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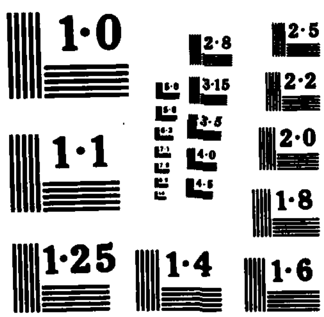
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A MATHEMATICAL MODEL OF SUBMERSED AQUATIC PLANTS

by

Carol Desormeau Collins, Richard A. Park, Charles W. Boylen

Center for Ecological Modeling
Rensselaer Polytechnic Institute
Troy, New York 12181

May 1985

Final Report

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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

Submersed aquatic plants or macrophytes often contribute significantly to primary production in lakes and reservoirs. Macrophyte growth and decomposition can influence the physical, chemical, and biological characteristics of aquatic ecosystems, including temperature and concentrations of dissolved oxygen, nitrogen, phosphorus, inorganic carbon, detritus, phytoplankton, and fish.

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20. ABSTRACT (Continued).

A mathematical model of submersed aquatic macrophyte growth and decomposition was developed for use with the US Army Corps of Engineers' one-dimensional reservoir water quality model, CE-QUAL-R1, which was developed under the Environmental and Water Quality Operational Studies (EWQOS). The ecological processes recommended for inclusion with the macrophyte compartment include gross production, dark respiration, photorespiration, nonpredatory mortality, and grazing. The influence of these processes on other compartments in CE-QUAL-R1 is described.

Select process equations have been validated using a stand-alone version of the recommended model based upon experimental results derived from the literature and other research at the US Army Engineer Waterways Experiment Station for two macrophyte species, *Myriophyllum spicatum* and *Hydrilla verticillata*. Management control strategies can be simulated for mechanical harvesting and chemical control of the plants.

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Preface

This investigation was supported by the Aquatic Plant Control Research Program (APCRP), sponsored by the Office, Chief of Engineers (OCE), and was managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. The OCE Technical Monitor was Mr. E. Carl Brown.

This is the final report for Contract No. DACW39-81-C-0036, "A Mathematical Model of Submersed Aquatic Plants," prepared by Rensselaer Polytechnic Institute (RPI), Troy, N. Y. Authors of this report were Drs. Carol Desormeau Collins, Richard A. Park, and Charles W. Boylen, RPI. The model was conceptualized and developed for incorporation into the US Army Corps of Engineers' reservoir water quality model, CE-QUAL-R1, which was developed during the conduct of the Environmental and Water Quality Operational Studies (EWQOS). CE-QUAL-R1 is a numerical, one-dimensional model that describes the vertical distribution of thermal energy and biological and chemical materials in a reservoir through time. The mathematical structure of the model is based on horizontal layers; temperature and materials concentration gradients are computed only in the vertical direction.

The original contract called for the development of algorithms and the programming of those algorithms for inclusion in CE-QUAL-R1. However, in subsequent discussions with the contract officer at the time, Mr. Joseph Norton, Environmental Research and Simulation Division (ERSD), and with other staff of the WES, Environmental Laboratory (EL), including Drs. Joseph H. Wlosinski and Allan S. Lessem, it was agreed that the programming should be done by the Environmental Laboratory staff most familiar with CE-QUAL-R1. The draft report was reviewed by Drs. Wlosinski and Lessem and Messrs. Mark S. Dortch and Jack B. Waide.

Manager of the APCRP was Mr. J. Lewis Decell. General supervision was provided by Mr. Donald L. Robey, Chief, ERSD. Chief of the EL during the conduct of this investigation was Dr. John Harrison.

Commanders and Directors of WES during the study and preparation of the report were COL Tilford C. Creel, CE, and COL Robert C. Lee, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

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Contents

A MATHEMATICAL MODEL OF SUBMERSED AQUATIC PLANTS

Introduction

Background

1. Submersed aquatic plants or macrophytes often contribute significantly to the productivity of lakes and reservoirs. Macrophytes can become so abundant that they become a nuisance to recreational and navigational activities. Their growth and decomposition also influence other biotic and abiotic components of the ecosystem. The littoral community of many eutrophic systems is often dominated by a single species of macrophyte. Under less eutrophic conditions, several species may coexist. The growth of aquatic plants is controlled by many factors, including (a) growth properties of the plant; (b) physical factors such as temperature, irradiance levels, and changes in water elevation; and (c) physiological characteristics of the plant such as nutrient requirements, photoadaptation, and sediment preference.

2. The importance of macrophytes to the aquatic ecosystem necessitated the development and incorporation of a macrophyte submodel in the US Army Corps of Engineers' one-dimensional reservoir water quality model, CE-QUAL-R1 (Environmental Laboratory 1982), which was developed during the conduct of the Environmental and Water Quality Operational Studies (EWQOS). This report describes the development and formulation of this macrophyte submodel for inclusion in CE-QUAL-R1. The model simulates growth and decomposition of macrophytes. The influence of the plants on other compartments in CE-QUAL-R1 is also included in the model.

3. To make the proposed submodel complementary with CE-QUAL-R1, the following recommendations are made regarding the computation and layering scheme of CE-QUAL-R1. Macrophytes should be regarded as occupying the bottom surface of each layer in the reservoir within the euphotic zone. As such, they are not subject to advection or diffusion and are not transported in inflowing or outflowing waters. The macrophyte compartment should have units of grams per layer. As the layers are resized in CE-QUAL-R1, dependent on the balance of inflowing and outflowing waters, the macrophyte biomass should be reapportioned to reflect the appropriate densities for those layers. If the surface elevation drops, macrophytes in the dewatered zone should no longer be included in the computation. If the water surface elevation increases and

inundates new areas, the macrophyte density in the new area should be given a small "seed" value to represent colonization.

4. Irradiance reaching a particular model layer determines the plants' growth response. Changes in water level can affect irradiance at a particular level. Drawdown may suddenly expose submersed plants to higher irradiances as the depth of water through which light is transmitted decreases. Conversely, an increase in reservoir pool elevation may result in greater light attenuation. Light attenuation for a particular layer in CE-QUAL-R1 is dependent upon the extinction coefficient of water and on shading by suspended solids, detritus, zooplankton, and phytoplankton. It is recommended that self-shading for macrophytes also be included in the model.

5. The following processes are recommended for inclusion in the macrophyte model: gross production, dark respiration, photorespiration, nonpredatory mortality, and grazing. Control measures affecting macrophytes, such as mechanical harvesting and herbicidal treatment, should also be included in the model as described in this report. Decomposition processes already modeled in CE-QUAL-R1 would be affected by macrophyte contributions to existing detritus and sediment compartments. A flow diagram of the interactions of the new macrophyte compartment with other model compartments summarizes the proposed changes to CE-QUAL-R1 (Figure 1).

