal data concerning Crater Lake are found in reports by Kemmerer et al. (1924), Hasler (1938), Utterback et al. (1942), Hoffman and Donaldson (1968), Phillips and Van Denburgh (1968) and Hoffman (1969).

The concentration of dissolved oxygen was nearly constant from a depth of 40 meters to a depth of 500 meters (Figures 11, 12). No attempt was made to sample below 500 m. As thermal stratification became more intense, the amount of dissolved oxygen below the thermocline approached a concentration that was 1 1/2 times greater than that measured in the epilimnion (Figures 11, 12). Robinson (1941) and Utterback et al. (1942), among others, have measured dissolved oxygen in Crater Lake and have reported similar conditions.

Odell Lake

Thermal stratification in Odell Lake was well-established by the end of June. Usually, the lake remained stratified until November when fall overturn occurred. In 1968, thermal stratification was evident as late as October 19. On November 26, the lake was homothermal at $6.77 \pm 0.15°$ C. During the following winter (1968-69), the lake froze over completely. From June through September, strong westerly winds pushed warm surface water toward the east half of the lake. There it piled up, displacing the thermocline (e.g., the thermocline at Station 3 was always three to five meters deeper than at Station 1). As a result, surface and perhaps internal seiches may have been generated regularly. Current systems such as these could be an important factor in the distribution of nutrients and heat energy throughout the lake. Summer heat incomes of 25,924 g cal/cm^2 and 26,659 g cal/cm^2 were computed for 1968 and 1969, respectively. In earlier studies of Odell Lake, temperatures were recorded vertically near Station 1 (Averett, 1966) and Station 2 (Newcomb, 1941).

The oxygen profiles at stations 1 and 3 approximated one another. During the summers of 1968 and 1969, the concentration of dissolved oxygen throughout the water column was essentially uniform (Figures 11, 13). Newcomb (1941) measured dissolved oxygen at depths of 0, 15, 38, and 55 meters. He reported a slight difference in measurements (i.e., 8.0 to 7.6 ppm of dissolved oxygen from the surface to maximal sampling depth).

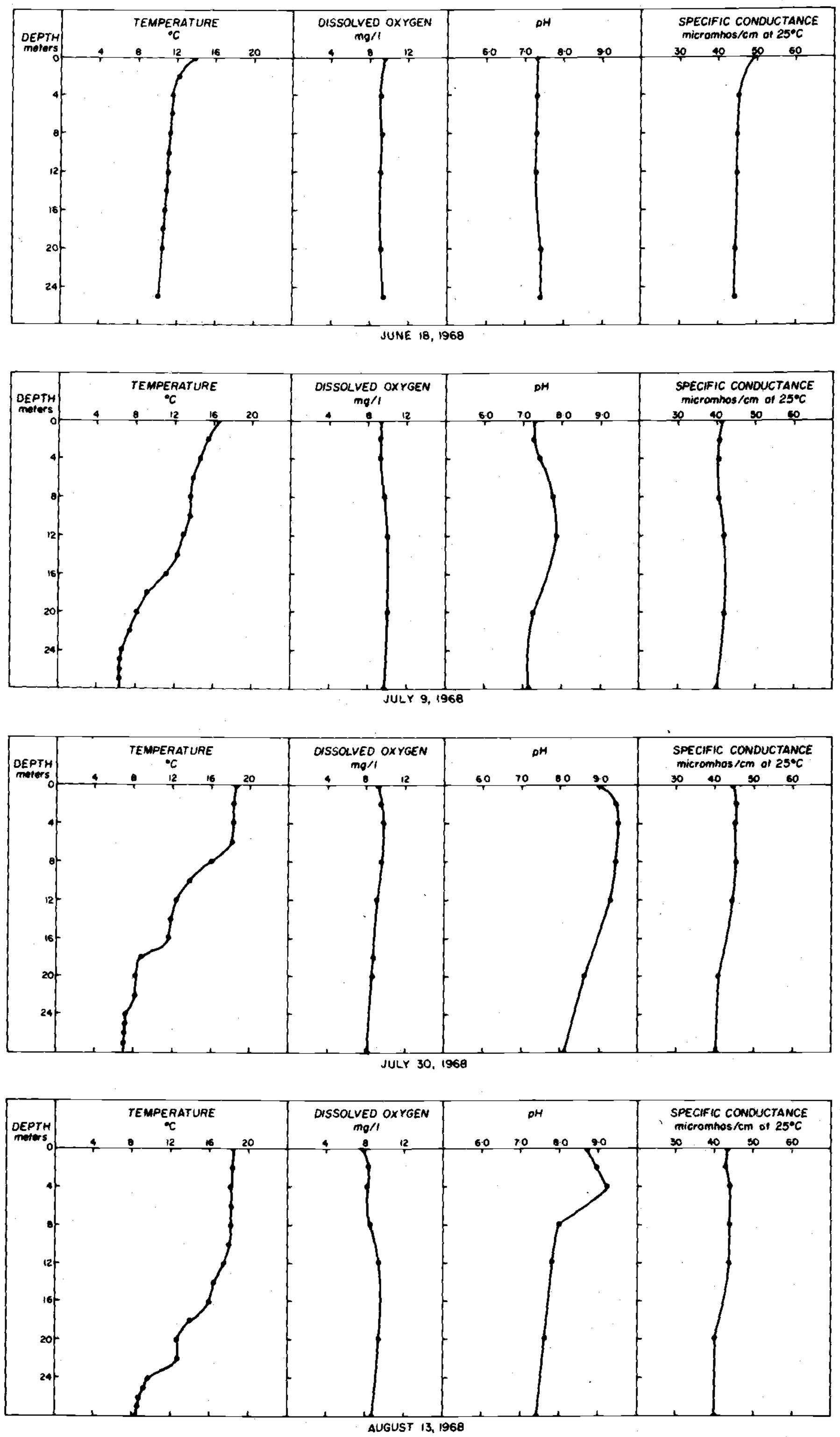


Figure 13. Temperature, oxygen, pH and conductivity profiles in Odell Lake, Oregon. June-August, 1968. Data collected at Station 1.

Waldo Lake

The vertical temperature gradients in Waldo Lake closely resemble those of Odell Lake (Figures 11, 14). On June 21, 1969, the surface temperature of Waldo Lake (to a depth of 4 m) was 11.2° C. This was 2.5° C lower than that recorded at Odell Lake two days earlier (on June 19). By July, however, the thermal profiles of both lakes were nearly identical.

For Waldo Lake, June through October was generally the period of thermal stratification (presumably, the lake freezes over during the winter). On October 3, 1969, the lake remained thermally stratified even though surface temperatures had fallen nearly 5° C in 37 days (i.e., from 17.0° C on August 28 to 12.4° C on October 3). Almost every afternoon throughout the summer, westerly winds reached velocities of 12 to 20 knots. This reinforced the thermal density gradient between the epi- and hypolimnia, which in turn created a more pronounced thermal profile (e.g., on August 6, 1969, metalimnetic temperatures fell rapidly from 16.3°C at 8 m to 6.6° C at 24 m). Whether wind action produced seiche-like currents is not known. A summer heat income of 21,496 g cal/cm^2 was computed from temperature data presented in Figure 11.

At all times, the maximum concentration of dissolved oxygen in Waldo Lake occurred several meters below the thermocline. Oxygen

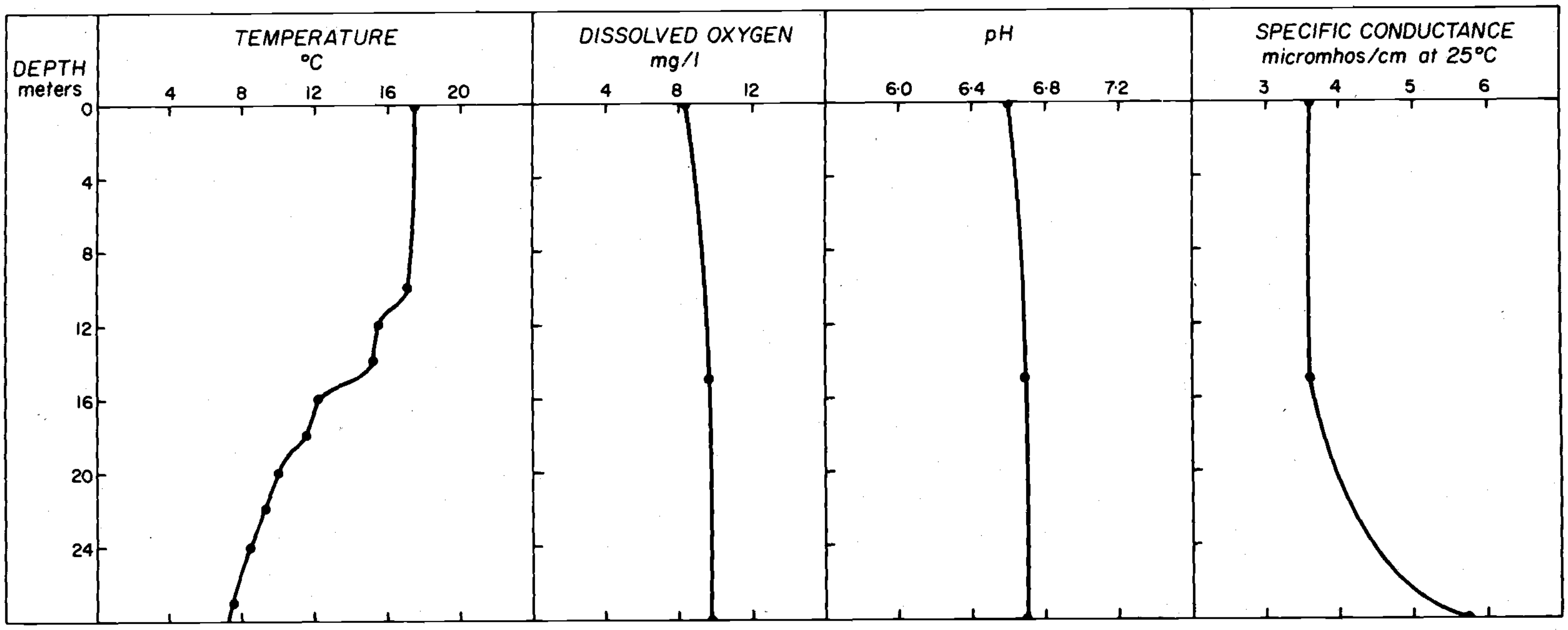


Figure 14. Temperature, oxygen, pH and conductivity profiles in Waldo Lake, Oregon. August 14, 1968. Data collected approximately 1.2 km NW of Station 9.

profiles were very similar to those determined for Crater Lake (Figure 11). Diurnal fluctuations in dissolved oxygen were not significant during the summer of 1969 (this was true also for Crater, Odell, and Woahink lakes). Carter et al. (1966) measured dissolved oxygen and temperature at a single depth (4 m) at eight widely scattered stations, and at two depths (4 and 60 meters) at a point near Station 9 (Figure 9). Their data compare with those obtained from this study.

Woahink Lake

Woahink Lake is classified as a warm monomictic type by virtue of its single yearly mixing period (occurring in the winter), during which time water temperatures at any depth are never less than 4° C. In addition, the lake is stratified in the summer.

From October to April (1968-69), Woahink Lake was swept continually by strong west-southwesterly winds that commonly reached velocities above 20 to 25 knots. This, in addition to cooler air temperatures, maintained continuous lake circulation during the winter months (i.e., from November to March). By April, with wind action lessening and air temperatures increasing, the lake developed a slight stratification (e.g., on April 14, 1969, temperatures in the water column ranged from 12.3° C at the surface to 9.9° C at 20 m). In June, the thermal profile was clearly indicated (Figure 11).

Earlier, it was mentioned that Woahink Lake exhibited thermal and oxygen curves that were generally parallel (Figures 11, 15). This suggests, perhaps, that the lake is, in fact, eutrophic. In 1968, for example, a hypolimnetic oxygen decrement was noted as early as June 26 (Figure 15). On July 1, 1969, the concentration of dissolved oxygen at 18 m was about 25% less than that measured at the surface to a depth of 12 meters. By September 3, there was a distinct oxygen deficit at 18 m (Figure 11). Ruttner (1952) described a small oligotrophic lake in which the shape of the oxygen profile was determined by the morphometry of the basin and the reducing power of the mud. Oxygen was consumed by reducing substances (generated at the mud-water interface at a rate which increased as the bottom (basin floor) was approached. In profile, the oxygen gradient showed little change as it passed through the thermocline and entered the hypolimnion. But at an indeterminate depth where the slope of the basin "wall" converged with the basin "floor," the oxygen profile responded by angling rather abruptly along a line that paralleled the bottom profile. Ruttner (1952) differentiated between lakes of this nature and eutrophic lakes in which a thermal density barrier, well-established in late summer between the epi- and hypolimnia, prevented oxygen from being circulated into the hypolimnion. There, the quantity of oxygen was gradually depleted. In the vicinity of the thermocline then, the oxygen gradient showed a tendency to parallel, instead, the thermal profile. Although this occurred in Woahink Lake (Figures

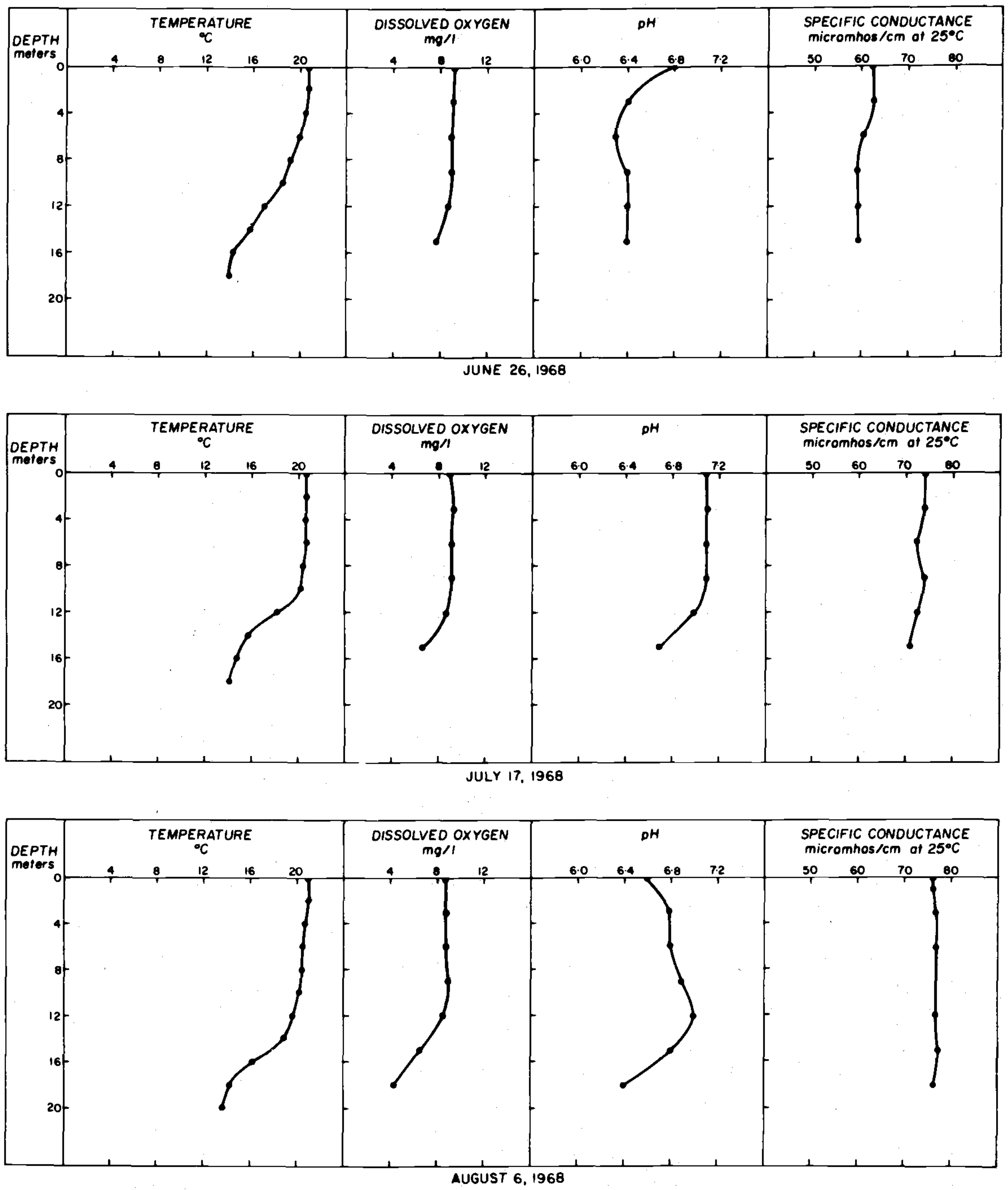


Figure 15. Temperature, oxygen, pH and conductivity profiles in Woahink Lake, Oregon. June-August, 1968. Data collected at Station 3.

11, 15), it is my opinion that the configuration of the oxygen profile resulted from the reducing power of the bottom mud. At a depth between 12 and 15 meters, the concentration of dissolved oxygen diminished rapidly (Figures 11, 15). McGie and Breuser (1962) found this also. The bathymetric chart of Woahink lake (Figure 10) shows the basin "walls" converging with the basin "floor" at a point located between 12 and 15 meters (i. e., between the 40 and 50-foot contours). This relationship between the basin profile and the oxygen gradient (in addition to other limnological features) leads me to believe that Woahink Lake is oligotrophic in the broadest sense of the term.

