MATHEMATICAL DOCUMENTATION FOR A LOTIC ECOSYSTEM MODEL

by

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Revision of the original FLEXFORM
by Curtis White

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The mathematical structure of the stream model reported here evolved during a six-year period; and with the exception of the periphyton module, most of the modeling was done between 1973 and 1976 at Oregon State University. The original version of the mathematical documentation—the FLEXFORM—was prepared by J. A. Colby during the fall of 1976. This version was revised by Curtis White in October, 1977. The revision altered the first version slightly to conform more closely to the format used in the FLEXFORM for several other existing models conceptualized in the FLEX paradigm. Furthermore, I have added a section entitled Related Concepts to provide a brief biological basis for the mathematical structure and for aid in the interpretation of some of the output variables.

The authors gratefully acknowledge the contributions of an interdisciplinary group of stream ecologists. Among this group, we are particularly indebted to J. R. Sedell, F. J. Triska, J. D. Hall, N. H. Anderson, E. Graflis, J. A. Speir, S. V. Gregory, K. W. Cummins, R. H. Boling, G. W. Minshall, G. W. Fowler, J. H. Wlosinski, C. E. Cushing, R. L. Vannote, and T. Bott for their unselfish willingness to share ideas and unpublished data. Very special thanks are due W. S. Overton for financing the revision of the FLEXFORM, and for his leadership in the development of FLEX2, a general model processor available at Oregon State University.

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INTRODUCTION

This report provides a detailed mathematical description of a stream ecosystem model. Model structure conforms to the FLEX paradigm (Overton, 1972, 1975) which is implemented by the program FLEX2, a general model processor that accommodates both holistic (FLEX mode) and mechanistic (REFLEX mode) representations (White and Overton, 1974). Complete technical documentation for the current, non-hierarchical version of the stream model is expressed in the FLEXFORM, the working document of the FLEX paradigm. FLEXFORM documentation provides a complete report of the conceptual model and specifies all variables, functions, and parameters according to the FLEX convention. A preliminary draft of the FLEXFORM for a hierarchical version of the model has been prepared by J. A. Colby. However, this version has not yet been implemented on a computer system and is therefore omitted from this report. Simulation runs at Oregon State University for the non-hierarchical version are performed by the FLEX2 processor on a CDC 3300 computer operating under OS-3.

The stream model is an expansion and modification of a model of periphyton processes developed by McIntire (1973). Conceptually, the model is hierarchically structured, consisting of seven basic processes that are subprocesses of three echelons of higher level processes. The model has 14 state variables associated with the seven basic processes, and is conceptualized in discrete time with a resolution of one day. The basic (fine-resolution) processes are periphyton dynamics, grazing, shredding, collecting, invertebrate predation, vertebrate predation, and detrital conditioning. Input and control variables include: light energy; allochthonous detritus; temperature; photoperiod; nutrient concentration; and stream discharge from which such variables as current velocity, shear stress, sediment load, and channel dimensions are derived. Output from the model tracks state variable dynamics and provides trajectories of process growth rates that aid in the interpretation of state variable dynamics. In addition, we recommend that programmers generate a summary table of selected variables of interest representing system dynamics at an annual time resolution. Examples of such output and the biological basis for the stream model are presented by McIntire and Colby (1978). Readers interested in the history of model development are referred to an earlier version of the stream model described by McIntire et al. (1975).
RELATED CONCEPTS

Ecosystem Processes and Process Capacity

On a basis of the level of biological organization, studies of ecological systems can be divided into five approaches: (1) investigations of populations and population interactions; (2) trophic level summation (Lindeman, 1941, 1942); (3) paraspecies summation, the functional group approach (Boling, et al., 1975); (4) process aggregation: quasi-organism viewpoint (McIntire, et al., 1975); and (5) process aggregation: process capacity viewpoint (McIntire and Colby, 1978). Approaches (2) and (3) involve the classification of taxonomic entities into groups of organisms considered to be similar to each other, usually with respect to trophic functions. Therefore, the dynamics of a trophic level or paraspecies is treated analytically (and conceptually) as a summation of activities associated with the constituent taxa of each functional group. In other words, the whole is treated as a sum of the parts. The paraspecies approach provides a refinement which allows a multistage representation of life history phenomena within a structure that can always be mapped into a trophic response. Here, we are concerned primarily with process aggregation, approaches (4) and (5), as they represent theoretical concepts upon which the lotic ecosystem model is based.

Theoretically, an ecosystem can be conceptualized as a hierarchical system of biological processes. For our purpose, a process is a systematic series of actions relevant to the dynamics of the system as it is modeled. Any process can be decomposed into a system of coupled subprocesses if project objectives justify the examination of system dynamics at a finer level of resolution. Alternatively, a process also can be considered as a component of some supraprocess, the behavior of which can be investigated either holistically or mechanistically. At each particular level of resolution, the details of each process can be elaborated in terms of the corresponding variables, functions, and parameters.

In large ecosystem studies, there is some question as to just what state variables associated with each process of interest should represent. This difficulty, the so-called "aggregation problem," was recognized by Overton (1977). In an early version of the stream ecosystem model, McIntire et al. (1975) selected state variables on the basis of the various functional activities of organisms recognized by current concepts of energy transfer in
lotic ecosystems. This approach -- here, referred to as the quasi-organism viewpoint -- designates each state variable as the biomass at any instant of time involved in a particular process. This convention ignores taxonomic position and is therefore different from paraspecies summation which combines taxonomic entities into ecologically similar groups. It is important to emphasize that the individual taxonomic entities are not missing from a process model. Rather, they are simply swept up into a higher level of aggregation to the degree that some of their detailed terminology is no longer appropriate. An analogous aggregation problem has generated controversy relative to connecting linkages between Forrester's World System Model and human values (Laszlo, 1973). Nevertheless, process aggregation in ecology avoids troublesome problems of dealing conceptually with large numbers of taxa individually and with individual organisms involved in more than one process. However, process modeling can create serious practical problems of parameter estimation, particularly when field data correspond to dynamics at the population level of organization. Unfortunately, field measurements of process rates in ecosystems are lacking, although measurements of primary production (e.g., Odum and Hoskin, 1958) and leaf pack studies that examine the shredding capacity in streams (e.g., Sedell et al. 1975) are notable exceptions. The paucity of field methods available for process studies is related to the relatively slow development of a corresponding conceptual framework or context within which the investigator can base his observations.

