T H E   U N I V E R S I T Y   O F   M I C H I G A N

SCHOOL OF NATURAL RESOURCES
Resource Ecology Program

Technical Progress Report

NUTRIENT CYCLING AND PRODUCTIVITY OF DYSTROPHIC LAKE-BOG SYSTEMS (PART A)

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TABLE OF CONTENTS

SCOPE OF WORK

December 1, 1970 - November 30, 1971

During the spring of 1971 work continued on data compiled from the second hypolimnion labeling experiment, carried out in 1970. This analysis together with previous findings provided an outline of the gross features of the phosphorus cycle within the basin, and demonstrated the major influence of external environmental perturbations in the control of nutrient supply. Two manuscripts have been prepared dealing with this phase of the study (Appendixes A and B).

The only remaining component of the phosphorus cycle not investigated until 1971 was the exchange between the mat and the open water of the lake. From earlier work and from previous studies (Coffin, et al., 1949) it was clear that exchange of phosphorus takes place between the large pool present in the mat and the lake water. There were indications that this exchange was largely mediated by weather conditions. Field work during the spring and summer of 1971 included a mat labeling experiment. This consisted of application of a ^{32}P-rhodamine mixture around approximately one-half of the mat surrounding the open lake. The treated zone extended shoreward from the open water to the approximate limit of the tree zone surrounding the lake (Fig. 3). The untreated half of the lake was left as a control and permitted measurement of flow through the entire system. After labeling, the following compartments of the system were sampled.

(1) Mat Interstitial Water. Three mat sampling stations were established on the treated area and three on the control area. At each station we sampled a transect extending from the open water to the tree line (Fig. 2). Three subsamples were taken in this transect at distances of approximately 1 m, 3 m, and 5 m from the open water. We measured the dissolved and particulate activity, and the rhodamine concentration in three replicates from each of these substations at 4-day intervals. A vertical series of samples was taken at each substation to measure penetration of activity within the mat. We also carried out an analysis of the phosphorus activity of particles of various size in the interstitial water. We were able to distinguish soluble organic activity from soluble inorganic activity by means of separation with hexanol.

(2) Open Lake Water. We established a total of seven sampling stations at which we collected vertical series of water samples. Three stations were adjacent to the mat on the treated side of the lake. Three marginal stations were located adjacent to the control area and a single station was located in open water near the center of the lake. At each station we collected samples for analysis of soluble and particulate activity at 4-day intervals. Stable phosphorus fractions were measured at 2-week intervals.

1

For Fig 1 and 2
see file copy

Fig. 1. Section of mat of North Gate
bog, showing labeled and control areas.
Labeled areas show pink rhodamine
stain.

Fig. 2. Labeled area of bog mat, showing walkway along
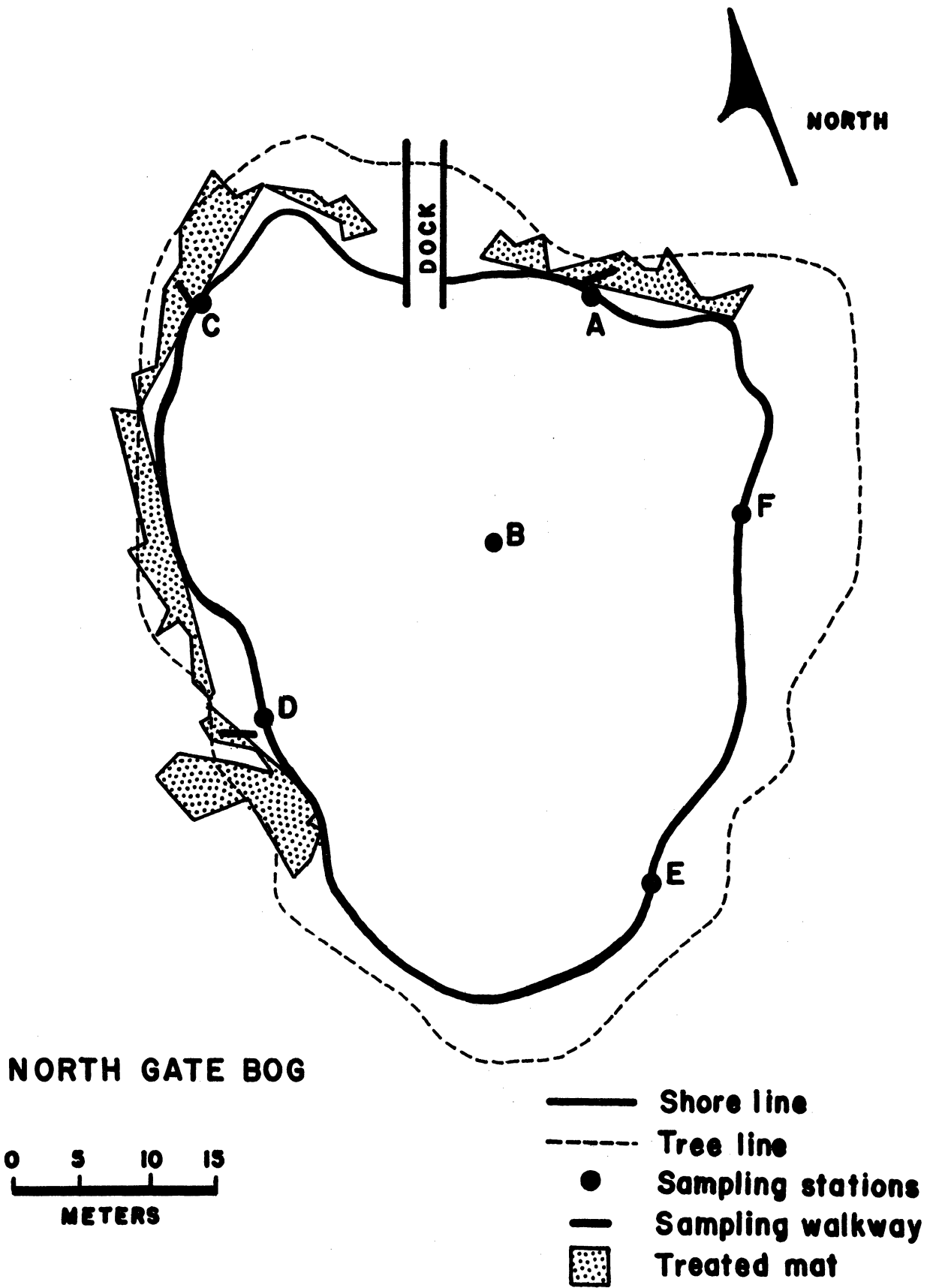transect at sampling station.

2

NORTH

NORTH GATE BOG

0   5   10   15
METERS

——— Shore line
------- Tree line
●   Sampling stations
—   Sampling walkway
▦   Treated mat

Fig. 3. Map of North Gate bog, showing treatment and control areas.

(3) Biological Compartments. We measured activity of two size catego-
ries of surface seston, zooplankton, Chaoborus, and Umbra at 4-day intervals
before and after treatment.

(4) Analysis of Organic Residues. At three locations in the lake (mat,
open water, and bottom water) we extracted phosphorus components by gradient
elution, and using procedures previously reported we measured the organic and
inorganic components in various eluted fractions, as well as the associated
radioactivity.

(5) Physical-Chemical Factors. At 4-day intervals we monitored physical-
chemical factors, such as pH, conductivity, dissolved oxygen, and temperature.
We also monitored weather conditions, measured rainfall, and collected rain
samples for the measurement of phosphorus. At the time of preparation of this
report, data from (4) above have been partially analyzed, and are reported in
Appendix C. Other segments of the data are in various stages of analysis.
Most of the data have been recorded on punchcards for analysis.

The initial application of the tracers was made on May 30. In this
treatment we mixed 50 gal of water with 120 mCi of ^{32}P and 100 g of rhodamine
WT, and sprinkled the mixture over the mat surface with 2-gal sprinkling cans.
It became apparent from both mat and open water sampling that little of the
activity from this treatment actually reached the interstitial water and only
traces entered the open lake. Most of the activity and most of the rhodamine
was adsorbed by the Sphagnum at the mat surface. Open water activities in-
creased to only a little above background, but there was exceedingly high ac-
tivity in the upper layer of the Sphagnum. Because this treatment did not
yield the desired information on exchange between mat and open water, it was
necessary to make a second treatment on June 24. On this date, 190 mCi was
used. In this application we added the label directly to the interstitial
water through holes punched in the mat at approximately 1-ft intervals. With
this technique we were successful in labeling the interstitial water, and
there was leaching of the tracers into the lake after the first rainfall.

Preliminary inspection of the data has revealed some interesting and
unexpected findings: (1) This treatment appears to have isolated rather
clearly the sources of input phosphorus into the entire system. Certain data
strongly suggest that input comes only from upland areas where there is sig-
nificant surface runoff input into the mat. (2) The mat labeling, followed by
lime treatment later in the summer, appears to have identified certain of the
conditions under which the organic components of the interstitial water are
modified and migrate into the lake. Iron-phosphorus organic complex from the
mat appears to release iron upon entering the epilimnion because of the higher
pH. There appears to be loss of Fe^{+++} iron to the hypolimnion at this point,
followed by utilization or uptake of the organophosphate remnant.

Hooper, Frank F. Origin and fate of organic phosphorus compounds in aquatic
systems. Review submitted for publication in: Environmental Phosphorus
Handbook; J. Griffith, Ed.

Hooper, Frank F., and David G. Imes. Physical and biological dispersion of
the hypolimnetic phosphorus of a bog lake system. (In press.) Trans-
actions of the 3rd National Symposium in Radioecology. Oak Ridge, Tenn.,
May 1971 (Appendix A).

Imes, David G. M.S. Thesis, The University of Michigan. The importance of
Chaoborus (Culicidae: Diptera) in the biological transport of phosphorus
in a meromictic bog.

Allan, John David. Ph.D. Thesis, The University of Michigan. Competition and
the relative abundance of two cladocerans. (Only logistic support,
tracers, supplies, and use of equipment, AEC funds.)

APPENDIX A

PHYSICAL AND BIOLOGICAL DISPERSION OF THE HYPOLIMNETIC
PHOSPHORUS OF A BOG LAKE SYSTEM

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PHYSICAL AND BIOLOGICAL DISPERSION OF THE HYPOLIMNETIC PHOSPHORUS OF A BOG LAKE SYSTEM*

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Abstract

The phosphorus of the 7- to 8-m stratum of a Michigan bog lake was labeled with ^{32}P in the early spring of 1969 and 1970. In 1969 the label was applied through ice cover and it spread horizontally throughout the 7- to 8-m stratum but moved very little vertically. The lake was meromictic in 1969 and the label remained in this part of the basin through the spring overturn and during the spring and summer. Isolation of the label in this stratum enabled study of biological transport in the absence of water movement. Larvae of the phantom midge Chaoborus carried radioactive phosphorus back and forth between the 7-m layer and the surface during their daily migration and appear to have liberated activity under the ice as a result of a heavy mortality in late spring. Little or no phosphorus was transported vertically from the hypolimnion by other species of zooplankton.

In 1970 when there was normal thermal stratification, we labeled water of the same depth and found that ^{32}P was carried into the epilimnion during three periods of high vertical turbulence. The quantity of phosphorus carried into the 0- to 2-m stratum during these periods was from 22 to 45% of the total phosphorus present in this layer before mixing and constituted a major fraction of the large quantity of phosphorus remaining in the 6- to 8-m zone after spring overturn. Each pulse of the phosphorus carried into the trophogenic waters by mixing was rapidly taken up by bacteria and plankton and soon appeared in Chaoborus and in Umbra. Uptake curves for Umbra and plankton appeared to reflect these pulses.

During daily migration Chaoborus larvae fed upon radioactive phytoplankton and carried an average of 0.6μg of phosphorus per larvae downward into the hypolimnion. A portion of this phosphorus was lost to the bottom water by excretion. However, net downward transport by Chaoborus appeared to be small when compared to quantities brought up by turbulent mixing.

Introduction

The seasonal redistribution of nutrients within stratified lakes is at the heart of many problems dealing with enrichment and eutrophication. The productive capacity of surface waters may be sustained by nutrient additions from outside the lake basin. However, exchanges of nutrients within the basin may be of great significance and may be obscured by steady-state equilibria and by the lack of markers or indicators of nutrient flow within the food chain. As a step in the analysis of the phosphorus flow of a northern Michigan bog, bog-lake system, we undertook two labeling experiments in which we attempted to (1) identify the mechanisms of transport of hypolimnetic phosphorus horizontally and vertically within the basin, and (2) follow quantitatively the flux of hypolimnetic phosphorus within the food chain of the trophogenic waters.

The salient features of the cycle of phosphorus and other elements within stratified lakes is well known (Juday, et al., 1928; Juday and Birge, 1931; Hutchinson, 1941, 1957; and Hutchinson and Bowen, 1950). The allochthonous input of phosphorus from groundwater or surface drainage furnishes one source utilized by photosynthetic organisms. Regeneration of phosphorus by limnetic bacteria and from the sediments of the littoral zone provides a mechanism for reutilization as long as wind-driven currents circulate materials within this zone. At depths greater than the thermocline, a major portion of the regenerated phosphorus may be stored for long periods before it is reintroduced into the upper water by mixing. The dynamics of phosphorus flow within the basin of stratified lakes is difficult to measure quantitatively because a number of processes may be occurring simultaneously. In any given stratum there may be: (1) regeneration of phosphorus from bottom sediments; (2) addition of material by sedimentation from upper strata in the form of plankton; (3) physical transport of phosphorus by water circulation from strata above or below; (4) in situ decomposition of phytoplankton and zooplankton; and (5) allochthonous input from the land drainage. The most successful approach to the study of these processes has been with the use of ^{32}P. Labeling of the surface water with ^{32}P demonstrated vertical movement within the basin into the hypolimnion (Hutchinson and Bowen, 1950) and the flow of phosphorus through the food chain of the littoral zone (Coffin, et al., 1949; Hayes, et al., 1952; Rigler, 1956).

Labeling of surface waters however does not permit examination of processes which transport phosphorus upward from strata below the thermocline and does not isolate the influence of hypolimnetic water movements upon the vertical distribution of nutrients. Possible mechanisms for transport of chemicals from the lower levels of the thermocline and hypolimnion into the epilimnion are (1) mixing arising from either wind stress at the lake surface or density differences within the water mass, and (2) biological transport arising from movement of organisms between these two strata.

10

In the present experiments we have attempted to isolate vertical transport processes by the injection of ^{32}P into the deeper strata and then monitoring its appearance within the trophogenic waters. We attempted to separate biological transport processes from physical transport by labeling a bottom stratum which in one year failed to mix with the upper water, and then labeling the same stratum a year later when mixing with upper water took place at frequent intervals.

Methods

This experiment was undertaken in North Gate Lake, a small bog lake located within Section 36 of T 45 N, R 42 W, Gogebic County, Michigan. The lake is one of numerous bog lakes on the 5500-acre reserve owned by the University of Notre Dame. It is approximately 50 m long and 40 m wide. The maximum depth is slightly over 8 m. The open water is surrounded by a Sphagnum mat which extends into a black spruce forest (Fig. 1). The bottom of the lake is relatively flat. The 7-m contour encloses approximately 2/3 of the surface area. There is an abrupt drop from the edge of the mat to the bottom. At many points, the 7-m depth is to be found 3 m or less from the edge of the mat. There are two small depressions slightly more than 8 m deep, near the central part of the basin (Fig. 1).

The procedure used in labeling the bottom water was as follows. We pumped 50 gal of water from the 7-m stratum into a steel drum. The intake used to pump the water from the bottom layer was so designed that the entering currents were horizontal and not vertical. We added approximately 40 g of rhodamine WT and 176 mCi of ^{32}P in the form of orthophosphate to the drum and mixed the contents thoroughly. This mixture was injected back into the stratum from which the water was collected in the following manner. In March 1969, when the treatment was made through an ice cover, we drilled 50 holes through the ice within the projection of the 7-m contour upon the surface. The holes were spaced in a 5-m grid network (Fig. 1). We then injected 1 gal of the mixture into the 7-m stratum at each of the 50 holes by pouring it through a 2-in. plastic tube fitted with the intake device used to collect the water, which directed the flow horizontally. The tube was then flushed with 3 gal of unlabeled water. This effectively dispersed the label horizontally from the injection site and removed traces of the labels from the tube so they did not contaminate upper layers when the tube was removed from the lake.