Light

Some optical properties of the four study lakes are shown in Figure 16. To the left of each row of k values (extinction coefficients) is the depth at which the values were obtained. Percent transmittance of incident radiation is read directly from the curve for any depth. Secchi disc transparency depths are included. Additional information is provided in Tables 2-5. The data presented (i. e., except for Secchi depths) were computed from photometric readings taken between 1200 and 1300 hours on the dates indicated. At Crater and Waldo lakes, light readings were taken under clear skies with no wind. At Odell Lake, the sky was clear but wind velocity varied from 8 to 10 knots. At Woahink Lake, wind velocity was negligible but the sky was

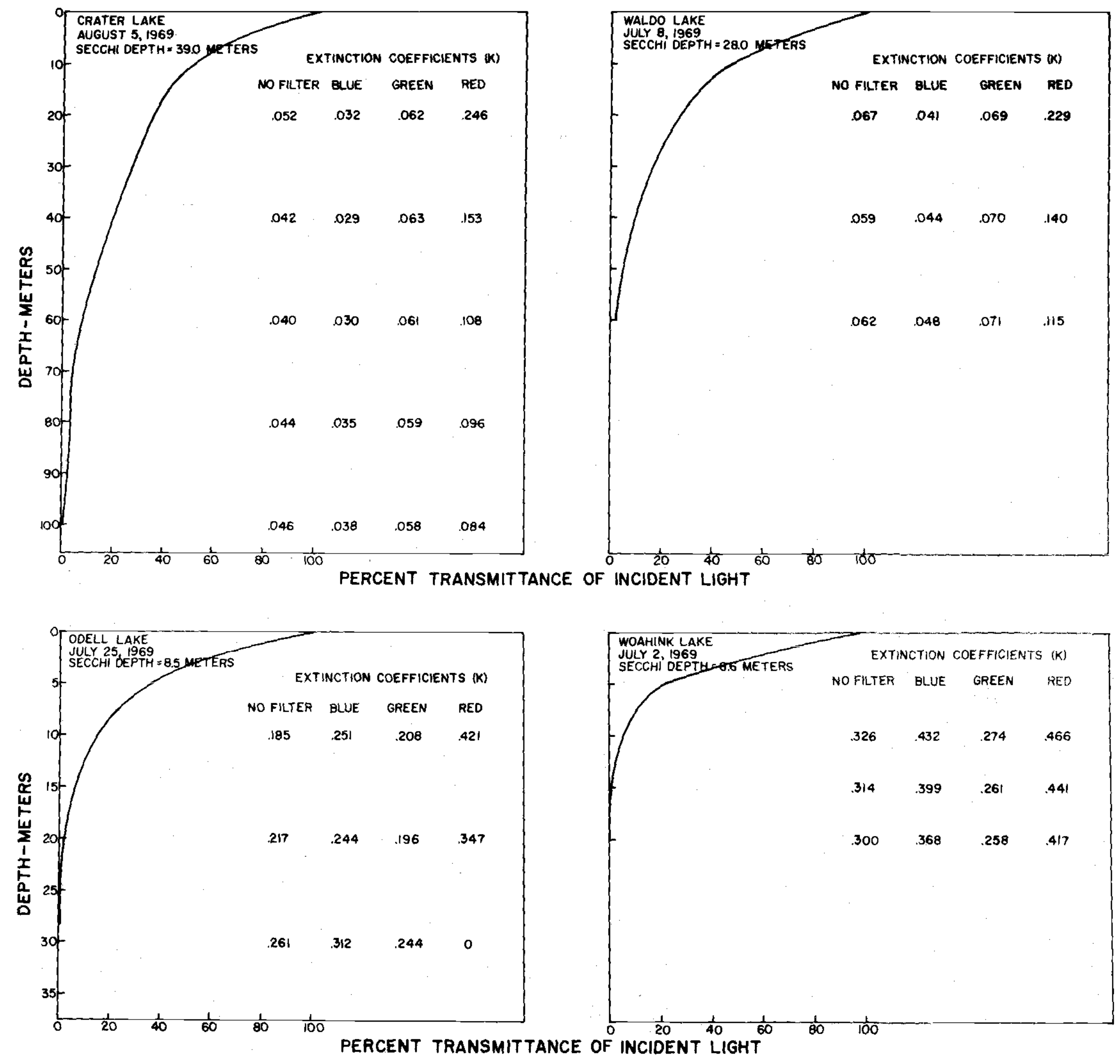


Figure 16. Optical data compared among the study lakes.

Table 2. Spectral data for Crater Lake, Oregon. Measurements taken August 5, 1969.

Depth (m)	No Filter		Blue		Green		Red	
	k*	T**	k	T	k	T	k	T
1	0.133	87.5	0.087	91.6	0.360	69.8	0.355	70.1
5	0.091	63.4	0.056	75.8	0.104	59.4	0.423	12.0
10	0.072	48.8	0.049	61.0	0.073	48.1	0.333	3.6
14	0.063	41.3	0.037	59.8	0.071	37.0	0.295	1.6
20	0.052	35.7	0.032	53.1	0.062	29.1	0.246	0.7
30	0.044	27.0	0.030	40.8	0.068	13.1	0.177	0.5
40	0.042	18.9	0.029	30.7	0.063	8.2	0.153	0.2
50	0.041	13.1	0.030	21.8	0.060	4.9	0.126	0.2
60	0.040	9.0	0.030	16.8	0.061	2.5	0.108	0.2
70	0.045	4.3	0.034	9.4	0.060	1.5	0.096	0
80	0.044	2.9	0.035	6.3	0.059	0.9	0.096	0
90	0.044	1.9	0.036	4.0	0.058	0.5	0.089	0
100	0.046	1.0	0.038	2.3	0.058	0.3	0.084	0

* Extinction coefficient.

** Percent transmittance.

Table 3. Spectral data for Odell Lake, Oregon. Measurements taken July 25, 1969.

Depth (m)	No Filter		Blue		Green		Red	
	k*	T**	k	T	k	T	k	T
1	0.247	78.1	0.205	81.4	0.044	95.7	0.551	57.6
5	0.210	34.9	0.250	28.7	0.167	43.4	0.398	13.7
10	0.185	15.7	0.251	8.2	0.208	12.5	0.421	1.5
14	0.214	5.0	0.243	3.3	0.189	7.0	0.396	0.4
20	0.217	1.3	0.244	0.8	0.196	2.0	0.347	0.2
25	0.248	0.2	0.296	0.1	0.231	0.3	0.349	0.1
30	0.261	0	0.312	0	0.244	0.1		
35	0.263	0			0.251	0		

* Extinction coefficient.

** Percent transmittance.

Table 4. Spectral data for Waldo Lake, Oregon. Measurements taken July 8, 1969.

Depth (m)	No Filter		Blue		Green		Red	
	k*	T**	k	T	k	T	k	T
1	0.165	84.8	.099	90.6	.097	90.7	.371	69.0
5	0.089	64.2	.061	73.6	.084	65.7	.371	15.7
10	0.077	46.5	.042	65.8	.081	44.4	.317	4.2
14	0.071	37.2	.046	52.2	.077	34.2	.296	1.6
20	0.067	26.0	.041	44.4	.069	24.9	.229	1.0
30	0.064	14.8	.043	27.5	.076	10.1	.169	0.6
40	0.059	9.3	.044	17.1	.070	6.0	.140	0.4
50	0.063	4.2	.047	9.6	.072	2.7	.122	0.2
60	0.062	2.5	.048	5.7	.071	1.5	.115	0.1

* Extinction coefficient.

** Percent transmittance

Table 5. Spectral data for Woahink Lake, Oregon. Measurements taken July 2, 1969.

Depth (m)	No Filter		Blue		Green		Red	
	k*	T**	k	T	k	T	k	T
1	0.326	72.2	.464	62.9	.263	76.9	.310	73.4
3	0.387	31.3	.552	19.1	.329	37.2	.664	13.6
5	0.319	20.3	.470	9.5	.279	24.8	.535	6.9
7	0.302	12.1	.439	4.6	.260	16.2	.500	3.0
10	0.326	3.8	.432	1.3	.274	6.5	.466	1.0
14	0.319	1.1	.407	0.3	.264	2.5	.447	0.2
20	0.300	0.2	.368	0.1	.258	0.6	.417	0.1

* Extinction coefficient.

** Percent transmittance

completely overcast.

From the surface to a depth of 10 meters, the red end of the spectrum was absorbed quickly. In all lakes, less than 5% of the red light (i.e., the bandwidth of 500 to 720 mμ) was transmitted below 10 m. Thus, the extinction coefficient for white light (i.e., unfiltered light) in the first two or three meters was proportionately higher than it was at greater depths. In Odell and Woahink lakes, however, little difference was observed among k values for white light, perhaps because the red component was absorbed more evenly throughout the water column.

In the four lakes studied, about 20% of the incident light was available at Secchi depth (Figure 16). Secchi transparency values increased from 39 to 44 meters in Crater Lake (on August 5), and from 28 to 35 meters in Waldo Lake (on July 8) when a larger disc (i.e., 1.0 m in diameter) was used.

Crater Lake

In considering the transmittance of radiant energy in all natural waters, that of Crater Lake is maximal (Smith and Tyler, 1967). The average extinction coefficient of blue light above 50 m in Crater Lake was 0.044. This compares with the average k of blue light above 50 m in clear seawater (Strickland, 1957) (Table 6). Note, however, that the "blue" bandwidth referred to by Strickland is distributed within the spectral range of the blue filter used in this study (i. e., 300 to 500 mμ).

Table 6. Suggested approximate extinction coefficient values (k) for different types of water (Strickland, 1957).

Water Type	Extinction Coefficients (k)		
	Blue (400-480 mμ)	Green (500-580 mμ)	Red (600-700 mμ)
All waters below 100 m.	0.025	0.015	0.15
Clear seawater, upper 50 m.	0.04	0.03	0.15
Moderately turbid inshore waters, upper 25 m.	0.12	0.08	0.2
Very turbid inshore waters, upper 10 m.	0.25	0.2	0.35

The blue segment of light (i. e., the wavelengths between 300 and 550 mμ) was transmitted the farthest in Crater Lake. At a depth of 100 m, 2.3% of the blue light had not been absorbed. The green segment (i. e., 460-660 mμ) was absorbed at a higher rate. The surface intensity of green light was reduced nearly 98% at 60 m. The fate of red light in Crater Lake was dealt with earlier.

At 60 m in Crater Lake, the extinction coefficient for white light was 0.040 (Figure 16). Riley (1956) applied the constant $k = 0.04$ to describe the attenuation of light in pure seawater that contained no chlorophyll a. This attests to the clarity of Crater Lake water.

Tyler (1965), Tyler and Smith (1966, 1967), Smith and Tyler (1967) and Smith (1968) have reported very precise optical data for Crater Lake. Utterback et al. (1942) derived average extinction coefficients at 0.033 in the blue (Schott filter, BG 12) and 0.060 in the green (Wratten filter, W61). Kemmerer et al. (1924) observed a 12 cm (diameter) Secchi disc at depths of 25 m (in August, 1913) and 27 m (in September, 1913). Hasler (1938) reported Secchi disc transparencies of 36, 39, and 40 m in August, 1937. The average Secchi disc transparency for June, July, and August, 1968, was 28.3 m. The mean of three Secchi readings taken during July and August, 1969, was 36.7 m.

Odell Lake

In Odell Lake, green light was transmitted the farthest. This was observed during every spectral measurement in 1968 and 1969. The rate of absorption of blue light was greatly increased over what it had been in Crater Lake. Red light was present to some extent throughout the depth of the photic zone (Table 3). Total illumination was quenched very rapidly. Almost 70% of the incident radiation was absorbed in the first five meters (Figure 16). In Odell Lake, light was transmitted at a rate one could expect for very turbid inshore waters (Table 6).

Secchi disc transparency averaged 5.6 m in 1968 (from seven readings taken during the period June through October), with the lowest value recorded during an algal bloom on July 30 (i. e., 3. 0 m). The mean of six readings taken in 1969 (June through September) was 7. 1 m. Newcomb (1941) reported a Secchi transparency of 12 m at a point near Station 2 on September 27, 1940.

Waldo Lake

Waldo Lake compared very well with Crater Lake in terms of subsurface light distribution (Tables 2, 4, Figure 16). The maximum transmission was in the blue. Green light was quenched more rapidly. About 96% of the red component was absorbed in the first 10 meters. At 10 m, 50% of the incident light was present (Figure 16).

From June through August, 1969, Secchi disc transparency varied between 23 and 28 m. Secchi readings taken at Station 5 on September 30 and on October 3, 1969, were reduced to 19. 5 and 19. 2 meters, respectively. Personnel from the Federal Water Pollution Control Administration (FWPCA) obtained a maximum Secchi disc reading of 32. 5 m during the summer of 1969. Carter et al. (1966) found no difference in turbidity from the surface to 60 m at a point near Station 9. Turbidity was reported to be 1. 2 JTU (Jackson Turbidity Units).

Woahink Lake

The waters of Woahink Lake were moderately stained, caused perhaps by humic materials that were brought in from the watershed. Consequently, blue light was absorbed about as rapidly as red. From 10 to 20 meters, the intensities of blue and red light were essentially equal (Table 5). Green light was least absorbed throughout the water column. Actual maximum transmission was probably in the yellow (i. e., 550 mμ), although, at the time, there was no way of determining this. Welch (1952) referred to lakes of this nature as moderately transparent types. Average extinction coefficients for white and blue light were considerably higher than they had been in the other study lakes.

Transmitted radiation was reduced by 50% in the first three meters. By 5 m, an additional 30% was lost (Figure 16). This rather rapid reduction of surface illumination was another distinguishing feature of Woahink Lake (Figure 16).

Secchi readings, taken almost every month throughout the 15-month sampling period, were found to be quite similar. The lowest reading (4.0 m) was recorded on October 14, 1968. The highest reading (7.3 m) followed in November. The reason for this is not known. The average Secchi disc transparency for the period June, 1968, to September, 1969, was 6.1 m. McGie and Breuser (1962) reported a Secchi depth of 3.6 m taken on August 16, 1960 near Station 3.

Chemistry

The chemical features of the four study lakes are compared in Figure 17. The data presented here are for 1969. pH and conductivity data, collected in 1968, are shown in vertical profile (Figures 12-15). Chemical determinations for both years, in addition to results published by other workers, are combined in Table 7.

Crater Lake

The water chemistry of Crater Lake was described by Van Winkle and Finkbiner (1913), Clarke (1924a), Robinson (1941), Utterback *et al*. (1942), Nelson (1961, 1967) and Phillips and Van Denburgh (1968). Their data are comparable with that resulting from this study.

Little or no variation in water chemistry was noted among the samples collected from several depths. Phillips and Van Denburgh (1968) found little difference between samples collected at the surface and at various depths, and between samples collected from widely scattered stations.

Among the lakes studied, Crater Lake exhibited the highest concentration of total dissolved solids--part of which included Na, K, Ca,

CHEMICAL FEATURES

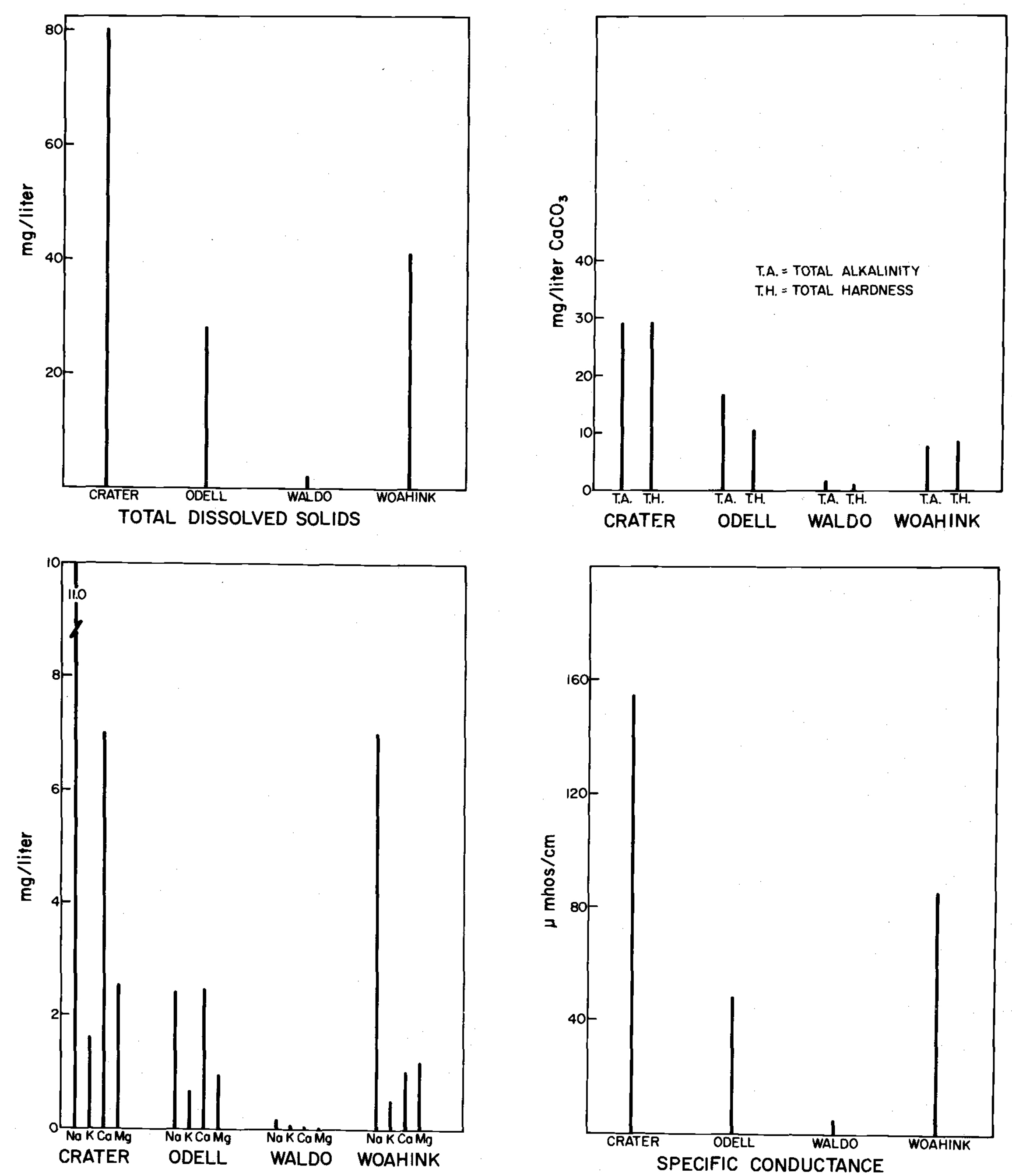


Figure 17. Chemical features compared among the study lakes.

