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THE AQUATIC ECOSYSTEM MODEL MS. CLEANER

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INTRODUCTION

MS.CLEANER represents over thirty man-years of development by a multidisciplinary team. The precursor CLEAN was formulated by twenty-five investigators from several institutions under the aegis of the International Biological Program, Eastern Deciduous Forest Biome (Park *et al.*, 1974). One of the guiding principles from the very beginning has been the inclusion of as much biologic realism as possible (Bloomfield *et al.*, 1973), and this has characterized the development of the succeeding versions of CLEANER (Scavia and Park, 1976; Clesceri, Park and Bloomfield, 1977; Youngberg, 1977), and MS.CLEANER (Grodén, 1977; Desormeau, 1978; Park, Grodén and Desormeau, 1978).

Because of the attention to general process-level constructs, the model is appropriate for application to diverse types of lakes and reservoirs and is capable of addressing many environmental problems such as nutrient enrichment, thermal pollution, siltation, impoundment, and fish removal (Park, Scavia and Clesceri, 1975; Park, 1975, 1977; deCaprariis *et al.*, 1977). Current development includes adaptation to coastal environments and coupling to a model for bioaccumulation of toxic substances. The model is programmed in FORTRAN IV and is virtually machine-independent. It is presently being used by a number of universities, consulting firms, and federal and foreign agencies.

STATE-VARIABLES

In order to be applicable to diverse ecosystems and environmental problems MS.CLEANER is structured to simulate up to twenty biotic and twenty abiotic state-variables in each of ten spatial segments simultaneously (Fig. 1). Furthermore,

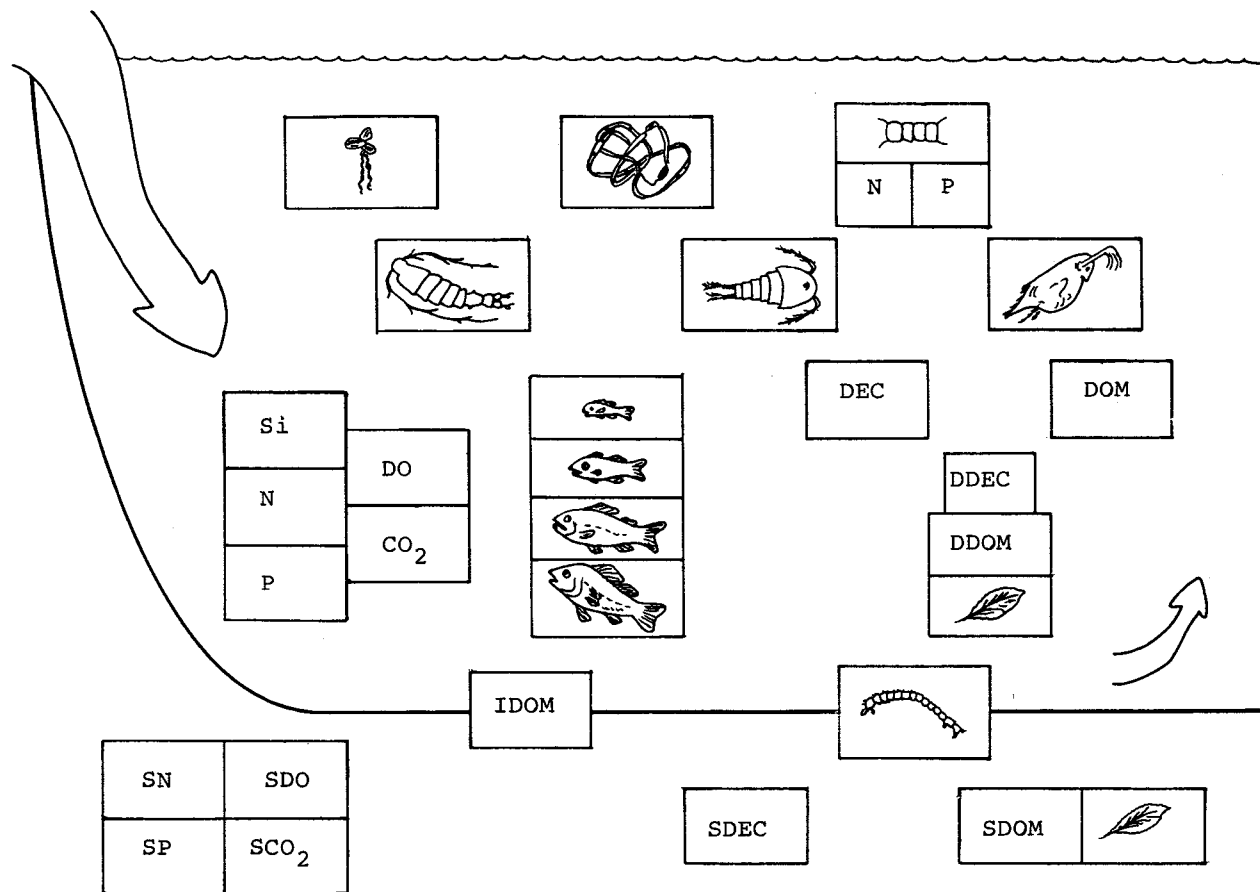


Figure 1 - Compartmental diagram of MS.CLEANER.

not only can the state-variables be reparameterized to represent different functional groups, but alternate formulations can be substituted, thus permitting representation of approximately ten alternative compartments with the present program.

