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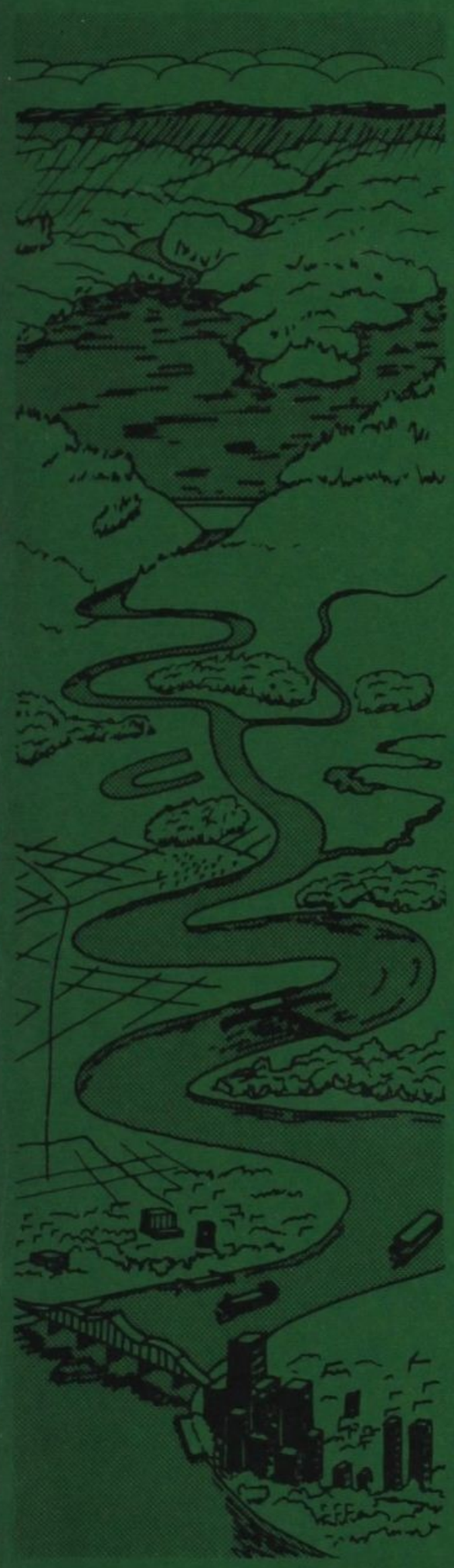

ENVIRONMENTAL & WATER QUALITY OPERATIONAL STUDIES

TECHNICAL REPORT E-83-15

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

by

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October 1983

Final Report

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Washington, D. C. 20314

Under EWQOS Work Unit IB.1

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE

READ INSTRUCTIONS BEFORE COMPLETING FORM

1. REPORT NUMBER
Technical Report E-83-15

2. GOVT ACCESSION NO.

3. RECIPIENT'S CATALOG NUMBER

4. TITLE (and Subtitle)
COEFFICIENTS FOR USE IN THE U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE-QUAL-R1

5. TYPE OF REPORT & PERIOD COVERED
Final report

6. PERFORMING ORG. REPORT NUMBER

7. AUTHOR(s)
Carol D. Collins and Joseph H. Wlosinski

8. CONTRACT OR GRANT NUMBER(s)

9. PERFORMING ORGANIZATION NAME AND ADDRESS
U. S. Army Engineer Waterways Experiment Station, Environmental Laboratory, P. O. Box 631, Vicksburg, Miss. 39180

10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
EWQOS Work Unit IB.1

11. CONTROLLING OFFICE NAME AND ADDRESS
Office, Chief of Engineers, U. S. Army
Washington, D. C. 20314

12. REPORT DATE
October 1983

13. NUMBER OF PAGES
120

14. MONITORING AGENCY NAME & ADDRESS(if different from Controlling Office)

15. SECURITY CLASS. (of this report)
Unclassified

15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)
Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, Va. 22151.

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)
Algorithms
CE-QUAL-R1 (Computer program)
Computer programs
Reservoirs
Water quality

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

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-QUAL-R1. 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

(Continued)

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

20. ABSTRACT (Continued).

Instruction Report E-82-1 entitled "CE-QUAL-R1: A Numerical One-Dimensional Model of Reservoir Water Quality; User's Manual," available from the Environmental Laboratory, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss.

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.

This report should be cited as follows:

> Collins, C. D., and Wlosinski, J. H. 1983. "Coefficients for the U. S. Army Corps of Engineers Reservoir Model, CE-QUAL-R1," Technical Report E-83-15, U. S. Army Engineer Waterways Experiment Station, Vicksburg, Miss.

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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
BENT2	62	198
BENT3	62	198
BENT4	62	198
BS2SED	60	197
DETT1	72	199
DETT2	72	199
DOMT1	84	209
DOMT2	84	209
EXCO	13	182
EXTINP	15	187
EXTINS	15	182
FEFFIC	69	203,204,205
FSHT1	66	203,204,205
FSHT2	66	203,204,205
FSHT3	66	203,204,205
FSHT4	66	203,204,205
FS2BEN	63	201
FS2FSH	63	201
FS2ZOO	63	201
F2ALG	64	202
F2DET	64	202
F2ZOO	64	202
F3BEN	64	202
F3SED	64	202
NH3T1	85	210
NH3T2	85	210
NO2T1	86	211
NO2T2	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
PS2CO2	38	191,192
PS2L	40	191,192
PS2N	34	190,192
PS2PO4	32	190,192
Q10COL	86	213
TBMAX	56	197
TBMORT	59	197
TBRESP	60	197
TCOLDK	80	207
TDETDK	77	207
TDOMDK	73	207
TDSETL	71	199
TFMAX	63	201
TFMORT	69	203,204,205
TFRESP	70	203,204,205
TNH3DK	75	207
TNO2DK	77	207
TPMAX	20	189,192
TPRESP	18	187
TSEDDK	84	207
TSETL	28	212
TSSETL	86	189,192
TZMAX	44	195
TZMORT	46	195
TZRESP	51	195
ZEFFIC	47	195
ZOOT1	53	196
ZOOT2	53	196
ZOOT3	53	196
ZOOT4	53	196
ZS2P	53	196

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 1/day. Assimilation efficiency is dimensionless and is multiplied by ingestion to account for the assimilation rate. In the literature, ingestion (I) 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 (S), eggs or young (Y), harvest (H), and the change in weight (WT).

7. In CE-QUAL-R1 predictions are made regarding WT. In the literature it usually equals

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

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 (1/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-R1 and CE-THERM-R1, 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 1-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-R1 and CE-THERM-R1. In CE-THERM-R1, 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 (SS) compartment has been incremented in value to include organic as well as inorganic particulates suspended in the water column, then EXTINS (1/m*mg/L) represents the extinction coefficient for all suspended solids, including inorganic matter, phytoplankton, zooplankton, and suspended detritus. However, if the SS compartment in CE-THERM-R1 does not include organic particulates--i.e., if the magnitude of SS is identical in CE-QUAL-R1 and CE-THERM-R1--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 EXTINS 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-R1 (1/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-R1 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 0.016/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 0.047/m*mg/L. Values near 0.10 have previously produced reasonable results (Environmental Laboratory 1982).

15. Light extinction by algae is computed from in situ light intensity measurements at depth intervals and in situ 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 a 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 1/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 chl a/L, and have been converted to units used in CE-QUAL-R1 assuming a C/chl ratio of 50 and a C/biomass ratio of 0.45.

Table 3

Self-shading coefficients due to particulate matter (1/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/Chl 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 (1/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 pO2 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 diel 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 1/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 1-hr time period.

Table 4

Phytoplankton dark respiration rates (1/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 (1/day). CE-QUAL-R1 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 ^{14}carbon 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 ^{14}carbon 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 $H^{14}CO3$ 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

$$dN/dt = k*N \tag{8}$$

where

N = the number or concentration of cells in the culture

t = the time

k = the growth constant - (1/t)

The solution to this equation is

$$k = \ln(N/N_o)/(t-t_o) \tag{9}$$

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

$$k_{10} = \log(N/N_o)/(t-t_o) \tag{10}$$

$$k_2 = \log_2 (N/N_o)/(t-t_o) \tag{11}$$

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 $\log_2$ units

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

$$N = 2$$
$$N_o = 1$$
$$t-t_o = 1$$

and

$$k = 0.693 = \ln 2 \tag{12}$$
$$k_{10} = 0.301 = \log_{10} 2,\ k = 2.3026\ k_{10} \tag{13}$$
$$k_2 = 1.0 = \log_2 2,\ k = 0.6931\ k_2 \tag{14}$$

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

$$N = 4$$
$$N_o = 1$$
$$t-t_o = 1$$

and

$$k = 1.386 = \ln 4 \tag{15}$$
$$k_{10} = 0.602 = \log_{10} 4,\ k = 2.3026\ k_{10} \tag{16}$$
$$k_2 = 2.0 = \log_2 4,\ k = 0.6931\ k_2 \tag{17}$$

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

$$N = 0.5$$
$$N_o = 1$$
$$t-t_o = 1$$

and let

$$k = -0.693 \tag{18}$$
$$k_{10} = -0.301,\ k = 2.3026\ k_{10} \tag{19}$$
$$k_2 = -1.0,\ k = 0.6931\ k_2 \tag{20}$$

