Eastern Deciduous Forest Biome
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LAKE GEORGE SITE SYNTHESIS - 1974-1975

By:

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INTRODUCTION

Synthesis activities at the Lake George Site have centered on primary productivity, viz. macrophyte function, secondary productivity, decomposition and nutrient cycling and aquatic modeling. Important advances were made in these areas and are described in the following sections.

A. Primary Productivity 1974-1975

Synthesis activities in primary productivity for the year ending August 31, 1975 have centered on the development and implementation of a less sophisticated submodel for the estimation of rooted macrophyte productivity. Such a model has allowed for considerable input of data not previously accessible by the submodel WEED.

1. Model implementation

The collection of considerable data prior to this year on the community structure of more than 30 major macrophyte species in Lake George has greatly increased our basic knowledge of the interactions of macrophytes with one another and the freshwater ecosystem as a whole (Ogden, et al., 1976). We have found that a substantial amount of data collected could not be used in the current macrophyte submodel WEED because of three major reasons:

a. We have found that rooted macrophytes inhabit depths of greater than 10 m; such inhabitation has not been previously documented for many of these species (Sheldon and Boylen, 1976b). Species growing over a wide range of depth dramatically change their growth habits such that plants growing in shallow water normally fruit and die back at the end of summer; whereas, plants of the same species remain vegetative if growing at depths greater than 5 m.

b. Plants which remain vegetative continue to maintain high standing crops even during the winter ice cover. Productivity of such species at 2°C is substantial and must be incorporated

into productivity estimates of all bodies of water in which such growth is occurring (Boylen and Sheldon, 1976).

c. Sloughing of macrophyte biomass does not occur only in the autumn die back but for those plants which remain vegetative, sloughing is continual and not limited to season. Some of these species are major macrophyte producers in Lake George. In the southern basin Potamogeton amplifolius produces a peak standing crop of 80 g ash-free dry weight/m^2 at 3 m and P. robbinsii, a peak standing crop of 50g ash-free dry weight/m^2 at 7m. Both of these species remain productive under the winter ice cover.

Therefore, to make use of such data, a new macrophyte submodel has been developed and implementation is presently underway (Scavia, et al., 1975). The current submodel is being implemented with data previously collected on the growth of 4 macrophyte species occurring in Lake George as well as data relating epiphyte and macrophyte productivities (Sheldon and Boylen, 1975).

2. Further synthesis activities

Attempts to approximate total yearly productivity in the Lake George littoral and pelagic zones are not yet completed. Data on phytoplankton, macrophyte (macroalgae and rooted aquatics) and epiphyte productivities are all available. Because of the implementation of the new submodel further synthesis with the decomposition and fish submodels will not be completed until mid-1976.

B. Secondary Productivity

1. Summary of synthesis results

The major effort during 1974-1975 was directed at rebuilding, calibrating and validating the resource allocation-predation model (McNaught and Bloomfield, 1973) for the herbivorous crustaceans, the dominant grazers in freshwater ecosystems. Calibration of this model, using data on grazing developed at Lake George, was followed by a very successful attempt at validation, using a large mass of data available

from a number of universities and federal agencies for the Lake Michigan ecosystem. This independent validation of the resource allocation-predation model has been accepted for publication (McNaught and Scavia, 1975) in a volume edited by R. P. Canale, entitled "Mathematical Modeling of Biochemical Processes in Aquatic Ecosystems." This publication, which deals with the application of the model to fisheries problems, will be followed by a more theoretical paper, dealing with the biological controls upon zooplankton production.

During investigations of the process of secondary production at Lake George, important discoveries regarding the role of herbivores in aquatic systems have been made. Such information is given in a study of selective grazing by zooplankton upon natural algal assemblages (Bogdan and McNaught, 1975) and a new technique for examining size-selective grazing, using dextran beads labeled with two radioisotopes (^{14}C, ^{3}H) in the form of alanine (Bogdan, 1975).

