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PRIMARY PRODUCTIVITY AND LIMITING FACTORS IN THREE LAKES OF THE ALASKA PENINSULA

by
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of the requirements for the degree of
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INTRODUCTION

The lakes draining into Bristol Bay along the base of the Alaska Peninsula are nurseries for juveniles of the red salmon, Onchorhynchus nerka (Walbaum), spawned in tributaries of the lakes. Although the other Alaskan Pacific salmons are also taken in the coastal fishery, the reds (sockeyes or blue-backs, as they are sometimes called) contribute most to making the Bristol Bay fishery one of the most valuable fisheries in the world. Fluctuations from year to year in the abundance of the red salmon have prompted many investigations. Despite continued effort, many aspects of red salmon ecology are as yet imperfectly understood.

The objectives of this investigation were to measure and compare the primary productivity of certain red salmon nursery lakes, find what factors were limiting, and determine how basic productivity might be increased. The opportunity to make the study arose through the interest of the United States Fish and Wildlife Service in ecological factors that might affect the numbers and condition of young of this important species. The field work was conducted from the Brooks Lake Research Station. This installation, established in 1940, has living quarters and laboratory facilities including electricity

and running water. It is supplied primarily by amphibious aircraft. Its overall research objective is to determine how physical, chemical, and biological factors affect populations of red salmon in fresh water.

Considerable evidence suggests that the abundance of this salmon is determined by conditions prevailing during its early life in fresh water (Barnaby 1944). The growth of the species in fresh water, although only a fraction of that achieved in the sea, is of great importance in determining the percentage of a given year class that reaches sexual maturity (Foerster 1954). That food supply is a limiting factor in some drainage systems was suggested by the inverse relationship between the average growth rate of juveniles and their numbers as found by Foerster (1944). Supporting the contention that food may be a very important limiting factor are the inverse correlations between available zooplankton and size of the populations of the red salmon, observed by Ricker as far back as 1937. More recently Nelson (1958), in following the growth of red salmon juveniles and smolts in fertilized Bare Lake, found a closer relationship between their growth rate and gross photosynthetic productivity than might have been expected in view of the large number of environmental factors to be considered in addition to food supply.

A logical point to begin the attack on the problem of food supply in the aquatic environment is at the level of the photosynthetic primary producers. These organisms are not all

restricted to photosynthetic production of organic matter, nor do they represent the only primary producers in the lake. The photosynthetic carbon fixation by phytoplankton and bacteria has, however, been demonstrated to represent the major portion of organic matter in lakes. Chemosynthetic productivity is of secondary importance (Kuznetsov 1956). Changes and differences in this basic productivity within lakes and among lakes may be expected to influence, although not always directly, the rate of accumulation of organic matter in successive trophic levels. The natural fertility or lack of fertility and rate of primary production in lake waters is therefore of fundamental importance for understanding and comparing lakes as biological units.

Techniques of measuring primary productivity by phytoplankton were developed late in the first quarter of this century. Steemann Nielsen (1952) credits Atkins (1922, 1923) with the first attempt at the indirect measurement of organic production in the sea. His estimates were based on loss of carbon dioxide and phosphate from the water as it was taken up by phytoplankton. Before this time, biologists had relied on a direct measure of standing crop, which, by its static nature, was of limited use in understanding a system in constant motion. A very important step in measuring the rate of photosynthesis was the development of the oxygen technique, as apparently first used by Putter (1924). Application of the oxygen method spread. Gaarder and Gran (1927), Schomer and Juday (1933), Vinberg and Iarovitzina (1939), Riley (1940), Nygaard (1955), and Odum and Odum (1955), to name a few, employed it. Chlorophyll content has also been used as a means of

estimating photosynthesis. Manning and Juday (1941), Riley (1940, 1941), Gardener (1943), Gessner (1949), and Ryther and Yentsch (1957) have extracted chlorophyll for this purpose. Daily variations in chlorophyll content are complicating factors in this technique (Yentsch and Ryther 1957). Verduin (1956) has used pH change as still another method of measuring photosynthesis. A major step in increased sensitivity at measuring primary productivity in natural water was achieved with the development of the C^{14} technique by Steemann Nielsen (1951, 1952). The relative merits of the oxygen, CO_2, nutrient uptake, C^{14}, and chlorophyll methods of measuring primary productivity are reviewed by Ryther (1956).

Paralleling the advance in techniques was growth in appreciation of the complexities of organic transfer through aquatic systems. From the first consideration of the lake as a microcosm (Forbes 1887) through the early diagrammatic representation of the food webs (Shelford 1913; Naumann 1925; Perfiliev 1929; and MacFadyen 1948) to the trophic dynamic approach of Lindeman (1942) and estimates of "bioactivity" by Ohle (1956), there has been a conceptual evolution in understanding the complexity of energy transfer through the ecosystem. The early work of Lindeman provided an important basis for development of the concept of productivity, although his early conception of trophic levels was criticized by Ivlev (1945) as an oversimplification of natural producer-consumer relations.

Confusion has arisen in the use of the words "production" and "productivity", because there has been a tendency to carry along

in their meaning the static and deep-rooted concept of biomass. Thienemann (1931), although the first to assess the terminology critically, was confused by considerations of energy and matter. Ivlev (1945) thought it inadvisable to use "potential productivity" because it does not reflect the existing state of the body of water in question. The terms and confusion of biomass and energy were generally clarified by MacFadyen (1948) and Dussart (1950). MacFadyen suggested the abandonment of "production" and the use of "productivity" as the rate of flow of matter. "Primary productivity" has been used in this study as the net rate of fixation of organic carbon by bacteria and phytoplankton in photosynthesis. During the summer of 1957 I made the first comparative measurements of primary productivity in three red salmon nursery lakes of the Alaska Peninsula with emphasis on physical and chemical factors which were limiting the process.

GEOGRAPHY

My studies in Alaska were centered some 260 air miles southwest of Anchorage, at the base of the Alaska Peninsula between latitudes 58° and 59° North, and longitudes 157° and 154° West (Fig. 1). With the exception of Lake Becharof, this area is all within the boundaries of the Katmai National Monument (Fig. 2). Six years after the famous volcanic eruption of 1912 the Monument was established. Later it was enlarged to include approximately 4,215 square miles.

The aquatic and terrestial ecology of this area has been profoundly influenced by its geological history. The eastern half of the Katmai Monument is a glaciated region characterized by the rugged young mountains and volcanoes of the Aleutian Range. Some of the volcanoes are still active and glaciers are numerous. To the west the land slopes with gentle irregularity beyond the Monument's border to Bristol Bay. This bay is formed from the Bering Sea by the peninsula to the east and the mainland to the north. The hundred miles of coast line on the eastern side of the peninsula included in the Monument are separated from Afognak and Kodiak Islands by Shelikof Strait.

The drainage pattern originating in part from the snow and glaciers of the mountains is dendritic on both the eastern and western sides of the peninsula. The proximity of the Aleutian Range

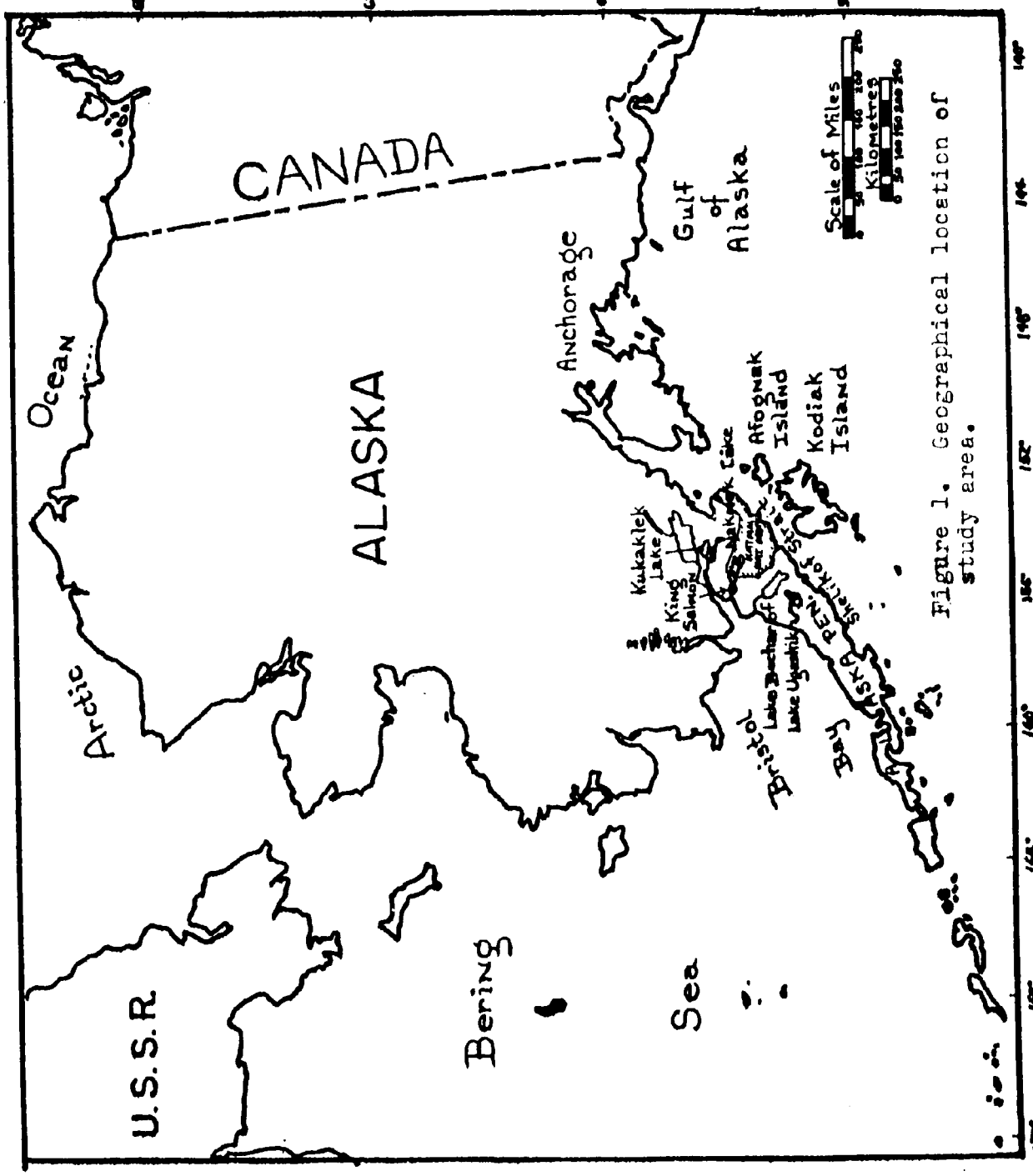
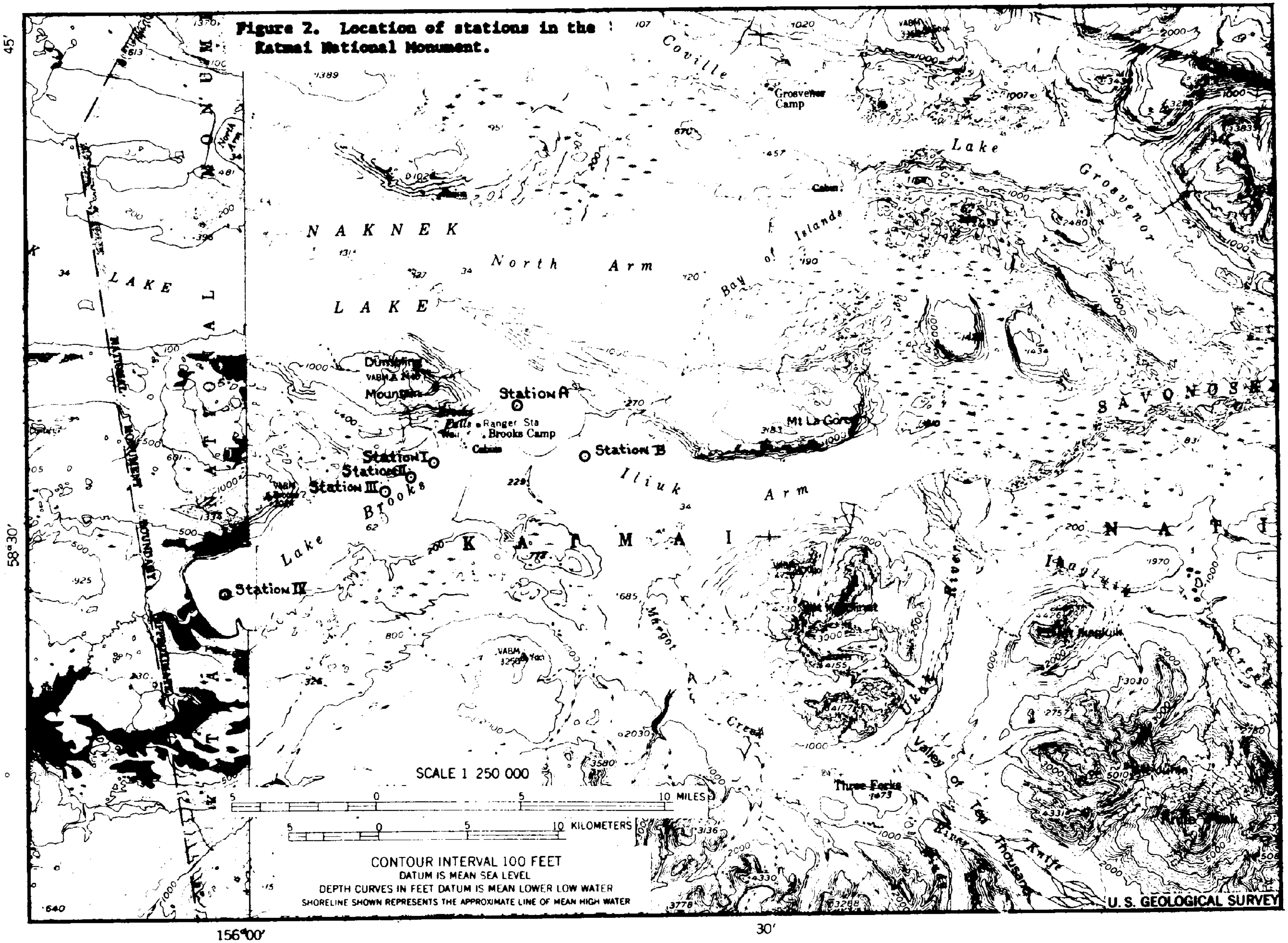


Figure 1. Geographical location of study area.

Figure 2. Location of stations in the Katmai National Monument.



to the eastern side gives the streams a steep gradient over their relatively short course to the coast. A few, nearly attaining base level, meander back and forth in the temporary channels on the valley floor before entering the Shelikof Strait. To the west of the divide, although the initial pattern is similar, the streams thread down the longer U-shaped valleys to lakes or, like King Salmon River, directly into the Bristol Bay. The low land is poorly drained. Small natural ponds and beaver impoundments dot an extensive area of tundra. Mud flats occupy extensive reaches of the immediate coast line.

Although volcanic origins may be considered for lakes in such a region, Atwood (1911), in a survey of the peninsula, suggested that the four large lakes (Kukaklek, Naknek, Becharof, and Ugashik) in the northeastern portion of the peninsula owed their depth and outline, if not their existence, to ice gouging. He further pointed out that except for Ugashik, all were in valley courses leading from the mountains to the shores of Bristol Bay.

The eruption of 1912, originally attributed solely to Mount Katmai, is now believed to have included the eruption of Novarupta. The total upheaval was of great magnitude, flooding what is now called the Valley of Ten Thousand Smokes with more than a cubic mile of tuff (Fenner 1923), as well as depositing a great quantity of silicious ash over a wide area. The Ukak River and its tributaries have now cut down through a hundred feet of this pumice and ash to form a narrow canyon. Since Robert F. Griggs led the first post-eruption expedition to the area, numerous geologists

have visited the area to study the sequence of geologic events that marked the eruption.

Ecologically the area is of considerable interest. The furthest southwestward advance of the white spruce (Picea glauca) forests covers a good portion of the monument. This spruce together with cottonwood (Populus deltoides Marsh.), balsam (Populus balsamifera L.), alder (Alnus), and birch (Betula) grade gradually into the tall arctic reed grasses (Calamagrostis sp.), which in turn yield to the lichens, mosses, and a variety of small flowering plants of the tundra. Short stands of willows (Salix spp.) surround the multitude of tundra ponds to the south and west. On the gentler mountain slopes a variety of shrubs and bushes flourish.

The climate is warmer than might be expected at this latitude and is generally maritime in nature. The proximity of the Alaska Current to the east and the Bering Sea to the west have a stabilizing effect on the temperature, although continental air masses cause infrequent extremes. U. S. Weather Bureau climatological data for King Salmon, Alaska, are available since 1928. This is the government weather station nearest to Brooks Lake which maintains complete records. A record low of -40°F (-40°C) was recorded in February, 1954. The average annual rainfall at King Salmon is 20.39 inches. During the summer of 1957 the four month total at Brooks Lake was 17% greater than at King Salmon. A comparison of summer rainfall at Brooks Lake and King Salmon since 1942 gives very similar values. Rainfall at Brooks Lake during

June, July, August, and September averaged 1.87, 2.30, 5.31, and 3.64 inches respectively during 1942-1957, exclusive of 1943, 1945, and 1946. Precipitation during the summer of 1957 was below these averages (United States Department of Commerce Weather Bureau 1957).

THE LAKES

Brooks

Brooks Lake is 10.7 miles long and varies in width from 2.5 to 4.0 miles. The surface area, exclusive of islands, is approximately 28.2 square miles (18,060 acres; 7308.5 hectares). It is 18.9 meters (62 feet) above mean sea level, and the long axis lies northeast by southwest. There are three prominent islands in the lake with a total surface area of 164 acres (66.4 hectares). During the 1957 field season the depth of the basin was carefully ascertained with a Raytheon depth recorder. Morphometry was calculated by Olson's system (1949). Maximum and mean depths were found to be 101.5 meters (333.0 feet) and 45 meters (147.6 feet) respectively. Shore development was 1.48. The northeast end has a broad, sandy littoral zone extending about a half mile from the shore. The other end of the lake has a similar shelf of about half the width. The northwestern side of the basin drops off more rapidly than the southeastern, reflecting the greater proximity of the mountains to the west.

The general U-shaped basin of Brooks Lake is a smaller and perhaps somewhat deeper model of the other basins of probable glacial origin in the area. An area of over 12 square miles of the lake has a depth of 61 meters (200 feet) or greater, and an area of about

five square miles has a depth of 73 meters (240 feet) or more. Mountains afford wind protection along the northwest and southwest sides. Both ends are open providing a maximum fetch for winds blowing in the direction of the long axis.

To the northeast, the Brooks River drains the lake into Naknek Lake, 9.2 meters (28 feet) below. At the southwest end of Brooks Lake, Headwater Creek, its major tributary, meanders across a broad valley with only a slight gradient near its mouth. A number of small tributaries are found along both sides of the roughly rectangular lake. Those along the southeast side are typically clean, gravel bottomed streams which find their source in the small ponds and low lands at the base of the mountains. All five species of Alaskan Pacific salmon utilize these streams, Headwater Creek, and, to a limited extent, the lake shore for spawning. The tributaries to the northwest are smaller and, for the most part, find their sources near the shore in beaver ponds or narrow gullys. During the 1956 and 1957 seasons, salmon were observed to spawn in only one of these streams.

Naknek

Naknek Lake, the largest body of water in the Monument, covers approximately 125,000 acres (50,586 hectares) at an elevation of 10.36 meters (34 feet). From the main lake, two arms extend to the east. The more northerly arm receives very little of the major drainage. The southerly Iliuk arm receives the outflow of Coville and Grosvenor lakes via the Savonoski River as well as the Ukak

River drainage from glaciers and the Valley of Ten Thousand Smokes. Although complete soundings have not been made in the various parts of this lake, extensive areas of water less than 25 meters in depth exist just off the mouth of the Brooks River. Contours based on 23 soundings in the southern portion of the lake (exclusive of the Iliuk arm) give an approximate mean depth of 20 meters (65.6 feet).

Both the Savonoski and the Ukak Rivers contain a great deal of suspended pumice and ash which reduces the transparency of Naknek Lake. The turbidity decreases progressively as one procedes away from the tributaries toward the Naknek River outflow, but is still quite evident near the mouth of Brooks River where the inflow of clear water is in sharp contrast.