A refinement of the quasi-organism viewpoint is to regard each state variable as the capacity to perform the corresponding process. For example, if the species composition of organisms involved in the process of grazing changes seasonally, the rate of food consumption per gram of biomass could exhibit corresponding changes. To account for such qualitative changes in biomass, we can consider the state variable as the capacity for grazing which is some function of biomass and other properties of the community that change with community composition (i.e., the genetic information in the system). Relative to process potential, a unit of capacity is time invariant, while a unit of biomass can vary over physiological, ecological, or evolutionary time. Therefore, the concept of capacity provides a theoretical basis for representing both qualitative and quantitative changes within each process in an ecosystem model. Problems of estimation and corresponding field methods associated with the capacity viewpoint of process aggregation are virtually
unexplored in ecosystem research, and may, in fact, prove to be insurmountable barriers to the practical application of the theory. Notwithstanding certain practical difficulties, the theory provides strong justification for monitoring community structure in some way during concurrent measurements of selected ecosystem processes.

During the development of the stream model, emphasis was placed on the responses of the processes of periphyton dynamics, grazing, shredding, collecting, predation, and detrital conditioning to inputs of energy, namely light and allochthonous detritus. State variables were conceptualized as biomasses associated with these processes (process aggregation: quasi-organism viewpoint). However, we were often forced to rely on data associated with the population level of organization for the estimation of many model parameters, and some of these values simply represent means for so-called functional groups of taxonomic entities. Therefore, model parameters are viewed as tentative and may be re-estimated as new field methods provide data more compatible with higher levels of aggregation. Hopefully, the concept of process aggregation will stimulate the development of such methods.

**SOME USEFUL VARIABLES**

The theory of consumer process dynamics in ecosystems can be examined relative to (1) the potential to expand process capacity; (2) process production; (3) the realized growth of process capacity; and (4) process regulation. In the discussion below, process capacity is stressed, but the concepts obviously apply to process biomass if the qualitative component of capacity is ignored.

The potential to expand process capacity at time $k$ is given by

$$g_0(k) = \frac{1}{S(k)} [aD(k) - C(k)]$$

where

- $S(k)$ = the state variable value at time $k$, i.e., the process capacity or biomass if quality is ignored;
- $D(k)$ = the process demand at time $k$;
- $C(k)$ = the cost of processing at time $k$; and
- $a$ = an efficiency parameter.
Process demand (D) is the rate of consumption of resources by the process (i.e., the process rate) if resources are in unlimited supply. The cost of processing (C) is the metabolic loss of energy during processing. The efficiency parameter (a) expresses the proportion of resource intake that is incorporated into process capacity and may, in fact, be a function of certain physical and biological control variables. The variable \( g_0 \) is the potential to expand process capacity per unit capacity in the absence of resource limitation and negative effects from other processes. Therefore, \( g_0 \) is theoretically unaffected by density-dependent factors and is a function of density-independent factors (e.g., temperature). Obviously \( g_0 \) goes to some maximum, say \( g_{0,\text{max}} \), as density-independent factors become optimal. If the state variable is expressed as capacity rather than biomass, \( g_{0,\text{max}} \) is a constant for each consumer process.

Process production for consumer processes is defined as the net elaboration of process capacity regardless of the fate of that capacity during the period under consideration. In other words, process production is analogous to the concept of secondary production (Ricker, 1958). The rate of process production is derived from the expression

\[
g_1(k) = \frac{1}{S(k)} [aR(k) - C(k)]
\]

where \( R(k) \) is the realized process rate at time \( k \), i.e., the actual rate at which resources are consumed by the process. The process production rate at time \( k \) is therefore \( aR(k) - C(k) \) or \( g_1(k)S(k) \). Moreover, while \( g_0 \) is a specific growth rate associated with unlimited resources, \( g_1 \) is the analogous rate when resources vary according to the system dynamics. A waste loss rate associated with processing (W) at time \( k \) is given by

\[
W(k) = R(k) - aR(k)
\]

Fecal discharge is the principal biological mechanism accounting for \( W \), and this waste usually represents a resource for another process or is exported from the system.
The realized growth of process capacity may be obtained after accounting for export and interactions with other processes. The equations are

\[ g_2(k) = \frac{1}{S(k)} [aR(k) - C(k) - E(k)] \]  
\[ g_3(k) = \frac{1}{S(k)} [aR(k) - C(k) - E(k) - B(k)] \]  
\[ g_4(k) = \frac{1}{S(k)} [aR(k) - C(k) - E(k) - B(k) - P(k)] \]  

Here, \( E(k) \), \( B(k) \), and \( P(k) \) correspond to the export of process capacity, losses of capacity to decomposer processes, and losses of capacity to predator processes, respectively. If process capacity is gained directly from outside the system (immigration), an additional term \( I \) must be added to equation (6) to account for this import. The variable \( g_T(k) \) is defined as the actual or realized specific growth rate associated with a process at time \( k \), and \( g_T(k)S(k) \) is the realized process growth rate. For a primary consumer process (e.g., grazing), \( g_T = g_4 \), while for a top predator process \( g_T(k) = g_3(k) \). If the process remains in a steady state relative to the time resolution under consideration, \( g_T \) fluctuates around a mean of zero.

Concepts related to autotrophic process dynamics are analogous to concepts associated with consumer process dynamics. When light energy and nutrients are not limiting,

\[ g_0(k) = \frac{1}{S(k)} [P_{g_{\text{max}}}(k) - C(k)] \]  

where \( P_{g_{\text{max}}} \) is the rate of gross primary production when resources are in unlimited supply. Again, \( g_0 \) can go to \( g_{0_{\text{max}}} \) when temperature and other relevant density independent factors are optimal. When resources vary with system dynamics,

\[ g_1(k) = \frac{1}{S(k)} [P_g(k) - C(k)] \]  

where \( P_g(k) \) is the realized rate of gross primary production at time \( k \). If
the process represents the function of autotrophic organisms only, the rate of net primary production at time \( k \) is \( g_1(k)S(k) \). However, it is often convenient to include the activities of tightly coupled heterotrophic microorganisms within the process boundary, as in the case of periphyton processes. If so, \( g_1(k)S(k) \) simply represents the net elaboration of autotrophic process capacity, and \( C(k) \), the cost of processing, expresses metabolic losses of energy from the activities of both autotrophic and heterotrophic organisms. Expressions analogous to equations (4), (5), and (6) for autotrophic processes are

\[
g_2(k) = \frac{1}{S(k)} \left[ P_g(k) - C(k) - E(k) \right], \quad (9)
\]

\[
g_3(k) = \frac{1}{S(k)} \left[ P_g(k) - C(k) - E(k) - B(k) \right], \quad (10)
\]

\[
g_4(k) = \frac{1}{S(k)} \left[ P_g(k) - C(k) - E(k) - B(k) - G(k) \right], \quad (11)
\]

where \( G(k) \) is the loss to the process of grazing and the other symbols are the same as above.