MS.CLEANER can simulate a variety of biotic variables (Table I), including four types of phytoplankton (two with internal storage of nitrogen and phosphorus); up to four types of submerged aquatic vegetation (macrophytes); five types of zooplankton; two or more types of fish, with or without as many as four life stages; two kinds of bottom-dwelling animals (zoobenthos); and three groups of decomposers (bacteria and fungi). An equal number of abiotic variables can be simulated including seven types of dissolved organic matter; four types of particulate organic matter; five types of inorganic nutrients in the water column and sediments; and four compartments for dissolved oxygen and inorganic carbon.

This potential state-variable complexity is seldom fully utilized, however. Normal applications require only a subset of perhaps twenty state-variables, and MS.CLEANER has been run with as few as two dynamic state-variables! Such flexibility is facilitated by an interactive editing routine that allows the user to specify the state-variables and the loadings for a particular simulation.

Several external variables and all the biotic state-variables can be used as loadings. External variables include water temperature, temperature and discharge rate of inflowing water, wind speed, light, dissolved inorganic nitrogen, orthophosphate, dissolved silica, dissolved organic material, and particulate organic material.

TABLE I
EQUATIONS FOR BIOTIC STATE VARIABLES

Phytoplankton

$$dBIOMAS/dt = PPROD-RESPIR-EXCR-MORT-SED-GRZ \quad (1)$$

PPROD = primary production rate
RESPIR = respiration rate
EXCR = excretion rate
MORT = mortality rate
SED = sedimentation rate
GRZ = grazing rate

Macrophytes

$$dBIOMAS/dt = MACPRD-RESPIR-EXCR-MORT-MACSLF-FTSH-GRZ \quad (2)$$

MACPRD = macrophyte primary production rate
MACSLF = macrophyte sloughing rate
FTSH = fruiting and shooting rate

Zooplankton

$$dBIOMAS/dt = CON-RESPIR-EXCR-MORT-DEF-GRZ+PROM+SWIM \quad (3)$$

CON = consumption rate
DEF = defecation
PROM = promotion rate
SWIM = swimming rate

Fish

$$dBIOMAS/dt = CON-RESPIR-EXCR-MORT-DEF-GRZ-FISH-GONAD+PROM+SWIM \quad (4)$$

FISH = fishing pressure
GONAD = spawning rate

Zoobenthos

$$dBIOMAS/dt = CON-RESPIR-EXCR-MORT-DEF-GRZ+PROM \quad (5)$$

Decomposers

$$dBIOMAS/dt = UPT-RESPIR-EXCR-MORT-GRZ+COL \quad (6)$$

COL = colonization rate
UPT = uptake rate

PROCESS REPRESENTATIONS

Phytoplankton Photosynthesis

Photosynthesis is represented as a function of factors for light and nutrients. Temperature is important in determining the maximum photosynthetic rate under light-saturating conditions and in determining the uptake rate for nutrients; however, it is not treated as an independent limitation factor for photosynthesis in MS.CLEANER as in previous versions (*cf.* Scavia and Park, 1976).

Previously, CLEANER used Steele's (1965) formulation for modeling the effect of differing light intensities on photosynthesis. However, based on the results of the tests of published formulations performed by Straškraba (1976) and Jassby and Platt (1976), the Smith (1936) equation is used for non-inhibiting conditions and the Steele (1965) equation is used for inhibiting conditions.

The effective light intensity at a given depth is calculated using Beer's Law and includes the effects of pure water, dissolved organic matter, suspended organic and inorganic particulate matter and plankton, and the incident light intensity at the surface, with only 50% of the total visible light being considered as available for photosynthesis (Strickland, 1958). Provision is made for modeling buoyant blue-green algae as well.

Many algae can adapt to varying light intensities by changing their concentration of chlorophyll; with increasing light intensities the concentration of chlorophyll decreases exponentially until it reaches a minimum value (Myers, 1946; Eppley and Sloan, 1966; Cloern, 1977). This relationship has been incorporated into MS.CLEANER (Fig. 2) (Grodén, 1977).