As mentioned previously, these lake basins appear to be the continuation of glacial valleys extending from the mountains to the east towards Bristol Bay. The Naknek Lake basin almost certainly has a deep deposit of pumice and ash from the eruption and from the tributary streams already noted. Rather steep mountains rim the lake. The highest of these is Mount Katolinat, rising abruptly from the south shore of the Iliuk arm to an elevation of about 1402 meters (4600 feet.)

Becharof

Lake Becharof, second largest of Alaska's inland lakes, is approximately 50 miles (80.5 kilometers) south of Naknek. Its long axis is about 40 miles (64.4 kilometers) in a general east-west direction. The greatest north-south dimension is approximately

15 miles (24.1 kilometers). The large Egegik River drains the lake into Bristol Bay, 35 miles (56.3 kilometers) to the west. The outlet, although a rapids strewn with boulders, is navigable to small boats. The lake's shoreline is more regular than that of Naknek Lake and lacks the rim of mountains except near the east end. It is beyond the advance of the white spruce forests and is bordered for the most part by a rocky shore with tundra beyond.

Soundings were taken to a distance of four miles east of the outlet. The bottom was rather flat and sandy in this area with a fairly uniform depth of about 25 meters (82 feet). Greater depths were encountered further east of the outlet. The drainage into the lake is through a number of small to moderate size tributaries.

METHODS USED FOR MEASURING PRIMARY PRODUCTIVITY WITH C^{14}

Lake Studies

The C^{14} technique for measuring primary productivity of phytoplankton populations in natural waters, first presented by Steemann Nielsen (1951), involves the addition of a small amount of radioactive carbon as sodium carbonate to water samples contained in clear glass bottles. Determination of the amount of carbon fixed is based on the assumption that rates of photosynthetic fixation of C^{14} and C^{12} differ only slightly because of the slower uptake of the heavier, radioactive isotope of carbon. This difference of 6%, called isotope effect, is corrected for in the calculations. Because preliminary experiments indicated that non-photosynthetic uptake of C^{14} exceeded the 1% of photosynthetic uptake suggested by Steemann Nielsen (1952), dark bottles were included with each experiment at selected depths at all stations to measure this.

Water samples were collected from selected depths at each station with a Kemmerer water sampler and transferred to 150 ml, clear, glass-stoppered bottles. Ordinarily, collections for an entire experiment were made within one hour. When all the samples for an experiment were on hand, five microcuries of C^{14} were added to each sample bottle. The sodium carbonate was prepared by Volk Radio

Chemical Company, Chicago, in 100 ml serum bottles with an activity of 2.5 microcuries per ml. An automatic hypodermic syringe (Cornwall No. 1251 B D) was adapted to facilitate its rapid injection into the 150 ml, clear, glass-stoppered bottles without danger of contamination (Figure 3). This procedure allowed a minimal time lapse for C^{14} addition among the bottles at each station and among stations. The time of C^{14} addition was carefully noted so that the isotope would be available to the algae for the same interval in each bottle. Each of these bottles had a metal snap tied to its neck for ease of attachment to hog rings secured at measured intervals to a line which, in turn, was attached to a float at each permanent station.

In Brooks Lake the three main study stations were located over depths of 5 (Station I), 35 (Station II), and 65 (Station III) meters, and were as representative as possible of the lake as a whole. The sites were marked by well anchored buoys. Each float was made from an inflated automobile inner tube securely lashed to a wooden crosspiece. A portable float of the same construction was also utilized as a supplementary station at the south end of Brooks Lake as well as in Naknek Lake and Lake Becharof.

Sample bottles were suspended at one-meter intervals from the surface to five meters at all stations. At Stations II and III bottles were also placed at 10, 15, 20, 25, and 35 meters. In addition, Station III had bottles at 50 and 65 meters. After four hours, the bottles in each series were retrieved and placed in a lightproof, insulated wooden box in which they were transported without delay to the laboratory for prompt filtration.



Figure 3. An automatic hypodermic syringe was adapted to facilitate rapid injection of $Na_2C^{14}O_3$ into sample bottles.

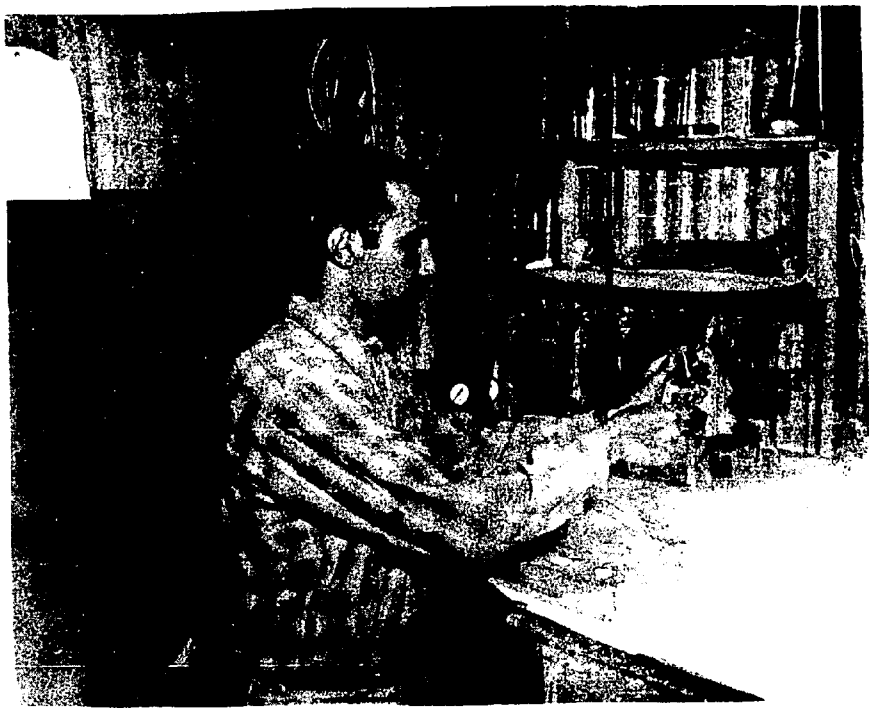


Figure 4. Millipore filtering of lake phytoplankton was done by a 110-volt centrifugal vacuum pump connected to six vacuum flasks.

Filtering equipment included a 110-volt centrifugal vacuum pump connected to six vacuum flasks (Figure 4). Each flask had a funnel which was fitted to a coarse porosity, fritted glass disk. Funnel and disk were held securely together by a removable, spring-loaded clamp. A precut, 1.1875 inch (3.016 centimeters) HA Millipore filter (Millipore Filter Corporation, Watertown, Massachusetts) was sealed between the funnel and the disk by the pressure of the clamp. The 0.5-micron HA Millipore filter was selected because of its ability to retain the nannoplankton (Goetz and Tsuneishi 1951; Goldberg et al. 1952).

Light meter readings, Secchi disk depths, and temperatures were recorded at each sampling period. To insure uniform light exposure, the sample bottles were taken one at a time from the lightproof insulated dark box and treated in the following manner. After shaking the sample to resuspend any settled plankton, 100 ml were pipetted into the funnel and filtered at a maximum vacuum of 15-20 lbs. per sq. inch. Two ml of a pale blue Janus Green B dye solution were added to the sample to show whether or not leakage occurred over the edge of the filter.

After the sample was filtered, ten ml of .003 N HCl were pipetted onto the filter to remove any residual carbonate adhering to it or to the organisms and to wash any organisms from the surface of the funnel to the filter. Addition of ten ml of 3% formalin for preservation of the organisms followed. Then the funnel was removed and the wet filter placed in a labeled 1.25 inch (3.18 centimeters) diameter aluminum sample pan for drying. After dessica-

tion, the filter was glued to the pan with a thin film of nitrate airplane dope and stored for subsequent counting.

Because radiation counting equipment was not available at the Brooks Lake Station, selected dried samples, glued to their aluminum pans, were air mailed to Ann Arbor, Michigan, for counting during the field season. The rest were stored and counted later. The results of the radioactivity determinations on the mailed lots were obtained within two weeks and provided a quality control for the field operations.

To assess total experimental error, duplicate samples were taken at each station once during the period of field operations. Each procedure was duplicated including the collection of two separate Kemmerer water samples at each depth, the preservation of separate plankton samples, etc. A simple wire harness was attached at each level so that the two samples could be suspended at exactly the same depth during the experimental period.

Nutrient Experiments by Culture

The sensitivity of culture techniques for determining the availability of nutrients for phytoplankton growth has been recognized for many years. Schreiber (1927) working with sea water, Strøm (1933) using Schreiber's approach in fresh water, Chu (1942), Edmondson and Edmondson (1947), Rodhe (1948), Potash (1956), and Provasoli et al. (1957), to name a few, have developed and used culture techniques with considerable success.

Phytoplankton population growth has been measured most frequently by direct cell counts (Serfling 1949), although light extinction coefficients (Åberg and Rodhe 1942), chlorophyll (Ryther and Yentsch 1957), volumetric, and gravimetric measurements have also been used. The low plankton concentrations encountered in the natural Alaskan waters used as media rendered all these techniques less applicable than the C^{14} method already discussed (Steemann Nielsen 1952). Therefore, the main experiments in this study involved a comparison of the rate of carbon assimilation in the different cultures. The measurement of growth was not dependent upon a significant increase in cell numbers during the culture period, but rather upon an increase in the rate of photosynthetic accumulation of organic carbon which may not be immediately manifest in a numerical increase. I was able to demonstrate the extreme sensitivity of this technique for detecting nutrient limiting factors in the laboratory at Ann Arbor, Michigan, before the field work was undertaken.

During the summer of 1957, fourteen culture experiments were conducted. In most of them, lake water with its natural plankton population (chiefly green algae and diatoms) was placed in screw top, widemouth, gallon or half-gallon jars in a floating crib near the lake outlet. Thus, the cultures were at lake surface water temperature and light conditions, and the rocking of the crib by current and wave action helped keep the algae in suspension. Jars were moved daily from place to place within the crib to eliminate any variability due to position. Vitamins B_1 and

B_{12}, KH_2PO_4, Na_2CO_3, $MnSO_4$, $MgSO_4$, $Ca(NO_3)_2$, and a variety of oligo-elements (Fe, Cu, Zn, and Co) chelated with EDTA (ethylenediamine tetra-acetic acid), as used by Provasoli and Pintner (1953), were tested separately and in certain combinations to determine which were most limiting. Other culturing was done with Brooks Lake water shipped to the laboratory in gallon polyethylene bottles. In addition to the above mentioned chemicals $Mg(NO_3)_2$, $NaNO_3$, Na_2SO_4, $CaSO_4$, K_2SO_4, and K_2HPO_4 were used in these cultures.

Bottom sediment extract was also assayed in order to determine its value as a phytoplankton nutrient. This extract was prepared from a sample of the bottom sediment collected at Station II. A volume of 400 ml was thoroughly mixed with an equal amount of lake water and allowed to settle for several hours. The liquid was then decanted and centrifuged twice in a Foerst Constant Speed Centrifuge. As a final treatment to remove microplankton and bacteria, the extract was passed through a Millipore filter. After analysis for phosphorous, nitrite, alkalinity, hardness, hydrogen-ion concentration, and silica, the filtrate was added to cultures in different percentages by volume. One or more controls were maintained with these as with all culture experiments.

Lake water for the culture media was collected from the surface in a clean, stainless steel bucket at Station I. After careful mixing, the total sample was divided into subsamples in gallon or half-gallon widemouth glass jars. Three liters of lake

water were used in the former size and 1.0 or 1.5 liters in the latter.

A measure of the rate of production in the cultures was accomplished by further subsampling with the addition of C^{14}. One hundred ml of each culture were pipetted into a 125 ml glass stoppered bottle after first shaking the jar to insure uniformity of plankton distribution. When all these subsamples had been taken, 2.5 microcuries of C^{14} were added to each. The sample bottles were then suspended in the river from a line stretched perpendicular to the direction of river flow in such a manner that the bottles remained just beneath the surface. One or more dark bottles were included as a measure of non-photosynthetic uptake of C^{14}. After a four-hour incubation period, samples were filtered and their radioactivity was measured in the same manner as the lake samples. To be certain that the addition of C^{14} as Na_2CO_3 was not altering the rate of photosynthesis, the oxygen method of measuring photosynthesis was used under controlled conditions. Various concentrations of $Na_2C^{14}O_3$ up to the highest quantity used in lake or culture experiments were tested. Rate of oxygen production was not measurably altered by the addition of sodium carbonate. (See p.62)

In mixed algal populations it is possible that the presence of one species may inhibit the growth of another (Akehurst 1931; Lefevre et al. 1949). Pratt (1943) on follow-up work with growth inhibiting substances from Chlorella vulgaris demonstrated the inhibitory effect of this substance on Chlorella pyrenoidosa as well as on mixed algal cultures. Rice (1954) and Proctor (1957)

showed the existence of similar antimetabolites with a number of different species of algae. In order to learn whether or not such an effect was extant in my experiments, unialgal culture series were conducted to eliminate possible interaction for comparison with cultures utilizing the natural lake plankton populations. A pure culture of the green algae, Ankistrodesmus falcatus (Rodhe), was obtained on proteose agar from the Algae Bank of the Indiana University Department of Botany. From this pure lot, the sterile Culture Solution VIII of Rodhe (1948) was inoculated.

The lake water used as a culture medium for the unialgal experiment was prepared by passing ten liters of surface water from Station I through a Millipore filter, thus removing bacteria, algae, and particulate matter. A liter of the filtrate was then placed in each of nine two-quart culture jars (clear glass). After filtering the Ankistrodesmus falcatus from Rodhe's Solution VIII, the algae were washed with and resuspended in distilled water. Following the addition of six ml (approximately 10,000 cells) to each culture, various nutrients were added. Periodic sampling of these cultures was accomplished in the manner already described, with one exception. Because of the smaller culture volume, only 50 ml subsamples of each were incubated. The C^{14} was correspondingly reduced to 1.25 microcuries. In this experiment, as in the others, duplicate samples of cultures were taken to determine the experimental error of the techniques employed. Ankistrodesmus falcatus was again used in subsequent pure culture experiments in the laboratory at Ann Arbor, Michigan.

It has been suggested that results of culture experiments may not be readily applied to the natural environment because restriction of plankton in a container does not duplicate the natural conditions and may favor the development of atypical forms. To offset this, in addition to using the natural lake plankton, every attempt was made to duplicate the natural lake light and temperature conditions in the experimental cultures. However, to strengthen the findings, a test was conducted in the lake itself of nutrients found to be limiting. Since direct application of nutrients to the lake as a whole was not possible and because the C^{14} technique was sufficiently sensitive to rapidly detect changes in the rate of photosynthesis, short term nutrient experiments were conducted at Station I.

Sampling Schedule

Radioactive carbon experiments were conducted from the first half of June to September, 1957, with reduced sampling to October. Lake studies were run every five days at the three permanent Brooks Lake stations simultaneously. A diurnal study was also initiated to determine variation in the daily photosynthetic rate. Naknek Lake was sampled every 15 days, and the south end of Brooks Lake at least once a month. Single comparative measurements were made in both Lake Becharof and the Iliuk arm of Naknek Lake. One to three culture experiments were continuously in progress during the summer. Sampling dates were usually staggered so that only one culture required attention on a given day.

Methods of Plankton Sampling and Water Chemistry

During the regularly scheduled C^{14} lake experiments, plankton was sampled by collecting 250 ml of water from the same Kemmerer water bottle samples used for the C^{14} uptake measurements, and by taking vertical hauls with a #20 Wisconsin closing net. During the first two sampling periods plankton were collected at each C^{14} sampling depth. After this they were taken on alternate C^{14} sampling dates (i.e. every ten days) at the surface and at depths of 5 meters at each station, 35 meters at Station II, and 35 and 65 meters at Station III. On the alternate sampling days, vertical hauls were made with the Wisconsin closing net from 5 meters to the surface at all three stations, 35 to 5 meters at Stations II and III, and 65 to 35 meters at Station III.

A ten-day schedule at the three permanent Brooks Lake stations was also established for chemical water analysis, Clarke-Bumpus plankton tows, and centrifuge plankton samples. Depths for this schedule were surface and 5 meters at Stations I, II, and III, 10 and 25 meters at Stations II and III, and 35 and 50 meters at Station III.

Laboratory Preparation and Analysis

From the 250 ml water samples taken for plankton analysis during the lake productivity experiments, 100 ml were preserved by adding formalin to make a 3% solution for inverted microscope analysis and another 100 ml were filtered on a gridded Millipore filter. To achieve a more random distribution of plankton on the

filter than could be obtained with the funnels used for C^{14} filtering, 0.875 inch inside diameter cylinders of plexiglass were fitted with flanges so that they could be clamped directly to the fritted disks of the vacuum system. After washing down any organisms adhering to the sides of the cylinders with 3% formalin, the filters were placed on clear, labeled, microscope slides and allowed to dry several hours in a dust free environment. After drying, the filters were cleared with two drops of cedarwood oil and one drop of terpineol. Mounting medium and a number one cover slip were then added. Vertical haul plankton samples were preserved immediately with formalin in the same manner as the inverted scope samples.

Two liters of water from each sampling depth were centrifuged in a Foerst Constant Speed Centrifuge. The sample was then placed in a calibrated centrifuge tube and hand centrifuged. After a wet volume determination was made, the sample was resuspended by shaking and subsamples were placed in a Sedgwick Rafter Counting Chamber for identification and enumeration of organisms.

Water analyses included the determination of phosphate, nitrite, silica, turbidity, dissolved oxygen, pH, alkalinity, and total hardness. Photocolorimetric determinations in ppm were made for phosphate, nitrite, and silicon, using standard procedures outlined in the Klett-Summerson photoelectric colorimeter "Industrial Manual."

Turbidity measurements were made with the colorimeter until 24 July when a Hellige turbidimeter became available. The early values were then converted to the Hellige readings. The

Hellige turbidimeter, sensitive to turbidity ranges below .80 ppm SiO_2, was more satisfactory than the Klett-Summerson because of the low turbidity encountered in Brooks Lake.

Total hardness determinations were made with a "BKH Water Hardness Outfit." Hydrogen-ion concentration values were obtained with a Hellige pocket comparator, glass disk type, using bromthymol blue-D indicator. Alkalinity was determined by titration with methyl orange indicator. Oxygen content was measured by the unmodified Winkler method as nitrogen was below 0.1 ppm (Standard Methods 1955). Water shipped to Ann Arbor in polyethylene containers was analyzed by flame spectrophotometer for magnesium, sodium, potassium, and calcium.

Radioactivity Determinations

The validity of conclusions based on the measurements of radioactivity depends upon the accuracy of the correction of errors in counting and, since no machine detects all the disintegrations, on the degree of accuracy attained in determining the efficiency of the machine employed. There is a definite probability at any given time of a nucleus disintegrating regardless of the atom's environment. The rate of disintegrations (which register as counts) therefore follow either a normal or Poisson distribution (Lapp and Andrews 1955). Because the standard deviation closely approximates the square root of the total counts, the desired accuracy can easily be achieved by adjusting the counting time. In this study samples were counted to $\pm$ 3% or better.

Natural cosmic and machine radiation must also be corrected for. Since samples from dark bottles were always included in the experiments reported here, these samples not only served to measure counts from non-photosynthetic uptake by chemosynthesis or adsorption, but also served as a basis for subtracting machine and sample background as well. Thus, in one subtraction all background and non-photosynthetic uptake could be eliminated without the necessity of determining these factors individually.

In determining the amount of C^{12} assimilated in photosynthesis it is necessary to know how much C^{14} was available. The $Na_2C^{14}O_3$ used was prepared with an activity of 2.5 microcuries per ml. This absolute activity was based on a National Bureau of Standards calibrated source with an accuracy of $\pm$ 10%. This figure reflects the extreme difficulty in determining the absolute activity of C^{14}. The error involved in preparing the $Na_2C^{14}O_3$ in 100 ml serum bottles was only about $\pm$ 0.3%.

As noted above, the C^{14} technique necessitates conversion of detected counts to absolute counts. Steemann Nielsen (1952) filtered barium carbonate-C^{14} of known activity onto a collodion filter and plotted a self-absorption correction curve. On the assumptions that the geometry of the filtered barium carbonate was identical with the geometry in measuring the activity of filtered plankton, and that because the weight of the plankton was always below 0.1 mg per three sq. cm, the activity of plankton could be directly compared with barium carbonate of known activity. Self-

absorption in the plankton were therefore disregarded.