In 1970, labeling was undertaken with open water conditions, approximately 3 weeks after the spring overturn. Water was again collected by pumping from the 7-m stratum and the label was injected with the apparatus used the previous year, but in this instance from an open boat. There was one important difference in the labeling procedure used in these 2 years. In 1969, the water used
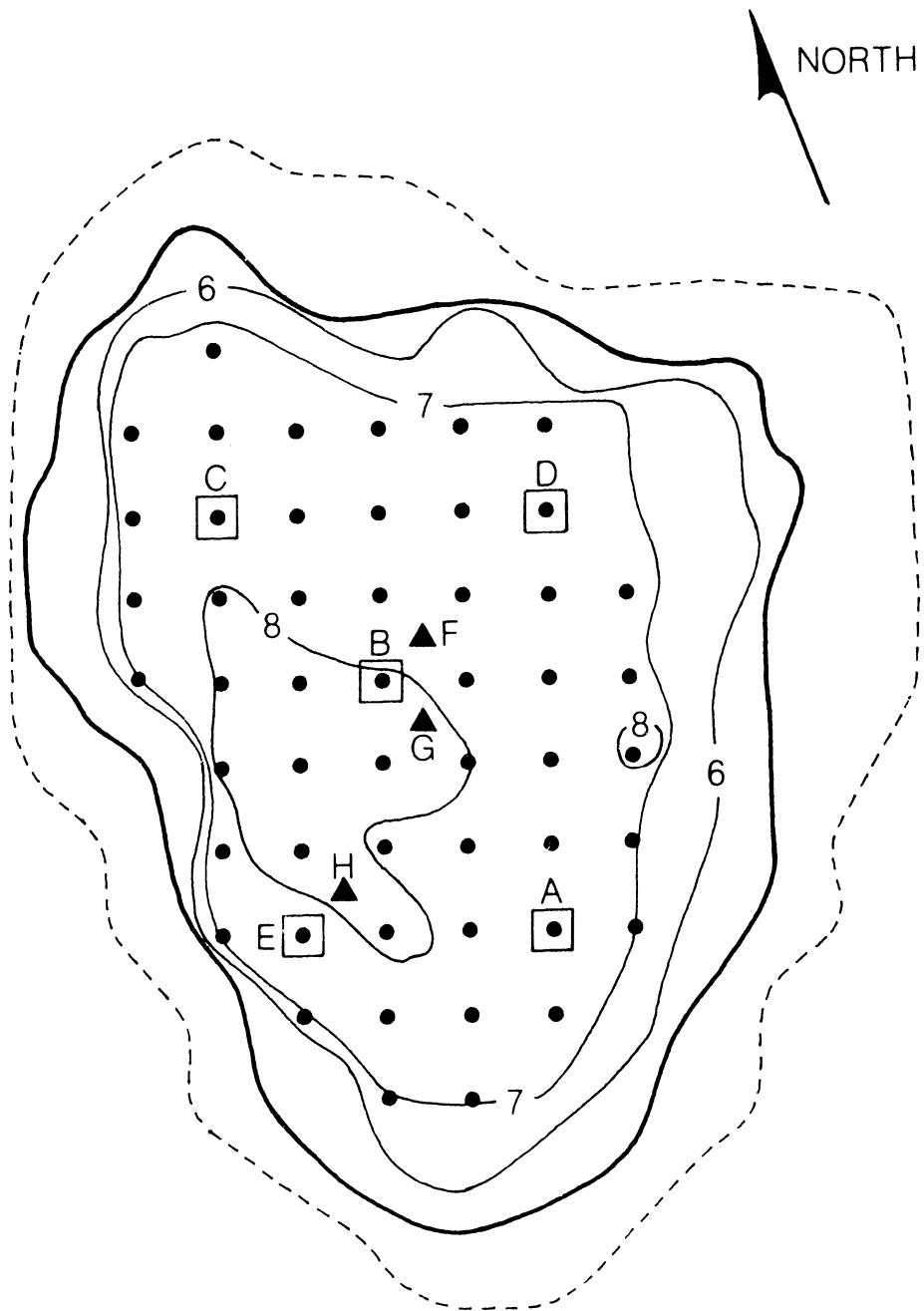
NORTH

NORTH GATE BOG

survey data 1969

(depth in meters)

● INJECTION SITES
▣ INJECTION SITES &
    SAMPLING STATIONS
▲ SAMPLING STATIONS

———— SHORE LINE
- - - - - - - - TREE LINE

Fig. 1. Hydrographic map of North Gate Lake, showing injection sites and sampling stations.

in flushing the tube was the same temperature as the 7-m water. This dispersed the label between the 7- and 8-m contours. In 1970, surface water was used to flush the apparatus. This water was slightly warmer than the bottom water and had the effect of dispersing the label through a thicker stratum (6-8 m).

Observations on the horizontal and vertical dispersion of the labels were made at frequent intervals after injection each year. We studied dispersion by measuring the concentration of the tracer at five of the injection sites, stations A, B, C, D, and E, and at three locations 3-5 m distant from the injection sites, stations F, G, H (Fig. 1). At each site we measured the rhodamine WT concentration and the concentration of soluble reactive phosphorus, soluble unreactive phosphorus and total phosphorus on three replicate samples. Procedures outlined by Strickland and Parsons (1965) were used in the latter analyses. We measured the radioactivity associated with each phosphorus fraction by pipetting 5 ml of the solution used in measurement of stable phosphorus onto a planchet, evaporating to dryness and counting the residue. All water samples were collected using a modification of the Hale water sampler (Welch, 1948). In this modification, the reservoir bottle encloses a single polyethylene bottle which is used as the sample bottle. The reservoir bottle had approximately five times the volume of the sample bottle. Thus a complete flushing of the sample bottle took place before samples were collected. The advantage of the modified Hale sampler for this investigation was that it enabled us to sample a relatively thin vertical stratum (0.2 m) and avoided possibility of contamination arising in the transfer of labeled materials from one container to another.

DISPERSION IN 1969 UNDER MEROMICTIC CONDITIONS

In 1969, after the injection of the labeled mixture through the ice, there appeared to be rapid horizontal dispersion, but vertical movement was minimal. Intensive sampling at stations A-E (Fig. 1) between March 15 and 21 indicated considerable horizontal variability in the concentration of both labels at 7 m and showed that the concentration at a given station fluctuated with time. These fluctuations appeared to be random and suggested horizontal water movements. This indication of horizontal flow was confirmed by measurements of the labels made at stations F and G. These two stations were located 3.5 m from the nearest injection site. By March 20 the concentrations of both tracers at these two stations were not significantly different from concentrations at adjacent injection sites, indicating that considerable horizontal mixing had occurred. These observations confirm findings of Hasler and Likens (1963) who observed horizontal movements of bottom water under the ice following labeling with radiosodium. Unlike the above study, in North Gate Lake there was little vertical movement within the water column. Within the first 5 days after labeling, significant quantities of activity were found only at 7-8 m and up to 6.7 m. Of 24 samples collected from 6 m at three stations between March 16-20, only 4 were above background.

Although we did not detect either tracer above the 6-m level between March 16 and 21, the next series of measurements made on April 13 showed an isolated layer with particulate ^{32}P activity immediately under the ice. We did not encounter measurable amounts of rhodamine WT at any depth above 7 m, and neither soluble nor particulate activity was detected in any stratum between the surface layer and 6.7 m on April 13. Thus, except for the particulate ^{32}P under the ice, there was no indication of vertical movement of either label above 6.7 m while ice was on the lake.

The lake was dichothermic when the label was injected on March 17 (Fig. 2). On this date there was an isothermal layer (3.95°C) between 4.5 and 6 m. The temperature was slightly higher (4.02°C) at 7 m and increased to 4.22°C at 8 m. A weak chemocline was indicated by an increase in calcium and conductivity from 7 to 7.5 m. Several sets of physical-chemical data collected between April 13 and 16 showed that the dichothermic condition was preserved during the spring overturn (Fig. 2).

There was little if any dispersion of the labels during vernal circulation. A second injection of rhodamine WT was made through the ice on April 16 to facilitate measurement of the tracer during the overturn. This increased the concentration at 7 m, however following the overturn, rhodamine was not detected above 6 m. Similarly, little or no vertical movement of ^{32}P was indicated (Fig. 3). A significant amount of particulate activity was detected at 6 m on April 20, however activity was not found between this layer and the surface. The particulate activity detected under the ice on April 13 was present on April 20. By May 6, this activity had moved down to the 3-m level (Fig. 3). Further warming of the lake effectively isolated bottom labels from upper strata and maintained dichothermic conditions during the entire summer (Fig. 2). The principal effect of vernal circulation upon the bottom water appears to have been a thickening of the layer below the 4.2°C isotherm (Fig. 2). This thickening must have taken place by an internal mixing process such as internal waves since there was no indication of water exchange between this stratum and upper layers.

BIOLOGICAL DISPERSION OF LABEL IN 1969

The absence of a vehicle for physical transport of labels into the trophogenic waters demanded close scrutiny of possible biological mechanisms. Two sets of data gave an indication of biological transport of ^{32}P within the lake basin. First, the large concentration of particulate activity under the ice sheet noted above was completely isolated from the source of activity in the bottom water. This activity occurred in water containing large numbers of dead phantom midges (Chaoborus). Although estimates of the total number of dead larvae were not made several hundred or more per square meter were present at all locations at which holes were cut through the ice. This species was previously collected in samples of labeled 7 m water between March 15-21,
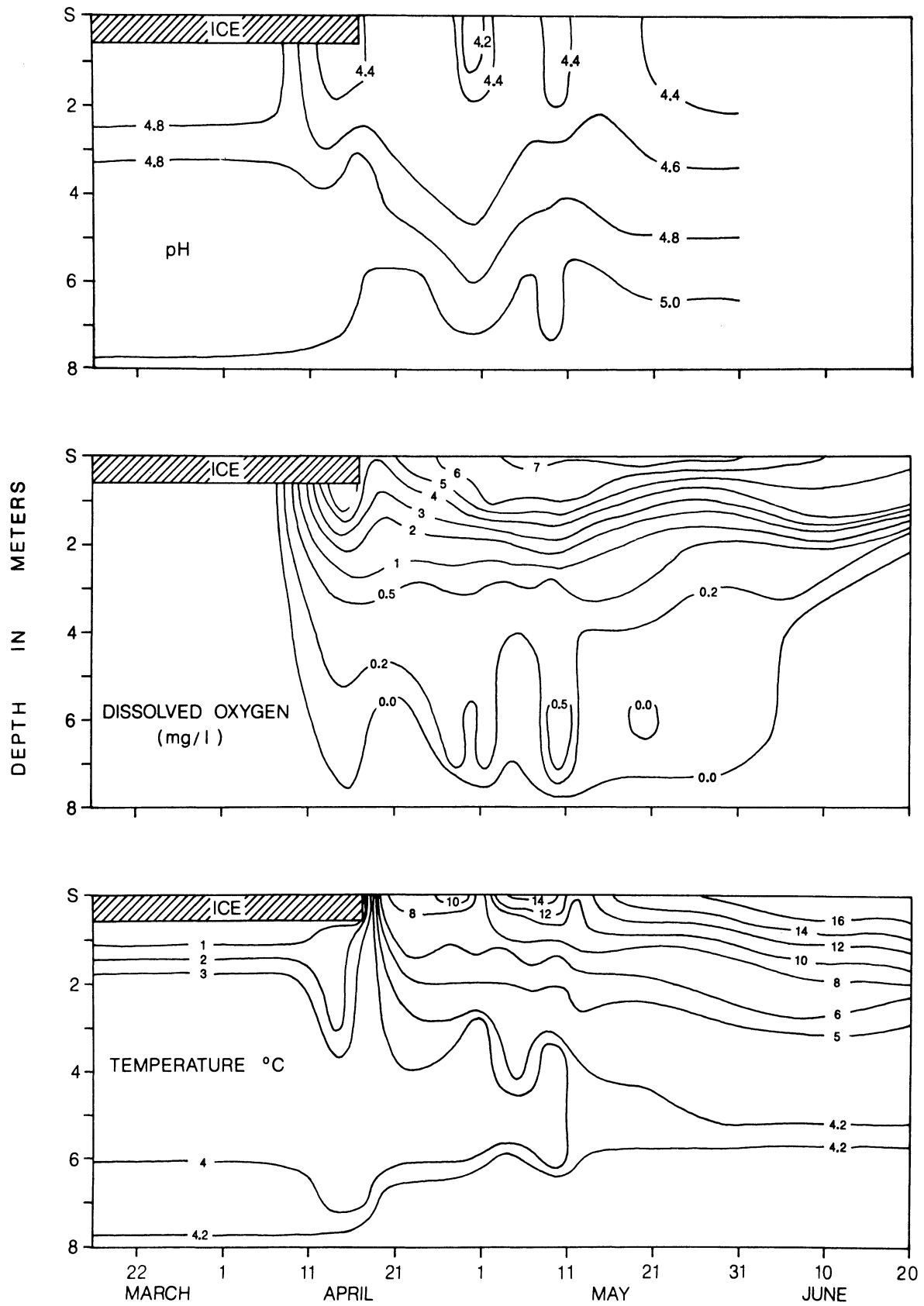
Fig. 2. Distribution of oxygen, pH, and temperature;
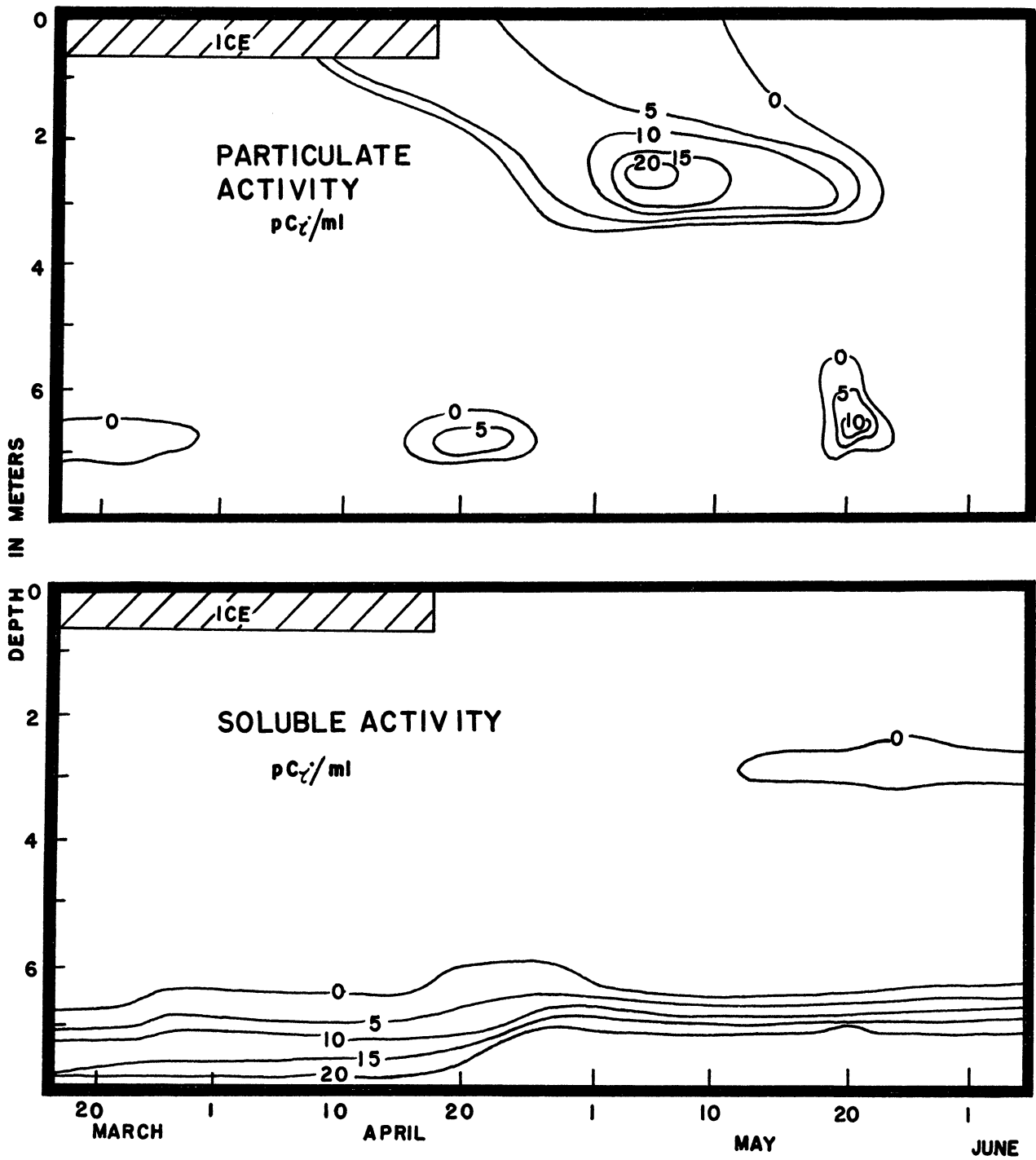North Gate Lake, 1969.

Fig. 3. Distribution of soluble and particulate radioactivity; North Gate Lake, 1969. Activity corrected for decay.

and the larvae were radioactive at this time. The localization of activity in
the stratum containing dead Chaoborus provided presumptive evidence that this
activity was brought to the surface by Chaoborus and subsequently released by
excretion and decay.

A second and direct observation of biological dispersion was noted
shortly after disappearance of the ice. At this time, net plankton samples
showed a large diurnal fluctuation in activity level. These fluctuations were
apparent at all depths (Fig. 4). It was soon discovered that this diurnal
fluctuation in activity was associated with the vertical migration pattern of
Chaoborus. Radioactive larvae appeared in the bottom water shortly before
sunset and within 1 hr or less they moved to the surface. Reverse migration
to the bottom occurred shortly before sunrise (Fig. 4). To determine whether
or not activity was transported by species other than Chaoborus, we collected
samples containing copepod nauplii, adult copepods, cladocera and rotifers at
four depths over a 24-hr period (Fig. 5). Few of these taxa occurred in water
below 3 m and we found no evidence of diurnal fluctuations in numbers except
in the surface and 2 m strata. Thus there was no evidence for vertical trans-
port of activity from the hypolimnion by species other than Chaoborus.

The fate of the activity noted under the ice cannot be traced precisely.
It spread throughout the epilimnion after the spring overturn and soon
appeared in the phytoplankton and zooplankton at 2 m (Fig. 3) and also in the
mudminnow, Umbra limi, which feeds almost exclusively upon Chaoborus.

