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LACUSTRINE PRODUCTIVITY AND THE DISTRIBUTION OF NUTRIENTS, DIATOMS, AND CLADOCERA

Thousands of fossil Cladocera and diatoms belonging to dozens of species are preserved in each cubic centimeter of typical lake mud. These fossils usually can be identified precisely and assigned to modern species. It has been demonstrated for the Cladocera and it is probably also true for the diatoms that there is negligible differential transport before deposition, and apparently little differential destruction after deposition (Mueller 1964, Frey 1960, Deevey 1964). Nevertheless, many of the changes in the populations of aquatic fossils during lacustrine history remain enigmatic because it is not known how the environment acts on living aquatic populations to regulate their distribution.

The biomass and population density of organisms in an environment is limited by the rate of photosynthetic production of organic matter, by primary production. The number of niches available for occupancy by different kinds of plants and animals, the biotic diversity in the environment and therefore the geographic distribution of organisms, is also limited primarily, although not entirely, by productivity. Therefore many of the fluctuations in the diversity and density of organisms during the history of lakes must be responses to fluctuations of primary productivity as it, in turn, responds to secular variations of climate and nutrient distribution. Studies of the productivity and the density and diversity of organisms in modern lakes should therefore increase considerably our understanding of the biotic changes during the history of lakes and this in turn would allow descriptions of changes in their productivity.

It is proposed here to initiate a study of lacustrine primary productivity in Minnesota during the summer of 1965 in an attempt to delineate the relationship between productivity and the distribution of nutrients, diatoms, and Cladocera. This study is feasible only because efficient techniques are now available, both for measuring productivity experimentally in the field and for determining the distribution and abundance of diatoms and Cladocera. Time-consuming plankton counts can be deferred until specific problems are formulated because the fossil assemblages of diatoms and Cladocera in surficial lake sediments are such faithful records of the living populations. It will be necessary only to examine one or at most a few sediment samples from each lake to determine the abundance of each species present in the entire lake. For most other aquatic organisms examinations of dozens of samples collected from each lake during several years would be required.

It is anticipated that this study will lay the groundwork for extensive studies of plankton dynamics and water chemistry in Minnesota. Because knowledge of lacustrine productivity is fundamental to understanding regional limnology, the information obtained will be pertinent not only to paleoecology but also to problems of nutrient supply and utilization by algae other than diatoms. A more exciting prospect, however, is that establishing the relationship between the modern environment and the biota will permit an assessment of the biostratigraphic record, particularly in the uppermost meter of sediments which are a record of the biotic changes during the century since European settlement. Examinations of short surface cores could be used to determine how different kinds of land use have affected the lakes, and to suggest how existing land use can be modified to minimize detrimental effects on our water resources.

Procedures

A. Measurements of productivity. Lacustrine primary productivity, i.e. the rate of phytoplankton photosynthesis, will be measured experimentally by use of the oxygen light-dark bottle technique. Samples of lake water are gathered from various depths, the oxygen content is measured by titration, and the water is transferred into light and dark bottles, which are suspended in the lake at the depth from which the samples were taken. After exposure for as much as 24 hours, the bottles are withdrawn and the oxygen change due to photosynthesis and respiration is measured. This technique was used in eutrophic Wisconsin lakes with eminent success many years ago (Manning and Juday 1941), and more recently in Indiana (Eberly 1959, 1964), but it is not sensitive enough to be used in Lake Superior (Putnam and Olson 1961). It should be adequate for most Minnesota lakes, with the possible exception of the oligotrophic lakes on crystalline bedrock along the Canadian border. The greater sensitivity achieved by measuring C-14 uptake instead of oxygen production during photosynthesis is probably unnecessary for most Minnesota lakes; the elaborate laboratory and counting facilities are not conveniently available, and there would be a time lag while samples are returned to the laboratory for counting. The major advantage of the oxygen technique for a survey of this sort is its economy. Very little specialised equipment is needed, and all analyses can be done as soon as the experiments are completed in the field, where they may be evaluated and repeated if necessary.