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

$$k = 2.3026\ k_{10} \tag{21}$$
$$k = 0.6931\ k_2 \tag{22}$$

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 (1/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	4	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	1.9	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	Castenholz 1964
Navicula minima	1.4	25	Hoogenhout and Amesz 1965
Navicula pelliculosa	2.0	20	Hoogenhout 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
Phaeodactylum tricornutum	2.7	19	Hoogenhout and Amesz 1965
Rhizosolenia fragillissima	1.20	21	Ignatiades & Smayda 1970
Skeletonema costatum	1.26	18	Fogg 1969
Skeletonema costatum	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	Castenholz 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		4.2	Hoogenhout and Amesz 1965
Chlorella pyrenoidosa	2.22	28	Shelef 1968
Chlorella ellipsoidea	3.6	25	Hoogenhout and Amesz 1965
Chlorella luteoviridis	0.56	22.4	Hoogenhout and Amesz 1965
Chlorella 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	Castenholz 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
Dunaliella tertiolecta	1.0	16	Hoogenhout and Amesz 1965
Dunaliella tertiolecta	0.77	36	Jitts et al. 1964
Haematococcus pluvialis	1.2	23	Hoogenhout and Amesz 1965
Nanochloris atomus	1.0	20	Hoogenhout and Amesz 1965
Platymonas subcordiformia	1.5	16	Hoogenhout and Amesz 1965
Scenedesmus sp.	1.34	20	Rhee and Gotham 1981b
Scenedesmus costulatus	2.0	24.5	Hoogenhout and Amesz 1965
Scenedesmus obliquus	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 al. 1972
Selenastrum westii	1.0	25	Hoogenhout and Amesz 1965
Stichococcus sp.	0.70	20	Hoogenhout and Amesz 1965
GOLDEN-BROWN			
Botrydiopsis intercedens	1.5	25	Hoogenhout and Amesz 1965
Bumilleriopsis brevis	2.9	25	Hoogenhout and Amesz 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
Monodus 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	Hoogenhout and Amesz 1965
Euglena gracilis	2.2	25	Hoogenhout and Amesz 1965
Euglena gracilis	0.00	36	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 polyedra	2.1	21.5	Hoogenhout and Amesz 1965
Gymnodinium splendens	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	Fogg 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 variabilis	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
Chloropseudomonas ethylicum	3.3	30	Hoogenhout and Amesz 1965
Cyanidium caldarium	2.4	40	Hoogenhout and Amesz 1965
Cylindrospermum sphaerica	0.17	25	Hoogenhout and Amesz 1965
Gloeotrichia echinulata	0.20	26.5	Hoogenhout and Amesz 1965
Microcystis aeruginosa	0.25	20	Holm and Armstrong 1981
Microcystis aeruginosa	1.6	23	Hoogenhout and Amesz 1965
Microcystis luminmosis	1.50	40	Castenholz 1969
Nostoc muscorum	2.9	32.5	Hoogenhout and Amesz 1965
Oscillatoria princips	0.50	40	Castenholz 1969
Oscillatoria subbrevis	5.52	38	Marre 1962
Oscillatoria terebriformis	3.36	40	Castenholz 1969
Oscillatoria rubescens	5.04	30	Zimmerman 1969
Rhodopseudomonas sphaeroides	10.8	34	Hoogenhout and Amesz 1965
Rhodospirllum rubrum	4.85	25	Hoogenhout and Amesz 1965
Schizothrix calcicola	3.4	30	Hoogenhout and Amesz 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 (m/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 1-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
Ditylum 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 (unpubl.)
Thalassiosira fluviatilis	0.60-1.10	Eppley et al. 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 al. 1967b
Coccolithus huxleyi	1.20	Eppley et al. 1967b
Cricosphaera carterae	1.70	Eppley et al. 1967b
Cricosphaera elongata	0.25	Eppley et al. 1967b
Cyclococcolithus fracilis	13.2	Bernard 1963
Cyclococcolithus fragilis	13.6	Bernard 1963
Cyclococcolithus 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 al. 1967b
Monochrysis lutheri	0.39	Eppley et al. 1967b
Monochrysis lutheri	0.39	Apstein 1910
GREENS EXPERIMENTAL		
Closterium parvulum	0.18	Burns and Rosa 1980
Dunaliella tertiolecta	0.18	Eppley et al. 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 (HSC) (mg/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 Monod kinetics. The value of the HSC can be calculated for the hyperbola using the Monod 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 al. 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	PS2PO4	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
Chlorella 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 Lembi 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 (NO3) or ammonium (NH4) by algae give hyperbolas when graphed against NO3 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 Monod 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 NO3 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 NO3 and NH4. 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 8

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

SPECIES	PS2N	N SOURCE	REFERENCE
DIATOMS			
Biddulphia aurita	0.056-.197	NO3	Underhill 1977
Chaetoceros gracilis	0.012	NO3	Eppley et al. 1969
Chaetoceros gracilis	0.007	NO4	Eppley et al. 1969
Coscinodiscus lineatus	0.161	NO3	Eppley et al. 1969
Coscinodiscus lineatus	0.036	NH4	Eppley et al. 1969
Cyclotella nana	0.025-.117	NO3	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	NH4	Eppley et al. 1969
Ditylum brightwellii	0.037	NO3	Eppley et al. 1969
Ditylum brightwellii	0.020	NH4	Eppley et al. 1969
Dunaliella teriolecta	0.013	NO3	Caperon and Meyer 1972
Dunaliella teriolecta	0.003	NH4	Caperon and Meyer 1972
Dunaliella teriolecta	0.087	NO3	Eppley et al. 1969
Fragilaria pinnata	0.037-.100	NO3	Carpenter & Guillard 1971
Leptocylindrous danicus	0.078	NO3	Eppley et al. 1969
Leptocylindrous danicus	0.013	NH4	Eppley et al. 1969
Navicula pelliculosa	0.923	NO3	Wallen and Cartier 1975
Phaeodactylum tricornutum	0.161	NO3	Ketchum 1939
Rhizosolenia robusta	0.186	NO3	Eppley et al. 1969
Rhizosolenia robusta	0.135	NH4	Eppley et al. 1969
Rhizosolenia stolterfothii	0.105	NO3	Eppley et al. 1969
Rhizosolenia stolterfothii	0.009	NH4	Eppley et al. 1969
Skeletonema costatum	0.027	NO3	Eppley et al. 1969
Skeletonema costatum	0.014	NH4	Eppley et al. 1969
BLUEGREENS			
Anabaena cylindrica	4.34	NO3	Hattori 1962
Anabaena cylindrica	2.48	NO2	Hattori 1962
Asterionella formosa	0.074-.093	NO3	Eppley and Thomas 1969
Asterionella formosa	0.062	NH4	Eppley and Thomas 1969
Microcystis aeruginosa	0.56-.207	NH4	Kappers 1980
Oscillatoria agarthii	0.22	NO3	van Liere et al. 1975
MICROFLAGELLATES			
Bellochia sp.	0.001-.016	NO3	Carpenter & Guillard 1971
Monochrysis lutheri	0.026	NO3	Caperon and Meyer 1972
Monochrysis lutheri	0.052	NH4	Caperon and Meyer 1972
Monochrysis lutheri	0.037	NO3	Eppley et al. 1969
Monochrysis lutheri	0.007	NH4	Eppley et al. 1969
COCCOLITHOPHORIDS			
Coccolithus huxleyi	0.006	NO3	Eppley et al. 1969
Coccolithus huxleyi	0.002	NH4	Eppley et al. 1969
Coccochloris stagnina	0.019	NO3	Caperon and Meyer 1972

(continued)

Table 8 (concluded)

SPECIES	PS2N	N SOURCE	REFERENCE
GREENS			
Chlorella pyrendoidosa	0.006-.014		Pickett 1975
Chlorella pyrendoidosa	1.15	NO2	Knudsen 1965
Pithophora oedogonia	1.236	NO3	Spencer and Lembi 1981
DINOFLAGELLATES			
Gonyaulax polyedra	0.589	NO3	Eppley et al. 1969
Gonyaulax polyedra	0.099	NH4	Eppley et al. 1969
Gymnodinium splendens	0.235	NO3	Eppley et al. 1969
Gymnodinium splendens	0.019	NH4	Eppley et al. 1969
Gymnodinium wailesii	0.223	NO3	Eppley et al. 1969
Gymnodinium wailesii	0.088	NH4	Eppley et al. 1969
CHRYSOPHYTES			
Isochrysis galbana	0.006	NO3	Eppley et al. 1969

PS2C02

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 CO2 limitation. PS2CO2 is defined as the concentration of CO2 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 CO2 availability limits the growth of aquatic populations. Johnson et al. (1970) demonstrated CO2 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 CO2 limitation (mg/L)

SPECIES	PS2CO2	pH RANGE	REFERENCE
Chlorella 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		Golterman 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 obliquus	0.16	7.1-7.2	Goldman and Graham 1981

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 Monod 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 Monod function used in CE-QUAL-R1. 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 ^{14}carbon, 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 ($kcal/m^2/hr$)

SPECIES	PS2L	PROCESS	REFERENCE
Amphidinium carteri	5.75		Dunstan 1973
Amphiprora sp.	6.42	growth	Admiraal 1977
Chlorella pyrenoidosa	12.7-38.0	photosyn	Myers and Graham 1961
Chlorophyte	1.2-4.2		Bates 1976
Chroomonas salina	6.25	growth	Hobson 1974
Coccolithus huxleyi	1.2		Parsons & Takahashi 1973
Coccolithus huxleyi	5.75		Dunstan 1973
Cryptomonas ovata	16.0	growth	Cloern 1977
Cyclotella nana	5.15	growth	Dunstan 1973
Ditylum brightwelli	5.4		Bates 1976
Fragilaria sp.	9.4	growth	Rhee and Gotham 1981b
Gonyaulax polyedra	15.4-18.9	growth	Prezelin and Sweeney 1977
Gonyaulax polyedra	15.4-19.1	photosyn	Prezelin and Sweeney 1977
Isochrysis galbana	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
Oscillatoria 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 costatum	0.18-4.2		Bates 1976
Thalassiosira fluvatilis	6.25	growth	Hobson 1974
Thalassiosira nordenskioldii	12.0	growth	Durbin 1974

ALGT1, ALGT2, ALGT3, ALGT4

52. All temperature coefficients are in degrees Celsius.

a. ALGT1 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 (ALGT1 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 (°C)

SPECIES	ALGT1	ALGT2	ALGT3	ALGT4	REFERENCE
Amphidinium carteri	18	24		35	Jitts et al. 1964
Anacystis nidulans		38	40		Castenholz 1969
Asterionella formosa		25	25		Rhee and Gotham 1981a
Asterionella formosa		25	29		Hutchinson 1967
Asterionella formosa	4	20	25		Talling 1955
Chlorella pyrenoidosa	1	28	38	40	Clendenning et al. 1956
Chlorella pyrenoidosa	7	38	40	42	Sorokin & Krauss 1962
Chlorella 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 brightwellii	5	23	26	30	Paasche 1968
Dunaliella 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
Rhizosolenia fragillissima	7	21			Ignatiades 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 al. 1964

Zooplankton

TZMAX

55. TZMAX is the maximum ingestion rate for zooplankton (1/day). The zooplankton compartment includes the groups Cladocera, Copepoda, and Rotatoria which are classified as either herbivores or as carnivores.

56. Two types of feeding behavior exist: filter feeding and grasping feeding. *Daphnia* and some copepods are filter feeders. They collect particulate matter, including algae and detritus, by sieving lake water through the fine meshes of their filtering apparatus (Jorgensen 1975). Algae are swept into the feeding appendages to the mouth region where they are ingested as boluses containing many cells. Filter-feeding zooplankton make up the greater proportion of the zooplankton community and have been studied in greater detail.

57. The filtering rate per animal decreases as food concentration increases; above a critical concentration of food, the feeding rate is independent of food concentration.

58. Factors that influence food consumption by filter-feeding zooplankton include (a) animal density, size, sex, reproductive state, nutritional or physiological state as well as (b) the type, quality, concentration, and particle size of food. Other factors include water quality and temperature.