Nutrient Limitation -- An internal nutrient submodel has been

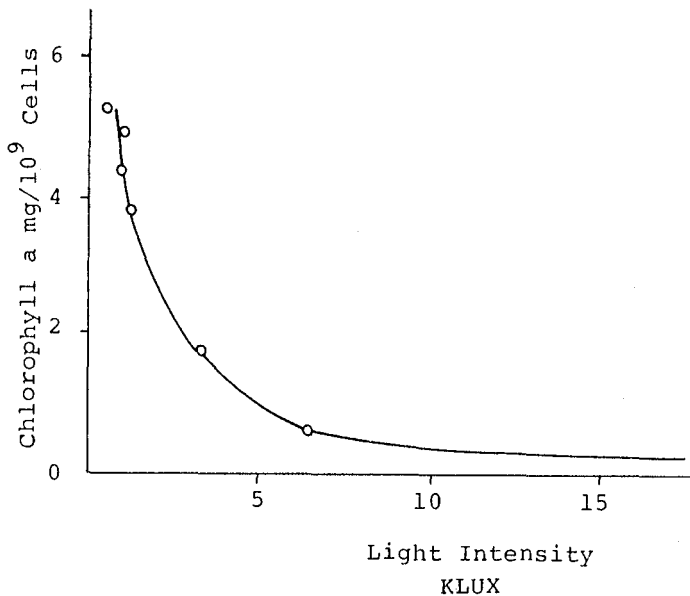


Figure 2 - Relationship between chlorophyll a in algal cells and light intensity from Nielsen and Jørgensen, 1968.

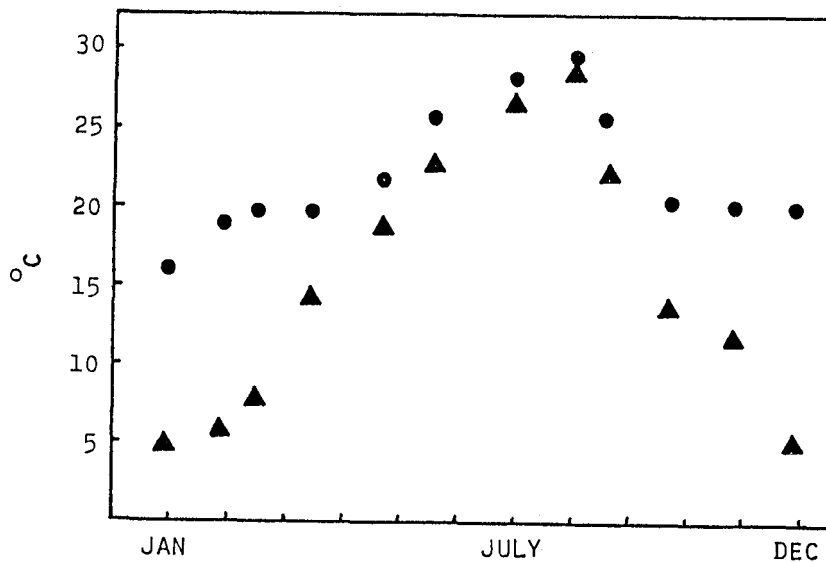


Figure 3 - Relationship between optimum temperature of phytoplankton (circles) and ambient temperature (triangles); after Straškraba (1976) using monthly data from Aruga (1965a).

developed for MS.CLEANER in order to predict the occurrence of phytoplankton blooms more accurately (Desormeau, 1978). Phytoplankton are able to store nutrients internally in excess of their needs, and later utilize the internal reserves if external nutrients become depleted. The state-variable equations for internal phosphorus and internal nitrogen have separate process equations for nutrient uptake and nutrient assimilation, where uptake is dependent on both internal and external nutrient levels and assimilation is dependent only on the internal nutrient concentration. This uncoupling of the uptake and assimilation processes enables accurate predictions in non-steady state systems. The subsistence quota, which represents the internal nutrient concentration per unit algal biomass (Droop, 1974), is an indicator of the nutrient status of the phytoplankton and is used to evaluate the nutrient limitation term for primary productivity. The atomic ratio of internal nutrients is compared with known thresholds (*cf.* Droop, 1974; Rhee, 1974, 1978) in order to predict which nutrient is actually limiting.

Temperature limitation -- Perhaps the most copied construct in CLEANER is the reduction factor for suboptimal temperature (Bloomfield *et al.*, 1973; Scavia and Park, 1976), which was slightly modified from a formulation developed by Shugart *et al.*, (1974). However, it is difficult to parameterize and yields values that are unreasonably high near 0°C. Therefore, a new equation has been developed using phytoplankton data from a variety of sources (Grodén, 1977).

Phytoplankton exhibit the ability to adapt to gradually changing temperatures (Aruga, 1965a; Brock, 1967; Boylen and

Brock, 1973) (Fig. 3). Straškraba (1976) has developed an empirical function for changing optimal temperature for growth of phytoplankton for temperate lakes; Groden (1977) generalized it for arctic, Alpine, and tropical lakes and incorporated it in MS.CLEANER.

Macrophyte Photosynthesis

The equation for production of macrophyte biomass is similar to that for phytoplankton, with additional empirical functions for substrate control (Scavia *et al.*, 1975) and the effect of water velocity on the boundary layer of the leaves (Titus *et al.*, 1975), both of which are indirectly related to the availability of nutrients. The extinction coefficient has an additional term to represent self-shading as a function of the leaf area index, which is a species-specific parameter relating biomass to surface area of leaves. The phosphate, nitrogen and carbon dioxide sources can be either sediment or water-column pools depending on the macrophyte group.