2. Contributions of resource allocation-predation model to understanding aquatic systems

This model illustrates one methodological and a number of ecological principles. First, it was developed and calibrated on Lake George, but permits an assessment of effects of predator populations upon zooplankton production in a very different oligotrophic-mesotrophic lake such as Lake Michigan. Thus the model, from a management viewpoint of assessing the impact of exotic fish introductions, may have universal application. From a theoretical standpoint, the model has been used to test assumptions regarding interactions between abundance of algal foods, the quality of such foods, and characteristics of different fish predators, upon the production and quality of the zooplankton fauna which a lake will support. Like much of the recent literature, this model suggests the overwhelming importance of selective predation in regulating zooplankton production. The interface between management of large systems and ecological modeling should be obvious. Introductions of exotic fishes may limit the natural control of algal populations by endemic herbivores,

especially if such fishes are fine particle feeders. In addition the model permits a realistic assessment of the degree to which exotic fishes must be controlled, once introduced, to permit the re-establishment of native herbivores.

3. Selective feeding studies

The field study of selective feeding (Bogdan and McNaught, 1975) illustrates that organisms characteristic of oligotrophic waters, like Diaptomus, have adapted to the algal resources (nannoplankton < 22 μ) characteristic of such waters. In contrast, the eutrophic Daphnia consumes a wide range of food sizes with equal efficiency. Such information is vital to model calibration, as evidenced from the results of the previously discussed model. As such, these investigations of selective feeding form an important segment of the calibration of our site model, CLEANER.

The laboratory study of selective feeding (Bogdan, 1975) illustrates a new technique which has been successfully applied to understanding the mechanisms (active or passive) of selective grazing. As a techniques paper, its contributions to ecosystem modeling lie in the areas of calibration of all herbivores, as selective or unselective feeders. It is a very specific technique which may find wide use in the future.

C. Aquatic Decomposition and Nutrient Cycling (with augmentation of submodels via conversion factor estimation)

Studies of the glucose assimilatory activity of the water column and the sediments have been made since 1971 in Lake George (Clesceri, 1972; Clesceri and Dazé, 1973). These measurements have been made for various depths in the water column, depths in sediment cores sampling sites, and time of the year.

To relate these activity measurements to biomass of the microflora in the water column, colony forming units (viable counts) have been estimated on dilute nutrient agar to maximize count. In the sediment, activity measurements have been related to the deoxyribonucleic acid

(DNA) content of the sediment since colony forming units have little significance in the sediments due to impregnation of particles, etc. DNA is a constant component of every living cell, degrades readily upon death of the cell in natural systems (Clesceri and Dazé, 1975), and is therefore a suitable choice.

Activity studies have been done primarily to be able to observe relative differences in microbial activity as influenced by time and place. Only secondarily and with significant uncertainty can one use these data to say something about the cycling of carbon, nitrogen and phosphorus since the release of these materials during metabolism is a function of: 1) physiological age of the organisms; 2) efficiency of conversion of energy substrates to biomass; 3) the chemical composition of the decomposing material (both chemical complexity and elemental composition); 4) nutrient composition of the environs; and 5) physical parameters, most important of which is temperature.

In order to give the data collected during decomposition process research more ecological realism and to make it of greater use to the modeling effort, a series of conversion factors have been developed.

1. Glucose assimilation studies

Under the conditions employed for the glucose assimilation studies for water and for sediment, the rate of glucose uptake was standardized by the addition of a constant known amount of nutrient (11 mg per 10 ml assay). This nutrient was composed of essential amino acids, cofactors and minerals from tryptone and yeast extract (10:1) as well as 8 micrograms of glucose from carrier in the labelled glucose. Early studies showing the influence of added nutrient indicated that the amount utilized in the field studies produced maximum uptake velocity of isotopic glucose i.e., the uptake was well into the plateau region of a Michaelis-Menten plot (Clesceri, 1972). This was checked periodically throughout the field studies and was always affirmed.

Since the decomposer submodel utilizes maximum uptake rates, these values converted to the uptake of grams of organic matter would

be of more use than the data in its present form which is in grams of glucose, thus further work was done.

Varying the ratio of the added components to glucose in the assay produced the same rate of glucose uptake as the standard assay as long as the level of glucose was greater than 4 micrograms. This occurred over a range of nutrient addition (tryptone plus yeast extract 10:1) of 8 micrograms to 11 mg with several samples of lake water and sediment. Thus, the organisms are fully saturated with the components of the additional nutrient as well as the glucose, under the conditions of the assay. In the absence of the added nutrient no incorporation was observed in a two hour incubation period for lake water. Incorporation was observed with sediment, but less than when nutrient is added. Thus the rationale of adding nutrient to the system to produce maximum uptake conditions seems valid for Lake George. The question remains, however, and that is how much of the unlabelled material is being assimilated along with the radioactive material?