In large ecosystem models, it is often difficult to understand mechanisms accounting for system dynamics from plots of state variables. In other words, values for state variables go up and down, but it is not always intuitively obvious why such variations occur. The concepts presented above provide a convenient basis for the investigation of regulatory mechanisms. From equations (1), (2), (4), (5), and (6),

\[
\begin{align*}
g_0 - g_1 & \text{ is the regulating effect of resource limitation;} \\
g_1 - g_2 & \text{ is the regulating effect of export losses;} \\
g_2 - g_3 & \text{ is the regulating effect of decomposer processes;} \quad \text{and} \\
g_3 - g_4 & \text{ is the regulating effect of predator processes.}
\end{align*}
\]

To analyze state variable dynamics, we simply plot \( g_0, g_r \), and all relevant \( g_i \) \( [i=1, 2, \ldots, g_{r-1}] \) against time and examine the areas between the curves relative to a plot of the corresponding state variable. Output from the stream model, the \( Y \) functions in the FLEX notation, provides state variable values \( y_2 - y_{14} \) on the FLEXFORM and values corresponding to variables expressed in equations 1 through 11 \( (y_1 \) and \( y_{15} - y_{41} \) on the FLEXFORM).
MODEL STRUCTURE

The stream model is conceptualized as a hierarchical system of biological processes (Fig. 1 and 2). At the ecosystem level of resolution, stream processes are considered mechanistically as two coupled subsystems representing processes of primary consumption and predation (Fig. 1). Primary consumption represents all processes associated with direct consumption and decomposition of both autotrophic organisms and detritus, including the internal production dynamics of the autotrophic organisms collectively. Predation includes processes related to the transfer of energy from primary to secondary consumers or from secondary to tertiary consumers. Behavior of each of these subsystems can be partitioned further and investigated in terms of their coupled subsystems. Figure 1 also illustrates the subsystems of the primary consumption and predation systems. The small, solid arrows represent energy flows, while the dotted arrows emphasize the influence of certain control variables. Predation includes the processes of invertebrate and vertebrate predation, and primary consumption is represented by processes of herbivory and detritivory. Herbivory consists of all processes associated with the production and consumption of autotrophic organisms within the system, whereas detritivory represents the consumption and decomposition of detrital inputs. In other words, herbivory and detritivory are analogous processes, the only important difference being related to whether the energy resource is generated within the system (autochthonous production) or from outside the system (allochthonous input). Figure 2 depicts the structure of the herbivory and detritivory subsystems in terms of each of their coupled subsystems. Herbivory partitions into grazing and periphyton processes. Periphyton processes include all processes that are tightly coupled to the primary producers, in this case the periphyton assemblage. Grazing is the set of processes associated with the flow of energy from periphyton to macroconsumers. Detritivory partitions into shredding, collecting, and detrital processes. Shredding and collecting are processes associated with flows of energy from large particle detritus (>1 mm) and fine particle detritus (<1 mm) to macroconsumers, shredders and collectors, respectively. Detrital processes include five state variables, each representing the biomass of an arbitrarily designated fraction of the total detrital biomass. Large particulate organic matter (LPOM) is fractionated into material that decomposes quickly (FLPOM) and material that has a relatively slow rate of decomposition (SLPOM). LPOM remains in the
Figure 1. Schematic representation of a lotic ecosystem showing the hierarchical decomposition of the Primary Consumption and Predation subsystems. The symbols refer to flows or control from processes of grazing (G), shredding (S), and collecting (C); large and small particle detritus (LPOM and FPOM); export (E); respiration (R); temperature (TEMP); stream discharge (FLOW); photoperiod (PHOT); and nitrate concentration (NO3).
Figure 2. Mechanistic structure of the Herbivory and Detritivory subsystems in a lotic ecosystem.
system as either FLPOM or SLPOM for periods representing the time it takes for micro-organisms to convert these fractions into states (CFLPOM and CSLPOM) suitable for consumption by macroconsumers. Sources of material for the fine particle detritus state variable (FPOM) include mechanical (nonbiological) transfers from CFLPOM and CSLPOM and from waste (fecal) materials associated with the processes of grazing, shredding, collecting, invertebrate predation, and vertebrate predation.

LITERATURE CITED


TITLE: Stream Ecosystem Model
INVESTIGATORS: McIntire and Colby
DATE: December, 1976
REVIEWED AND REVISED BY: White
REVISION DATE: October, 1977

TIME RESOLUTION: 1 day (360 days = 1 year)

QUANTITY MODELED: Biomass equivalents

SYSTEMS DIAGRAM: (See attached figures 1 and 2)

VARIABLES AND FUNCTIONS:

<table>
<thead>
<tr>
<th>X List</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>x1</td>
<td>Not used</td>
<td>-</td>
</tr>
<tr>
<td>x2</td>
<td>Biomass-grazing</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>x3</td>
<td>Biomass-shredding</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>x4</td>
<td>Biomass-collecting</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>x5</td>
<td>Biomass-vertebrate predation</td>
<td>g m(^{-2})</td>
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<td>x6</td>
<td>Biomass-invertebrate predation</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>x7</td>
<td>Biomass-periphyton processes</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>x8</td>
<td>Biomass-fine particulate organic matter (FPOM)</td>
<td>g m(^{-2})</td>
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<tr>
<td>x9</td>
<td>Conditioned allochthonous biomass-slow rate (CSLPOM)</td>
<td>g m(^{-2})</td>
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<tr>
<td>x10</td>
<td>Conditioned allochthonous biomass-fast rate (CFLPOM)</td>
<td>g m(^{-2})</td>
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<td>x11</td>
<td>Unconditioned allochthonous biomass-slow rate (SLPOM)</td>
<td>g m(^{-2})</td>
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<tr>
<td>x12</td>
<td>Unconditioned allochthonous biomass-fast rate (FLPOM)</td>
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<td>x13</td>
<td>SLPOM conditioning gate</td>
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</tr>
<tr>
<td>x14</td>
<td>FLPOM conditioning gate</td>
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</tr>
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</table>
2. Z Functions

\[ z_1 = b_4 + b_5 \sin \left( \frac{2\pi k}{360} - \frac{\pi}{2} \right), \]

where

- \( b_4 = 12 \), the mean annual temperature,
- \( b_5 = 6 \), the amplitude of temperature variation,
- \( \pi = 3.1416 \)

\[ z_2 = \begin{cases} s_1 (k, \text{EXLITE}, 360, 2) & \text{if } r_{13} < 0, \\ r_{13} & \text{otherwise}, \end{cases} \]

where

- \( r_{13} \) is a constant light input,
- EXLITE is a table of light input for one year at two-day resolution.