Respiration in Plants

Plant respiration can be separated into endogenous respiration and photorespiration. Riley (1963) has shown that endogenous respiration increases exponentially with temperature, whereas carbon dioxide release through photorespiration is a relatively constant percentage of primary production. Combining these processes MS.CLEANER now has a realistic representation of respiration (Groden, 1977).

Excretion in Plants

Extracellular release of photosynthate appears to be dependent

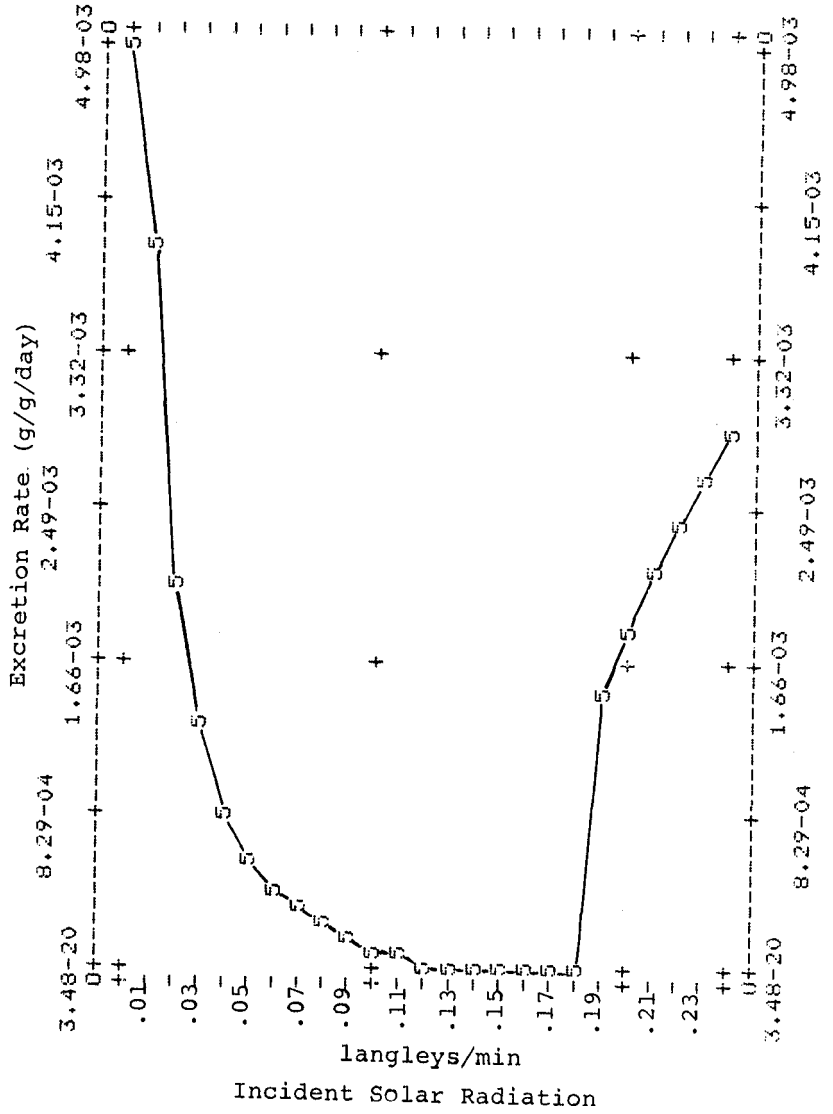


Figure 4 - Predicted algal excretion rate as a function of light intensity.

on light intensity, carbon dioxide concentration and oxygen levels. In general, any environmental condition that permits photo-assimilation but prohibits cell multiplication will result in release of photosynthate. This is especially true for light (Watt, 1966; Fogg *et al.*, 1965). Therefore, the excretion equation in MS.CLEANER has been reformulated so that extracellular release is now a function of primary production and inversely related to the adaptive light curve (Fig. 4) (Desormeau, 1978). Limited data prohibits including the effects of dissolved oxygen and carbon dioxide levels in the excretion process equation at this time.

Nonpredatory Mortality in Plants

The internal nutrient compartments used by MS.CLEANER allow continuous monitoring of the physiological status of the cells. If the internal nutrient level goes below the subsistence quota, senescence occurs, accompanied by increased bacterial colonization and eventual lysis. This and the effect of critically high levels of temperature are both represented in the nonpredatory mortality equation.

Macrophyte Sloughing

An important loss term in the macrophyte equation is sloughing of leaves. Sloughing is initiated under deteriorating conditions where self-shading and metabolic cost of maintaining biomass are disadvantageous. It occurs when the leaf area index is greater than the optimal leaf area index, which is computed as the ratio of leaf surface area to lake surface area that results in maximum net photosynthesis (Shugart *et al.*, 1974; Park *et al.*, 1974).

Macrophyte Die-back

Autolysis of the major portion of individual macrophyte plants, as opposed to sloughing of individual leaves and mortality affecting the whole population, occurs after the production of fruit or overwintering shoots. The cue for fruit or shoot production may be a particular photoperiod level or a particular temperature level; fruiting is not permitted if the depth of water exceeds the maximum depth at which fruiting can occur.