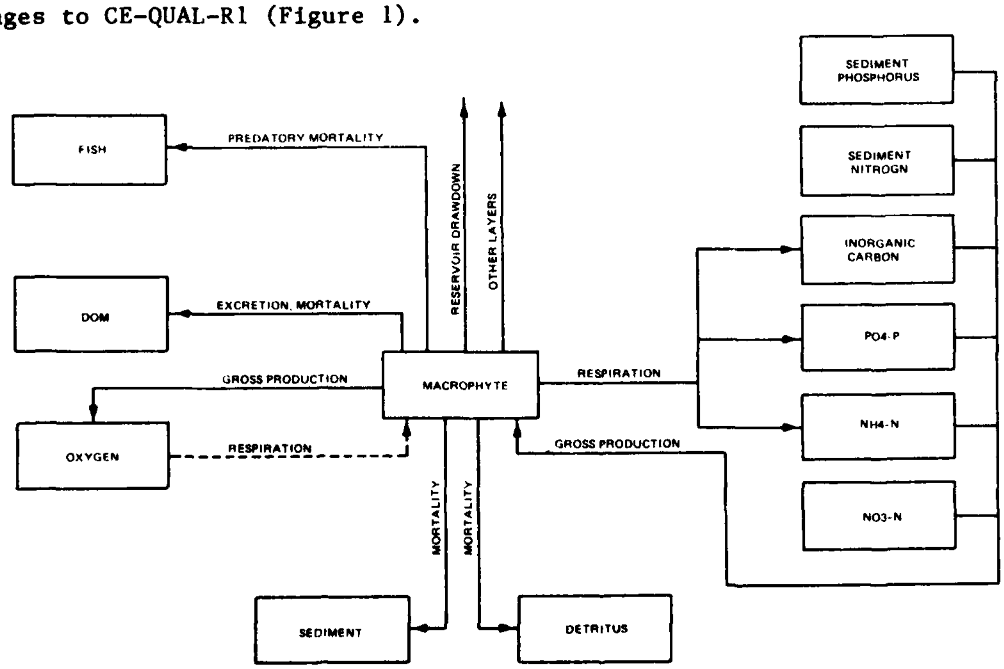

Figure 1. Compartment diagram of macrophyte model recommended for CE-QUAL-R1

Report composition

6. In the following section the specific physiological processes recommended for inclusion in a new macrophyte subroutine are formulated for incorporation into CE-QUAL-R1. Next, a geometric scheme for apportioning macrophyte biomass among model layers is discussed. The next major section contains recommendations for the simulation of macrophyte control measures (mechanical harvesting, herbicidal treatment). The next section discusses the validation of select process formulations based upon published data on two macrophyte species, *Myriophyllum spicatum* and *Hydrilla verticillata*. The final section summarizes the major recommendations contained in this report. Two appendices are also included. Appendix A presents equations included in a stand-alone version of the macrophyte submodel used in the process validation studies, while Appendix B lists representative values for parameters included in the proposed macrophyte submodel based on published research on *M. spicatum* and *H. verticillata*. The material contained in this report will be included in a final, revised edition of the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) scheduled for publication in 1985.

Recommended Physiologic Processes

7. The differential equation for the macrophyte state variable expresses conservation of mass in each horizontal model layer. The solution provides material concentrations as functions of time and depth. The equation is mathematically expressed as follows:

$$\begin{bmatrix}\text{rate of}\\ \text{change}\\ \text{of mass}\\ \text{g day}^{-1}\end{bmatrix} = \left[\begin{matrix}\text{macrophyte}\\ \text{biomass}\end{matrix} * \begin{matrix}\text{gross}\\ \text{production}\\ \text{rate}\end{matrix} - \begin{matrix}\text{dark}\\ \text{respiration}\\ \text{rate}\end{matrix} - \begin{matrix}\text{photorespiration}\\ \text{rate}\end{matrix} \right.$$

$$\left. - \begin{matrix}\text{grazing}\\ \text{rate}\end{matrix} - \begin{matrix}\text{nonpredatory}\\ \text{mortality}\\ \text{rate}\end{matrix} - \begin{matrix}\text{mechanical}\\ \text{or}\\ \text{chemical}\\ \text{harvesting}\\ \text{rate}\end{matrix}\right] \qquad (1)$$

Each of the individual terms in this equation is discussed in the subsections which follow. The style of presentation follows that contained in the

CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) which should be consulted for further details. The overall structure of CE-QUAL-R1 will not be presented here. Only those macrophyte process terms specifically included in the proposed new macrophyte submodel will be documented plus their interactions with other compartments in CE-QUAL-R1.

Macrophyte processes

8. Gross production. The daily photosynthetic or gross production rate is a function of temperature, light intensity, and nutrient concentration:

$$PLTGRO = PLTMAX * RMULT1(T) * RMULT2(T) * MIN(XLIMN,XLIMP,XLIMC) * XLIML \quad (2)$$

where

PLTGRO = photosynthetic rate, day^{-1}

PLTMAX = user-specified maximum photosynthetic rate, day^{-1}

RMULT1,2(T) = temperature limitation functions, unitless

XLIMN = limitation function for nitrogen, unitless

XLIMP = limitation function for phosphorus, unitless

XLIMC = limitation function for carbon, unitless

XLIML = limitation function for light intensity, unitless

9. Temperature limitation is calculated using the equations developed by Thornton and Lessem (1978):

$$RMULT1(T) = \begin{cases} 0 & T \le T_1 \\ \dfrac{K_1 e^{\lambda_1(T-T_1)}}{1 + K_1 e^{\lambda_1(T-T_1)} - 1} & T > T_1 \end{cases}$$

$$RMULT2(T) = \begin{cases} \dfrac{K_4 e^{\lambda_2(T_4-T)}}{1 + K_4 e^{\lambda_2(T_4-T)} - 1} & T < T_4 \\ 0 & T \ge T_4 \end{cases} \quad (3)$$

where

$$\lambda_1 = \frac{1}{T_2 - T_1} \ln \frac{K_2(1 - K_1)}{K_1(1 - K_2)}$$

$$\lambda_2 = \frac{1}{T_4 - T_3} \ln \frac{K_3(1 - K_4)}{K_4(1 - K_3)}$$

As is the case in the parent model CE-QUAL-R1, T_1 and T_4 represent the user-specified lower and upper lethal temperatures for the processes in question, while T_2 and T_3 (also user specified) define the range of optimum temperatures over which the process occurs at near the maximum rate (Environmental Laboratory 1982). The term T represents the computed temperature of a specific layer in the model CE-QUAL-R1. The corresponding user-specified K values define the relative rates (i.e., on a 0 to 1 basis) at which the process occurs at each of these temperatures.

10. Nutrient limitation is dependent upon the concentrations of nitrogen and phosphorus in the water column and sediment and on the carbon concentration in the water column. The nutrient determined to be limiting based upon the following Monod equation is used in the photosynthesis calculation (Equation 2):

$$XLIM(N,C,P) = \frac{C}{K_{1/2} + C} \tag{4}$$

where

$XLIM(N,C,P)$ = nutrient limitation function for nitrogen, carbon, and phosphorus, unitless

C = concentration of respective nutrient in the water column (N, C, P) or sediment (N, P), g m^{-3}

$K_{1/2}$ = user-specified half-saturation coefficient for the respective nutrient, g m^{-3}

The limiting nutrient is defined in this context as the one giving the minimum value of Equation 4.

11. Many nutrients used by freshwater submersed macrophytes, including both nitrogen and phosphorus, are obtained primarily through the roots from sediment (Best and Mantai 1978; Bole and Allan 1978; Carignan and Kalff 1980; DeMarte and Hartman 1974; Nichols and Kinney 1976). CE-QUAL-R1 has

APPENDIX A: MACROPHYTE MODEL STAND-ALONE VERSION

Introduction

1. A stand-alone version of the macrophyte model was developed to verify and validate several of the recommended process equations for a single model layer. This appendix provides a list of the state variable equations used in this version of the model. Seven compartments are represented by the model, including macrophytes, dissolved oxygen, particulate organic matter (POM), dissolved organic matter (DOM), phosphorus, nitrogen, and organic sediment. The individual process equations which together comprise the state variable equations are also described herein. A parameter list (Table A1) describes each of the parameters used in the process equations and the values used in running the stand-alone version.