The total quantity of activity within the epilimnion did not increase
significantly after the spring overturn. Thus there was no evidence of fur-
ther inputs of activity from migrating Chaoborus. An increase in particulate
and soluble phosphorus in bottom strata arising from sedimentation of sus-
pended matter and subsequent mineralization might have been predicted. This
is the normal seasonal pattern in stratified lakes (Juday and Birge, 1931).
For the period between May 6 and June 26, there appears to have been little or
no change in the quantity of particulate stable phosphorus at 7 m. During
this period there was a slow decrease both in soluble activity and in soluble
reactive phosphorus at this depth. Means of the specific activity of soluble
phosphorus on five sampling dates during this period were not significantly
different. Failure to find a decrease in specific activity suggests that very
little unlabeled stable phosphorus was released into the 7 m layer by way of
sedimentation and regeneration or from excretion by Chaoborus.

DISPERSION WITH NORMAL THERMAL STRATIFICATION, 1970

In 1970, at the vernal overturn, partial mixing took place to the 8 m
depth. Injection of the tracer in 1970 was not as well localized in the water
column as in 1969. Although concentrated at 7 m, small amounts moved upward
in the water column to slightly above 6 m and downward to the 8 m stratum
(Fig. 6). Horizontal dispersion was poor and resulted in considerable
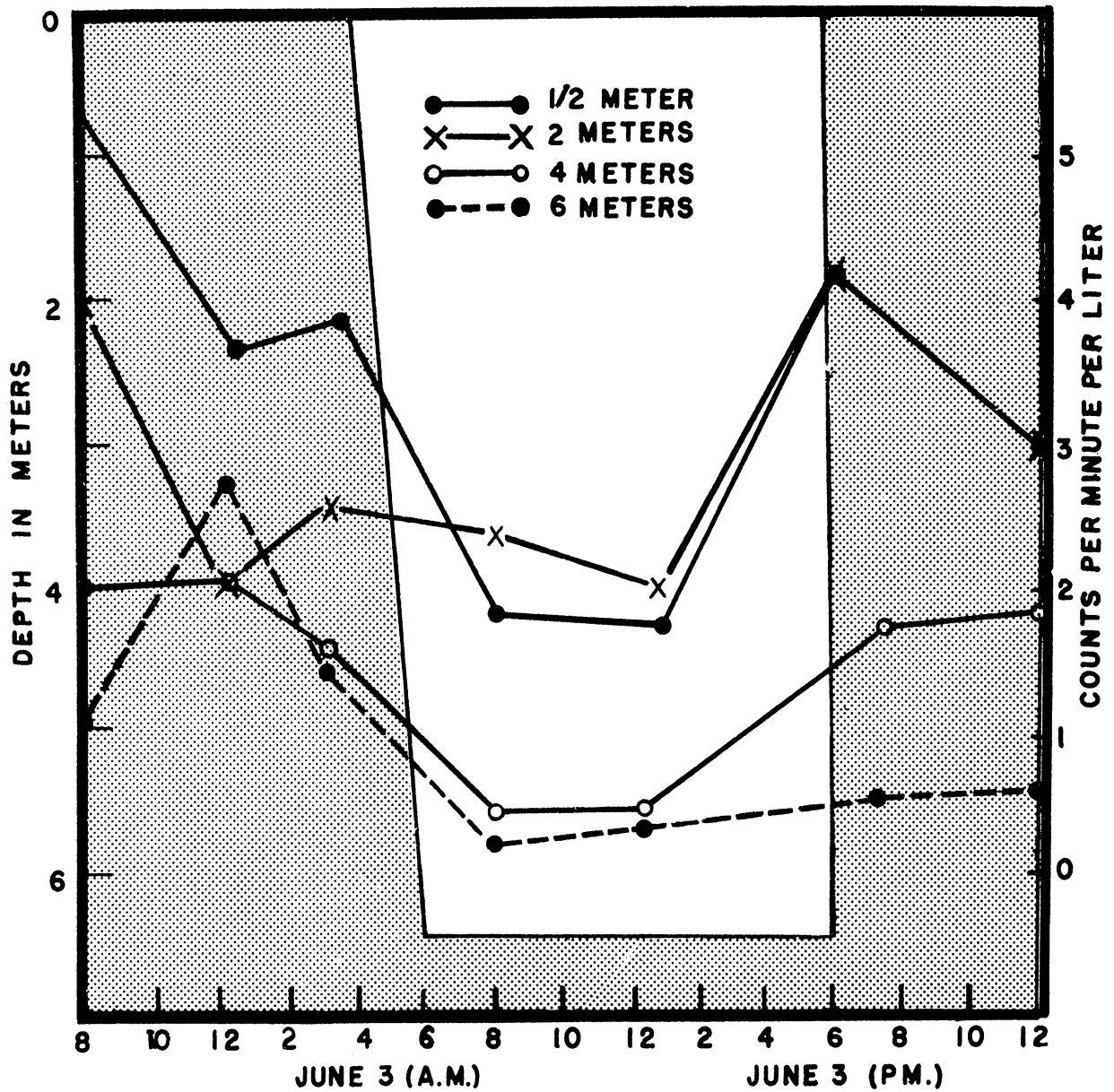
Fig. 4. Activity of plankton samples collected from various depths in North Gate Lake on June 2-3, 1969. Plankton collected by straining 10 liters through a 20μ nytex net. Shaded area shows the depths at which Chaoborus was collected during this period. Activity corrected for decay.

Fig. 5. Diurnal changes in the numbers of zooplankters in North Gate Lake, May 27-28, 1969.

Fig. 6. Distribution of total water radioactivity (pCi/ml) in 1970. Activity corrected for decay.

20

horizontal variation in activity within the 7 m stratum. On May 17, the day after injection, values of ^{32}P varied from 4 to 143 pCi/ml at stations A-E. At station B the concentration remained at 64-65 pCi/ml until a major redistribution both horizontally and vertically occurred b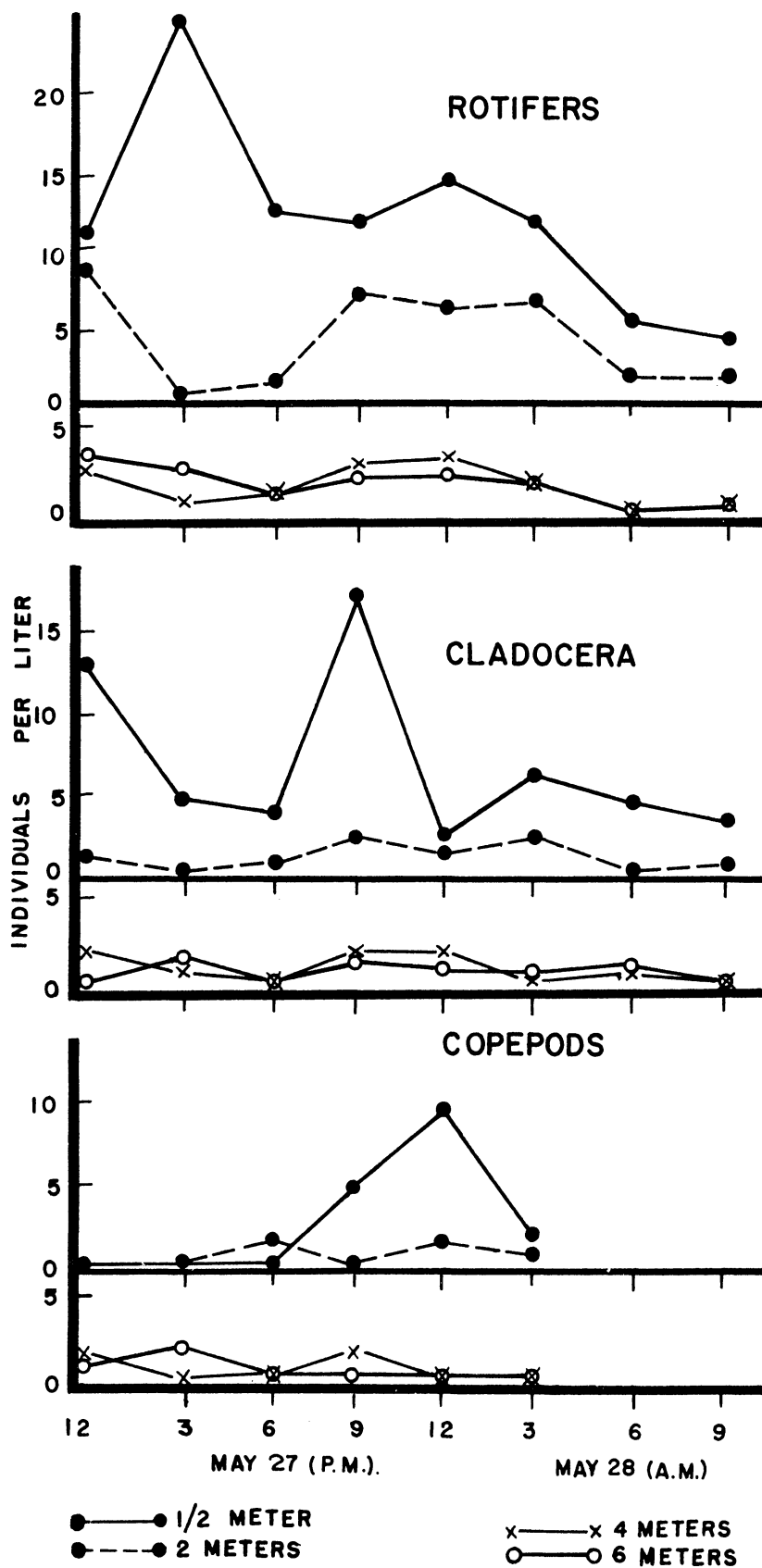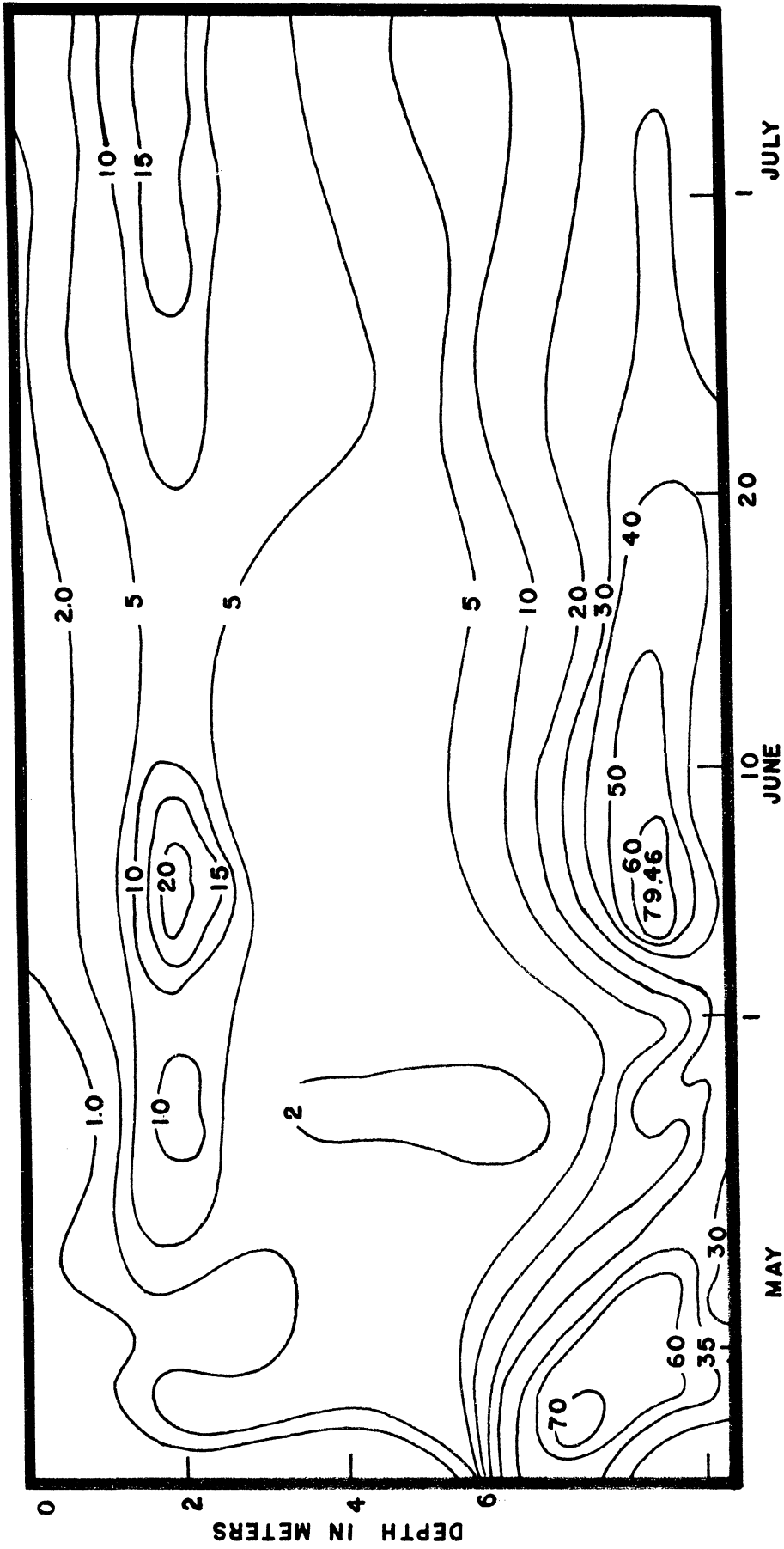etween May 19-21 (Fig. 6). At this time, the concentration at station B fell to 15-16 pCi/ml and concurrently a large increase in activity was detected in the epilimnion. The activity injected into the epilimnion appeared as particulate matter although activity encountered below 3 m was chiefly filterable. Thus phosphorus carried into the upper waters was rapidly incorporated into bacteria and plankton. The physical-chemical data collected during this period confirm the water movements of May 19-21. A second movement of label into the upper layers occurred between June 1-5. Again there was a large increase in activity at 2 m and large horizontal redistribution within the 6- to 8-m zone. At station B the tracer concentration increased at 7 m to the levels encountered before May 19 (Fig. 6). After this period of circulation, horizontal variations appeared to have been small, which indicated that the tracer had been mixed rather well in the bottom water. A third major upward movement of tracer occurred between June 17-25. This greatly reduced the amount of activity in the 6- to 8-m layer, and increased activity in the 1- to 2-m stratum and at intermediate depths. During each of these periods of water movement, we noted corresponding changes in the distribution of rhodamine WT and other physical and chemical parameters.

The pattern of activity changes of the 0- to 2-m layer was the same in all three instances. After vertical mixing, the activity fixed in the particulate matter of the 0- to 2-m stratum decreased slowly. The fate of activity lost from this stratum between pulses cannot be identified with certainty. However, since there was no increase in particulate activity at lower levels, it would appear that activity was lost by horizontal dispersion, perhaps by movement into the bog mat. Exchange of ^{32}P between open water and the bog mat has been described previously (Coffin, et al., 1949).

Since the specific activity of the phosphorus of all strata was known, the quantity of stable phosphorus carried into the 1- to 3-m zone can be estimated from changes in the distribution of radioactivity (Table I). The quantities of phosphorus transported vertically during the three periods of mixing constituted major fractions of the phosphorus present in the receiving strata. Increases in the 1- to 2-m layer were from 22.4 to 44.8% of the total phosphorus present. It is also clear that these injections brought to the upper water major fractions of the phosphorus remaining in the 6- to 8-m stratum at the conclusion of vernal circulation (Table II).

BIOLOGICAL DISPERSION IN 1970

The 1970 data provided no evidence for vertical transport of phosphorus by Chaoborus. There was very little activity in Chaoborus and the biota of the epilimnion between May 16-19. Mixing between May 19-20 carried activity

Table I. Estimates of stable phosphorus from 6- to 8-m stratum carried into 0- to 2-m zone during periods of high vertical mixing in 1970. Estimates made from changes in ^{32}P distribution.

Dates of mixing	Total Phosphorus Entering 0- to 2-m Zone		
	Grams	Percentage of total P present 0-2 m	Percentage of total P, 6- to 8-m stratum at labeling (May 16)
May 21-23	41.2	22.4	8.0
June 1-3	136.0	44.8	27.7
June 17-18	89.1	26.5	18.1

Table II. Dry weight, activity, and phosphorus content of Chaoborus during vertical migration on June 27-28, 1969.

Time	Chaoborus				
	Number	Average dry weight (mg)	Average activity (pCi)	Average phosphorus (µg)	Specific activity (pCi/µg P)
10:15 p.m.	97	0.247	221	6.29	35.14
10:15 p.m.	97	0.247	220	6.04	36.42
4:15 a.m.	96	0.250	244	6.81	35.82
4:15 a.m.	98	0.253	238	6.84	34.80

into this stratum and brought about a rapid build-up of activity in phytoplankton, zooplankton, Chaoborus, and Umbra. The specific activity curve of plankton collected with a 10μ plankton net does not show a steady increase but changes in rate. Periods of accelerated uptake appeared to follow the injections of phosphorus into the upper water. Plateaus or decreases in plankton activity occurred when water activity remained constant or decreased (Fig. 7). The specific activity of the muscle tissue of Umbra does not show a steady increase but rather stepwise changes which might be related to changes in water activity (Fig. 7). The specific activity pattern of Chaoborus, on the other hand, was sigmoid and did not show periods in which activity decreased. In late June, Chaoborus reached a higher specific activity level than that encountered in plankton. The higher activity of Chaoborus could arise from the selection of plankton food of a higher activity than the mean of the plankton samples analyzed or this species could have increased its activity during residence in the high activity bottom water.

Discussion

Isolation of the biological transport process in 1969 provided the opportunity to examine two questions of interest regarding the phosphorus cycle of stratified lakes: (1) What is the direction of net transport of phosphorus by Chaoborus during its daily migration cycle? (2) Considering emergences, daily transport, and predation in the surface waters, how does the quantity of phosphorus carried upward by biological processes compare with the quantities brought up by turbulent mixing?

