COEFFICIENTS FOR USE IN THE U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE·QUAL·R1

ARMY ENGINEER WATERWAYS EXPERIMENT STATION, VICKSBURG, MS. ENVIRONMENTAL LAB

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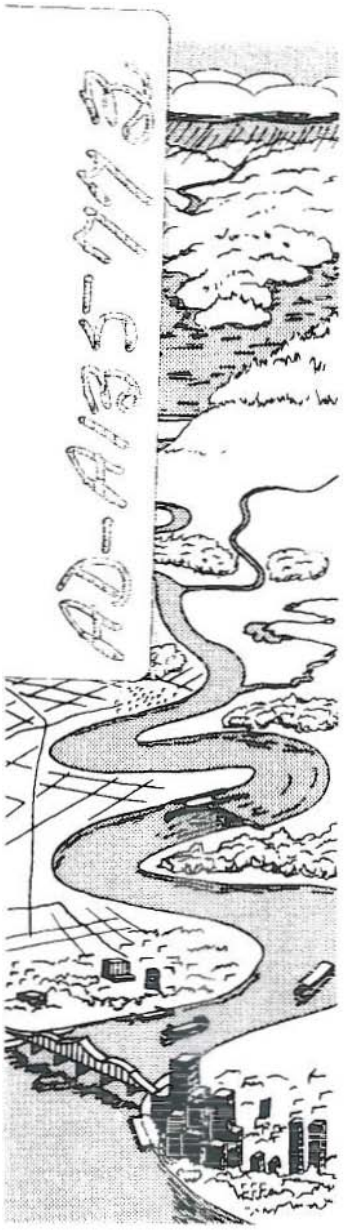

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COEFFICIENTS FOR USE IN THE U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE-QUAL-R1

by

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This report supplies information about, and literature values for, many of the coefficients needed for the U. S. Army Corps of Engineers Reservoir Model, CE-OUAL-Rl. Most of the information presented concerns biological processes of gross production, ingestion, respiration, mortality, and decomposition. Coefficients specified are suitable for the algorithms described in the

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PREFACE

This report was sponsored by the Office, Chief of Engineers (OCE), U. S. Army, as part of the Environmental Water Quality and Operational Studies (EWQOS) Work Unit IB.1 entitled Improved Description of Reservoir Ecological and Water Quality Processes. OCE Technical Monitors for EWQOS were Mr. John Bushman, Mr. Earl Eiker, and Mr. James L. Gottesman.

Work for this report was conducted during the period January 1982-September 1982 by Dr. Carol D. Collins and Dr. Joseph H. Wlosinski, Water Quality Modeling Group (WQMG) of the Environmental Laboratory (EL), U. S. Army Engineer Waterways Experiment Station (WES). The draft report was reviewed by Mr. Jack Waide and Drs. Allan Lessem and John Barko, all of EL.

The study was conducted under the direct supervision of Mr. Aaron Stein, Acting Chief, WQMG, and under the general supervision of Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and Dr. John Harrison, Chief, EL, WES. Program Manager of EWQOS was Dr. Jerome L. Mahloch, EL.

Commander and Director of WES during this study and the preparation of this report was Col. Tilford C. Creel, CE. Technical director was Mr. F. R. Brown.

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COEFFICIENTS FOR USE IN THE U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE-QUAL-R1

PART I: INTRODUCTION

Background

1. A numerical one-dimensional model (CE-QUAL-R1) of reservoir water quality is being developed as part of the Environmental and Water Quality Operational Studies (EWQOS). A User's Manual (Environmental Laboratory 1982), which describes the model and lists the data required, is available from the U. S. Army Engineer Waterways Experiment Station (WES). One of the major types of input to the model is a set of coefficients used in equations which describe rates of change for various water quality variables. Although a description of the coefficients is included in the User's Manual, no values are supplied for many of them. Most of these deal with biological processes which are extremely difficult, and very costly, to measure; in fact, for a pre-impoundment study, many coefficients cannot be measured. For these reasons, users of CE-QUAL-R1 will have to use coefficient estimates found in the literature.

Purpose

2. The purpose of this report is to aid the users of CE-QUAL-R1 by supplying information about, and values for, many of the coefficients needed for use of the model. Table 1 lists those coefficients for which information is supplied in this report. The coefficients presented are

suitable for the version of the model described in the User's Manual (Environmental Laboratory 1982). Neither the information concerning coefficient measurements nor the coefficient values listed should be considered to represent an exhaustive search of the literature. In many cases, the parameter values found in the literature were inappropriate to use in the model because of (a) the lack of information necessary to convert the value to the proper units or (b) improper experimental design. Therefore, this report includes literature values for experiments that were already in appropriate form for use in CE-QUAL-R1 or were readily transformable.

3. Although parameter values for a given coefficient may range over several orders of magnitude, it was felt inappropriate to recommend a single value for a parameter. Instead, experimentally determined values are presented to provide the user with a range of values.

Table 1

Alphabetical listing of coefficients in this report

COEFFICIENT	PAGE NUMBERS* THIS REPORT	USER'S MANUAL
ALGT1	42	193,194
ALGT2	42	193,194
ALGT3	42	193,194
ALGT4	42	193,194
BEFFIC	59	197
BENT1	62	198
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BS2SED	60	197
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FSHT3	66	203,204,205
FSHT4	66	203,204,205
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FS2Z00	63	201
F2ALG	64	202
F2DET	64	202
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NH3T2	85	210
N02T1	86	211
N02T2	86	211
PREF1	49	195
PREF2	49	195

(Continued)

*The page numbers reflect a cross-reference between this document and the User's Manual (Environmental Laboratory 1982).

Table 1 (Concluded)

COEFFICIENT	PAGE NUMBERS* THIS REPORT	USER'S MANUAL
PREF3	49	195
PS2C02	38	191,192
PS2L	40	191,192
PS2N	34	190,192
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PART II. COEFFICIENTS

Coefficient Types

4. For those coefficients that are involved in equations as rates of change, the user must supply values that are appropriate to continuous exponential functions. These values should be appropriate for the equation:

$$X(t) = X_o \exp(K_c t) \qquad (1)$$

where

$X(t)$ = final condition

X_o = initial condition

K_c = coefficient in units of 1/day in continuous form

t = time in days

5. For those coefficients that are negative (e.g., mortality rate), the negative sign is introduced internally by the model. If values are reported in the discrete form suitable for the equation

$$X(t) = X_o (1+K_d)^n \qquad (2)$$

where

K_d = coefficient in units of 1/day *in* discrete form

n = the number of time steps in days

the coefficient must be transformed. If the user has coefficients *in* the discrete form in units of 1/day, they can be transformed to the proper continuous form by using the following relationship:

$$K_c = \ln(1+K_d) \qquad (3)$$

For a detailed explanation of the type of coefficients used by CE-QUAL-R1, please refer to the User's Manual, pages 41 through 47 (Environmental Laboratory 1982). Values included in this report are in the continuous form. This entailed transforming values for those citations that were reported in the discrete form; transformations of units to the form used by the model were also necessary.