Table 7. Chemical features

	Crater			Odell		Waldo		Woahink	
	1964*	1968	1969	1968	1969	1966**	1969	1968	1969
pH	7.4	7.2	7.3	8.5	7.9	6.1	6.6	7.1	7.2
Specific cond. (μ mhos/cm)	117	123	154	46	48	7	5	80	85
Total dissolved solids (mg/l)	75	82	79	25	28	5	2	44	41
Total alkalinity (mg/l $CaCO_3$)		28.3	29.1	16.8	16.5	0.2	1.5	8.2	7.7
Total hardness (mg/l $CaCO_3$)	28.0	27.7	28.9	11.1	10.6	3.0	1.2	8.9	8.5
Sodium (mg/l)	11.0				2.39		0.16		7.04
Potassium (mg/l)	1.6				0.62		< 0.1		0.51
Calcium (mg/l)	7.0				2.46		0.09		0.97
Magnesium (mg/l)	2.5				0.85		0.04		1.18
Sulfate (mg/l)	10.0								
Chloride (mg/l)	9.5								
Zinc (ppb)					3.93		3.97		5.33
Ammonia-N (mg/l)						< 0.01			
Nitrate-N (mg/l)	0					0.11			
Phosphate-P (mg/l)						< 0.01			
Silica (mg/l)	16.0								
Turbidity (Jackson unit)	0					1.2			

* Phillips and Van Denburgh (1968). Water samples collected 6.9 km north 47° E. of Crater Lake lodge at a depth of 0.3 m on August 5, 1964.

** Carter, et al. (1966). Water samples collected at Station 9 at a depth of 3.6 m on July 27, 1966.

and Mg. It followed that alkalinity (as $CaCO_3$), hardness (comprising Ca and Mg) and specific conductivity would also be higher (Figure 17, Table 7). The major sources of dissolved inorganic ions in Crater Lake (including SO_4, SiO_2, Cl and $CO_3^{=}$) were discussed earlier.

During the study, no attempt was made to analyze water samples for inorganic nitrogen, phosphorus or silica--all of which are basic algal nutrients. Several investigators have done so at Crater Lake. Van Winkle and Finkbiner (1913) reported concentrations of 0.38 and 0.01 mg/liter for nitrate and phosphate, respectively. Clarke (1924a) reported an identical concentration for phosphate (i.e., 0.01 mg/l), but a higher amount of nitrate (i.e., 0.47 mg/l). In addition, he found silica to be 22.5 mg/l. Lipman (1940) presented values of 0.01 and 0.037 mg/l for nitrate and phosphate, respectively. Robinson (1941) and Utterback et al. (1942) found what they considered to be high concentrations of soluble phosphorus (i.e., 0.014 mg/l) and silica (i.e., 8.5 mg/l) at several depths extending to 425 m. They concluded that both elements were extracted from volcanic rock at a rate which accounted for their relative abundance. More recent analyses by Edmondson (1953) showed Crater Lake water to contain 0.358 mg/l of total nitrogen and 0.105 mg/l of total phosphorus. Van Denburgh (1961) reported silica and nitrate to be 18.0 and 0.38 mg/l, respectively.

The above reports suggest that at least three essential nutrients (i.e., soluble nitrate, phosphorus, and silica) were not deficient in Crater Lake. Sawyer (1947, 1952, 1954) found that algal blooms occurred in Wisconsin lakes when nitrogen and phosphorus reached concentrations of 0.30 and 0.01 mg/l, respectively. Müller (1953) stated that excessive growths of algae could be expected when the level of nitrate exceeded 0.3 mg/l. Minimal phytoplankton production could be sustained in seawater when concentrations of phosphate and nitrate were 0.017 and 0.12 mg/l, respectively (Curl and Small, 1968).

Phillips and Van Denburgh (1968) estimated that Crater Lake received anywhere from 90,000 to 100,000 acre-feet (i.e., 29×10^9 to 32×10^9 gallons) of precipitation annually. Precipitation in non-industrial areas contained approximately 0.64 mg/l NH_3, 0.196 mg/l NO_3, 0.03 mg/l total P, 0.1 to 10 mg/l Ca, 0.5 mg/l Cl, 2.0 mg/l SO_4, and 0.1 mg/l Mg (Hutchinson, 1957). Thus, precipitation was probably an important source of nitrogen and phosphorus as well as other essential ions in Crater Lake. Since most of the water loss in Crater Lake was through evaporation, it stands to reason that these nutrients would become more concentrated than in lakes where the major loss would be through outflowing tributaries.

Odell Lake

Newcomb (1941) reported very little information about the chemistry of Odell Lake. His values for pH ranged from 7.2 at the surface to 6.9 at 55 m. Methyl orange alkalinity (bicarbonate) averaged 27.0 mg/l for the same water column. Phenolphthalein alkalinity (carbonate) did not exist.

In 1968, mid-summer and early fall algal blooms had a marked effect on pH and alkalinity (Figure 13). During a dense bloom in July, 1968, the pH soared to 9.5 in the upper portion of the photic zone due to the removal of free CO_2 and HCO_3^- by phytoplankton. An increase in $CO_3^=$ was indicated by phenolphthalein alkalinity titration. During August and September, pH at a depth of 4 m never fell below 9.0. Phenolpthalein alkalinity was determined as late as October 18, 1968. In 1969, algal blooms were less pronounced; consequently, pH values never exceeded 8.9. Phenolphthalein alkalinity was never more than 1.3 mg/l as $CaCO_3$ (which contrasted with 1968 when values ranged from 4.5 to 3.7 mg/l as $CaCO_3$).

Values for specific conductance and total dissolved solids in Odell Lake were third highest among the study lakes. Odell was second only to Crater Lake, however, in total alkalinity and total hardness (Figure 17, Table 7). The concentrations of K and Ca in Odell Lake exceeded those present in either Waldo or Woahink.

No historical information was available concerning phosphorus and nitrogen in Odell Lake. Apparently, human activities was a major source of these as well as other essential nutrients in the Odell Lake basin. A discussion concerning the use and the pollution of Odell Lake will follow.

Waldo Lake

Waldo Lake featured an unusual water chemistry (Figure 17, Table 7). The values from the 1969 study (Table 7) represent surface water. However, samples were collected and analyzed from depths of 6, 12, 24, 30, and 40 meters. Surface and deeper samples exhibited near-identical chemical characteristics. Carter et al. (1966), in comparing samples collected at 4 and 60 meters, found little or no difference in water chemistry. In 1968, specific conductance was higher below 15 m. This may have been related to the thermocline which occurred also at that depth.

An extreme paucity of buffering compounds existed in Waldo Lake as shown in the values for total alkalinity and hardness (Figure 17, Table 7). pH ranged from 6.0 to 6.6 (Figure 14, Table 7). pH values below 6.0 were recorded consistently by the FWPCA in 1969 (J. Tilstra, personal comm.). The cations Na, K, Ca, and Mg were present in trace amounts (Figure 17, Table 7). The values for specific conductance and total dissolved solids were perhaps the lowest ever recorded for natural waters. Phosphorus and nitrate were found to be generally less than 0.002 and 0.1 mg/l, respectively (FWPCA, 1969). Carter et al. (1966) found the concentration of NO_3^- to be slightly higher (Table 7).

In general, the quality of Waldo Lake water was very similar to that of distilled water. A comparison between rainwater (J. Wagner, personal comm.) and water from Waldo Lake showed the latter to contain the lowest concentrations of every major element compared.

Woahink Lake

Values for specific conductance and total dissolved solids in Woahink Lake were second highest among the study lakes (Figure 17, Table 7). A comparatively high concentration of Na, which enhanced values for conductivity and TDS, was noted (Figure 17). Nearly 20% of the total dissolved solids consisted of Na. The mean percentage of Na in North American inland waters is 7.46 (Clarke, 1924b). Because Woahink Lake is located less than 5 km inland from the Pacific Ocean, it is possible that sea spray and sand particles, carried aloft by wind, were deposited in the lake. The concentration of Na in seawater is about 10,000 mg/l (Hem, 1959).

The basin soils, composed entirely of sand and sandy loam, generally accounted for the low alkalinity and hardness of the water (Griffith and Yeoman, 1938; McGie and Breuser, 1962). This may have been an important factor in limiting production in the lake.

During the period of thermal stratification in 1968 and 1969, the pH was observed to decrease gradually below the thermocline

(Figure 15). Under reducing conditions at the mud-water interface (during summer stratification), the concentrations of dissolved oxygen and carbon dioxide are inversely related. The consumption of oxygen near the bottom is associated with an increase in CO_2 which lowers the pH effectively (Mortimer, 1942).

LIMNETIC PLANKTON AND PRODUCTIVITY

Biological productivity in a lake environment begins with the phytoplankton. These are the primary producers, the productivities of which are controlled by temperature, light, and nutrients. The trophy of a lake is determined at this first trophic level, then, by the response of the phytoplankton to its environment.

The fact that the four study lakes are classified as oligotrophic has been discussed. That the lakes have been so grouped suggests that the annual rates of phytoplankton production would not be expected to differ appreciably. A significant difference in their trophy would imply a lack of sensitivity in the trophic scheme of classification.

Algal blooms have been known to occur infrequently, during the summer months, in oligotrophic lakes (Welch, 1952; Prowse, 1955). Taken over the entire year, however, the rates of phytoplankton production among oligotrophic lakes are expected to be comparable (Prowse, 1955).

The Composition of the Plankton

Crater Lake

Several of the Crater Lake studies have dealt with the plankton. Kemmerer *et al*. (1924) identified the zooplankton (including the rotifers) as Daphnia pulex, Bosmina longispina, Notholca longispina, Anuraea aculeata and Asplanchna sp. These were concentrated at depths between 60 and 80 m in August (1913), and between 50 and 60 m in September (1913). Zooplankton were not observed at depths above 30 m. The filamentous green algae Mougeotia sp. was most abundant at depths of 60 to 80 m in August, and 100 to 150 m in September. The only diatom to be found, Asterionella sp., was distributed, generally, from 100 to 200 m. Recently, Sovereign (1958) has shown the diatoms to be more diverse.

Brode (1935) found Daphnia pulex, Nostoc sp. (a blue-green algae) and Zygonema sp. (a green, filamentous algae) in the stomachs of fish collected in Crater Lake. Daphnia pulex made up 35% of the total. Later, Brode (1938) identified several species of algae in Crater Lake including Mougeotia sp., Nostoc sp., Asterionella sp., Calothrix sp., Spirogyra sp., Oscillatoria sp., Chrococcus sp., Zygnema sp., Ulothrix aequalis, and Cladophora keutzingianum. Also, he listed four crustaceans (Daphnia pulex, Bosmina longispina, Hyalella azteca and Astacus nigrescens) and two rotifers (Notholca longispina and Anuraea aculeata).

Hasler (1938) and Hasler and Farner (1942) examined stomachs of fish taken from Crater Lake and found Daphnia sp. and Hyalella sp. to be a major part of the diet. In addition, they collected benthic mosses, Fontinalis sp. and Drepanocladus sp., from a depth of 120 m.

Utterback et al. (1942) found that most of the phytoplankton in Crater Lake consisted of the blue-green, Anabaena sp. Also collected were Mougeotia sp., Asterionella sp., Synedra sp., and Nitzschia sp. About 90 to 95% of the algae occurred between depths of 70 and 150 meters with the first 20 meters being devoid of any viable cells.

Recent studies by Hoffman and Donaldson (1968) and Hoffman (1968) have centered on the dynamics of zooplankton populations in Crater Lake, particularly the distribution and vertical migration of two species, Daphnia pulex and Bosmina longispina.

The data in Table 8 represent hauls taken in 1968 and 1969. Algae collected in August, 1969 were identified to genera (Table 9). Chlorophyll a concentrations ranged from 8.385 to 59.950 mg/m^2 (Table 10).

Table 8. Numbers of zooplankton collected in 100 m vertical tows at Crater Lake, Oregon (Malick, unpublished data.)*

Date	Daphnia longispina/m^3	Bosmina longispina/m^3	Total no. /m^3
15 June 68	76.5	147.4	253.9
4 July 68	55.9	171.6	227.5
25 July 68	14.7	95.1	109.8
8 Aug 68	130.7	233.6	364.3
28 Aug 68	624.6	566.6	1,191.2
17 July 69	255.8	3.7	259.5
31 Aug 69	572.1	3.0	575.1

*Sampling site approximately 1.6 km south-southeast of indicated station location (Figure 7). Both adults and juveniles are represented. Vertical tows taken with a no. 20 mesh net (intake diameter equaled 0.5 m).

Table 9. Some representative phytoplankton genera collected during 1969. Identifications courtesy of Dr. H. K. Phinney, Department of Botany, Oregon State University.

	Genera			
Lake and Date	Chlorophyta	Cyanophyta	Chrysophyta	Mastigophora (flagellates)
Crater, 31 Aug.	Spirogyra Staurastrum		Asterionella Synedra Fragilaria Coscinodiscus Gomphonema Epithema Melosira Stipitococcus	Ceratium Dinobryon
Odell, 24 Sept.	Planktosphaeria Oedogonium Staurastrum		Asterionella Synedra Fragilaria Coscinodiscus Melosira Cyclotella Stephanodiscus Suriella Cocconeis	Ceratium Eudorina Colacium
Woahink, 5 Aug.	Planktosphaeria Staurastrum	Gomphosphaeria Anacystis Merismopedia	Synedra Fragilaria	Volvox
Waldo, 6 Aug.		Stigonema Scytonema		
Waldo, 30 Sept.	Oedogonium Mougeotia Planktosphaeria Hyalotheca Pleurotaenium	Anacystis Tolypothrix Nostoc** Stigonema	Synedra Fragilaria	
Waldo, 24 July	Oedogonium Microspora Spirogyra* Staurastrum		Synedra Suriella	

* Sample composed almost entirely of this genus.

** One species identified as Nostoc microscopicum.

Table 10. Detectable concentrations of chlorophyll a in milligrams per meter square for Crater Lake, Oregon (July 16 to August 31, 1969). Samples for chlorophyll analyses were obtained from depths of 0, 20, 40, 70, 110, and 200 meters.

Date	mg chlorophyll a/m^2	mg chlorophyll a/m^3 (average)
16 July	59.950	0.300
5 August	35.000	0.175
31 August	8.385	0.044

Odell Lake

The average volume of plankton collected in Odell Lake in September, 1940, was 1.8 mg/m^3 of water (Newcomb, 1941). Thereafter, the production of plankton increased considerably. In 1968 and 1969, the September hauls yielded 15 to 25 mg of plankton/m^3 (very rough estimates by the author).

Newcomb (1941) was perhaps the first investigator to identify the plankton in Odell Lake. The zooplankton included *Epischura sp.*, *Diaptomus sp.*, *Bosmina sp.* and *Holopedium sp.* He identified the phytoplankton as *Asterionella sp.*, *Anabaena sp.*, *Spirogyra sp.*, and *Staurastrum sp.* The results of another study (Malick, unpublished data) are presented in Table 11.

Algae collected in September, 1969, were identified to genera (Table 9). Concentrations of chlorophyll a (Table 12) ranged from 52.716 to 150.741 mg/m^2.

Table 11. Numbers of zooplankton collected in vertical tows at Odell Lake, Oregon (Malick, unpublished data).*

Date	Tow Depth (m)	*Daphnia longispina*/m^3	*Cyclops bicuspidatus*/m^3	Total no./m^3
17 June 68	30	286.0	6,264.4	6,550.4
9 July 68	30	2,886.3	1,978.3	4.864.6
30 July 68	30	36,598.3	2,899.1	39,497.4
13 Aug 68	30	56,274.5	6,617.6	62,892.1
6 Sept 68	28	11,960.7	11,352.9	129,313.6
25 Sept 68	28	38,051.4	132,702.2	170,753.6
19 Oct 68	30	7,795.0	81,198.1	88,993.1
10 July 69	30	1,638.6	31,974.7	33,613.3
24 July 69	30	9,130.4	10,409.2	19,539.6
8 Aug 69	30	21,512.0	5,938.9	27,450.9

*Sampling site located at Station 1 (Figure 8). Both juveniles and adults are represented. Vertical tows taken with a no. 6 mesh net (intake diameter equaled 0.5 m).

Table 12. Detectable concentrations of chlorophyll a in milligrams per meter square for Odell Lake, Oregon (June 19 - September 24, 1969). Samples for chlorophyll analyses were obtained from depths of 0, 2, 4, 6, 12, and 30 meters.

Date	mg chlorophyll a/m^2	mg chlorophyll a/m^3 (average)
19 June	52.716	1.757
10 July	59.641	1.988
25 July	78.608	2.621
7 August	150.741	5.025
29 August	107.130	3.571
24 September	142.977	4.766

Waldo Lake

The plankton in Waldo Lake was indeed sparse. Carter et al. (1966) towed plankton nets horizontally through the surface waters for several minutes both during the day and at night collecting only a "few" diatoms. Throughout the summer of 1969, 60 to 80 meter vertical tows with no. 6 mesh nets (intake diameter equaled 0.5 m), yielded no more than 13 zooplankters per haul (Table 13). Chlorophyll a concentrations were similarly low, ranging from 0.263 to 9.436 mg/m^2 (Table 14). Algae collected during three sampling dates (July 24, August 6, and September 30, 1969) were identified to genera (Table 9).

The benthic community in Waldo Lake was described by Carter et al. (1966). It consisted primarily of aquatic mosses including

Table 13. Numbers of zooplankton collected periodically at Station 9, Waldo Lake, Oregon.

Date	Tow Depth (m)	No./Tow *Daphnia* Sp.	*Cyclops* Sp.	*Polyphemus* Sp.	*Diaptomus* Sp.	Total	Total No./m^3
8 July 69	60	3	2			5	0.55
8 July 69	60		2			2	0.24
24 July 69	70		2			2	0.26
24 July 69	80		1			1	0.13
24 July 69	78		1		1	2	0.19
24 July 69	70	2			1	3	0.27
6 Aug 69	60	9	3	1		13	1.40
6 Aug 69	60	6			2	8	0.97

Sphagnum sp. in the littoral zone (seldom occurring at depths greater than 2 m) and Drepanocladus sp. in deeper water. The latter form was collected at depths of 70 to 75 meters. Associated with the deep-water mosses were at least two species of diatoms (Cymbella ventricosa Kuetz and Tabellaria flocculosa Kuetz) and several desmids (Staurastrum sp., Cosmarium sp., Netrium sp. and Micrasterias sp.). Diatoms and a blue-green algae (Anabaena sp.) commonly occurred in the Sphagnum clumps.