A mixture composed of ^{14}C-glucose and ^{14}C-amino acids (21 in equal proportion) to give the same organic content as the standard assay (8 micrograms of glucose and 11 mg. of other nutrient) was used to examine this question with several samples of lake water and sediment.

	cpm assimilated	
Minutes	Standard glucose assay*	Isotope mixture **
0	620	799
30	26,015	75,462
60	51,149	149,561
90	70,562	201,225

* 8 μc ^{14}C-glucose (U) in 8 micrograms glucose, 10 mg. of tryptone, and 1 mg. yeast extract

** 8 μc ^{14}C-glucose (U) in 8 micrograms glucose and 11/21 mg. of each of 21 ^{14}C-amino acids (U), 1 μc each.

These data, which are typical, seem to indicate that the amount of organic material which is assimilated during a standard glucose

assimilatory assay is about three times that represented by the assimilated radioactive glucose alone. This has been studied with a wide variety of Lake George water samples and is only a working conversion, but a value that seems reasonable in terms of the relative ease of glucose and amino acid assimilation for many microorganisms.

Thus after correction for quenching (70% efficiency for water samples and 65% for sediment samples), one can convert the corrected count to micrograms glucose and multiply by 3 to estimate the total organic material assimilated during the standard glucose assimilatory assay which is equivalent then to the maximum uptake of organic material.

Another quest on with respect to the glucose assimilatory assay is the degree of cellular multiplication occurring during the course of the assay. This is difficult to assess for lake water samples since these samples are processed by an overlay technique (Clesceri and Garber, 1973), and the cells are almost uniformly associated with particles such that colonization on the particle occurs during the glucose assimilatory assay. Thus, a frequently occurring organism (Aeromonas liquefacians) that was isolated from Lake George was used to determine the degree of cellular multiplication occurring during the assay.

Significant cell division was found to occur at 25°C as indicated below by cells grown up on the medium.

Time (hr.)	Flask 1 (cells/ml)	Flask 2 (cells/ml)
0	1.2×10^2	1.2×10^4
1/2	3.2×10^2	2.6×10^4
1	6.6×10^2	4.6×10^4
24	2.4×10^8	2.0×10^9

It appears that during the glucose assimilatory assay, of one hour cells are multiplying generally to the extent of about two or three generations as confirmed by studies with several other organisms (pseudomonads, unidentified lake isolates, etc.).

When these organisms were maintained in dilute medium (same

composition but total organic nutrient only 10 mg/l) for 12 hours prior to the glucose assimilatory assay, a similar pattern was observed.

2. Plate counts

The amount of biomass generated, either during the glucose assimilatory assay or in the lake, depends upon the mass of an organism as well as the generation time. An organism like Pseudomonas oleovorans will produce less biomass in two generations than a Cellulomonas sp. (isolate #21), however the generation time of the pseudomonad is less. Thus the amount of mass produced in unit time for Ps. oleovorans exceeds that of Cellulomonas as seen below.

Time	Pseudomonas		Cellulomonas	
(hr.)	(Cells/ml)	(picogm)*	(cells/ml)	(ng)*
0	2.8×10^3, 3.9×10^3	81, 113	7.5×10^3, 6.0×10^3	90, 72
1/2	8.1×10^3, 9.3×10^3	234, 269	1.0×10^4, 9.2×10^3	120, 110
1	6.2×10^4, 7.3×10^4	1792, 2110	1.7×10^4, 1.5×10^4	200, 180
2	7.5×10^4, 8.1×10^4	2168, 2341	3.0×10^4 2.7×10^4	360, 324

plate count on 1/2 strength agar

* dry weight (duplicate values)

A figure for the conversion to biomass from cell numbers is quite variable among different species of organisms. For the above organisms (Ps. oleovorans and Cellulomonas isolate 21), one sees that an average cell weight for the pseudomonad is 0.029 picogram whereas the cellulose hydrolyzer (Cellulomonas) is 12 picograms. Thus more than a 400 fold difference is seen between these two organisms. The efficiency with which one can count viable cells by plate count is of course another factor in the consideration of a conversion figure between cell numbers and biomass.