\[ z_3 = \begin{cases} s_1 (k, \text{XNUTR}, 1080, 30) & \text{if } r_{11} < 0, \\ r_{11} & \text{otherwise}, \end{cases} \]

where

- \( r_{11} \) is a constant nutrient input,
- XNUTR is a table of nutrient input for three years at thirty-day resolution.

\[ z_4 = \begin{cases} s_1 (k, \text{STRFLOW}, 360, 1) & \text{if } r_{12} < 0, \\ r_{12} & \text{otherwise}, \end{cases} \]

where

- \( r_{12} \) is a constant stream flow,
- STRFLOW is a table of stream flow rates for one year at daily resolution.
\[ z_5 = \begin{cases} s_1 (k, \text{SALLOC, 360, 5}) & \text{if } r_{14} < 0, \\ r_{14} & \text{otherwise}, \end{cases} \]

where
\( r_{14} \) is a constant allochthonous input, SALLOC is a table of slowly conditioned allochthonous input for one year at five-day resolution.

\[ z_6 = \begin{cases} s_1 (k, \text{FALLOC, 360, 5}) & \text{if } r_4 < 0, \\ r_4 & \text{otherwise}, \end{cases} \]

where
\( r_4 \) is a constant allochthonous input, FALLOC is a table of fast conditioned allochthonous input for one year at five-day resolution.

\[ z_7 = b_8 (b_{11} + b_{10} z_4 + b_9 z_4^2 + z_4^3) \]

where
\( b_8 = 1.97 \times 10^{-4} \),
\( b_9 = -94.4 \),
\( b_{10} = 9.42 \times 10^3 \),
\( b_{11} = 1.08 \times 10^3 \).

(b parameters estimated for Oak Creek flow schedule)

\[ z_8 = b_{12} z_4^{-b_{13}} \]

where
\( b_{12} = 4.88 \times 10^{-2} \),
\( b_{13} = 8.83 \times 10^{-2} \).

(b parameters estimated for Oak Creek flow schedule)

\[ z_9 = b_{16} z_4^{b_{17}} \]

where
\( b_{16} = 1.07 \),
\( b_{17} = 0.633 \).

(b parameters estimated for Oak Creek flow schedule)

<table>
<thead>
<tr>
<th>Description</th>
<th>Units</th>
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<tbody>
<tr>
<td>Allochthonous input (slow conditioned)</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>Allochthonous input (fast conditioned)</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>Suspended load</td>
<td>mg l⁻¹</td>
</tr>
<tr>
<td>Roughness coefficient</td>
<td>-</td>
</tr>
<tr>
<td>Stream cross-sectional area</td>
<td>ft²</td>
</tr>
</tbody>
</table>
\[ z_{10} = b_6 z_4^{b_7} \]
where
\[ b_6 = 0.114, \]
\[ b_7 = 0.581. \]
(b parameters estimated for Oak Creek flow schedule)

\[ z_{11} = b_{14} z_4^{b_{15}} \]
where
\[ b_{14} = 10.2, \]
\[ b_{15} = 2.95 \times 10^{-3}, \]
(b parameters estimated for Oak Creek flow schedule)

\[ z_{12} = z_9 / (2z_{10} + z_{11}) \]
where
\[ z_9 \] is the cross-sectional area,
\[ z_{10} \] is the stream depth,
\[ z_{11} \] is the stream width.

\[ z_{13} = (45.42 z_{12}^{2/3} b_2^{1/2}) / z_8 \]
where
\[ b_2 = 0.0139, \] the channel slope,
\[ z_8 \] is the roughness coefficient,
\[ z_{12} \] is the hydraulic radius.

\[ z_{14} = \min \left[ 1, 0.2 + \frac{b_3 z_{13}}{1 + b_3 z_{13}} \right] \]
where
\[ b_3 = 0.057, \]
\[ z_{13} \] is the current velocity.
\[ z_{15} = 304.73 \times b_2 z_{12} \]

where

\[ b_2 = 0.0139, \text{ the channel slope} \]

(estimated for Oak Creek),

\[ z_{12} \text{ is the hydraulic radius.} \]

\[ z_{16} = z_2 \exp \left[ -z_{10} \times 0.305 \times \min \left\{ 3, \max (0.03, 0.03z_7 + 0.2) \right\} \right] \]

where

\[ z_2 \text{ is the light intensity,} \]

\[ z_{10} \text{ is the stream depth,} \]

\[ z_7 \text{ is the suspended load.} \]
\[ z_{17} = b_{43} + b_{44} \sin \left( \frac{2 \frac{k - \pi}{360}}{2} \right) \]

where

- \( b_{43} = 12 \), the mean annual photoperiod,
- \( b_{44} = 4 \), the fluctuation amplitude,
- \( \pi = 3.1416 \).

(graph similar to that for \( z_1 \), with \( b_{44} = b_5 \))

3. G Functions

\[ g_1 = x_2 (b_{81} + r_1 z_1) \]

where

- \( b_{81} = 1.46 \times 10^{-2} \)
- \( r_1 = 4.46 \times 10^{-3} \)

\( z_1 \) is the water temperature,
\( x_2 \) is the process biomass for grazing.

\[ g_2 = x_2 b_{100} \begin{cases} 
0.046 z_1 & \text{if } z_1 < 2, \\
0.0268 z_1 + 0.0388 & \text{if } 2 \leq z_1 < 18, \\
-0.0435 z_1 + 1.305 & \text{if } 18 \leq z_1 < 30 \\
0 & \text{if } z_1 \geq 30
\end{cases} \]

where

- \( b_{100} = 1 \),
- \( z_1 \) is the water temperature,
- \( x_2 \) is the process biomass for grazing.
\[ g_3 = x_2 b_{85} \left[ s_1(k, \text{GEMER}, 360, 15)/15 \right] \]

where
- \( b_{85} = 0.8 \), the scaling factor,
- GEMER is a table of 15-day emergence totals for one year at 15-day resolution,
- \( x_2 \) is the process biomass for grazing.