Because of the low energy Beta emission of the C^{14} atom (0.155 Mev), I felt that self-absorption should not be ignored nor should a counting efficiency be based on a barium carbonate standard if a better one could be devised. To circumvent these problems, my calibration was based on filtered algae of known activity. To prepare and calibrate this source, duplicate samples of the alga, Ankistrodesmus falcatus, and nannoplankton grown in a C^{14} rich medium were killed with formalin, filtered, washed, and resuspended in distilled water.

One set of the duplicate samples was dessicated in flasks, burned to CO_2 (Van Slyke and Folch 1940), and counted in accordance with the gas phase counting method of Bernstein and Ballentine (1950). The high efficiency gas phase counts were then converted to absolute counts with an efficiency value determined by combusting and counting a number of calibrated samples (Series A, June 1949, S. S. No. GS3849, PO No. 155382, National Bureau of Standards).

Quadruplicate samples, taken for the second set, were Millipore filtered, dessicated, and counted with the same equipment used for all the experimental counts. The algae suspension was sufficiently dilute to provide single cell thickness on the filters. The true efficiency of the equipment used in counting an algal source of known activity could thus be obtained by comparison with the gas counts. By removing the C^{14} from the algae and counting it as CO_2, the problems of self-absorption and geometry have been eliminated.

The replicated samples from gas conversion counts and Millipore filter counts allowed a statistical evaluation of the ratio derived (Arkin and Colton 1953). This efficiency was equal to 31.63% with a standard deviation of $\pm$ 0.64% (31.63 $\pm$ 0.20).

RESULTS

The Primary Productivity of Brooks, Naknek, and Becharof Lakes

The need and the desire to classify lakes has long been a motivating force in limnology. In the past a great variety of geographical, physical, chemical, and biological criteria have been employed for this purpose with varying degrees of success. Recently Nygaard (1955) has added productivity to the list. Since productivity must necessarily be a synthesis of the host of variables acting in any lake, it is likely to emerge the most important. Nygaard, who compares his Compound Index with primary productivity measurements, points out the danger of predicting productivity with chemical measurements alone and the improbability of founding the concepts of oligotrophy and eutrophy exclusively on the basis of productivity.

In the study reported here, regular biweekly measurements of photosynthesis with C^{14} were made in Naknek Lake for comparison with the more intensive sampling in Brooks Lake. A single measurement in Lake Becharof was included because of the lake's size, importance, and decidedly different typology. Estimates of productivity on both a unit volume and surface area basis were possible because sufficient measurements were made at each sampling to construct a curve of the variation in rate with depth. By computing the total area under each curve by planimetry, the total

carbon fixation in the euphotic zone was obtained. The mean productivity per unit volume was calculated by dividing this figure by the depth of the euphotic zone. The mean primary productivity per unit of surface area was obtained by multiplying the average productivity per cubic meter by the depth of the euphotic zone or by the mean depth depending upon which value was lower. This is an important consideration if a meaningful comparison of primary productivity among lakes is to be made on a surface area basis. If the euphotic zone exceeds the mean depth, as was the case in Brooks Lake, the average surface area productivity is limited by the mean depth. In contrast, the estimated mean depth of Naknek Lake is greater than the euphotic zone. An areal estimate of productivity in this lake must therefore be restricted to the depth of the euphotic zone.

A marked diurnal variation in the rate of photosynthesis by plankton populations has been noted by Doty and Oguri (1957) and further investigated by Verduin (1957). A diurnal study was made at Brooks Lake, and the curve (Figure 5) for the rate of carbon fixation per hour formed the basis for converting the 4-hour measurements to daily net photosynthesis. Solar energy reduced to the photosynthetic range in Langley's per minute (15°C gram-calories/centimeter^2/minute) taken from Brooks Lake pyrheliometer recordings during the diurnal study is also given.

All measurements were corrected for seasonal variation in the visible portion of the spectrum (4000 Å to 7000 Å) penetrating a smooth water surface at sea level. The solar radiation values used

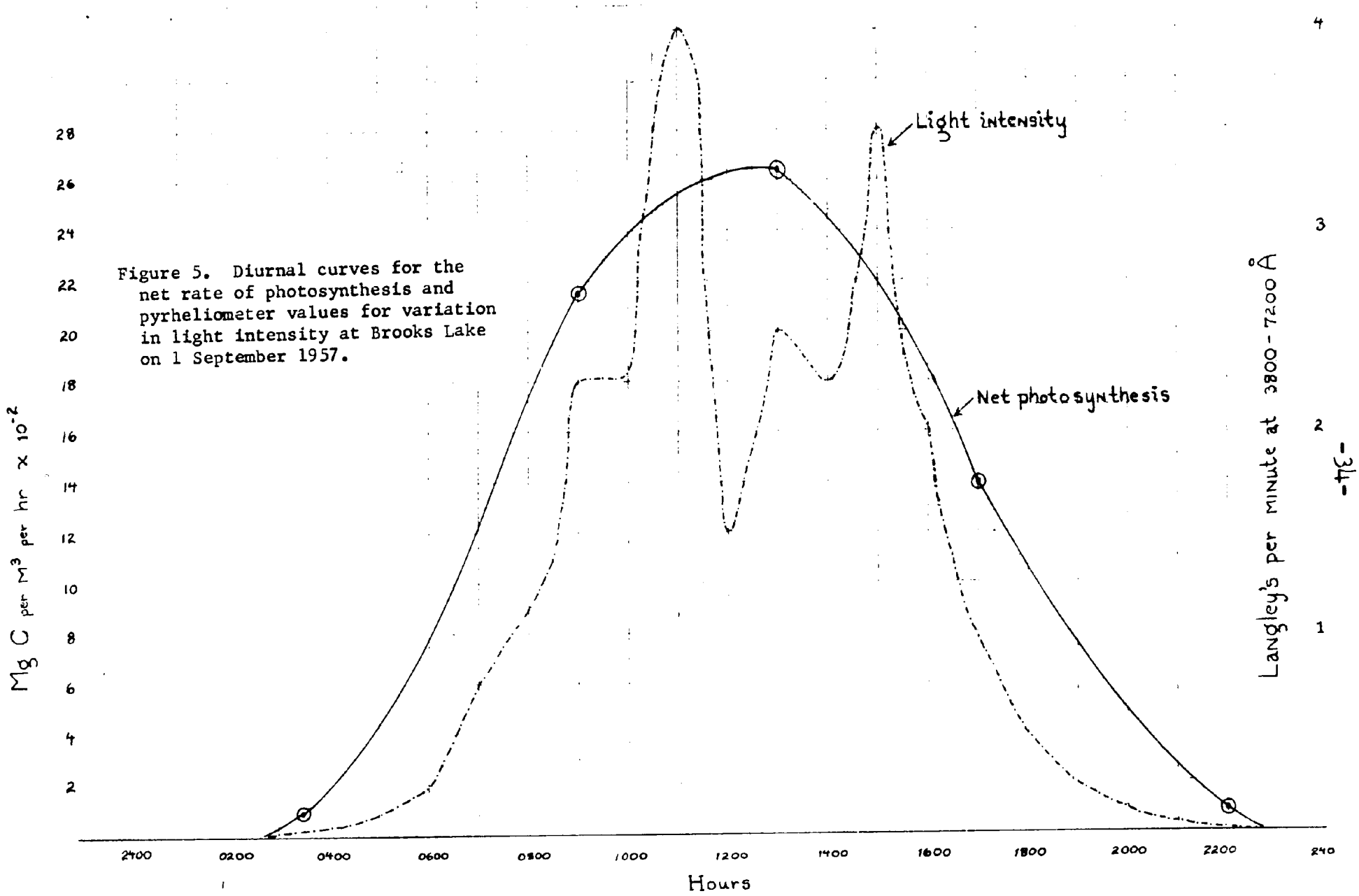


Figure 5. Diurnal curves for the net rate of photosynthesis and pyrheliometer values for variation in light intensity at Brooks Lake on 1 September 1957.

were monthly averages of the U. S. Weather Bureau as compiled by Gotaas and Ozwald (unpublished), interpolated to 58°30' North latitude, and corrected for average monthly sunrise to sunset cloud cover during 1957 (Figure 6). Average monthly cloud cover data were obtained for the King Salmon Weather Station (58°41' North, 156°39' West) from the Weather Bureau, U. S. Department of Commerce.

The most striking feature of a comparison between the productivity of these lakes is the much higher rate per unit volume in Naknek Lake as compared with either Brooks or Becharof Lakes (Table 1). Because of the limited euphotic zone in the shallow south arm of Naknek Lake, and despite a rate of carbon fixation per unit volume over three times that of Brooks Lake and 17 times that of Lake Becharof, the difference in productivity per square meter of surface area between Brooks and Naknek Lakes is not great. This has been generally recognized in other lakes (Ruttner 1952; Ohle 1956). No estimate for Lake Becharof is included because the mean depth is not known. On the basis of transparency, however, the euphotic zone probably exceeds 70 meters at mid-day. The accuracy in estimation of the euphotic zone is dependent upon the degree of precision in determining the average "compensation point" (the place at which photosynthesis balances respiration; Jenkin 1937). This depth necessarily moves upward with decreases in light penetration and downward with increases. Estimates for compensation depth vary from seven meters at Woods Hole harbor to 100 meters in the Sargasso Sea (Clarke 1954). Talling (1957) reviews the subject briefly in a formation for "Respiration losses and the 'compensation point.'"

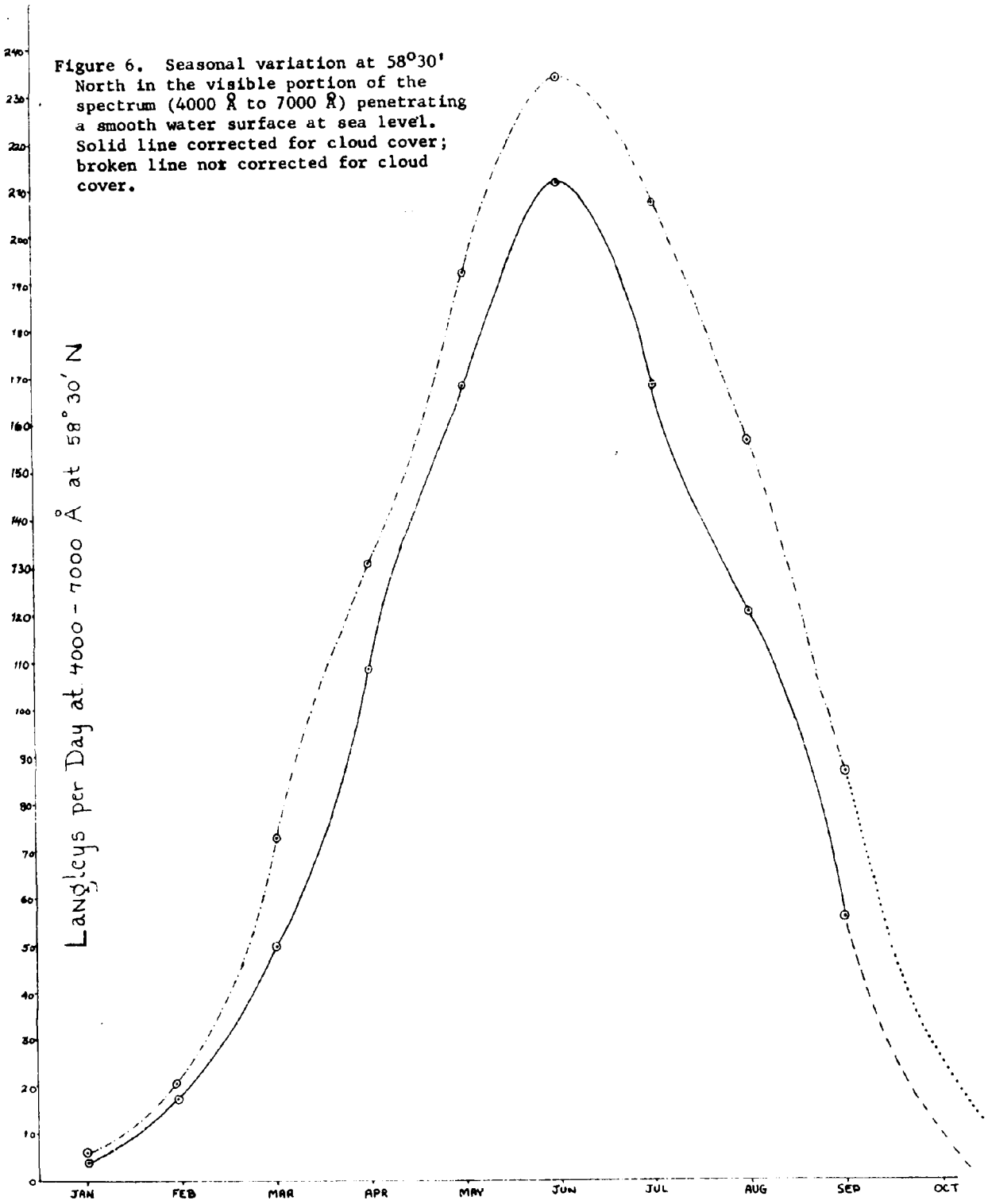


Figure 6. Seasonal variation at 58°30' North in the visible portion of the spectrum (4000 Å to 7000 Å) penetrating a smooth water surface at sea level. Solid line corrected for cloud cover; broken line not corrected for cloud cover.

Table 1. Rates of photosynthetic carbon fixation in three lakes of the Alaskan Peninsula in 1957.

Naknek[1]			Brooks[2]			Becharof	
Date	mg C/M^3/Day	mg C/M^2/Day	Date	mg C/M^3/Day	Mg C/M^2/Day	Date	mg C/M^3/Day
20 June (10)[3]	4.39	70.24	18 June (10)	1.63	73.35		
6 July (9)	6.03	96.48	3 July (8)	2.09	94.05		
20 July (5)	4.63	74.08	23 July (8)	1.80	81.00		
4 August (9)	3.74	59.84	2 August (2)	1.33	59.85		
19 August (4)	4.47	71.52	22 August (2)	0.84	37.80	23 August (2)	0.27
5 September (9)	4.59	73.44	2 September (8)	1.37	61.65		
Mean	4.64	74.27		1.51	67.95		0.27
Experimental Error	± .04			± .07			

1. Estimate of mean depth 20 meters based on 23 soundings. Euphotic zone 16 meters.
2. Mean of Stations II and III. Mean depth of Brooks Lake 45 meters.
3. Estimated cloud cover (10.0 equals complete cloud cover.)

In Brooks Lake the vertical euphotic zone varied in depth from about 25 meters to over 50 meters, with an average of 46 meters for the seasonal sampling periods. This is fortuitously close to the mean depth of 45 meters which is used in this study for the areal estimate of productivity in the lake. The considerable variation in the rate of carbon fixation on a clear day as opposed to a rainy day is illustrated by Figure 7. On these two days the $mgC/M^3/day$ is within about 10% of being proportional to the available light energy, as measured by pyrheliometer. The production on the extremely dark day (17 August) corresponds to Nygaard's (1955) figure for reduction of light intensity to about 10% of that encountered on a bright day. In contrast to the deeper stations, Station I exhibited light inhibition (Edmondson 1956) on the bright day as evidenced by higher productivity on the dark day.

In Naknek Lake the minimum compensation depth was found to be about 14 meters. Extreme fluctuation in transparency coupled with those of light intensity would extend this zone considerably on bright days if lake depth allowed. Strickland (1958) has noted that the steady compensation depth at noon will only be four to five meters below the 24 hour mean compensation depth. Although the mean depth of Naknek Lake is not known, an estimate of 20 meters was made from 23 soundings in approximately 60 sq. miles of lake west of the Iliuk arm. All measurements of photosynthesis in Naknek Lake extended to 13 meters and some to 17, and the depth of the euphotic zone averaged about 16 meters; this depth was used for an approximation of carbon fixation per square meter of surface area. Because

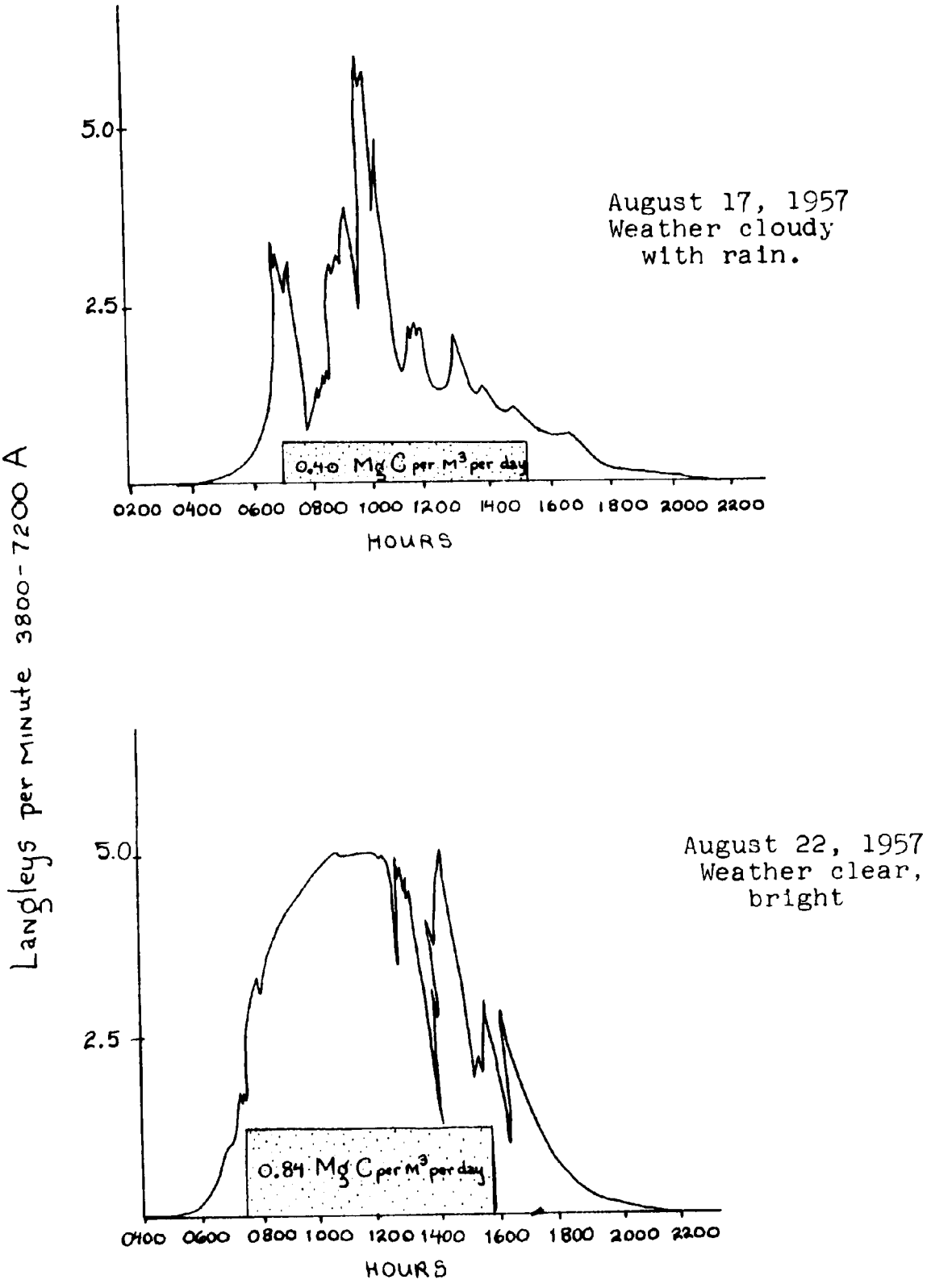


Figure 7. Variation in Photosynthesis with solar radiation at Brooks Lake Stations I and II.

sampling dates in Brooks Lake bracketted those in Naknek Lake, the dates showing the greatest similarity in weather conditions were used for comparison in Table 1.