59. A second type of feeding behavior, raptorial or grasping feeding, is exhibited by most copepods and some cladocerans. They pursue prey and grasp large particles, including algae and detritus. Apparently, some copepods can switch feeding modes.

60. Several experiments have been able to demonstrate a maximum grazing rate allowing for long-term acclimation to food concentration above the incipient limiting level. Values for TZMAX range from 0.045 to 3.44 1/day.

61. Dissolved organic matter (DOM) is another potential source of food for zooplankters, although this feeding transfer is not modeled in CE-QUAL-R1. Values for maximum ingestion rates for zooplankton are given in Table 12.

Table 12

Maximum ingestion rates for zooplankton (1/day)

PREDATOR	VALUE	FOOD SOURCE	REFERENCE
Bosmina	0.01	detritus	Bogdan and McNaught 1975
Brachionus rubens	3.438	Chlorella vulgaris	Pilarska 1977
Cladocerans	0.15	detritus	Bogdan and McNaught 1975
Copepods	0.10	detritus	Bogdan and McNaught 1975
Daphnia	0.01	detritus	Bogdan and McNaught 1975
Daphnia magna	0.251	Saccharomyces cervisiae	McMahon and Rigler 1965
Daphnia magna	0.452	Tetrahymena pyriformis	McMahon and Rigler 1965
Daphnia magna	0.301	Chlorella vulgaris	McMahon and Rigler 1965
Daphnia magna	0.045	Escherichia coli	McMahon and Rigler 1965
Daphnia magna	0.760	Chlorella vulgaris	Kersting and Van De Leeuw-Leegwater 1976
Daphnia magna	0.350	Saccharomyces cerivisiae	Rigler 1961
Daphnia magna	1.9	Chlorella vulgaris	Ryther 1954
Daphnia magna	2.2	Navicula pelliculosa	Ryther 1954
Daphnia magna	2.3	Scenedesmus quadricauda	Ryther 1954
Daphnia pulex	0.120	Chlorococcum sp.	Monokov and Sorokin 1961
Daphnia rosea	0.900	Rhodotorula glutinis	Burns and Rigler 1967
Diaptomus	0.47	detritus	Bogdan and McNaught 1975
IN SITU EXPERIMENTS			
Heart Lake, Canada	0.801	Various	Haney 1973
Lake Vechten, The Netherlands	0.24	Various	Gulati 1978
Lake Krasnoye, USSR	1.20	Various	Andronikova 1978

TZMORT

62. TZMORT is the maximum nonpredatory mortality rate for zooplankton (1/day). Nonpredatory mortality rate may be obtained by measuring total mortality and predatory mortality and subtracting to obtain the difference (a direct approach is to measure mortality rate and eliminate predators altogether). Nonpredatory mortality may be influenced by oxygen concentration, temperature, diet, age, and population density. Nonpredatory mortality rates are normally less than 1 percent per day. Values for maximum nonpredatory mortality rate are given in Table 13.

Table 13

Zooplankton mortality rates (1/day)

SPECIES	TZMORT	REFERENCE
Calanus helgolandicus	0.003-0.048	Paffenhoffer 1976
Calanus helgolandicus	0.024	Mullin and Brooks 1970
Carnivorous zooplankton	0.002-0.013	Petipa et al. 1970
Ceriodaphnia reticulata	0.0016	Clark and Carter 1974
Copepod nauplii	0.006-0.017	Petipa et al. 1970
Daphnia galeata	0.017	Hall 1964
Daphnia pulex	0.012	Craddock 1976
Daphnia pulex	0.018-0.027	Frank et al. 1957
Daphnia retrocurva	0.001	Clark and Carter 1974
Daphnia rosea	0.001-0.007	Dodson 1972
Daphnia rosea	0.001	Clark and Carter 1974
Daphnia spp.	0.002	Wright 1965
Diaptomus clavipes	0.004-0.155	Gehrs and Robertson 1975
Diaphanosoma leuchtenbergiana	0.001	Clark and Carter 1974
Omnivorous zooplankton	0.010-0.013	Petipa et al. 1970
Paracalanus sp.	0.003-0.006	Petipa et al. 1970
Rhincalanus nasutus	0.006-0.015	Mullin and Brooks 1970
Simocephalus serrulatus	0.003	Hall et al. 1970

ZEFFIC

63. ZEFFIC, the zooplankton assimilation efficiency (A/G) (dimensionless), is the proportion of food consumed (G) to food assimilated (A), i.e., food actually absorbed from an individual's digestive system. The assimilation efficiency is used to modify consumption and to determine the quantity of energy entering an individual or population.

64. Of the factors affecting assimilation efficiency, the most significant is food type. For herbivores-detrivores, the range in ZEFFIC is wide because these animals often consume foods of varying energy content and digestibility. Among the carnivores, for which food type varies little, A/G ranges between 0.80 and 0.95. Values for zooplankton assimilation efficiency are given in Table 14.

Table 14

Zooplankton assimilation efficiency coefficients (dimensionless)

SPECIES	ZEFFIC	REFERENCE
Acartia clausi	0.66-0.73	Penchen'-Finenko 1977
Bosmina coregoni	0.09-0.77	Semenova 1974
Bosmina longirostris	0.32-0.31	Gutel'mackher 1977
Calanus firmarchicus	0.48-0.96	Marshall and Orr 1956
Calamoecia lucase	0.63-0.67	Green 1975
Ceriodaphnia reticulata	0.106	Czeczuga & Bobiatynska-Ksok 1970
Ceriodaphnia reticulata	0.47-0.73	Czeczuga & Bobiatynska-Ksok 1970
Cyclops strennus	0.50	Schindler 1971
Cyclops vicimus	0.80	Monakov 1972
Daphnia longispina	0.10-0.25	Monakov & Sorokin 1961
Daphnia longispina	0.42	Monakov 1972
Daphnia magna	0.60-0.84	Schindler 1968
Daphnia pulex	0.14-0.31	Richman 1958
Daphnia schodleri	0.60-0.90	Hayward & Gallup 1976
Daphnia sp.	0.08-0.25	Cohn 1958
Diaptomus graciloides	0.81	Penchen'-Finenko 1977
Diaptomus graciloides	0.45-0.50	Klekowski & Shushkina 1966
Diaptomus siciloides	0.40-0.83	Comita 1972
Diaptomus oregonensis	0.77	Richman 1964
Eurycercus lamellatic	0.07-0.32	Smirnov 1962
Holopedium gibberrum	0.10-0.47	Gutel'mackher 1977
Leptodora kindtii	0.40	Cummins et al. 1969
Leptodora kindtii	0.87	Hillbricht-Ilkowska & Karabin 1970
Macrocyclops albidus	0.45-0.50	Klekowski & Shushkina 1966
Mesocyclops albidus	0.20-0.75	Klekowski & Shushkina 1966
Polyphemus pediculus	0.42	Monokov 1972
Sida crystallima	0.17-0.99	Monakov 1972
Simocephalus espinosus	0.46	Sorokin 1969
Simocephalus vetulus	0.31-0.72	Klekowski 1970
Simocephalus vetulus	0.31-0.72	Ivanova & Klekowski 1972
10 herbivores	0.476	Comita 1972

PREF1, PREF2, PREF3

65. All zooplankters are selective feeders resulting from a combination of (a) an organism's mechanical limitations in capturing and processing food items of varying size and configuation, (b) the chemical composition of the food items, and (c) feeding behavior. Food preference is demonstrated if an organism consumes a food item in a proportion different from the food item's relative contribution to the total of all available foods in the environment. If all foods occur at the same concentration, then the preference factors equal the fractions of ingestion contributed by each food compartment. Seasonal abundance of phytoplankton, bacteria, and detritus may be the main factor determining the percent composition of these components in the diets of many zooplankters.

66. Filamentous bluegreen algae are generally not considered to be as assimilable as are other algal species. They are seldom found in the guts of zooplankton, because they either are not eaten or are actively rejected. Most species of green algae and diatoms are filtered at about the same rate and digested. However, it is not necessarily the taxonomic position of the alga that makes it suitable or unsuitable as food, but rather the attributes of each algal species such as size, shape, and toxicity.

67. Although ample evidence exists to show that detritus is consumed by zooplankton, no evidence exists to show that it is consumed preferentially; rather, detritus is ingested in proportion to its composition in the environment. When detritus is included as a food source in a grazing formulation, it should be given equal ranking with other suitable foods. It should be noted that bacteria that colonize detritus constitute an important source of protein in the diet.

68. Filter feeders discriminate among particles on the basis of size, shape, and texture. There are upper and lower limits to the sizes of particles that can be managed by zooplankton feeding appendages. Particles of 0.8 μ and larger can be retained; an upper limit is related to the size of the animal. Algae that clog the filtering appendages are rejected from them by a claw on the lower abdomen.

69. Raptorial feeders can sieze large prey and tear it apart before eating (Ambler and Frost 1974, Brandl and Fernando 1975), but there are limits to the size of prey they capture.

70. PREF1 is the preference factor of zooplankton for the ALGAE1 compartment, PREF2 is the preference factor of zooplankton for the ALGAE2 compartment, and PREF3 is the preference factor of zooplankton for the detritus compartment. The food preference factors are dimensionless; the total of the three factors must equal 1. Values for these preference factors are given in Table 15.

Table 15

Food preference factors of zooplankton (dimensionless)

PREDATOR	PREF	PREY	REFERENCE
Bosmina	0.33	nannoplankton	Bogdan and McNaught 1975
Bosmina	0.33	netplankton	Bogdan and McNaught 1975
Cladocerans	0.30	nannoplankton	Bogdan and McNaught 1975
Cladocerans	0.30	netplankton	Bogdan and McNaught 1975
Cladocerans	0.20	bluegreen algae	Bogdan and McNaught 1975
Copepods	0.45	nannoplankton	Bogdan and McNaught 1975
Copepods	0.15	netplankton	Bogdan and McNaught 1975
Copepods	0.20	bluegreen algae	Bogdan and McNaught 1975
Daphnia	0.33	nannoplankton	Bodgan and McNaught 1975
Daphnia	0.17	netplankton	Bogdan and McNaught 1975
Diaptomus	0.40	nannoplankton	Bogdan and McNaught 1975
Diaptomus	0.17	netplankton	Bogdan and McNaught 1975

TZRESP

71. TZRESP is the maximum zooplankton respiration rate (1/day). Respiration is the sum of all physical and chemical processes by which organisms oxidize organic matter to produce energy. Respiration rates of aquatic invertebrates usually are estimated directly by monitoring oxygen consumption. By multiplying oxygen consumed times an oxycaloric coefficient (i.e., 4.83 cal/ml 02 (Winberg et al. 1934)) and the energy-to-carbon relation for aquatic invertebrates (i.e., 10.98 cal/mg C (Salonen et al. 1976)), the amount of carbon metabolized can be determined and converted to biomass.