\[ g_4 = g_{13} \max \left[0, (x_2 - b_{96})\right] \]

where
- \( b_{96} = 0.3 \),
- \( g_{13} \) is the coefficient of predation on the process of primary consumption,
- \( x_2 \) is the process biomass for grazing.
\[ g_5 = x_3(b_{82} + r_2z_1) \]

where
\[ b_{82} = 2.86 \times 10^{-2} \]
\[ r_2 = 4.46 \times 10^{-3} \]
\[ z_1 \] is the water temperature,
\[ x_3 \] is the process biomass for shredding.

\[ g_6 = x_3(1 + b_{89})b_{88}\min\left[\frac{1.2b_{99}z_1}{1 + b_{99}z_1}, 1\right] \]

where
\[ b_{88} = 0.7, \]
\[ b_{89} = 0.237, \]
\[ b_{99} = 0.167, \]
\[ z_1 \] is the water temperature,
\[ x_3 \] is the process biomass for shredding.

**Description**

**Units**

<table>
<thead>
<tr>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration associated with shredding</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>Shredding demand for CSLPOM and CFLPOM</td>
<td>g m(^{-2})</td>
</tr>
</tbody>
</table>
\( g_7 = x_3 b_{86} [s_1(k, \text{SEMER, 360, 15})] / 15 \)

where

\( b_{86} = 12, \)

SEMER is a table of 15-day emergence totals for one year at 15-day resolution,

\( x_3 \) is the process biomass for shredding.

\( g_8 = g_{13} \max [0, (x_3 - b_{97})] \)

where

\( b_{97} = 0.3, \)

\( g_{13} \) is the coefficient of predation on all primary consumers,

\( x_3 \) is the process biomass for shredding.
\[ g_9 = x_4(b_{83} + r_3z_1) \]

where
\[ b_{83} = 1.46 \times 10^{-2}, \]
\[ r_3 = 4.46 \times 10^{-3}, \]
\[ z_1 \] is the water temperature,
\[ x_4 \] is the process biomass for collecting.

\[ g_{10} = x_4 \begin{cases} 0.12z_1 & \text{if } z_1 < 2, \\ 0.015z_1 + 0.21 & \text{if } 2 \leq z_1 < 18, \\ -0.04z_1 + 1.2 & \text{if } 18 \leq z_1 < 30, \\ 0 & \text{if } 30 \leq z_1. \end{cases} \]

where
\[ z_1 \] is the water temperature,
\[ x_4 \] is the process biomass for collecting.
\[ g_{11} = x_4 b_{87} [s_1(k, \text{CEMER, 360, 15})]/15 \]

where
\[ b_{87} = 0.35, \text{ the scaling factor,} \]
\[ \text{CEMER is a table of 15-day} \]
\[ \text{emergence totals for one year} \]
\[ \text{at 15-day resolution,} \]
\[ x_4 \text{ is the process biomass} \]
\[ \text{for collecting.} \]

\[ g_{12} = g_{13} \max [0, (x_4 - b_{98})] \]

where
\[ b_{98} = 0.3, \]
\[ g_{13} \text{ is the coefficient of} \]
\[ \text{predation on all primary consumers,} \]
\[ x_4 \text{ is the process biomass} \]
\[ \text{for collecting.} \]
\[ g_{13} = \begin{cases} 0 & \text{if } g_{21} \leq 0 \\ \frac{(g_{57} + g_{58})}{g_{21}} & \text{otherwise} \end{cases} \]

where

- \( g_{21} \) is the primary consumer biomass available for consumption,
- \( g_{57} \) is food consumption of primary consumers by invertebrate predation,
- \( g_{58} \) is food consumption of primary consumers by vertebrate predation.

\[ g_{14} = \begin{cases} \frac{b_{78}z_3}{1 + b_{78}z_3} & \text{if } z_3 < b_{68} \\ 1 - \left( \frac{1}{1 + b_{68}b_{78}} \right) \frac{b_{69} - z_3}{b_{69} - b_{68}} & \text{if } b_{68} < z_3 < b_{69} \\ 0 & \text{if } b_{69} \leq z_3 \end{cases} \]

where

- \( b_{68} = 1 \times 10^{-3} \),
- \( b_{69} = 0.5 \),
- \( b_{78} = 2.68 \times 10^2 \),
- \( z_3 \) is the nutrient (NO\textsubscript{3} \textsuperscript{-}) concentration.

\[ g_{15} = \begin{cases} \frac{b_{71}z_{16}}{1 + b_{71}z_{16}} & \text{if } z_{16} < b_{90} \\ 1 - \left( \frac{1}{1 + b_{90}b_{71}} \right) \frac{b_{91} - z_{16}}{b_{91} - b_{90}} & \text{if } b_{90} \leq z_{16} < b_{91} \\ 1 & \text{if } b_{91} \leq z_{16} \end{cases} \]

Nutrient limiting effect coefficient for primary production

Light limiting effect coefficient for primary production

<table>
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<tr>
<th>Description</th>
<th>Units</th>
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</thead>
<tbody>
<tr>
<td>Coefficient of predation on all primary consumers</td>
<td>none</td>
</tr>
<tr>
<td>Nutrient limiting effect coefficient for primary production</td>
<td>none</td>
</tr>
<tr>
<td>Light limiting effect coefficient for primary production</td>
<td>none</td>
</tr>
</tbody>
</table>
where
\[ b_{71} = 2.1 \times 10^{-3}, \]
\[ b_{90} = 1 \times 10^3, \]
\[ b_{91} = 2.4 \times 10^5, \]
\[ z_{16} \] is the effective light intensity at the stream bottom.