Consumer Ingestion

The general consumption term described by Park *et al.* (1974) and Scavia and Park (1976), has been modified to differentiate between saturation-kinetic and uniform-rate feeding strategies. Saturation-kinetic feeding is represented by a function containing a maximum ingestion rate, modified by the availability of preferred prey at concentrations above a minimum level, as well as a half-saturation construct for feeding and an intracompartamental competition term; it is used in modeling organisms such as copepods and fish. Filtering at a constant rate, as demonstrated by cladocerans, is represented as a linear relationship with terms for weighting the available prey according to preference or capturability and for representing the maximum rate at which the prey may be removed from the water column. At high prey concentrations, the production of pseudofeces is simulated by comparing the filtering rate with the maximum consumption rate and treating the excess as particulate organic matter.

Both feeding equations are further modified by functions representing changes in behavior caused by ecologic and physiologic responses to various environmental stimuli, such as oxygen depletion.

A function intended to correct for changing process rates associated with a maturing population is discussed by Scavia and Park (1976); because the function is often unsatisfactory, it will not be discussed here. If large differences in feeding rates are of concern, compartments can be disaggregated, linked by the promotion function, and assigned different parameter values.

The consumption term is also utilized for the determination of grazing pressure on prey populations. The defecation term is expressed as the proportion of food consumed but not assimilated.

Consumer Respiration and Excretion

The respiration equation involves two terms. One represents endogenous respiration with an exponential increase in rate with increasing temperature. There is also a complex density-dependent factor to represent increased respiration as the carrying capacity is approached (Shugart *et al.*, 1974). This factor can be negative to represent the opposite response in schooling fish and other organisms. The second term in the equation is analogous to "specific dynamic action", as used by fish specialists, and accounts for the metabolic cost of catching and utilizing food, with a proportionality constant relating respiration to the food consumed. The entire function can be multiplied by a reduction factor to simulate the effect of decreasing oxygen levels (Youngberg, 1977).

Excretion rate is related linearly to respiration by means of a proportionality constant. A separate routine is used to represent the excretion of excess internal nutrients by zooplankton.

In actuality, excretion is not directly related to the stoichiometry of prey (Conover, 1964; Martin, 1968; Omori, 1970), but this simplification is necessary to maintain mass balance of nutrients in the model.

Consumer Mortality

Nonpredatory mortality is treated as a function of critically high temperature, with the capability of representing effects of population, age structure, crowding, and behavior. Because starvation is an important form of mortality in zooplankton (Argentesi, deBernardi, DiCola, 1977) and higher organisms, it should be included in the model. However, insufficient data are available (Park, Groden, Desormeau, 1978). Predatory mortality utilizes the general consumption equation. Fishing pressure is handled by a parameter for the average daily catch limited by the legal season.

Spawning

The time of onset of spawning may be either specified or calculated with an empirical equation based on the photoperiod as a function of latitude (Leung, 1978). Because gonadal products may account for a significant proportion of biomass loss in many fish, a function has been developed to represent their release throughout the spawning period.

Promotion

Promotion can be simulated in MS.CLEANER as the transfer of biomass between state-variables representing separate age or size classes. If state-variables are based on size, the rate of growth will determine the extent to which promotion occurs. This

function is a simplification of a complex response that depends on the mean weight or size of the individuals. However, simulation of mean weight would require modeling both biomass and numbers of individuals — twice as many equations. The function seems to be adequate for simulating organisms such as chironomids (Park, 1978). If state-variables are based on age, a function similar to that for spawning is used, where a normal probability curve is assumed for the interval of time during which promotion occurs (Leung, 1978).

Decomposition

Microbial dynamics are modeled explicitly, with separate state-variable equations for water decomposers, detrital decomposers, sediment decomposers, labile and/or refractory particulate and dissolved organic matter, and inorganic nutrients occurring in the water column, interstitial water, and the sediment. The biomass of decomposers is determined by functions for substrate utilization, nonpredatory mortality, respiration, consumption and sedimentation. Decomposer remineralization is represented by several process equations for nutrient uptake, hydrolysis of organic matter, colonization of detritus and endogenous shedding as a function of growth rate (Clesceri, Park, and Bloomfield, 1977).

This compartmental and process resolution, including feedback mechanisms, confers a stabilizing effect on the simulations. MS.CLEANER can be used to represent the differential degradation of different types of organic material including pollutants, the cycling of nutrients, and the production of microbial biomass.

SEGMENT LINKING

MS.CLEANER has the capability to simulate up to ten different segments simultaneously. The segments are used to represent spatial heterogeneties by allowing for variation in chemical, physical, and biotic characteristics within the body of water. The vertical and horizontal distribution and extent of each segment is defined by the user. A linking language is used to specify the transfer processes that act on each state-variable in effecting transfers among sections and loss from the system. As shown in Fig. 5, transfer processes include gains or losses due to sedimentation (S), turbulent mixing (T), resuspension from the bottom sediments (R), and biotic migrations (B). Also calculated are density-determined inflows (I), the reduction of incident solar radiation ($I\phi$) through vertically arrayed segments, and losses due to outflow (O) as functions of retention times.