2. The macrophyte process equations correspond to those given in the main body of this report (although several variable names have been changed in this version of the model). Equations for the other six state variables contain terms reflecting the impacts of macrophyte processes on other components of aquatic ecosystems. This stand-alone version of the model is appropriate for implementation on a microcomputer.

3. There are some differences between the stand-alone version of the model and that recommended for CE-QUAL-R1. For the stand-alone version, (a) it was assumed that macrophyte production was not nutrient limited, (b) contributions to nutrients from macrophyte respiration were not included, and (c) contributions to nutrients from macrophyte nonpredatory mortality are included. Additionally, CE-QUAL-R1 does not include harvesting as the stand-alone version does.

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Recommendations

31. It is recommended that the model for submersed aquatic plants described in this report be incorporated in the CE-QUAL-R1 model with due consideration of the following points:

- a. The light response function should permit representation of photoinhibition (this same algorithm should be used for algae in CE-QUAL-R1).
- b. Because nutrients are an explicit part of the photosynthesis algorithm, limitation should be based on the Monod function for the nutrient shown to be limiting using threshold ratios.
- c. The spatial relationships of the rooted zone of macrophytes to the model layers should be accounted for based on the intersection of model layers with the reservoir bottom, creating a two-dimensional array of cells for macrophyte computations; the macrophytes should be apportioned into the vertical layers based on cell-by-cell computations and a comparison with a user-specified maximum macrophyte density in each cell; this algorithm can also be used to determine the biomass of macrophytes cut by a mechanical harvester set at a particular depth.
- d. Chemical control can be modeled using dose-response relationships.

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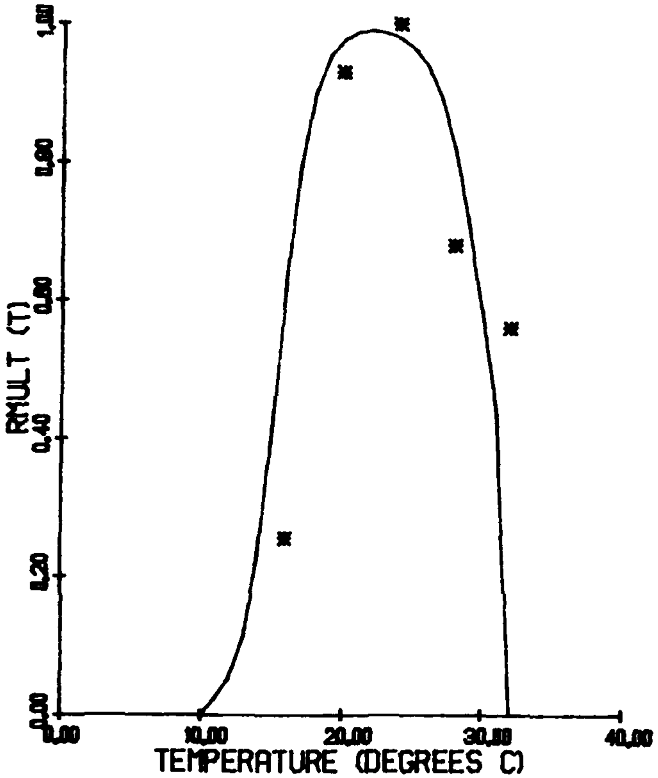

Figure 5. Process validation plot using the Thornton and Lessem (1978) equation, RMULT, as a temperature rate multiplier to predict the effect of temperature on photosynthetic rate. Asterisks represent normalized experimental results from Barko et al. (1980). Process parameter values are given in text

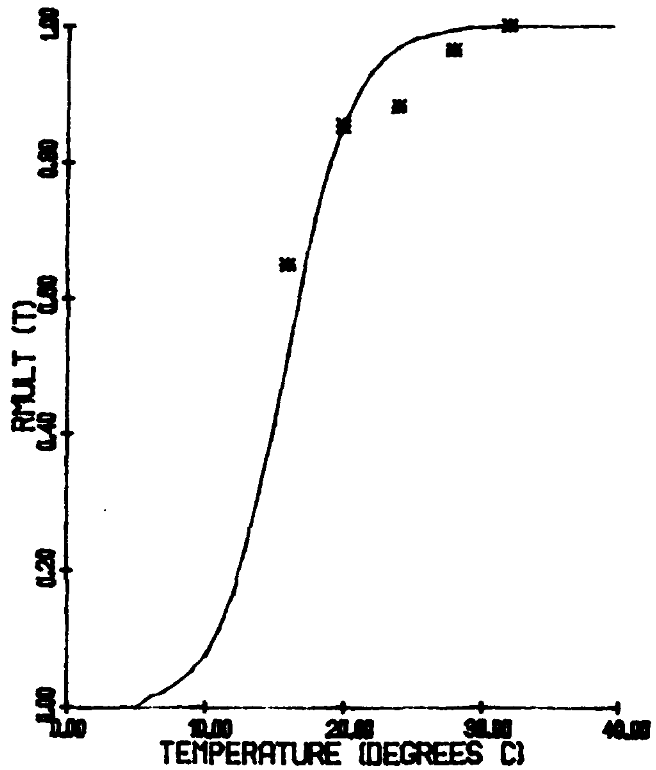

Figure 6. Process validation plot using the rising limb of the Thornton and Lessem (1978) equation, RMULT, as a temperature rate multiplier to predict the effect of temperature on dark respiration rate. Asterisks represent the normalized experimental results from Barko et al. (1980) for *H. verticillata*. Process parameter values are given in text

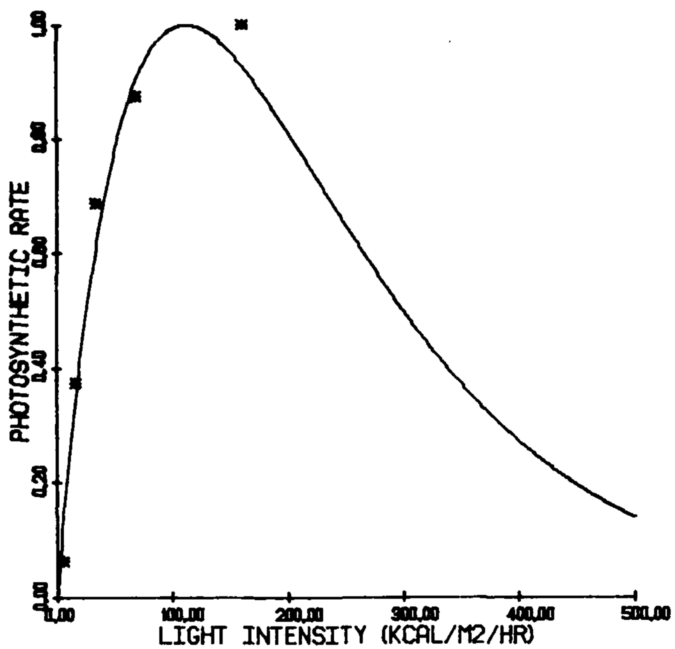

Figure 3. Process validation plot using Steele's (1962) equation to represent the photosynthetic light intensity response of *M. spicatum*. Asterisks represent normalized experimental results from Van, Haller, and Bowes (1976). Process parameter values are given in text