Physiological Processes

6. For zooplankton, fish, and benthos, the physiological processes modeled are ingestion, respiration, and assimilation efficiency. The units for ingestion are l/day. Assimilation efficiency is dimensionless and is multiplied by ingestion to account for the assimilation rate. In the literature, ingestion (1) or consumption is equal to assimilation (A) + egestion (E). The amount assimilated may be separated into (a) that amount respired (R) and (b) growth (G). The products of growth may be separated into excretion (X), predatory mortality (PM), nonpredatory mortality (NM), exuviae (V), secretion (5), eggs or young (Y), harvest (H), and the change in weight (WT) •

7. In CE-QUAL-Rl predictions are made regarding WT. In the literature it usually equals

$$WT = I - E - R - X - PM - NM - V - 5 - Y - H \qquad (4)$$

Ingestion, respiration, predatory mortality, nonpredatory mortality, and harvest are explicitly modeled. Egestion is calculated using ingestion and the assimilation efficiency. Eggs or young are not considered lost in the model and are not included in the equation. Excretion, exuviae, and secretion are considered as part of the nonpredatory mortality term. Values for growth should be used with caution. Model users must know exactly what is included in the growth term so that correct coefficient estimates can be made.

8. The rates used in the model represent the maximum rate for each process under conditions normally

found in reservoirs. These maximum rates are scaled down *in* the model due to predicted conditions such as temperature, nutrient, or food concentrations. Values found in the literature for rates are often measured at a set of specific conditions and may not represent a true maximum rate. Values found in this report may not necessarily be maximum rates, but the authors felt that the information may still be of use in setting coefficients. The ingestion rate must be greater than the combined mortality and respiration rates divided by the assimilation efficiency.

9. Data input and coefficient selection are discussed in detail. Guidance will be given with respect to how the data item is used in the model and how the data item can be calculated or determined. Values for the coefficients are also given in tables based upon results from laboratory and in situ experimental results. With careful specification of coefficient values, calibration efforts can be held to a minimum.

Light Extinction

10. Solar radiation is distributed vertically in the water column in subroutine HEAT (which is called from subroutine MIXING). The distribution is due in part to the absorption of light by water, including dissolved substances, and by absorption by particulate organic and inorganic materials. Care must be taken when estimating or measuring extinction coefficients, for the same coefficient may have a different meaning depending on whether it is used in CE-QUAL-R1 or CE-THERM-R1. Two extinction coefficients are used in CE-THERM-R1: EXCO and EXTINS; EXTINP is used only in CE-QUAL-R1.

EXCO

11. EXCO is the extinction coefficient for water, including dissolved substances (l/m). It can be estimated from the equation (Williams et al. 1981)

$$EXCO = 1.1*Z**(-0.73) \quad (5)$$

given the Secchi depth (Z) in meters, or it can be measured directly with a photometer using the Beers-Lambert Law

$$EXCO = (\ln I - \ln I_z)/Z \quad (6)$$

where

I = irradiance at water surface

I_z = irradiance at depth z

However, in situ measurements for EXCO are likely to overestimate the extinction coefficient because it includes extinction due to detritus, phytoplankton, zooplankton, and inorganic suspended solids. Thus, the manual carefully states on p. 182 that the calculated value of EXCO should reflect the maximum light penetration (i.e., the maximum Secchi depth). This should minimize the overestimation problem. In CE-QUAL-Rl and CE-THERM-Rl, self-shading due to these components is handled separately.

12. The light extinction coefficient for an ultra-oligotrophic to oligotrophic lake ranges from 0.03 to 1.0/m; for mesotrophic lakes the figures are from 0.1 to 2.0/m; for eutrophic lakes, from 0.5 to 4.0/m; and for dystrophic lakes, from 1.0 to 4.0/m (Likens 1975). The extinction coefficient of monochromatic light by a I-m column of distilled water ranges from 0.0255 at 380 nm, 0.0054 at 460 nm, 0.078 at 580 nm, 0.455 at 680 nm, to 2.42 at 820 nm (Hutchinson 1957). Other values are given in Table 2 for photosynthetically active radiation (PAR) and other wavelengths.

Table 2

Extinction coefficients for Water (1/m)

SITE	DESCRIPTION	EXCO	REFERENCE
Lake Tahoe, California	oligotrophic	0.2	Wetzel 1975
Wintergreen Lake, Michigan	eutrophic	0.46-1.68	Wetzel 1975
Crystal Lake, Wisconsin	oligotrophic	0.2	Wetzel 1975
Crater Lake, Oregon	oligotrophic, almost pure, blue	0.18	Spence 1981
Loch Borralie, Scotland	calcareous water, blue green	0.34	Spence 1981
Neusiedlersee, Austria	turbid water, sediment colored	3.31	Spence 1981
Loch Unagan, Scotland	yellow substances	0.93	Spence 1981
Black Loch, Scotland	brown substances (peaty)	1.53	Spence 1981
Loch Leven, Scotland	turbid, dense phytoplankton	2.58	Spence 1981
Lake Paajarvi, Finland	brown-stained	0.7	Verduin 1982
Highly stained lakes	average	4.0	Wetzel 1975

EXTINS and EXTINP

13. EXTINS is the self-shading coefficient due to particulate inorganic material in both CE-QUAL-RI and CE-THERM-R1. In CE-THERM-Rl, because organic particulate materials are not explicitly modeled, the light attenuation due to these materials must be handled through either EXTINS or EXCO. If the suspended solids (55) compartment has been incremented in value to include organic as well as inorganic particulates suspended in the water column, then EXTIN5 (l/m*mg/L) represents the extinction coefficient for all suspended solids, including inorganic matter, phytoplankton, zooplankton, and suspended detritus. However, if the 55 compartment in CE-THERM-Rl does not include organic particUlates--i.e., if the magnitude of 55 is identical in CE-QUAL-Rl and CE-THERM-Rl--then light attenuation by organic matter suspended in the water column cannot be handled by EXTINS. Rather, the value of EXCO must be increased to handle the "extra" attenuation due to phytoplankton, zooplankton, and detritus. In either case, the magnitude of EXTIN5 should be the same in both models. It should typically be of the same order of magnitude as EXTINP.

14. EXTINP is the self-shading coefficient due to organic particulate matter in CE-QUAL-Rl (l/m*mg/L). The self-shading coefficient represents the decreased light penetration or increased light extinction resulting from phytoplankton, zooplankton, and detritus suspended in the water column. The light extinction coefficient in subroutine HEAT is modified as a function of the concentrations of these three constituents. Most measurements of EXTINP refer only to algal biomass; it is assumed in CE-QUAL-RI that light extinction due to

zooplankton and detritus is numerically equivalent to that due to phytoplankton. Megard et al. (1980) and Smith and Baker (1978) determined that each microgram per liter of chlorophyll increased the light extinction coefficient by about 0.022 and O.OI6/m, respectively. Assuming a ratio of carbon to algal biomass of 0.45 and a carbon/chlorophyll (C/chl) ratio of 50, then algebraically each milligram per liter of algal biomass should increase the light extinction coefficient by about 0.20 to 0.14/m, respectively. The range of C/chl ratios, however, varies from 25-150, resulting in a range of self-shading coefficients from 0.40/m*mg/L to O.047/m*mg/L. Values near 0.10 have previously produced reasonable results (Environmental Laboratory 1982).

15. Light extinction by algae is computed from <u>in situ</u> light intensity measurements at depth intervals and <u>in situ</u> determinations of chlorophyll a using the modified Lambert-Bouguer Law (Megard et al. 1980). Bannister (1979) extracted chlorophyll from cell suspensions and measured the absorption spectrum to obtain the mean extinction coefficient. Theoretical estimates for attenuation of photosynthetically active radiation by chlorophyll <u>a</u> in algae range between 0.06 and 0.018, depending on the size and chlorophyll content of cells and colonies (Kirk 1975). The extinction coefficient was determined to range between 0.0066 and 0.0205 l/m*mg/m3 in laboratory analysis (Bannister 1979). Values for self-shading coefficients are given in Table 3. Values shown in this table were originally reported in units of 1/m*µg chI ai L, and have been converted to units used in CE-QUAL-R! assuming a C/chl ratio of 50 and a C/biomass ratio of 0.45.