72. Conover (1960) has indicated that carnivores have higher respiration rates than herbivores. Values for maximum zooplankton respiration rates are given in Table 16.

Table 16

Zooplankton maximum respiration rates (1/day)

SPECIES	TZRESP	REFERENCE
Bosmina coregoni	0.170	Manuilova 1958
Bosmina longirostris	0.185	Sushchenya 1958
Ceriodaphnia reticulata	0.18-.50	Gophen 1976
Copepoda	0.075-.204	Bishop, 1968
Copepod adults	0.043-.131	Williams 1982
Copepod copepodites	0.054-.171	Williams 1982
Copepod nauplii	0.165-.695	Williams 1982
Copepod total	0.056-.183	Williams 1982
Daphnia ashlandii	0.447-.74	Duval and Geen 1976
Daphnia clavipes	0.117-.165	Comita 1968
Daphnia cuculata	0.161	Manuilova 1958
Daphnia galeata	0.13-.772	LaRow et al. 1975
Daphnia hyalina	0.179	Blazka 1966
Daphnia longispina	0.121-.135	Tezuka 1971
Daphnia longispina	0.16	Manuilova 1958
Daphnia longispina	0.146	Shushkina and Pecen' 1964
Daphnia magna	0.085-.175	Kersting and Van De Leeuw-Leegwater 1976
Daphnia magna	0.014	Sushchenya 1958
Daphnia oregonesis	0.194	Richman 1964
Daphnia pulex	0.582	Buikema 1972
Daphnia pulex	0.18-.19	Tezuka 1971
Daphnia septopus	0.008-.18	Comita 1968
Daphnia siciloides	0.006-.52	Comita 1968
Diaphanosoma brachyurum	0.272	Sushchenya 1958
Diaptomus kenai	0.272-.448	Duval and Geen 1976
Leptodora kindtii	0.471	Moshiri et al. 1969
Leptodora kindtii	0.125	Hillbricht-Ilkowska and Karabin 1970
Simocephalus vetulus	0.131	Sushchenya 1958
Simocephalus vetulus	0.154	Manuilova 1958
Simocephalus vetulus	0.096-.201	Ivanova and Klekowski 1972
Total zooplankton	0.063-.210	Williams 1982

ZS2P

73. ZS2P is the zooplankton half-saturation coefficient for grazing on algae and detritus (mg/L). It has been found that zooplankton exhibit reduced feeding rates at high food concentrations; the relationship between feeding rate and food concentration has been reported to be curvilinear by a number of investigators (Burns and Rigler 1967, Parsons et al. 1967, McQueen 1970, Frost 1972, Monakov 1972, Gaudy 1974, and Chisholm et al. 1975).

74. The most realistic calculation of zooplankton grazing rate is based on their rate of removal of biomass of food (Mullin 1963); therefore, it is important that investigators report results in terms of biovolume or biomass instead of cell number. The method most used to determine ingestion rate is to count prey in controls and experimental chambers after feeding zooplankton. Values for zooplankton HSC are given in Table 17.

Table 17

Zooplankton half-saturation coefficients (mg/L)

SPECIES	ZS2P	REFERENCE
Bosmina coregoni	4.0	Scavia and Eadie 1976
Daphnia magna	9.6-15.0	Scavia and Eadie 1976
Daphnia rosea	0.16	Scavia and Eadie 1976
Diaptomus oregonensis	1.6	Scavia and Eadie 1976

ZOOT1, ZOOT2, ZOOT3, ZOOT4

75. Values for zooplankton temperature coefficients are given in Table 18.

a. ZOOT1 is the lower temperature bound at which metabolism continues to occur. It is generally 0°C.

b. ZOOT2 is the lowest temperature at which processes are occurring near the maximum rate (°C).
c. ZOOT3 is the upper temperature bounding the range of maximum rates (°C).
d. ZOOT4 is the upper lethal temperature (°C).

Table 18

Zooplankton temperature coefficients (°C)

SPECIES	ZOOT1	ZOOT2	ZOOT3	ZOOT4	REFERENCE
Calamoecia lusasi	NA*	20	24	NA	Green 1975
Ceriodaphnia reticulata	NA	24	27	NA	Gophen 1976
Daphnia galeata	NA	20	24	NA	Burns 1969
Daphnia longispina	NA	16	18	NA	Nauwerck 1959
Daphnia magna	NA	24	26	35	McMahon 1965
Daphnia magna	NA	25	NA	NA	Burns 1969
Daphnia middendorffiana	NA	24	25	NA	Kryutchkova and Kondratyuk 1966
Daphnia pulex	NA	20	24	NA	Burns 1969
Daphnia pulex	NA	20	24	NA	Geller 1975
Daphnia pulex	NA	NA	25	NA	Geller 1975
Daphnia rosea	NA	20	24	NA	Burns & Rigler 1967
Daphnia rosea	NA	14	15	NA	Kibby 1971
Daphnia schedleri	NA	20	22	NA	Burns 1969
Daphnia schedleri	NA	20	24	NA	Hayward & Gallup 1976
Diaptomus sp.	NA	16	18	NA	Nauwerck 1959

* NA = not available.

76. As with the phytoplankton, zooplankton are able to adapt to the ambient temperature with time. This is demonstrable throughout the different regions of the United States and at different times of the year. Zooplankton found in temperate regions of the United States are exposed to lower average temperatures throughout the year and consequently have lower temperature factors (i.e., ZOOT1, ZOOT2, ZOOT3, and ZOOT4) than those found in more southern regions. Again, these values are unavailable from the literature but have been estimated by Leidy and Ploskey (1980) based upon acclimation temperatures (Table 19).

Table 19

Acclimation temperature, upper and lower lethal temperature, and the temperature range for a constant maximum grazing rate for zooplankton exposed to rapid temperature stress (°C) (from Leidy and Ploskey 1980)

Accl. Temp.	ZOOT1	ZOOT2	ZOOT3	ZOOT4
5	0	5	6	25
10	0	10	12	30
15	2	15	18	33
20	5	20	24	33
25	7	25	30	34
29	10	29	34	34
30	10	30	34	34
31	12	31	34	34
34	15	34	34	34
35		lethal		

Table 20

Daily ration of benthic organisms (from Leidy and Ploskey 1980) (l/day)

SPECIES	FOOD	RATION	REFERENCE
NEMATODA			
Aphelenchus avenae	fungal mycelia	0.26	Soyza 1973
Plectus palustris	Acinetobacter sp.	6.50	Duncan et al. 1974
MOLLUSCA			
Dreissena polymorpha	bacteria	0.01-.12	Sorokin 1966
Goniobais clavaeformis	aufwucks	0.01-.24	Malone and Nelson 1969
ARTHROPODA			
Hyalella azteca	sediments	0.17-1.03	Hargrave 1970
Pontogammarus robustoides	Cladophora sp.	0.007-.98	Kititsyna 1975
Pontogammarus robustoides	Tubifex sp.	0.187-1.63	Kititsyna 1975
PODOCOPA			
Chaoborus flavicans	natural phytoplankton population	0.036-.114	Kajak and Dusoge 1970
Herpetocypris reptans	Spirogyra sp.	1.28	Yakovleva 1969
Herpetocypris reptans	Zygnema sp.	0.93	Yakovleva 1969
Herpetocypris reptans	Mougeotia sp.	0.93	Yakovleva 1969
Herpetocypris reptans	Chironomus plumosus	0.66	Yakovleva 1969
Herpetocypris reptans	Asellus aquaticus	0.66	Yakovleva 1969
Herpetocypris reptans	fish fry	1.09	Yakovleva 1969
Procladius choreus	Chironomidae	0.007-.11	Kajak and Dusoge 1970
EPHEMEROPTERA			
Stenonema pulchellum	Navicula minima	0.234	Trama 1972
PLECOPTERA			
Acroneuria californica	Hydropsyche sp.	0.002-.087	Heiman and Knight 1975

Benthos

TBMAX

77. TBMAX is the maximum ingestion rate for benthos (1/day) and is measured at food densities above the incipient limiting food concentration. The food source for this compartment is organic sediment; its dominant members for most reservoir benthic communities are the aquatic oligochaetes and Chironomidae. Filter feeders, predators, deposit feeders, and surface grazers are all represented in most benthic communities.

78. Daily rations (an approximation of the daily grazing rate) of some benthic species compiled by Leidy and Ploskey (1980) are listed in Table 20. Other values for maximum ingestion rate are given in Table 21.

Table 21

Benthos maximum ingestion rates (1/day)

SPECIES	TBMAX	REFERENCE
Acroneuria californica	0.002-.09	Heiman and Knight 1975
Asellus aquaticus	0.25	Prus 1972
Carnivores	0.0282	Bigelow et al 1977
Chaoborus flavicans	0.036-.114	Kajak and Dusoge 1970
Deposit feeder	0.111	Gordon 1966
Hyalella azteca	0.17-1.3	Hargrave 1970
Omnivores	0.043	Bigelow et al. 1977
Pontagammarus robustiodes	0.074-.98	Kititsyna 1975
Procladius choreus	0.07-.11	Kajak and Dusoge 1970
Selective deposit feeder	0.05	Bigelow et al. 1977
Stenonema pulchellum	0.21-.23	Trama 1972

TBMORT

79. TBMORT is the nonpredatory mortality rate for benthos (1/day). Leidy and Ploskey (1980), in their review of the literature, show most benthos nonpredatory mortality rates to be between 0.001 and 0.02/day.

BEFFIC

80. BEFFIC is the assimilation efficiency for benthos (dimensionless). The assimilation efficiency is multiplied by the ingestion rate to obtain an assimilation rate. Values for benthos assimilation efficiency are given in Table 22.