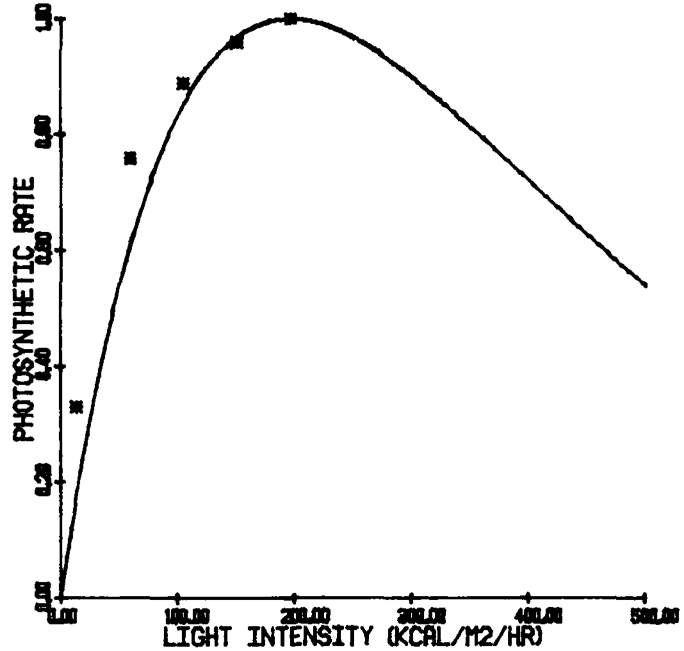

Figure 4. Process validation plot using Steele's (1962) equation to represent the photosynthetic light intensity response of *H. verticillata*. Asterisks represent normalized experimental results from Barko et al. (1980). Process parameter values are given in text

Depending on how the chemical control program is implemented, the macrophyte mass killed can be transferred as appropriate to other model compartments (detritus, sediment, dissolved organic matter).

Process Validation

27. Select process equations included in the proposed macrophyte submodel have been validated based on experimental results from the literature and published experimental results performed at the US Army Engineer Waterways Experiment Station by Dr. John Barko and colleagues. Data on two macrophyte species of particular interest to the Corps were used in this validation procedure, *M. spicatum* and *H. verticillata*. Results of validating several specific equations in the macrophyte model are discussed in the following paragraphs.

28. The equation used to represent the photosynthetic light response is that of Steele (1962) (see Equation 5 and Appendix B). Figures 3 and 4 demonstrate that this equation fits experimental data from Van, Haller, and Bowes (1976) for *M. spicatum* and from Barko et al. (1980) for *H. verticillata*. The parameter PISAT, which describes the saturating light intensity for photosynthesis, was set at 112 and 196 kcal m^{-2} hr^{-1}, respectively, for *M. spicatum* and *H. verticillata* (Appendix B). Photoinhibition at high light intensities can also be predicted using this equation. Although this type of response of these two species to high light intensities has not been observed, other species demonstrate photoinhibition which could be significant during reservoir drawdown.

29. The effect of temperature on photosynthesis is represented using the equation of Thornton and Lessem (1978) (Equation 3). Validation of this equation for *H. verticillata*, based on results of Barko et al. (1980), is demonstrated in Figure 5. The parameter values used in this equation are as follows: T1 = 10°C, T2 = 20°C, T3 = 24°C, T4 = 32°C, K1 = 0.01, K2 = 0.98, K3 = 0.98, and K4 = 0.30 (Appendices A and B).

30. Validation of the equation representing dark respiration (Equation 6) is represented in Figure 6 for *H. verticillata*. The parameter values used are as follows: T1 = 5°C, T2 = 25°C, K1 = 0.01, and K2 = 0.98 (Appendix B).

The index J ranges from 1 (top layer) up to a user-specified value indicating the maximum number of layers in which macrophytes can occur (actually, the maximum rooting depth in metres). If all the mass in that column can be contained in the bottommost cell, it is placed there. Otherwise, Equation 9 is iterated (i.e., the value of J is increased sequentially) until the calculated total macrophyte mass for that column is apportioned among cells in that column, such that the mass in each cell is less than or equal to the maximum calculated with Equation 9. The total macrophyte mass is then calculated for each model layer by summation, and for the entire reservoir.

Management Control Processes

25. In addition to ecological processes, the model can also simulate management control processes including mechanical harvesting and chemical control of the plants. Macrophyte mass removed by mechanical harvesting is a function of plant rooting depth and mass density as well as the cutting depth of the mechanical harvester. Having determined macrophyte biomass in each model layer, the amount cut (MBIOCUT) by a mechanical harvester set at a particular cutting depth (CUTZ) can be calculated by summation. If the cutting depth falls between layer boundaries, then an appropriate fraction of the macrophyte mass in that layer can be removed since mass is assumed to be distributed homogeneously within layers.

26. Chemical control is a function of the following dose-response curve for the herbicide used:

$$MCHEM(I) = MACRO(I) * CHEM/(LC50 + CHEM) \tag{10}$$

where

MCHEM(I) = macrophyte biomass killed in layer I, g

MACRO(I) = total macrophyte biomass in layer I, g

CHEM = user-specified ambient environmental concentration of herbicide applied, $\mu g \ \ell^{-1}$

LC50 = user-specified herbicide concentration which will kill 50 percent of the macrophytes, $\mu g \ \ell^{-1}$

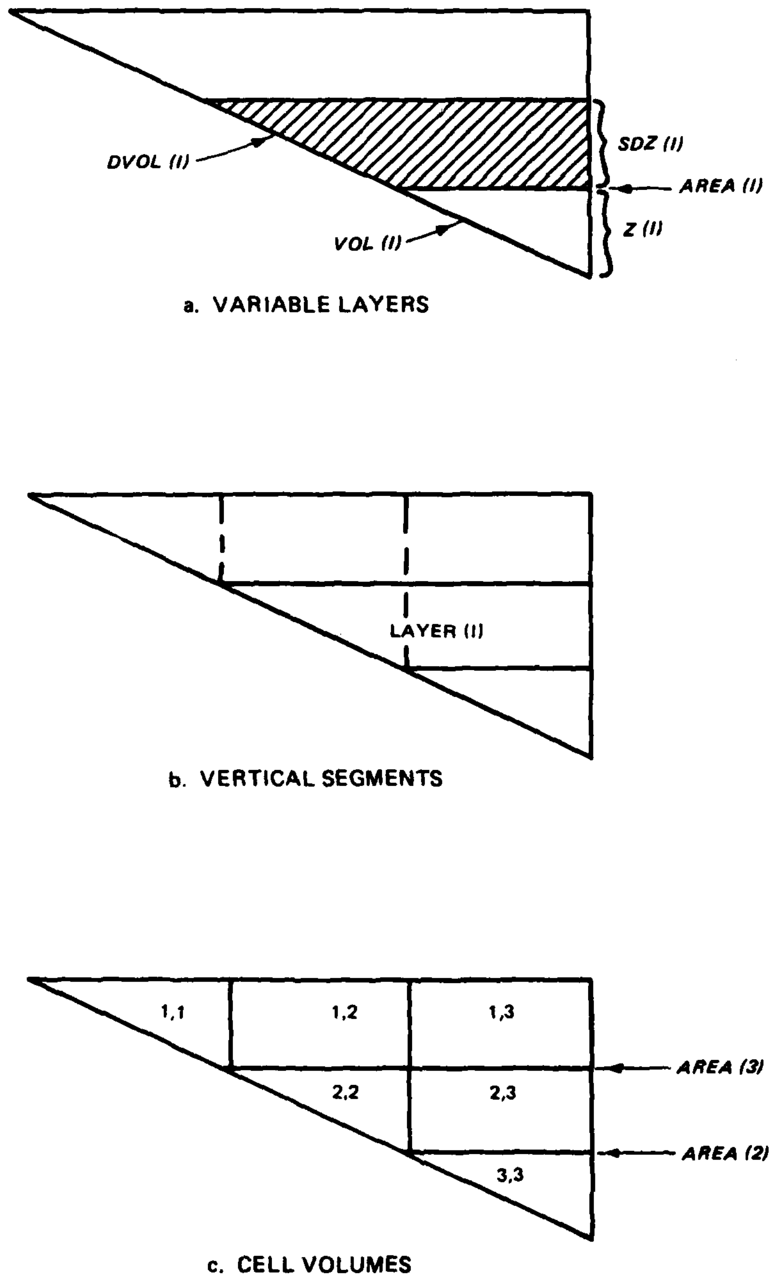

Figure 2. Model structure for macrophyte distribution

the Ith layer. The actual volume of the Ith layer, DVOL(I), is calculated as the difference between VOL(I+1) and VOL(I). Both volume and area are typically represented as power functions of elevation.