Table 3

Self-shading coefficients due to particulate matter (l/m*mg/L)

TYPE	COMMENT	VALUE	REFERENCE
Suspensoids	average	0.12	Verduin 1982
Suspensoids	Lake Paajarvi, Finland	0.24	Verduin 1982
Organic matter	Pacific Ocean	0.047	Verduin 1982
Phytoplankton	Pacific Ocean	0.033	Verduin 1982
Phytoplankton - diatoms	C/Chl ratio = 120 dry wt/C ratio = 4	0.058	Verduin 1982
Phytoplankton diatoms	C/Chl ratio = 30 dry wt/C ratio = 4	0.014	Verduin 1982
Phytoplankton greens	C/Ch1 ratio = 100 dry wt/C ratio = 2	0.024	Verduin 1982
Phytoplankton greens	C/Chl ratio = 30 dry wt/C ratio = 2	0.007	Verduin 1982
Phytoplankton	Shagawa Lake, Minnesota	0.03	Megard et al. 1980

Phytoplankton

TPRESP

16. TPRESP is the maximum phytoplankton respiration rate (l/day). Although two compartments are available to simulate phytoplankton, a single respiration rate coefficient is used and should reflect the composite nature of the species assemblages. TPRESP should include dark respiration and photorespiration. Endogenous or dark respiration (mitochondrial) refers to the oxygen consumption associated primarily with oxidative phosphorylation and which produces carbon dioxide. Photorespiration, commonly refered to as excretion, is the release of dissolved organic matter (glycolate) and carbon dioxide that occurs during light periods; it is the oxygen-sensitive loss of carbon dioxide during photosynthesis, stimulated by an increase in temperature or oxygen concentration (Birmingham et al. 1982).

17. Measurement of dark respiration in the light is hampered by the presence of photosynthetic oxygen production and photorespiratory oxygen consumption; this precludes direct measurement in the light using a p02 electrode. Oxygen consumption in the dark depends on the previous light history in several ways. The duration, spectrum and magnitude of light, as well as other factors, determine the type and amount of photosynthate produced. Subsequent respiration in the dark will be affected by the metabolism of the photosynthate and by certain dieI rhythms. The previous light history thus may affect the dark respiration for many hours after a light-dark transition. Transient phenomena in oxygen exchange also are noted for approximately 10 min after the light-dark

transition. Therefore, determination of oxygen consumption should be made after a 5- to 10-min acclimation to a dark environment. It can be measured polarographically using an oxygen electrode, manometrically, or chemically.

18. Respiration rates, in many instances, are expressed as milliters of oxygen consumed per milligram of organism dry weight per hour. Since the model formulation requires units of l/day, these values must be converted. For values in this report, the method outlined on page 188 of the User's Manual (Environmental Laboratory 1982) was used. In addition, respiration values in Table 4 are in continuous form.

19. The amount of excretion of organic matter by phytoplankton is commonly expressed as a percent of photoassimilated carbon. It is measured using ^{14}C as a tracer in photosynthetic uptake rate studies. After incubation and filtration of the algae, the filtrate is then acidified and either (a) bubbled with air for 2 hr or (b) allowed to stand overnight in a dessicator of sodium hydroxide pellets. Rates of carbon dioxide release in the light are lower than rates of dark respiration (Birmingham et al. 1982). Percent extracellular release (PER) values reported in the literature range from 7 to 50 for natural phytoplankton populations (Nalewajko 1966). Berman (1976) reported PER values of 3 to 32 for natural phytoplankton populations in Lake Kinneret.

20. The values given in Table 4 for dark respiration rates are usually determined for a I-hr time period.

Table 4

Phytoplankton dark respiration rates (l/day)

SPECIES	TPRESP	REFERENCE
Mesodinium rubrum	0.05	Smith 1979
Thalassiosira allenii- small cells	0.14-0.59	Laws and Wong 1978
Thalassiosira allenii- large cells	0.05-0.42	Laws and Wong 1978
Monochrysis lutheri	0.15-0.32	Laws and Wong 1978
Dunaliella teriolecta	0.12-0.46	Laws and Wong 1978
Anabaena variabilis	0.10-0.92	Collins and Boylen 1982a
Coscinodiscus excentricus	0.075-0.11	Riley and von Aux 1949
Chlorella pyrenoidosa	0.01-0.03	Myers and Graham 1961
Phytoplankton	0.05-0.10	Ryther 1954

TPMAX

21. TPMAX is the maximum gross photosynthetic rate (l/day). CE-QUAL-RI uses gross production rates to simulate the rate of change of algal biomass through time.

22. The physiological processes of phytoplankton that are being modeled are gross production and respiration. Gross production is the total rate of photosynthesis, which includes the storage rate of organic matter by the phytoplankton (net production) plus the organic matter used by phytoplankton in respiration. That is,

$$\text{gross production} = \text{net production} + \text{respiration} \quad (7)$$

23. Net production is the organic matter used for other processes such as zooplankton grazing, sinking, excretion, and nonpredatory mortality. Extreme care must be used in estimating these rates because the rates are

often dependent on the experimental design. For example, the maximum growth rate *is* often used in modeling studies (see, for example, the Preliminary Generalized Computer Program, Water Quality for River-Reservoir Systems, Oct. 1978, u. S. Army Engineer Hydrologic Engineering Center, Davis, Calif.). The respiration rate is subtracted from the maximum growth rate in order to predict a new mass. However, the values of growth found in the literature are most equivalent to net production in the above equation and have already accounted for respiration; in other words, the model may predict low phytoplankton values because respiration is being accounted for twice. If growth is measured as the difference in mass between two points in time, it must be realized that algae may have been lost to grazing, sinking, etc. Also, the true growth figure is actually higher than reported.

24. Values are often reported as "production" without mention as to whether the figures represent gross or net production. and the reader may have to evaluate the experimental design to determine the correct value.

25. There are four general methods used to measure phytoplankton primary productivity (Janik et al. 1981). These involve the measurement of (a) changes in the oxygen content of water, (b) changes in the carbon dioxide.content of water, (c) incorporation of 14carbon tracers into the organic matter of phytoplankton, and (d) measures of chlorophyll. Readers should refer to Janik et al. (1981) to gain insight into the problems associated with the four methods. For example, the 14carbon technique gives a measurement which is between net and gross production, depending on the length of the experiment (Whittaker 1975).

26. The most frequently used method for measuring primary production by phytoplankton has been photosynthetic

oxygen evolution and ^{14}C uptake. The light- and dark-bottle ^{14}C technique of Steemann-Nielsen (1952) requires the lowering of pairs of bottles injected with $H^{14}CO_3$ to fixed depths in the water column for time periods of 1-5 hrs or by incubating the bottles under known conditions of light and temperature.

27. Under optimal conditions, a culture grows so that the rate of addition of cells is proportional to the number present (i.e., exponential growth). Cells divide in a characteristic time called the division, generation, or doubling time. Population growth follows the solution to the equation

$$dN/dt = k*N \qquad (8)$$

where

N = the number or concentration of cells in the culture

t = the time

k = the growth constant - (l/t)

The solution to this equation is

$$k = \ln(N/N_0)/(t-t_0) \qquad (9)$$

Subscripts denote values at a known initial time, and ln indicates natural logarithms.