Table 22

Benthos assimilation efficiencies (dimensionless)

SPECIES	VALUE	REFERENCE
Anatopina dijari	0.30	Teal 1957
Asellus aquaticus	0.30	Klekowski 1970
Asellus aquaticus	0.26-0.44	Prus 1971
Bandsiola crotchii	0.31-0.40	Winterbourn 1974
Calopsectra dives	0.20	Teal 1957
Carnivores	0.20-0.97	Lawton 1970
Gammarus pseudolimnaeus	0.10-0.20	Barlocher and Kendrick 1975
Gammarus pseudolimnaeus	0.42-0.75	Barlocher and Kendrick 1975
Gammarus pseudolimnaeus	0.10	Marchant and Hynes 1981
Gammarus pulex	0.30-0.40	Nilsson 1974
Glossosoma nigrior	0.17-0.32	Cummins 1973
Hedriodiscus	0.59	Stockner 1971
Hyalella azeteca	0.05-0.80	Hargrave 1970
Hydrophilus triangularis	0.55	Hallmark and Ward 1972
Lepidostoma	0.07-0.12	Grafius 1973
Lestes sponsa	0.36	Klekowski et al. 1970
Lethocerus americanus	0.07	Guthrie and Brust 1969
Limnodrilus hoffmeisteri	0.5	Teal 1957
Most invertebrates	0.5	Monakov 1972
Potamopyrgres jenkinsi	0.04	Heywood and Edwards 1962
Potomophylax cingulatus	0.10-0.30	Otto 1974
Pteronarcys scotti	0.11	McDiffett 1970
Pyrrhosoma	0.77-0.91	Lawton 1970
Simulium	0.57	McCullough 1975
Stenonema	0.52	Trama 1957
Tricorythodes minutus	0.07-0.55	McCullough 1975
Tubifex tubifex	0.5	Ivlev 1939

BS2SED

81. BS2SED is the half-saturation coefficient for benthos feeding on organic sediment (g/m^2). Leidy and Ploskey (1980), after a thorough review of the literature, wrote that they were unable to find a single reference that documented, in units convertible to carbon, the change in benthic grazing as a function of food concentration. In addition, the value of the coefficient depends on the depth of the sediment being modeled, which is itself a variable. The authors of the present report recommend using values slightly smaller than half the initial condition for the sediment, which is reported in g/m^2.

TBRESP

82. TBRESP is the maximum respiration rate for benthos (1/day). Respiration rates are estimated directly by monitoring benthic oxygen consumption by manometric, chemical, or polarographic methods. Values for the respiration rate for benthos are given in Table 23.

Table 23

Maximum respiration rates for benthos (1/day)

SPECIES	TBRESP	TEMP °C	REFERENCE
Acartia	0.129-.215	NA*	Williams 1982
Ancylus fluviatilis	0.035-.049	16	Berg 1952
Baetes sp.	0.47-.72	10	Fox et al. 1937
Bithynia tentaculata	0.020	13	Berg & Ockelmann 1959
Bithynia leachi	0.031	13	Berg & Ockelmann 1959
Chironomus anthracinus	0.005	11	Berg et al. 1962
Chironomus strenzkei	0.12-.14	30	Plpatzer-Schultz 1970
Chloeon dipterum	0.16-.46	10-16	Fox and Simmonds 1933
Coenis sp.	0.075	10	Fox et al. 1935
Corethra flavicans	0.002	11	Berg et al. 1962
Corycaeus	0.051-.270	NA	Williams 1982
Echyonurus venosus	0.17-.34	10	Fox et al. 1935
Ephemera simulans	0.063	20	Olson and Rueger 1968
Ephemera vulgata	0.072-.19	10	Fox et al. 1935
Ephemera damica	0.095-.21	10	Fox et al. 1935
Ephemerella ignita	0.24	10	Fox et al. 1935
Erpobdella oculata	0.034	20	Mann 1956
Erpobdella testacea	0.052	20	Mann 1956
Gammarus pulex	0.10-.12	NA	Fox and Simmonds 1933
Gastropoda, Veliger	0.107	NA	Williams 1982
Glossiphonia complanata	0.044	20	Mann 1956
Helobdella stagnalis	0.052	20	Mann 1956
Ilyodrilus hammoniensis	0.0009	11	Berg et al. 1962
Larvaceans	0.014-.043	NA	Williams 1982
Lumbricillus rivalis	0.006	11	Berg et al. 1962
Lymnaea aricularia	0.016	13	Berg & Ockelmann 1959
Lymnaea palustris	0.027	13	Berg & Ockelmann 1959
Lymnaea pereger	0.023	13	Berg & Ockelmann 1959
Many groups	0.0001-.04	NA	Olson and Rueger 1968
Myxas glutinosa	0.026	13	Berg & Ockelmann 1959
Oligotrichs	0.257	NA	Williams 1982
Physa fontinalis	0.041	13	Berg & Ockelmann 1959
Piscicola geometra	0.088	20	Mann 1956
Procladius sp.	0.002	11	Berg et al. 1962
Tintinnids	0.245	NA	Williams 1982
Tubifex barbatus	0.005	11	Berg et al. 1962
Tubifex tubifex	0.001	11	Berg et al. 1962
Valvata piscinalis	0.041	13	Berg & Ockelmann 1959

* NA = not available.

BENT1, BENT2, BENT3, BENT4

83. Values for benthos temperature coefficients are given in Table 24.

a. BENT1 is the lower temperature bound at which metabolism continues to occur; it is usually 0 °C.
b. BENT2 is the lowest temperature at which processes are occurring near the maximum rate.
c. BENT3 is the upper temperature bounding the range of maximum rates.
d. BENT4 is the upper lethal temperature.

Table 24

Temperature coefficients for benthos metabolism (°C)

SPECIES	BENT1	BENT2	BENT3	BENT4	REFERENCE
Asellus aquaticus	0	15	NA*	NA	Moore 1975
Gammarus pulex	0	18	NA	NA	Moore 1975
Gammarus pseudolimnaeus	0	20	NA	NA	Marchant & Hynes 1981

* NA = not available.

Fish

84. CE-QUAL-R1 has three fish compartments for simulating piscivorous, planktivorous, and benthic-feeding assemblages in a reservoir. Since many fish species are omnivorous, however, the weighting procedure for computing composite compartment rates is different from other compartments. A report by Leidy and Jenkins (1977) provides all the information necessary to compute the required composite rate coefficients.

85. In the model, the piscivorous fish (compartment 1) feed only on the other two fish compartments. Fish in the second compartment feed on detritus, zooplankton, and the two algal groups; fish in the third compartment feed on

sediment and benthos.

TFMAX

86. TFMAX,1 is the maximum ingestion rate (1/day) for the piscivorous fish compartment. The composite rate for the compartment should be computed based on the mean annual standing crop estimate. Ingestion rates vary as a function not only of species, but also of other factors such as condition or age class; the ingestion rate should reflect these factors by using, for example, average age class estimates.

87. TFMAX,2 is the maximum ingestion rate for planktivorous fish (1/day). The planktivorous fish consume zooplankton, algae, and detritus.

88. TFMAX,3 is the maximum ingestion rate for benthic fish (1/day). Benthic-feeding fish ingest both benthos and organic sediment.

89. In general, a TFMAX coefficient of 0.01 represents maintenance without growth; 0.04 to 0.05 represents optimum growth efficiency (Leidy and Jenkins 1977).

FS2BEN, FS2ZOO, FS2FSH

90. To adjust the ingestion rate of fish due to the available food supply, the fishery model uses half-saturation constants; these represent the amount of food present that results in fish ingestion at half the maximum growth rate. It has been suggested that the half-saturation constant be considered to be 5 percent of fish wet body weight consumed per day at 20 °C (Leidy and Jenkins 1977). Five percent of the body weight consumed per day corresponds closely with the food intake rate for optimum efficiency in growth (4 to 5 percent for many species). User's of CE-QUAL-R1 should refer to Leidy and Jenkins (1977) because

of the difficulty in estimating half-saturation coefficients. Estimates of fish half-saturation coefficients are given in Table 25.

a. FS2BEN is the benthic-feeding fishes' (FISH3) half-saturation coefficient for benthos and sediment grazing (mg/L).
b. FS2ZOO is the planktivorous fishes' (FISH2) half-saturation coefficient for zooplankton, detritus, and algae (mg/L).
c. FS2FSH is the piscivorous fishes' (FISH1) half-saturation coefficient for feeding on FISH3 and FISH2 (mg/L).

Table 25

Estimated half-saturation coefficients for fish growth (mg/L) (from Leidy and Jenkins 1977)

SPECIES	FOOD TYPE	VALUE	REFERENCE
Largemouth bass	minnows	4.6	Thompson 1941
Smallmouth bass	minnows	7.2	Williams 1959
Muskellunge	minnows	5.6	Gammon 1963
Reticulate sculpin	midge larvae	4.4	Davis and Warren 1965
Sockeye salmon	mixed diet	3.9-7.9	Brett et al. 1969
Channel catfish	mixed diet	3.1	Andrews and Stickney 1972

F2ALG, F2DET, F2ZOO, F3BEN, F3SED

91. Preference factors for fish compartments 2 and 3 are as follows:

a. F2ALG is the preference of FISH2 for algae (dimensionless).
b. F2DET is the preference of FISH2 for detritus (dimensionless).
c. F2ZOO is the preference of FISH2 for zooplankton (dimensionless).
d. F3BEN is the preference of FISH3 for benthos (dimensionless).
e. F3SED is the preference of FISH3 for sediment (dimensionless).

Information relating to fish preference factors is supplied in Leidy and Jenkins (1977) and is reprinted here in Table 26 below. Unfortunately, the different fish foods are expressed as fractions of the total diet rather than as quantities (i.e. grams) consumed, making preference factors difficult to estimate from this information.

Table 26

Fish food expressed as a fraction of the diet (from Leidy and Jenkins 1977)

SPECIES	PLANT	DETRITUS	ZOOPL	BENTHOS	FISH
Gizzard shad	0.10	0.80	0.05	0.05	
Threadfin shad (young)	0.30	0.50	0.10	0.10	
Threadfin shad (old)	0.30	0.05	0.15	0.55	0.10
Rainbow trout	0.05		0.60	0.15	
Brook trout			0.90	0.05	
Carp	0.30	0.40	0.20	0.10	
Minnows	0.20		0.20	0.60	
Carpsuckers	0.15	0.65	0.05	0.15	
Suckers	0.15	0.65	0.05	0.15	
Hogsuckers		0.80	0.05	0.15	
Buffalofish	0.05	0.40	0.05	0.15	
Redhorse			1.00		
Bullhead	0.10	0.25	0.50		0.15
Catfish	0.27	0.10			0.80
Madtoms			0.55		0.18
Silversides			0.20	0.80	
Temperate bass			0.20	0.10	0.70
Sunfish	0.10	0.05	0.65		0.05
Black bass			0.08		0.86
Crappie	0.05	0.05	0.20	0.15	0.55
Perch			0.20	0.20	0.60
Freshwater drum		0.08	0.58		0.34

92. An example is given for calculating preference factors for the third fish compartment when actual quantities consumed are known. Suppose a particular species of fish consumes 2 g out of an available 16.0 g of benthos and 0.26 g out of an available 120.0 g of sediment. The preference factor (P) for the ith food category equals

$$P_i = (E_i/A_i)/SUM_i(E_i/A_i)) \qquad (22)$$

where

E_i = the amount of the ith food consumed

A_i = the amount of the ith food available

For the above examples the preference factors would be

P(benthos) = (2.0/16.0)/0.127166 = 0.983

P(sediment) = (0.26/120.0)/0.127166 = 0.017

FSHT1, FSHT2, FSHT3, FSHT4

93. Upper and lower temperature tolerances for fish ingestion are presented as follows:

a. FSHT1 is the lower temperature boundary, usually 0 °C, at which metabolism continues.
b. FSHT2 is the lowest temperature at which processes are occurring at the maximum rates.
c. FSHT3 is the upper temperature bounding the range of maximum rates.
d. FSHT4 is the upper lethal temperature.