INTERACTIVE CAPABILITY

MS.CLEANER, as a user-oriented model, features a machine-independent namelist editor and a set of simple commands. The namelist editor enables the user to list and make changes in parameter values while running the model. Parameter values also can be obtained by using a command that lists values to blocks. The set of commands also enables the user to: list all the commands with a brief description of each; initiate an integration; terminate the integration in the event of instability; reset the initial conditions to the values at the last time-step in order to restart the integration; plot the state-variable concentrations, rates for various processes, and loadings to the model; and

transform the state-variable values into "environmental perception" characteristics such as water turbidity, fish catch, and concentrations of noxious algae. The option to save all the parameter changes made during a run is also available.

VERIFICATION

The model has been calibrated and verified with data from a number of lakes of diverse types. It was originally applied to Lake George, New York. Subsequent versions have been calibrated for Loch Leven, Scotland; Slapy Reservoir, Czechoslovakia; Balaton Lake, Hungary; Lakes d'Endine and Mergozzo, Italy; Lake Esrum, Denmark; and Lake Paijanne, Finland. A version that incorporates all the latest improvements, including storage of internal nutrients in phytoplankton, has been calibrated for subalpine Øvre Heimdalsvatn, Norway, and verified with data from Vorderer Finstertaler See, Austria, without changing parameter values (Desormeau, 1978). With only minor changes it gives reasonable results for Lake Mergozzo, a mesotrophic, stratified lake (Fig. 6).

PERTURBATIONS AND SENSITIVITY ANALYSIS

The loadings of nutrients, temperature, and light can be perturbed using the editing capability of MS.CLEANER to set the perturbation parameters. The perturbations can be either additive or multiplicative, and either constant or as a pulse of user-specified duration and timing.

An algorithm was developed to facilitate analysis of the sensitivity of MS.CLEANER to changes in values of parameters and driving variables. Using a random number generator, values with a normal or uniform distribution are used to vary loadings or

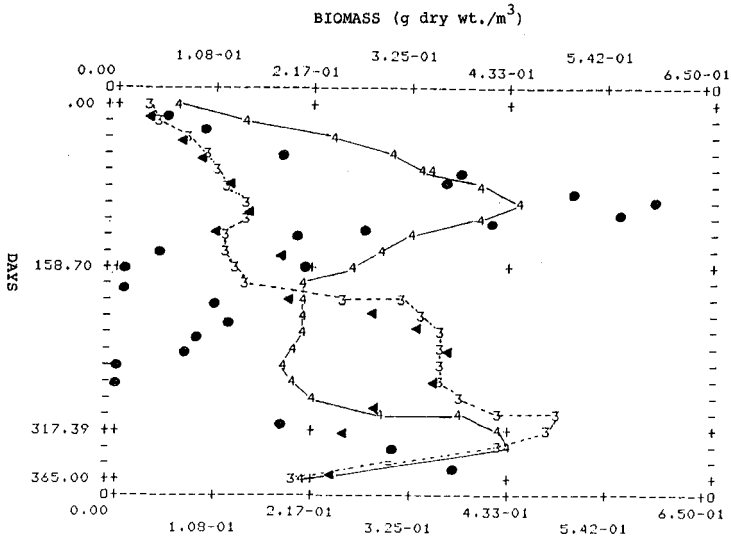


Figure 6 - Comparison of predicted and observed values for diatoms (4, circles) and blue-green algae (3, triangles) in Lake Mergozzo, Italy; data courtesy of Delio Ruggiu.

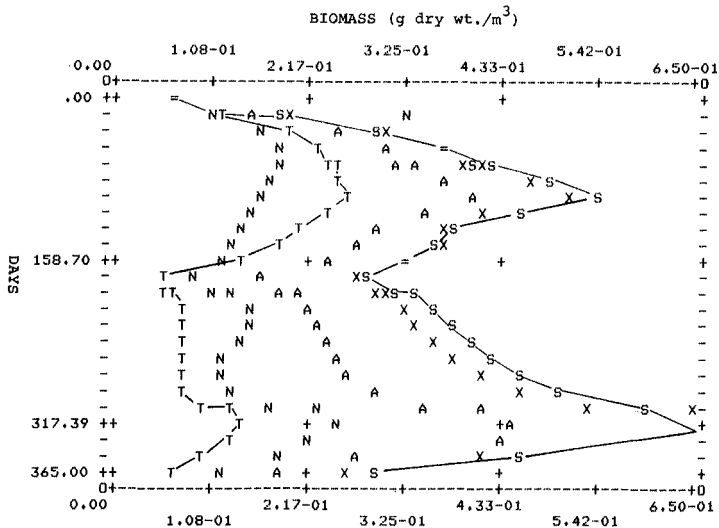


Figure 7 - Sensitivity analysis of maximum photosynthetic rate for diatoms in Lake Mergozzo, Italy; ± 1 standard deviation in biomass indicated by lines, "A" = mean for five simulations.

parameters within a specified range. The simulation is repeated a given number of times with different perturbations, and the results are summarized. The parameters are perturbed at the beginning of each simulation; the loadings are perturbed at each step.