The relationship of Secchi depth to the compensation point has received attention in the literature since Poole and Atkins (1929) calculated an approximate ratio of 1.7/Secchi depth in meters for the extinction coefficient of visible rays. Verduin (1956), in reviewing some of the literature on the subject, gives values of 2.5 to 5.0 times the Secchi depth for estimations of the compensation point. The ratio of the mean depth of the euphotic zone and the mean Secchi depth in Brooks Lake gives a factor of 3.6 with variation at least as great as those noted above. Naknek Lake, with an average Secchi depth of only 3.9 meters, had a ratio of 4.5. This difference probably resulted from the human eye's being more sensitive to the longer wave lengths of a given light energy favored by turbid water (Sverdrup et al. 1942). The approximate nature of Secchi disk conversion factors may result in errors of 25% or more from variation in back-scattering of light encountered in natural waters (Strickland 1958).

Variation in Primary Productivity within Brooks and Naknek Lakes

The sites of Stations I, II, III, and IV (Figure 2) were selected not only to provide a good average estimate of the primary productivity of Brooks Lake, but also to serve as an accurate comparison between different areas in the lake. The first three Brooks stations, each sampled 16 times during the summer, formed a matrix of 96 measurements for a comparison of carbon fixation in the first five meters of Stations I, II, and III, 144 for the first 20 meters of Stations II and III, and 176 measurements for the first 35 meters of these last two stations.

For easier comparison with the four sampling dates at Station IV, these data have been arbitrarily grouped in Tables 2, 3, and 4 as the means of four consecutive dates covering each of four 15-day periods. This grouping of Stations I, II, and III has the further advantage of combining a variety of light conditions since each group includes at least one bright day and never more than two.

Even preliminary comparison of sample radioactivity counts by variance analysis indicated a very significant statistical difference between stations. Although the average starting time differential between Stations I and III was only 20 minutes, this difference, because of peak photosynthesis about noon, was found to favor the earlier starting time. In the three comparative tables (2, 3, and 4), the values for Stations I, II, and III were corrected on the basis of the diurnal curve to the same starting time on each

date before statistical comparison of the rates of productivity. This correction, although slightly reducing the differences between the three permanent stations, did not alter the trend or the significance of these differences.

The primary productivity at Station IV can be considered as only an approximate comparison because productivity measurements could not be taken there on the same day at the three permanent stations. Meteorological conditions could therefore bias the results of sampling carried out on four dates. In this respect, it is of interest that two of the measurements were made on cloudy days and two on clear days.

Table 2. Rates of primary productivity in $mgC/M^3/day$ for the first 5 meters of four Brooks Lake Stations.

Dates	Station I (5 meters)	Station II (35 meters)	Station III (65 meters)	Station IV* (35 meters)
18 June to 3 July	1.97	2.08	2.38	1.67
8 July to 23 July	1.25	1.11	1.71	1.46
28 July to 12 August	1.21	1.58	1.54	2.07
17 August to 2 September	1.08	1.16	1.42	2.38
Mean	1.38	1.48	1.76	1.90
Standard Error	.02	.02	.05	.08
No. of Measurements	96	96	96	24

*Measurements made on 26 June, 22 July, 15 August, and 6 September respectively.

In comparing the first five meters of Stations I, II, and III, it is evident that an inverse relationship exists between the average rate of primary productivity in the first five meters and the depth of the stations (Table 2). In addition and perhaps more important is the trend for higher production per unit volume as one proceeds away from the outlet in the direction of the major tributaries.

When all 16 dates are compared, Station II is just significantly higher in production at the 0.05% level by Wilcoxon sum than Station I. Predominant WSW winds during July caused a concentration of plankton in the vicinity of Station I. If the four measurements in July are excluded the difference is significant at the 0.01% level.

When Station II is compared with Station III the degree of significance by the same test increases to slightly above the 0.025% level. The greatest difference (significant at above the 0.01% level) is obviously between Stations I and III. This trend in higher production rates is retained by Station IV.

A comparison of the first 20 meters of the three stations yields very similar results to a comparison of the first five (Table 3). Station IV again retains the trend, even if the unusually high productivity of 8 August were excluded from the average. Table 2 when compared with Table 3 further illustrates that the rate of carbon fixation per unit volume is higher between the surface and 20 meters than it is from the surface to five meters. This is also the case for Station IV except on 6 September when peak production was at a depth of only four meters.

Table 3. Rates of primary productivity in $mgC/M^3/day$ in the first 20 meters of three Brooks Lake Stations.

Dates	Station II (35 meters)	Station III (65 meters)	Station IV* (35 meters)
18 June to 3 July	2.58	2.61	2.54
8 July to 23 July	1.05	2.06	1.89
28 July to 12 August	1.39	1.64	4.23
17 August to 2 September	1.04	1.20	1.80
Mean	1.52	1.88	2.62
Standard Error	.03	.05	.06
No. of Measurements	144	144	39

*Measurements made on 26 June, 22 July, 15 August, and 6 September respectively.

A decrease in average productivity per cubic meter is evident when an additional 15 meters of depth is included in the comparison (Table 4). Station III is consistently more productive in the first 35 meters than Station II, at a significant level above 0.005%. The only date when measurements extended to a depth of 35 meters at Station IV was 15 August. This was a bright day and the warmest of the summer with a record high of 82° F. recorded at the King Salmon weather station. The clear conditions that prevailed

and the high phytoplankton population doubtless provided a higher than average production there, but even at half the rate, the trend of higher productivity toward the tributary end of the lake is maintained.

Table 4. Rates of primary productivity in $mgC/M^3/day$ in the first 35 meters of three Brooks Lake Stations.

Dates	Station II (35 meters)	Station III (65 meters)	Station IV* (35 meters)
18 June to 3 July	1.91	2.08	
8 July to 23 July	0.94	1.74	
28 July to 12 August	1.22	1.81	3.51
17 August to 2 September	0.77	0.96	
Mean	1.21	1.65	3.51
Standard Error	.02	.03	.09
No. of Measurements	176	176	12

*Measurement made on 15 August.

On 4 August parallel primary productivity measurements were made in the Iliuk arm (Station B) and the regular station (Station A) on Naknek Lake three miles to the west of Station B (Figure 2). These measurements were to compare the primary productivity of the

water at Station A with water nearer the mouths of the Savonoski and Ukak Rivers. Because of the contribution of ash, pumice, and glacial outwash from these two streams, the Secchi depth at Station B was only 2.5 meters as compared with 6.5 at the regular station. Although temperature recording equipment was inadequate for precision, thermometer values from the water samples at each depth above 10 meters show an average increase of 1.8° F. from Station B to Station A. Below ten meters the temperatures of the two stations were identical.

The rate of carbon fixation at different depths at Stations A and B in the two water columns is illustrated in Figure 8. Although light inhibition at the surface was more the rule than the exception in Naknek Lake as well as in Brooks Lake, the measurements of 4 August were made under cloudy conditions. This is the probable explanation for the high photosynthetic rate at the surface, as there was not a significant difference in the plankton between the surface and one meter. The variability in productivity with depth reflects the heterogeneous distribution of phytoplankton which was evident from centrifuge and inverted microscope analyses of plankton in both Brooks and Naknek Lakes. The mean productivity for 13 meters at Station A was 3.74 $mgC/M^3/day$ as compared to 2.62 $mgC/M^3/day$ at Station B. Station A is more productive than Station B at all depths except between 4.0 and 6.5 meters. The lower productivity of the water column at Station B is probably not the result of lower temperature, since Station B is cooler between 4.0 and 6.5 meters than Station A and still has higher production

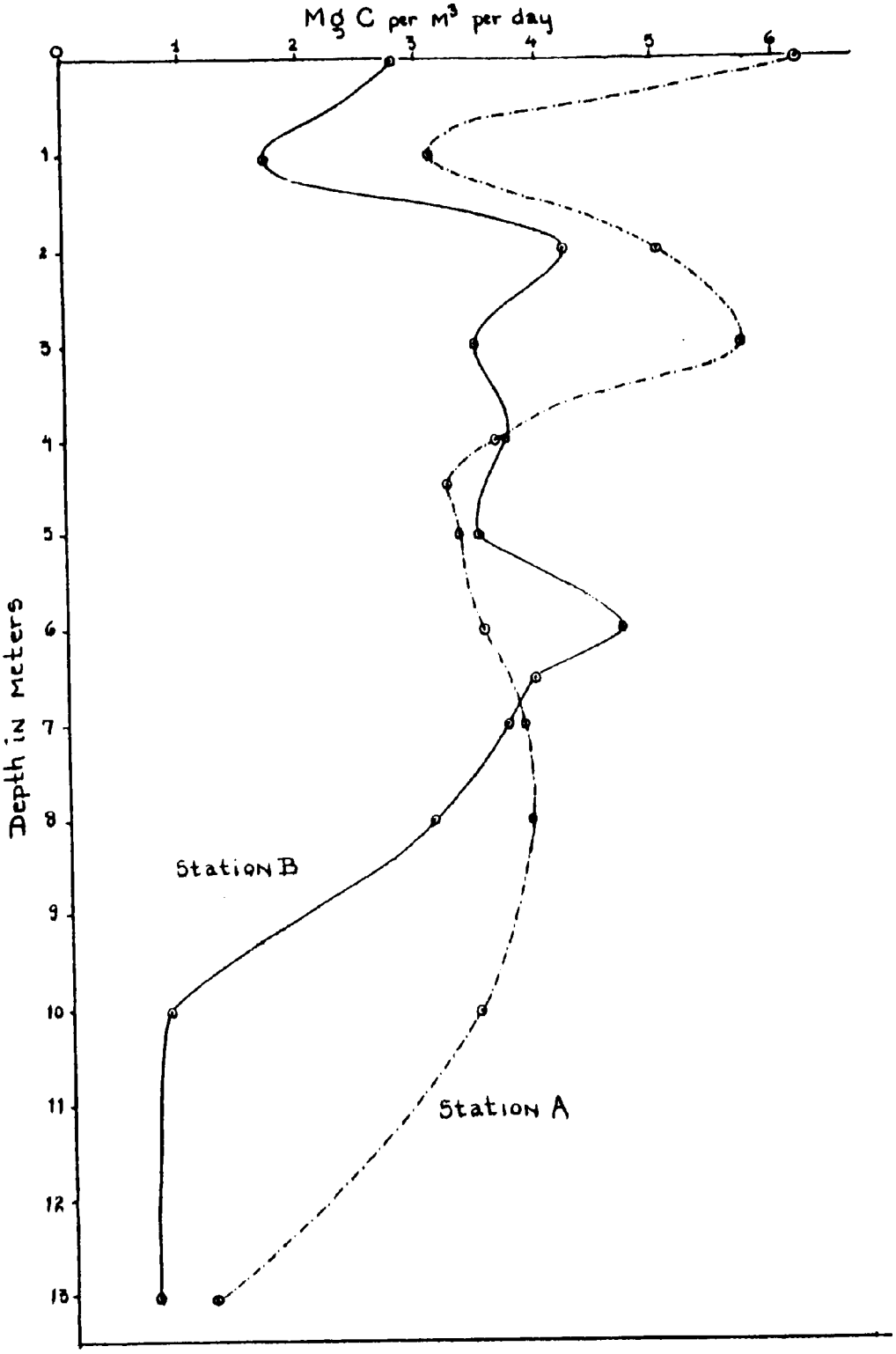


Figure 8. Changes in photosynthetic rate with depth at Naknek Lake Stations A (solid line) and B (broken line), 4 August 1957.

between these depths. Lower temperatures tend, also, to reduce respiration more than they reduce the rate of photosynthesis (Spoehr 1926).

The rapid decline in photosynthesis below seven meters at Station B suggests that light limitations imposed by the higher turbidity are responsible.

A comparison of all routine water analyses during the summer shows little detectable difference among the stations (Table 5). Analysis for phosphorus and nitrogen were near their limits of detectability with values below 0.0008 ppm registering as 0. When all depths are included at Stations I and III, there is a trend towards higher phosphorus content as one proceeds from Station I to III. If, however, only the first five meters are included in the comparison, the trend is reversed. Nitrite nitrogen is appreciably higher at Station IV than it is at the other Brooks stations. Silicon increases towards Station IV regardless of whether only the first five meters or the entire water columns are considered.

A comparison of Naknek Stations A and B similarly show only small differences in the amounts of the elements measured. Station B, nearer the main tributaries gave slightly higher average silicon, phosphorus, and total hardness values with nitrogen and alkalinity slightly lower than at Station A. Phosphorus and nitrogen values are probably at or close to their extreme range of reliability. In respect to the amount of silicon, which is very likely the most reliable of the photocolorimetric determinations

Table 5. Water quality in three Alaskan Lakes, 1957. Values in ppm.

LAKES	Brooks[1]				Naknek[2]		Becharof[3]
STATIONS	I	II	III	IV	A	B	
Phosphorus	.0065	.0070	.0073	--	.0087	.0095	.0083
Nitrite	.0015	.0012	.0019	.0038	.0083	.0050	.0030
Silicon	10.45	10.58	10.77	11.95	10.90	11.60	1.04
Total Hardness or ppm $CaCO_3$	36.13	35.17	35.48	--	69.50	71.0	24.90
Bound CO_2 as ppm $CaCO_3$	31.79	31.48	32.00	31.54	35.30	35.10	18.00

1. Stations I, II, III, and IV, all comparative values July 4 to September 3, 1957.

2. 4 August 1957 Mean of 0 and 13 meters.

3. 23 August 1957 Mean of 0, 15, and 35 meters.

reported here, it is of interest that the 13-meter value (11.6 ppm) at Station A is the same as the mean value of the surface and 13 meters at Station B. The surface value at A is lower (10.2 ppm). This difference might result from silica removal by diatoms in the surface layers, but more probably, since temperatures were the same below 10 meters at the two stations, from the presence of the denser water mass from Station B close to the bottom at Station A.

The variation in productivity in Brooks and Naknek lakes from June to October is illustrated by the curves in Figure 9. Both of these show a steady decline in primary productivity imposed by diminishing light as the season progresses. This is generally recognized as a dominant factor at higher latitudes (Livingstone et al. 1958). Thermal stratification, although not as severe as in more southerly latitudes, set in firmly by late June and remained until early September when there was evidence of mixing to 35 meters. Temperatures in Naknek Lake were about two degrees warmer than in Brooks Lake during the summer, although daily variations were large in the shallower waters of both.

The seasonal change in the total phytoplankton of Brooks Lake (derived from the means of Stations I, II and III) is in rather good agreement with productivity measurements and lends support for a usable relationship between standing crop and rate of production estimates for major changes in productivity during a season (Figure 9). Verduin (1956) presents a formula for such estimates from standing crop measurements. Unfortunately, if nutrient or other factors are limiting, a crop built up before this deficiency may be producing

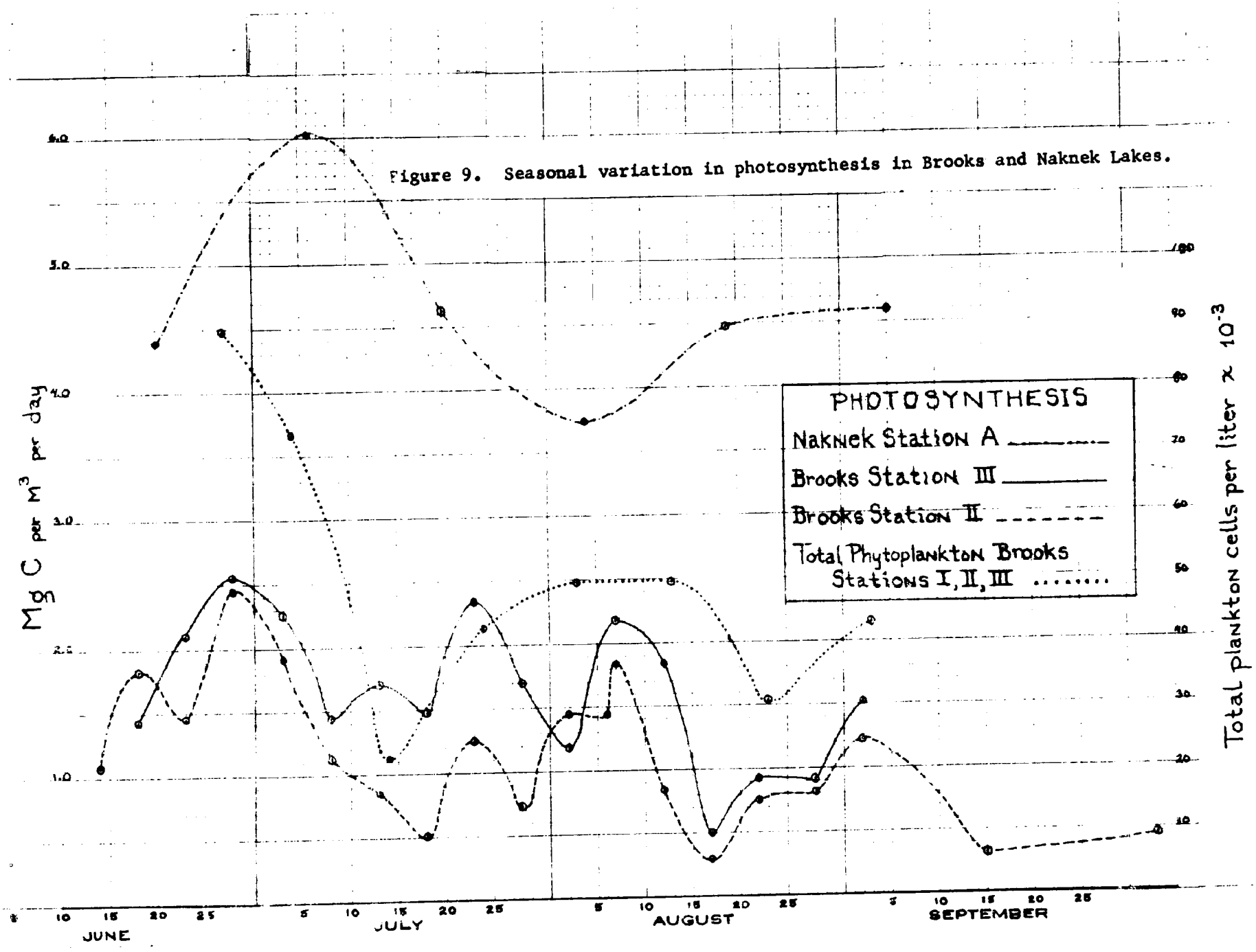


Figure 9. Seasonal variation in photosynthesis in Brooks and Naknek Lakes.

very little additional organic matter at the time the estimate is made. In this situation standing crop measurements would give unreliable values for the rate of production.

As might be expected at this northern latitude the dominating Phylum (Division) was the Chrysophyta. Its important genera were Melosira, Stephanodiscus, Fragilaria, Asterionella, Tabellaria, Synedra, and Navicula. The diatom population followed and was primarily responsible for the trimodal curve shown in Figure 9. Next in abundance of both species and numbers were the Chlorophyta. The green algae were at or near their peak development in late June, and declined gradually throughout the rest of the summer except for a short lived increase at Stations III and IV in early August. Phacotus, Pediastrum, Ankistrodesmus, and Dictyosphaerium were the most abundant genera. Of the Cyanophyta, Microcystis and Lyngbya were the only representatives throughout the summer. They formed a significant portion of the phytoplankton in the second half of August.

The total zooplankton population in Brooks Lake (measured at Stations I, II, and III) declined steadily throughout the season. The copepods were more abundant in the lake than cladocerans.

Experiments on Nutrient Factors Limiting Productivity

The mere presence of chemical substances in the environment, although recognized as a valuable guide for pure culture studies (Provasoli and Pintner 1953), does not necessarily prove their biological availability (Potash 1956). Nevertheless because of the intricacies of growth factors in natural waters (Hutchinson 1944), bioassay may be expected to reflect limiting factors better than chemical analysis of the environment.

As described under "Methods," culture series were run to identify the role of various nutrient factors in phytoplankton production in Brooks Lake during the summer portion of the red salmon growing season with three experiments in Naknek Lake and Lake Becharof for comparison. By starting Brooks Lake cultures at regular intervals during the field season, it was possible, further, to detect progressive changes in these limiting factors.

Although cultures were maintained for a sufficient time to allow significant population increases in them, the effect of specific nutrients on rate of carbon fixation was detectable (with C^{14} as a tracer) within a few minutes or hours after their addition to the media.