94. For most warmwater species, upper and lower temperature tolerances are similar, the lower limit being reached at 0°C and the upper limit between 33 and 37 °C; the optimum temperature is about 27°C. Coldwater species such as salmonids reach a lower temperature limit at 0°C, but the upper limit is near 25°C; the optimum temperature is about 14°C. Temperature tolerance values and the various acclimation temperatures (ACCL), where available, are given in Table 27.

Table 27

Temperature coefficients for fish ingestion (°C)
(from Leidy and Jenkins 1977)

SPECIES	ACCL	FSHT1	FSHT2	FSHT3	FSHT4	REFERENCE
Pickerals		0		24	34.4	Leidy and Jenkins 1977
Minnows		0	27		33.4	Leidy and Jenkins 1977
Catfish		0	30		37.1	Leidy and Jenkins 1977
Sunfish		2.5	27.5		35.7	Leidy and Jenkins 1977
Black bass		1.6	27		36.5	Leidy and Jenkins 1977
Crappie			23		32.5	Leidy and Jenkins 1977
Yellow perch		0	24.2		30.9	Leidy and Jenkins 1977
Yellow perch				29		Schneider 1973
Fingerling salmon			15			Brett et al. 1969
Bluntnose minnow	5				26.0	Hart 1947
Bluntnose minnow	10				28.3	Hart 1947
Bluntnose minnow	15	1.0			30.6	Hart 1947
Bluntnose minnow	20	4.2			31.7	Hart 1947
Bluntnose minnow	25	7.5			33.3	Hart 1947
Flathead minnow	10				28.2	Hart 1947
Flathead minnow	20	1.5			31.7	Hart 1952
Flathead minnow	30	10.5			33.2	Hart 1952
Creek chub	5				24.7	Hart 1952
Creek chub	10				27.3	Hart 1952
Creek chub	15				29.3	Hart 1952
Creek chub	20	0.7			30.3	Hart 1952
Creek chub	25	4.5			30.3	Hart 1952
Chub	14				27.1	Black 1953
Finescaled sucker	14				26.9	Black 1953
White sucker	25				31.2	Brett 1944
White sucker	5				26.3	Hart 1947
White sucker	10				27.7	Hart 1947
White sucker	15				29.3	Hart 1947
White sucker	20	2.5			29.3	Hart 1947
White sucker	25	6.0			29.3	Hart 1947
White sucker			27			McCormick and Mischuk 1973
Brown bullhead	5				27.8	Hart 1952
Brown bullhead	10				29.0	Hart 1952
Brown bullhead	15				31.0	Hart 1952
Brown bullhead	20				32.5	Hart 1952
Brown bullhead	25				33.8	Hart 1952
Brown bullhead	30				34.8	Hart 1952
Brown bullhead	34				34.8	Hart 1952
Black bullhead	23				35	Black 1953
Channel catfish	25				35.5	Allen and Strawn 1968
Channel catfish	35				38	Allen and Strawn 1968
Channel catfish			18			Andrews and Stickney 1972
Channel catfish	15	0.0			30.3	Hart 1952
Channel catfish	20	2.5			32.8	Hart 1952
Channel catfish	25	6.0			33.5	Hart 1952
Bluegill	15	2.5			30.7	Hart 1952
Bluegill	20	5.0			31.5	Hart 1952
Bluegill	25	7.5				Hart 1952

Table 27 (concluded)

SPECIES	ACCL	FSHT1	FSHT2	FSHT3	FSHT4	REFERENCE
Bluegill	30	11.1			33.8	Hart 1952
Bluegill			22		33.8	McComish 1971
Longear sunfish	25				35.6	Neill et al. 1966
Longear sunfish	30				36.8	Neill et al. 1966
Longear sunfish	35				37.5	Neill et al. 1966
Pumkinseed	25				24.5	Brett 1944
Smallmouth bass	35	1.6	26.3		35.0	Horning and Pearson 1973
Smallmouth bass			28.3			Peck 1965
Largemouth bass			27.5	30		Strawn 1961
Largemouth bass			25			Niimi and Beamish 1974
Largemouth bass	20	5.5			32.5	Hart 1952
Largemouth bass	25				34.5	Hart 1952
Largemouth bass	30	11.8			36.4	Hart 1952
Yellow perch	5				21.3	Hart 1947
Yellow perch	10	1.1			25.0	Hart 1947
Yellow perch	15				27.7	Hart 1947
Yellow perch	25	3.7			29.7	Hart 1947
Yellow perch-juvenile	24		20	23.3		McCauley and Read 1973
Yellow perch-adult	24		17.6	20.1		McCauley and Read 1973
Yellow perch	8		18.6			Ferguson 1958
Yellow perch	10		19.3			Ferguson 1958
Yellow perch	15		23.0			Ferguson 1958
Yellow perch	20		23.1			Ferguson 1958
Yellow perch	25		24.5			Ferguson 1958
Yellow perch	30		26.7			Ferguson 1958
Sockeye salmon-fry	5	0			22.2	Brett 1952
Sockeye salmon-fry	10	3.1			23.4	Brett 1952
Sockeye salmon-fry	15	4.1			24.4	Brett 1952
Sockeye salmon-fry	20	4.7			24.8	Brett 1952
Sockeye salmon-juvenile	15		15	17		Brett et al. 1969
Coho salmon	5	0.2			20.9	Brett 1952
Coho salmon	10	1.7			23.7	Brett 1952
Coho salmon	15	3.5			24.3	Brett 1952
Coho salmon	20	4.5			25.0	Brett 1952
Chinook salmon			18.4			Olson and Foster 1955
Northern pike	25				32	Scott 1964
Lake trout			11.7			McCauley and Tait 1970
Lake trout			8	10.9		Rawson 1961
Rainbow trout	18		17	20		McCauley and Pond 1971
Brook trout	5				23.7	Fry et al. 1946
Brook trout	10				24.4	Fry et al. 1946
Brook trout	15				25.0	Fry et al. 1946
Brook trout	20				25.3	Fry et al. 1946
Brook trout	25	0.5			25.3	Fry et al. 1946
Brook trout			14	19		Graham 1949

FEFFIC

95. FEFFIC, the assimilation efficiency for fish (dimensionless), ranges from 0.66 to 0.98; a value of 0.80 is realistic for most fish (Leidy and Jenkins 1977). The assimilation efficiency is multiplied by the ingestion rate to obtain an assimilation rate. Values for fish assimilation efficiency are given in Table 28.

Table 28

Assimilation efficiencies of fish (dimensionless)

SPECIES	FEFFIC	REFERENCE
Bleak	0.80	Mann 1965
Blueback herring	0.80	Burbridge 1974
Bluegill	0.80	Pierce and Wissing 1974
Bluegill	0.97	Gerking 1955
Carnivorous fish	0.80	Wingerg 1956
Carp	0.74	Ivlev 1939a
Carp	0.95	Kobashi and Deguchi 1971
Cichlasoma bimaculatum	0.69-0.89	Warren and Davis 1967
Cutthroat trout	0.84-0.86	Krokhin 1959
Ctenopharyngodon	0.14	Fisher 1970
Dace	0.79	Mann 1965
Goldfish	0.71-0.86	Davies 1964
Green sunfish	0.94	Gerking 1952a
Longear sunfish	0.94-0.97	Gerking 1952a
Northern pike	0.72	Johnson 1966
Perca fluvatilis	0.35	Klekowski et al. 1970
Perch	0.79	Mann 1965
Reticulate sculpin	0.74-0.84	Davis and Warren 1965
Roach	0.78	Mann 1965
White bass	0.66-0.69	Wissing 1974

TFMORT

96. TFMORT is the nonpredatory mortality rate for fish (1/day). Mortality rate is that fraction of fish biomass that is converted to detritus by death. Nonpredatory mortality rates can be highly variable depending on species, age, exploitation rate, and numerous environmental variables.

The average rate calculated by Leidy and Jenkins (1977) is 0.001 for exploited populations.

97. Ricker (1945) has reviewed techniques for calculating various mortality rates (total, instantaneous, conditional, natural, and fishing). Values for nonpredatory mortality are given in Table 29.

Table 29

Fish nonpredatory mortality rates (1/day)

SPECIES	TFMORT	REFERENCE
American shad	0.002	Walburg 1961
Bluegill	0.002	Patriarche 1968
Bluegill	0.0002	Gerking 1952b
Bluegill	0.001	Ricker 1945
Brook trout	0.001	Latta 1962
Brook trout	0.003-.004	Alexander and Shetter 1961
Brook trout	0.56-1.34	Hatch and Webster 1961
Brown bullhead	0.001	McCammon and Seeley 1961
Brown bullhead	0.001	Rawstron 1967
Channel catfish	0.001	Ricker 1958
Cutthroat trout	0.001-.002	Hansen 1971
Cutthroat trout	0.001	Ball and Cope 1961
Freshwater drum	0.001	Butler 1965
Largemouth bass	0.00037	Mraz and Threinen 1955
Longnose sucker	0.002	Geen et al. 1966
Northern pike	0.002	Groebner 1960
Northern pike	0.002	Johnson and Peterson 1955
Rock bass	0.002	Ricker 1947
Walleye	0.001	Olson 1957
White catfish	0.001	McCammon and Seeley 1961

TFRESP

98. TFRESP is the fish respiration rate (1/day). There are three types of respiration that can be defined: (a) standard respiration--oxygen consumed in the absence of measurable movement (i.e., nonactive respiration, basal of resting metabolism), (b) routine respiration--rate of

oxygen consumption of fish showing normal activity, and (c) active respiration--maximum rate of oxygen consumption under continuous forced active respiration. It would appear that the best estimates of the rate of respiration for normal active fish are values for routine metabolism (i.e., type 2 above) (Winberg 1956). Values for fish respiration rate are given in Table 30.

Table 30

Fish maximum respiration rates (1/day)

SPECIES	TFRESP	TYPE	REFERENCE
Brown bullhead	0.001	routine	Beamish 1964
Brook trout	0.003	routine	Beamish 1964
Carp	0.001	routine	Beamish 1964
Lake trout	0.001	standard	Gibson and Fry 1954
Rainbow trout	0.002	standard	Florke et al. 1954
Salvelinus fontinalis	0.006-.024	standard	Madsen et al. 1977
Salvelinus fontinalis	0.019-.101	active	Madsen et al. 1977
Sockeye salmon	0.002	standard	Brett 1944
White sucker	0.002	routine	Beamish 1964

Other Coefficients

TDSETL

99. TDSETL is the detrital settling velocity (m/day). Detrital settling velocities vary from 0.001 to over 200 m/day depending on the detrital characteristics and reservoir hydrodynamics. Settling rates should be obtained from quiescent settling chamber studies because advective and turbulent forces in the mixed layer that can reduce settling in a reservoir are modeled separately. For most studies, settling velocities are in the range of 0.05 to 1.0 m/day.