To answer question 1, on June 27 and 28, 1969, we measured the dry weight, activity, and stable phosphorus content of larvae collected at 10:15 p.m. during upward migration and compared these values with data from larvae collected at 4:15 a.m. during their downward migration (Table II). Chaoborus captured moving down in the morning had a higher phosphorus content, a higher average dry weight, and a higher average activity than larvae moving upward. Since the downward moving larvae had a higher stable phosphorus content, as well as higher activity, the specific activity of upward and downward moving larvae remained essentially unchanged. Chaoborus larvae were eating radioactive plankton in the uppwer water and the difference in stable phosphorus between morning and evening migrating larvae indicated that about 0.6μg of phosphorus per Chaoborus was taken from the epilimnion into the hypolimnion. Migrating larvae collected on this date and introduced into activity-free water lost activity at the rate of 2.31 pCi per larva per hour, which was equivalent to 0.07μg per larva per hour. Thus it would appear that migrating larvae enrich the hypolimnion with phosphorus excreted after their return from surface feeding.
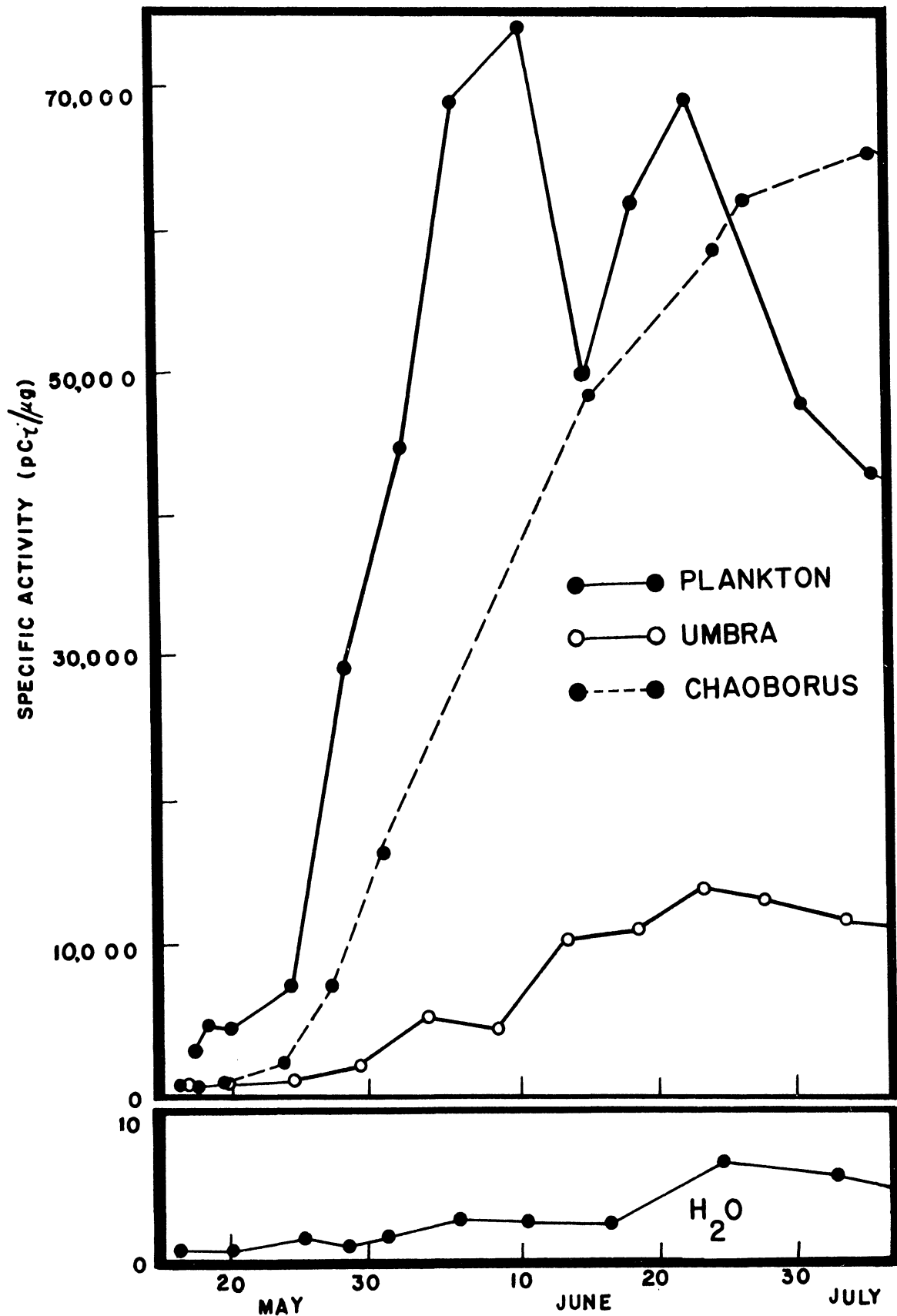
Fig. 7. Average specific activity of water, plankton, Chaoborus, and Umbra of 0- to 2-m stratum after labeling in 1970. Activity corrected for decay.

The net downward movement during daily migration however, may be quantitatively insignificant as regards the phosphorus cycle. The total amount of phosphorus in the Chaoborus population in 1969 was estimated to be less than 24 g. This appears to be less than 2% of the total phosphorus present in the lake water. The different in phosphorus content between upward and downward moving larvae was 9% of their phosphorus content and some of this phosphorus must be lost in transit. It would appear that the input into the bottom water from migration is small and may be overbalanced by losses to the epilimnion arising from predation, emergence, and other sources of mortality. A mudminnow may consume 20 Chaoborus larvae during a 24-hr period, and since the lake contains from 1000 to 2000 mudminnows, the amount of phosphorus excreted and egested by Umbra in the upper water may be greater than that carried down by daily migration.

Our estimates of the quantity of phosphorus carried vertically by way of circulation indicate that this process brings much larger quantities (up to 136 g in a 2- to 3-day period) into surface waters than does biological transport (Table II). These inputs into the trophogenic waters constitute a major renewal of the phosphorus resources and doubtlessly sustain production for a considerable period.

A second major source of phosphorus for the lake system is the bog mat. Phosphorus additions from this source also occur at irregular intervals. Data collected in 1970 indicate that enrichment from this source occurs when the Sphagnum mat is flooded by rain, and there is a flow of interstitial water from the mat into the lake.

The overall picture that emerges is one of aperiodic enrichments, controlled by weather phenomena, which arise from these two sources. The lack of littoral sediments as a source for renewal of phosphorus gives bog systems such as North Gate low predictability as regards their nutrient supply and makes such systems highly dependent upon the vertical intrusion described above.

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APPENDIX B

FURTHER STUDIES OF THE DISPERSION OF HYPOLIMNETIC
PHOSPHORUS IN A BOG LAKE SYSTEM

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FURTHER STUDIES OF THE DISPERSION OF HYPOLIMNETIC PHOSPHORUS IN A BOG LAKE SYSTEM

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This manuscript further describes the vertical and horizontal dispersion of phosphorus compounds within a small bog lake labeled with ^{32}P in 1969-70. It presents data upon the method of vertical transport of phosphorus from the hypolimnion and its fixation within the photosynthetic zone. It will also present data on the horizontal dispersion of phosphorus within the lake basin and data on the effects of an application of lime upon distribution of phosphorus.

Details of the procedures used in labeling the bottom stratum in 1969-70 have been described elsewhere (Hooper and Imes, 1969, 1970). Briefly, in 1970 we labeled the bottom water of the lake 3 weeks after the spring overturn by injecting a mixture of 120 g of rhodamine WT and 200 mCi of ^{32}P, as orthophosphate, into the 7-m stratum. Two-gal aliquots of a 50-gal mixture of the above two ingredients and lake water were poured through a 2-in. plastic tube into the bottom layer. By flushing the tube with several additional gallons of lake water, the label was dispersed horizontally and mixed within the 6 and 8-m contours. After labeling, we followed horizontal and vertical movement of the tracers by sampling vertical strata between 0 and 8 m at a series of stations upon the lake surface (station A-E; Fig. 1). Water samples were collected and analyzed for radioactivity at approximately weekly intervals. For these measurements, from 25 to 100 ml (depending upon activity) of water was evaporated to dryness in an evaporating dish. The residue was removed by washing with 5 ml of 0.1 N HCL and was transferred to a planchet, evaporated to dryness, and counted. In addition to measuring the concentration of rhodamine WT, soluble and particulate ^{32}P activity, we also monitored the concentration of stable phosphorus in the water at a series of depths, and we measured the stable phosphorus and ^{32}P within the surface plankton, within the phantom midge Chaoborus, and within the principal predator of the lake, the mudminnow Umbra.

Vertical Movement of Labels in the Lake Basin

There was no indication of residual ^{32}P activity from 1969 in the spring

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*Present address: Hebron, Maine.
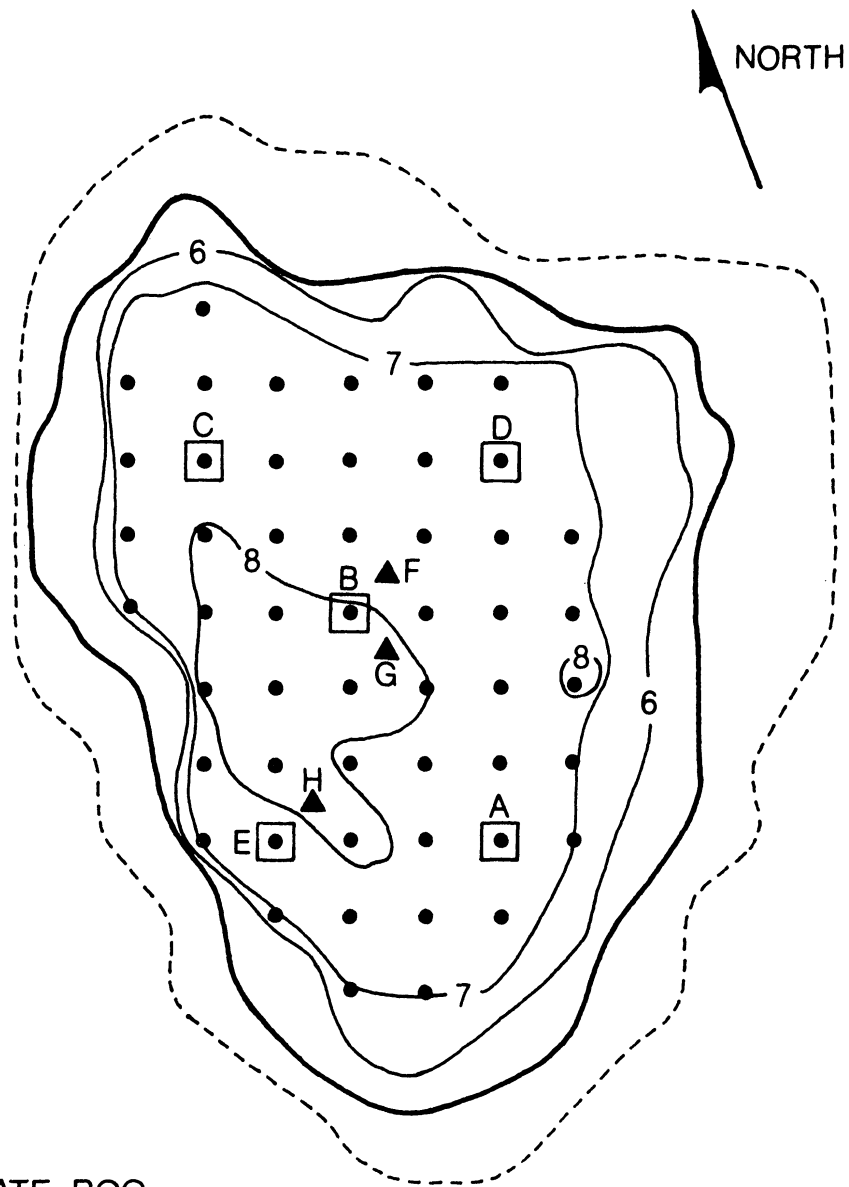
NORTH

NORTH GATE BOG
survey data 1969
(depth in meters)

● INJECTION SITES
▣ INJECTION SITES &
SAMPLING STATIONS
▲ SAMPLING STATIONS

———— SHORE LINE
- - - - - - - TREE LINE

Fig. 1. Map of North Gate Lake, showing sampling locations.

of 1970. However rhodamine introduced in the spring of 1969 persisted in the water column in the 6-8 m zone. The concentration present on May 6, 1970, at 8 m was approximately the same as present on August 22, 1969 (Table I). Since the lake was dichothermic and the bottom layers failed to mix with the upper layers in 1969, the persistence of a large quantity of rhodamine at 8 m was not unexpected. Above this layer the rhodamine appeared to be distributed uniformly. On May 6 concentration ranged between 3 and 8 ppb (Table I). Temperature data of May 5-11 (Fig. 2) show a tongue of cold water remaining from the spring overturn between 4 and 7 m, and warmer water both above and below this layer. This monimolimnion persisted between 7 and 8 m through most of the summer. As in 1969, the 6-8 m zone was rich in phosphorus. On May 8, over 200 μg/l of soluble reactive phosphorus (SRP) was present at 7 m.

The two tracers were injected into the bottom water in a grid pattern. Application was made at horizontal intervals of 5 m. Although we attempted to disperse the label by flushing the injection tube with unlabeled water, this procedure only partially dispersed the labels within the 6-8 m stratum. Large horizontal variations appeared in this stratum and persisted until June 2-5. The injected material was confined vertically to the 5.5-8 m zone. Maximum concentration was at 7 m but relatively large quantities appeared upward as far as 5.5 m.

Significant upward movement of the labels was first detected in the data of May 21. At this time there had been movement of ^{32}P from 6-8 m upward into the 3-5 m zone. This upward displacement therefore seems to have been confined to the hypolimnion and thus must be associated with an internal mixing process rather than a mixing process arising at the surface. Further upward transport was detected in samples collected on May 26. At this time a large concentration of ^{32}P appeared at 1.8 m and smaller quantities at 0.9 m and at the surface. This upwelling seemed to be associated with changes in weather conditions. On May 21 exceedingly heavy rains occurred in the area. These were followed by passage of a cold front and freezing temperatures on the night of May 23 (Fig. 3). This may have caused vertical mixing from the surface and may have brought the tracers into the upper strata.

High horizontal variability in activity was apparent both in the surface layers and in the deeper strata in the data of May 26. Extreme horizontal patchiness was apparent in nearly all strata and suggests that up until this point both horizontal and vertical dispersion had been localized within the lake basin.

Greater horizontal uniformity in the concentration of tracers was established during the week of June 1-5 when there was large-scale mixing within the basin. Evidence of mixing first appeared in the temperature data of June 5, but the mixing almost certainly took place the night of June 2 and 3 when air temperatures fell after passage of a cold front (Fig. 3). Clear skies and a cold polar air mass brought rapid cooling of surface water and

Table I. Concentration of rhodamine WT (ppm) at stations on North Gate Lake after labeling mat with rhodamine on May 6. Stations A, C, D, F, and O are near the mat margin. Station B is near the center of the open water.

Depth (meters)	May 6 Station						May 11 Station					
	A	B	C	D	F	O	A	B	C	D	F	O
sfc	17	9	9	7	16	12	29	31	36	31	31	31
0.91	5	3	38	7	50	6	12	27	34	18	23	9
1.8	6	5	8	5	7	5	8	6	7	7	6	8
2.7	6	3	8	5	10	5	6	6	7	6	6	7
3.6	7	7	8	5	6	6	6	6	10	6	6	7
4.6	5	6	10	6	5	6	7	8	8	6	6	8
5.5	5	8	9	8	5	8	6	7		7	7	7
6.4	5	11		8	5	17	6	11		9	10	8
7.3	15	41		14	14	49	21	43				46
8.2		51						49				52
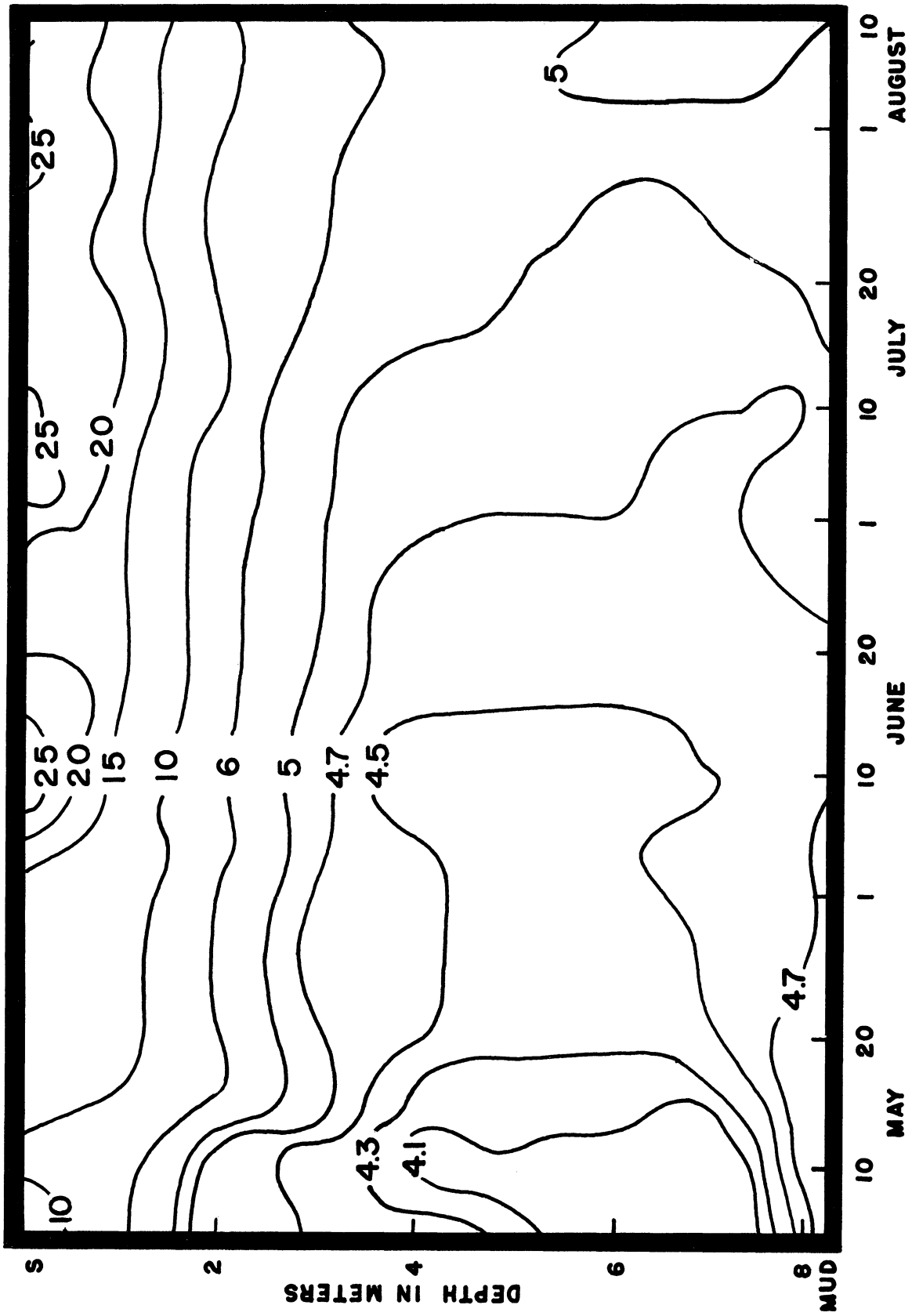
Fig. 2. Temperature (°C) distribution, North Gate Lake, 1970.