Table 14. Detectable concentrations of chlorophyll a in milligrams per meter square for Waldo Lake, Oregon (June 20 - October 3, 1969). Samples for chlorophyll analyses were obtained from depths of 0, 6, 12, 24, 30, and 40 meters.

Date	mg chlorophyll a/m^2	mg chlorophyll a/m^3 (average)
20 June	0.263	.0066
7 July	2.870	.0718
23 July	4.439	.1109
6 August	2.932	.0733
28 August	8.477	.2119
30 September*	9.436	.2359
3 October*	8.518	.2129

*Samples collected at Station 5. All others are from Station 9.

Carter et al. concluded in their 1966 report that the benthos, particularly the mosses, was contributing most to the primary productivity of Waldo Lake. They surmised that the few algal cells (mostly diatoms) collected in the limnetic zone had not originated as plankton but as benthic forms washed into the open water.

Stomachs of fish collected in Waldo Lake on October 1, 1969 were examined. The major food item for all species (i.e., *Salvelinus fontinalis*, *Salmo gairdneri*, and *Oncorhynchus nerka kennerlyi*) appeared to be chironomid larvae. Traces of plankton, too digested to be counted or identified, were found.

Woahink Lake

The zooplankton in Woahink Lake was studied intensively in 1968 and 1969 (Table 15, Malick, unpublished data).

Cladocerans were the most important source of food for Kokanee salmon, *Oncorhynchus nerka kennerlyi* in Woahink Lake (McGie and Breuser, 1962). Opossum shrimps (Mysidacea), mayflies (Ephemeroptera) and crane flies (Tipulidae) were included in the diet.

The benthos of Woahink Lake was relatively unproductive. Ekman dredge samples taken throughout the basin yielded very few organisms (McGie and Breuser, 1962).

In Table 9, some of the algae that occurred in Woahink Lake are identified. Cyanophyta appeared to be more common than in the other study lakes. Concentrations of chlorophyll *a* (Table 16) were reasonably uniform from July to September, 1969.

Table 15. Numbers of zooplankton collected in vertical tows at Woahink Lake, Oregon (Malick, unpublished data).*

	Tow Depth (m)	*Daphnia longispina*/m^3	*Cyclops bicuspidatus*/m^3	*Diaphanosoma brachyurum*/m^3	*Diaptomus franciscanus*/m^3	*Epischura nevadensis*/m^3	Total no./m^3
17 July 68	16		105.7	280.8	943.4	84.2	1,414.1
6 Aug 68	17		39.2	2,150.9	1,541.1	21.5	3,752.7
3 Sept. 68	17.5	72.5	569.6	27.9	5,020.4	117.2	5,807.6
19 Sept 68	15	860.2	1,014.7	114.7	1,305.8	30.8.	3,326.2
14 Oct 68	17	3,492.6	765.9	2,015.9	747.5	18.3	7,042.2
13 Nov 68	16	255.2	253.2	205.2	165.4	68.4	947.4
9 Dec 68	16	113.3	36.5	50.1	41.2	424.0	665.1
23 Feb 69	16	16.6		0.8	731.5	73.9	822.8
13 Apr 69	16	46.0		9.8	3,007.0	15.9	3,743.8
25 May 69	16	93.0	42.5	152.7	1,630.4	13.2	1,931.8
13 June 69	16	287.7	37.0	758.3	2,721.6	145.8	3,950.4
1 July 69	16	443.3	3.3	5,058.2	1,411.6	44.9	6,961.3
1 Aug 69	16	602.5	516.5	95.4	613.9	42.4	1,870.8

* Sampling site located at Station 3 (Figure 10). Both juveniles and adults are represented. Vertical tows taken with a no. 6 mesh net (intake diameter equaled 0.5 m).

Table 16. Detectable concentrations of chlorophyll a in milligrams per meter square for Woahink Lake, Oregon (June 13 - September 28, 1969). Samples for chlorophyll analyses were obtained from depths of 0, 2, 4, 8, 12, and 18 meters.

Date	mg chlorophyll a/m^2	mg chlorophyll a/m^3 (average)
13 June	11.870	0.659
2 July	24.476	1.360
2 August	24.839	1.380
3 September	29.783	1.655
28 September	25.062	1.392

Limnetic Phytoplankton Productivity Estimates

The net productivity of the phytoplankton was estimated periodically for each of the four study lakes. Measurements of carbon fixed per incubation period were converted to approximate daily values. This was done by dividing the 4-hr *in situ* production measurement by an appropriate energy fraction (Function F; Vollenweider, 1965). An energy fraction was that portion of the total daily radiation which was incident during the incubation period (Platt and Irwin, 1968). The results that are presented in Tables 18-21 are based on the energy fractions computed and modified from Vollenwider (1965) by Platt and Irwin (1968). When bimonthly sampling occurred, a monthly average was derived from the two measurements.

Net phytoplankton productivities (in mgC/m^2/hr) among the four study lakes for 1968 and 1969 are compared in Figure 18. The values

Table 17. Rate of phytoplankton photosynthesis per unit of chlorophyll a at the depth of maximum productivity (assimilation number).

Lake	Date	Assimilation Number (mg C hr^{-1} per mg chlorophyll a)
CRATER	16 July 69	1.50
	5 Aug 69	4.20
	31 Aug 69	3.50
		$\bar{x}$ = 3.07
ODELL	10 July 69	2.34
	25 July 69	7.60
	7 Aug 69	5.10
	29 Aug 69	3.10
	24 Sept 69	3.20
		$\bar{x}$ = 4.27
WOAHINK	2 July 69	2.10
	2 Aug 69	3.10
	3 Sept 69	4.30
	28 Sept 69	4.90
		$\bar{x}$ = 3.80
WALDO	8 July 69	0.89
	23 July 69	1.05
	6 Aug 69	1.47
	28 Aug 69	1.58
	3 Oct 69	2.30
		$\bar{x}$ = 1.46

Table 18. Phytoplankton primary productivity for Crater Lake, Oregon. Total production for the periods June 14 to August 27, 1968, and July 16 to August 31, 1969 estimated to be 19.0 gC/m^2 and 11.9 gC/m^2, respectively.

Date	$mgC/m^2/hr$	Energy Fraction (F)*	$mgC/m^2/day$ (approximated)
14 June 68	27.280	0.37	294.92
23 July 68	19.659	0.38	206.94
27 Aug 68	28.052	0.40	280.52
16 July 69	21.413	0.38	225.40
5 Aug 69	20.683	0.40	206.83
31 Aug 69	32.718	0.40	327.18

*Modified after Vollenweider (1965) by Platt and Irwin (1968).

Table 19. Phytoplankton primary productivity for Odell Lake, Oregon. Total production for the periods June 18 to October 19, 1968, and June 19 to September 24, 1969 estimated to be 231.3 gC/m^2 and 118.1 gC/m^2, respectively.

Date	$mgC/m^2/hr$	Energy Fraction (F)*	$mgC/m^2/day$ (approximated)
18 June 68	31.928	0.37	345.17
9 July 68	170.771	0.38	1797.59
31 July 68	396.772	0.38	4176.55
13 Aug 68	206.103	0.40	2061.03
6 Sept 68	196.496	0.50	1571.97
25 Sept 68	195.151	0.50	1561.21
19 Oct 68	165.444	0.54	1225.51
19 June 69	10.354	0.37	111.74
10 July 69	56.779	0.38	597.67
25 July 69	149.889	0.38	1577.78
7 Aug 69	223.027	0.40	2230.27
29 Aug 69	172.709	0.40	1727.09
24 Sept 69	112.696	0.50	901.57

*Modified after Vollenweider (1965) by Platt and Irwin (1968).

Table 20. Phytoplankton primary productivity for Waldo Lake, Oregon. Total production for the period June 21 to October 3, 1969 estimated to be 4.225 gC/m^2.

Date	$mgC/m^2/hr$	Energy Fraction (F)*	$mgC/m^2/day$ (approximated)
21 June 69	0.107	0.37	1.16
8 July 69	2.185	0.38	23.00
23 July 69	2.264	0.38	23.83
6 Aug 69	4.474	0.40	44.74
28 Aug 69	5.050	0.40	50.40
3 Oct 69	9.880	0.54	73.19

*Modified after Vollenweider (1965) by Platt and Irwin (1968).

Table 21. Phytoplankton primary productivity for Woahink Lake, Oregon. Total production for the periods June 27 to December 9, 1968, and February 2 to September 28, 1969 estimated to be 28.3 gC/m^2 and 35.4 gC/m^2, respectively.

Date	$mgC/m^2/hr$	Energy Fraction (F)*	$mgC/m^2/day$ (approximated)
27 June 68	37.051	0.37	400.55
18 July 68	23.136	0.38	243.54
7 Aug 68	27.031	0.40	270.31
4 Sept 68	22.326	0.50	198.61
19 Sept 68	26.434	0.50	211.47
15 Oct 68	8.218	0.54	60.87
12 Nov 68	13.134	0.60	87.56
9 Dec 68	1.984	0.72	11.02
24 Feb 69	3.949	0.64	24.68
14 Apr 69	5.889	0.46	51.21
10 May 69	16.579	0.42	157.89
26 May 69	12.525	0.42	119.29
13 June 69	2.501	0.37	27.04
2 July 69	22.443	0.38	236.24
2 Aug 69	36.708	0.40	367.08
3 Sept 69	42.550	0.50	340.40
28 Sept 69	45.959	0.50	367.67

*Modified after Vollenweider (1965) by Platt and Irwin (1968).

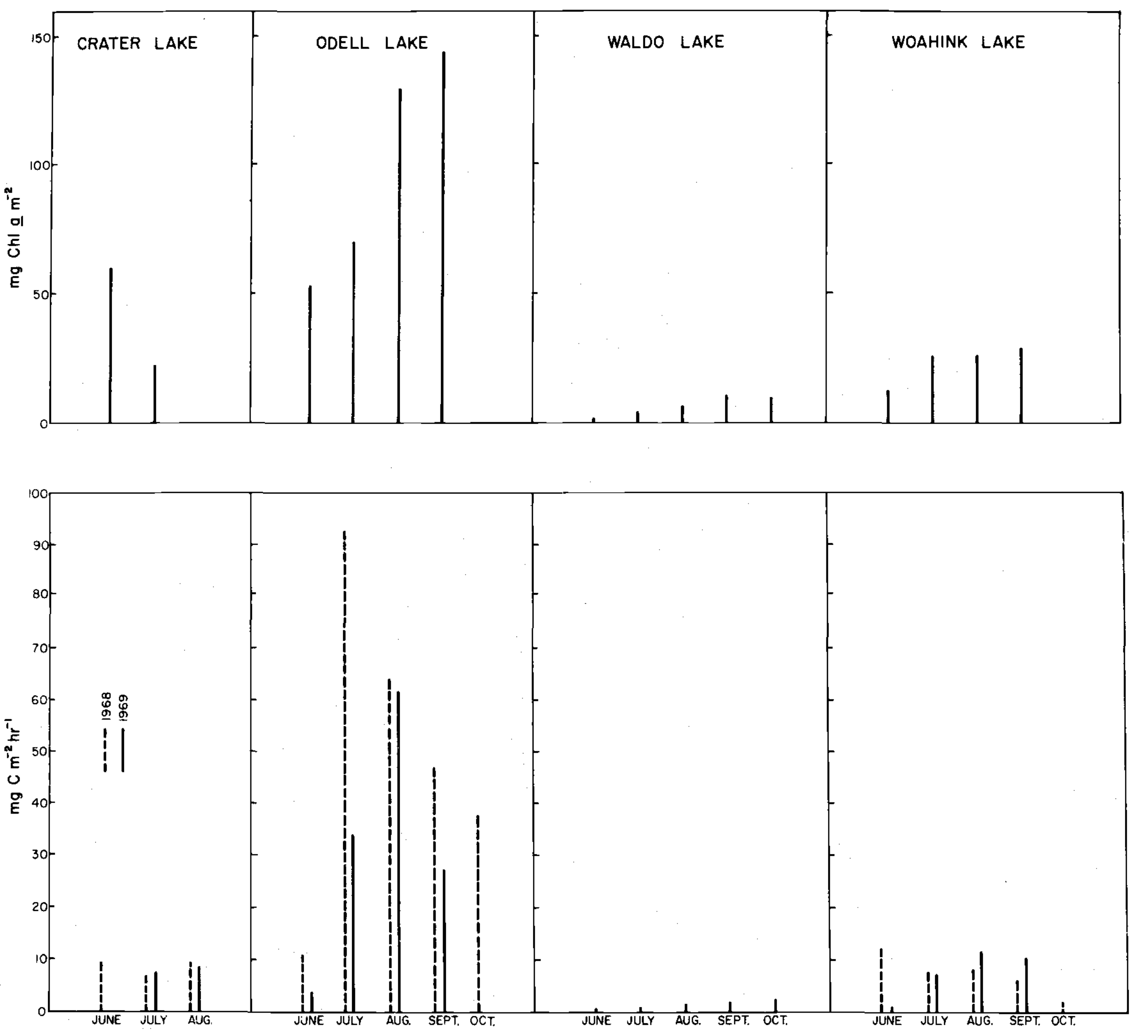


Figure 18. The monthly average rates of production (lower panel) and concentrations of chlorophyll a per meter squared. Chlorophyll data taken only in 1969.

for 1969 are related to concentrations of chlorophyll a per square meter (Figure 18). Assimilation numbers for the four lakes are summarized in Table 17. The values represent the amount of carbon that is synthesized by phytoplankton per hour per mg of chlorophyll a. The number may be related to nutrient availability (Curl and Small, 1965; Fogg, 1966). That is, the low availability of nutrients would be reflected by low assimilation numbers. At sea, in a region of nutrient enrichment caused by upwelling, the average assimilation number was found to be 13. Conversely, in an area where upwelling did not occur (i.e., a region where nutrients were perhaps less available), the mean was reduced to about 6 (Small, et al. in press). An average assimilation number of 3 has been determined for natural lake populations (Gessner, 1949). Other values obtained for lake populations were 2 (Manning and Juday, 1941) and 4 to 6 (Gessner, 1943). Assimilation numbers in eutrophic environments may exceed those under oligotrophic conditions by a factor of 4 or more (Ichimura, 1958).

Crater Lake

Net productivity for Crater Lake--often regarded as being extremely low in biological production (Nelson, 1967)--averaged 6.70 g C/m^2/month (June - August, 1968) and 6.61 g C/m^2/month (July - August, 1969). Estimates of net phytoplankton productivity for

75 days from June 14 to August 27, 1968 and 47 days from July 16 to August 31, 1969 are presented in Table 18.

Rates of photosynthesis per cubic meter are shown in vertical profiles (Figure 19). The zone of maximum production was usually between depths of 70 and 100 meters. For no apparent reason, total production throughout the water column on July 23, 1968 was relatively low. At that time, production was rather uniform throughout the water column. The zone of maximum production increased on August 27, 1968. Severe storms which occurred before and after that time probably mixed the water column and distributed the phytoplankton more evenly. This resulted in a lower Secchi reading than usual (i. e., 18 m).

Again in 1969 production was maximal between 70 and 100 m (Figure 19). During both sampling periods in August, a pulse in production occurred in the first 10 m. Here, one would expect strong illumination to reduce photosynthesis; however, the algal cells that occupied this region were obviously well acclimated to high light intensity. Higher temperatures in the first 20 m may have compensated for the photoinhibitory effects. The thermal gradient on both dates ranged from about 16° C at the surface to 7 or 8° C at 20 m (Figure 11). Chlorophyll a was not detected in water samples collected at depths of 0 and 20 m on July 16 and August 31, 1969. On August 5, the concentrations of chlorophyll a at these depths stood at 0. 086 and

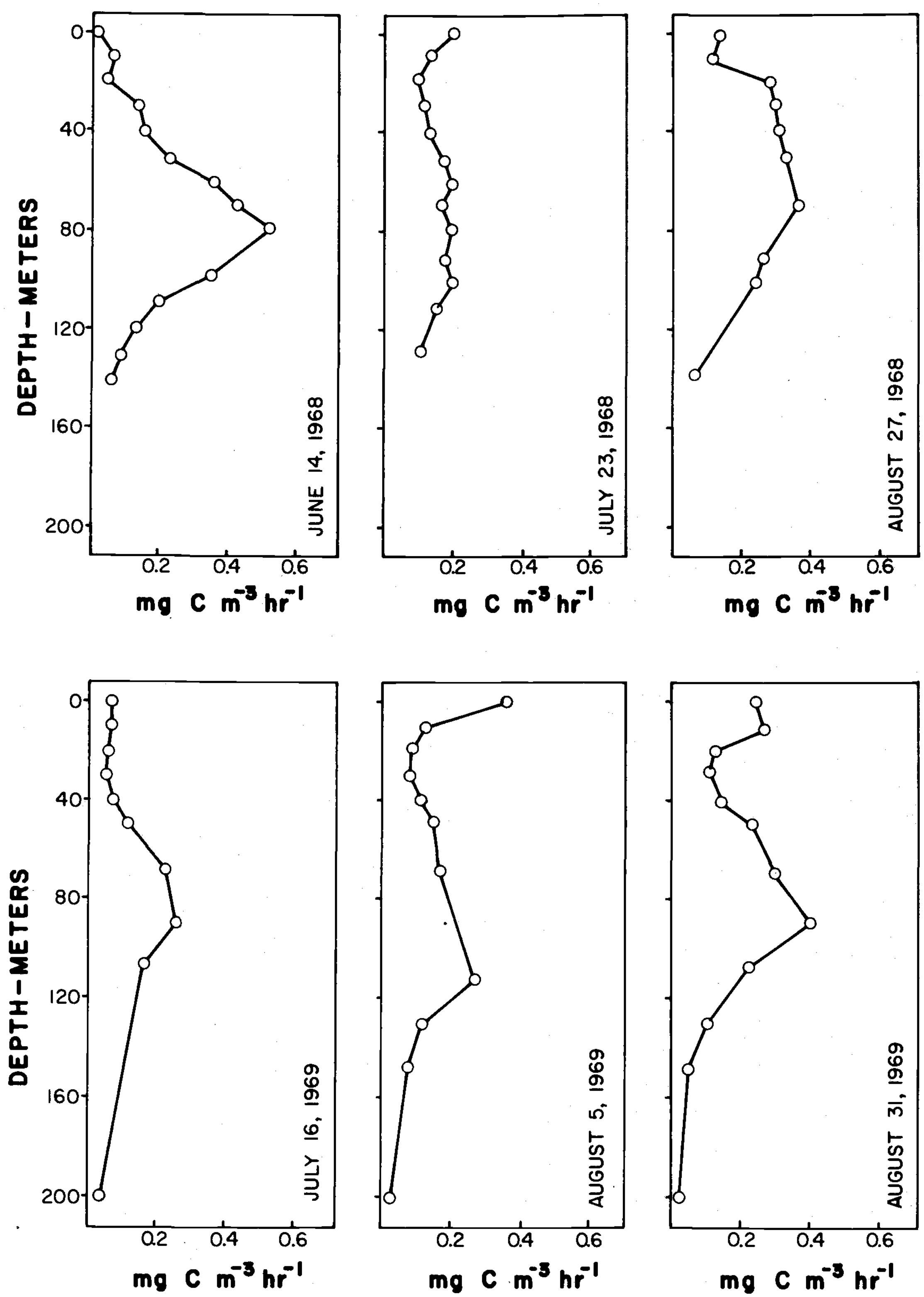


Figure 19. Vertical profiles of phytoplankton photosynthetic rates for Crater Lake, Oregon, 1968-1969.