To demonstrate the efficiency of the method before field work was undertaken, a nitrogen deficient culture of Scenedesmus quadricauda Turp. was divided into two equal volumes. Five ppm of nitrogen was added as $Ca(NO_3)_2$ to one; the other was maintained as a control. Equal amounts of C^{14} were added to both. These were then subsampled four times during the 30-minute period immediately

following the addition of $Ca(NO_3)_2$ and C^{14}. Figure 10 illustrates the high sensitivity of this technique for measuring the increase in rate of photosynthesis initiated by the addition of $Ca(NO_3)_2$ to the nitrate deficient culture. Steemann Nielsen and Al Kholy (1956) have demonstrated that the C^{14} technique is applicable under conditions of phosphorus and nitrogen deficiency. This is a rather important consideration since many of the measurements in the Alaskan lakes studied as well as in cultures were made under sub-optimal concentrations of these two elements.

The first Brooks Lake culture experiment was started on 23 June and was maintained until 8 July. Of the variety of nutrients added, $MgSO_4$ was most conspicuous as a stimulant to photosynthesis (Figure 11). Although evident throughout the summer, the increase in the rate of carbon fixation stimulated by the addition of 9 ppm $MgSO_4$ was most pronounced in June. That this nutrient was still in short supply in early July is evidenced by a significantly higher production value in the culture of that month to which $MgSO_4$ had been added (Figure 12). Similarly, the pure culture experiment started on the last day of July showed an appreciable gain upon the addition of this nutrient (Figure 13).

In testing various concentrations of $MgSO_4$ with natural plankton populations, the quantity used initially, amounting to 9.0 ppm (1.82 ppm of Mg and 7.18 ppm of SO_4), was found to be about optimum. This concentration is within the range used by Rodhe (1948) to obtain optimum growth with Ankistrodesmus falcatus and is close to the quantity used by Potash (1956) in pond water with the green alga, Kirchneriella subsolitaria G. S. West, as an indicator organism.

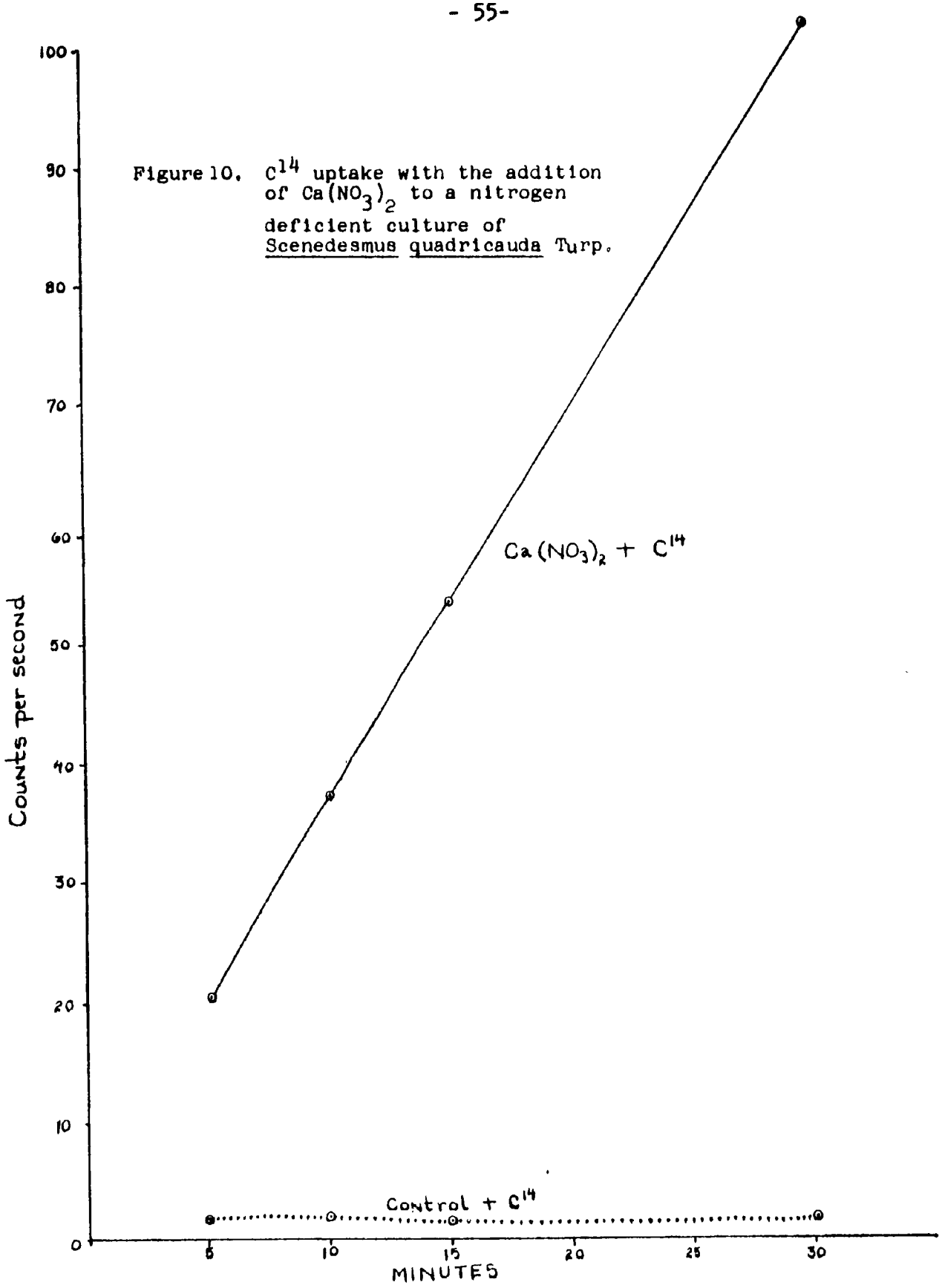


Figure 10. C^{14} uptake with the addition of $Ca(NO_3)_2$ to a nitrogen deficient culture of Scenedesmus quadricauda Turp.

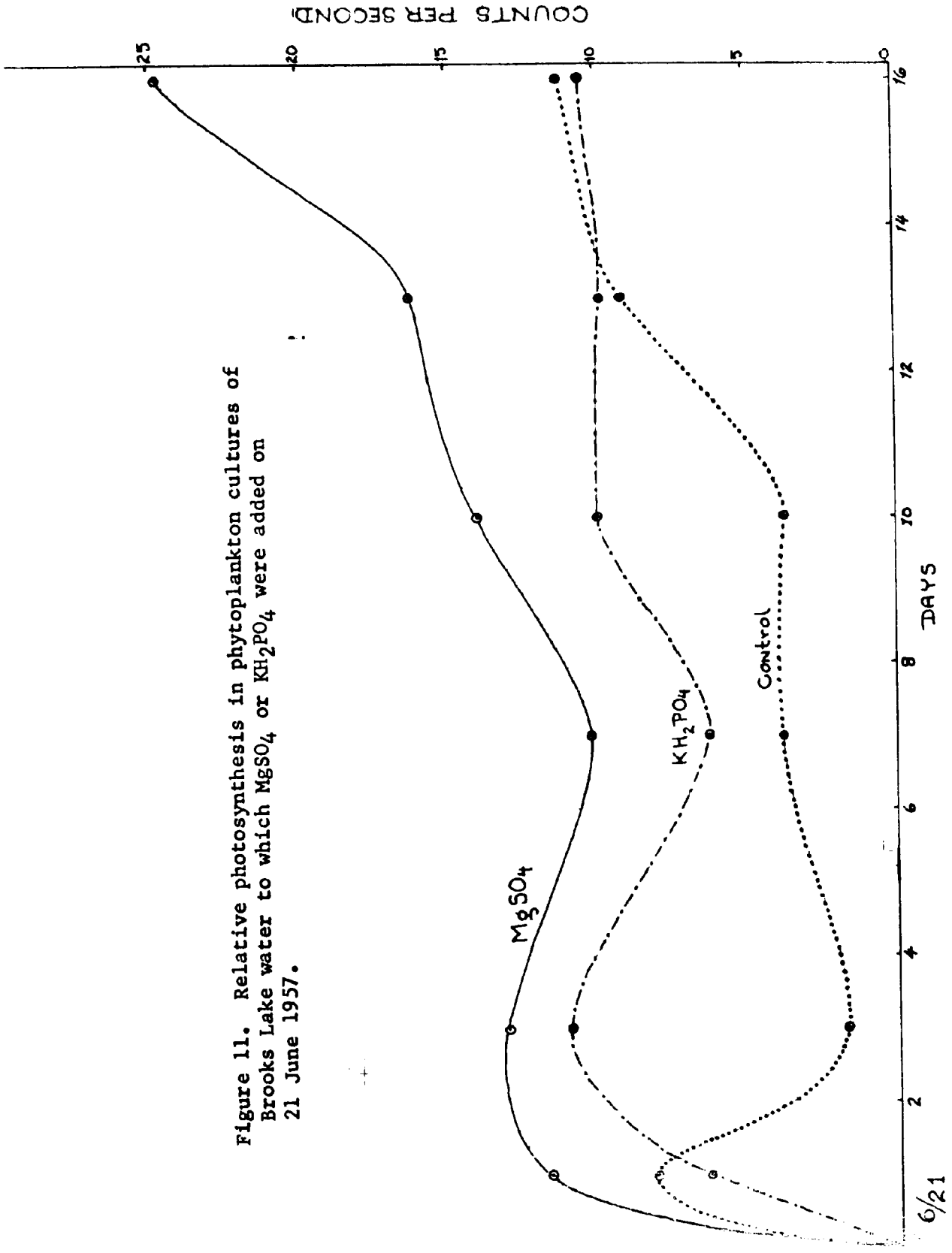


Figure 11. Relative photosynthesis in phytoplankton cultures of Brooks Lake water to which $MgSO_4$ or KH_2PO_4 were added on 21 June 1957.

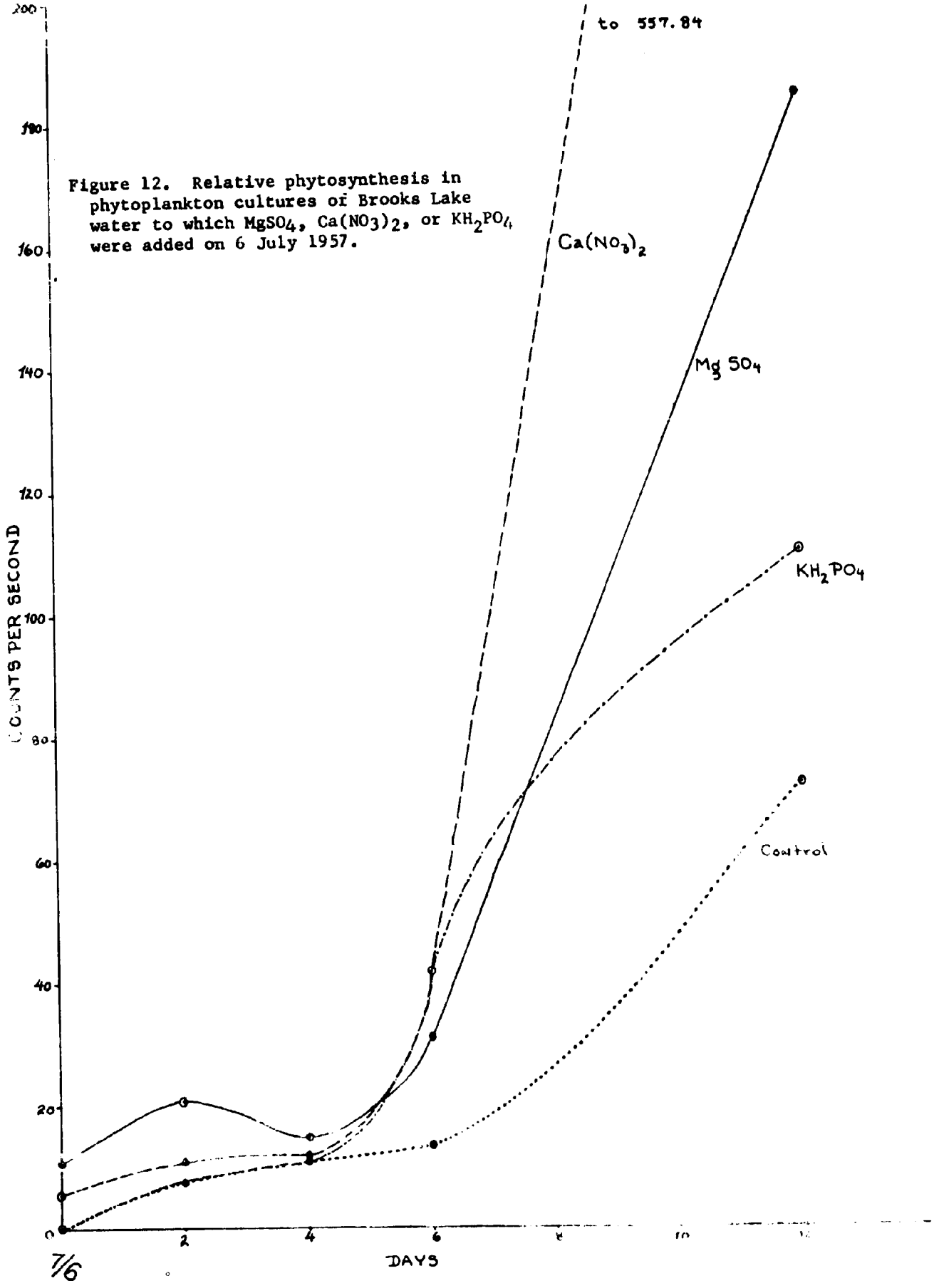
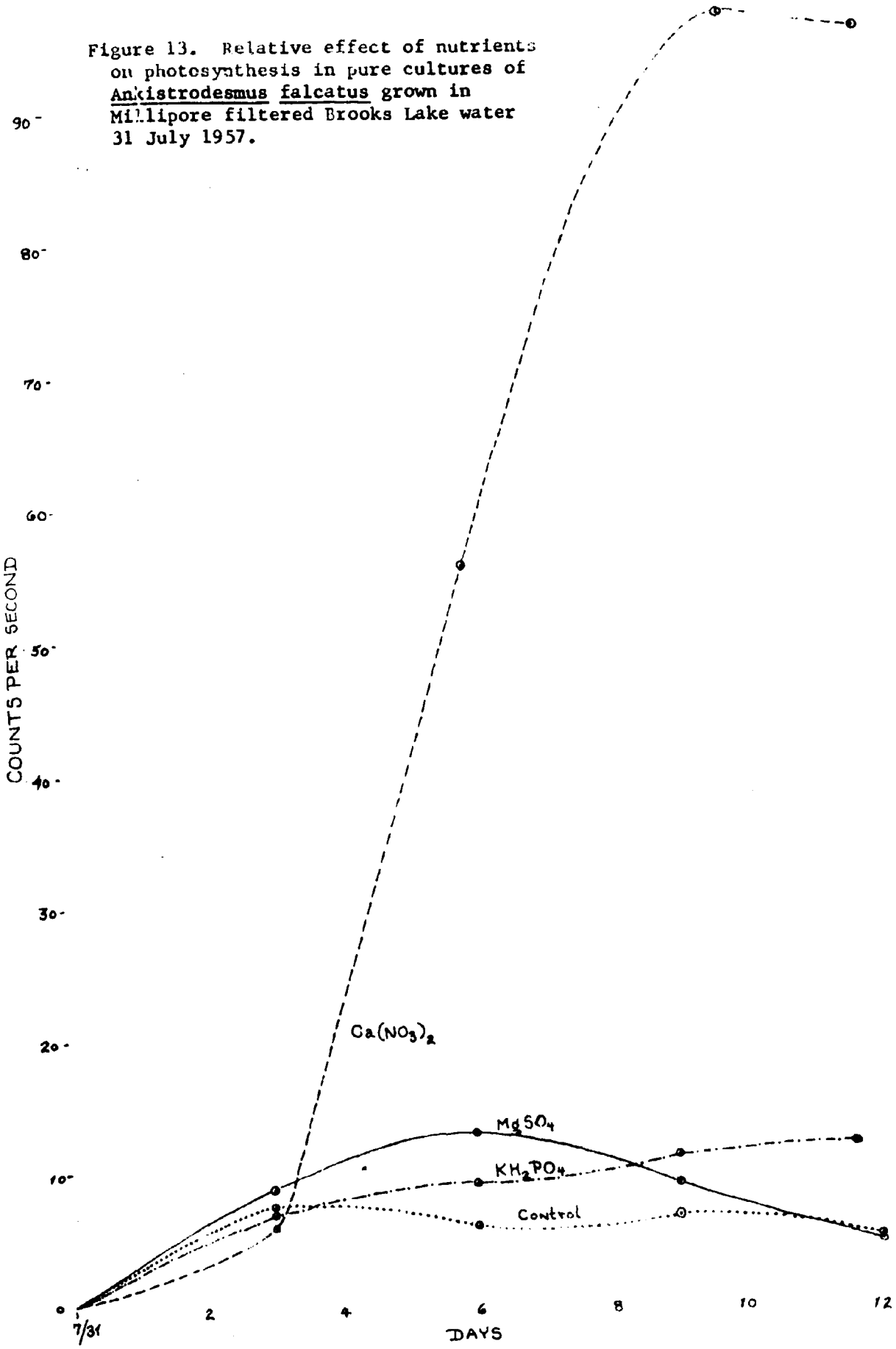


Figure 12. Relative phytosynthesis in phytoplankton cultures of Brooks Lake water to which $MgSO_4$, $Ca(NO_3)_2$, or KH_2PO_4 were added on 6 July 1957.

Figure 13. Relative effect of nutrients on photosynthesis in pure cultures of Ankistrodesmus falcatus grown in Millipore filtered Brooks Lake water 31 July 1957.



Analysis by Beckman flame spectrophotometer of Brooks Lake water collected in February 1958 indicated that 1.2 ppm of magnesium were present. Since the importance of magnesium as a limiting factor declined towards the end of the summer (Figure 14) it is probable that lower magnesium levels or unfavorable cation ratios (Pravasoli et al. 1954) existed in June and July. Turbidimetric determinations (Standard Methods 1955) gave 7.6 ppm sulfate. The addition of sulfate as $CaSO_4$, Na_2SO_4, and $MnSO_4$ in all possible combinations to water taken from Brooks Lake in February 1958 was stimulating to growth, but unless nitrate was provided, this stimulation was short lived.

To determine the relative importance of magnesium in different parts of the lake, surface water was collected at Station I, III, and IV on 22 July. Each sample was subsequently divided into three 2-liter cultures. Because KH_2PO_4 and $Ca(NO_3)_2$ were also fairly consistent in initiating increases in the rate of carbon fixation above that of the control they were added together with Na_2CO_3 in two of the three cultures from each station. $MgSO_4$ was then added to one of these. The third was maintained as a control. A high rate of productivity in cultures was attained by the addition of $MgSO_4$ when other nutrients were not allowed to become limiting (Figure 15). The deficiency of magnesium although evident at all stations decreases somewhat in the direction of the lakeb main tributary.