PRECIPITATION (inches)

▦ 0-0.25　　▨ 0.25-0.5　　▧ 0.5-1.0　　■ <1.0

AVERAGE CLOUD COVER

□ <0.1　　▦ >0.1-<0.5　　▨ >0.6-<0.9　　■ >0.9

MINIMUM AIR TEMPERATURE

Fig. 3. Weather data, 1970; U.S. Forest Service, Watersmeet, Michigan, Ranger Station.

34

mixing throughout the basin. At this time there was heat input and changes in pH and oxygen in the lower thermocline. This upwelling of tracer more than doubled the concentration of ^{32}P at the surface, 0.9, and 1.8 m strata.

During the week of June 5-11, a warming trend brought about large increases in air and water temperatures (Fig. 3). During this period there was little or no heat input into the thermocline and no indication of upwelling of tracer (Fig. 2). Warm weather continued until June 18 when there was another cold front passage and falling air temperatures (Fig. 3). This weather change again brought about a response in lake temperatures. Surface temperatures fell and there was mixing in the lower thermocline. Tracer data collected on June 25 again showed an increase in ^{32}P at the surface, 0.9, and 1.8 m. This increase, however, was somewhat smaller than the increase on June 5. During the early part of the week of June 26-July 3 the cold trend continued and there was a further upwelling of tracer and thermal changes in the thermocline.

The rhodamine WT introduced along with the ^{32}P at 7 m on May 16 also showed a gradual upward dispersion. Rhodamine data are incomplete for the period between May 16 and June 6, and have been extrapolated (Fig. 4). For the period for which adequate data are available, it appears that the major intrusions of rhodamine coincide with major inputs of ^{32}P. Upward movement was apparent from data collected on June 18 and again between June 26 and July 3. The rhodamine data thus appear to confirm that upward movement of tracer was restricted to short periods when there were thermal changes within intermediate layers of the lake.

Data collected from the time of treatment of the lake with tracer (May 16) until the time of treatment with lime (July 6) point to a strong relationship between upwelling of tracer and weather conditions. Inputs of tracer into the strata above 1.8 m occurred only during periods of cool weather after cold front passages. This brought on lower surface water temperatures. In two instances, vertical mixing was associated with clear nights and cold air masses which would combine strong back radiation with convective cooling at the surface.

There were no indications of upwelling during warm periods when surface temperatures were increasing or remained relatively high, or with warm and cloudy weather. The observed weather responses indicate that lake systems of this morphometry and thermal structure have exceedingly low resiliency to meteorological changes. Responses of the system to short-term weather fluctuation go beyond thermal changes and must include enrichment from nutrient sources deep in the lake basin.
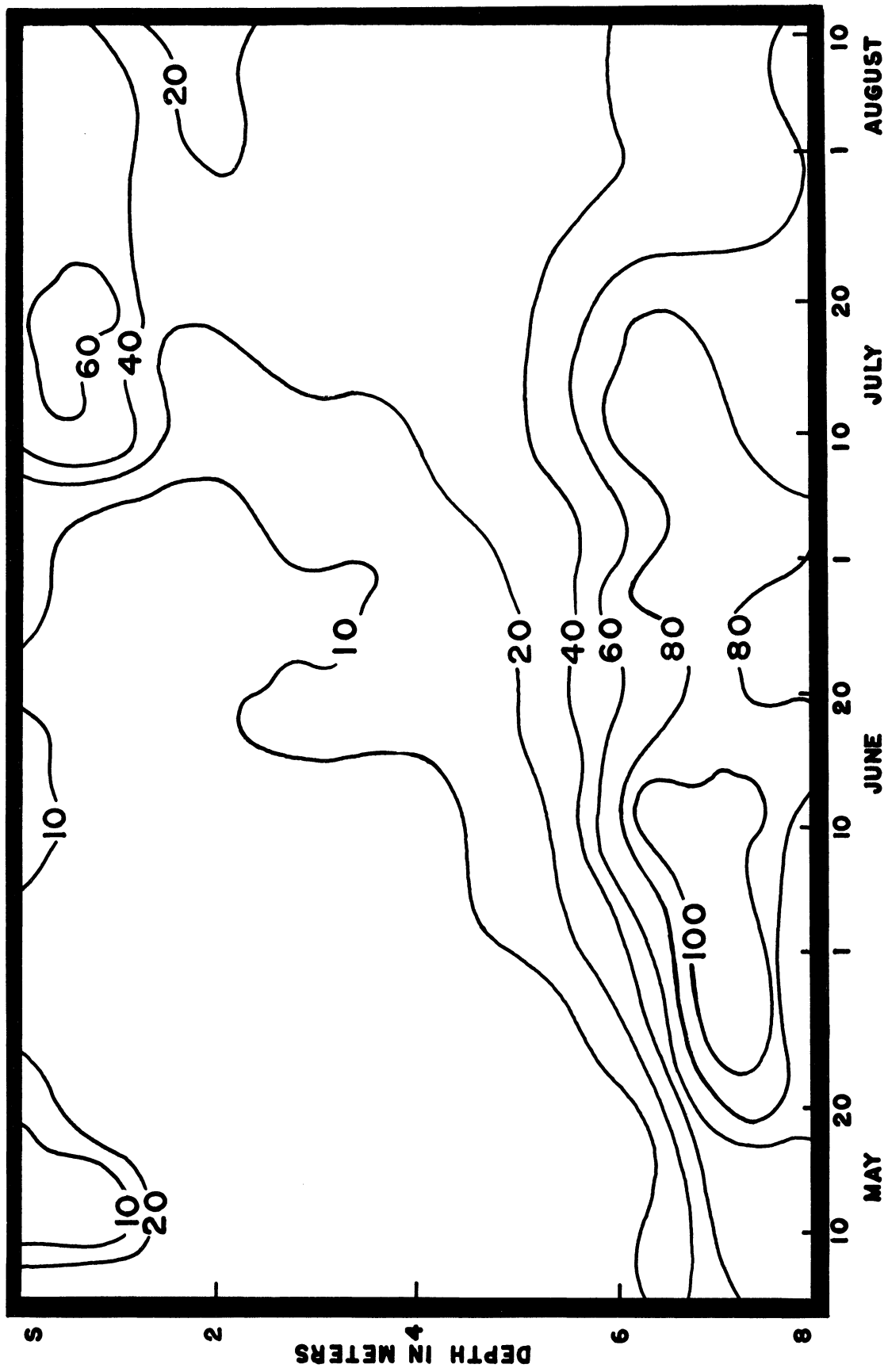
Fig. 4. Distribution of Rhodamine WT; North Gate Lake, 1970.

Role of the Biota in the Vertical Transport of Phosphorus

Comparison of the rate of upward movement of the biologically conservative label (rhodamine WT) with that of the nonconservative label (^{32}P) afforded an opportunity to investigate the influence of biological processes in vertical dispersion. Although rhodamine is adsorbed on certain organic particulates, it appears to resist biological uptake and breakdown. Rhodamine introduced in 1969 was present in the spring of 1970. The quantity encountered in the spring of 1970 in the monimolimnion layer was only slightly less than that present in the fall of 1969. During residence in the stratum at which they were introduced (6-8 m) all of the rhodamine and about 68% of the ^{32}P was filterable through a 0.45 μ filter. The phosphorus activity must have been soluble reactive (SRP) since little or no soluble unreactive (SUP) was recorded in this layer (Fig. 5).

Above the labeled stratum the percentage of soluble activity decreased and little was encountered above 5 m (Fig. 5). Activity transported above the 5-6 m layer was converted into particulate form. The phosphorus concentrated in the 1.2 - 2.1 m layer was almost entirely particulate. The small quantities of soluble activity (up to 2 pCi/ml) that appeared sporadically in this zone may have been activity released from particulates. However, other than the large input of SUP which entered the lake water from the mat late in July (discussed below), there was little soluble activity within the euphotic zone during the summer.

Fixation of phosphorus in particulate form in the lower part of the thermocline appears to have accelerated the flow of phosphorus upward from the bottom water. This becomes apparent upon comparing the change in vertical dispersion of phosphorus with that of rhodamine. On June 6 less than 0.5% of the rhodamine introduced in the water column had moved to the 1.2 - 2.1 m zone while 20% of the phosphorus activity had moved upward to or above this zone. On July 3 approximately 35% of the phosphorus had moved to the 1.2 - 2.1 m layer or above, while less than 2% of the rhodamine had reached this depth or above (Fig. 6). Thus biological fixation of activity appears to have made nearly a 20-fold increase in the efficiency of vertical transport.

The nature of the process concentrating ^{32}P in particulate form within the 1.2 - 2.1 m zone cannot be identified with certainty. It must have been either biological uptake or adsorption on debris concentrated in this zone. Vertical transport of the nuclide occurred at irregular intervals and was concurrent with thermal changes in the lower thermocline in the hypolimnion and with upward movement of rhodamine. The pattern observed was not that expected if upward displacement was by the daily migration of Chaoborus. If upward displacement was entirely by eddy diffusion, then there must have been selective uptake of ^{32}P compared to rhodamine by particulates which resisted sinking.
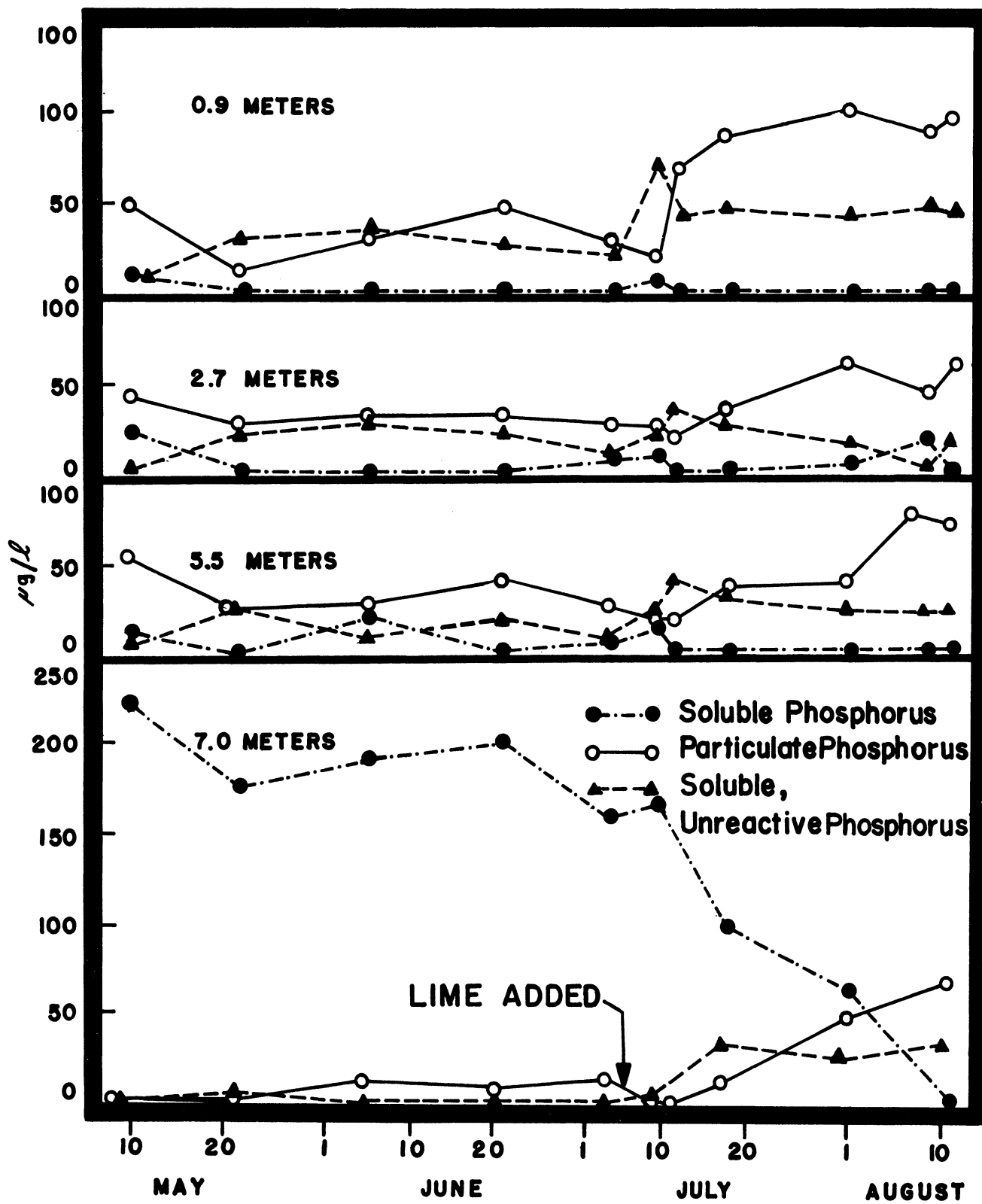
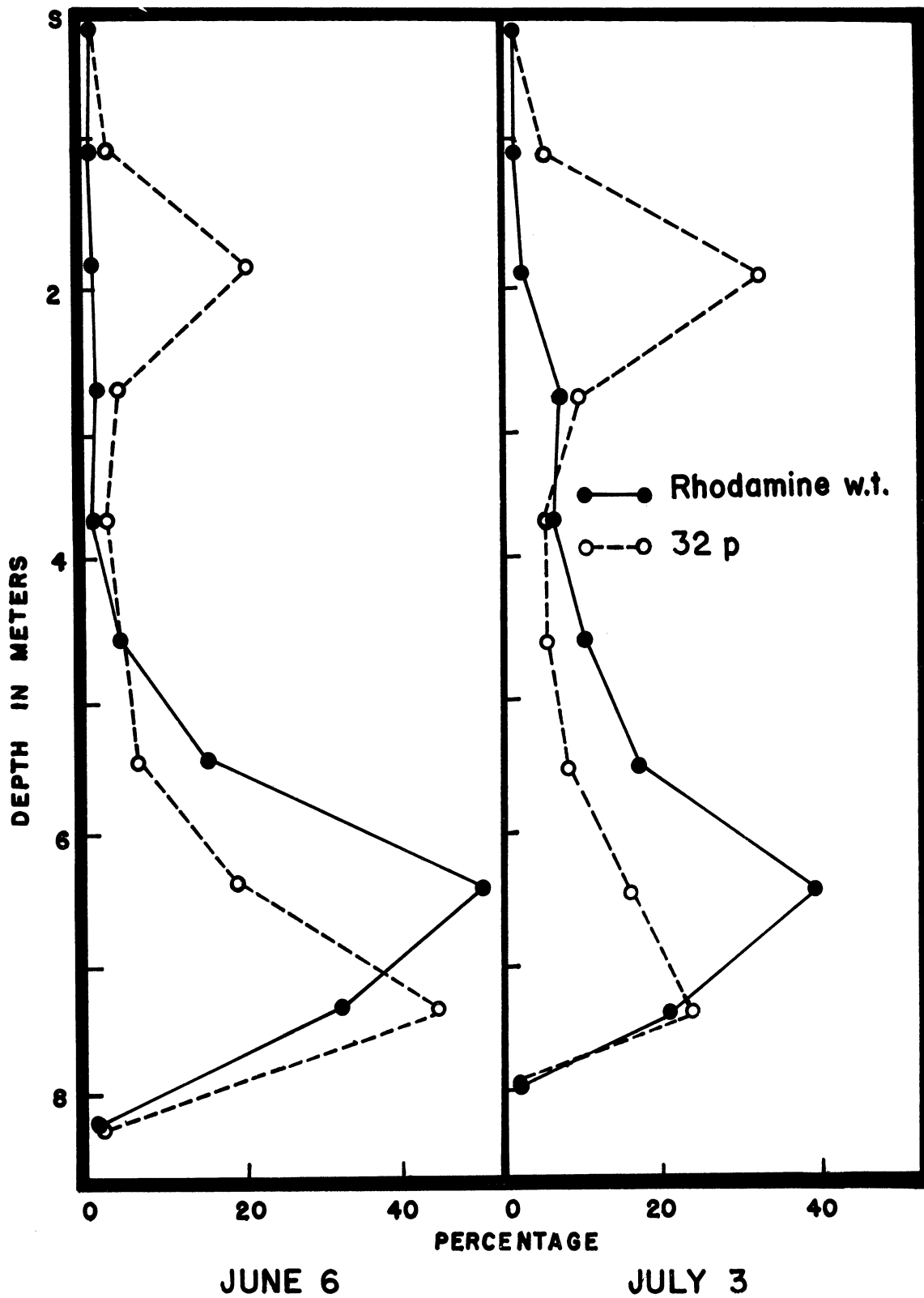Fig. 5. Concentration of stable phosphorus fractions at selected depths during 1970.