23. Using this scheme, a series of vertical segments or columns can be superimposed at the points at which boundary layers intersect the reservoir bottom (Figure 2b), creating a series of two-dimensional cells for macrophyte computations (Figure 2c). To simplify the computational sequence, these cells are numbered from the reservoir surface down, and from upstream toward the dam. A given cell is indexed (i,j) with i referring to row position and j to column. Because each of the layers in the model representation of a reservoir is extremely long and thin, the bottom surface area in which macrophytes root can be approximated as the difference AREA(I+1) - AREA(I). Similarly, the volume of each computational cell can be approximated as this bottom surface area times the thickness (SDZ) of the layer in which that cell occurs. These bottom areas and cell volumes are used in macrophyte computations as described in the following paragraph.

24. Macrophytes are associated with the bottom sediments in which they are rooted and with the overlying water column. In order to determine how macrophyte mass is apportioned among the cells in a given vertical column, the assumption is made that the volumetric density of macrophyte dry mass cannot exceed a user-specified maximum value (PLDENS, g m^{-3}). At each model time step, the macrophyte differential equation (Equation 1) is solved on a cell-by-cell basis using a simple Euler procedure and the mass is calculated at the previous time step as an initial value. Then macrophyte mass is summed over all cells in a given column. Beginning with the bottommost cell (i.e., the one nearest the sediment), this summed mass is apportioned among cells by comparing it with the maximum mass which each cell can contain. For cells in the Ith column, this maximum is calculated as

$$\mathrm{DATA(J,I) = PLDENS * SDZ(J) * (AREA(I+1) - AREA(I))} \qquad (9)$$

where

DATA(J,I) = maximum macrophyte mass which can be contained in the cell in layer J and column I, g

PLDENS = user-specified maximum macrophyte volumetric density, g m^{-3}

SDZ(J) = thickness of Jth model layer, m

AREA(I) = bottom surface area at layer I, m^2

coefficients are involved. In a similar manner, grazing represents a direct transfer of mass to fish, without conversion. As a consequence of nonpredatory mortality, macrophyte biomass is transferred to dissolved organic matter, detritus, and sediment compartments. The "dead" biomass is apportioned between the three receiver compartments based on user-specified coefficients.

20. Included in Appendix A is a stand-alone version of the macrophyte model which was used in validating the various process equations just discussed. In addition to containing the equations describing macrophyte physiological processes (Equations 1-8), this version of the model also contains equations for oxygen, particulate organic matter, dissolved organic matter, phosphorus, nitrogen, and sediment. This model thus illustrates the way in which macrophyte terms enter into equations for other water quality constituents included in CE-QUAL-R1. In Appendix B, representative values for the parameters included in Equations 1-8 of the macrophyte model (as defined in Appendix A) are listed, based on research on two macrophyte species of particular interest, *Myriophyllum spicatum* and *Hydrilla verticillata*. CE-QUAL-R1-related parameters and coefficient values are also listed in Appendix B.

Spatial Relationships

21. In order to describe vertical growth of macrophytes in a one-dimensional, variable-layer model like CE-QUAL-R1, it was necessary to devise a means of geometrically segmenting the model into a matrix of rows (layers) and columns. This matrix defines the volume of each segment and the proximity of one segment to another. A description of how the matrix can be incorporated into the CE-QUAL-R1 model follows.

22. CE-QUAL-R1 is a one-dimensional model with multiple layers. Thermal energy and materials are assumed to be uniformly distributed within each model layer. Reservoir morphometry is represented in the model by a variable-layer approach (i.e., layer dimensions vary over time based on inflows and cutflows and on user-specified morphometric relationships of area and volume to elevation above the reservoir bottom). Relationships among elevation, area, and volume are depicted in Figure 2a. A given layer (numbered I, from the bottom up) is specified as being Z(I) metres above the bottom and SDZ(I) metres thick. The area of the Ith layer, AREA(I), is defined at the lower boundary of that layer. A volume, VOL(I), is also defined up to the lower surface of

calculated as the product of the two temperature limitation functions, RMULT1 and RMULT2 (Equation 3), times a user-specified maximum fish grazing rate, times a Monod function similar in form to Equation 4. In this fish-grazing limitation function, the role of C (Equation 4) is played by the sum, over all types of food (including macrophytes) ingested by fish, of products of a user-specified preference factor for that food type and the concentration of that food type. For this grazing function, $K_{1/2}$ (in Equation 4) would again be a user-specified half-saturation coefficient for fish grazing. The reader should consult the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) for further details. An additional preference factor would need to be included in the model, specifying the fractional preference of fish for macrophytes.

Interactions with other compartments in CE-QUAL-R1

18. As depicted in Figure 1, those macrophyte processes discussed above also impact a variety of other compartments in CE-QUAL-R1. Thus, corresponding to the process equations given above (Equations 1-8), terms will need to be added to or subtracted from other equations in the model. These terms represent the addition or removal of mass to or from other compartments in the modeled reservoir. These terms will be briefly described here. Although the actual equations will not be provided, they correspond exactly to the form of the equations listed previously.

19. As a result of macrophyte photosynthetic processes, oxygen is evolved. This is modeled as an "equivalent oxygen concentration," calculated as the product at the gross production rate of concentration and a user-specified oxygen-to-biomass stoichiometric coefficient, which is added directly to the oxygen differential equation. Similarly, dark respiration removes oxygen. This removal, a subtraction from the oxygen equation, is calculated as the product of the dark respiration rate of concentration and another user-specified stoichiometric coefficient. Gross production and respiration also result in the uptake and release, respectively, of nutrients (N, P, C) from and to the water column and sediments (Figure 1). These transfers are calculated as the product of the production and respiration rates of concentration and user-specified nutrient-to-biomass stoichiometric coefficients. Photorespiration represents a direct addition of mass to the ammonia-nitrogen, phosphorus, and dissolved organic matter compartments; no conversion

mathematically using only the rising limb of the temperature equation of Thornton and Lessem (1978) (Equation 3):

$$MRESP = MKRESP * RMULT1(T) \tag{6}$$

where

MRESP = dark respiration rate, day^{-1}

MKRESP = user-specified maximum dark respiration rate, day^{-1}

15. Photorespiration. Photorespiration or excretion is important because it results in the phenomenon known as "nutrient pumping," whereby nutrients are transferred from bottom sediments to water. This process also increases the amount of organic matter dissolved in the water column. Excretion is a function of light intensity. Under conditions of very high or very low light intensities, the rate of extracellular release increases. Mathematically this is represented as

$$MEXCR = (1 - XLIML) * MKEXCR \tag{7}$$

where

MEXCR = excretion rate, day^{-1}

MKEXCR = user-specified maximum excretion rate, day^{-1}

16. Nonpredatory mortality. Nonpredatory mortality is temperature-dependent when the change in temperature (increase or decrease) over a 7-day period exceeds a critical maximum temperature TMPMAX . Therefore, if $|TMPTUR(1) - TMPTUR(7)| > TMPMAX$:

$$MMORT = MKMORT \tag{8}$$

where

TMPTUR(1) and TMPTUR(7) = water temperature over 7-day period, °C

TMPMAX = maximum temperature change, °C

MMORT = nonpredatory mortality rate, day^{-1}

MKMORT = user-specified maximum nonpredatory mortality rate, day^{-1}

17. Grazing. Grazing of macrophytes by fish is modeled with the same type of grazing function as used in CE-QUAL-R1. Thus, the grazing rate is

compartments representing sediment nitrogen and phosphorus; therefore, limitation of nutrients obtained through the roots can occur, although this is rare in nature. This process is most important in allowing "nutrient pumping" from the sediments into the water column.