\[ g_{16} - g_{18} \]
\[ g_{19} = \max \{ 0, x_6 - b_{50} \} \]
where
\[ b_{50} = 0.3, \]
\[ x_6 \] is the process biomass for invertebrate predation.
\[ g_{20} = (1 - b_{92})g_{51} + \left( 1 - \frac{b_{93}}{1 + b_{89}} \right)g_{52} + (1 - b_{94})g_{53} \]
\[ FPOM \] generated by primary consumption

where
\[ b_{89} = 0.237, \] the fraction of consumption by shredding that represents mechanical transfer of LPOM to FPOM,
\[ b_{92} = 0.55, \] assimilation ratio for grazing,
\[ b_{93} = 0.18, \] assimilation ratio for shredding,
\[ b_{94} = 0.21, \] assimilation ratio for collecting,
\[ g_{51} \] is the consumption of periphyton by grazing,
\[ g_{52} \] is the consumption of CSLPOM and CFLPOM by shredding,
\[ g_{53} \] is the consumption of FPOM by collecting.
\[ g_{21} = \max[0, x_2 - b_{96}] + \max[0, x_3 - b_{97}] + \max[0, x_4 - b_{98}] \]
where
\[ b_{96} = 0.3, \]
\[ b_{97} = 0.3, \]
\[ b_{98} = 0.3, \]
\[ x_2, x_3, \text{and } x_4 \text{ are process biomasses for grazing, shredding, and collecting, respectively.} \]
\[ g_{22} = x_6(b_{56} + r_6z_1) \]
where
\[ b_{56} = 1.88 \times 10^{-2}, \]
\[ r_6 = 0, \]
\[ z_1 \text{ is the water temperature,} \]
\[ x_6 \text{ is the process biomass for invertebrate predation.} \]
\[ g_{23} = x_6b_{59}\min\left[ \frac{1.2 \times b_{60}z_1}{1 + b_{60}z_1}, 1 \right] \]
where
\[ b_{59} = 0.05, \]
\[ b_{60} = 100, \]
\[ z_1 \text{ is the water temperature,} \]
\[ x_6 \text{ is the process biomass for invertebrate predation.} \]
\[ g_{24} = x_6 b_{57} \left( s_1(k, PEMER, 360, 15) \right) / 15 \]

where

\[ b_{57} = 0.42, \text{ a scaling factor,} \]

PEMER is a table of 15-day emergence totals for one year at 15-day resolution,

\[ x_6 \] is the process biomass for invertebrate predation.

\[ g_{25} = b_{52} \left( g_{27} + g_{54} + g_{58} \right) + x_5 \left( b_{53} + r_5 z_1 + b_{54} \right) \]

where

\[ b_{52} = 0.1, \]

\[ b_{53} = 1.87 \times 10^{-3}, \]

\[ b_{54} = 2.5 \times 10^{-3}, \]

\[ r_5 = 1.44 \times 10^{-4}, \]

\[ g_{27} \] is vertebrate predation demand for food,

\[ g_{54} \] is vertebrate predation of drifting organisms,

\[ g_{58} \] is vertebrate predation of primary consumer organisms,

\[ x_5 \] is the process biomass for vertebrate predation.

Description

Emergence losses associated with invertebrate predation

Units

\( g \ m^{-2} \)

Respiration and mortality losses associated with vertebrate predation

Units

\( g \ m^{-2} \)
\[ g_{26} = x_5 b_{55} \]
where
\[ b_{55} = 2.6 \times 10^{-2}, \]
\[ x_5 \] is the process biomass for vertebrate predation.

\[ g_{27} = \begin{cases} 
0 & \text{if } g_{19} \leq 0 \\
g_{56} \left( \frac{g_{19}}{g_{19} + g_{21}} \right) & \text{otherwise}
\end{cases} \]
where
\[ g_{19} \] is invertebrate predator biomass available for consumption,
\[ g_{21} \] is primary consumer biomass available for consumption,
\[ g_{56} \] is vertebrate predation capacity to reduce primary consumer and invertebrate predator biomass.

\[ g_{28} = (1 - b_{51})(g_{27} + g_{54} + g_{58}) + (1 - b_{58})g_{57} \]
where
\[ b_{51} = 0.86, \]
\[ b_{58} = 0.82, \]
\[ g_{27} \] is consumption of invertebrate predator biomass by vertebrate predation,
\[ g_{54} \] is consumption of drifting organisms by vertebrate predation,
\[ g_{58} \] is consumption of primary consumers by vertebrate predation,
\[ g_{57} \] is consumption of primary consumers by invertebrate predation.
\[ g_{29} = \frac{x_7 z_{14} r_7}{[1 + \exp(1.7 - b_{80} z_1)]} \]

where 
- \( b_{80} = 0.187 \),
- \( r_7 = 5.85 \times 10^{-2} \),
- \( z_1 \) is the water temperature,
- \( z_{14} \) is the current velocity effect,
- \( x_7 \) is the periphyton biomass.

\[ g_{30} = 0.937 b_{79} g_{31} g_{14} g_{15} z_{14} z_{17} \]

where 
- \( b_{79} = 2.95 \),
- \( g_{31} \) is the biomass and temperature limiting effect coefficient,
- \( g_{14} \) is the nutrient limiting effect,
- \( g_{15} \) is the light limiting effect,
- \( z_{14} \) is the current velocity effect,
- \( z_{17} \) is the photoperiod.

\[ g_{31} = \left( \frac{b_{76} x_7}{1 + b_{76} x_7} \right) \left( \frac{b_{77} z_1}{1 + b_{77} z_1} \right) \]

where 
- \( b_{76} = 0.1 \),
- \( b_{77} = 0.4 \),
- \( z_1 \) is the water temperature,
- \( x_7 \) is the periphyton biomass.
\[ g_{32} = x_7(b_{75} + b_{70}z_{15}) \]

where
\[ b_{75} = 1.08 \times 10^{-3}, \]
\[ b_{70} = 1.92 \times 10^{-2}, \]
\[ z_{15} \text{ is the shear stress,} \]
\[ x_7 \text{ is the periphyton biomass.} \]

\[ g_{33} = x_7(b_{73} + b_{74}z_{15}) \]

where
\[ b_{73} = 0, \]
\[ b_{74} = 7.40 \times 10^{-3}, \]
\[ z_{15} \text{ is the shear stress,} \]
\[ x_7 \text{ is the periphyton biomass.} \]

\[ g_{34} = \max[0, x_7 - b_{72}] \]

where
\[ b_{72} = 0.7, \]
\[ x_7 \text{ is the periphyton biomass.} \]

\[ g_{35} = r_8(1 + b_{37}z_1) \]

where
\[ b_{37} = 0.294, \]
\[ r_8 = 9.11 \times 10^{-4}, \]
\[ z_1 \text{ is the water temperature.} \]
\[ g_{36} = b_{39} + b_{41}z_{15} \]

where
- \( b_{39} = 1.28 \times 10^{-4} \),
- \( b_{41} = 1.38 \times 10^{-3} \),
- \( z_{15} \) is the shear stress.

\[ g_{37} = r_9(1 + b_{38}z_1) \]

where
- \( b_{38} = 2.03 \),
- \( r_9 = 1.99 \times 10^{-4} \),
- \( z_1 \) is the water temperature.
\[ g_{38} = b_{40} + b_{42}z_{15} \]

where
\[ b_{40} = 1.28 \times 10^{-4}, \]
\[ b_{42} = 1.38 \times 10^{-3}, \]
\[ z_{15} \] is the shear stress.