Much higher values are often reported for fecal pellets, as shown in Table 20; however, such high settling coefficients may be questionable because they produce unrealistically low detritus values in the modeling studies. Values for detritus settling velocities are given in Table 31.

Table 31

Detritus settling velocities (m/day)

SOURCE	TDSETL	REFERENCE
Ceratium balticum	9.0	Apstein 1910
Chaetoceros borealis	5.0	Apstein 1910
Chaetoceros didymus	0.85	Eppley et al. 1967b
Cricosphaera carterae	1.70	Eppley et al. 1967b
Ditylum brightwellii	2.0	Apstein 1910
Fecal pellets:		
Acartia clausii	116.0	Smayda 1971
Fecal pellets:		
Euphausia krohnii	240.0	Fowler and Small 1972
Fecal pellets:		
Euphausia pacifica	43.0	Osterberg et al. 1963
Fecal pellets:		
Pontella meadii	54.0-88.0	Turner 1977
Phaeodactylum tricornutum	0.02-.04	Riley 1943
Rhizosolenia herbetata	0.22	Eppley et al. 1967b
Stephanopyxis tunis	2.1	Eppley et al. 1967b
Tabellaria flocculosa	0.46-1.5	Smayda 1971
Thalassiosira psuedonana	0.85	Hecky and Kilham 1974

DETT1, DETT2

100. DETT1 is the lower temperature boundary at which decomposition continues to occur. It is usually 0 °C.

101. DETT2 is the temperature at which decomposition occurs near the maximum rate. Temperature coefficients for decomposition are given in Table 32.

Table 32

Temperature coefficients for decomposition (°C)

SUBSTRATE OR SITE	DETT1	DETT2	REFERENCE
Pseudomonas fluorescens: natural substrate	0	25-30	Tison and Pope 1980
E. coli: natural substrate	0	37	Tison and Pope 1980
Glucose: Lake George, New York	0	25	Tison et al. 1980
Glucose	0	20-30	Bott 1975
Glucose: Lake Wingra, Wis.		25-30	Boylen and Brock 1973

TDOMDK

102. TDOMDK is the dissolved organic matter (DOM) decay rate (1/day). DOM in natural waters is the organic substrate for heterotrophic metabolism. The composition of natural DOM is highly variable and little understood, but its sources are generally grouped into (a) excretion from phytoplankton and macrophytes, (b) decomposition of phytoplankton and macrophytes, (c) excretion by animals, and (d) allochthonous drainage (e.g., humic compounds from upstream sources).

103. Aquatic bacteria appear to be chiefly responsible for the removal of DOM compounds from the water; they are the major agents for bacterial mineralization of organic solutes in fresh water (Wright 1975), using organic matter as an energy source. Various methods have been tested to determine the decay rate of DOM in water. Modification of the basic Parson and Strickland (1963) technique have been developed to quantify the kinetics.

104. DOM decomposition rates have also been represented by filtered carbonaceous biochemical oxygen demand (BOD) decay rates. If sufficient oxygen is available, the

aerobic biological decomposition of organics will continue until all the DOM is consumed. In the standard test for BOD, a sample is diluted with water containing a known amount of oxygen. The loss of oxygen after the sample has been incubated for 5 days at 20 °C is known as the 5-day BOD. The value of the first-order decay rate is generally about 0.05 to 0.20 per day.

105. The BOD test suffers from several serious deficiencies. The test has no stoichiometric validity, for example: the arbitrary 5-day period usually doesn't correspond to the point where all the organic matter is consumed.

106. Contributing to the errors involved in measuring decay rates of DOM is the extensive variability in the composition and stage of decomposition of DOM. Allochthonous inputs of DOM are likely to be more refractory than autochthonous inputs, and as a result, decomposition rates will be slower and decay may be incomplete; therefore, the length of time the organic matter is available for decomposition is important. In addition, as particles sink out of the euphotic zone, both dissolved and detrital organic substrates may be limited to more resistant fractions thereby arresting attached microbial growth. Therefore, the rate of DOM decomposition may be lower in the hypolimnion of a stratified reservoir.

107. Oxygen consumption rate (mg O_2/L/hr) can be transformed into a mineralization rate of organic carbon (mg C/L/hr) by application of a conversion factor of 0.29 (Seepers 1981). Values for DOM decay rate are given in Table 33.

Table 33

DOM decay rates (1/day)

COMPOUND	TDOMDK	REFERENCE
Acetate	0.2	Wright 1975
Amino acids	0.64	Williams et al. 1976
Glucose	0.24	Williams et al. 1976
Glucose	0.32-.50	Toerien and Cavari 1982
Glucose	0.111	Wright 1975
Glutamate	0.11-.625	Carney and Colwell 1976
Glycine	0.312-.45	Vaccaro 1969
Glycine	0.048	Vaccaro 1969
Glycolate	0.024-.432	Wright 1975
Glycolate	0.012-.25	Wright 1975
Glycolic acid	0.004	Tanaka et al. 1974

TNH3DK

108. TNH3DK is the ammonia decay rate (i.e., the rate at which ammonia is oxidized to nitrite) (1/day). Ammonia is generated by heterotrophic bacteria as the primary end product of decomposition of organic matter, either directly from proteins or from other nitrogenous organic compounds. Although ammonia is a major excretion product, this nitrogen source is minor in comparison to decomposition.

109. Nitrification is the biological conversion of organic and inorganic N compounds from a reduced state to a more oxidized state (Alexander 1965). The nitrifying bacteria capable of oxidation of NH4+ to NO2- are largely confined to the species Nitrosomonas, bacteria which are mesophilic (1-37 °C).

110. Nitrification rate can be determined by a number of different techniques. Courchaine (1968) has plotted nitrogenous BOD on a logarithmic scale and determined the decay rate from the slope of the line. Thomann et al. (1971) used a finite-difference approximation to solve a

set of simultaneous linear equations.

111. Laboratory measurements for the ammonia decay rate can produce results that differ from what might be measured in situ. Several environmental factors influence the rate of nitrification, including pH, temperature, suspended particulate concentration, hydraulic parameters and benthos.

112. Nitrification can be measured as a one- or two-step process. In the one-step method, only the end product of the entire reaction, nitrate, is measured. In the two-step method, (a) nitrite accumulation is measured as ammonia is oxidized to nitrite and (b) nitrate accumulation is measured as nitrite is oxidized to nitrate. Oxidation of ammonia to nitrite is the rate-limiting step in the total reaction; therefore, experiments that measure the rate of the total reaction (i.e., the one-step method) can be used to estimate this parameter. Ammonia oxidation rates are given in Table 34.

Table 34

Ammonia oxidation rates (1/day)

SITE	TNH3DK	REFERENCE
Wastewater treatment plant	0.05-0.30	Wild et al. 1971
Grand River, Ill.	0.80	Bansal 1976
Grasmere Lake, U.K.	0.001-.013	Hall 1982
Truckee River, Nev.	0.09-1.30	Bansal 1976
Upper Mohawk River, N.Y.	0.23-0.40	Bansal 1976
Middle Mohawk River	0.30	Bansal 1976
Lower Mohawk River	0.30	Bansal 1976
Ohio River	0.25	Bansal 1976
Big Blue River, Neb.	0.17-0.25	Bansal 1976
Flint River, Mich.	0.76-0.95	Bansal 1976

TNO2DK

113. TNO2DK is the decay rate of nitrite to nitrate (1/day).

TDETDK

114. TDETDK is the detritus decay rate (1/day). Detritus as defined by Wetzel et al. (1972) consists of organic carbon lost from an organism by nonpredatory means (including egestion, excretion, secretion, etc.) from any trophic level component, or input from sources external to the ecosystem that enter and cycle in the system (i.e., allochthonous organic carbon). For CE-QUAL-R1, this should be considered to be particulate material only.

115. The rate of detritus decay can be determined by measuring the use of oxygen during decomposition, with results expressed as a first-order decay coefficient (k base e = mg oxygen used/mg/day). Many workers have measured rates of oxygen uptake by detritus, suggesting that oxygen uptake is related to the organic matter available for decomposition. Odum and de la Cruz (1967) and Fenchal (1970), for example, demonstrated an inverse relation between detritus particle size and oxygen consumption. Oxygen uptake is an integrative measure of all oxidative processes occurring in the sample, both chemical and biological: reducing substances are usually rapidly oxidized; respiration of the organisms associated with detritus is primarily bacterial, although algae, protozoa, and fungi may also contribute. Measurement of the oxygen uptake reflects the metabolism of communities of microorganisms involved in the decomposition of natural substances.

116. As a detrital particle decomposes with time, there is a decline in oxygen uptake accompanied by succession of communities of microorganisms; this decline occurs

as the matter changes from labile to refractory; refractory matter often accumulates in the sediment. Rates of decay are generally high initially and slow down as the material becomes refractory; the rate is influenced by temperature, detrital composition, and age of the detritus. Macrophyte communities are the primary source of detritus in most systems. Submersed and floating macrophytes generally decay more rapidly than the highly lignified emergent species. Particulate organic matter of dead bluegreen algae decomposes much faster than that derived from green algae diatoms and desmids. Particulate organic matter (POM) is especially resistant (Gunnison and Alexander 1975). As detritus decays, there is a decrease in the C:N ratio as a result of a buildup of microbial protein (Mann 1972). A 1-g sample of detritus at 20 °C consumes about 1 mg oxygen/hr (Hargrave 1972).

117. Plant litter consists of a variety of compounds (i.e., sugars, hemicellulose, lignin, waxes) which decay at different rates. The decay curves initially tend to follow the exponential decay functions of the more readily degradable fractions, particularly aquatic macrophytes, which account for a large proportion of the weight of plant litter; therefore, the majority of the litter's weight loss occurs in the first year. Over the long term, the decay rates change, especially for deciduous leaf litter which has a larger proportion of decay-resistant material than do aquatic macrophytes and therefore decays at a much slower rate.

118. Decay rates can also be measured by suspending a nylon mesh bag of detrital material _in situ_ or under controlled conditions and determining weight loss with time. This actually measures weight loss due to enzymatic decomposition by bacteria and fungi, solution of soluble sub-

stances, and loss of fragments through the container pores.