As an example, the technique was applied to the model of Lake Mergozzo to determine sensitivity of the phytoplankton simulations to changes in the maximum photosynthetic rate. A standard deviation of 0.00055 units about a mean observed value of .00091 was used in 5 simulations of diatoms (Fig. 7).

SUMMARY

The aquatic ecosystem model MS.CLEANER has had a long history of development involving numerous individuals from different disciplines. As a result, fifty different state-variables can be represented (up to forty simultaneously) and a high level of biologic realism has been achieved by giving careful attention to process-level constructs. As many as ten different ecosystem segments can be simulated simultaneously, with dynamic linkages such as circulation and fish migration specified by the user. The model has a set of simple commands and a machine-independent namelist editor for efficient usage.

The model is programmed so as to facilitate perturbation and sensitivity analysis. Calibration and verification has utilized data from diverse lakes and reservoirs. Agreement with observed data has been good.

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REFERENCES

- Argentesi, F., deBernardi, R., and CiCola, G., 1977. Some mathematical methods for the study of population dynamics. In Proceedings 1st World Conference on Mathematics at the Service of Man, Barcelona, Spain, 25 pp.
- Aruga, Y., 1965a. Ecological studies of photosynthesis and matter production of phytoplankton -- I. Seasonal changes in photosynthesis of natural phytoplankton. Bot. Mag. Tokyo, 78:280-288.
- Aruga, Y., 1965b. Ecological studies of photosynthesis and matter production of phytoplankton -- II. Photosynthesis of algae in relation to light intensity and temperature. Bot. Mag. Tokyo, 78:360-365.
- Bloomfield, J. A., Park, R. A., Scavia, D., and Zahorcak, C. S., 1973. Aquatic modeling in the eastern deciduous forest biome, U. S. International Biological Program. In: E. J. Middlebrooks, D.

H. Falkenberg and T. E. Maloney (Editors), Modeling the Eutrophication Process. Utah State University, Logan, Utah, pp. 139-158.

Boylen, C. W. and Brock, T. D., 1973. Effects of thermal additions from the yellowstone geyser basins on the benthic algae of the firehole river. *Ecology*, 54:1282-1291.

Brock, T. D., 1967. Micro-organisms adapted to high temperatures. *Nature*, 214:883-885.

Clesceri, L. S., Park, R. A., and Bloomfield, J. A., 1977. General model of microbial growth and decomposition in aquatic ecosystems. *Appl. Environ. Microbiol.*, 33(5):1047-1058.

Cloern, J. E., 1977. Effect of light intensity and temperature on *Cryptomonas ovata* (Cryptophyceae) growth and nutrient uptake rates. *Jour. Phycol.*, (in press).

Conover, R. J., 1964. Food relations and nutrition of zooplankton. Occasional publ., Proc. Sym., Exp. Mar. Ecol., 2:81-91.

deCaprariis, P., Park, R. A., Haines, R., Albanese, J., Collins, C., Desormeau, C., Groden, T., Leung, D., and Youngberg, B., 1977. Utility of the complex ecosystem model MS.CLEANER. In Proceedings of the International Conference on Cybernetics and Society, pp. 87-89.

Desormeau, C. J., 1978. Mathematical modeling of phytoplankton kinetics with application to two alpine lakes. Report #4, Center for Ecological Modeling, Rensselaer Polytechnic Institute, Troy, N.Y., 21 pp.

Droop, M. R., 1974. The nutrient status of algal cells in continuous culture. *Journal of Marine Biology Ass., U.K.*, 54: 825-855.

Eppley, R. W. and Sloan, P. R., 1966. Growth rates of marine phytoplankton: correlation with light adsorption by cell chlorophyll a. *Physiol. Plant.*, 19:47-59.

Fogg, G. E., Nalewajko, C., and Watt, W. D., 1965. Extracellular products of phytoplankton photosynthesis. *Proc. R. Soc. B.*, 162:517-534.

Groden, T. W., 1977. Modeling temperature and light adaptation of phytoplankton. Report #2, Center for Ecological Modeling, Rensselaer Polytechnic Institute, Troy, N.Y., 17 pp.

Jassby, A. D. and Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.*, 21:540-547.

Leung, D. K., 1978. Modeling the bioaccumulation of pesticides in fish. Report #5, Center for Ecological Modeling, Rensselaer Polytechnic Institute, Troy, N.Y., 18 pp.