28. The growth constant k is the number of the logarithm-to-the-base-e units of increase per day. Growth rate is sometimes expressed as logarithm-to-base-10 units of increase per day, k_{10}; or as logarithm-to-base-2 units per day, k_2, where

$$k_{10} = \log(N/N_0)/(t-t_0) \qquad (10)$$

$$k_2 = \log_2(N/N_0)/(t-t_0) \qquad (11)$$

Conversions among the expressions are as follows: let

k = growth rate measured in ln units

k_{10} = growth rate measured in $\log_{10}$ units

k_2 = growth rate measured in 1092 units

Now let an algal population of interest double in one day. Then

$N = 2$

$N_o = 1$

$t - t_o = 1$

and

$$k = 0.693 = \ln 2 \qquad (12)$$

$$k_{10} = 0.301 = \log10\ 2, \quad k = 2.3026\ k_{10} \qquad (13)$$

$$k_2 = 1.0 = \log_2 2, \quad k = 0.6931\ k_2 \qquad (14)$$

Or, let the algal population quadruple in one day. Then

$N = 4$

$N_0 = 1$

$t - t_0 = 1$

and

$$k = 1.386 = \ln 4 \qquad (15)$$

$$k_{10} = 0.602 = \log10\ 4, \quad k = 2.3026\ k_{10} \qquad (16)$$

$$k_2 = 2.0 = \log_2 4, \quad k = 0.6931\ k_2 \qquad (17)$$

Similarily, let the algal population halve in one day. Then

$N = 0.5$

$N_o = 1$

$t - t_0 = 1$

and let

$$k = -0.693 \qquad (18)$$

$$k_{10} = -0.301, \quad k = 2.3026\ k_{10} \qquad (19)$$

$$k_2 = -1.0, \quad k = 0.6931\ k_2 \qquad (20)$$

Thus, the relation between the various growth rates is given by

$$k = 2.3026\ k_{10} \qquad (21)$$

$$k = 0.6931\ k_2 \qquad (22)$$

The composite gross production rate for this compartment should also represent a weighted contribution for the dominant species, or the dominant functional groups, to be simulated by this compartment.

29. Literature values for TPMAX are given in Table 5.

Table 5

Gross production rates of phytoplankton (l/day)

SPECIES	TPMAX	TEMP °C	REFERENCE
DIATOMS			
Asterionella formosa	0.81	20	Holm and Armstrong 1981
Asterionella formosa	0.69	10	Hutchinson 1957
Asterionella formosa	1.38	20	Hutchinson 1957
Asterionella formosa	1.66	25	Hutchinson 1957
Asterionella formosa	1.71	20	Fogg 1969
Asterionella formosa	0.28	●	Talling 1955
Asterionella formosa	0.69	10	Talling 1955
Asterionella formosa	1.38	20	Talling 1955
Asterionella formosa	2.2	20	Hoogenhout and Amesz 1965
Asterionella formosa	1..	18.5	Hoogenhout and Amesz 1965
Asterionella japonica	1.19	22	Fogg 1969
Asterionella japonica	1.3	18	Hoogenhout and Amesz 1965
Asterionella japonica	1.7	25	Hoogenhout and Amesz 1965
Biddulphia sp.	1.5	11	Castenholz 1964
Coscinodiscus sp.	0.55	18	Fogg 1969
Cyclotella meneghiniana	0.34	16	Hoogenhout and Amesz 1965
Cyclotella nana	3.4	20	Hoogenhout and Amesz 1965
Detonula confervacea	0.62	2	Smayda 1969
Detonula confervacea	1.4	10	Hoogenhout and Amesz 1965
Ditylum brightwellii	2.1	20	Paasche 1968
Fragilaria sp.	0.85	20	Rhee and Gotham 1981b
Fragilaria sp.	1.7	11	Castenholz 1964
Melosira sp.	0.7	11	Castenho1z 1964
Navicula minima	1..	25	Hoogenhout and Amesz 1965
Navicula pelliculosa	2.0	20	Hoogenhaut and Amesz 1965
Nitzschia closterium	1.66	27	Harvey 1937
Nitzschia palea	2.1	25	Hoogenhout and Amesz 1965
Nitzschia turgidula	2.5	20	Paasche 1968
Phaeodactylum tricornutum	1.66	25	Fogg 1969
Phaeodactylwn tricornuturn	2.7	19	Hoogenhout and Amesz 1965
Rhizosolenia fragillissima	1.20	21	Ignatiades & Smayda 1970
Skeletonema costatum	1.26	18	Fogg 1969
Skeletonema costaturn	2.30	20	Jorgensen 1968
Skeletonema costatum	1.52	20	Steemann-Nielsen and Jorgensen 1968
Skeletonema costatum	1.23	20	Jitts et al. 1964
Synedra sp.	1.2	11	Castenho1z 1964
Thalassiosira nordenskioldii	0.77	13	Jitts et al. 1964
natural diatom community	3.10	20	Verduin 1952
GREENS			
Ankistrodesmus braunii	2.33	25	Hoogenhout and Amesz 1965
Chlamydomonas moewusii		'.2	Hoogenhout and Amesz 1965
Chlorella pyrenoidosa	2.22	28	She1ef 1968
ChIorella ellipsoidea	3.6	25	Hoogenhout and Amesz 1965
ChIarella luteoviridis	0.56	22.4	Hoogenhout and Arnesz 1965
ChIarella miniata	0.87	25	Hoogenhout and Amesz 1965
Chlorella pyrenoidosa	2.14	25	Fogg 1969

Table 5 (continued)

SPECIES	TPMAX	TEMP °C	REFERENCE
Chlorella pyrenoidosa	1.95	25.5	Sorokin and Myers 1953
Chlorella pyrenoidosa	9.00	39	Castenho1z 1969
Chlorella pyrenoidosa	9.2	39	Hoogenhout and Amesz 1965
Chlorella seccharophilia	1.2	25	Hoogenhout and Amesz 1965
Chlorella variegata	0.86	25	Hoogenhout and Amesz 1965
Chlorella vulgaris	2.9	25	Hoogenhout and Amesz 1965
Chlorella vulgaris	1.59	20	Goldman and Graham 1981
Ounaliella tertiolecta	1.0	1.	Hoogenhout and Amesz 1965
Ounalie11a tertiolecta	0.77	3.	Jitts et a1. 1964
Haematococcus pluvialis	1.2	23	Hoogenhout and Amesz 1965
Nanochloris atornus	1.0	20	Hoogenhout and Amesz 1965
Platymonas subcordiformia	1.5	1.	Hoogenhout and Amesz 1965
Scenedesmus sp.	1.34	20	Rhee and Gotham 1981b
Scenedesmus costulatus	2.0	24.5	Hoogenhout and Amesz 1965
Scenedesmus obliquu8	2.11	20	Goldman and Graham 1981
Scenedesmus obliquus	2.2	25	Hoogenhout and Amesz 1965
Scenedesmus quadricauda	4.1	25	Hoogenhout and Amesz 1965
Scenedesmus quadricauda	2.29	27	Goldman et al. 1972
Selenastrum capricornutum	2.45	27	Goldman et a1. 1972
Selenastrum westii	1.0	25	Hoogenhout and Amesz 1965
Stichococcus sp.	0.70	20	Hoogenhout and AmeS2 1965
GOLDEN-BROWN			
Botrydiopsis intercedens	1.5	25	Hoogenhout and Amesz 1965
Bumi11eriopsis brevis	2.9	25	Hoogenhout and Ames2 1965
cricosphaera carterae	0.82	18	Fogg 1969
Isochrysis galbana	0.55	20	Fogg 1969
Isochrysis galbana	0.80	25	Hoogenhout and Amesz 1965
Monochrysis lutheri	1.5	15	Hoogenhout and Amesz 1965
Monochrysis lutheri	0.39	24	Jitts et al. 1964
Monod.us subterraneus	0.93	25	Hoogenhout and Amesz 1965
Monodus subterraneus	0.39	30	Fogg 1969
Tribonema aequale	0.70	25	Hoogenhout and Amesz 1965
Tribonema minus	1.00	25	Hoogenhout and Amesz 1965
Vischeria stellata	0.70	25	Boogenhout and Amesz 1965
Euglena gracilis	2.2	25	Hoogenhout and Amesz 1965
Euglena gracilis	0.00	3.	Marre 1962
DINOFLAGGELATE			
Amphidinium carteri	1.88	18	Fogg 1969
Amphidinium carteri	0.32	32	Jitts et al. 1964
Ceratium tripos	0.20	20	Fogg 1969
Gonyaulax po1yedra	2.1	21.5	Hoogenhout and Amesz 1965
Gymnodinium sp1endens	0.92	20	Hoogenhout and Amesz 1965
Peridinium sp.	0.90	18	Hoogenhout and Amesz 1965
Prorocentrium gracile	0.83	18	Hoogenhout and Amesz 1965
Prorocentrium micans	0.71	25	Hoogenhout and Amesz 1965
Prorocentrium micans	0.30	20	F099 1969