119. Decay rates have also been determined by measuring the mineralization rates of carbon, nitrogen, and phosphorus (Otuski and Hanya 1972). Decomposition of detritus generated from planktonic communities of surface lake water occurs at rates on the order of 10 percent per day (Saunders 1972), based upon radioactive carbon tracer studies.

120. Consideration should be given to the primary or expected sources of detritus. Decomposition rates for allochthonous detrital sources are generally lower than for autochthonous sources to reflect the more refractory nature of allochthonous material after its transport through the upper portions of the reservoir. While a one-dimensional model like CE-QUAL-R1 assumes instantaneous dispersal of inflow constituents, much of the decomposition in the prototype reservoir system occurs in the headwater area. The labile fraction of autochthonous detritus produced in the pelagic zones of the lower reservoir will decompose more rapidly in the water column and should have a higher decomposition rate than allochthonous detritus. However, in a stratified reservoir the POM in the hypolimnion may not be exchanged with the epilimnetic waters. The POM becomes more refractory with time, and rates of decomposition decrease.

121. Microbial decomposition of detritus can be represented by three stages: a very quick solution of soluble organic components, a relatively rapid decomposition of labile organic constituents, and slow decomposition of refractory organic constituents. Detritus decay rates are given in Table 35.

Table 35

Detritus decay rates (1/day)

DETRITUS SOURCE	TDETDK	REFERENCE
Beech	0.001-.004	Hanlon 1982
Cladophera glomerata	0.007	Piecznska 1972
Dead green algae	0.016-.076	Otsuki and Hanya 1972
Dead mixed algae	0.007-.111	Jewell and McCarty 1971
Dead mixed algae	0.007-.06	Fitzgerald 1964
Gloeotrichia echinulata	0.001-.007	Piecznska 1972
Isoetes lancustris	0.003-.015	Hanlon 1982
Leaf packs	0.005-.017	Sedell et al. 1975
Osier	0.001-.005	Hanlon 1982
Potamogeton crispus	0.002-.004	Rogers and Breen 1982
Potomogeton perfoliatus	0.002-.007	Hanlon 1982

TCOLDK

122. TCOLDK is the coliform decay rate (1/day). Estimates of coliform die-off rates may be obtained in the laboratory or *in situ*. *In situ*, where there are no flow regime data, or where flows are of a transient nature, a commonly used method is to add a slug of a conservative tracer substance (a dye, rare element, or radioisotope) to steady-state discharge. The discharge plume is sampled, dilution is estimated from the concentration of tracer, and the decay rate is estimated from the dilution-corrected coliform counts. This technique gives misleading results in cases where the tracer is diluted by water heavily contaminated with the same discharge. Since the tracer was introduced as a slug, there is no way to know how many of the surviving coliforms originated in the tracer-dosed effluent and how many came from pre- or post-dosing effluent. This problem is reduced where the flow regime is sufficiently stable (Zison et al. 1978).

123. There are two approaches to estimating die-off rates. Frost and Streeter (1924) were able to estimate the die-off rate using seasonal averages of coliform counts from a downstream station, by assuming plug flow in the river. Errors in the rates determined by this approach are attributable to (a) dilution and to longitudinal mixing that produced overestimates and (b) unconsidered sources of coliforms that produced underestimates.

124. In a second approach, a mathematical model of the flow and mixing in the system is used to correct the measurements for the effects of dilution. In this manner Marais (1974) analyzed coliform die-off in wastewater maturation ponds as a first-order decay reaction in a series of completely mixed steady-state reactors. Errors in the decay rates determined in this way are primarily attributable to the reliability of the system model.

125. Table 36 gives decay rates for coliform and fecal streptococcus. In Table 37 from Mitchell and Chamberlain (1978), the median die-off value was 0.040/hr for freshwater coliform. In general, the die-off follows first-order decay kinetics, although a significant increase in coliform levels is commonly observed in the first several miles downstream from the outfall.

126. Factors affecting coliform decay rate include sedimentation, solar radiation, nutrient deficiencies, predation, algae, bacterial toxins, and physiochemical factors.

Table 36

Coliform and fecal streptococcus decay rates (1/day)

SPECIES	TCOLDK	REFERENCE
Fecal coliform	0.048-.096	Evans et al. 1968
Fecal streptococci	0.063	Evans et al. 1968
Fecal streptococci	0.004-.013	Geldreich et al. 1968
Total coliform	4.48-5.52	Kittrell and Furfari 1963
Total coliform	0.199-.696	Klock 1971
Total coliform	1.99	Marais 1974
Total coliform	0.168-1.56	Geldreich et al. 1968
Total coliform	0.009-.028	Klock 1971
Total coliform	0.021-.038	Evans et al. 1968
Total coliform	0.045-.049	Frost and Streeter 1924
Total coliform	0.024-.105	Hoskins et al. 1927
Total coliform	0.48-2.04	Mitchell and Chamberlain 1978

Table 37

Freshwater die-off rates of coliform bacteria measured in situ (1/day) (from Mitchell and Chamberlain 1978)

SITE	TEMP/SEASON	RATE	REFERENCE
Ohio River	Summer 20°C	1.175	Frost and Streeter 1924
Ohio River	Winter 5°C	1.08	Frost and Streeter 1924
Upper Illinois River	June-Sept.	2.04	Hoskins et al. 1927
Upper Illinois River	Oct.-May	2.52	Hoskins et al. 1927
Upper Illinois River	Dec. Mar.	0.576	Hoskins et al. 1927
Upper Illinois River	Apr.-Nov.	1.032	Hoskins et al. 1927
Lower Illinois River	June-Sept.	2.04	Hoskins et al. 1927
Lower Illinois River	Oct.-May	0.888	Hoskins et al. 1927
Lower Illinois River	Dec.-Mar.	0.624	Hoskins et al. 1927
Lower Illinois River	Apr.-Nov.	0.696	Hoskins et al. 1927
Shallow turbulent stream	Summer	15.12	Kittrell and Koschtitzky 1947
Missouri River	Winter	0.48	Kittrell and Furfari 1963
Tennessee River (Knoxville)	Summer	1.03	Kittrell and Furfari 1963
Tennessee River (Chattanooga)	Summer	1.32	Kittrell and Furfari 1963
Sacramento River, Calif.	Summer	1.752	Kittrell and Furfari 1963
Cumberland River, Md.	Summer	5.52	Kittrell and Furfari 1963
Groundwater stream	10°C	0.504	Wuhrmann 1972
Leaf River, Miss.	NA	0.408	Mahloch 1974
Wastewater lagoon	7.9-25.5°C	0.199-.696	Klock 1971
Maturation ponds	NA	1.99	Marais 1974
Maturation ponds	19°C	1.68	Marais 1974
Oxidation ponds	20°C	2.59	Marais 1974

TSEDDK

127. TSEDDK is the organic sediment decomposition rate (1/day). While sediment consists primarily of settled organic detritus, the decomposition rate should reflect the changing nature of the detritus as it reaches the sediment; i.e., it becomes more refractory since the labile portion of the organic detritus decomposes as it settles through the water column. In addition, since the initial value for sediment is in g/m^2, the thickness of the sediment layer, along with TSEDDK, will affect the amount of predicted decomposition. Thus, if high initial values are used for sediment, TSEDDK may have to be lowered since only the top few centimeters of sediment are usually involved in aerobic decomposition. Hargrave (1969) found the following relationship between the rate of oxygen comsumption by sediments (ml $O2/m^2/hr$) and the temperature (T, °C):

$$\ln (O_2 \text{ consumption rate}) = 1.74*\ln(T)-1.30 \qquad (23)$$

At 6° C this would be 214.3 mg $02/m^2$/day, assuming a constant rate for the day and the conversion formula found in the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982, p. 188). At 25° C the rate would be 2567 mg/m^2/day. The amount of sediment (in mg/m^2) times the value for TSEDDK times 1.4 (i.e., the stoichiometric equivalent of oxygen uptake to sediment decay) should be near the 6-25 °C range.

DOMT1, DOMT2

128. DOMT1, the critical low temperature for DOM decay, is usually 0 °C.

129. DOMT2 is the optimum temperature for DOM decay (°C). Temperature coefficients for DOM decay are given in Table 38.

Table 38

Temperature coefficients for DOM decay (°C)

SUBSTRATE	DOMT1	DOMT2	REFERENCE
Glucose	5.0	35.5	Toerien and Cavari 1982
Glucose: Lake George, N.Y.	0	25	Tison et al. 1980
Glucose	0	20-30	Bott 1975
Glucose: Lake Wingra, Wis.	0	25-30	Boylen and Brock 1973

NH3T1, NH3T2

130. Researchers have generally found temperature to affect nitrification rates, especially in the range of 10 to 35 °C.

a. NH3T1 is the lower temperature boundary at which ammonium nitrification continues. It is generally 0 °C.
b. NH3T2 is the optimum temperature for oxidation of NH3-N. The optimum temperature for nitrification is generally accepted to be between 25 and 30 °C.

Temperature factors for ammonia oxidation are given in Table 39.

Table 39

Temperature coefficients for ammonia oxidation (°C)

SPECIES OR SITE	NH3T1	NH3T2	REFERENCE
Nitrosomonas	5	30	Knowles et al. 1965
Wastewater treatment plant	5	25	Wild et al. 1971
Ann Arbor, Michigan	2	20	Borchardt 1966

NO2T1, NO2T2

131. NO2T1 is the lower temperature boundary at which nitrate nitrification occurs (°C).

132. NO2T2 is the lowest temperature (°C) at which the oxidation of nitrite to nitrate occurs near the maximum rate.

TSSETL

133. TSSETL is the suspended solids settling velocity (m/day). The settling rate is dependent on the type of particle, grain size, density, temperature, viscosity, and turbulence. Most of the larger particles entering a reservoir settle very quickly and should not be included in the inflow. Lane (1938) gives figures of 0.86 to 860.0 m/day for particle diameters of 0.002 to 0.1 mm. Particles found in the main body of a reservoir are usually at the lower end of this scale.

Q10COL

134. CE-QUAL-R1 uses a Q10 formulation to modify the coliform die-off rate as a function of temperature. All other rates are modified by temperature through the RMULT function in CE-QUAL-R1. The Q10 coefficient is usually 1.04.

PART III: RECOMMENDATIONS

135. This report provides information about, and values for, many of the coefficients needed for use of the version of the model CE-QUAL-R1 described in the User's Manual (Environmental Laboratory 1982).

136. Research on processes described in this report is likely to provide more information needed to refine the equations used in the model. Future versions of the model may therefore require additional coefficients.

137. This report may be updated to provide information about, and values for, any additional coefficients needed for use of future versions of the model.

138. Application, calibration, and verification of the model to a variety of sites is likely to identify coefficient values that are best suited to the model. These values may be included in updates to this report.

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