This counting efficiency was indicated in an earlier report (Clesceri, 1972) which showed that the maximum plate count for lake organisms was

obtained by plating on half strength nutrient agar.

Repeated microscopic examination of Lake George water reveals that there are very few unattached bacteria and that most seem to be associated with very small suspended particles. The plate counts observed are "colony forming units" produced mostly by colonized particles containing apparently from 2-3 organisms per particle. Further work in this area is progressing in another study concerning the microdynamics of detritus in lake systems. The question of attached vs. unattached organisms in marine systems is discussed by Wiebe and Pomeroy (1972).

In general it would appear that more realism could be attained from Lake George plate count values by multiplying plate count values from lake water by two and recognizing perhaps a 400 fold factor between small and large microorganisms in trying to estimate biomass. The distribution of large and small microorganisms probably favors the smaller ones, at least in sediments, as seen in the DNA studies which follow.

3. DNA values

In the sediment where DNA values have been used to estimate biomass, one again is confronted with the problem of large and small cells in the computation. Clesceri and Dazé (1973) have shown that there is a substantial difference between the number of small cells (eg., E. coli) per mg DNA and the number of large cells (eg., Bacillus subtilis) per mg DNA. In studying the DNA content of a group of frequently occurring Lake George isolates, it has been estimated that 5.0×10^9 cells per mg DNA is a good average value for converting DNA level to numbers of cells. This value favors the smaller cells which seem to occur more frequently in the lake.

In further studies, a relationship between the mg of DNA, biomass and cell numbers was established. Organisms were grown in nutrient broth at 25°C.

Organism	mg DNA / mg dry wgt	no. of cells / mg dry wgt	no. of cells / mg DNA
Bacillus subtilis	0.221	2.01×10^8	9.09×10^8
Bacillus megaterium	0.056	3.74×10^7	6.69×10^8
Escherichia coli	0.102	1.73×10^{10}	1.69×10^{11}
Pseudomonas oleovorans	0.204	3.46×10^{10}	1.69×10^{11}
Lake George isolate #21	0.484	8.33×10^7	1.72×10^8

One observes that the number of cells/mg DNA is about an order of magnitude larger than that achieved when cells are grown in the more dilute glucose assimilatory broth (Clesceri and Daze, 1973). This was not expected and reflects perhaps variation incurred in the perchloric acid extraction of DNA. Nonetheless, the relative proportions between the organisms remain the same in both studies implying some systematic error.

Under dilute nutrient conditions (25 mg/l of organic material) resembling more closely the oligotrophic environment, generation times of 6-10 hours have been observed with the isolate Aeromonas liquifaciens at 25°C in chemostat studies. A level of 2×10^4 cells per ml is maintained at this substrate concentration with 10% of the substrate utilized. Similar generation time data have been reported earlier (Clesceri, 1972) for lake water samples. However the level of organisms achieved in the Aeromonas study exceeds that of the lake water study. This reflects the higher concentration of limiting component (readily metabolizable C) in the Aeromonas study. The Aeromonas study gives an extremely small yield (0.000082%) of biomass on the 25 mg/l substrate which is composed of peptides and amino acids (Difco nutrient broth formulation). This is assuming a weight of 0.03 picogram per cell since the Aeromonas is a small organism comparable in size to Pseudomonas oleovarans studied above.

These calculations would tend to imply an extremely inefficient conversion of reduced carbon to biomass at this level of substrate. Highly efficient (20%) systems can be obtained when high levels of substrate

are used. The number of studies done are insufficient to determine whether this extremely low yield is an artefact of a highly dilute system or not, i.e., cell mass adhering to surfaces and thus not entering into the yield determination. It is suspected however that efficiency figures for the conversion of reduced carbon to biomass in highly dilute systems have been considerably overestimated.

4. Conclusion

The application of these conversion factors is being made for a publication presently in draft form by Clesceri and Bloomfield (1976).

D. Biome Aquatic Model - Evaluation and Simplification of CLEAN

Synthesis efforts have resulted in the validation, documentation, and evaluation of sensitivity of the Biome model CLEAN and the Lake George version, CLEANER. The model is valid for both mesotrophic and eutrophic conditions. The constructs are founded on biologic functionalities, and the parameter values are in accord with laboratory and field results. The model is judged to be too sensitive to changes in certain parameters. It is suggested further modeling should focus on the representation of adaptive shifts in environmental response.