0.159 mg/m^3, respectively. These were about 50% less than the concentrations measured at depths between 40 and 110 m. Tyler (1965) reported that the first 20 m in Crater Lake approximated chlorophyll-free water.

Phytoplankton production was measured at depths greater than 100 m (Figure 19). In Crater Lake, the compensation depth (i.e., the depth to which 1% of the total incident light is transmitted; Curl and Small, 1968; Lund, 1969), was between 90 and 100 m (Figure 16). The photometric instrument used in this study indicated that incident light was reduced to zero at 100 m (Figure 16). Smith and Tyler (1967) were able to predict however, from data obtained with the highly sensitive Scripps Spectroradiometer, that down-welling irradiance reached maximum depth (i.e. 589 m) in Crater Lake.

Odell Lake

At all times, primary productivity in Odell Lake greatly exceeded that of any other study lake (Figure 18). Vertical profiles of productivity for 1968 and 1969 are compared in Figures 20 and 21 (note that the scales along the x-axis in Figure 20 differ from those in Figure 21).

Productivity was generally higher in 1968 than in 1969. Total production by phytoplankton for the period June 18 to October 19, 1968 was 231.3 gC/m^2. In 1969, production was measured over a shorter

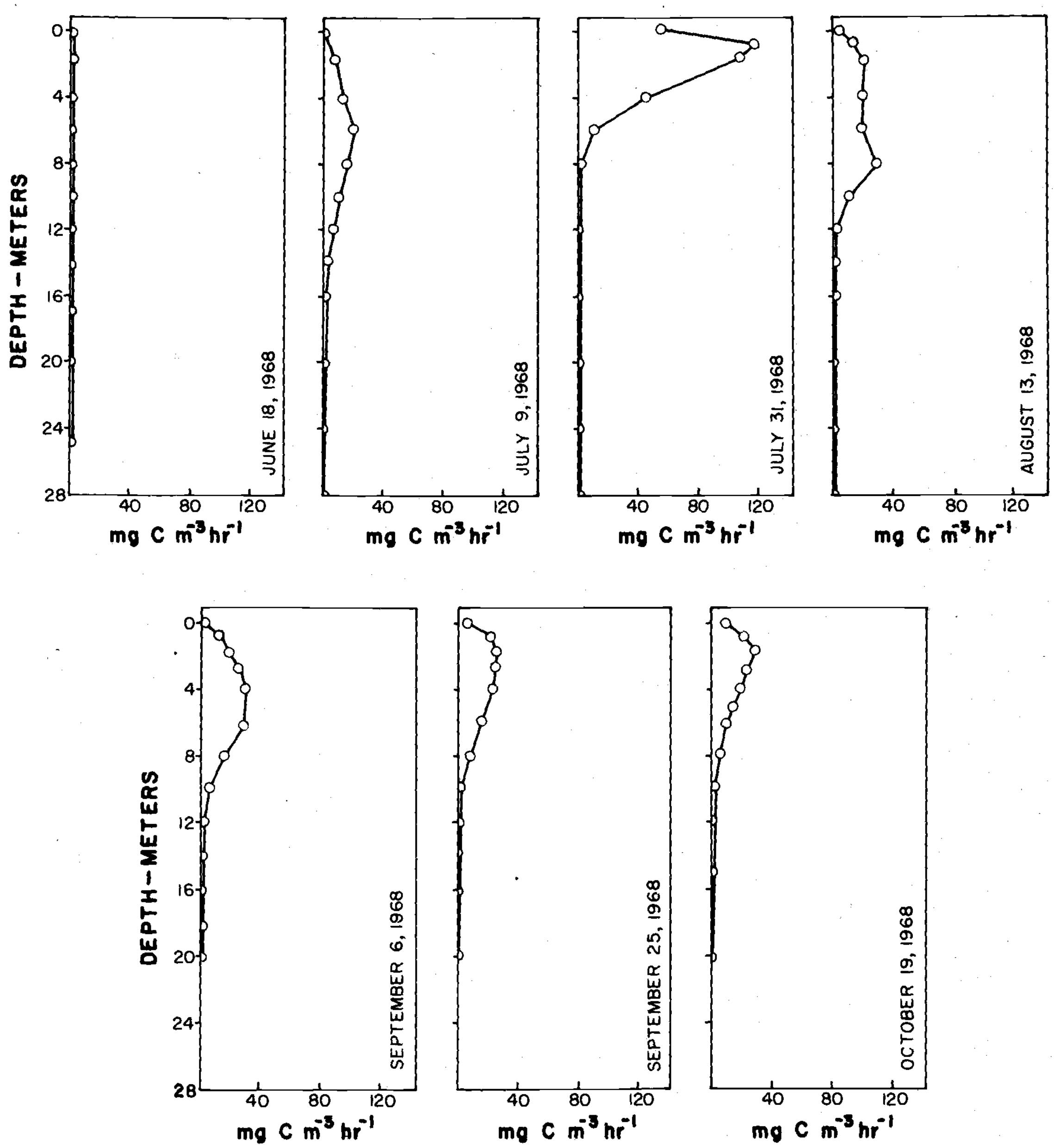


Figure 20. Vertical profiles of phytoplankton photosynthetic rates for Odell Lake, Oregon, 1968. Data taken at Station 1.

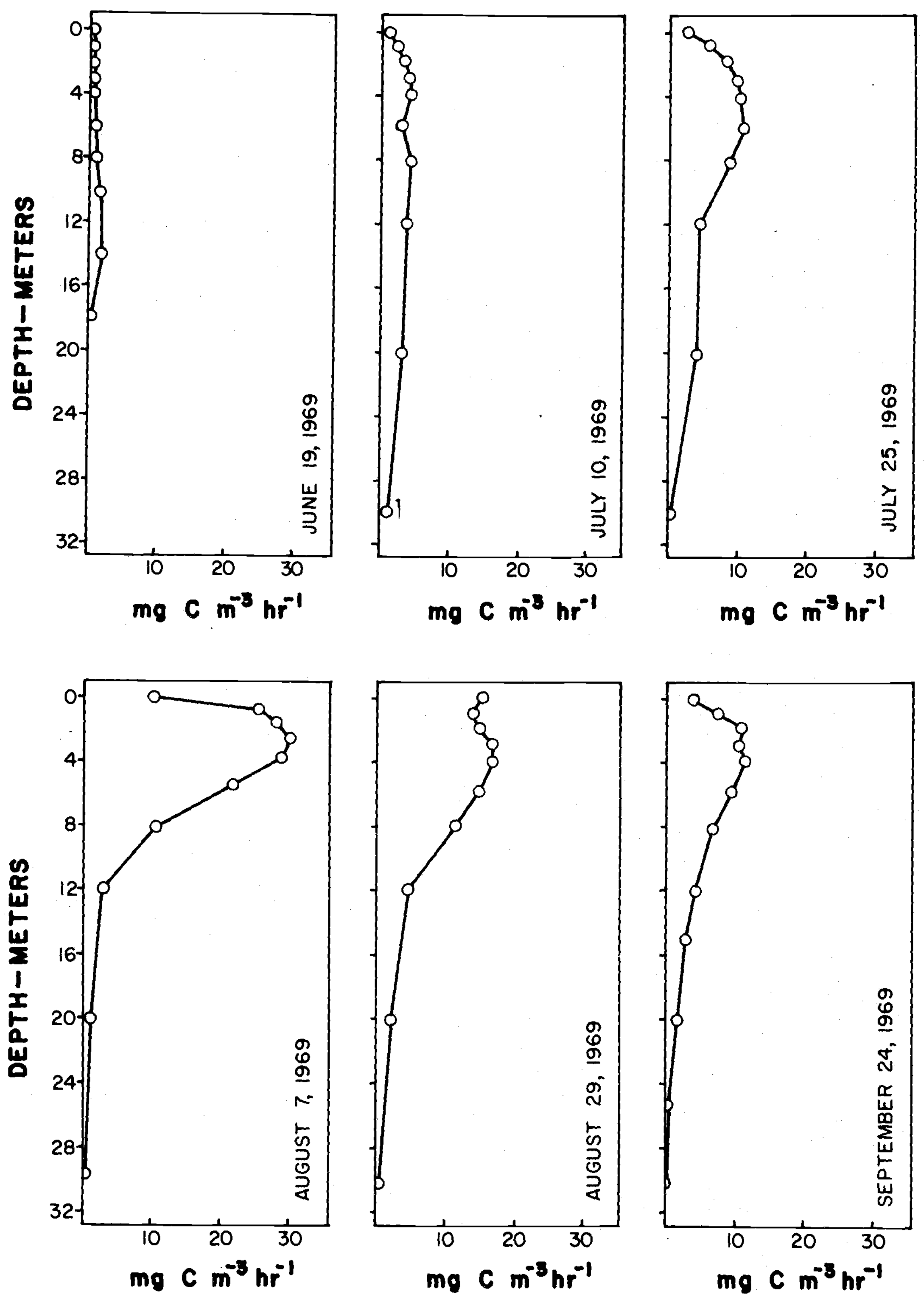


Figure 21. Vertical profiles of phytoplankton photosynthetic rates for Odell Lake, Oregon, 1969. Data taken at Station 1.

period (i.e., June 19 to September 24) and totalled 118.1 g C/m^2 (Table 19).

In 1968, production was relatively low during June. An algal bloom (unidentified) reached maximum proportions in late July (Figure 20). Throughout the remainder of the summer and fall, production diminished rather slowly (Figures 18 and 20; Table 19). Weather conditions prohibited sampling beyond October.

The cycle of summer production developed similarly in 1969. June was a period of limited production. The seasonal maximum occurred in late July or early August (Figure 21). Earlier, in May, a diatom bloom had been reported. Another bloom (unidentified) was observed in November (S. Lewis, personal comm.). Both pulses were thought to be quite unusual for Odell Lake.

Waldo Lake

Waldo Lake certainly ranks as one of the most oligotrophic and consequently, the least productive, freshwater temperate lakes ever encountered (Figure 18; Table 20). Hobbie (1964), after estimating the primary productivity of two Alaskan arctic lakes, concluded that they were the "least productive ever extensively measured." Lake Peters produced 0.9 gC/m^2/year while net productivity estimates for Lake Schrader varied from 6.6 to 7.5 gC/m^2/year.

An estimate of net phytoplankton productivity for a 103-day sampling period (June 21 to October 3, 1969) in Waldo Lake is presented in Table 20. For September, when weather conditions prohibited in situ ^{14}C experiments, it was assumed that production increased linearly between August 28 and October 3.

The total production estimate given in Table 20 (i. e., 4.225 $gC/m^2/103$ days) represents perhaps 75-80 percent of the annual phytoplankton production in Waldo Lake. Presumably, during the November to April period, low light and temperature conditions greatly restrict phytoplankton production. In Waldo Lake, this period of restriction may include May and June as well (Figure 22). However, this is yet to be ascertained through yearlong sampling.

The comparatively high production for October 3 (Figure 22; Table 20) is explained perhaps by the use of Station 5 as an alternate sampling site. Station 5, located at the south end of the lake in a relatively sheltered area, is less than 1000 meters from shore. These features are considerably different from those encountered at Station 9. Strong northwesterly winds, persisting for several days prior to October 3, may have produced a concentration of plankton in the vicinity of Station 5.

Woahink Lake

In terms of phytoplankton production per unit area, Woahink and Crater lakes closely resembled one another (Figure 18; Tables 18 and 21).

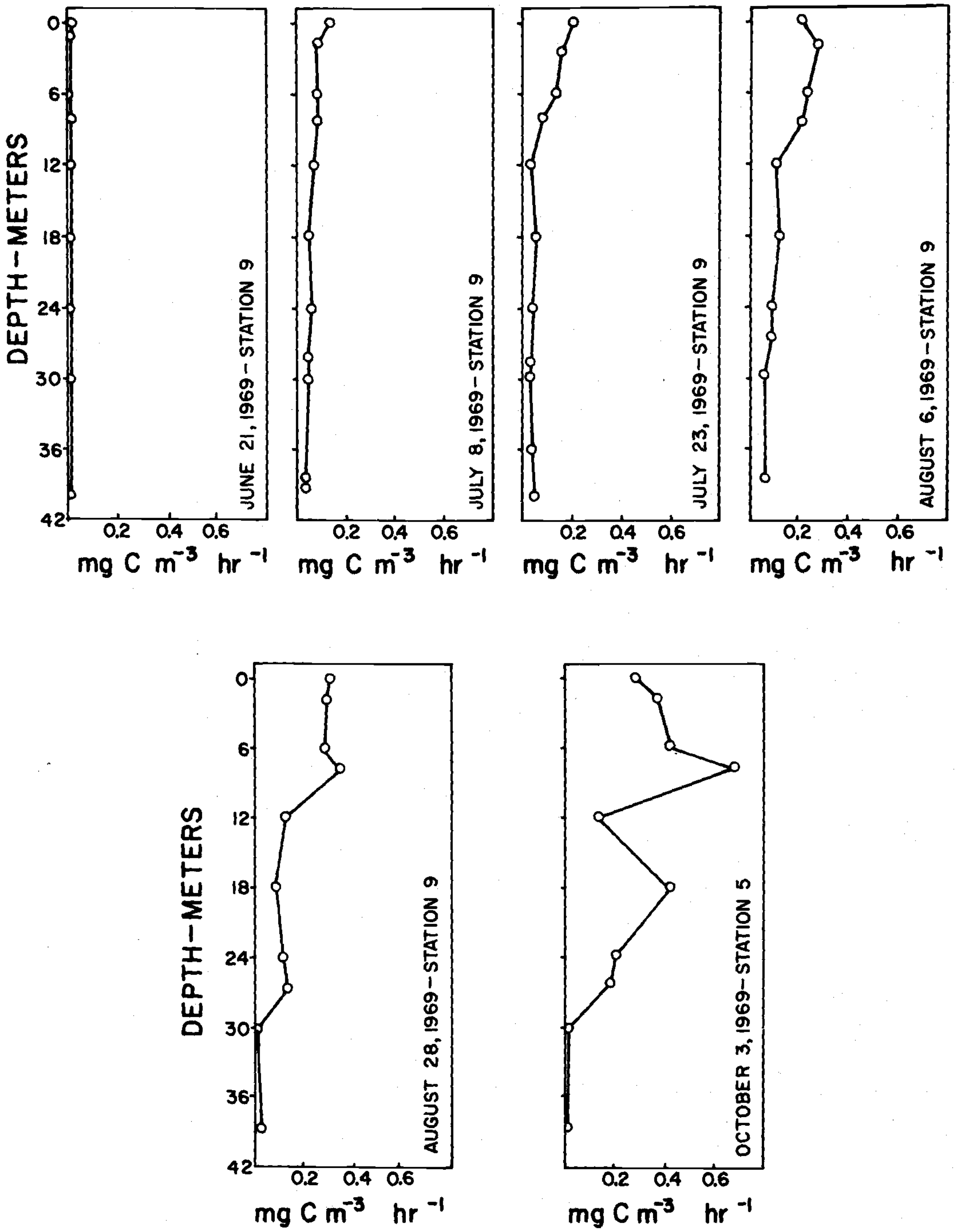


Figure 22. Vertical profiles of phytoplankton photosynthetic rates for Waldo Lake, Oregon, 1969.

Net productivity for Woahink Lake averaged 7.9 g C/m^2/month (July-August, 1968) and 9.4 g C/m^2/month (July-August, 1969). Total annual productivity (June 27, 1968 to June 13, 1969) was calculated to be 37.2 g C/m^2/year.

In Woahink Lake, the zone of maximum production during the summer and fall months was generally between depths of 2 and 6 m (Figures 23 and 25). In reference to Figure 16, about 20% of the incident light penetrated to 6 m in Woahink Lake. At 16 m, incident radiation had been reduced to zero.

During the June through September periods in 1968 and 1969, there were relatively slight fluctuations in productivity per unit area (Table 21; Figures 23 and 25). In fact, it was not possible to distinguish a marked seasonal maximum (Figures 23 and 25). Algal blooms never appeared while the lake was being studied.

Coincidental with the fall overturn in October, 1968 (Figure 23) was a steep decline in production. Photosynthetic rates by phytoplankton were minimal during the winter months (Figures 23 and 24). Starting in April, a pulse in production developed (Figure 24). By June, the bloom had ended; the level of production returned to what it had been during the winter (Figure 25; Table 21).