Table 5 (concluded)

SPECIES	TPMAX	TEMP °C	REFERENCE
BLUEGREENS			
Agmenellum quadriplaticum	8.0	39	Hoogenhout and Amesz 1965
Anabaena cylindrica	0.96	25	Hoogenhout and Amesz 1965
Anabaena variabi1is	3.9	34.5	Hoogenhout and Amesz 1965
Anacystis nidulans	2.9	25	Hoogenhout and Amesz 1965
Anacystis nidulans	8.28	38	Marre 1962
Anacystis nidulans	11.00	40	Castenholz 1969
Ch1oropseudomonas ethylicurn	3.3	30	Hoogenhout and Amesz 1965
Cyanidium ca1darium	2.4	40	Hoogenhout and Amesz 1965
Cy1indrospermurn sphaerica	0.17	25	Hoogenhout and Amesz 1965
G1oeotrichia echinu1ata	0.20	26.5	Hoogenhout and Amesz 1965
Microcystis aeruginosa	0.25	20	Holm and Armstrong 1981
Microcystis aeruginosa	1..	23	Hoogenhout and Amesz 1965
Microcystis 1urninmosis	1.50	40	Castenho1z 1969
Nostoc muscorum	2.9	32.5	Hoogenhout and Amesz 1965
Oscillatoria princips	0.50	40	Castenho1z 1969
Oscillatoria subbrevis	5.52	38	Marre 1962
Osci11atoria terebriformis	3.36	40	Castenholz 1969
Oscil1atoria rubescens	5.04	30	Zimmerman 1969
Rhodopseuaomonas sphaeroides	10.8	34	Hoogenhout and Amesz 1965
Rhodospir1lurn rubrurn	4.85	25	Hoogenhout and Amesz 1965
Schizothrix calcicola	3.4	30	Hoogenhout and Arnesz 1965
Synechococcus lividus	4.98	40	Castenholz 1969
synechococcus sp.	8.0	37	Hoogenhout and Amesz 1965
Tolypothrix tenuis	4.0	38	Hoogenhout and Amesz 1965
Leptocylindrus danicus	0.67-2.0	10-20	verity 1981
Anabaena variabilis	0.07-2.0	10-35	Collins and Boylen 1982a

TSETL

30. TSETL is the phytoplankton settling rate (rn/day). Mechanisms of suspension can influence the settling or sinking rate of algae. Morphological mechanisms include cell size, colony formation, cyclomorphosis, protuberances, and flagella. Physiological mechanisms include fat accumulation; regulation of ionic composition of cell sap; and the response of an organism to light, photoperiod, and nutrient concentration. Physical mechanisms include water viscosity and the role of water movements.

31. Two methods used to measure sinking rates experimentally are (a) the settling chamber method with or without the use of a microscope, and (b) the photometric technique. In the settling chamber, the descent time is determined (a) by following with a microscope or, in the case of large particles, with the naked eye, the cell trajectory between two marks at a known distance apart; (b) by measuring the time a cell takes to fall to the bottom of a settling chamber of known height placed on the stage of an inverted scope; or (c) using a l-mm-deep Sedgwick Rafter counting chamber with a compound microscope. Estimation of relative sinking rate has been obtained by placing a well-mixed suspension of phytoplankton into a graduated cylinder and determining the concentration in various layers after a given time.

32. Photometric determination of sinking rate measures changes in optical density of a phytoplankton suspension measured at 750 nm after introducing the phytoplankton suspension into a cuvette.

33. These techniques are influenced by the "wall-effect," that *is,* the effect of the settling chamber wall and convection current on the sinking velocity. To provide adequate fall for attainment of terminal velocity and to

minimize overcrowding, the selection of chamber size is important.

34. The sinking rates of natural populations have also been determined by comparing changes *in* population density with depth and calculating a mean rate of descent. However, determination of sinking rate in situ is complicated by water movements and losses due to grazing. Mathematical expressions may also be used to determine sinking rates (Riley et al. 1949).

35. The application of experimentally determined sinking rates to natural populations or ecosystem models must be qualified and used with caution. In lakes and reservoirs, vertical gradients of light, temperature, and nutrient concentration contrast with the constancy of the settling chamber and photometer cuvette environments in sinking experiments. The influence of light and nutrients on sinking rates together with the turbulent motion of the natural environment suggest that in vitro sinking results may not be particularly representative of natural populations. Values for settling rates are given in Table 6.

Table 6

Phytoplankton settling rates (m/day)