\[ g_{39} = x_8 z_{14} \left[ \frac{r_{10}}{1 + \exp(1.7 - b_{45}z_1)} \right] \]

where
\[ b_{45} = 0.187, \]
\[ r_{10} = 5.85 \times 10^{-2}, \]
\[ z_{14} \] is the current velocity effect.

\[ g_{40} = x_8 (b_{46} + b_{47}z_{15}) \]

where
\[ b_{46} = 2.33 \times 10^{-3}, \]
\[ b_{47} = 1.74 \times 10^{-2}, \]
\[ z_{15} \] is the shear stress,
\[ x_8 \] is the FPOM biomass.
\[ \mathcal{G}_{41} = (x_9 + x_{11})g_{35} + (x_{10} + x_{12})g_{37} \]

where
- \( g_{35} \) is decomposition of CSLPOM and SLPOM,
- \( g_{37} \) is decomposition of CFLPOM and FLPOM,
- \( x_9 \) is the CSLPOM biomass,
- \( x_{10} \) is the CFLPOM biomass,
- \( x_{11} \) is the SLPOM biomass,
- \( x_{12} \) is the FLPOM biomass.

\[ \mathcal{G}_{42} = (x_9 + x_{11})g_{36} + (x_{10} + x_{12})g_{38} \]

where
- \( g_{36} \) is export of CSLPOM and SLPOM,
- \( g_{38} \) is export of CFLPOM and FLPOM,
- \( x_9 \) is the CSLPOM biomass,
- \( x_{10} \) is the CFLPOM biomass,
- \( x_{11} \) is the SLPOM biomass,
- \( x_{12} \) is the FLPOM biomass.

\[ \mathcal{G}_{43} = z_5 + z_6 \]

where
- \( z_5 \) is slow-conditioned allochthonous input,
- \( z_6 \) is fast-conditioned allochthonous input.
\[ g_{44} = \min[x_{11}, \max(0, b_{31}(x_{11} - x_{13}))] \]

where
\[ b_{31} = 9.95 \times 10^{-2}, \]
\[ x_{11} \text{ is the SLPOM biomass,} \]
\[ x_{13} \text{ is the SLPOM conditioning gate.} \]

\[ g_{45} = \min[x_{12}, \max(0, b_{32}(x_{12} - x_{14}))] \]

where
\[ b_{32} = 0.465, \]
\[ x_{12} \text{ is the FLPOM biomass,} \]
\[ x_{14} \text{ is the FLPOM biomass.} \]

\[ g_{46} = \frac{b_{21}g_{34}}{1 + b_{21}g_{34}} \]

where
\[ b_{21} = 4, \]
\[ g_{34} \text{ is the periphyton biomass available to grazing.} \]

\[ g_{47} = \min\left[1, \frac{1.2 b_{28}(x_{9} + x_{10})}{1 + b_{28}(x_{9} + x_{10})}\right] \]

where
\[ b_{28} = 3.5, \]
\[ x_{9} \text{ is the CSLPOM biomass,} \]
\[ x_{10} \text{ is the CFLPOM biomass.} \]

\[ g_{48} = g_{56} - g_{27} \]

where
\[ g_{26} \text{ is the consumption of invertebrate predator biomass by vertebrate predation,} \]
\[ g_{56} \text{ is vertebrate predation capacity to reduce primary consumer biomass in the absence of competition with invertebrate predation.} \]

\[ g_{49} \text{ and } g_{50} \text{ not used.} \]
\[ g_{51} = \min[g_2 g_{46}, g_{34}] \]

where
- \( g_2 \) is grazing demand for periphyton,
- \( g_{34} \) is the periphyton biomass available to grazing,
- \( g_{46} \) is the food density limiting factor for grazing.

\[ g_{52} = \min[g_6 g_{47}, x_9 + x_{10}] \]

where
- \( g_6 \) is shredding demand for CSLPOM and CFLPOM,
- \( g_{47} \) is the food density limiting factor for shredding,
- \( x_9 \) is CSLPOM biomass,
- \( x_{10} \) is CFLPOM biomass.

Description

Consumption of periphyton biomass by grazing

Units

\( g \ m^{-2} \)
\[ g_{53} = \min \left( g_{10} \left( \frac{b_{29} x_8}{1 + b_{29} x_8} \right), x_8 \right) \]

where

- \( b_{29} = 3.5 \),
- \( g_{10} \) is collecting demand for FPOM,
- \( x_8 \) is FPOM biomass.

\[ g_{54} = \min \left( b_{23} (g_3 + g_7 + g_{11} + g_{24}), b_{25} x_8 \right) \]

where

- \( b_{23} = 1 \),
- \( b_{25} = 0.5 \),
- \( g_3 \) is emergence loss (grazing),
- \( g_7 \) is emergence loss (shredding),
- \( g_{11} \) is emergence loss (collecting),
- \( g_{24} \) is emergence loss (invertebrate predation),
- \( g_{26} \) is vertebrate predation demand for food.

\[ g_{55} = g_{23} \begin{cases} \frac{g_{21}}{10b_{20}} & \text{if } g_{21} < b_{20}, \\ 0.9 - 0.8 \left( \frac{b_{24} - g_{21}}{b_{24} - b_{20}} \right) & \text{if } b_{20} \leq g_{21} < b_{24}, \\ \min \left[ 1, 0.9 + \frac{0.1(g_{21} - b_{24})}{b_{20}} \right] & \text{if } g_{21} \geq b_{24} \end{cases} \]

Description

Consumption of drift by vertebrate predation

Consumption of FPOM by collecting

Description

Invertebrate predation capacity to reduce primary consumer biomass
where

\[ b_{20} = 1.5, \]
\[ b_{24} = 4, \]

\( g_{21} \) is primary consumer biomass available for consumption,
\( g_{23} \) is invertebrate predation demand for primary consumers.

\[ g_{56} = (1-b_{25})g_{26} \left[ \frac{b_{18}}{b_{18} + b_{19}\exp(-b_{18}(g_{19} + g_{21}))} \right] \]

Vertebrate predation capacity to reduce primary consumer and invertebrate predator biomass

where

\[ b_{18} = 1.1, \]
\[ b_{19} = 1.6 \times 10^2, \]
\[ b_{25} = 0.5, \]