12. In some cases where nutrient concentrations in the water are high, it becomes advantageous for the plant to draw nutrients from the water column. In water with a phosphorus concentration of 2.0 mg ℓ^{-1}, characteristic of eutrophic reservoirs, *Myriophyllum spicatum* took phosphorus from the water column (Bole and Allan 1978). This is modeled using a species-specific parameter to indicate the water concentration above which nutrients are taken from the water column. Whenever the water column concentration of nitrogen or phosphorus equals or exceeds this user-specified concentration, it is the water concentration of that nutrient which is entered into the Monod equation (Equation 4). Otherwise, it is the sediment concentration of nitrogen or phosphorus which is used in Equation 4.

13. Light limitation is represented using Steele's equation (1962):

$$XLIML = \left(\frac{0.5 * SWSA}{PISAT}\right) \exp\left[1 - \left(\frac{0.5 * SWSA}{PISAT}\right)\right] \tag{5}$$

where

SWSA = average irradiance for a specific model layer, kcal m^{-2} hr^{-1} (calculated in Subroutine HEAT in CE-QUAL-R1)

PISAT = user-specified irradiance level at which the photosynthetic rate is saturated (i.e., occurs at maximum rate), kcal m^{-2} hr^{-1}

The coefficient value 0.5 is used in Steele's equation to represent the fraction of total irradiance that is photosynthetically active radiation (PAR). PAR is in the range of 400 to 700 nm. Steele's equation can predict photoinhibition of photosynthesis at high light intensities, above the level specified by PISAT. Solar radiation is distributed vertically in the water column in CE-QUAL-R1 based upon the extinction coefficient for water. Light is also attenuated by self-shading by algae, zooplankton, detritus, and suspended solids. An additional self-shading coefficient should be included in the model to account for the effect of macrophyte biomass on light attenuation.

14. <u>Dark respiration</u>. Dark respiration is a function of temperature. As with other respiratory rates in CE-QUAL-R1, it is represented

State Variable Equations*

Macrophyte

$\dot{\mathrm{MACRO}}$ = MPROD - MRESP - MEXCR - MMORT - MHVST

macrophyte = photosynthesis - dark respiration - excretion (photo-respiration) - mortality - harvesting

Oxygen

$\dot{\mathrm{OXYGEN}}$ = OTST + OMAC - ANIT - OPDK - ODDK - OSDK

Oxygen = oxygen saturation + contribution from macrophytes - equivalent loss from nitrogen decay - equivalent loss from POM decay - equivalent loss from DOM decay - equivalent loss from sediment decay

Particulate organic matter

$\dot{\mathrm{POM}}$ = PMAC - PDK - PSTL

POM = contribution from macrophyte mortality and harvesting - loss from POM decay - loss from settling

Dissolved organic matter

$\dot{\mathrm{DOM}}$ = DMAC + DEXCR + DDK - DBAC

DOM = contribution from macrophyte mortality and harvesting + contribution from macrophyte excretion + contribution from POM decay - loss from bacterial respiration

Phosphorus (water column)

$\dot{\mathrm{PO4}}$ = FMAC + FDK + FEXCR - FSINK

PO4 = contribution from macrophyte mortality and harvesting + contribution from decay of POM and sediments + contribution from macrophyte excretion - loss to algal production

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* Each equation represents the time rate of change of the state variable for a model layer. The units of MACRO are grams per square metre per day per model layer. The units of all other state variables are grams per square metre per day per metre of model layer.

Nitrogen (water column)

$\dot{N}$ = NMAC + NDK + NEXCR - NSINK

N = contribution from macrophyte mortality and harvesting
+ contribution from decay of POM and sediments
+ contribution from macrophyte excretion - loss to algal production

Organic sediment

$\dot{SED}$ = SMAC - SDK

SED = contribution from macrophyte mortality and harvesting
- loss from sediment decay

Process Equations

Macrophyte

$$MPROD = PMAX * RMULT1(T) * RMULT2(T) * LIGHT * MACRO$$

where

PMAX = maximum photosynthetic rate, day^{-1}

RMULT1(T) = temperature limitation function, unitless

RMULT2(T) = temperature limitation function, unitless

T = ambient water temperature, °C

LIGHT = light limitation function, unitless

MACRO = macrophyte biomass, g m^{-2}

$$LIGHT = \frac{e}{\varepsilon(Z2-Z1)}\left\{ e^{\left[\frac{(-0.5\cdot IO)}{ISAT}\, e^{-\varepsilon Z2}\right]} - e^{\left[\frac{(-0.5\cdot IO)}{ISAT}\, e^{-\varepsilon Z1}\right]} \right\}$$

where

ε = extinction coefficient

Z2 = depth at the bottom of the simulated section, m

Z1 = depth at the top of the simulated section, m

IO = irradiance at the water surface, kcal m^{-2} sec^{-1}

ISAT = saturating irradiance for photosynthesis, kcal m^{-2} sec^{-1}

$$MRESP = KRESP * RMULT1(T) * MACRO$$

where

KRESP = user-specified maximum respiration rate, g g^{-1} day^{-1}

$$MEXCR = KEXCR * (1-LIGHT) * MACRO$$

where

KEXCR = user-specified maximum excretion rate, g g^{-1} day^{-1}

If, $|TMPTUR(1) - TMPTUR(7)|$ is greater than TMPMAX, then

$$MMORT = KMORT * MACRO$$

where

KMORT = nonpredatory mortality rate, g g^{-1} day^{-1}

TMPMAX = critical maximum temperature difference over a 7-day period, °C

TMPTUR(1) and TMPTUR(7) = water temperatures over a 7-day period, °C

$$MHVST = CHEM * MACRO$$

where

CHEM = rate of die-off of macrophyte dependent upon type of chemical used, g g^{-1} day^{-1}

NOTE: Mechanical harvesting is calculated outside the differential equation as follows:

$$MWH \div MACRO = MHT$$
$$Z - MHT = TPLT$$
$$CUTZ - TPLT = MCUT$$
$$MWH \div MCUT = MBIOCUT$$

where

MWH = species-specific weight-to-height ratio, g m^{-1}

MHT = macrophyte height, m

Z = depth of water column, m

TPLT = top of plant, m

CUTZ = cutting depth of mechanical harvester, m

MCUT = amount of macrophyte cut, m

MBIOCUT = biomass of macrophyte cut, g m^{-2}

<u>Oxygen</u>

OTST = (14.6 * exp(-(0.027767 - 0.00027 * T
+ 0.000002 * T * T) * T)) * Z

OMAC = (OMACEQ1 * MPROD) - (OMACEQ2 * MRESP)