SPECIES	TSETL	REFERENCE
DIATOMS		
EXPERIMENTAL STUDIES		
Asterionella formosa	0.26-0.76	Smayda 1974
Asterionella formosa	0.4	Margalef 1961
Bacteriastrum hyalinum	0.39-1.27	Smayda & Boleyn 1966
Chaetoceros didymus	0.85	Eppley et al. 1967b
Chaetoceros lauderi	0.46-1.54	Smayda & Boleyn 1966
Chaetoceros lauderi	0.46-1.54	Smayda & Boleyn 1966
Chaetoceros spp.	0.25	Margalef 1961
Chaetoceros spp.	5.0	Sverdrup et al. 1942
Chaetoceros spp.	4.0	Allen 1932
Coscinodiscus wailesii	7.0-30.2	Eppley et al. 1967b
Coscinodiscus sp.	1.95-6.83	Eppley et al. 1967b
Coscinodiscus sp.	14.7	Eppley et al. 1967b
Cyclotella meneghiniana	0.08-0.24	Titman and Kilham 1976
Cyclotella nana	0.16-0.76	Eppley et al. 1967b
Ditylum brightwellii	0.60-3.09	Eppley et al. 1967b
Oitylum brightwellii	2.	Eppley et al. 1967b
Ditylum brightwellii	5.8-8.6	Gross & Zeuthen 1948
Fragilaria crotonensis	0.27	Burns and Ross 1980
Leptocylindrus danicus	0.08-0.42	Margalef 1961
Melosira agassizii	0.67-1.87	Titman and Kilham 1976
Nitzschia closterium	0.52	Margalef 1961
Nitzschia seriata	4.0	Allen 1932
Nitzschia seriata	0.35-0.50	Smayda , Boleyn 1965
Phaeodactylum tricornutum	0.05-0.06	Riley 1943
phaeodactylum tricornutum	0.02-0.04	Riley 1943
Rhizosolenia hebetata f. semispina	0.22	Eppley et al. 1967b
Rhizosolenia setigera	0.11-2.23	Smayda & Boleyn 1966
Rhizosolenia setigera	0.10-6.30	Smayda & Boleyn 1966
Rhizosolenia stolterfothii	1.0-1.9	Eppley et al. 1967b
Rhizosolenia spp.	0-0.72	Margalef 1961
Skeletonema costatum	0.30-1.35	Smayda & Boleyn 1966
Stephanopyxis turris	1.1	Eppley et al. 1967b
Stephanopyxis turris	2.1	Eppley et al. 1967b
Thalassionema nitzschiodes	0.35-0.78	Smayda (unpub1.)
Thalassiosira fluviatilis	0.60-1.10	Eppley et a1. 1967b
Thalassiosira cf. nana	0.10-0.28	Smayda & Boleyn 1965
Thalassiosira rotula	1.15	Eppley et al. 1967b
Thalassiosira rotula	0.39-2.10	Smayda & Boleyn 1965
Thalassiosira spp.	0-0.16	Margalef 1961
THEORETICAL		
Diatoms	0.3	Bramlette 1961

Table 6 (concluded)

SPECIES	TSETL	REFERENCE
DINOFLAGELLATES EXPERIMENTAL STUDIES		
Gonyaulax polyedra	2.8-6.0	Eppley et al. 1967b
COCCOLITHOPHORIDS EXPERIMENTAL STUDIES		
Coccolithus huxleyi	0.28	Eppley et a1. 1967b
Coccolithus huxleyi	1.20	Eppley et a1. 1967b
Cricosphaera carterae	1.70	Eppley et a1. 1967b
Cricosphaera elongata	0.25	Eppley et a1. 1967b
Cyclococcolithus fracilis	13.2	Bernard 1963
Cyclococcolithus fragilis	13.6	Bernard 1963
Cyclococco1ithus fragilis	10.3	Bernard 1963
THEORETICAL		
Coccoliths	1.5	Bramlette 1961
MICROFLAGELLATES EXPERIMENTAL STUDIES		
Cryptomonas erosa	0.31	Burns and Rosa 1980
Cryptomonas marsonii	0.32	Burns and Rosa 1980
Rhodomonas minuta	0.07	Burns and Rosa 1980
Dunaliella tertiolecta	0.18	Eppley et a1. 1967b
Monochrysis lutheri	0.39	Eppley et al. 1967b
Monochrysis lutheri	0.39	Apstein 1910
GREENS EXPERIMENTAL		
Closterium parvu1um	0.18	Burns and Rosa 1980
Dunaliella tertiolecta	0.18	Eppley et a1. 1967b
Lagerhaemia quadriseta	0.08	Burns and Rosa 1980
Scenedesmus acutiformis	0.10	Burns and Rosa 1980
Selenastrum minutum	0.15	Burns and Rosa 1980
BLUEGREENS EXPERIMENTAL		
Anabaena spiroides	0.10	Burns and Rosa 1980
Gomphosphaeria lacustris	0.11	Burns and Rosa 1980

PS2P04

36. PS2P04 *is* the phosphorus half-saturation coefficient (HSe) (rng/L). In practical terms, the HSC of a nutrient approximately marks the upper nutrient concentration at which growth ceases to be proportional to that nutrient. The modeled uptake of phosphorus by algae follows Monad kinetics. The value of the HSe can be calculated for the hyperbola using the Monad equation. PS2P04 is defined as the concentration of phosphorus at which the rate of uptake is one-half the maximum.

37. Half-saturation coefficients generally increase with nutrient concentrations (Hendrey and Welch 1973, Carpenter and Guillard 1971, and Toetz et a1. 1973). This fact reflects both the change in species composition of the phytoplankton assemblage and the adaptation of the plankton to higher nutrient levels. A reservoir characterized by low nutrient concentrations is generally also characterized by low half-saturation coefficients. Phosphorus *is* commonly the nutrient that limits the growth of algae in lakes and reservoirs.

38. The procedure of measuring a phosphorus half-saturation coefficient involves the measurement of the net rate of loss of dissolved orthophosphate from the medium in which the experimental population is suspended.

39. Units of measurement must be expressed in terms of the chemical element and not the compound; i.e., the half-saturation constant for phosphorus should be specified as mg/L of phosphorus and not mg/L of orthophosphate. Micromoles per liter or microgram-atom values may be converted by multiplying by the molecular weight of the element times 10^{-3}. Values for the HSC are given in Table 7.

Table 7

Phytoplankton half-saturation coefficients for P limitation (mg/L)

SPECIES	PS2P04	REFERENCE
Asterionella formosa	0.002	Holm and Armstrong 1981
Asterionella japonica	0.014	Thomas and Dodson 1968
Biddulphia sinensis	0.016	Quasim et al. 1973
Cerataulina bergonii	0.003	Finenko and Krupatikina 1974
Chaetoceros curvisetus	0.074-.105	Finenko and Krupatikina 1974
Chaetoceros socialis	0.001	Finenko and Krupatikina 1974
ChIarella pyrenoidosa	0.38-.475	Jeanjean 1969
Cyclotella nana	0.055	Fuhs et al. 1972
Cyclotella nana	0.001	Fogg 1973
Dinobryon cylindricum	0.076	Lehman (unpubl. data)
Dinobryon sociale var. americanum	0.047	Lehman) (unpubl. data)
Euglena gracilis	1.52	Blum 1966
Freshwater phytoplankton	0.02-.075	Halmann and Stiller 1974
Microcystis aeruginosa	0.006	Holm and Armstrong 1981
Nitzschia actinastreoides	0.095	von Muller 1972
Pediastrum duplex	0.105	Lehman (unpubl. data)
Pithophora oedogonia	0.098	Spencer and Lemhi 1981
Scenedesmus obliquus	0.002	Fogg 1973
Scenedesmus sp.	0.002-.05	Rhee 1973
Thalassiosira fluviatilis	0.163	Fogg 1973

PS2N

40. PS2N is the nitrogen (N) half-saturation coefficient (mg/L). Uptake rates of nitrate (N03) or ammonium (NH4) by algae give hyperbolas when graphed against N03 or NH4 concentration in the environment. Half-saturation coefficients (i.e., the concentration of N at which the rate of production is one-half the maximum) can be calculated for the hyperbolas using the Monad equation. This constant reflects the relative ability of phytoplankton to use low levels of nitrogen.

41. The role of N as a growth-limiting factor has been relatively neglected when compared with phosphorus, presumably because the latter is the growth-limiting factor in most natural fresh waters. However, it has been found that nitrogen becomes the limiting nutrient where phosphorus is abundant because of its release from geological deposits or from external loadings.