1. Validation

CLEANER was validated using an independent data set from Saratoga Lake (NY), a eutrophic lake quite dissimilar to Lake George. Silicon limitation was added in order to simulate the observed diatom, green, blue-green algal succession, and certain parameters (such as nutrient half-saturation constants) were adjusted to account for adaptation to enriched conditions.

The results were encouraging: biomass levels and seasonal patterns were well represented. However, the patterns exhibited a time-lag that could not be corrected. Based on the experience of other modelers, we suspect that this is an artifact of not using internal nutrient concentrations in the phytoplankton submodel. It is also possible that the time-lag merely reflects inappropriate parameter values for

autolysis of the phytoplankton and accelerated remineralization through decomposition of labile organic matter. Otherwise, CLEANER was shown to be valid for modeling the eutrophic conditions.

2. Documentation

In order to complete the description of the Biome model that was begun two years previously, the construct formulations and parameter values were documented, with numerous references to the ecologic literature. This documentation is being published in the open literature (Scavia and Park, 1975).

With few exceptions, the constructs are well founded on known ecologic and physiologic functionalities. Departures of the CLEANER constructs from accepted functionalities fall into two categories: 1) constructs that are intended to represent assemblage responses as opposed to the population responses studied by most ecologists, and 2) constructs that are conceded to be gross simplifications necessitated by the overall exigencies of the ecosystem model.

Most parameter values used in the modeling can be justified by published studies. Interestingly, when parameter values were changed in order to achieve conformity with reported values, subsequent simulations were usually more accurate!

3. Sensitivity analysis

Because of the complexity of the model, the sensitivity was primarily evaluated qualitatively. However, a new quantitative procedure is currently being refined (Kohberger and Scavia, in prep.).

The importance of each term through time was evaluated by plotting the time-course of the rates (Scavia and Park, 1975). Thus the relative contribution of each process, such as respiration, grazing, photosynthesis, and nutrient remineralization, could be evaluated for the respective submodels and functional groups.

Comparison with the results from detailed laboratory studies of process rates confirmed the validity of the simulations. However, measurement of most of the processes *in situ* through time is impossible;

therefore, this is seen to be an important product or "emergent property" of the model - a result not feasible with traditional limnological methodologies.

The response of each of the constructs was determined by varying the parameter values. The resulting families of curves graphically portrayed the sensitivities of the constructs to the parameter values (Scavia and Park, 1975).

Additional insights were obtained by varying the form of selected constructs. The original intention was to find simpler formulations requiring less computer time; the result was just the opposite: simplifications resulted in model instability and lengthy integrations.

The conclusion is that the model is too sensitive to the form and parameter values of many of the constructs. It is strongly suggested that, rather than trying to simplify the constructs, future modeling effort should focus on incorporating representations of the additional complexity of adaptive shifts in environmental response.

Furthermore, sensitivity to temperature has significant implications in trying to model animals that undergo diurnal migration. Clearly, a point model utilizing mean temperature values for the water column is inappropriate if temperature control is at all important. Therefore, a two-layered version of CLEANER, representing stratification with a concomitant dichotomy in temperature, has been developed.

4. Communication of results

Two open-literature papers have been published this year (Park, Scavia and Clesceri, 1975; Scavia and Park, 1975). Some of the results and discussion of approach were presented at a AAAS Symposium and widely circulated in mimeographed form (Park and others, 1975). Although not directly supported by the contract, contributions based on the IBP modeling experience were incorporated in the NAS/TIE publication "Methods of Ecosystem Analysis" and in an EPA report "Secondary Impacts of Urbanization on Ecosystems Assessment Methodology" (Park and Carlisle, 1975; Carlisle and Park, 1975).

Numerous lectures and presentations in the United States and Europe, including the International Congress of Ecology and eight foreign institutions, were an important aspect of the synthesis effort. In addition, magnetic tapes of the computer program for CLEAN have been sent to five laboratories and institutions and another five will be sent shortly. Reprint requests are continuing to be answered, as well. Thus, the results of the modeling study are being widely disseminated.

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