ANIT = ONEQ * NMAC

OPDK = OPEQ * PDK

ODDK = ODEQ * DDK

OSDK = OSEQ * SDK

<u>Particulate organic matter</u>

PMAC = (MMORT * M1) + (MHVST * H1)

PDK = KPOM * POM * RMULT1(T)

PSTL = (PMSTL * MMORT) + (PHSTL * MHVST)

KPOM = 0.01192 * 1/NTC(2) + 0.00672

<u>Dissolved organic matter</u>

DMAC = (MMORT * M2) + (MHVST * H2)

DEXCR = MEXCR * E2

DDK = PDK * P2

DBAC = KDOM * DOM * RMULT1(T)

KDOM = 0.024 * 1/NTC(3) + 0.0192

<u>Phosphorus</u>

FMAC = (MMORT * M3) + (MHVST * H3)

FDK = (PDK * P3) + (SDK * S3)

FEXCR = MEXCR * E3

FSINK = photoplankton biomass * FRS

Nitrogen

NMAC = (MMORT * M4) + (MHVST * H4)

NDK = (PDK * P4) + (SDK * S4)

NEXCR = MEXCR * E4

NSINK = photoplankton biomass * NRS

Sediments

SMAC = (MMORT * M5) + (MHVST * H5)

SDK = KSED * SED * RMULT1(T)

KSED = 0.00519 * 1/NTC(4) + 0.00346

Table A1

Stand-Alone Version Macrophyte Model Parameter List

Parameter	Parameter Description	Value	Reference
Z	Depth of water column, m	Specified by user	
CHEM	Chemical dependent rate of macrophyte die-off, g g^{-1} day^{-1}	Specified by user	
CUTZ	Cutting depth of mechanical cutter, m	Specified by user	
TMPMAX	Critical maximum temperature difference for nonpredatory mortality, °C	5	Boylen, unpublished data
ISAT	Saturating light intensity for photosynthesis, kcal m^{-2} sec^{-1}	112 196	Van, Haller, and Bowes (1976) Barko et al. (1980)
KEXCR	Excretion rate for macrophyte, g g^{-1} day^{-1}	0.023 0.017	Stanley and Naylor (1972) Bowes et al. (1977)
KMORT	Mortality rate for macrophyte, g g^{-1} day^{-1}	0.001	Calibrated
KSED	Decay rate for sediment, g g^{-1} day^{-1}	0.001 - 0.015	Hargrave (1972)
KPOM	Decay rate for POM, g g^{-1} day^{-1}	0.007 - 0.06 dead mixed algae 0.002 - 0.007 Potomogeton	Fitzgerald (1964) Hanlon (1972)
KRESP	Respiration rate for macrophyte, g g^{-1} day^{-1}	0.027 0.016 - 0.039	Bowes et al. (1977) McGahee and Davis (1971)
KDOM	Decay rate (bacterial respiration) for DOM, g g^{-1} day^{-1}	0.238	Carpenter (1980)
PMAX	Maximum photosynthetic rate, g g^{-1} day^{-1}	0.48 - 0.6 0.02 - 0.6	Van, Haller, and Bowes (1976); Ikusima (1965) Adam, Titus, and McCracken (1974)
ONEQ	Oxygen equivalent for nitrogen decay or mineralization, unitless	3.43	Calculated
OPEQ	Oxygen equivalent for POM mineralization or decay, unitless	1.3	Jewell (1971)
ODEQ	Oxygen equivalent for DOM mineralization or decay, unitless	1.3	Jewell (1971)
OSEQ	Oxygen equivalent for sediment mineralization or decay, unitless	1.3	Jewell (1971)

(Continued)

Table A1 (Continued)

Parameter	Parameter Description	Value	Reference
OMACEQ	Oxygen equivalent for macrophyte photosynthesis and respiration, unitless	1.0 1.2	Brylinsky and Mann (1973) Strickland (1960)
PMSTL	Mortality fraction of POM that sediments	20 to 50%	Calibrated
PHSTL	Harvested fraction of POM that sediments	10 to 40%	Calibrated
NRS	Nitrogen uptake rate by phytoplankton, $g\ g^{-1}\ day^{-1}$	0.012 to 0.035	Healey (1976)
PRS	Phosphorus uptake rate by phytoplankton, $g\ g^{-1}\ day^{-1}$	0.3 to 0.6	Healey and Hendzel (1975)
M1	Fraction of dying macrophyte that goes to POM, unitless	29%	Godshalk and Wetzel (1978)
M2	Fraction of dying macrophyte that goes to DOM, unitless	1 to 10%	Wetzel and Manny (1975)
M3	Fraction of dying macrophyte that goes to phosphorus, unitless	0.13 to 0.60%	Wile (1978)
M4	Fraction of dying macrophyte that goes to nitrogen, unitless	1.2 to 2.8%	Wile (1978)
M5	Fraction of dying macrophyte that goes to sediment, unitless	18%	Carpenter (1976)
H1	Fraction of harvested macrophyte that goes to POM, unitless	Specified by user; dependent on harvesting method	
H2	Fraction of harvested macrophyte that goes to DOM, unitless		
H3	Fraction of harvested macrophyte that goes to phosphorus, unitless		
H4	Fraction of harvested macrophyte that goes to nitrogen, unitless		
H5	Fraction of harvested macrophyte that goes to sediment, unitless		

(Continued)

Table A1 (Continued)

Parameter	Parameter Description	Value	Reference
E2	Fraction of excretion that goes to phosphorus, unitless	4 to 6% *Egeria densa* 7 to 29% *Hydrilla verticillata* 1 to 4% *Myriophyllum spicatum*	Barko and Smart (1980)
E3	Fraction of excretion that goes to nitrogen, unitless	11%	Wetzel and Manny (1975)
E4	Fraction of excretion that goes to DOM, unitless	1 to 10%	Wetzel and Manny (1975)
P2	Fraction of decaying POM that goes to DOM, unitless	15 to 46%	Godshalk and Wetzel (1978)
P3	Fraction of decaying POM that goes to phosphorus, unitless	0.12%	de la Cruz and Gabriel (1974)
P4	Fraction of decaying POM that goes to nitrogen, unitless	0.40%	de la Cruz and Gabriel (1974)
S3	Fraction of decaying sediment that goes to phosphorus, unitless	0.10 to 0.15%	Calibrated
S4	Fraction of decaying sediment that goes to nitrogen, unitless	0.40 to 1.0%	Calibrated
MACRO	Initial macrophyte biomass, $g\ m^{-2}$	Specified by user	
OXY	Initial oxygen concentration, $g\ m^{-3}$		
POM	Initial POM concentration, $g\ m^{-3}$		
DOM	Initial DOM concentration, $g\ m^{-3}$		
P	Initial phosphorus concentration, $g\ m^{-3}$		
N	Initial nitrogen concentration, $g\ m^{-3}$		
SED	Initial sediment concentration, $g\ m^{-3}$		
K1	Temperature rate factor for photosynthesis and respiration at $T = T_1$	0.01	Calibrated
K2	Temperature rate factor for photosynthesis and respiration at $T = T_2$	0.98	Calibrated

(Continued)

Table A1 (Concluded)