38

Fig. 6. Comparison of the percentages of rhodamine WT with quantity of ^{32}P transported vertically in water column on 2 dates in 1970. Percentages are:

$$\frac{\text{Sum of increases in tracer at indicated depth}}{\text{Quantity of tracer added to 7-m stratum on May 16}}$$

39

Movements of Mat Water Into the Lake Basin

On May 6 we labeled the interstitial water of the mat adjacent to the open water with approximately 100 g of rhodamine WT. The dye was dissolved in water and broadcast from a boat over the section of the mat 2 m from the open water. The purpose of this application was to determine whether or not there was vertical intrusion of mat water into subsurface strata of the open lake during early spring. Intrusions of mat water into bottom strata were suspected after observing horizontal movements of both the ^{32}P and rhodamine label added to the 7 m layer the preceding spring (Hooper and Imes, 1969). We hypothesized that sudden drops in air temperature cooled the interstitial mat water adjacent to the open lake and thereby produced density currents flowing vertically into deeper strata. After labeling, we made two sets of observations at stations around the basin (station A-E; Table I) in an attempt to detect vertical movement. At each of the stations we sampled the water column a distance of approximately 1 m from the margin of the mat.

It was clear that the label moved vertically only to the 0.91 m layer (Table I). Between 0.9 m and 5.5 m there were minor variations in concentration which were not significantly different from readings before treatment. The zone between 6.4 and 8.2 m showed the residual rhodamine from the 1969 experiments but did not show a significant change after the mat treatment. The data of May 6 indicated more rapid vertical movement of the tracer into the open water at stations C and F than at other stations. A large concentration developed at the 0.9 m depth at these stations before the dye was dispersed in the surface layer at other stations. By May 11 the dye was well distributed horizontally at the surface, and higher concentrations appeared at 0.9 m at marginal stations (A,C,D,F,O) and at the open water station (station B).

Although labeling demonstrated that the interstitial water moved vertically a distance of approximately 1 m, the experiment failed to verify intrusions to greater depths. Weather in 1970 was milder than in 1969 and temperatures which produced ice over flooded portions of the mat were not encountered in 1970.

Rhodamine introduced into the mat water persisted in the open lake at levels greater than 20 ppm for approximately 2 weeks. Surface concentrations fell to 10 ppm thereafter and remained near this level until after the lime treatment on July 6. This loss from the surface waters was not accompanied by increases at other depths within the basin. This suggests movement into the bog mat.

Differences in the mobility of mat interstitial water at different points in the mat were demonstrated by the mat labeling experiment. Although the label was applied uniformly around the lake, movement was not uniform around

the perimeter. At stations adjacent to an upland area (stations A, C, and F) the dye was visible in the mat for only 2 to 3 weeks following treatment. However at stations distant from upland areas (stations D and E), dispersion was exceedingly slow and the dye was visible one year after the application.

Effect of Lime Treatment Upon Distribution of Labels

On July 6, the lake was treated with 230 lb of agricultural lime (Griffing, 1971). The lime was broadcast at the surface as a slurry. The day after treatment there was a large increase in rhodamine at the surface, and at 0.9 and 1.8 m (Fig. 4). During the next 2 weeks concentrations continued to rise at these depths and reached a maximum which was in excess of 60 ppb. There is little doubt but that this increase was associated with the action of lime. The principal source of rhodamine in upper strata was that broadcast into the mat in early May. Hence it would appear that with high pH and calcium levels, adsorbed rhodamine was released back into the lake water from the basin.

On July 8, 2 days after addition of lime to the lake, a large increase in water activity appeared in the 0-0.6 stratum but not at 0.6 - 1.2 m or at greater depths. This increase was chiefly particulate activity but included a dissolved component. The dissolved activity must have been SUP since there was no SRP in the surface water at this time (Fig. 5). This activity must have been released from the mat system since there was high vertical stability in underlying layers and no indications of upwelling during this period. This increase occurred simultaneously with the increase in rhodamine WT noted above, but was restricted to the 0-0.6 m layer while increases in rhodamine appeared at 0.9 and 1.8 m.

The addition of lime brought about a large change in the ionic balance of water in contact with the mat and underlying portions of the lake basin since large increases in pH and alkalinity were observed at all depths (Griffing, 1971). Since there were increases in rhodamine but not in ^{32}P activity at 0.9 and 1.8 m, it would appear that "releasable" ^{32}P was concentrated in the mat while "releasable" rhodamine was stored at greater depths in the basin. Particulate activity release by the lime treatment did not include particulates of plankton size (10 μ and above). This fraction of both activity and stable phosphorus decreased rapidly in the 0-0.6 m stratum after lime treatment. This also indicates that little if any of the released activity was incorporated into seston.

Table II. Estimates of stable phosphorus from labeled stratum carried into the 0-2 m zone and quantities entering seston of 0-0.6 m zone after upwelling between May 16 and July 6, 1970.

Dates of upwelling	Total Phosphorus Entering 0-2 m Zone			Dates of calculation of seston uptake	Upwelled Seston Phosphorus 0-0.6 m Zone	
	Grams	Percentage of total P present 0-2 m zone	Percentage of total P, 6-8 m zone at labeling		μg/l	Percentage of total seston P
May 19-21	41.2	22.4	8.0	May 25	0.172	1.1
June 1-3	136.0	44.8	27.7	June 11	2.36	64.8
June 17-18	89.1	26.5	18.1	June 23	1.37	77.8

Utilization of Upwelled Phosphorus by Seston

During the growing season, the layer between the surface and 0.6 m is more or less completely mixed by wind and thus represents the counterpart of the epilimnion of larger stratified lakes. Our analysis of seston was confined to this layer. The small volume of this stratum makes it exceedingly vulnerable to weather changes. Temperature changes in the order of 4-5°C in a 24-hr period were not at all uncommon in the 0-0.6 m layer, and an increase of 10 degrees occurred between June 3 and 5.

Seston of this stratum (0-0.6 m) was sampled by dipping a pail 0.4 m into the zone and pouring a 20-1 sample through a 10 μ nytex plankton net. The ^{32}P activity of each sample was measured by digesting the concentrate with nitric acid, evaporating to dryness, muffling, and counting. A duplicate sample of each net seston collection was preserved for measurement of stable phosphorus. Activity and the stable phosphorus content of seston collected in this manner was measured at approximately weekly intervals from May 6 to August 12 (Fig. 7).

Between May 14 and 17 there was a major increase in the standing crop of sestonic phosphorus (Fig. 7). The source of this phosphorus cannot be identified precisely but probably came from upwelling of bottom water since there was a loss from 7 m during this period (Fig. 5). Thus at the time of labeling (May 16) there was a large crop of seston with a high phosphorus content. This was the situation when a measurable quantity of activity arrived in water of the 0-0.6 m layer on May 25. This brought an immediate increase in seston activity, and the seston appeared to reach an equilibrium with water activity during the period between May 29 and June 2. The crop of sestonic phosphorus decreased until June 2 but thereafter increased as did seston activity. This increase in the labeled sestonic phosphorus followed the upwelling of June 2-3 and appears to be phosphorus labeled in the 7 m stratum on May 16. This crop of sestonic phosphorus developed during the warming trend in the surface water between June 3-11. After June 11 the water again began to cool and there was a decrease in seston activity and stable phosphorus. Between June 18-26 stability was high in the 0.6-1.2 m layer. Thus although there was a large increase in water activity of the 0.6-1.2 m zone, there was no measurable increase in activity of the 0-0.6 m water. Even though water activity did not appear to respond to this input, both plankton activity and plankton phosphorus increased, indicating that labeled phosphorus was made available and was incorporated into seston without significant changes in the water activity level.

After June 2 there was a strong correlation between plankton activity and plankton phosphorus. Changes in the level of activity reflect the utilization of upwelled phosphorus of the 6-8 m stratum in the surface water. By using the specific activity of the soluble phosphorus at the 7 m stratum after

Fig. 7. Total basin water activity of selected strata, surface plankton (seston) activity, and surface plankton (seston) phosphorus in North Gate Lake, 1970. All activity data corrected for decay.

44

labeling, the contribution of stable phosphorus from the 6-8 m stratum to the sestonic phosphorus crop can be calculated (Table II). The upwelled phosphorus made up only 1.1% of sestonic phosphorus on May 25 but increased to 64.8% after the upwelling of June 1-3. Although the upwelling of June 17-18 did not increase water activity of the 0-0.6 m stratum significantly, there was a significant increase in both stable and labeled phosphorus, and the percentage of upwelled phosphorus increased to 77.8%. These calculations indicate that seston crops in late spring and early summer develop after phosphorus upwellings from the 6-8 m stratum and suggest that fertilization from this source is a major factor in sustaining plankton growth during this season.

Fate of ^{32}P in the Lake Basin

On May 19 we estimated that 185 mCi (corrected for decay) of the 200 mCi introduced on May 16 was dispersed within the lake water. The high variability in bottom water activity between May 21 and 29 led to some uncertainty as to the quantity of activity within the 6-8 m zone. However after the mixing between June 1-3, horizontal variation was reduced and we were able to make good estimates of activity in the basin by sampling at the central station (station B).

The total activity within the basin (corrected for decay) indicates loss of ^{32}P from the basin (Fig. 7) but it is clear that the rate of loss was not uniform. The pattern observed was a rapid fall in activity during periods in which there was little or no movement within the water column followed by reappearance of a major part of the lost activity during periods of vertical mixing (Fig. 7). This redispersion occurred on June 1-3, June 8-25, July 1-3, and between July 23-30. In each of these instances, increases in ^{32}P within the euphotic zone and at intermediate depths were correlated with upward movement of rhodamine and downward movement of heat. These periodic redispersions however were clearly superimposed upon a steady loss of ^{32}P from the basin (Fig. 7). The average overall loss between May 16 and August 6 was 1.2 mCi/day.

Various strata within the basin behaved quite differently in their loss and gain of radioactivity. For the 4.9-8.0 m stratum, the loss rate decreased with time and became asymtotic with the X axis (Fig. 8). Inputs into upper strata were not at all similar. Periods of mixing brought about relatively small increases in the 2.1-4.9 m layer; however the percentage of the activity in this layer increased steadily throughout the summer. The layer showing the largest input of activity was 1.2-2.1 m. There were large increases in this zone during each period of mixing. Following each increase, activity decreased slowly until the next period of mixing. The fate of activity lost cannot be established; however there was no evidence of vertical dispersion into layers above or below.
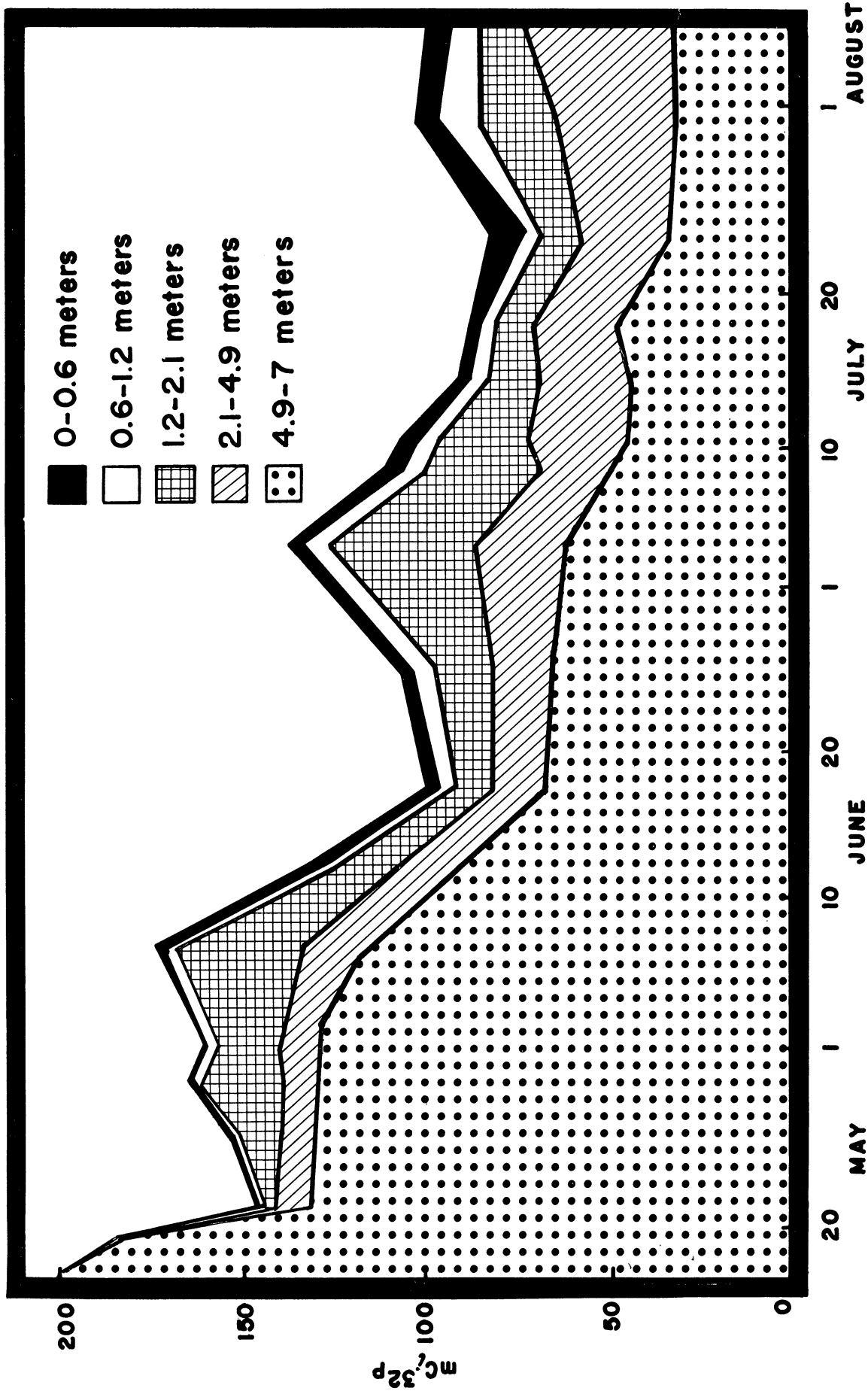
Fig. 8. Quantity of ^{32}P in various strata of lake after labeling 7-m stratum in 1970. Activity corrected for decay.

Activity within the 0.6-1.2 m and the 0-0.6 m layers was always a small fraction of the activity between 1.2-2.1 m. Losses from the 1.2-2.1 m layer were not followed by increases in the upper layers. However temperatures and rhodamine data indicated that mixing took place between the 1.2-2.1 m layer and upper strata frequently (June 1-3, June 26-July 3). Since no increases were observed following periods of vertical turbulence, it would appear that upward transport into the 0-1.2 m layer was followed by rapid horizontal dispersion and loss from the open water. Water in the 0-1.2 m layer was in contact with Sphagnum. Movement of ^{32}P from open water into Sphagnum has been previously recorded (Coffin, et al., 1949). Thus transport into the surface water was probably promptly followed by horizontal movement into the mat.

Model of Phosphorus Flow

To clarify features of the phosphorus cycle so far investigated, we propose a tentative model of phosphorus flow in the North Gate system (Fig. 9). This model is still being developed and will be improved and perhaps redesigned when all data from the 1971 experiment are available. The 1971 experiment will furnish further details on exchange between the mat and open water.