A separate study was initiated in April, 1969, to determine whether brisk wind action (common for the Woahink basin) and an unusually high shoreline development had any effect on phytoplankton

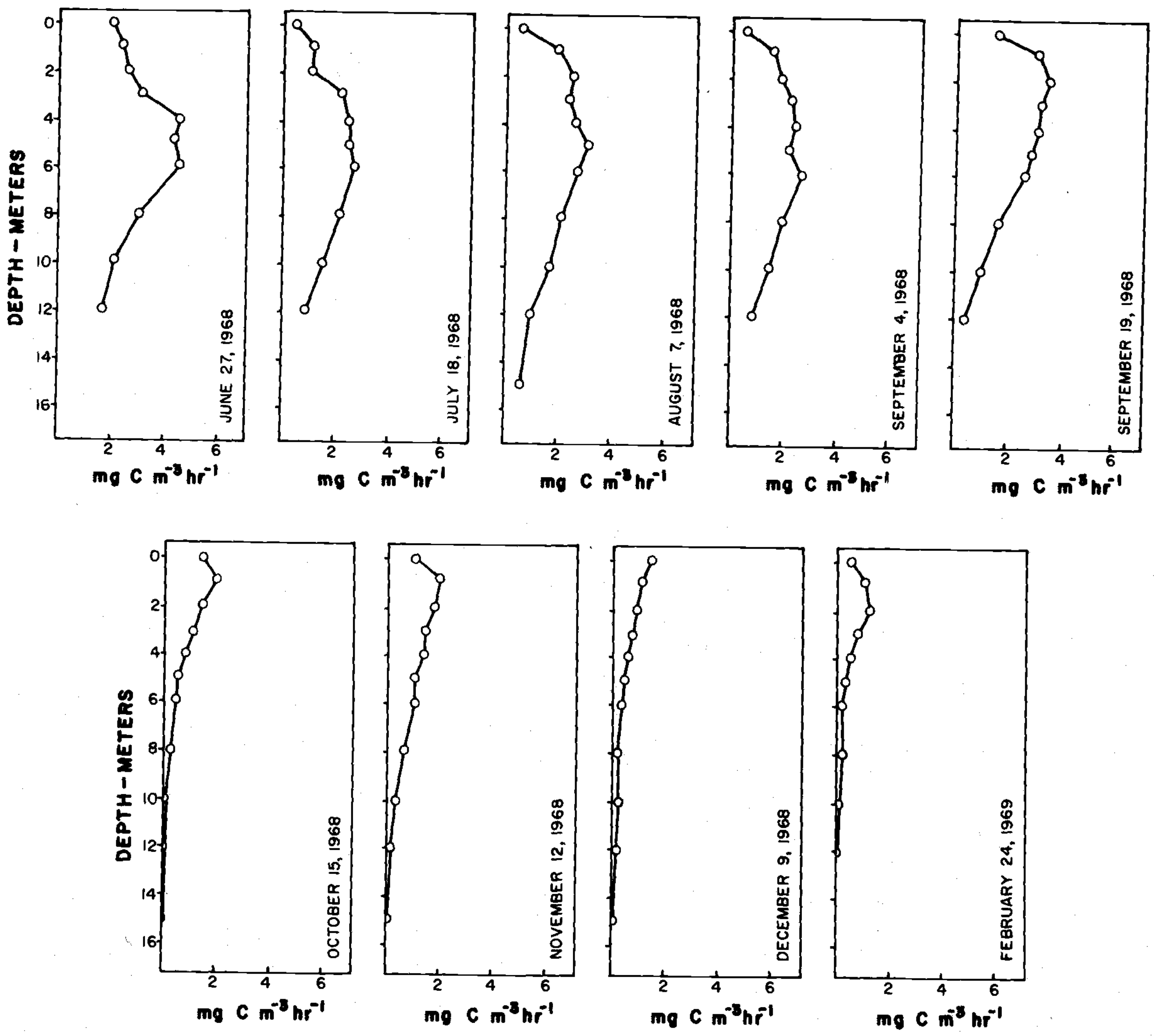


Figure 23. Vertical profiles of phytoplankton photosynthetic rates for Woahink Lake, Oregon, June, 1968 to February, 1969. Data taken at Station 3.

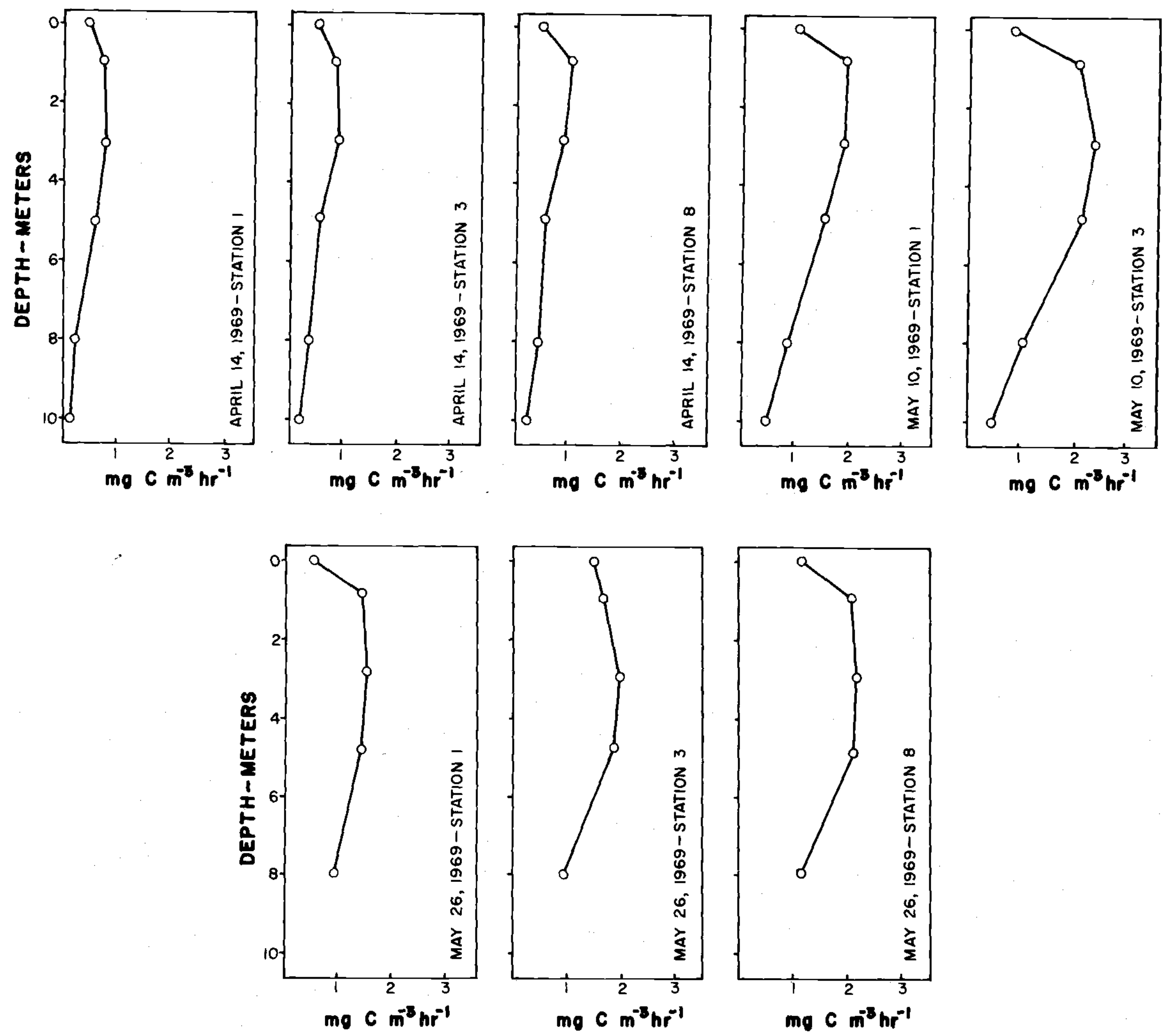


Figure 24. Vertical profiles of phytoplankton photosynthetic rates for Woahink Lake, Oregon, 1969. Data compared among stations on three separate occasions.

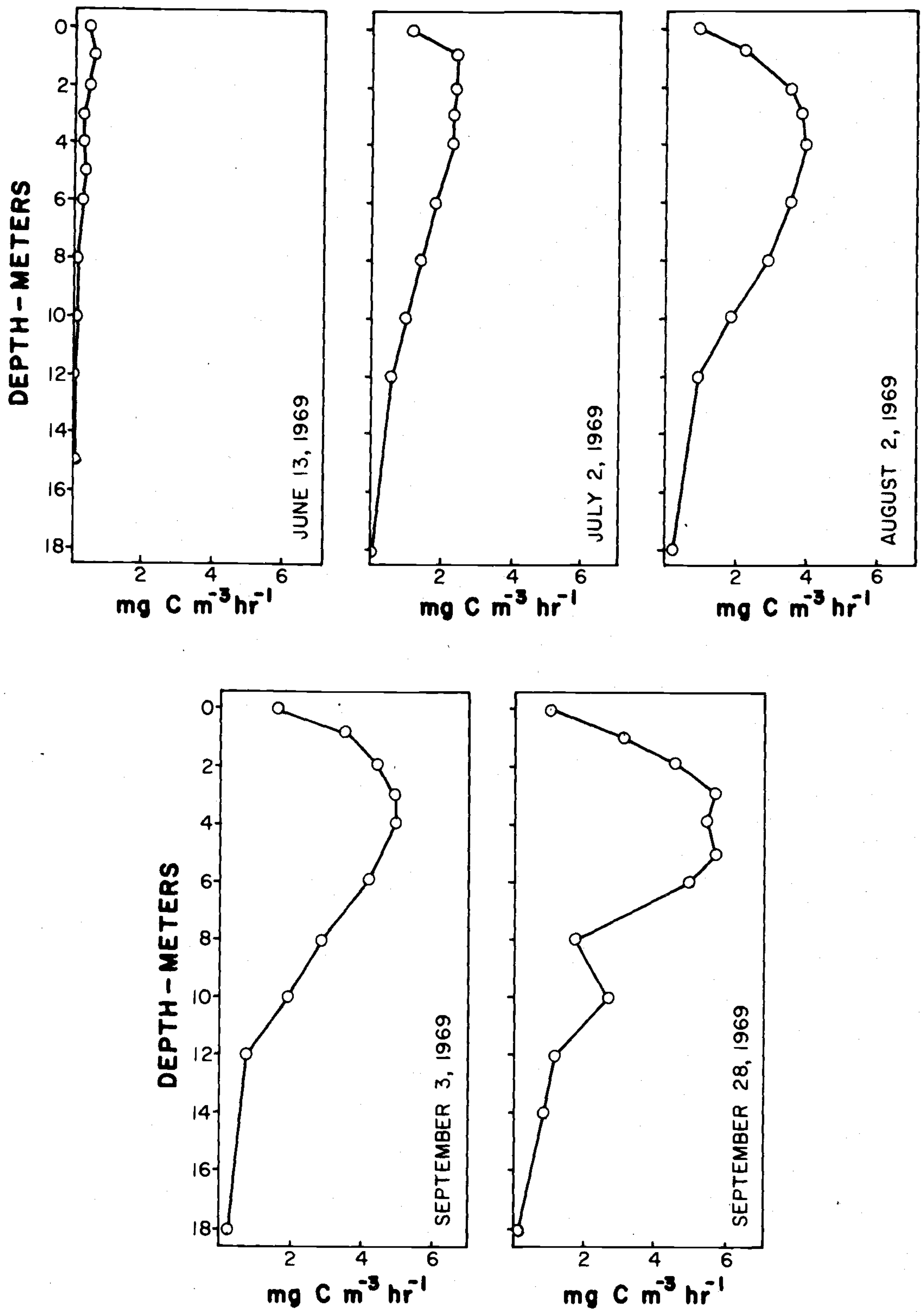


Figure 25.. Vertical profiles of phytoplankton photosynthetic rates for Woahink Lake, Oregon, 1969. Data taken at Station 3.

production estimates in Woahink Lake. Normally, production was measured from a single index station (Station 3) located at the approximate center of the lake (Figure 10). I was interested in knowing whether the estimate made at that point was a reasonable representation for the entire lake.

In all lakes, the spatial distribution of phytoplankton is influenced considerably by the morphometry of the basin--especially the configuration of the shoreline and local prevailing winds. Welch (1952) discussed, in general, the effects of wind on the horizontal and vertical distribution of plankton. He noted that wind action caused plankton to drift and become concentrated, especially in bays and in smaller indentations along the lake shoreline. Tucker (1948), Verduin (1951) and Pomeroy, Haskin and Ragotzkie (1956) found that during periods of low wind velocity, phytoplankters became concentrated, resulting in patchy distribution. These aggregations were dispersed by high wind velocities creating a more uniform distribution of cells throughout the epilimnion.

The combined effect of shoreline development and wind action may complicate the sampling design that is being used to estimate production. Several authors (Verduin, 1951; Rodhe, 1958; Fogg, 1966) have criticized the view that samples obtained from a single station located at mid-lake are, for all practical purposes, representative of the lake as a whole. They contend that production estimates gained from a single station can be misleading--particularly if wind action is a prominent feature of the basin climate. In order to achieve greater accuracy in the estimation of phytoplankton production, Small (1963) suggested that sampling stations be selected with reference to wind effects on a particular lake.

If primary production is being estimated *in situ*, a multi-station system may be difficult to maintain. In a lake with a deep photic zone, a sizeable amount of time may be required to draw water samples from depth, inoculate them with a ^{14}C-carrier and return them for incubation (in Crater Lake, about 1 hr was needed to obtain, prepare, and return water samples to *in situ* positions, located at various intervals down to 200 m). Furthermore, travel-time between stations might be considerable, depending on inter-station distances and the speed of transport. As a result, a period of 1 to 2 hrs may lapse between the actual deployments (for *in situ* incubation) of water samples at the first and second (and additional) stations. Goldman (1960) conducted near-simultaneous primary production *in situ* experiments at three stations in a large Alaskan lake. He reported a significant statistical difference among stations even when the three starting times differed by only 20 minutes.

In order to obtain some idea of the between-station differences, three stations in Woahink Lake (Station 1, 3 and 8; Figure 10) were sampled on April 14 and May 26, 1969. Only two stations (stations 1 and 3) could be reached on May 10. Wind data for the three dates are shown in Table 22.

Table 22. Wind data for Woahink Lake, Oregon (approximate values)*.

Date (1969)	Velocity (knots)	Direction
12 April	35	SW
13 April	7	SW
14 April	4	SW
8 May	5	SW
9 May	0	--
10 May	12	WNW
24 May	15	SW
25 May	10	SW
26 May	20	SSW

*Courtesy of the U. S. Coast Guard, Siuslaw River Station, Florence, Oregon.

The vertical profiles (Figure 24) were integrated to obtain $mgC/m^2/hr$. Results of each sampling date were handled separately. A statistical analysis of primary production, using a randomized-block design followed by analysis of variance test, showed no significant differences among stations at the $\alpha = 0.025$ level. Surface concentrations of chlorophyll a were analyzed, also. The results indicated no significant differences among stations at the $\alpha = 0.025$ level.

The above suggests that despite the unusual wind action and shoreline development of the Woahink basin, the phytoplankton in the lake are distributed rather uniformly on a horizontal plane. Therefore, samples obtained from a single station were sufficient to estimate the productivity of Woahink Lake.

Factors that Influence Production

Crater Lake

The fact that Crater Lake is a deep, steep-walled basin with very low shoreline development may be related to its low productivity. Generally, lakes of this kind are much less productive than shallow lakes with extensive shoal areas. Welch (1952) associated high shoreline development with increased production by noting that plankton was more dense in the protected "indentations" (coves, bays) along the shores of lakes. Rawson (1952, 1955, 1961) noted that biological productivity in lakes decreased, generally, with an increase in average depth. Arbitrarily, he established a mean depth of 18 m as a point of separation between eutrophic and oligotrophic lakes.

The nutrient status in Crater Lake was discussed. Several references were made concerning the relatively high concentrations of phosphorus, nitrogen, and silica in the lake. It was concluded from this that these and perhaps other essential nutrients were not restricting production. One of several micronutrients could have been limiting, but no attempt was made to determine this. The results of a nutrient bioassay experiment, conducted in July, 1969 (Figure 26), showed that various nutrient additives (Ref. Table 23) had little or no effect on the rate of photosynthesis. The nutrient that appeared to be most effective was phosphorus (i.e., P at a concentration of 0.10 mg/l).

Temperature may have had the greatest effect on productivity in Crater Lake. Although the summer heat budget is exceptionally high for a freshwater lacustrine environment (34,910 g cal/cm^2 in 1968) the temperature at any one place and time is not very warm. By June 14, 1968, the temperature at the surface of the lake had risen to only 6.8° C. On July 22, the surface temperature stood at 14.8° C. In August, the lake began to cool (Figure 12). The summer temperature cycle in 1969 was very similar.

Temperatures below 40 m were usually less than 6° C (Figures 11 and 12). Significant production in the water column was achieved between depths of 40 and 120 m (Figure 19). Light conditions at these depths were probably optimal for shade-acclimated phytoplankton. However, temperatures there were possibly less than optimal which restricted a higher rate of production. This is not to say that temperature was a limiting factor. Eaton (1967) and Round (1968) concluded that, although minimal temperatures would reduce productivity, temperature by itself was not limiting.