At the time and place of an experiment, the vertical oxygen, temperature, and pH profiles in the lake will be determined. The Limnological Research Center now has the necessary portable galvanic-cell oxygen analysers, thermisters, and pH meters so that these determinations can be done immediately in the boat without transporting samples to a laboratory. However, plankton samples and water samples will be collected for study and complete chemical analysis in the Limnological Research Center laboratories.

The light-dark bottle technique is essentially a bioassay that provides a numerical index of productivity. Its use in this survey will furnish a spectrum of numbers by which lakes can be compared in the future. Blooms of nuisance algae, excessive stands of water weeds, and replacement of game fish by rough fish all tend to occur as productivity increases. Influx of industrial, domestic, and agricultural waste water usually encourages these undesirable trends because they increase the concentration of phosphorus and other nutrients in the lakes, even when extensive sewage treatment is practiced. Controlling the undesirable features of highly productive lakes, therefore, often hinges on reducing the supply and availability of nutrients. The light-dark bottle technique offers a bioassay of nutrient concentrations that can be used to identify areas within lakes where nutrient levels are high, to chose among alternative nutrient control measures, and to monitor the effect of these measures after they are applied.

B. Analysis of diatoms and Cladocera. For most aquatic organisms it would be necessary to examine dozens of plankton collections taken throughout the year to obtain a comprehensive species list for a single lake. To do this for more than a few lakes normally requires years of effort. Cladocera and diatoms are resistant to bacterial decomposition, however, and as they die (or molt in the case of Cladocera) the frustules and exoskeletons accumulate in the surficial sediments. Thus, it was possible for Frey (1960) to compile a list of the chydorid Cladocera living in each of the five lakes in the vicinity of Madison, Wisconsin, simply by examining a single sample of surface sediments taken from near the middle of each lake. In fact he recovered several species which E.A. Birge overlooked during 25 years of collecting in those lakes.

The fossils in the sediments integrate seasonal and annual fluctuations in the living populations and permit a quantitative expression of the relative dominance of each species, something that can be done only subjectively by examining plankton collections. Also, expressing the results as absolute numbers of fossils per cubic centimeter of mud describes quantitatively the rate of fossil production relative to the rate of sedimentation.

By examining samples of surface sediments from only 40 lakes, DeCosta (1964) determined the effect of latitude on the distribution and relative abundance of the Cladocera in the Mississippi River Valley, from its source in northern Minnesota to its delta in Louisiana. The same principles will be exploited here to relate productivity of lakes to the diatom flora and Cladoceran fauna. At least one mud sample will be taken with an Ekman dredge from each lake whose productivity is measured. The mud samples will be stored for processing and examination during the winter by R.C. Bright and by R.O. Megard.

Establishing the relationship between the modern diatom and cladoceran assemblages with modern lacustrine productivity will permit the utilization of the fossil assemblages as bioassays of past lacustrine productivity, just as the light-dark bottle experiment is a bioassay of present productivity.

Biostratigraphic studies usually indicate that lacustrine productivity increases as sediment accumulates in the basin. With most lakes increased productivity may be an inevitable consequence of lake evolution. Human activity, which generally increases the rate of sedimentation and delivery of nutrients to lakes, usually accelerates this trend. Continued studies of the fossils will contribute, therefore, to deciding whether this trend is, in fact, inevitable. Presumably proper watershed management can retard the rate of evolution or, more hopefully, reverse it.

Although the light-dark bottle experiments might be used to monitor changes of productivity in connection with pollution-abatement programs, each experiment measures only the conditions of the moment; numerous experiments through the years would be required to determine "average" or "typical" conditions. The fossils in the surficial sediments, however, integrate seasonal and annual fluctuations. Once the diatom floras are "calibrated" against measured productivities, spot analyses of surficial sediments might be the most effective bioassay for diagnosing lakes with unduly high levels of production or detecting unusual chemical or physical conditions.