- Martin, J. H., 1968. Phytoplankton-zooplankton relationships in Narragansett Bay. III. Seasonal changes in zooplankton excretion rates in relation to phytoplankton abundance. *Limnol. Oceanogr.*, 13:63-71.
- Myers, J., 1946. Culture conditions and the development of the photosynthetic mechanism -- IV. Influence of light intensity of photosynthetic characteristics of *Chlorella*. *Jour. of Gen. Physiol.*, 29:429-440.
- Nielsen, E. S., and Jørgensen, 1968. The adaptation of plankton algae -- I. General part. *Physiol. Plant.*, 21:401-413.
- Omori, M., 1970. Variations of length, weight, respiratory rate, and chemical composition of *Calanus cristatus* in relation to its food and feeding. In: J. H. Steele (Editor), *Marine Food Chains*. University of California Press, Berkeley, pp. 113-126.
- Park, R. A., 1975. Theoretical implications of models of aquatic systems. Presented at AAAS, Biological Sciences Meeting, New York City.
- Park, R. A., 1977. Predicting the impact of man on lake ecosystems, (abs.). In: P. Biro (Editor), *Human Effects on Life in Fresh Water*, Hungarian Academy of Sciences, Tihany.
- Park, R. A., 1978. A model for simulating lake ecosystems. Report #3, Center for Ecological Modeling, Rensselaer Polytechnic Institute, Troy, N.Y., 19 pp.
- Park, R. A., O'Neill, R. V., Bloomfield, J. A., Shugart, H. H., Booth, R. S., Goldstein, R. A., Mankin, J. B., Koonce, J. F., Scavia, D., Adams, M. S., Clesceri, L. S., Colon, E. M., Dettmann, E. H., Hoopes, J., Huff, D. D., Katz, S., Kitchell, J. F., Kohberger, R. C., LaRow, E. J., McNaught, D. C., Peterson, J., Titus, J., Weiler, P. R., Wilkinson, J. W. and Zahorcak, C. S., 1974. A generalized model for simulating lake ecosystems. *Simulation*, 23(2):33-50.
- Park, R. A., Scavia, D. and Clesceri, N. L., 1975. CLEANER, the Lake George model. In: C. S. Russell (Editor), *Ecological Modeling in a Resource Management Framework*. Resources for the Future, Inc., Washington, D. C., pp. 49-82.
- Park, R. A., Groden, T. W. and Desormeau, C. J., 1978. Modifications to the model CLEANER requiring further research. In: D. Scavia and A. Robertson (Editors), *Perspectives on Aquatic Ecosystem Modeling*, Ann Arbor Science Publishers, Inc.
- Rhee, G-Yull, 1974. Phosphate uptake under nitrate limitation by *Scenedesmus* spp. and its ecological implications. *J. Phycol.*, 10:470-475.
- Rhee, G-Yull, 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol. Oceanogr.*, 23:10-25.

- Riley, G. A., 1963. Theory of food-chain relations in the ocean. *The Sea*, 2.
- Scavia, D., Boylen, C. W., Sheldon, R. B., and Park, R. A., 1975. The formulation of a generalized model for simulating aquatic macrophyte production. FreshWater Institute Report #75-6, Rensselaer Polytechnic Institute, Troy, N.Y.
- Scavia, D. and Park, R. A., 1976. Documentation of selected constructs and parameter values in the aquatic model CLEANER. *Ecol. Mod.* 2(1):33-58.
- Shugart, H. H., Goldstein, R. A., O'Neill, R. V. and Mankin, J. B., 1974. TEEM: A terrestrial ecosystem energy model for forests. *Oecol. Plant.*, 9(3):231-264.
- Smith, E. L., 1936. Photosynthesis in relation to light and carbon dioxide. *Nat. Acad. Sci. Proc.*, 22:504-511.
- Steele, J. H., 1965. Notes on some theoretical problems in production ecology. In: C. R. Goldman (Editor), *Primary Production in Aquatic Environments*. Univ. of Calif. Press, Berkeley, Calif., pp. 393-398.
- Straškraba, M., 1976. Development of an analytical phytoplankton model with parameters empirically related to dominant controlling variables. In: R. Glaser, K. Unger and M. Koch (Editors), *Umwelbiophysik*. Akademik Verlag, Berlin, G. D. R., pp. 33-65.
- Strickland, J. D. H., 1958. Solar radiation penetrating the ocean -- a review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. *J. Fish Res. Bd. Canada*, 15:453-493.
- Titus, J., Goldstein, R. A., Adams, M. S., Mankin, J. B., O'Neill, R. V., Weiler, P. R., Jr., Shugart, H. H., and Booth, R. S., 1975. A production model for *Myriophyllum spicatum* L. *Ecology*, 56:1129-1138.
- Walshe, B. M., 1950. The function of haemoglobin in *Chironomus plumosus* under natural conditions. *J. Exp. Biol.*, 27:73-95.
- Watt, W. D., 1966. Release of dissolved organic material from the cells of phytoplankton populations. *Proc. R. Soc. B.*, 164:521-551.
- Youngberg, B. A., 1977. Application of the aquatic model CLEANER to a stratified reservoir system. Report #1, Center for Ecological Modeling, Rensselaer Polytechnic Institute, Troy, N.Y., 22 pp.