The addition of $MgSO_4$ to a single culture of Naknek Lake water did not produce an increase in carbon fixation. With Lake

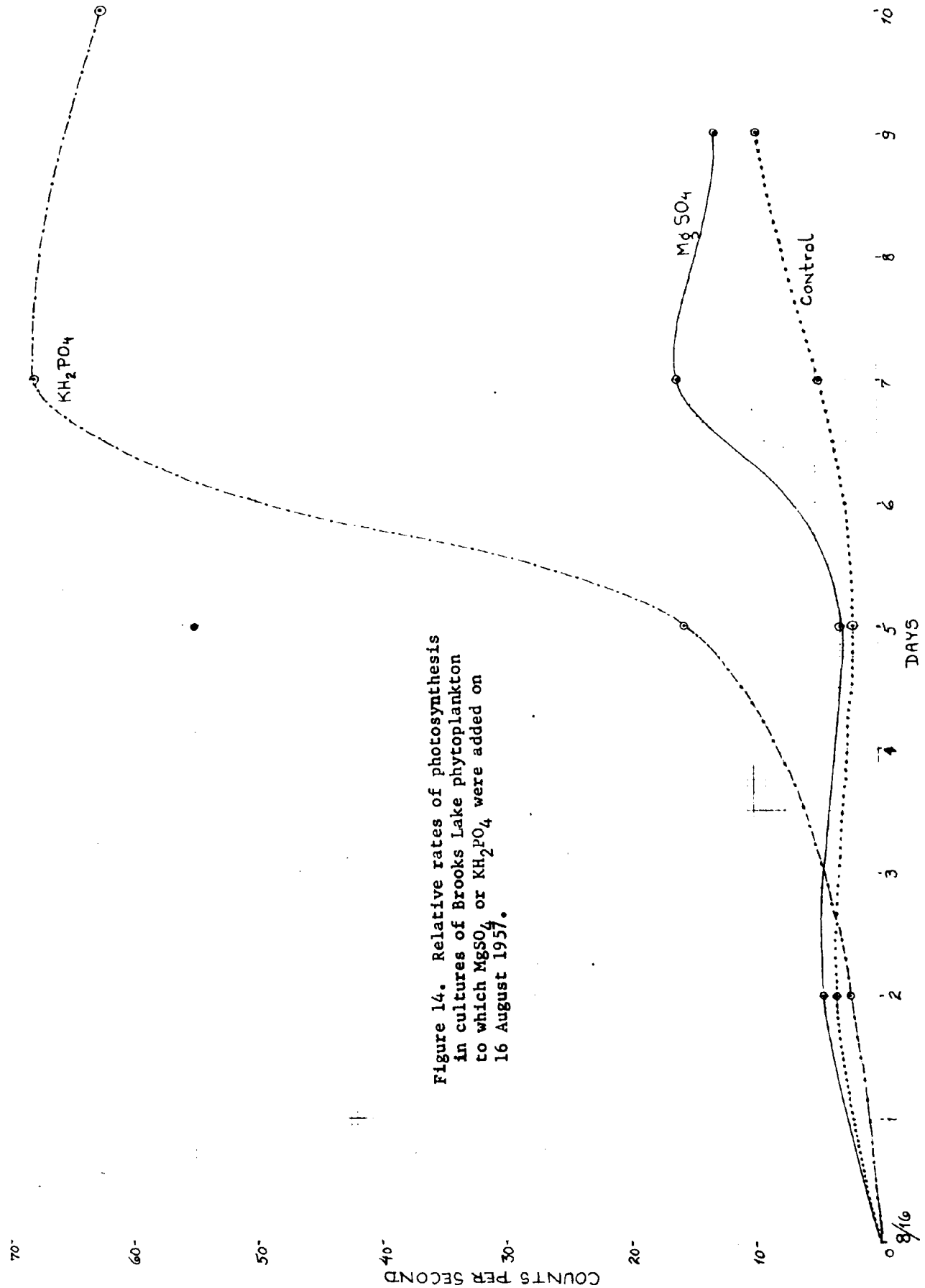


Figure 14. Relative rates of photosynthesis in cultures of Brooks Lake phytoplankton to which $MgSO_4$ or KH_2PO_4 were added on 16 August 1957.

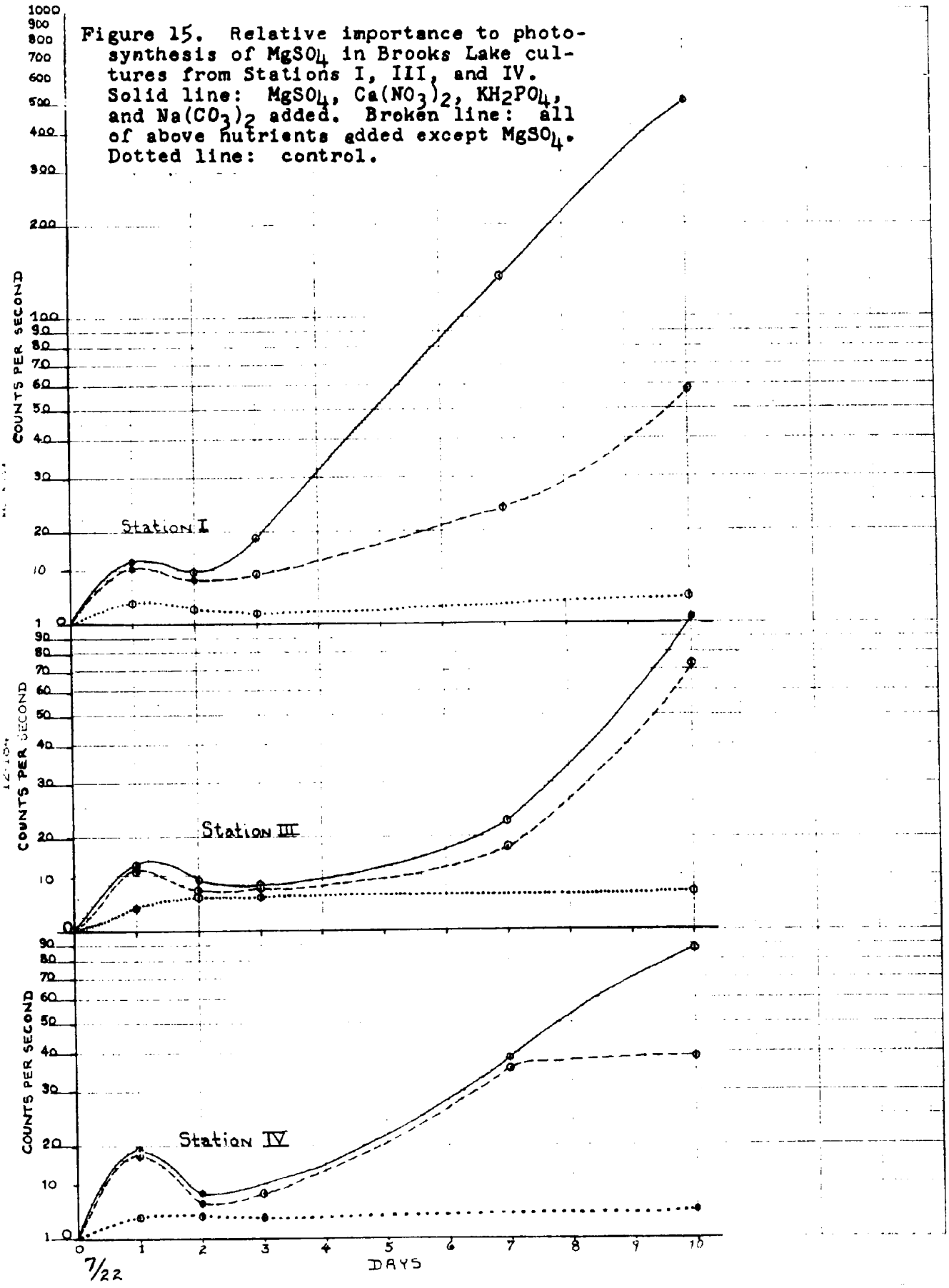


Figure 15. Relative importance to photosynthesis of $MgSO_4$ in Brooks Lake cultures from Stations I, III, and IV. Solid line: $MgSO_4$, $Ca(NO_3)_2$, KH_2PO_4, and $Na(CO_3)_2$ added. Broken line: all of above nutrients added except $MgSO_4$. Dotted line: control.

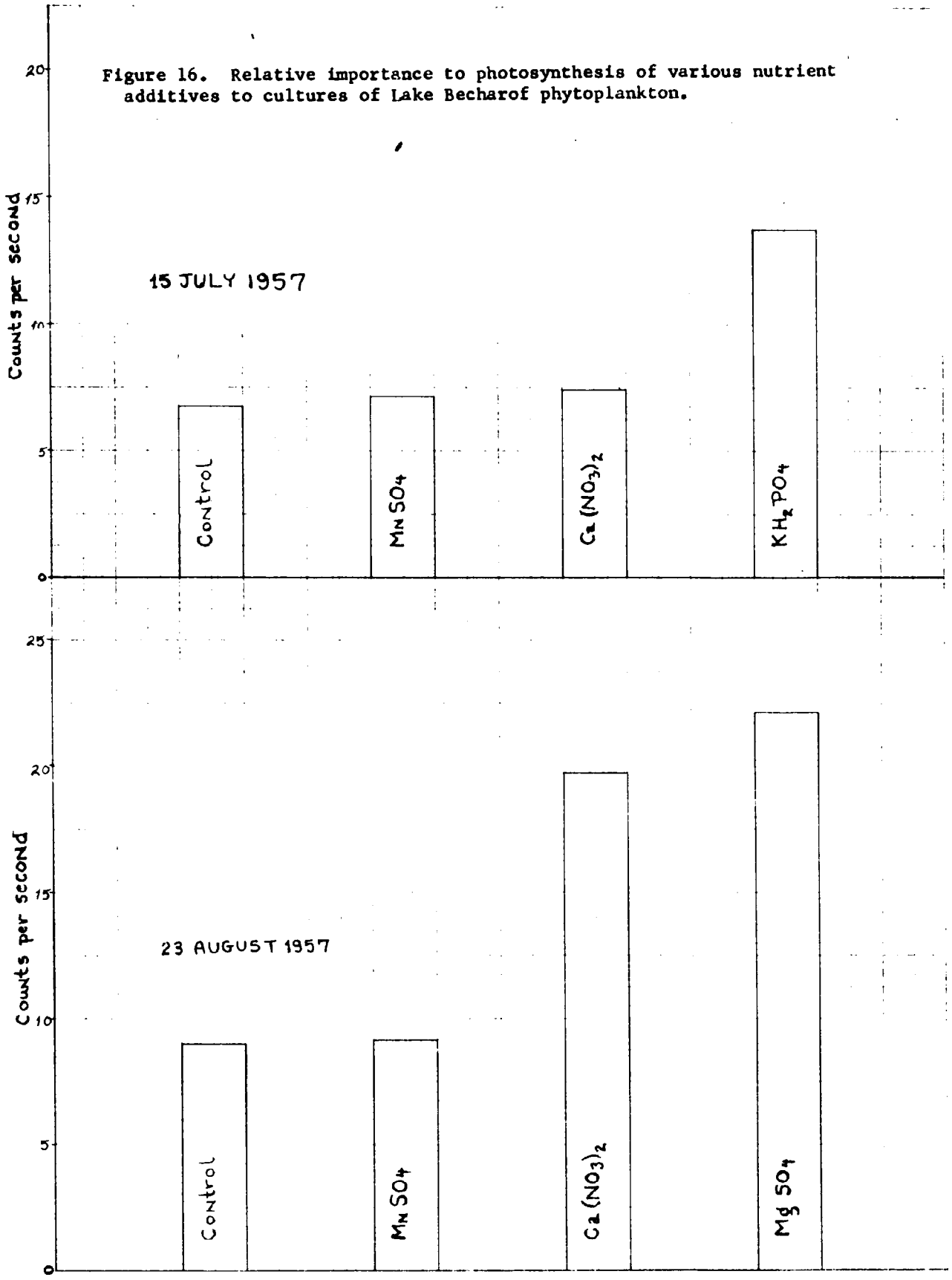
Becharof water, however, $MgSO_4$ gave the highest rate of photosynthesis in the culture experiment conducted on 23 August (Figure 16).

To be certain that the addition of $MgSO_4$ or $Na_2C^{14}O_3$ to the cultures was not initiating the uptake of carbon by ion exchange mechanisms other than photosynthesis (e.g. by absorption into outer or apparent free space; Kramer 1957) an oxygen production experiment was run in addition to the regular maintenance of dark bottle controls with C^{14} experiments. Net O_2 production over a five-day period with 0.0, 2.5, and 5.0 microcuries of $Na_2C^{14}O_3$ added, was 0.72, 0.70, and 0.73 ppm of O_2 respectively. In a fourth sample 5.4 ppm of $MgSO_4$ produced 1.3 ppm of oxygen.

As a final check on the limiting nature of $MgSO_4$ in Brooks Lake, the same wire spreaders that were used for suspending duplicate samples for determining experimental error in the regularly scheduled lake experiments were utilized to determine if there was a significant difference in C^{14} uptake between duplicate samples of lake phytoplankton at Station I. Because of the difficulty of assuming randomness even in dilute plankton populations, a non-parametric test (Wilcoxon Matched Pairs Signed Ranks Test; Siegel 1956) was utilized. The high efficiency (95%) with small samples made this test an excellent statistical treatment for these data.

When the Wilcoxon sum (10) was found to be well below the .05 level of significancy (Table 6), the null hypothesis (H_o) was accepted and parallel samples were again taken. To one of each pair, 6 ppm of the nutrient being tested were added together with

Figure 16. Relative importance to photosynthesis of various nutrient additives to cultures of Lake Becharof phytoplankton.



$Na_2C^{14}O_3$. The other, the control, was inoculated only with $Na_2C^{14}O_3$. These pairs were resuspended at meter intervals from 0 to 5 meters for four hours of incubation; then their contents were filtered. This rapid bioassay technique had the advantage of measuring the immediate change in carbon fixation initiated by the addition of specific nutrients at a variety of depths without allowing time for population shifts, which, although not detected in the cultures, might conceivably have occurred in the nannoplankton.

Table 6. Relative rates of C^{14} assimilation (counts/second) of algae from duplicate samples suspended at Station I

Depth in meters	0	1	2	3	4	5
Sample A	2.21	1.68	1.11	3.26	2.01	1.80
Sample B	1.58	2.10	1.00	2.94	2.49	1.96

Decision: Accept H_o

Carbon uptake increased at each depth of incubation in all samples to which 6 ppm of $MgSO_4$ had been added. On a single end-test basis, the Wilcoxon sum of 0 is significant at the .025 level (Table 7).

Calcium nitrate did not produce very significant increases in growth until July. In the culture started on 6 July (Figure 12), the deficiency of this nutrient was not pronounced until the fourth day when the culture carrying an addition of $Ca(NO_3)_2$ began a rapid increase in rate of carbon assimilation. Twenty-five days later the lack of this nutrient in the lake water was even more pronounced as

evidenced by the pure culture (Figure 13) started on 31 July. The response at that time to the addition of $Ca(NO_3)_2$ resembles the preliminary laboratory experiment with Scenedesmus quadricauda (Figure 10).

Table 7. Relative rates of C^{14} assimilation (counts/second) of algae from samples of Brooks Lake water suspended at Station I with and without $MgSO_4$ added.

Depth in meters	0	1	2	3	4	5
Control	2.30	1.73	1.84	1.72	2.12	2.34
$MgSO_4$ added	2.62	2.85	2.09	2.13	2.52	2.96

Decision: Reject H_o

Unfortunately the only nitrogen determinations that reagents were available for during the field season were for nitrite rather than the more stable and preferable nitrate. The relationship between ammonia, nitrate, and nitrite is apt to be unstable, although nitrate values are likely to be higher. The nitrite values are included in this study because they appear to show a relationship between the available nitrogen in the lake and results of culture experiments. The bioassay technique provides the best basis for assessing nitrogen deficiency.

It is of interest that in the single culture experiment in late August utilizing Naknek Lake water with its natural phytoplankton population, the only nutrient that significantly stimulated carbon assimilation above that of the control was $Ca(NO_3)_2$. At this time nitrite nitrogen values for the lake were appreciably higher

than they were in Brooks Lake. The same experiment with Lake Becharof water on 15 July and 23 August showed only a slight photosynthetic increase in July by the addition of $Ca(NO_3)_2$, but in August the stimulating effect of this nutrient was very marked (Figure 16). Lake Becharof nitrite nitrogen for 23 August was at a level above the mean Brooks Lake determination for the same day.

Rodhe (1948), using Ankistrodesmus falcatus, found $Ca(NO_3)_2$ to be a better source of nitrogen for this organism than NH_4Cl and recommended 29.4 mg $Ca(NO_3)_2$ per liter as the lowest level for achieving optimum growth. Only 6.1 mg per liter were used in the Brooks Lake study.

In Brooks Lake water there was a decrease in nitrogen, measured as nitrite, during late July and early August (Figure 17), concomitant with the deficiency noted in the pure culture experiment (Figure 13). As already mentioned, in reference to the $MgSO_4$, Brooks Lake water collected in February and used in pure culture experiments in the laboratory gave elevated rates of production when nitrate was added in combination with any one of the following: calcium, magnesium, or sodium. Cultures of Ankistrodesmus falcatus to which the three foregoing cations were added individually soon turned from green to yellow with a decrease in rate of photosynthesis. When nitrate was added to these cultures they recovered. This clearly demonstrated that nitrogen was the deficient element.

With the advent of a new limiting factor in the July cultures, it seemed advisable to repeat the experiment in situ at Station I. This time $Ca(NO_3)_2$ instead of $MgSO_4$ was added to one of

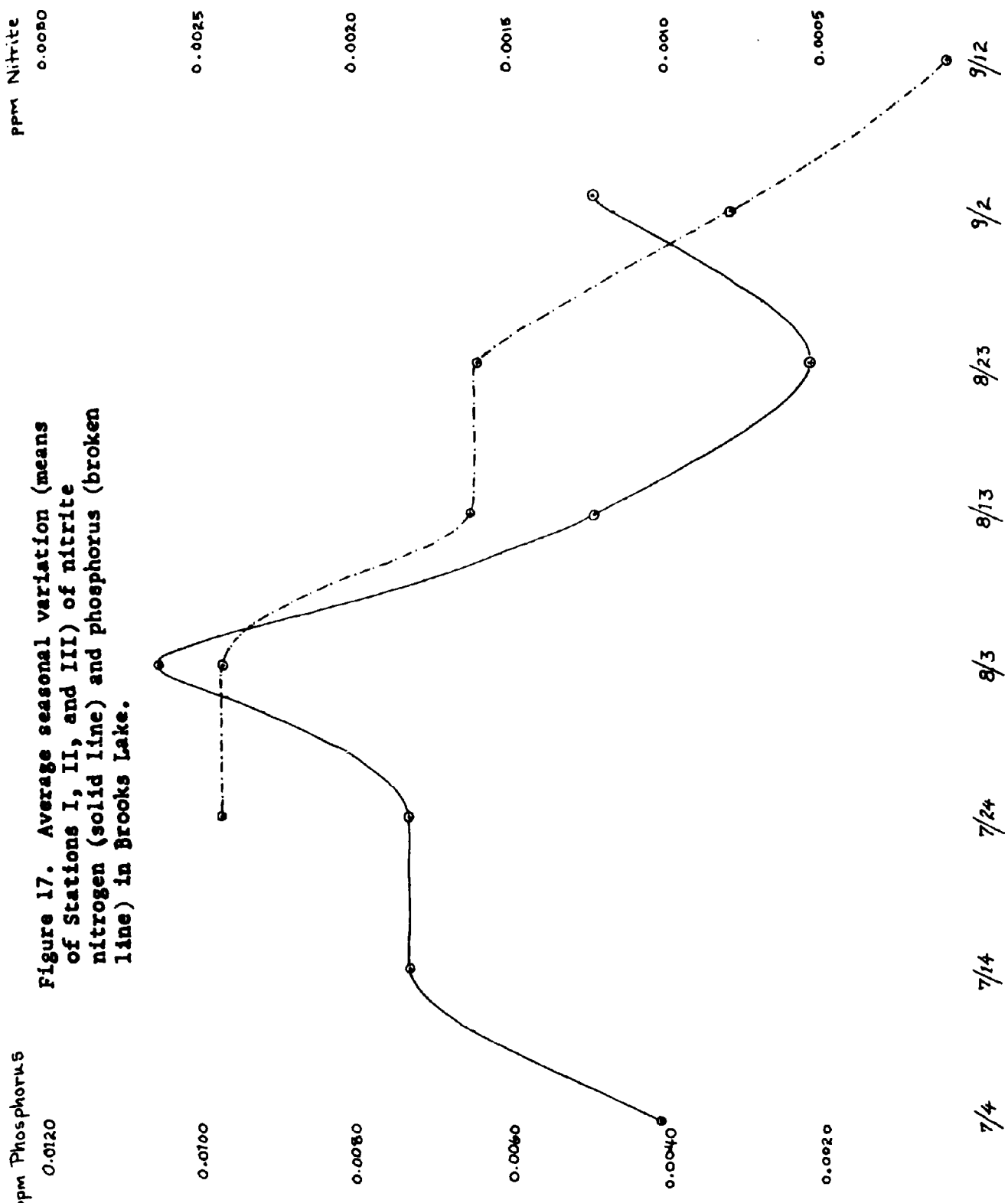


Figure 17. Average seasonal variation (means of Stations I, II, and III) of nitrite nitrogen (solid line) and phosphorus (broken line) in Brooks Lake.

each of the parallel samples (Table 8). Again utilizing the Wilcoxon Matched Pairs Signed Ranks Test, the increase in carbon assimilation initiated by the addition of $Ca(NO_3)_2$ gives a significant Wilcoxon sum of 1.0 (.05 level = 2.1, .025 level.