We conceive of North Gate bog as a system in which the flow of essential nutrients is controlled by external environmental perturbation. These external influences are chiefly rainfall which creates hydrostatic flow through the mat system into the lake, and secondly, conditions of temperature, wind, and cloud cover which bring about upwelling. These external perturbations are not periodic but occur within the time limits of the period of westerly waves in the atmosphere. In the spring, spring-summer season this time span would ordinarily be in the order of 2 or 3 weeks. The details of mat flushing by rain are incomplete but data indicate that this process returns the interstitial mat water to the lake. Upwelling brings residual hypolimnetic phorphorus into the upper water. Upwards flow is not continuous but in many cases appears to be interrupted at a depth of about 2 m by what we tentatively call a concentration zone. Here there is biological uptake by heterotrophic organisms. Flow to the surface from the concentration layer appears to be more frequent than flow from the hypolimnion and doubtlessly arises from relatively minor thermal changes at the surface. Flow of SRP into the photosynthetic zone appears to be immediately utilized and, as in most waters, there appears to be a very small pool of SRP in this layer. Recycling within the photosynthetic zone and within the concentration layer occurs not only through degradation of particulates but also by excretion of SUP compounds by bacteria. This creates a pool of partly degraded phosphorus within both the euphotic zone and the concentration layer. Internal recycling appears to occur between these strata. However there does not appear to be extensive losses to the hypolimnion since in 1969 little or no activity was observed to return to this stratum. Upward
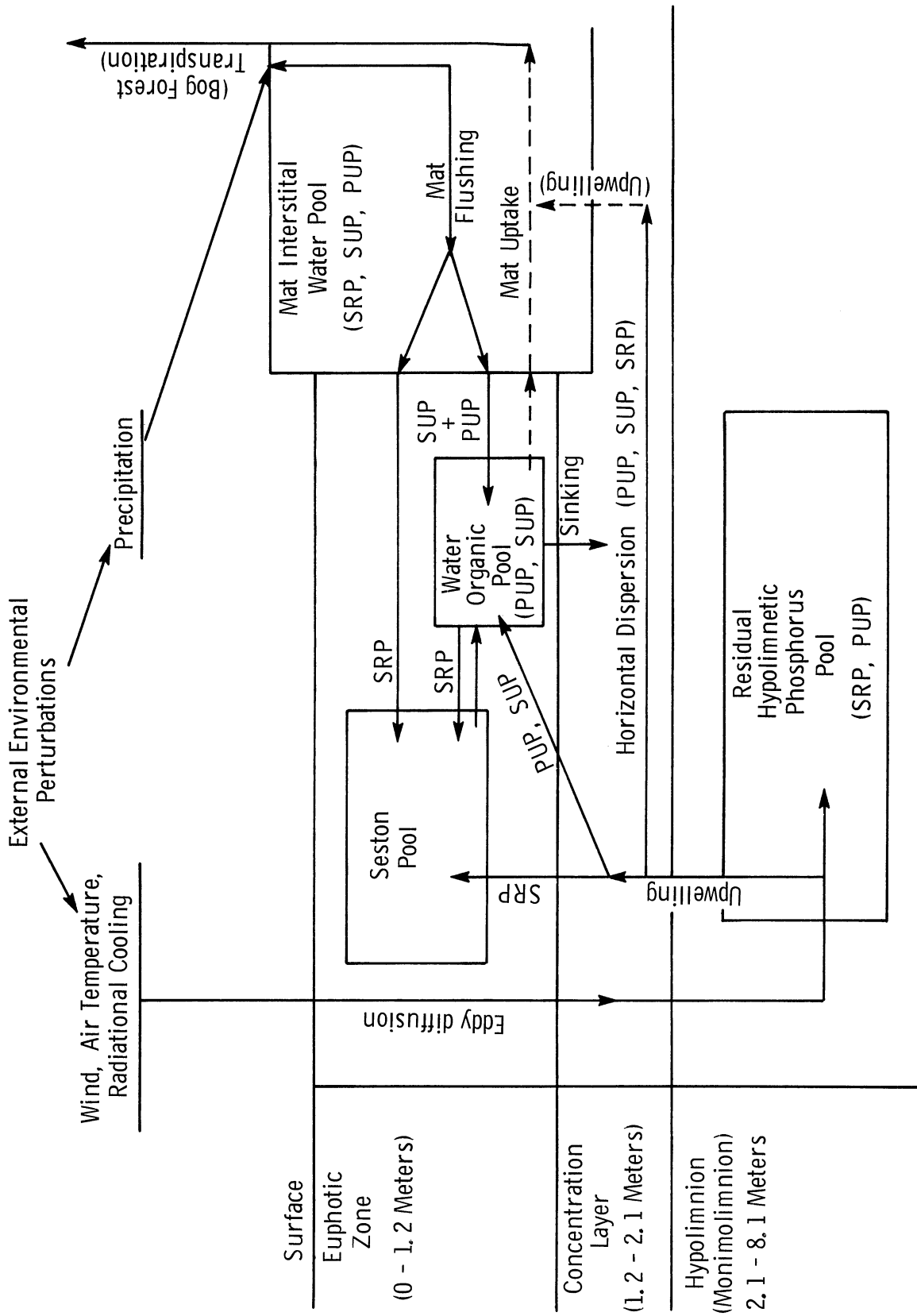
Fig. 9. Tentative model of phosphorus flow in North Gate bog, bog-lake system.

48

dispersion of phosphorus into the concentration zone appears to be accompanied by horizontal movement into the mat. Thus there is a major flow upward into the mat system and a return from the mat to the water which are largely regulated by external environmental factors.

The overall picture that emerges at this time is that climatic regulation is the paramount influence in production. The mat acts as a buffering and storage device which has little counterpart in eutrophic lake systems. Of great interest is the concentration zone which appears to be at the heart of the metabolic processes of the lake. Here there is intimate relationship between chemical, biological, and physical processes. It is clear from preceding years' data that the chemical influence of this zone extends into the mat and influences processes in this part of the system. It is also clear that the internal cycling between this zone and the surface water is of far greater consequence than its counterpart in eutrophic lakes.

Summary

By labeling residual phosphorus in the bottom water after the spring overturn with ^{32}P and rhodamine WT we analyzed the vertical and horizontal dispersion of phosphorus in the basin of a small bog, bog-lake system. Upwelling of phosphorus occurred as the water surface cooled following passage of cold fronts. The rate of upwelling of ^{32}P was approximately 20-fold greater than of rhodamine because of high uptake of phosphorus on particulates in the lower thermocline. Upward movement of ^{32}P was followed by biological uptake and by horizontal movement into the bog mat system. Treatment of the lake with 230 lb of lime mobilized both ^{32}P and rhodamine from the mat and returned these tracers to the lake water.

The phosphorus brought into the euphotic zone from three major upwellings was incorporated into the seston. After the second upwelling approximately 65% of the sestonic phosphorus was phosphorus from the hypolimnion.

Loss of ^{32}P from the water column averaged 1.2 mCi/day but the rate of loss was not uniform. There was a rapid fall in ^{32}P activity when there were no vertical water movements. This was followed by reappearance of much of the lost activity during periods of vertical mixing. Flow of phosphorus in the system appears to be in large part regulated by external weather conditions.

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APPENDIX C

PRELIMINARY REPORT ON THE DIFFERENTIAL DISTRIBUTION
OF PHOSPHORUS COMPOUNDS IN A DYSTROPHIC BOG

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It is difficult to describe the precise nature of the organic and inorganic
phosphorus compounds in natural water from the gross information received from
routine chemical analysis. Adding ^{32}P to the system provides information con-
cerning the rates of phosphorus movement from one class of compounds to another.
While this adds tremendously to the information available from a system, it
still does not enable the elucidation of many details.

In 1970 a method was developed to differentiate certain of the forms of
phosphorus in natural waters.[12] This allows the previously described categories
to be broken down into their components. This procedure, in combination with
radioactive tracer labeling, allowed a much more detailed view of phosphorus
flow and a better understanding of the composition of the compounds in the var-
ious physical compartments of the ecosystem. This composite procedure was
applied to the waters of North Gate Lake in the summer of 1971.

Methods

Ion exchange chromatography was used to separate the inorganic and organic
phosphorus compounds. For organic compounds, Dowex 1-8x, 200-400 mesh ion ex-
change resin was changed from chloride form to a formate form with formic acid.
Since Dowex 1 is a strongly basic resin, it can separate the weaker inorganic
acids as well as the stronger organic acids of phosphorus.

One liter of lake water was collected on different days at the surface
(0-15 cm), at 6.5 m in the hypolimnion, and at the mat surface (0-15 cm). One
set of samples was collected in the spring, a second in the summer, and a third
in the fall. A sample was taken at the surface on July 12 (0-15 cm) 6 days
after the addition of hydrated lime to the lake. A second was taken approxi-
mately 2 1/2 months after the addition of the lime. The pH of the samples was
reduced to 1.0-1.5 by the addition of sulfuric acid. Samples were then taken
to the laboratory and filtered through 0.45μ membranes. The filtrate was cooled

in an ice-water bath until it could be applied to the resin column. Phosphorus-free distilled water was added to the acidified sample to increase the pH, then the sample was applied to the column at a rate of 3-4 ml/minute. The column was then washed with distilled water and set up for a 0.01-0.5 N formic acid gradient elution. Fifteen-ml fractions were collected on a Warner-Chilcott automatic fraction collector with the elution rate of $\leq$ 1 ml/min. After the gradient elution, 0.5 N formic acid plus 0.2 N sodium formate was applied to the resin, followed by a distilled water wash.

A subsample of all the columns' eluates was collected to be analyzed for radioactivity as well as phosphorus content. Five ml of the fractions were pipeted on to previously monitored and numbered planchets. These were then dried and counted on a Nuclear-Chicago low background beta counting system.

NON-PHOSPHORUS COMPOUNDS

The eluate from the tea-colored lake water sample was clear, indistinguishable from distilled water. A banding pattern from the colored organic matter of the bog and from the organic dye rhodamine WT appeared on the resin column. This latter compound, used to label the mat water, acted as a biologically conservative organic acid. Organic stains of bog lakes are considered to be an organo-mineral complex (i.e., a cation-anion interaction) with a net negative charge,[1,5] and since rhodamine is a weak carboxylic acid, uptake of these compounds by the resin is consistent with their chemical natures.[2]

The gradient elution with formic acid did not remove either the organo-mineral complex or the rhodamine. However, the acid gradient completely removed and separated the inorganic and organic phosphorus compounds from the resin.

PHOSPHORUS COMPOUNDS

Elution Patterns Previously Observed

The activity peaks exhibited by the fractions after gradient elution represent compounds which differ from each other in their capacity to bond with the resin bead, and then to be exchanged with the eluting formate ion. Nucleotides of different lengths differ in their negative charges. Thus the number of electrically charged groups often determines the elution pattern.[3] Therefore, the order of the eluted materials is usually directly proportional to the number of electrically charged (acid) groups present, i.e., the more phosphorus groups, the later the compound appears in the elution pattern. Dinucleotides and other polynucleotides which are not completely hydrolyzed will appear in the elution pattern according to the number of active phosphate groups present.

The elution order of the various single ribonucleotides depends to a great extent on the nature of the eluting solution. For example, at a pH of 2 the elution order, under a formic acid elution, is first cytidylic acid followed by adenylic, guanglic, and uridylic acids (i.e., C. A. G. U.). At a pH of 4, under an ammonium formate elution, the order changes slightly with uridylic acid directly following cytidylic acid (i.e., C. U. A. G).[4] It appears that the net negative charge of the nucleotides, which changes differentially with a pH shift due to the amino groups present on the bases, is the main determinant of the elution order. However, the elution order predicted from the net charge is not fully realized because of further changes caused by the differential sorbtion of purine bases over pyrimidine bases by the exchange resins.[17] Also present within any elution order is the minor effect of the position of the phosphate group. Generally, the 5'-ribonucleotides come off the resin first, followed by the 2', then the 3'-ribonucleotides.[8] This seems to be caused by minor differences in the acid dissociation constants of these compounds. However, even though the specific nucleotide order may be different in various elution patterns, it is important to realize that as a group the monophosphate nucleotides appear first in the elution patterns followed by the diphosphate nucleotides and then by the triphosphate nucleotides.[4]

Inorganic phosphorus compounds are also arranged in order of their phosphorus contents with ortho- appearing first followed by the pyro-, tri-, tetrameta-, and trimeta-phosphate ions.[6,7] Inorganic phosphorus (ortho) always appears in the organic elution pattern within the monophosphate section. At an eluting pH of 1-3, for example, the orthophosphate peak is towards the end of this section while at a pH of 4-6, the peak is towards the beginning. Generally then, the amount of phosphorus contained in a compound increases from left to right along the elution pattern. This hold true only when the inorganic and the organic elution patterns are considered separately, for when the two patterns are considered together there is considerable overlap in phosphorus content per compound.

Elution Patterns from North Gate Lake Water

Two problems which underlie the proposed study of nutrient distributions are (1) the primary source of new nutrients to the bog, and (2) the differential effect of the biota of different habitats upon the nutrients supplied. The properties of organic phosphorus compounds are dependent upon the organisms forming them. The endemic organisms at each station will vary tremendously because of the totally different environmental conditions. Therefore, the compounds exhibited in the elution pattern of each station should be qualitatively different and should reflect the differences in the environment and in the biota. Most of the water entering the open water passes through the surface of the <u>Sphagnum</u> mat due to the lower water conductivity of the peat with increasing depth[9,10]; therefore most of the nutrients supplied to the epilimnion arise from this source, i.e., the mat is analogous to the littoral zone of a

eutrophic lake.

The ^{32}P labeled phosphorus was in inorganic form when added to the mat water, so there should be a large peak of radioactivity appearing early in the mat elution pattern. It is reasonable to suspect that this same peak would occur at all stations sampled since only a small amount would be high in activity. Figures 1-4 depict this peak. It occurs at all three sampling areas in fractions 32-37. In the data from the previous summer (1970) (Figs. 1-3), there is a peak of inorganic phosphorus at almost the same point in the elution curves of the three stations (fractions 22-35). The 1970 data are used in the interpretation of activity peaks.

Using the activity peaks (fractions 32-37) and the inorganic phosphorus peaks (fractions 22-35) as a base, it is possible to describe the nutrient interrelationships of the three stations and to partially identify the remaining compounds. While the activity data show a peak for this inorganic phosphate, the quantity of this compound varies from station to station. In the mat, where the label was added, there is a considerable quantity of inorganic phosphate (Fig. 2) but in the epilimnion (Fig. 1) the amount is small, probably due to its assimilation by the phytoplankton. The amount of orthophosphate increases unexpectedly in the hypolimnion; this might be due to three different mechanisms (1) leakage of the compound from the mat into the hypolimnion, (2) loss of the inorganic phosphorus from the epilimnion, and (3) reconversion of detrital phosphorus compounds by bacteria back into inorganic phosphate (Fig. 3).

The activity peak distribution of the mat water (Fig. 2) closely corresponds with the proposed components of these peaks. It is evident that the first activity peak (35) contains most of the inorganic phosphorus present in the sample, while the second peak (70) and perhaps the third (82) consist of most of the organic compounds present in the sample. So the potential supply of nutrients to the epilimnion consists of both inorganic phosphate (ortho) and organic phosphorus compounds. What appears in the epilimnion (Fig. 1) is indeed the inorganic peak (32); however the organic phosphorus peak (70-80) is entirely missing. It appears that either the plankton have removed the supplied form of the organic phosphorus and have altered it into another organic form represented by activity peak (50), or it never entered the open water. The organic fraction of the mat, at least, has the potential to move into the water, for the elution curve (Fig. 4) of the epilimnion after the addition of the lime now contains the peaks of activity (78-90) that did not appear in the earlier elution curve for the epilimnion (Fig. 1). Aqueous extracts of decomposing peat have been shown to contain purine and pyrimidine bases, together with phosphoric acid, in nucleotide and di-nucleotide form.[12]

The organic phosphorus (fraction 50, Fig. 1) attributed above to the plankton also appeared in the epilimnion even after the addition of the lime (Fig. 4, fraction 56). Both of these peaks consist of an organic compound
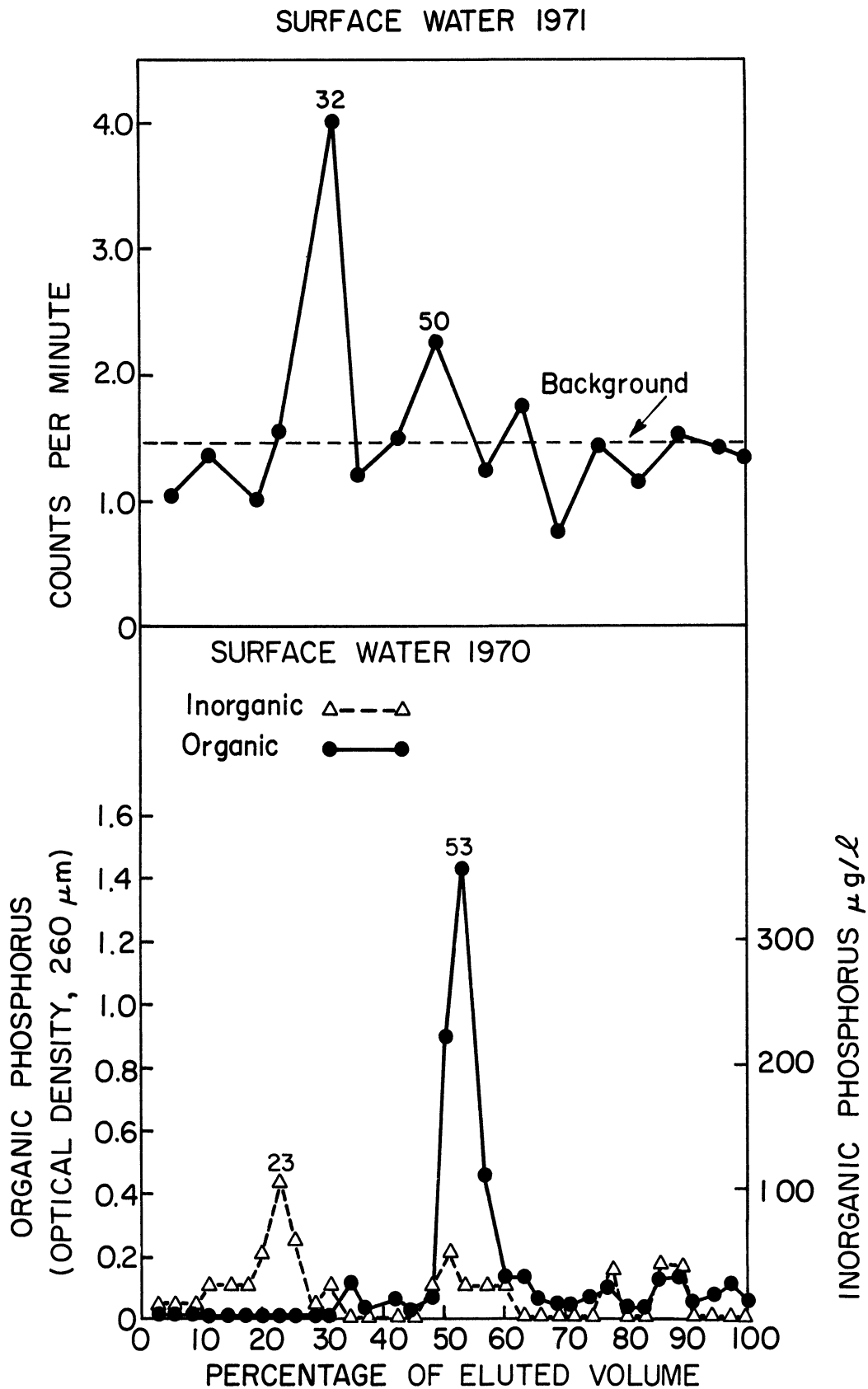
56