For freshwater lakes, several authors (Rodhe, 1948; Lund, 1965;

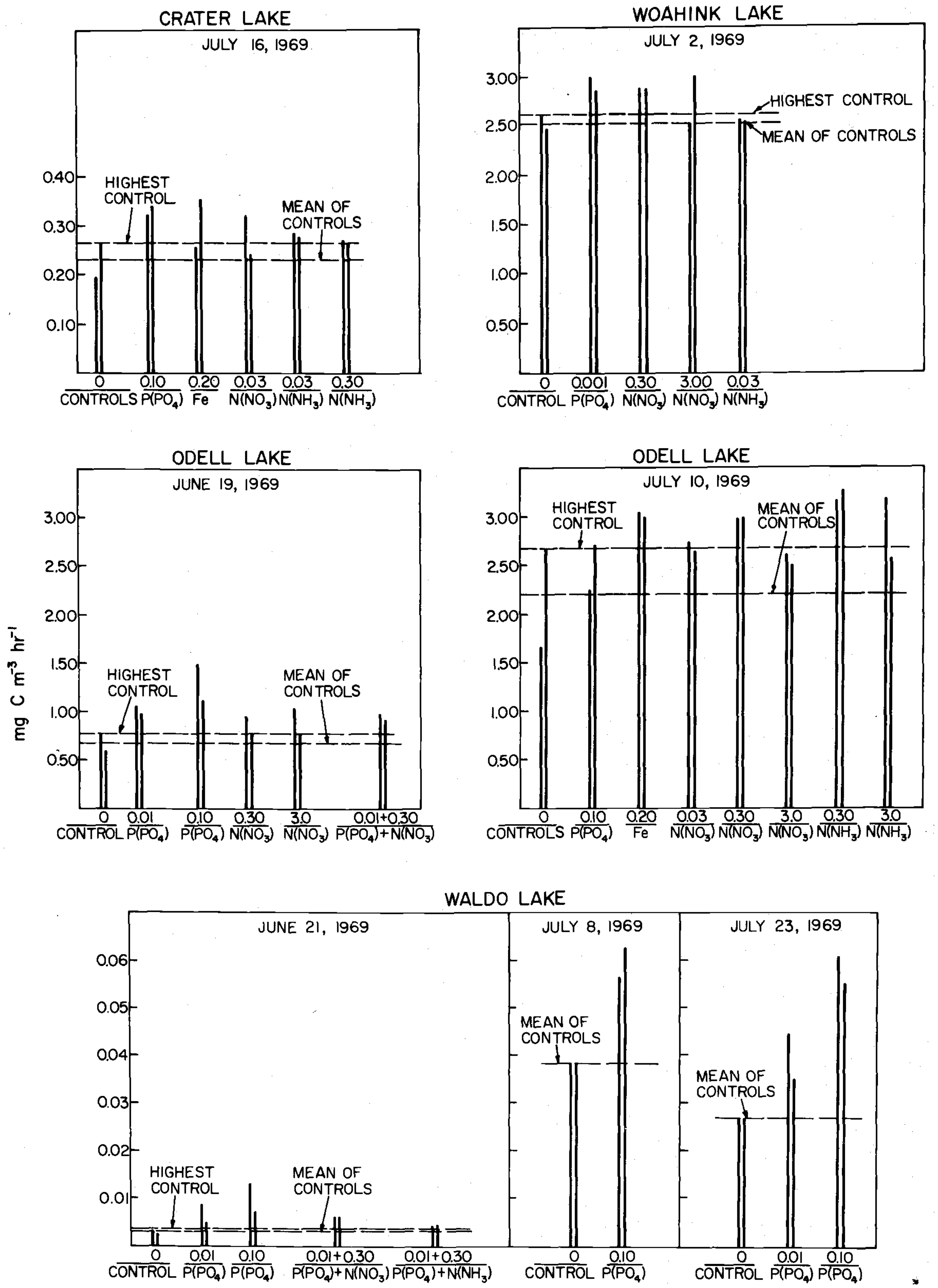


Figure 26. Response of lake phytoplankton populations to nutrient enrichment bioassays.

Table 23. Types and concentrations of algal nutrients employed during bioassay experiments in 1969.

Lake and Date	Nutrient Additives	Concentrations (mg/liter)		
Crater, 16 July	$P(KH_2PO_4)$	0.001	0.01	0.10
	$Fe(FeCl_3)$	0.002	0.02	0.20
	$N(NaNO_3)$	0.003	0.03	0.30
	$N(NH_4Cl)$	0.003	0.03	0.30
Odell, 19 June	$P(KH_2PO_4)$	0.001	0.01	0.10
	$N(NaNO_3)$	0.03	0.30	3.00
	$N(NH_4Cl)$	0.03	0.30	3.00
	$P + N(NO_3)$	0.01 +	0.30	
	$P + N(NO_3)$	0.10 +	3.00	
	$P + N(NH_3)$	0.01 +	0.30	
Odell, 10 July	$P(KH_2PO_4)$	0.001	0.01	0.10
	$Fe(FeCl_3)$	0.002	0.02	0.20
	$N(NaNO_3)$	0.03	0.30	3.00
	$N(NH_4Cl)$	0.03	0.30	3.00
Woahink, 2 July	$P(KH_2PO_4)$	0.001	0.01	0.10
	$N(NaNO_3)$	0.03	0.30	3.00
	$N(NH_4Cl)$	0.03	0.30	3.00
	$P + N(NO_3)$	0.001 +	0.30	
	$P + N(NO_3)$	0.01 +	3.00	
Waldo, 21 June	$P(KH_2PO_4)$	0.001	0.01	0.10
	$N(NaNO_3)$	0.03	0.30	3.00
	$N(NH_4Cl)$	0.03	0.30	3.00
	$P + N(NO_3)$	0.01 +	0.30	
	$P + N(NO_3)$	0.10 +	3.00	
	$P + N(NH_3)$	0.01 +	0.30	

Table 23. (Continued)

Lake and Date	Nutrient Additives	Concentrations (mg/liter)		
Waldo, 8 July	$P(KH_2PO_4)$	0.001	0.01	0.10
	$Fe(FeCl_3)$	0.002	0.003, 0.02	0.20
	$N(NaNO_3)$	0.03	0.30	3.00
	$N(NH_4Cl)$	0.03	0.30	3.00
Waldo, 23 July	$P(KH_2PO_4)$	0.001	0.01	0.10
	$Fe(FeCl_3)$	0.002	0.02	0.20
	$N(NaNO_3)$	0.003	0.03	0.30
	$N(NH_4Cl)$	0.003	0.03	0.30

Canter and Lund, 1966; Round, 1968) stated that temperature was as important as light in initiating phytoplankton growth in the spring. Moreover, the growth of Chlorococcales (Rodhe, 1948) and Cyanophyta (Round, 1968) during the summer period was very much dependent upon temperature. In Crater Lake, the period for summer growth is relatively short. Quite possibly, "winter" ends in June and resumes in late August.

During the study, no attempt was made to determine the size of individual algal cells that occurred in Crater Lake. In view of temperature, light, and nutrient conditions, cell size could relate strongly to phytoplankton growth and production. Rodhe (1955) investigated highly oligotrophic arctic lakes during the winter months and found moderately dense (i.e., 1×10^6 to 1×10^7 cells/liter) populations of extremely small (i.e., none larger than 2 μ) green algae. In the lakes he studied, nearly all the incident light was obscured by a surface layer of ice and snow. Water temperatures throughout were less than 2.5° C. Yet, the populations proceeded to grow, and where light was available immediately beneath the ice, photosynthesize. In complete darkness, growth was maintained by heterotrophic processes. The energy intake efficiencies of these populations had to have been very high to contend with such an environment.

Populations of ultraplankton (i.e., cell size < 5-10 μ) are characteristic of oligotrophic lakes (Goldman and Wetzel, 1963). These very small cells have a high surface area to volume ratio which facilitates a high rate of nutrient absorption and an efficient use of light energy. Thus, in lakes where the availabilities of nutrients and light are limited, ultraplankton are well-adapted, and, as a rule, will exhibit a higher rate of production per unit volume than larger-bodied forms.

Similar populations of highly-efficient, very minute "μ-algae" (Rodhe, 1955) may comprise a major part of the phytoplankton in Crater Lake. If so, the productivity of the lake could well have been underestimated. That is, in the process of filtering in situ culture samples with AA-type Millipore filters (pore size equaled 0.8 μ), so as to determine the rate of uptake of ^{14}C, significant numbers of μ-algae may have been lost.

Odell Lake

Temperature, light and nutrients appeared to favor productivity in Odell Lake. High production was sustained during the summer and fall. Algal blooms were not uncommon. Large densities of zooplankton were observed on almost every sampling occasion.

During the June bioassay experiment (Figure 26), the response of phytoplankton to several nutrient additives (Ref. Table 23) was, as a whole, not significant. In July, prior to the summer pulse, productivity was stimulated to some extent following the addition of most nutrient solutions. The significance of these results was not tested. In all probability they do not reflect nutrient deficiencies in the lake. Considering the level of phytoplankton biomass and productivity (including assimilation numbers, Table 17), it is reasonable to assume that Odell Lake is nutrient-enriched.

The concentration of total dissolved solids in Odell Lake was about one-third that for Crater Lake. Yet, production in Odell Lake was 8 to 10 times greater. This is not completely in line with Northcote and Larkin (1956) and Larkin and Northcote (1958) who stated that "total dissolved solid content is by far the most important factor in determining standing crops of organisms in British Columbia lakes." This generalization would probably apply only to remote regions where man's limited presence has had little effect on the trophy of the lakes.

In addition, it should be noted that six elements in Crater Lake water (i.e., Na, Ca, Mg, Cl, Si, S) comprise 75% of the total dissolved solids. This would suggest that although the value of TDS is relatively high still certain essential ions could be deficient. In Odell Lake, on the other hand, there is probably a better-balanced supply of ions with none being deficient.

The soils in the Odell basin were described. Perhaps the most salient feature of the soil profile was the large porosity and highly permeable nature of the underlying pumiceous layers. As stated before, the subsurface percolation of water through these materials would be very rapid, thereby facilitating the transport of dissolved nutrients and suspended materials into the lake.

Waldo Lake

Nutrient deficiency was easily the most important factor in determining production in Waldo Lake. The total water chemistry of the lake approximated that of distilled water (Figure 17, Table 7). Rainwater was thought to contain higher concentrations of essential nutrient ions (J. Wagner, personal comm.).

Water analyses by Carter *et al.* (1966) showed that the level of phosphate in Waldo Lake was less than 0.01 mg/l. Recently, the FWPCA (1969) reported the concentration of total phosphorus to be lower than 0.002 mg/l. Throughout the bioassay experiments, phosphate appeared to have a large effect on rates of photosynthesis, especially during July (Figure 26). This may indicate the importance of phosphorus in the nutrient economy of the lake.

Personnel from the FWPCA have cultured populations of algae in water collected from Waldo Lake. They concluded, tentatively, that carbon was limiting algal production (W. Miller, personal comm.). This is, perhaps, a reasonable assessment in view of the extremely low alkalinity, low hardness and poor buffering capacity (low concentration of HCO_3^-) of the water.

Apparently, very little in the way of nutrients is derived from the Waldo Lake watershed. The description of the basin implied that the soils, as a whole, are relatively barren and unproductive. No permanent tributaries enter the lake. Water is supplied primarily through rainwash and temporary meltwater streams.

Woahink Lake

Climate and morphometry play an important role in determining the rate of production in Woahink Lake. Due to a combined set of conditions, the lake probably undergoes a high rate of flushing and water renewal. Thus, perhaps often during the year, portions of the phytoplankton standing crop are removed from the lake. Presumably, nutrients are lost as well. Furthermore, the "new" water that replenishes the lake volume may diminish productivity for a considerable length of time thereafter (Findenegg, 1965).

Periodic flushing of Woahink Lake is brought about by (1) the small storage capacity of the lake basin as indicated by low seasonal fluctuations in the level of the lake (e.g., variations were less than 0.5 m), (2) moderately heavy precipitation during the period October through April (approximately 87% of the total annual precipitation of 203 cm occurs then), (3) heavy runoff from the surrounding terrain (the drainage area is 14.2 km^2), and (4) a high volume development of the basin (i.e., 1.50). Robertson (1954) attributed high rates of flushing in a similar lake in British Columbia to (1) small storage capacity, (2) heavy precipitation (about 300 cm per year, 60 to 70% of which occurred in the period September through March), (3) heavy runoff from a small drainage area (9.3 km^2) and (4) a high volume development (i.e., 1.53).

Nutrient bioassay experiments were not conclusive (Figure 26). Generally, the response of phytoplankton to various nutrient solutions (Table 23) was negligible. Miller (FWPCA, personal comm.) suggested, in light of their culture bioassays, that carbon may be limiting (Ref. chemical description of Woahink Lake in which low pH, alkalinity and total hardness were noted). Other factors (e.g., temperature and light) appeared to be favorable for production during the growing season.

CULTURAL IMPACT ON LAKE EVOLUTION

Many of the excellent lake environments in Oregon are being exploited for recreational use and, as a result, are becoming more productive biologically. The problems that are brought on by increased biological production have been well-documented in the literature (Hasler, 1969). The general effect of artificial enrichment is a shift to a higher level of trophy in respondent lakes.

The use to which each of the study lakes is being put has been discussed. Where human activities are restricted, eutrophication will proceed at a rate that is determined primarily by the natural factors of the basin environment. On the other hand, where the lake is used for any number of purposes, eutrophication is likely to accelerate beyond natural limits.

Rodhe (1969) established rather precise boundaries in graphically depicting the various stages in lake evolution (Figure 27). The relative positions of the study lakes in Figure 27 are most interesting in view of how each is being used. Waldo Lake is certainly where one would expect it to be--as is Woahink Lake. The degree to which Odell Lake has approached eutrophication on Rodhe's scale is somewhat alarming. The position of Crater Lake is the most surprising, being as far up the scale as it is.

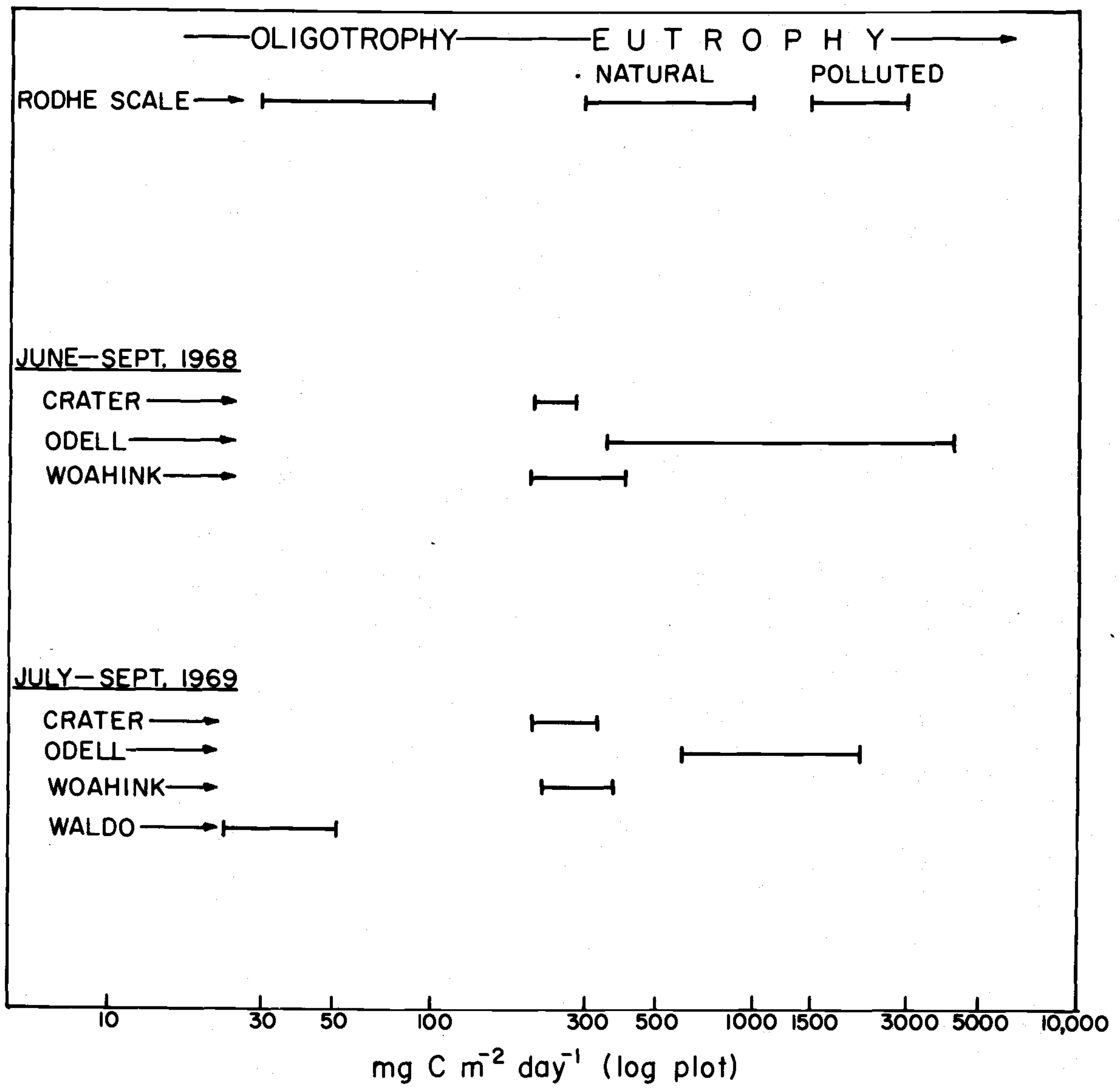


Figure 27. Approximate ranges of phytoplankton primary productivities for the study lakes compared with the Rodhe (1969) scale for oligotrophic and eutrophic lakes.

Crater Lake

The Crater Lake environment, by virtue of its being preserved in a national park, receives an extremely limited use. Access to the lakeshore is along a precipitous trail that zig-zags for nearly 2 km down the caldera wall. At the base of the trail, one finds a concession stand, a rowboat rental service and two toilet facilities, all of which represent the total recreational development in the basin (i.e., along the lakeshore). Six excursion boats carry tourists on scenic trips around the lake. A boat storage and repair facility, property of the park concessionaire, is located on the southwest shore of Wizard Island.

Odell Lake

Odell Lake serves various interest groups, including those that fish, camp, boat, and waterski. The lake is easily reached by State Highway 58 which parallels, closely, the shoreline to the north and east.

The U. S. Forest Service maintains five campgrounds and three boating facilities in the Odell basin. The use of these has increased at a rate of about 9% per year (J. H. Nunan, personal comm.). All Forest Service toilet facilities are of the vault-type with one exception, this being at the Pebble Bay campground. The vaults are pumped two or three times during the summer and fall and the contents are removed from the basin (J. H. Nunan, personal comm.).

Included in the total development of the lake are two privately-owned resorts, a marina, and 67 summer homes, most of which are situated at the west end of the lake. The homes are occupied usually from May until September. Sewage wastes are removed by drainage-field or pit-type systems. These are located, as a rule, at least 60 m back from the shoreline and 30 m from any water course (J. H. Nunan, personal comm.).

Since 1965, angler use of Odell Lake has nearly doubled. Creel census data, collected by the State of Oregon Game Commission, show that the number of boat hours spent on Odell Lake increased from 46,000 in 1965 (Averett, 1966) to over 69,000 in 1968 (S. Lewis, personal comm.).