C. Selection of lakes. There is a remarkable environmental gradient in Minnesota, expressed most notably by the transition from coniferous forest in the north and northeast, through deciduous forest in the central and southeast, to the grasslands in the west and southwest. Precambrian metamorphic and igneous rocks are the dominant bedrock in the northeast, while in the west, south, and southeast Cretaceous and Paleozoic sedimentary rocks are the most abundant. Many lakes in the northeast occupy crystalline bedrock basins; elsewhere the basins are in glacial drifts of varying age, texture, and lithology. Lakes in the northeast have soft water and they are low in nutrients and fish production. Water hardness, nutrient supply, and fish production increase toward the west and south (Moyle 1954, cited by Swain 1954). Whereas DeCosta's (1964) transect of the Mississippi Valley traversed a temperature-latitude gradient, Minnesota presents a gradient of nutrient supply as well as climate.

It is proposed to select an array of 20 or more lakes extending from the northeast corner of the state toward the southwest that traverses the gradients of environment and substrate outlined above. The selection will be from among those lakes for which the Minnesota Department of Conservation has prepared bathymetric charts, so that productivity can be computed both on an areal and a volumetric basis. The Department of Conservation also has accummulated a backlog of chemical data from a variety of lakes, and this will provide another criterion for selection.

The environmental gradients are steepest in northwestern Minnesota, along a line extending 30 - 50 miles west of the University of Minnesota Biological Station in Itasca State Park. The Biological Station provides a logical base of operations for this reason and because the limnological resources and Cladoceran fauna of the region are relatively well known (Megard 1964). It is planned to perfect the logistics of the field operations on a nucleus of lakes that are already under study in the Itasca vicinity and to extend the survey from there, both to the northeast and to the southwest.

D. Plan of operations and Personnel. The instrumental analyses of the vertical profiles of oxygen, temperature, and pH, the plankton tows and collection of water samples will be done at the time of the light-dark bottle experiments are begun. The Winkler titrations for oxygen changes in the experimental bottles must be done immediately after the termination of the experiments. The equipment and reagents for these determinations can be transported into the field, so there should be little need for additional immediate laboratory work, except for alkalinity and hardness titrations, which may be done any time after collection of the samples.

A full-time field assistant, preferably a graduate student with training in limnology, will be required to aid in handling boats and equipment, to assist with routine chemical analyses, and to continue the survey independently in late summer. A part-time student laboratory assistant who could enroll for 1/2 the normal course load at the Itasca Biological Station will be required to do those laboratory analyses which do not need to be done in the field, such as hardness and alkalinity determinations.

It is desirable to extend the productivity transect from the northeastern corner to the southwestern corner of the state, a distance of about 400 miles, in order to achieve maximum differences of productivity. Therefore, except for the initial studies in the Itasca region where the samples can be returned to the laboratory for analysis in case of inclement weather, a mobile laboratory is virtually essential for an efficient operation. Accordingly the budget includes a camper unit, such as sportsmen mount on the back of trucks, which could be converted into a mobile laboratory with little alteration. If this were available the tentative plan is to spend the last weeks of June studying the lakes in the Itasca region and perfecting techniques and to spend the first part of July studying the lakes southwest and south of there. The lakes in the Itasca vicinity would be visited again in late July and the lakes in northeast Minnesota would be studied in early August, with a return to Itasca in late August. A total of 30 days away from the Itasca Laboratory is estimated.

A major difficulty of experimenting over such a large area is that the planktonic flora changes as the season advances and the productivity varies accordingly. Although some of the seasonal variations in the lakes of the Itasca vicinity will be monitored by the proposed schedule, most of the other lakes can probably be visited only once. After the logistics of the field operations are mastered and the survey is well under way, it is hoped that an airplane with pontoons can be rented for moving from lake to lake. Experiments could thus be conducted over a much wider area in a short time interval. This might be attempted on a trial basis late in the summer to explore the feasibility of subsequently using an airplane routinely.

The budget also includes an item for a boat, motor, and trailer. These items and the mobile lab will become permanent additions to the equipment of the Limnological Research Center, to be used on future projects suggested by the productivity survey.

The echo sounder will be required to orient the experimental and collection sites to the bathymetry of unfamiliar lakes that are studied. The planimeter is used to measure the area enclosed by depth contours of bathymetric charts during computations of lake area and volume.

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