42. There are several methods for measuring half-saturation constants for N limitation. The chemostat method requires the measurement of the remaining nitrogen concentration at a number of fixed dilution rates (i.e., growth rates) in nitrogen-limited chemostat cultures. Culture media are prepared with nitrate or ammonium as the nitrogen source, with one-fifth or less than the usual amount of N03 or NH4 added to the culture media to ensure that during growth, nitrogen will be depleted before other nutrients. A second, less desirable, method is to use nitrogen-starved cells as an innoculum for cultures containing known concentrations of nitrogen and then (a) measure the concentration of nitrogen in the extracellular fluid at some later time to determine the rate of nitrogen uptake and (b) measure the increasing cell concentration to determine growth kinetics. The problems associated

with this method are that the organisms are poorly adapted to their subsequent growth environment, so growth can occur only after uptake of a substantial amount of nitrogen.

43. Some trends can be seen in the data for half-saturation coefficients: (a) organisms with a high HSC for nitrate usually have a high HSC for ammonium uptake as well, (b) large-celled species tend to show higher HSC's, (c) fast-growing species tend to have lower HSC's than slow growers.

44. The nitrogen HSC as used in CE-QUAL-R1 should reflect the uptake of both NO_3 and NH_4. Both compounds are taken up for use in production in proportion to their concentration *in* the layer.

45. A factor that will lead to selection for a particular functional group or species is the availability of combined nitrogen. In situations where the level of combined nitrogen is relatively low compared with other essential elements like phosphorus, those bluegreen species that can fix nitrogen will be at a selective advantage. Nitrogen fixation is not explicitly included in the model formulation for phytoplankton; however, if bluegreen algae are an important component in one of the compartments, the nitrogen half-saturation coefficient may have to be reduced to a low value to reflect nitrogen fixation. Values for the HSC for nitrogen are given in Table 8.

Table B

Phytoplankton half-saturation coefficients for N limitation (mg(L)

SPECIES	PS2N	N SOURCE	REFERENCE
DIATOMS			
Biddulphia aurita	0.056-.197	NO]	Underhill 1977
Chaetoceros gracilis	0.012	NO]	Eppley et al. 1969
Chaetoceros gracilis	0.007	N04	Eppley et a1. 1969
Coscinodiscus lineatus	0.161	NO]	Eppley et a1. 1969
Coscinodiscus lineatus	0.036	NH4	Eppley et al. 1969
Cyclotella nana	0.025-.117	NO]	Carpenter & Guillard 1971
Cyclotella nana	0.111		MacIssac and Dugdale 1969
Cyclotella nana	0.027		Caperon and Meyer 1972
Cyclotella nana	0.031		Eppley et al. 1969
Cyclotella nana	0.007	Na4	Eppley et a1. 1969
Ditylum brightwel1ii	0.037	NO]	Eppley et a1. 1969
Ditylum brightwellii	0.020	NH4	Eppley et al. 1969
Dunaliel1a terio1ecta	0.013	NO]	Caperon and Meyer 1972
Dunaliella terio1ecta	0.003	Na4	Caperon and Meyer 1972
Duna1iella teriolecta	0.087	NO]	Eppley et a1. 1969
Fragilaria pinnata	0.037-.100	NO]	carpenter & Gui11ard 1971
Leptocy1indrous danicus	0.078	NO]	Eppley et al. 1969
Leptocylindrous danlcus	0.013	Na4	Eppley et al. 1969
Navicula pelliculosa	0.923	NO]	Wallen and Cartier 1975
Phaeodactylum tricornutum	0.161	NO]	Ketchum 1939
Rhizoso1enia robusta	0.186	NO]	Eppley et al. 1969
Rhizoso1enia robusta	0.135	NH4	Eppley et al. 1969
Rhizosolenia stolterfothii	0.105	NO]	Eppley et al. 1969
Rhizoso1enia sto1terfothii	0.009	Na4	Eppley et al. 1969
Skeletonema costatum	0.027	NO]	Eppley et al. 1969
Ske1etonema costatum	0.014	N84	Eppley et al. 1969
BLOEGREENS			
Anabaena cylindrica	4.34	NO]	Battori 1962
Anabaena cylindrica	2.48	N02	Hattori 1962
Asterionella formosa	0.074-.093	NO]	Eppley and Thomas 1969
Asterionella formosa	0.062	NH4	Eppley and Thomas 1969
Microcystis aeruginosa	0.56-.207	Na4	Kappers 1980
Osci11atoria agarthii	0.22	NO]	van Liere et a1. 1975
MICROFLAGELLATES			
Bellochia sp.	0.001-.016	NO]	Carpenter & Guil1ard 1971
Monochrysis lutheri	0.026	NO]	caperon and Meyer 1972
Monochrysis 1utheri	0.052	Na4	Caperon and Meyer 1972
Monochrysis lutheri	0.037	NO]	Eppley et al. 1969
Monochrysis lutheri	0.007	NH4	Eppley et al. 1969
COCCOLITHOPHORIDS			
Coccolithus huxleyi	0.006	NO]	Eppley et al. 1969
Cocco1ithus huxleyi	0.002	NH4	Eppley et al. 1969
Coccoch1oris stagnina	0.019	NO]	Caperon and Meyer 1972

(continued)

Table 8 (concluded)

SPECIES	PS2N	N SOURCE	REFERENCE
GREENS			
Chlorella pyrendoidosa	0.006-.014		Pickett 1975
Chlore1la pyrendoidosa	1.15	N02	Knudsen 1965
Pithophora oedogonia	1.236	N03	spencer and Lemhi 1981
DINOFLAGELlATES			
Gonyaulax polyedra	0.589	N03	Eppley et al. 1969
Gonyaulax po1yedra	0.099	NH'	Eppley et a1. 1969
Gymnodinium splendens	0.235	N03	Eppley et a1. 1969
Gymnodinium splendens	0.019	NH'	Eppley et al. 1969
Gymnodinium wailesii	0.223	N03	Eppley et a1. 1969
Gymnodinium wailesii	0.088	NH'	Eppley et a1. 1969
CHRYSOPHYTES			
Isochrysis ga1bana	0.006	N03	Eppley et a1. 1969

PS2CQ2

46. PS2C02 is the half-saturation coefficient for carbon dioxide (mg/L). The coefficient is used in the Monod equation to determine the rate factor for C02 limitation. PS2C02 is defined as the concentration of C02 at which the rate of production is one-half the maximum. In practical terms, the HSC approximately marks the upper nutrient concentation at which growth ceases to be proportional to that nutrient.

47. There is a diversity of opinions as to whether inorganic carbon (C) limits photosynthesis in phytoplankton. Goldman et al. (1974) have argued that inorganic carbon almost never limits growth in natural algal populations. In contrast, King (1970) has shown that *C02* availability limits the growth of aquatic populations. Johnson et al. (1970) demonstrated C02 limitation in lakes contaminated by acid mine wastes, and Schindler and Fee (1973) demonstrated C limitation in a lake during the summer when nitrogen and phosphorus were available. Carbon dioxide limitation is clearly pH dependent. For example, the HSC for carbon dioxide given in Table 9 for Scenedesmus capricornutum increases with increasing pH. This is related to the effect of pH on the relative proportions of the inorganic carbon species of carbon dioxide, bicarbonate ion, and carbonate ion in solution. Half-saturation coefficient values for carbon dioxide are given in Table 9.