Parameter	Parameter Description	Value	Reference
K3	Temperature rate factor for photosynthesis at $T = T_3$	0.98	Calibrated
K4	Temperature rate factor for photosynthesis at $T = T_4$	0.30	Calibrated
T1	Critical low temperature for photosynthesis and respiration, °C	10°C	Barko et al. (1980); Van, Haller and Bowes (1976)
T2	Optimum low temperature for photosynthesis and respiration, °C	16°C 20°C	Van, Haller, and Bowes (1976) Barko et al. (1980)
T3	Optimum high temperature for photosynthesis, °C	24°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis, °C	32°	Barko et al. (1980)
MWH	Species-specific weight-to-height ratio, g m^{-1}	0.78 2.40	Boylen, unpublished data Miller (1981)
NTC(1)	Nitrogen to carbon ratio for macrophytes	0.03 to 0.08	Godshalk and Wetzel (1978)
NTC(2)	Nitrogen to carbon ratio for POM	0.05	Harrison and Mann (1975)
NTC(3)	Nitrogen to carbon ratio for DOM	0.09 to 0.16	Otsuki and Hanya (1972)
NTC(4)	Nitrogen to carbon ratio for sediments	0.06 to 0.16	Olah (1972)

(Sheet 4 of 4)

APPENDIX B: MACROPHYTE MODEL PARAMETER LIST

Tabulated in Table B1 in this Appendix are values for specific parameters included in the state variable and process equations which comprise the macrophyte model proposed in the main body of this report (as intended for inclusion in CE-QUAL-R1). These values were either derived from published literature sources or established in the process validation studies described earlier. Most values tabulated here apply to one or two macrophyte species of interest, *Myriophyllum spicatum* or *Hydrilla verticillata*.

Table B1

Macrophyte Model Parameter List Recommended for CE-QUAL-R1

Parameter	Description	Species	Value	Converted Value	Reference
PISAT	Saturating light intensity for photosynthesis	*M. spicatum*	600 $\mu E\ m^{-2}\ sec^{-1}$	112 $kcal\ m^{-2}\ hr^{-1}$	Van, Haller, and Bowes (1976)
PISAT		*M. spicatum*	1050 $\mu E\ m^{-2}\ sec^{-1}$	196 $kcal\ m^{-2}\ hr^{-1}$	Barko et al. (1980)
PISAT		*H. verticillata*	600 $\mu E\ m^{-2}\ sec^{-1}$	112 $kcal\ m^{-2}\ hr^{-1}$	Van, Haller, and Bowes (1976)
PLTMAX	Maximum photosynthetic rate	*M. spicatum*	3.3 $\mu mole\ CO_2\ mg\ chl^{-1}\ hr^{-1}$	0.04 $g\ g^{-1}\ hr^{-1}$	Van, Haller, and Bowes (1976)
PLTMAX		*M. spicatum*	0.8 - 4.6 $\mu mole\ CO_2\ mg\ chl^{-1}\ hr^{-1}$	0.09 - 0.05 $g\ g^{-1}\ hr^{-1}$	Adams, Titus, and McCracken (1974)
PLTMAX		*H. verticillata*	4.6 $\mu mole\ CO_2\ mg\ chl^{-1}\ hr^{-1}$	0.05 $g\ g^{-1}\ hr^{-1}$	Van, Haller, and Bowes (1976)
PLTMAX		*H. verticillata*	5 $mg\ CO_2\ g^{-1}\ hr^{-1}$	0.05 $g\ g^{-1}\ hr^{-1}$	Ikusima (1965)
MKRESP	Dark respiration	*M. spicatum*	2.5 $\mu mole\ CO_2\ g^{-1}\ hr^{-1}$	0.027 $g\ g^{-1}\ hr^{-1}$	Bowes et al. (1977)
MKRESP	Dark respiration	*H. verticillata*	1.5 - 3.6 $\mu moles\ mg\ chl^{-1}\ hr^{-1}$	0.016 - 0.039 $g\ g^{-1}\ hr^{-1}$	McGahee and Davis (1971)
MKEXCR	Photorespiration rate	*M. spicatum*	0.023 $g\ g^{-1}\ hr^{-1}$	0.023 $g\ g^{-1}\ hr^{-1}$	Stanley and Naylor (1972)
MKMORT	Nonpredatory mortality rate			0.001 $g\ g^{-1}\ hr^{-1}$	Calibrated

(Continued)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
TMPMAX	Maximum 7-day temperature change for non-predatory mortality			5°C	Boylen, unpublished data
T1	Critical low temperature for photosynthesis	*M. spicatum*	10°C	10°C	Van, Haller, and Bowes (1976)
T1	Critical low temperature for photosynthesis	*H. verticillata*	10°C	10°C	Barko et al. (1980)
T2	Low optimum temperature for photosynthesis	*M. spicatum*	16°C	16°C	--
T2	Low optimum temperature for photosynthesis	*H. verticillata*	20°C	20°C	Barko et al. (1980)
T3	High optimum temperature for photosynthesis	*M. spicatum*	35°C	35°C	--
T3	High optimum temperature for photosynthesis	*H. verticillata*	24°C	24°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis	*M. spicatum*	44°C	44°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis	*H. verticillata*	32°C	32°C	Barko et al. (1980)

(Continued)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
K1	Temperature rate multiplier for photosynthesis	*M. spicatum*	0.01	0.01	Calibrated
K1	Temperature rate multiplier for photosynthesis	*H. verticillata*	0.01	0.01	
K2		*M. spicatum*	0.98	0.98	
K2		*H. verticillata*	0.98	0.98	
K3		*M. spicatum*	0.98	0.98	
K3		*H. verticillata*	0.98	0.98	
K4		*M. spicatum*	0.28	0.28	
K4		*H. verticillata*	0.30	0.30	
T1	Critical low temperature for dark respiration	*M. spicatum*	5°C	5°C	
T1	Critical low temperature for dark respiration	*H. verticillata*	5°C	5°C	
T2	Low optimum temperature for dark respiration	*M. spicatum*	20°C	20°C	
T2	Low optimum temperature for dark respiration	*H. verticillata*	25°C	25°C	

(Continued)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
K1	Temperature multiplier for respiration	*M. spicatum*	0.01	0.01	Calibrated
K1		*H. verticillata*	0.01	0.01	
K2		*M. spicatum*	0.98	0.98	
K2		*H. verticillata*	0.98	0.98	
HTW	Average height-to-weight ratio	*M. spicatum*	1.27 m g^{-1}	1.27 m g^{-1}	Boylen, unpublished data
HTW	Average height-to-weight ratio	*H. verticillata*	0.416 m g^{-1}	0.416 m g^{-1}	Miller (1981)
O2FAC	Oxygen equivalent for macrophyte photosynthesis	*M. spicatum*	1.0	1.0	Brylinsky and Mann (1973)
O2RESP	Oxygen equivalent for macrophyte dark respiration	*M. spicatum*	1.2	1.2	Strickland (1960)
PLXGO(1)	Fraction of excreted matter released as PO_4-P	*M. spicatum*	1 - 4%	0.01 - 0.04	Barko and Smart (1980)
PLXGO(1)	Fraction of excreted matter released as PO_4-P	*H. verticillata*	7 - 29%	0.07 - 0.29	Barko and Smart (1980)

(Continued)

(Sheet 4 of 5)

Table B1 (Concluded)

Parameter	Description	Species	Value	Converted Value	Reference
PLXGO(2)	Fraction of excreted matter released as NH_4-N		11%	0.11	Wetzel and Manny (1975)
PLXGO(3)	Fraction of excreted matter released as dissolved organic matter (DOM)		1 - 10%	0.01 - 0.10	Wetzel and Manny (1975)
PLDIGO(1)	Fraction of dead macrophyte that goes to DOM		1 - 10%	0.01 - 0.10	Wetzel and Manny (1975)
PLDIGO(2)	Fraction of dead macrophyte that goes to detritus		29%	0.29	Godshalk and Wetzel (1978)
PLDIGO(3)	Fraction of dead macrophyte that goes to sediment		18%	0.18	Carpenter (1976)

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