Fig. 1. Activity of fractions eluted from surface water of North Gate Lake after mat labeling in 1971 compared with inorganic and organic phosphorus components eluted from the surface water in 1970. Numbers on graphs indicate percentage at peaks.
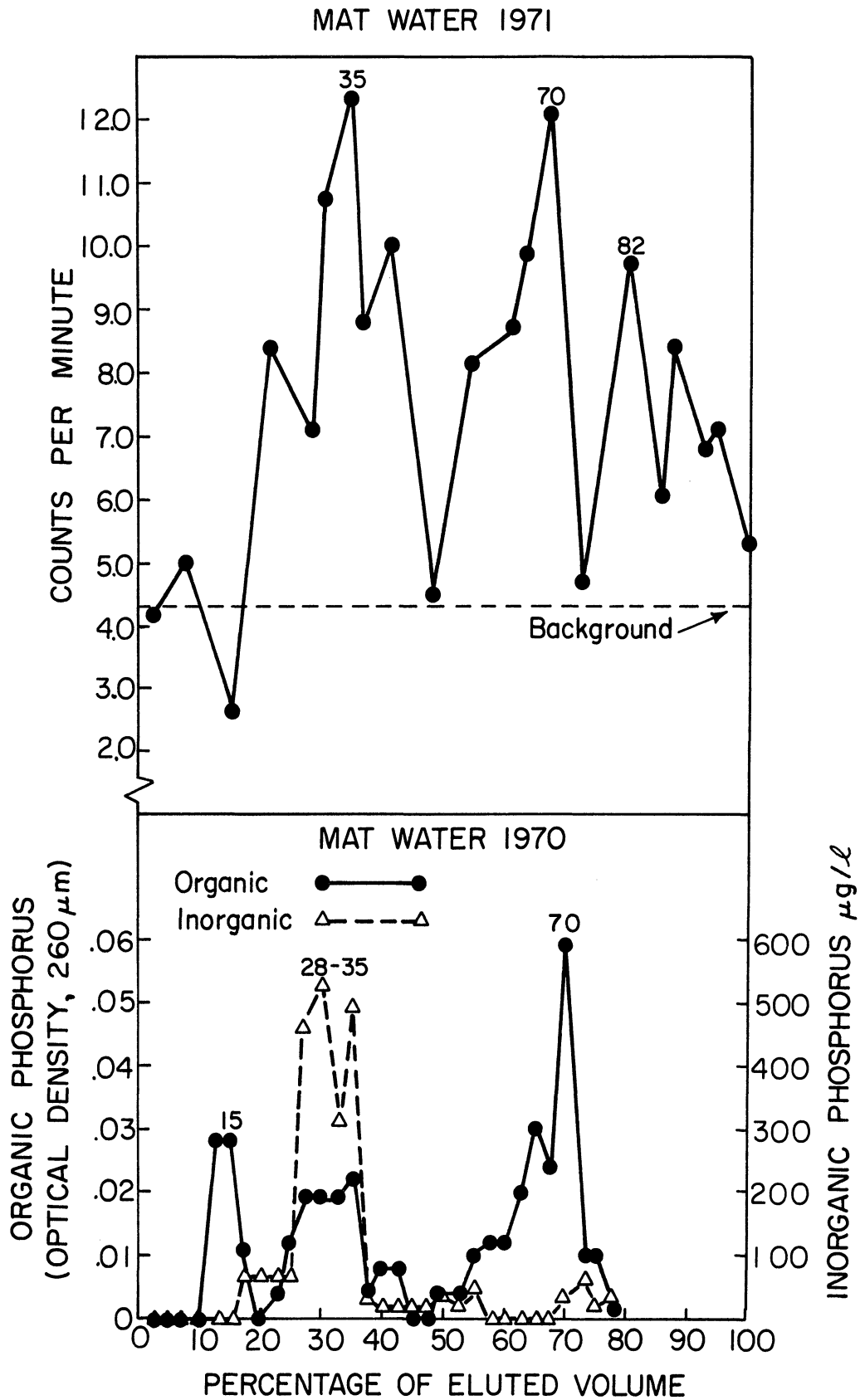
Fig. 2. Activity of fractions eluted from mat water of North Gate bog after mat labeling in 1971, compared with inorganic and organic phosphorus components eluted from mat water in 1970.
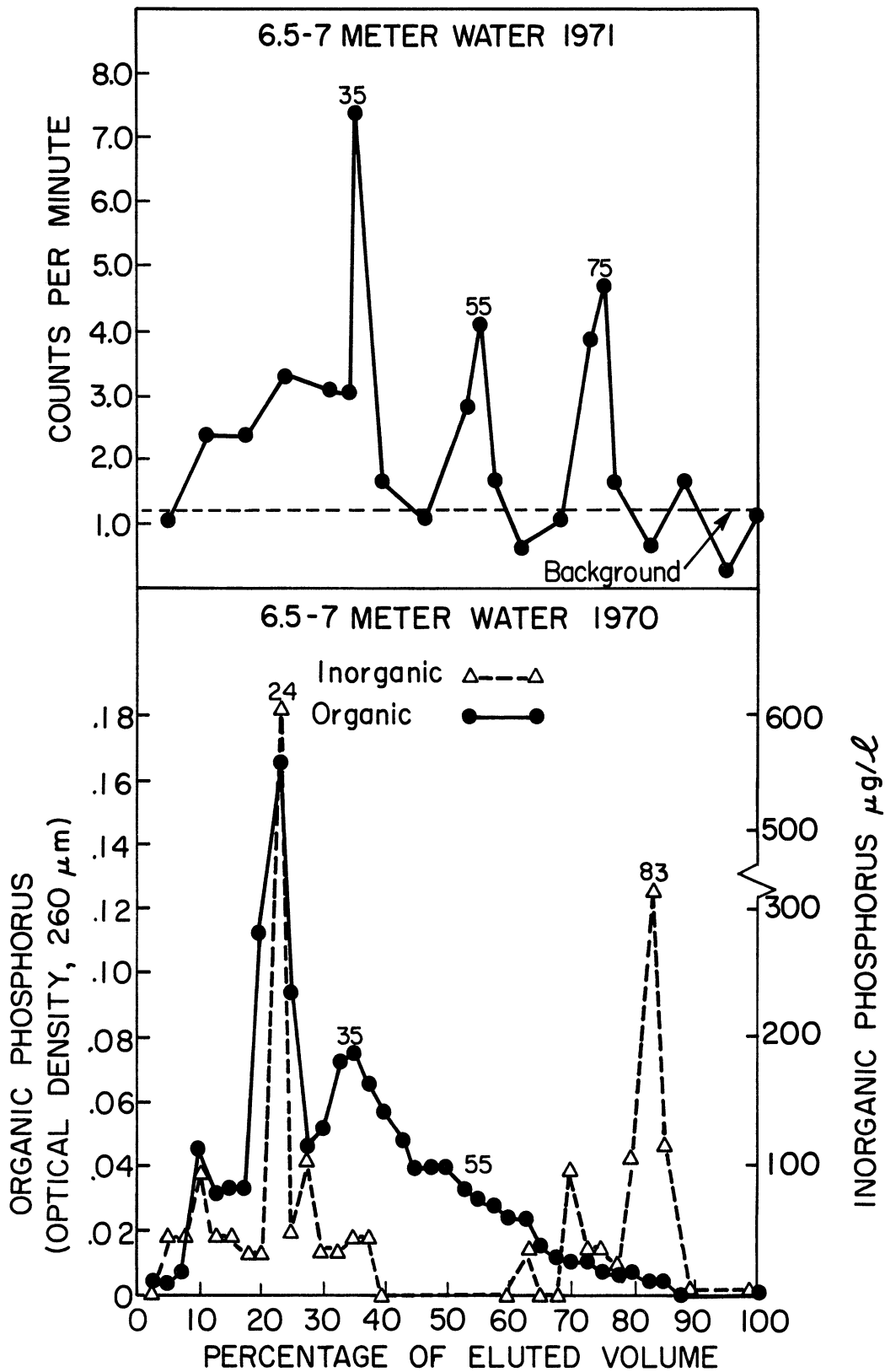
Fig. 3. Activity of fractions eluted from 6.5 - 7 m water of North Gate Lake after mat labeling in 1971, compared with inorganic and organic phosphorus components eluted from 6.5 - 7 m water in 1970. Numbers on graphs indicate percentage at peaks.
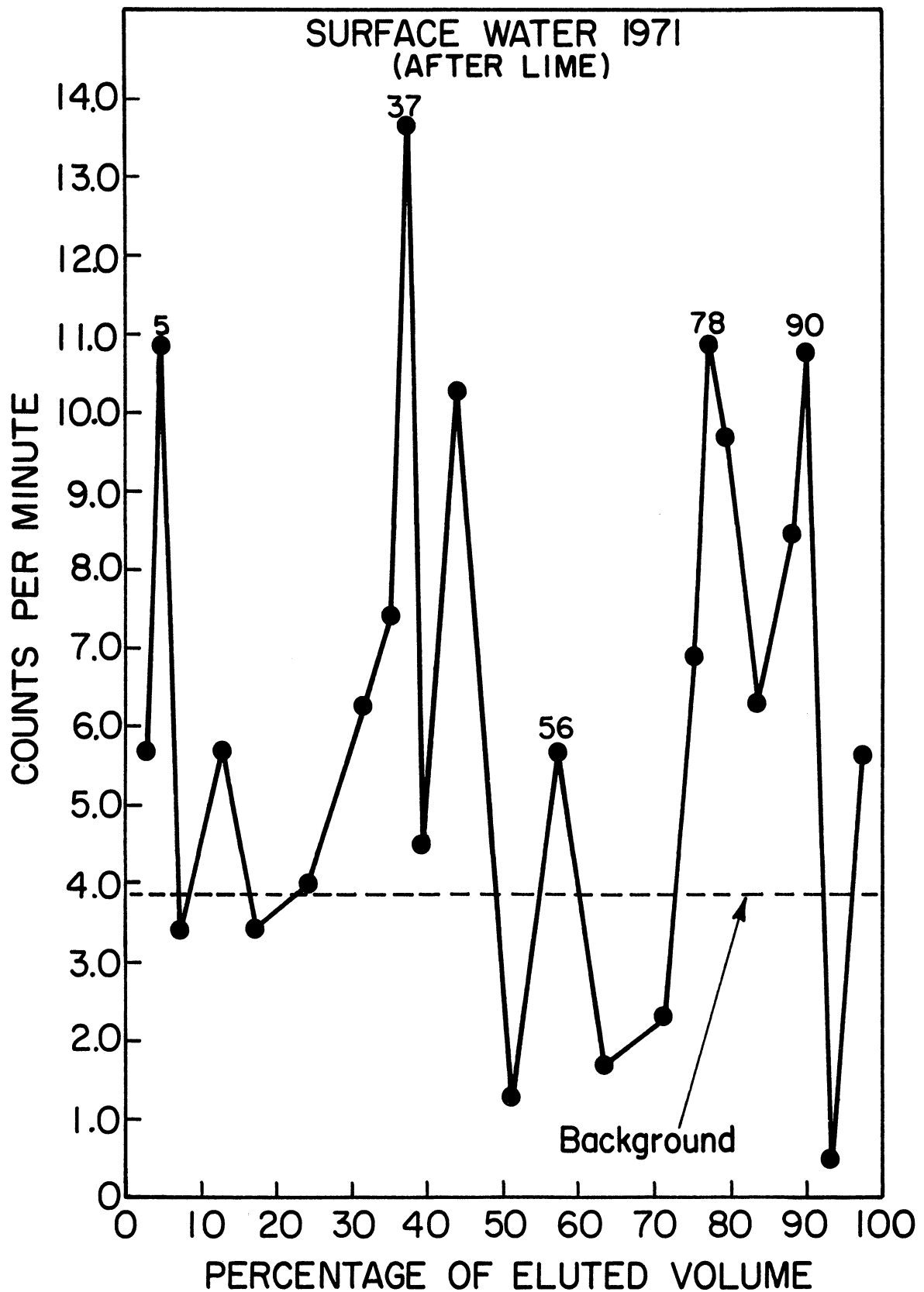
Fig. 4. Activity of fraction eluted from surface water of North Gate Lake after treatment with lime in 1971.

represented by peak 53 in the characterization curve (Fig. 1) of the epilimnion. This peak contains most of the organic compounds present in the epilimnion before the addition of the lime, and appears to be produced solely in this zone.

The varied composition of the activity peaks in the hypolimnion (Fig. 3) makes interpretation more difficult but not impossible. The activity peaks are for those compounds that were manufactured out of the inorganic labeled phosphorus both in the mat and in the epilimnion (peaks 35, 55, and 75; Fig. 3). These compounds are represented in the characterization data (Fig. 3). For example, activity peak 55 has to be an organic compound because of the lack of any inorganic phosphorus at that point on the characterization curve. The activity peak (35) is represented by the great amount of inorganic phosphorus in the characterization pattern around fraction 24.

The many remaining unlabeled fractions, both organic and inorganic, are to be expected in the lower water zone since the primary role of the anaerobic bacteria present on the bottom of the bog is the mineralization of the compounds falling out of the water. This is the accumulation zone for all the bog and for the products of subsequent decomposition. This is amply illustrated by the large organic fraction appearing around peak 24 of the hypolimnion characterization curve (Fig. 3). There was a small peak of the same fraction in the mat water sample (Fig. 2), and this high peak therefore may represent an accumulation of this compound. However peak 83 of the hypolimnion water (Fig. 3) is an accumulation of an inorganic polyphosphate from either bacterial origin or from the autolysis of algae. These compounds are common to both organisms and they do not appear at any other station.

Tentative Conclusions

From the known elution rates of inorganic and organic phosphorus compounds, and by using the known orthophosphate peak as a base, it is possible to identify the remaining peaks in North Gate Lake's elution patterns. Compounds produced in the mat have been chemically identified and previously characterized as the hydrolysis products of ribonucleic acids, i.e., its four nucleotides.[12] These same compounds have been shown by their ultraviolet absorbtion spectra to occur in the mat water of North Gate Lake.[13] It appears then that the mat contains an organic phosphorus fraction consisting mainly of ribonucleotides. These compounds, which have been shown to exist in the aqueous portion of the mat, can be flushed out into the open water. The addition of hydrated lime to the lake triggered a massive influx of these compounds into the open water through a pH change, i.e., a rise in hydroxyl ion concentration. Under normal conditions the plankton could quickly and completely utilize the injected compounds. However, due to both the large increase in the supply rate of these compounds and to the negative effect of the pH and ion shock on the algae

population,[14-15] the injected compounds remained in the surface waters. The remaining algae could not utilize all the nutrients presented. It appears that unlike the mat water, whose organic compounds consist of two triphosphate nucleotides and/or a dinucleotide, the organic phosphorus compound normally predominant in the epilimnion is a diphosphate nucleotide. Organic compounds present in natural waters are known to be both produced and used by the phytoplankton present. The free mono-, di-, and triphosphates of the common ribonucleotides (i.e., A, G, C, and U) have been found in algal cells.[15] The diphosphate nucleotide predominant in the undisturbed epilimnion probably was produced by the phytoplankton out of the nutrients provided from the mat. The organic phosphorus compounds appearing in the hypolimnion consist mainly of the mono- and diphosphate ribonucleotides with a minor amount of triphosphate nucleotides.

While the inorganic phosphorus in the epilimnion and in the mat water is predominantly orthophosphate, the hypolimnial waters contain a considerable inorganic pool consisting of both ortho- and a polyphosphate containing three to four phosphate groups. Polyphosphates (open chains) and metaphosphates (closed chains) have also been isolated from algal, bacterial, and fungal cells.[16] So the polyphosphate compounds, which show an accumulation only in the hypolimnion, appear to be products of the autolysis of algae and the decomposition activity of bacteria.

In summary, one of the nutrient sources for the bog during the summer stagnation period is the Sphagnum mat. When it rains, the water movement off the watershed and through the mat flushes the nutrient compounds into the epilimnion of the bog. Here the phytoplankton assimilate all the provided nutrients and secrete their own metabolic products into the open water. Through leakage from the mat and from the epilimnion, the compounds produced are deposited in the lower hypolimnial waters. Further organic and inorganic input may be provided by falling detrital remains of the zoo- and phytoplankton. Upon decomposition of the detritus, which also includes many bacteria, by either the living anaerobic bacteria or by free enzymes many compounds are released and many new ones are formed. These include the poly- and metaphosphates as well as a myriad of organic compounds. By combining a knowledge of distribution of the compounds that are characteristic of certain biotas with a method of tracing these compounds, it appears to be possible to analyze the nutrient degradation and transformation processes in an aqueous system.

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63

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