The overall use of Odell Lake has grown rapidly, especially within the last 10 years (Atkinson, Odell Lake marina owner, personal comm.). Lake users have brought a substantial load of nutrients into the basin that otherwise would not have been available. As expected, the algae responded positively. Now, frequent pulses by phytoplankton populations and a relatively high rate of primary production throughout the growing season are features of the lake's biology. Algal blooms were never observed in the years prior to 1960 (Atkinson, personal comm.).

In 1940, the State of Oregon Game Commission conducted a biological survey of forty lakes, including Odell Lake, in the Upper Deschutes River Watershed (at that time, construction of the Willamette Highway no. 58 had just been completed; Newcomb, 1941). Part of the task was to quantify the benthic and planktonic communities and to classify the lakes accordingly. Each lake was assigned a numerical grade (or index value) that ranged between 1.0 and 2.5. The magnitude of the number depended upon the degree of eutrophy (i.e., the more eutrophic the lake, the larger the number). The number itself was based on a set of limnological conditions that were common to each lake. If a lake received a number between 1.0 and 1.5, it was classified as oligotrophic (implying that the value 1.0 represented ultra-oligotrophy). The ensuing ranges of values from 1.6 to 2.0 and 2.1 to 2.5, designated lakes that were eutrophic and advanced eutrophic, respectively. Interestingly enough, Odell Lake was graded 1.4.

Waldo Lake

The extreme oligotrophic nature of Waldo Lake, Oregon, was first reported in a document prepared by the State of Oregon Sanitary Authority (presently the State of Oregon Department of Environmental Quality) and the U. S. Forest Service (Carter et al. 1966). Data reported from the study suggested that Waldo Lake may be one of the most oligotrophic lakes in the world. Subsequent research as a part of this study verified the 1966 report.

Before 1969, Waldo Lake was nearly inaccessible to vehicular traffic. Use estimates by the U. S. Forest Service for the period 1966-1968 showed a yearly average of 33,000 visitor days (e.g., one person visiting the lake for 12 hours equals one visitor-day). In June, 1969, a paved highway was opened leading to several newly constructed campsites situated along the east shore of the lake. Consequently, visitor-day estimates for 1969 and future years were expected to rise dramatically.

In view of this and because of the near-pristine condition of Waldo Lake, a study of the lake's productivity was initiated in 1969. The purposes were: (1) to further document the unusual limnological features of Waldo Lake, particularly at this time when the lake is in a very early stage of evolution, (2) to record phytoplankton standing stock and productivity measurements that may be unique for a temperate freshwater lake, (3) to begin a continuous year-to-year surveillance of algal production, which is expected to increase due to recreational development and (4) to establish Waldo Lake as a "eutrophication baseline" in an attempt to predict the effects of expanded use and subsequent enrichment on other high-quality lakes in the Cascades Range.

It is difficult to predict how the recreational development and use of Waldo Lake will affect various components in the lake's ecology.

Certainly, some aspects of the environment will likely be altered. The degree of alteration will depend, for the most part, on the implementation of policies currently proposed by the Federal Water Pollution Control Administration and the U. S. Forest Service (1969).

The lake changed little, if at all, during the time before 1969 when the number of users was limited. Now that the lake is easily accessible and construction projects are disturbing the watershed, continuous limnological monitoring is essential. This research will hopefully provide a reference point, allowing responsible agencies to estimate periodically the effects of population impact on the Waldo Lake basin.

Woahink Lake

Among the study lakes, Woahink Lake probably receives the widest variety of uses. And, the lake is used continually throughout the year.

Use-estimates for Woahink Lake were not available. As one would expect, recreation ranks highest among all uses received. The number of persons who visit the lake for this purpose has increased noticeably over the last 5 to 10 years (C. Mulvey, Woahink Lake resort owner, personal comm.).

More than 150 summer cabins and permanent residences line the shore of Woahink Lake. Nearly 20% of these have been constructed since 1964) (C. Mulvey, personal comm.). Domestic sewage is handled by septic tanks and drainfields.

Water is pumped from the lake and, sans treatment, is used for drinking and other domestic purposes. This is approved by the Lane County Health Department which periodically examines the water to see that it conforms with accepted bacteriological standards of purity. They have insured that domestic wastes will not be discharged directly into the lake. Samples of water tested for coliform bacteria resulted in MPN values ranging from 2 (June, 1964) to 22 (July, 1969) (R. Burns, personal comm.).

During the tourist season (June - August), weather and daylight permitting, a commercial floatplane makes, on the average, four takeoffs and landings per hour. The quantity of oil that is put into the water by this operation is indeterminable. In places along the shoreline, an oil scum will develop, usually, following a period of intensive floatplane use.

Several land-development projects have denuded large watershed areas that adjoin the lake. Most notable among these is an extensive recreational facility situated on the terminus of the north-central peninsula. The work has generated a considerable amount of exposed, unconsolidated material, much of which has been consumed by erosion and discharged into the lake. Consequently, the water in the vicinity of the peninsula has become extremely turbid (Larson and Malick, aerial observation, August, 1969).

A DIAGNOSTIC APPROACH TO LAKE CLASSIFICATION

A brief discussion concerning ecological energy efficiency can be found in Odum (1959). He expressed the view that maximum production per unit time is obtained when photosynthetic efficiencies by phytoplankton are low.

A method for determining energy intake efficiencies in phytoplankton was presented by Platt (1969). He defined the extinction coefficient k as the sum of two components, k_p (light attenuated at depth due to physical processes) and k_b (light absorbed in photosynthesis). k_b represents, approximately, the ratio of production (expressed in calories) to radiation (also in calories) at any depth. That is:

$$k_b \simeq P_{(z)} / I_{(z)}$$

where $P_{(z)} = (\mathrm{mgC/m^3/hr})\ (15.8)$

noting that $\mathrm{mgC/m^3/hr}$ represents net productivity, and 15.8 the number of kilocalories per gram of carbon that is assimilated in photosynthesis (T. Platt, personal comm.).

and where $I_{(z)} = I_o e^{-kz}$

A strong correlation was found to exist between k_b and the concentration of chlorophyll a (Platt, 1969). The implication is that an increase in biomass is associated with an increase in the amount of light being absorbed in photosynthesis (k_b).

In this study, k_b was determined at several depths. The values were averaged to give $\bar{k}_b$ for the vertical productivity profile. In Figure 28, $\bar{k}_b$ (total profile) and k_b at the depth of maximum production (DMP) are compared.

The rate of photosynthesis (mgC/m^3/hr) was plotted against K_b for the DMP (Figure 28). A near-linear relationship developed between the two variables. The lakes are compared in the distribution of plotted data.

Similarly, photosynthetic rate for the total profile (mgC/m^2/hr) was plotted against $\bar{k}_b$. Here, the Crater Lake data deviated from linearity (Figure 28). East and Paulina lakes, both of which are caldera lakes located in Newberry Crater in central Oregon, were included for comparison.

From the grid labelled "total profile" (Figure 28), one can interpret a set of environmental conditions that influence productivity from each of the nine quadrates:

Quadrate I: nutrient deficient; light and temperature within the limits of tolerance.

Quadrate II: temperature may be a limiting condition (ref. Figure 29 in which photosynthetic rate is controlled by temperature in spite of optimal light conditions);

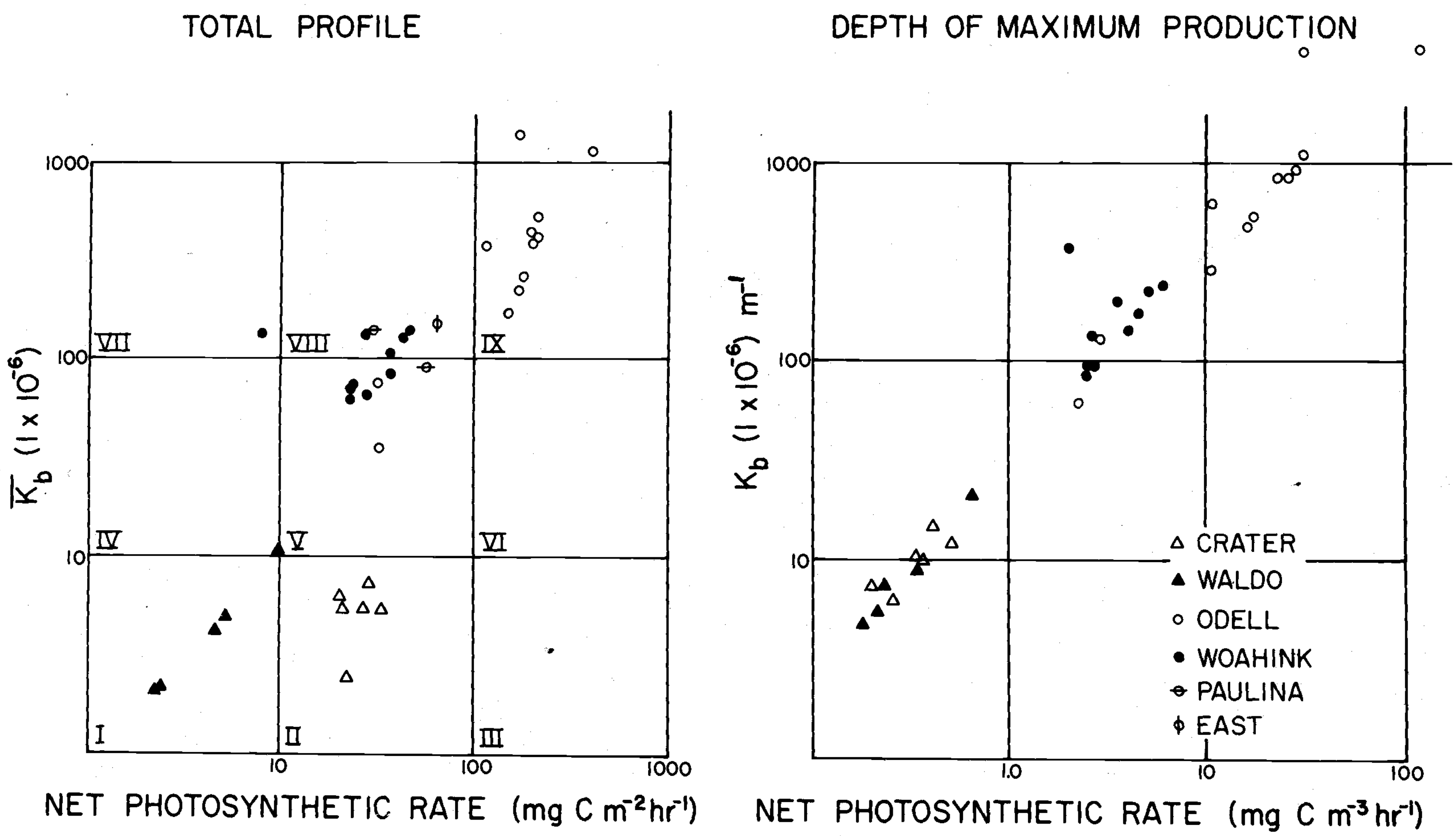


Figure 28. Relationships between phytoplankton primary productivity and radiant energy absorbed by cells in photosynthesis.

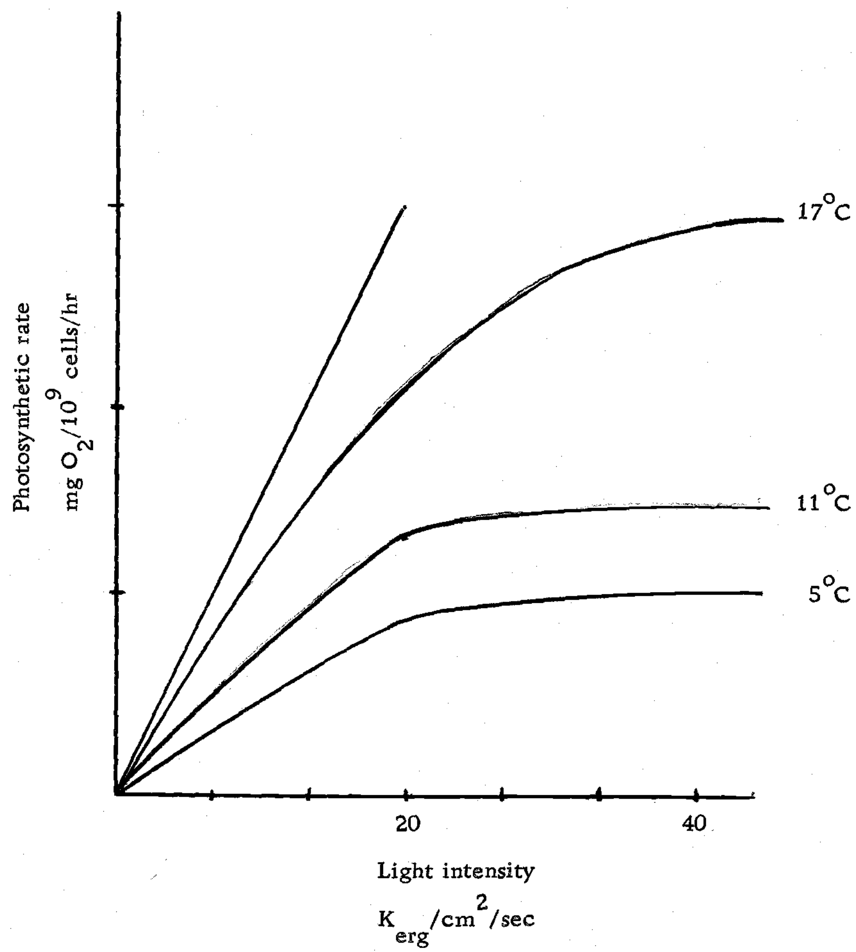


Figure 29. The limitation by temperature of the light controlled rate of photosynthesis in <u>Asterionella sp</u>. (Talling, 1957).

nutrients may be optimal; light within limits of tolerance; high photosynthetic efficiency.

Quadrate III: nutrients, temperature and light are perhaps optimal; a very high photosynthetic efficiency.

Quadrate IV: light and nutrients may exceed the limits of tolerance; temperature probably favorable; low photosynthetic efficiency.

Quadrate V: lake becoming more nutrient-enriched; light and temperature probably within the limits of tolerance; increase in biomass results in a higher rate of production; photosynthetic efficiency lower than Q II but higher than Q IV.

Quadrate VI: conditions less favorable than in Q III; still, a highly efficient use of available light and nutrients.

Quadrate VII: light, temperature and nutrients may or may not be favorable; very low photosynthetic efficiency (i. e., large biomass, but very low production); possibly indicative of senescent populations.

Quadrate VIII: conditions similar to those in Q V; however, lower photosynthetic efficiency and perhaps larger biomass.

Quadrate IX: nutrient-enriched; high yield at a relatively low efficiency; light and temperature well within limits of tolerance.

Quadrate X (directly above IX): rate of eutrophication increasing rapidly; lower photosynthetic efficiency than in Q IX.

Some basic information can be gained about the lakes by noting their positions on the grid. An initial inspection might indicate the following: (1) the factor or factors that are restraining or accelerating the rate of eutrophication and (2) the efficiency of energy intake by phytoplankton (one would expect that phytoplankton in enriched lakes use light and nutrients less efficiently). Thereafter, periodic plotting of productivity data on the grid would make it possible to (1) determine the extent to which the lakes have evolved in response to certain environmental factors and (2) determine the rate at which the lakes are currently evolving because of these factors.

It is proposed that the grid be used to classify lake environments. The system will serve to diagnose, to a degree, the causes of lake eutrophication, and will continue to provide an instantaneous assessment of lake productivity.

IN RETROSPECT

As has been pointed out in an earlier section, it is possible to classify each of the four study lakes as oligotrophic because of certain limnological features that they possess. Nevertheless, as the study showed, the lakes were found to be quite different in primary productivities and planktonic standing stocks. This, then, would place the lakes at different levels of trophy, whereupon the term "oligotrophy" would become a misrepresentation.

The lakes were divergent in response to certain environmental factors. Human involvement had, by far, the greatest effect. Thus, the grouping of these lakes into an identical trophy category simply because they possess all the traditional attributes of an oligotrophic lake is not realistic and does not provide an accurate assessment of individual lake productivity. Neither does it indicate how rapidly certain lakes are eutrophicating due to artificial (man-induced) enrichment.

Two fundamental problems are encountered when attempting to classify one or more lakes: first, a lake classification system is built upon a rather discrete set of taxonomic categories which are derived with the intent of accounting for all the lakes that are being considered. Recall, for example, the attempts to classify lakes on the basis of biological productivity by using three basic categories (i. e., oligotrophy, eutrophy, dystrophy). In nature, as one might suspect, lakes exist as a continuous array of environments, ranging from the biological extremities of ultra-oligotrophy (e.g., Waldo Lake) to the middle-aged status of mesotrophy (e.g., Odell and perhaps even Woahink and Crater lakes) to the final phases of advanced eutrophication (e.g., Klamath Lake, Oregon; Hazel, 1969). Any lake that can be placed, confidently, into one of these three basic trophy categories is the exception rather than the rule. Recognizing this, one is faced with the task of either subdividing the three basic categories, or deriving some additional ones so as to include more lakes than the exceptional few. But, as we saw, various endeavors to do this have resulted in a confusion of lake typology as exemplified in Jarnefelt's (1958) proposed classification. Thus, in the final analysis, we must admit that every lake is a unique environment and the attempt to approach it systematically is controversial.

A second problem is brought out by the fact that lakes are undergoing continuous physical, chemical, and biological changes in response to natural or cultural impositions. As a result, lakes will evolve or age by advancing to a higher level of trophy. Thus, a lake classification that was once fitting may no longer be applicable (e.g., consider the trophy change that has taken place in Odell Lake over the past few years in spite of its "oligotrophy" classification). What is needed then, is a periodic re-assessment of lake productivity and, if possible, a re-assignment of respondent lakes to an advanced trophy status.

The need for an adaptable classification system that would take into account the continuous process of lake evolution was emphasized. Such a system, based on the relationship between phytoplankton primary productivity and light energy absorbed by phytoplankton for photosynthesis, was proposed. The system will provide a more precise set of criteria for classifying lakes and, most important, will have predictive power. Certainly this will be needed, considering that most of our valuable water resources are being threatened by man's involvement with nature.

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