Table 8. Relative rates of C^{14} assimilation (counts/second) of algae from samples of Brooks Lake water suspended at Station I with and without $Ca(NO_3)_2$ added.

Depth in meters	0	1	2	3	4	5
Control	5.11	7.24	7.17	4.46	3.11	3.47
$Ca(NO_3)_2$ added	6.31	9.25	7.04	6.03	3.37	5.40

Decision: Reject H_o

Phosphorus, as KH_2PO_4, although a consistent stimulant to culture growth throughout the summer (Figures 11, 12, and 13), did not increase the photosynthetic rate in the cultures to the extent that $MgSO_4$ and $Ca(NO_3)_2$ did until middle August (Figure 15). An environmental decline in phosphate is in close agreement with culture results. Despite a very low potassium level of 0.94 ppm the addition of potassium as K_2SO_4 to pure cultures did not produce a significant photosynthetic increase.

In Lake Becharof, KH_2PO_4 was the most conspicious stimulating nutrient in the July experiment (Figure 16). The August cultures of Lake Becharof water did not demonstrate this deficiency, and water analysis at this time showed phosphorus to be at a higher level than in Brooks or Naknek Lakes.

It is common knowledge to aquatic biologists that a large percentage of nutrient material, both organic and inorganic, is lost to the ecosystem by deposition as bottom sediment or by binding in aquatic plants (e.g. Hutchinson and Bowen 1950; Hayes et al. 1952). Under natural conditions no large-scale release of nutrients occurs unless the oxidized layer of the surface muds disappears (Mortimer 1949). Sedimentation, as in Danish fiords, can be assumed to take place at a faster rate than regeneration (Grøntved and Steemann Nielsen 1957). The recirculation of nutrients freed for reutilization in the system by decomposition is accomplished by eddy diffusion or by overturn in spring and fall. Mechanical agitation (Zicker et al. 1956) or artificially turning over a lake (Hooper et al. 1953) has been suggested as a possible means of increasing the efficiency of the system.

While using SCUBA equipment to inspect the shelf area of Brooks Lake, the author noted that clouds of bottom sediment billowed up as he walked along the bottom. The extremely fine texture of the superficial bottom deposits suggests that mechanical resuspension might easily be achieved if it could be demonstrated that release of soluble nutrients in such bottom material would indeed be beneficial to the metabolism of the lake.

In Brooks Lake, analysis of sediment extract indicated that it contained .062 ppm of phosphorus as compared to the lake's .0057 ppm. It also had .023 ppm of nitrite as compared to the lake's .0012 ppm, and 6.0 ppm more SiO_2 than the lake water. Additions of

one and two percent by volume of this extract to cultures of Brooks Lake water increased the rate of photosynthesis appreciably (Table 9).

Table 9. Assay with C^{14} of the nutrient contribution of bottom sediment extract to cultures of Brooks Lake phytoplankton, in counts/second..

Amount of extract added	Days				
	1	2	5	7	11
0% (Control)	3.63	6.50	5.81	2.56	3.47
1%	6.17	8.64	5.98	4.56	--
2%	9.17	10.28	9.60	6.84	5.32

DISCUSSION

The importance of lake basin morphometry in influencing lake productivity has received considerable attention since the pioneer work of Thienemann (1927) and Naumann (1929). Because morphometry affects temperature, thermal and chemical stratification, and dilution and circulation of nutrients, mean depth, as the best indicator of morphometry, has been suggested as a dominant factor in productivity (Rawson, 1952). The extreme variability between lakes precluding any sharp delineation between types has, however, led Larkin and Northcote (1958) to conclude that only the total dissolved solid content could be used as an index of production in their studies.

The information gained from the studies reported here indicate that, if the productivity of the water alone is considered, the quantity and quality of replenished nutrients by the inflow of tributary streams is a much more important factor than depth in Brooks Lake. Important considerations in this respect, however, are the benthic development in the littoral zone which would certainly increase the productivity on a surface area basis and antimetabolites which might cause antagonistic interactions between plankton and sessile algae (Jorgensen 1956).

Traditionally the productivity per unit of surface area has been used for comparing different water bodies. On this basis,

as in the comparison of Brooks and Naknek lakes, a long euphotic zone may compensate for a lower production per unit volume. There can be little doubt, however, that zooplankton or fish can feed at a faster rate if their food supply is concentrated. Richmond (1957) has demonstrated an increase in net efficiency of young production (from 52.08 to 70.46%) by Daphnia pulex with increase in the concentration of food supply. Since the food levels he used were well above those encountered in Brooks Lake, higher phytoplankton densities may support a faster rate of zooplankton production. This might be an important factor in the larger average size of red salmon migrating from Naknek Lake compared with those migrating from Brooks Lake. Supporting this speculation is the recent work (Nelson 1958) on the relationship between photosynthesis and growth of the juvenile red salmon in Bare Lake.

Eicher and Rounsefell (1957), working from fishery statistics, crude soil tests, chemical analyses of lake water, plankton production, and tree growth rings, have suggested that lake fertility may have been significantly increased in the lakes that received volcanic ash during the eruptions of 1912 and 1913. This is especially pertinent to the discussion because Brooks and Naknek Lakes were the only ones on the peninsula thought to have received the ash. Martin (1913) reported that the ash fall extended only as far west as Brooks Lake and the Iliuk arm of Naknek Lake. This reached a maximum thickness of 20 inches, and, although covered by a thin layer of humus, is still clearly visible in the area when a shallow excavation is made.

Perhaps the greatest weakness in considering the pumice and ash as a nutrient source is evident from its chemical composition. Griggs (1920), who investigated the recovery of vegetation at Kodiak, makes rather a strong argument of this. He points out the basic difference between this geologically fresh, acid ash and the lava of the Columbian region and further notes that the former has practically the same composition as pulverized granite. He goes on to state that the widespread idea that luxuriant growth of vegetation was due to some fertilizer in the ash was erroneous. He attributes recovery of vegetation to mulching and reduced competition. Attempts at growing wheat in the ash failed, as death ensued as soon as the nutrients stored in the seed were exhausted.

In comparing his analysis of the ash with the composition of the average igneous rock (Pettijohn 1957), the latter is higher in almost every element except silicon. White pumice, hurled out by the eruption, was composed of rhyolitic magma with a silica content of 75%. The high concentration of this important element (Lund 1950) in Brooks and Naknek Lakes is in sharp contrast to Lake Becharof whose watershed did not receive the volcanic pumice or ash. The important water soluble salt potash (K_2O) was especially low in Brooks Lake. Griggs (1919) also noted that rankest growth of Calamagrostis langsdorfii occurred where evaporation was evidently concentrating the meager salts.

The greatest deficiency in the ash from the standpoint of plant growth, however, was nitrogen (Griggs ibid). The first plant invader of the ash was the lupine (Lupinus nootkatensis) which has

its own nitrogen-fixing bacteria. Shipley (1919a), chemist for the 1917 Katmai expendition, noted that the high ferrous sulfate content of the ash was not only directly injurious to plant growth, but also inhibited the action of nitrifying bacteria, thereby indirectly reducing the supply of an essential element.

The sub-optimal level of nitrogen in Brooks Lake evidenced by cultures and chemical analyses during July and August is of special interest since meteorological and geological evidence from the region are in good agreement with these findings. Ruttner (1953) and Welch (1952) have observed that the primary source of nitrogen is from the atmosphere. Hutchinson (1957) concludes, however, that in most lakes the origin of fixed nitrogen is to be found in the soils of the drainage basin. It is worth noting at this point that atmospheric nitrogen may not be as efficient for growth of algae as ammonia or nitrate (Kratz and Myers 1955). Shipley (1919b), who was more than casually interested in the nitrogen problem in this area, made numerous determinations for the ammonia and the nitrous nitrogen in the rainwater of southwestern Alaska. Using Nessler's reagent, he found an almost entire absence of ammonia in the rainfall of this region in striking contrast to similar measurements made at about the same latitude in Europe. His highest value was 0.015 ppm NH_3 as compared with the lowest value observed in Scotland of 0.44 ppm. He found nitrate nitrogen in the rainfall along Shelikof Strait from August to September averaged only 0.0018 ppm and noted that nitrites were not transformed to nitrates.

Nitrogen fixation by algae has been recognized for some time (Fogg 1951; Williams and Burris 1952) and has been demonstrated to increase the yields of rice fields (Watanabe 1956). Studies now underway on Afognak Island may provide an evaluation of the importance of nitrogen in the lake waters of this region. The carcasses of spawned-out salmon might also provide a significant amount of nitrogen and phosphorus if the escapement is of great size (Nelson and Edmondson 1955). Unfortunately most of this contribution comes at a time of rapidly declining light intensity and the normal nutrient recirculation by the fall overturn.

The nitrogen contribution of spring or melt water would appear negligible, as Shipley (1919b) commented that it was not necessary to prepare distilled water because of the almost total absence of either nitrous nitrogen or ammonia nitrogen in the spring and creek waters of the district as well as water obtained from melting snow. While the volcanic ash in question contains less than 1% of the nitrogen found in cultivated soil, the tundra of the region has a total nitrogen content of 43.0 ppm which is appreciably higher than Illinois prairie soils or the black loam of the Red River Valley, which Shipley (1919c) used for comparison. He associated this high nitrogen content with a low rate of nitrification in the cold, shallow tundra soil.

Another soil source of nitrogen which has received attention in recent years (Virtanen et al. 1955; Virtanen 1957) and which may have been a factor in Shipley's measurements is the alder shrub (Alnus). These plants are abundant in the area and have nitrogen-fixing

bacteria in root nodules. Although some of the nitrogen leaks directly into the soil, most is deposited in the leaves, which, falling to the ground, add to the soil annually as much as 140 pounds of nitrogen per acre (Lawrence 1958). The possible contribution of alders to lake fertility is certainly worthy of investigation.

From the above it would appear that the most important source of nitrogen in the area may be from such streams as Headwater Creek, which have their source in the tundra and alder thickets. This hypothesis finds support in the increase in productivity towards the tributary end of the lake as well as in the chemical analysis summarized in Table 5. On 22 July (after a 0.30 in. rain on 21 July) the nitrite nitrogen at Station IV was over twice the average at the other three Brooks stations measured the following day. Thus it would appear that rainfall soaking through the nitrogen rich tundra before entering tributary streams may be a significant factor in the lake fertility of the region. In Brooks Lake, as observed in the sea (Ketchum 1947; Steemann Nielsen 1958), the rate of replenishment of nutrients rather than the concentration at any given time, determines the fertility of the environment.

Recently sulfate has been found to be a limiting factor in Lake Victoria, Africa (Fish 1955). Even without the chemical analyses and experimentation by addition of sulfate in various forms, the geology of the Alaska Peninsula and analysis of the ash might well suggest a deficiency of magnesium rather than sulfate in this region. Average igneous rock contains almost 3.5% magnesia

(MgO). The ash that blanketed the area discussed contained less than 0.5%.

One thing that the eruption certainly did contribute to the area was sulfate. Following the eruption, rain containing high concentrations of sulfuric acid fell over large areas of Alaska (Griggs 1917). As far away as Prince William Sound, 300 miles (483 kilometers) to the east, concentrations were high enough to burn the flesh. Even before the eruption, however, Spurr (1898), in a reconnaissance in southwestern Alaska, noted precipitates of iron and sulfur in hot springs of the Katmai pass. Thawing has been noted in upper Naknek Lake (the Iliuk arm) with air temperatures of 15° F (-9.6°C). This was also considered indicative of hot springs by early explorers (Griggs 1922).

Magnesium, occupying the center of the chlorophyll molecule and estimated as occupying about two percent of the earth's crust (Mason 1958), is essential for both plant growth and chlorophyll formation. Experimental increase of magnesium concentration in Chlorella cultures, even at levels which do not appreciably increase the chlorophyll content, results in an increase in photosynthetic rate (Hill and Whittingham 1955). Like potassium, magnesium has long been recognized as a necessity for life but has not been considered as a limiting factor for phytoplankton development in lakes (Rodhe 1948).

After converting the extensive ionic water analysis of Lohammar (1938) to percentages of equivalents, Rodhe (1949) found close agreement between these and his own analysis of Swedish lakes

as well as with those of the world (Clarke 1924). Cations in Brooks Lake as determined by flame spectrophotometer were converted to percentages of equivalents for comparison with these figures (Table 10). This table illustrates a divergence from the usual concentrations in two important respects. First the Ca/Mg ratio is higher in Brooks Lake and secondly the magnesium-sodium relationship is reversed from the usual. The first is of interest in respect to the work by Pravasoli et al. (1954) which indicates that below monovalent-divalent ratios of 1.3 the range of favorable Ca/Mg ratios for growth of Synura sp. is restricted. In contrast the above-mentioned workers found Fragilaria capucina does well below this level. The diatom predominance in Brooks Lake is therefore in accord with the low monovalent-divalent ratio. The second is of interest in relation to the culture work. Magnesium, demonstrated to be very stimulating to phytoplankton growth during much of the season, is less available for plants in the presence of increased quantities of sodium or potassium (Leeper 1952).

Table 10. A comparison of cation percentages of equivalents.

Cation	The Whole World (Clarke 1924)	Brooks Lake	Uppland, 1-21 (Lohammar 1938)
Ca^{++}	63.5	63.6	67.3
Mg^{++}	17.4	13.2	16.9
Na^{+}	15.7	20.1	13.6
K^{+}	3.4	3.1	2.2

It would appear from the evidence at hand that although potassium uptake by cells is independent of the presence or absence of sodium (Scott and Hayward 1954), the already low magnesium level in comparison to other cations is made less available in Brooks Lake by the presence of relatively higher quantities of sodium. The slightly higher levels of phosphorus and nitrogen evident early in the summer are therefore of limited use to the phytoplankton population. Uptake during this period may represent luxury consumption above the phytoplankton requirements (Gerloff and Skogg 1954). As the levels of nitrogen decline, the relative optimum levels of $MgSO_4$ may also be depressed to the actual level of the environment. This situation was observed in cultures of the fungus Mucar hiemalis by Fothergill (1954). He found that with lower NH_4NO_3 concentrations optimal growth was obtained at reduced levels of $MgSO_4$ and that K_2HPO_4 has little influence on this relationship.

Very little published data are available on primary productivity in arctic lakes. Those that are available are difficult to compare because of the variety of techniques used. Early studies were made by the oxygen method and were usually reported in terms of gross photosynthesis. This is apparently the case in the measurements near Point Barrow, Alaska, by Comita and Edmondson (1953), and the measurements at Bare Lake before and during fertilization (Nelson and Edmondson 1955). The very limited freshwater work with C^{14} is listed by Lund and Talling (1957).

Before the completion of this study, however, Frey and Stahl (1958) made measurements of primary productivity with C^{14}

on 13, 16, 19, and 20 August, 1957 in a pond and a lake on Southampton Island in the Canadian arctic. Although the two measurements in the lake (designated S-7) were made for periods of 20 and 24.5 hours, their daily estimates are of interest for comparison with measurements in Brooks, Naknek, and Becharof Lakes during the same period. After correcting their two measurements at S-7 to $mgC/M^3/day$, it is obvious that the difference between the two was not of significant magnitude to necessitate the inclusion of both in the comparison they made with Imikpuk and Bare Lakes. The estimate for $mgC/M^3/day$ is 1.5 in S-7, as compared with 0.84 in Brooks Lake on 22 August, 4.47 for Naknek Lake on 19 August, and 0.27 in Lake Becharof on 23 August. The alkalinity of S-7 was over twice that of the three lakes just compared. Since variations in Brooks Lake with seasonal and meteorogical conditions range from well below 0.84 to a maximum of 4.23, there is little point in carrying the comparison further than to note that these lakes were all coverting solar energy at a rather low rate in comparison to other lakes of the world (Vollenweider 1956).

If the primary productivity in Brooks Lake continued to follow the light values downward after the last sampling date in October (a not unreasonable assumption), about half of the annual production was measured during the season. On this basis an estimate of productivity for Brooks Lake is extremely close to that of the Sargasso which Steemann Nielsen and Jensen (1957) estimate at 1 $mgC/M^3/day$, or 50 $mgC/M^2/day$.

Problems in connection with fertilization have been covered by a number of authors (e.g. Hutchinson and Bowen 1950; Hasler and Einsele 1948). The experiments reported here provide a feasible approach to the establishment of a rationale for increasing basic productivity, and the C^{14} technique as adapted in these studies provides the fastest and most sensitive means yet devised for assessing nutrient limiting factors in natural waters. The Brooks Lake shelf areas hold a great store of nutrients that might be released by mechanical agitation. Since light is frequently inhibiting in very shallow water the increase in turbidity might be more beneficial than detrimental. If fertilization is to be tried in a lake on a trial basis, it should be done with due respect to the factors actually limiting productivity, and should be balanced so as to supplement, not replace, the contribution of the watershed. The work reported here demonstrates the seasonal variation in these factors as well as marked differences in lakes of the same region. A careful investigation of the plankton nutrient requirements, seasonal changes in these requirements, and the trophic relationships of the consumers in individual lakes is of great importance in future work of this kind.

SUMMARY

1. The C^{14} technique was utilized for both bioassay of nutrient limiting factors and direct measurement of primary productivity in Brooks, Naknek, and Becharof Lakes. The efficiency of counting radioactivity was based on conversion of plankton to CO_2, thereby eliminating problems of geometry and self-absorption.

2. Comparisons of daily photosynthetic rate in Naknek and Brooks Lakes on a unit volume basis indicate a threefold higher rate in the former.

3. When photosynthetic rate is compared on a surface area basis, the difference is small.

4. The euphotic zone in Brooks Lake varied from about 25 meters to over 50 meters with an average for the season of 46 meters.

5. The average primary productivity of Brooks Lake was higher on bright days than it was on cloudy days. The reverse was frequently the case in shallow water where light inhibition was especially evident.

6. The depth of the euphotic zone in Naknek averaged about 16 meters with considerable variation with changes in light and turbidity.

7. The possible relationships of Secchi depth to the euphotic zone are discussed with emphasis on the approximate nature of such comparisons.

8. Comparisons of the four Brooks Lake stations indicate that primary productivity per unit volume at comparable depths consistently increases towards the tributary end of the lake.

9. Comparisons of the primary productivity of Naknek Lake Stations A and B indicate a higher rate at the less turbid Station A.

10. Primary productivity measurements in Brooks Lake compare favorably with variations in total phytoplankton. Phytoplankton and zooplankton abundance both followed the seasonal decline in light energy so evident at these northern latitudes.

11. The sensitivity of the C^{14} technique was demonstrated in the laboratory with a nitrate deficient culture of Scenedesmus quadricauda Turp.

12. Magnesium was found to be a limiting factor for phytoplankton production throughout the summer by both culture and in situ lake experiments. The relative importance of magnesium decreases somewhat towards the major tributary and with deficiences in other nutrients.

13. Magnesium deficiency was also noted in Lake Becharof in late August.

14. Nitrate deficiency was evident in Brooks Lake cultures in July and August concomitant with a decline in lake nitrites. Results were verified in experiments in situ.

15. The single culture experiment in Naknek Lake indicated nitrate deficiency in late August. The Lake Becharof experimental cultures in July showed only slight stimulation with the addition of

nitrate; in the August culture, the nitrate addition was considerably more stimulating.

16. Phosphorus, although consistently stimulating to photosynthesis, did not appear as critical as $MgSO_4$ or $Ca(NO_3)_2$ until middle August. An evironmental decline was observed at this time. In Lake Becharof, although phosphorus was of primary importance in July, by August environmental levels were above those in Brooks and Naknek Lakes and the cultures derived no measurable benefit from its addition.

17. Brooks Lake bottom sediment extract was very stimulating to cultures of the natural phytoplankton population.

18. A discussion is given on published work related to the problems of primary productivity and fertility in arctic lakes.

REFERENCES

The standard abbreviations of A World Periodicals List for Fisheries Science, 1st draft, Rome, F. A. O., 1957 are used throughout wherever possible. Where periodicals were not cited the list style was adopted for the abbreviations.

Åberg, B., and W. Rodhe
1942. Über die Milieufaktoren in einigen südschwedischen Seen. Symb. Bot. Ups., 5: 1-256.