Table 9

Phytoplankton half-saturation coefficients for C02 limitation (mg/ L)

SPECIES	PS2C02	pH RANGE	REFERENCE
Chlore11a vulgaris	0.20	7.1-7.2	Goldman and Graham 1981
Chlorella emersonii	0.068-.411		Beardall and Raven 1981
Mixed bluegreen algae	0.088		Golterrnan 1975
Mixed bluegreen algae	0.031		Forester 1971
Mixed bluegreen algae	0.057		Shamieh 1968
Scenedesmus quadricauda	0.14	7.1-7.2	Goldman et al. 1974
Scenedesmus quadricauda	0.36	7.25-7.39	Goldman et al. 1974
Scenedesmus quadricauda	0.54-.71	7.44-7.61	Goldman et al. 1974
Scenedesmus capricornutum	0.40-.41	7.05-7.2	Goldman et al. 1974
Scenedesmus capricornutum	0.63-1.0	7.25-7.39	Goldman et al. 1974
Scenedesmus capricornutum	1.2-1.5	7.43-7.59	Goldman et al. 1974
Scenedesmus ob1iquU5	0.16	7.1-7.2	Goldman and Graham 19B1

PS2L

48. PS2L is the light half-saturation coefficient expressed as kcal/m^2/hr. It is the light intensity at which the rate of production is at one-half the maximum rate.

49. The shape of the curve relating light and production has been studied extensively. It is generally known that (a) at lower light intensities, production proceeds linearly with increasing light intensity and (b) as intensity is increased further, the production rate tends towards a maximum value. The simplest representation of this response is the Monad function.

50. It has been shown that the photosynthetic rate of certain algal species is inhibited at high light intensities. This phenomenon cannot be simulated by the Monad function used in CE-QUAL-Rl. Other formulations have been developed to represent this effect (Steele 1962). Photoinhibition at high light intensities may be more important in oligotrophic waters than in eutrophic waters.

51. The value of this parameter can be obtained by running a set of experiments to determine the production rate at various light intensities ranging from light-limiting to light-saturating conditions. The value can be determined for net photosynthetic rate by measuring l4carbon, fixed or oxygen evolved, at different light levels. The light half-saturation constant for growth rate can be determined by measuring growth rate (i.e., by measuring either dry weight, cell volume, chlorophyll concentration, or optical density) at variuos light intensities. Values for the HSC for light intensity are given in Table 10.

Table 10

Phytoplankton half-saturation coefficients for light limitation

(kca1/m^2/hr)

SPECIES	PS2L	PROCESS	REFERENCE
Amphidinium carteri	5.75		Dunstan 1973
Amphiprora sp.	6.42	growth	Admiraal 1977
ChIarella pyrenoidosa	12.7-38.0	photos}'n	Myers and Graham 1961
Chlorophyte	1.2-4.2		Bates 1976
Chroomonas salina	6.25	growth	Hobson 1974
Caccolithus hux1eyi	1.2		Parsons & Takahashi 1973
Coccolithus huxleyi	5.75		Dunstan 197)
Cryptomonas ovata	16.0	growth	Cloern 1977
Cyclotella nana	5.15	growth	Dunstan 1973
Ditylum brightwelli	5••		Bates 1976
Fragi1aria sp.	9.'	growth	Rhee and Gotham 1981b
Gonyaulax polyedra	15.4-18.9	growth	Preze1in and Sweeney 1977
Gonyaulax polyedra	15.4-19.1	photosyn	Preze1in and Sweeney 1977
Isochrysis ga1bana	6.18		Dunstan 1973
Isochrysis sp.	5.0	growth	Hobson 1974
Mixed population	16.0	growth	Gargas 1975
Navicula arenaria	6.42	growth	Admiraal 1977
Nitzschia dissipata	6.64	growth	Admiraal 1977
Oscil1atoria agardhii	0.8	growth	van Lierre et al. 1978
Phaeodactylum tricornutum	51.0-71.4	photosyn	Li and Morris 1982
Prorocentrum micans	5.66		Dunstan 1973
Scenedesmus protuberans	2.57	growth	van Lierre et al. 1978
Scenedesmus sp.	6.0	growth	Rhee and Gotham 1981b
Scenedesmus sp.	6.8	photosyn	Rhee and Gotham 1981b
Skeletonema costaturn	0.18-4.2		Bates 1976
Thalassiosira fluvatilis	6.25	growth	Hobson 1974
Thalassiosira nordenskioldii	12.0	growth	Durbin 1974

ALGTI, ALGT2, ALGT3, ALGT4

52. All temperature coefficients are in degrees Celsius.

a. ALGTl is the lower temperature bound at which phytoplankton metabolism continues.

b. ALGT2 is the lowest temperature at which processes are occurring near the maximum rate.

c. ALGT3 is the upper temperature at which processes are occurring at the maximum rate.

d. ALGT4 is the upper lethal temperature. Biological temperature curves are generally asymmetrical, with the maximum rates occurring nearer the upper lethal temperatures than the lower temperatures.

53. Temperature acclimation. The temperature coefficients for algal production are dependent upon the acclimation temperature and the length of time the alga has been exposed to this temperature (Collins and Boylen 1982b) since algae are exposed to seasonal temperature changes in various regions of the United States. For example, algae growing in a northern reservoir will have a lower optimum temperature (ALGT2 and ALGT3) than algae growing in a southern reservoir because the northern algae have become acclimated to different climatic regimes. The lower and upper temperature boundaries (ALGTl and ALGT4) will also be affected by acclimation and will differ substantially among different functional groups of algae.

54. Unfortunately, there is no set rule to determine these coefficients based upon site-specific temperature regimes. One can estimate these values for a given species or functional group based upon reported experimental conditions or in situ study conditions. Several investigators have determined these values based upon studies where several physical factors such as light intensity,

temperature, and day length have been varied simultaneously. Often the algae were preconditioned at a specific combination of these factors, which may help in parameter estimation for a particular site. Values for the temperature coefficients are given in Table 11.

Table 11
Temperature coefficients for phytoplankton (OC)

SPECIES	ALGT1	ALGT2	ALGT3	ALGT4	REFERENCE
Amphidinium carteri	18	24		35	Jitts et al. 1964
Anacystis nidulans		38	40		Castenholz 1969
Asterionella formosa		2S	25		Rhee and Cotham 1981a
Asterionella formosa		25	29		Hutchinson 1967
Asterionella formosa	4	20	2S		Talling 1955
Chlorella pyrenoidosa	1	28	38	40	Clendenning et al. 1956
Chlorella pyrenoidosa	7	38	40	42	Sorokin & Krauss 1962
ChIorella sp.		20	25		Tamiya et al. 1965
Detonula confervacea	0	10	12	16	Guillard , Ryther 1962
Detonula confervacea	1	10	13	15	Smayda 1969
Ditylum brightwel1ii	5	23	26	30	Paasche 1968
Ounaliella teriolecta	8	31	33	36	Eppley and Sloan 1966
Dunaliella teriolecta	12	26	28	36	Jitts et al. 1964
Microcystis aeruginosa		38	40		Castenholz 1969
Monochrysis lutheri	9	19	22		Jitts et al. 1964
Nitzschia closterium		27	30		Harvey 1955
Nostoc muscorum	1	31	33	36	Clendenning et al. 1956
Oscillatoria terebriformis		38	40		Castenholz 1969
Phaeodactylum tricornutum	0	20	21	30	Li and Morris 1982
Rhiz.osolenia fragillissima	7	21			Jgnatiades and Smayda 1970
Scenedesmus sp.		19	20	21	Rhee and Gotham 1981a
Skeletonema costatum	1	20			Jorgensen 1968
Skeletonema costatum	2	20			Steemann-Nielsen and Jorgensen 1968
Thalassiosira nordenskioldii	4	13	14	16	Jitts et a1. 1964