Akehurst, S. C.
1931. Observations on pond life, with special reference to the possible causation of swarming of phytoplankton. J. R. Micr. Soc., 51: 237-265.

American Public Health Association, et al.
1955. Standard methods for the examination of water, sewage and industrial wastes. 10th Ed. New York, American Public Health Association. 522 p.

Arkin, H., and R. R. Colton
1953. Statistical methods. New York, Barnes and Noble, Inc. 4th Ed. 224 p.

Atkins, W. R. G.
1922. Hydrogen-ion concentration of sea water in its biological relation. J. Mar. Biol. Ass. U. K., 12: 717.

Atkins, W. R. G.
1923. Phosphate content of waters in relationship to growth of algal plankton. J. Mar. Biol. Ass. U. K., 13: 119-150.

Atwood, W. W.
1911. Geology and mineral resources of parts of the Alaskan Peninsula. Bull. U. S. Geol. Surv., 467. 137 p.

Barnaby, J. T.
1944. Fluctuations in abundance of red salmon, Oncorhynchus nerka (Walbaum), of the Karluk River, Alaska. Fish. Bull. U. S. F. W. S., 39 (50): 237-295.

Bernstein, W., and R. Ballentine
1950. Gas phase counting of low energy Beta-emitters. Rev. Sci. Instruments, 21: 158-162.

Chu, S. P.
1942. The influence of the mineral composition of the medium on the growth of planktonic algae. I. Methods and culture media. J. Ecol., 30: 284-325.

Clarke, F. W.
1924. The data of geochemistry. Bull. U. S. Geol. Surv., 770. 5th Ed. 841 p.

Clarke, G. L.
1954. Elements of ecology. New York, John Wiley & Sons. 534 p.

Comita, G. W., and W. T. Edmondson
1953. Some aspects of the limnology of an arctic lake. Publ. Stanford Univ., Biol. Sci., 11: 7-13.

Doty, M. S., and M. Oguri
1957. Evidence for a photosynthetic daily periodicity. Limnol. Oceanogr., 2(1): 37-40.

Dussart, B.
1950. La productivité de l'eau de mer. Conf. Cent. Rech. Etud. Oceanogr., 6. 6 p.

Edmondson, W. T.
1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, 37: 161-174.

Edmondson, W. T., and Y. H. Edmondson.
1947. Measurements of production in fertilized salt water. J. Mar. Res., 6: 228-246.

Eicher, G. J., and C. A. Rounsefell
1957. Effects of lake fertilization by volcanic activity on abundance of salmon. Limnol. Oceanogr., 2: 70-76.

Fenner, C. N.
1923. The origin and mode of emplacement of the Great Tuff Deposit of the Valley of Ten Thousand Smokes. Tech. Pap. Nat. Geogr. Soc., Katmai Ser., 1. 74 p.

Fish, G. R.
1955. Chemical factors limiting growth of phytoplankton in Lake Victoria. J. E. African Agric., 21: 152-158.

Foerster, R. E.
1944. The relation of lake population density to size of young sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada, 6: 267-280.

Foerster, R. E.
1954. On the relation of adult sockeye salmon returns to known smolt seaward migrations. J. Fish. Res. Bd. Canada, 11: 339-350.

Fogg, G. E.
1951. Nitrogen fixation by Mastigocaldus laminosus Cohn. J. Exp. Bot., 2: 117-120.

Forbes, S. A.
1887. The lake as a microcosm. Republished in 1925. Bull. Ill. Nat. Hist. Surv., 15: 537-550.

Fothergill, P. G.
1954. The mineral nutritional requirements of Mucar hiemalis. J. Gen. Microbiol., 10: 17-26.

Frey, D. G., and J. B. Stahl
1958. Measurements of primary production on Southhampton Island in the Canadian Arctic. Limnol. Oceanogr., 3: 215-221.

Gaarder, T., and H. H. Gran
1927. Investigations of the production of plankton in the Oslo Fjord. J. Cons. Int. Explor. Mer., 42: 1-48.

Gardener, A. C.
1943. Measurement of phytoplankton population by the pigment extraction method. J. Mar. Biol. Ass. U. K., 25: 739-744.

Gerloff, G. C., and F. Skoog
1954. Cell contents of nitrogen and phosphorus as a measure of their availability for growth of Microcystis aeruginosa. Ecology, 35: 348-353.

Gessner, F.
1949. Der Chlorophyllgehalt im See und seine photosynthetische Valenz als geophysikalische Problem. Schweiz. Z. Hydrol., 11: 378-410.

Goetz, A., and N. Tsuneishi
1951. The application of molecular filter membranes to the bacteriological analysis of water. J. Amer. Wat. Wks. Ass., 43: 943-969.

Goldberg, E. D., M. Baker, and D. L. Fox
1952. Microfiltration in oceanographic research. I. Marine sampling with the molecular filter. J. Mar. Res., 11: 194-204.

Gotaas, H. B., and W. J. Ozwald
(Unpublished). Utilization of solar energy for waste reclamation. Report on research supported by the National Institutes of Health, United States Public Health Service, and the University of California. 28 p.

Grøntved, J., and E. Steemann Nielsen
1957. Meddelelser fra Kommissionen for Danmarks Fiskeriog Havundersogelser. Serie: Plankton. Bind 5. 52 p.

Griggs, R. F.
1917. IV. The character of the eruption as indicated by its effects on vegetation. Ohio J. Sci., 19(3): 173-209.

Griggs, R. F.
1919. IX. The beginning of revegetation in Katmai Valley. Ohio J. Sci., 19: 318-342.

Griggs, R. F.
1920. The recovery of vegetation at Kodiak. Bull. Ohio State Univ., 24(15): 1-57.

Griggs, R. F.
1922. The Valley of Ten Thousand Smokes. Washington, The National Geographic Society. 341 p.

Hasler, A. D., and W. G. Einsele
1948. Fertilization for increasing productivity of natural inland waters. Trans. N. Amer. Wildl. Conf., 13: 527-555.

Hayes, F. R., J. A. McCarther, M. L. Cameron, and D. A. Livingstone
1952. On the kinetics of phosphorus exchange in lakes. J. Ecol., 40: 202-216.

Hill, R., and C. P. Whittingham
1955. Photosynthesis. London, Methuen and Co., Ltd. 165 p.

Hooper, F. F., R. C. Ball, and H. A. Tanner
1953. An experiment in the artificial circulation of a small Michigan lake. Trans. Amer. Fish. Soc., 82(1952): 222-241.

Hutchinson, G. E.
1944. Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake water. Ecology, 25: 3-26.

Hutchinson, G. E.
1957. A treatise on limnology. Vol. I. New York, Wiley and Sons. 1015 p.

Hutchinson, G. E., and V. T. Bowen
1950. Limnological studies in Connecticut. IX. A quantitative radio-chemical study of the phosphorus cycle in Linsley Pond. Ecology, 31: 194-203.

Ivlev, V. S.
1945. The biological productivity of waters. (In Russian, Preliminary Translation by W. E. Ricker) Adv. Mod. Biol., Moscow, 19: 98-120.

Jenkin, P. M.
1937. Oxygen production by the diatom Coscinodiscus excentricus Ehr. in relation to submarine illumination in the English Channel. J. Mar. Biol. Ass. U. K., 22: 301-342.

Jorgensen, E. G.
1956. Growth inhibiting substances formed by algae. Physiol. Plant. 9: 712-726.

Ketchum, B. H.
1947. The biochemical relations between marine organisms and their environment. Ecol. Monogr. 17: 309.

Kramer, P. J.
1957. Outer space in plants. Science, 125 (3249): 633-635.

Kratz, W. A., and J. Myers
1955. Nutrition and growth of several bluegreen algae. Amer. J. Bot., 42: 282-287.

Kuznetsov. S. I.
1956. Application of radioactive isotopes to the study of processes of photosynthesis and chemosynthesis in lakes. Proceedings of the International Conference on Peaceful Uses of Atomic Energy. 12: Radioactive Isotopes and Ionizing Radiations in Agriculture, Physiology, and Biochemistry. pp. 368-376.

Lapp, R. E., and H. L. Andrews
1955. Nuclear radiation physics. New York, Prentice-Hall. 532 p.

Larkin, P. A., and T. G. Northcote
1958. Factors in lake typology in British Columbia, Canada. Verh. Int. Ver. Limnol., 13: 252-263.

Lawrence, D. B.
1958. Glaciers and vegetation in Southeastern Alaska. Amer. Sci., 46(2): 89-122.

Leeper, G. W.
1952. Factors affecting availability of inorganic nutrients in soils with special reference to micronutrient metals. Annu. Rev. Pl. Physiol., 3: 1-15.

Lefèvre, M., M. Nisbet, and E. Jakob
1949. Actions des substances excretees en culture, par certaines especes d'Algues sur le metabolisme d'autres especes d'Algues. Verh. Int. Ver. Limnol., 10: 259-264.

Lindeman, R. L.
1942. The trophic-dynamic aspect of ecology. Ecology, 23: 399-418.

Livingstone, D. A., K. Bryan, Jr., and R. G. Leahy
1958. Effects of an Arctic environment on the origin and development of freshwater lakes. Limnol. Oceanogr., 3: 192-214.

Lohammar, G.
1938. Wasserchemie und höhere Vegetation schwedischer Seen. Symb. Bot. Ups., 3: 1-252.

Lund, J. W. G., and J. F. Talling
1957. Botanical limnological methods with special reference to the algae. Bot. Rev., 23: 489-583.

Lund, J. W. G.
1950. Studies on Asterionella formosa Hass. II. Nutrient depletion and the spring maximum. J. Ecol. 38: 1-35.

MacFadyen, A.
1948. The meaning of productivity in biological systems. J. Anim. Ecol., 17: 75-80.

Manning, W. M., and R. E. Juday
1941. The chlorophyll content and productivity of some lakes in northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett., 33: 363-393.

Martin, G. C.
1913. The recent eruption of Katmai volcano in Alaska. Nat. Geogr. Mag., 24: 131-181.

Mason, B.
1958. Principles of geochemistry. New York, John Wiley & Sons. 310 p.

Mortimer, C. H.
1949. Seasonal changes in chemical conditions near the mud surface in two lakes of the English Lake District. Verh. Int. Ver. Limnol., 10: 353-356.

Naumann, E.
1925. Handbuch der biologischen Arbeitsmethoden. Abt. IX, Methoden zur Erforschung der Leistungen des tierschen Organismus, Teil 2, 1. Halfte, Heft 3: 543-652.

Naumann, E.
1929. Einige neue Gesichts punke zur Systematik der Geswassertypen, mit besonderer Berucksichtingung der Seetypen. Arch. Hydrobiol., 20: 191-198.

Nelson, P. R.
1958. Relationship between rate of photosynthesis and growth of juvenile red salmon. Science, 128(3317): 205-206.

Nelson, P. R., and W. T. Edmondson
1955. Limnological effects of fertilizing Bare Lake, Alaska. Fish. Bull. U. S. F. W. S., 56(102): 415-436.

Nygaard, G.
1955. On the productivity of five Danish waters. Verh. Int. Ver. Limnol., 12: 123-133.

Odum, H. T., and E. P. Odum
1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll, Ecol. Monogr., 25: 291-320.

Ohle, W.
1956. Bioactivity, production, and energy utilization of lakes. Limnol. Oceanogr., 1: 139-149.

Olson, F. C. W.
1949. A system of morphometry. Tallahassee, The Oceanographic Institute, Florida State University. Contr. 21. 20 p.

Perfiliev, B. W.
1929. Zur Mikrobiologie der Bodenablagerungen. Verh. Int. Ver. Limnol., 4: 107-143.

Pettijohn, F. J.
1957. Sedimentary rocks. New York, Harper Brothers. 718 p.

Poole, H. H., and W. R. G. Atkins
1929. Photo-electric measurements of submarine illumination throughout the year. J. Mar. Biol. Ass. U. K., 16: 297-324.

Potash, M.
1956. A biological test for determining the potential productivity of water. Ecology, 37: 631-639.

Pratt, R.
1943. Studies on Chlorella vulgaris. VI. Retardation of photosynthesis by a growth-inhibiting substance from Chlorella vulgaris. Amer. J. Bot., 30: 32-33.

Proctor, V. W.
1957. Studies of algal antibiosis using Haematococcus and Chlamydomonas. Limnol. Oceanogr., 2: 125-139.

Provasoli, L., and I. J. Pinter
1953. Ecological implications of in vitro nutritional requirements of algal flagellates. Ann. N. Y. Acad. Sci., 56: 839-851.

Provasoli, L., J. J. A. McLaughlin, and M. R. Droop
1957. The development of artificial media for marine algae. Arch. Mikrobiol., 25: 392-428.

Pravasoli, L., J. A. McLaughlin, and I. J. Pinter
1954. Relative and limiting concentrations of major mineral constituents for the growth of algal flagellates. Trans. N. Y. Acad. Sci., Ser. 2, 16: 412-417.

Putter, A.
1924. Der umfang der Kohlensaurerreduktion durch die Planktonalgen. Pflugers Arch. Physiol., 205: 293-312.

Rawson, D. W.
1952. Mean depth and the fish production of large lakes. Ecology, 33: 513-521.

Rice, T. R.
1954. Biotic influences affecting population growth of planktonic algae. Fish. Bull. U. S. F. W. S., 54(87): 227-254.

Richman, S.
1957. The transformation of energy by Daphnia pulex. Doctoral dissertation. Ann Arbor, University of Michigan. 61 p.

Ricker, W. E.
1937. The food and the food supply of sockeye salmon (Oncorhynchus nerka, Walbaum) in Cultus Lake, British Columbia, J. Biol. Bd. Canada, 3: 450-468.

Riley, G. A.
1940. Limnological studies in Connecticut. Part III. The plankton of Linsley Pond. Ecol. Monogr., 10: 279-306.

Riley, G. A.
1941. Plankton studies, III. Long Island Sound. Bull. Bingham Oceangr. Coll., 7: 1-93.

Rodhe, W.
1948. Environmental requirements of fresh-water plankton algae. Symb. Bot. Ups., 10: 149 p.

Rodhe, W.
1949. The ionic composition of lake waters. Verh. Int. Ver. Limnol., 10: 377-386.

Ruttner, F.
1952. Planktonstudien der Deutschen Limnologischen Sunda Expedititon. Arch. Hydrobiol., Suppl., 21. 274 p.

Ruttner, F.
1953. Fundamentals of Limnology. Toronto, University of Toronto Press. 242 p.

Ryther, J. H.
1956. The measurement of primary production. Limnol. Oceanogr., 1: 72-84.

Ryther, J. H., and C. S. Yentsch
1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr., 2: 281-286.

Schomer, H. A., and C. Juday
1933. Photosynthesis of algae at different depths in some lakes of northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett., 29: 173-193.

Schreiber, W.
1927. Der Reinkultur von marinem phytoplankton und deren Bedeutung für die Erforschung der Produktions fähigkeit des Meerwassers. Wiss. Meeresuntersuch., 16: 1-34.

Scott, G. T., and H. R. Hayward
1954. Evidence for the presence of separate mechanisms regulating potassium and sodium distribution in Ulva lactuca. J. Gen. Physiol., 37: 601-620.

Serfling, R. E.
1949. Quantitative estimation of plankton from small samples of Sedgwick-Rafter cell mounts of concentrate samples. Trans. Amer. Micr. Soc., 68: 185-199.

Shelford, V. E.
1913. Animal communities in temperate America. Chicago, University of Chicago Press. 362 p.

Shipley, J. W.
1919a. The water soluble salt content, the ferrous iron content and the acidity of volcanic ash. Ohio J. Sci., 19: 224-229.

Shipley, J. W.
1919b. Ammonia and nitrous nitrogen in the rain water of south-western Alaska. Ohio J. Sci., 19: 230-234.

Shipley, J. W.
1919c. The nitrogen content of volcanic ash in the Katmai eruption of 1912. Ohio J. Sci., 19: 213-223.

Siegel, S.
1956. Nonparametric statistics. New York, McGraw-Hill Book Co. 312 p.

Spoehr, H. A.
1926. Photosynthesis. New York, New York Chemical Catalogue Co., Inc. 393 p.

Spurr, J. E.
1898. A reconnaissance in S. W. Alaska. Ann. Rep. U. S. Geol. Surv., 20. 146 p.

Steemann Nielsen, E.
1951. Measurement of the production of organic matter in the sea by means of carbon 14. Nature, 167: 684-685.

Steemann Nielsen, E.
1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J. Cons. Int. Explor. Mer., 18: 117-140.

Steemann Nielsen, E.
1955. The production of antibiotics by plankton algae and its effect upon bacterial activities in the sea. Pap. Mar. Biol. Oceanogr., Suppl. to Vol. 3 of Deep-Sea Res., pp. 281-286.

Steemann, Nielsen, E., and A. A. Al Kholy
1956. Use of C^{14}-Technique in measuring photosynthesis of phosphorus to nitrogen deficient algae. Physiol. Plant., 9: 144-153.

Steemann Nielsen, E., and E. A. Jensen
1957. Primary oceanic production. Galathea Rep., 1: 49-136.

Steemann Nielsen, E.
1958. The balance between phytoplankton and zooplankton in the sea. J. Cons. Int. Explor. Mer., 23: 178-188.

Strickland, J. D. H.
1958. Solar radiation penetrating the ocean. A review of requirements; data and methods of measurement, with particular reference to photosynthetic productivity. J. Fish. Res. Bd. Canada, 15: 453-493.

Strøm, K. M.
1933. Nutrition of algae. Experiments upon: the feasibility of the Schreiber method in fresh waters; the relative importance of iron and manganese in nutritive medium; the nutritive substances given off by lake bottom muds. Arch Hydrobiol., 25: 38-47.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming
1942. The oceans. Their physics, chemistry, and general biology. Englewood Cliffs, N. J., Prentice-Hall, Inc. 1087 p.

Talling, J. F.
1957. The phytoplankton population as a compound photosynthetic system. New Phytol., 56: 133-149.

Thienemann, A.
1927. Der Bau des Seebeckens in seiner Bedeutung für den Alblauf des Lebens im See. Verh. Zool.-Bot. Ges. Wien, 77: 87-91.

Thienemann, A.
1931. Der produktionsbergriff in der Biologie. Arch. Hydrobiol., 22: 616-622.

United States Department of Commerce Weather Bureau
1957. Local climatological data with comparative data. Alaska, King Salmon. 4 p.

Van Slyke, D., and J. Folch
1940. Manometric carbon determinations. J. Biol. Chem., 136: 509-541.

Verduin, J.
1956. Energy fixation and utilization by natural communities in western Lake Erie. Ecology, 37: 40-50.

Verduin, J.
1956. Primary production in lakes. Limnol. Oceanogr., 1: 85-91.

Verduin, J.
1957. Daytime variations in phytoplankton photosynthesis. Limnol. Oceanogr., 2: 333-336.

Vinberg, G. G., and L. I. Iarovitsina
1939. Daily changes in the quantity of dissolved oxygen as a method for measuring the value of primary production. Trud. Limnol. Stantsii Kosine, 22: 128-143.

Virtanen, A. I.
1957. Investigations on nitrogen fixation by the alder. II. Associated culture of spruce and inoculated alder without combined nitrogen. Physiol. Plant., 10: 164-169.

Virtanen, A. I., T. Moisio, R. M. Allison, and R. H. Burris
1955. Fixation of nitrogen by excised modules of the alder. Acta Chem. Scand., 9: 184-186.

Vollenweider, R. A.
1956. Das Strahlungsklima des Lago Maggiore und seine Bedeutung für die Photosynthese des Phytoplanktons. Mem. Ist. Ital. Idrobiol. de Marchi, 9: 293-362.

Watanabe, A.
1956. On the effect of the atmospheric nitrogen-fixing blue-green algae on the yield of rice. Bot. Mag. (Tokyo), 69: 530-535.

Welch, Paul S.
1952. Limnology. New York, McGraw-Hill. 538 p.

Williams, A. E., and R. H. Burris
1952. Nitrogen fixation by blue-green algae and their nitrogenous composition. Amer. J. Bot., 39: 340-342.

Yentsch, C. S., and J. H. Ryther
1957. Short-term variations in phytoplankton chlorophyll and their significance. Limnol. Oceanogr., 2: 140-142.

Zicker, E. L., K. C. Berger, and A. D. Hasler
1956. Phosphorus release from bog lake muds. Limnol. Oceanogr., 1: 296-303.