\( g_{19} \) is invertebrate predator biomass available for consumption by vertebrate predation,
\( g_{21} \) is primary consumer biomass available for consumption by predation,
\( g_{26} \) is vertebrate predation demand for food.
\[ g_{57} = \min \left[ g_{55}, b_{22} g_{21} \left( \frac{g_{55}}{g_{55} + g_{48}} \right) \right] \]

where

- \( b_{22} = 0.8 \)
- \( g_{21} \) is primary consumer biomass available for consumption by predation,
- \( g_{48} \) is vertebrate predation capacity to reduce primary consumer biomass,
- \( g_{55} \) is invertebrate predation capacity to reduce primary consumer biomass.

\[ g_{58} = \min \left[ g_{48}, (1 - b_{22}) g_{21} \left( \frac{g_{48}}{g_{55} + g_{48}} \right) \right] \]

where

- \( b_{22} = 0.8 \)
- \( g_{21} \) is primary consumer biomass available for consumption by predation,
- \( g_{48} \) is vertebrate predation capacity to reduce primary consumer biomass,
- \( g_{55} \) is invertebrate predation capacity to reduce primary consumer biomass.

\[ g_{59} = \begin{cases} 
0 & \text{if } x_7 < b_{64}, \\
 x_7 b_{65} \left( \frac{x_7 - b_{64}}{b_{84} - b_{64}} \right) & \text{if } b_{64} \leq x_7 < b_{84}, \\
 x_7 b_{65} & \text{if } b_{84} \leq x_7 
\end{cases} \]

where

- \( b_{64} = 15 \)
- \( b_{65} = 0.01 \)
- \( b_{84} = 3 \)
- \( x_7 \) is the periphyton biomass.
\[ g_{60} = b_{66} \exp (b_{67}g_{30}) - 1] + g_{59} \]

where

- \( b_{66} = 2.8 \times 10^{-2} \),
- \( b_{67} = 0.583 \),
- \( g_{30} \) is periphyton primary production,
- \( g_{59} \) is leakage of dissolved organic matter from periphyton biomass.

**Description**
Total export of dissolved organic matter from periphyton

**Units**
\( g \ m^{-2} \)

---

4. **F Functions:**

\[ f_{1,1} \]

\[ f_{2,2} = b_{92}g_{51} - g_{1} - g_{3} - g_{4} \]

where

- \( b_{92} = 0.55 \),
- \( g_{1} \) is respiration associated with grazing,
- \( g_{3} \) is emergence loss associated with grazing,
- \( g_{4} \) is predation loss for grazing,
- \( g_{51} \) is consumption of periphyton by grazing.

**Description**
Biomass update increment for grazing

**Units**
\( g \ m^{-2} \)

**Not used**

\[ f_{3,3} = \left( \frac{b_{93}}{1 + b_{89}} \right) g_{52} - g_5 - g_7 - g_8 \]

where
- \( b_{89} = 0.237 \)
- \( b_{93} = 0.18 \)
- \( g_5 \) is respiration associated with shredding,
- \( g_7 \) is emergence loss associated with shredding,
- \( g_8 \) is predation loss for shredding,
- \( g_{52} \) is consumption of LPOM by shredding.

\[ f_{4,4} = b_{94} g_{53} - g_9 - g_{11} - g_{12} \]

where
- \( b_{94} = 0.21 \)
- \( g_9 \) is respiration associated with collecting,
- \( g_{11} \) is emergence loss associated with collecting,
- \( g_{12} \) is predation loss for collecting,
- \( g_{53} \) is consumption of FPOM by collecting.

\[ f_{5,5} = b_{51} (g_{27} + g_{54} + g_{58}) - g_{25} \]

where
- \( b_{51} = 0.86 \)
- \( g_{25} \) is respiration and mortality losses for vertebrate predation,
- \( g_{27} \) is consumption of invertebrate predator biomass by vertebrate predation,
- \( g_{54} \) is consumption of drift by vertebrate predation,
- \( g_{58} \) is consumption of primary consumer biomass by vertebrate predation.

<table>
<thead>
<tr>
<th>Description</th>
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<tbody>
<tr>
<td>Biomass update increment for shredding</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>Biomass update increment for collecting</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>Biomass update increment for vertebrate predation</td>
<td>g m(^{-2})</td>
</tr>
</tbody>
</table>
\[ f_{6,6} = b_{58}g_{57} - g_{22} - g_{24} - g_{27} \]

where

\( b_{58} = 0.82, \)

\( g_{22} \) is respiration associated with invertebrate predation,

\( g_{24} \) is emergence loss associated with invertebrate predation,

\( g_{27} \) is consumption of invertebrate predator biomass by vertebrate predation,

\( g_{57} \) is consumption of primary consumers by invertebrate predation.

\[ f_{7,7} = g_{30} - g_{29} - g_{32} - g_{33} - g_{51} - g_{60} \]

where

\( g_{29} \) is periphyton respiration,

\( g_{30} \) is periphyton primary production,

\( g_{32} \) is fine particle export of periphyton,

\( g_{33} \) is large particle export of periphyton,

\( g_{51} \) is consumption of periphyton by grazing,

\( g_{60} \) is export of dissolved organic matter from periphyton.

\[ f_{8,8} = g_{20} + g_{28} - g_{39} - g_{40} - g_{53} \]

where

\( g_{20} \) is FPOM generated by primary consumption,

\( g_{28} \) is FPOM generated by predation,

\( g_{39} \) is decomposition of FPOM,

\( g_{40} \) is FPOM export,

\( g_{53} \) is consumption of FPOM by collecting.
\[ f_{9,9} = \begin{cases} \frac{x_9}{x_9 + x_10} & \text{if } x_9 \leq 0, \\ \frac{x_9}{x_9 + x_10} - x_9(g_35 + g_36) & \text{otherwise} \end{cases} \]

\[ f_{10,10} = \begin{cases} \frac{x_10}{x_9 + x_10} & \text{if } x_{10} \leq 0, \\ \frac{x_10}{x_9 + x_10} - x_{10}(g_37 + g_38) & \text{otherwise} \end{cases} \]

\[ f_{11,11} = z_5 - g_{44} - x_{11}(g_35 + g_36) \]

\[ f_{12,12} = z_6 - g_{45} - x_{12}(g_37 + g_38) \]

where:
- \( g_35 \) is decomposition of CSLPOM,
- \( g_36 \) is export of CSLPOM,
- \( g_44 \) is transfer of SLPOM to CSLPOM,
- \( g_{52} \) is consumption of LPOM by shredding,
- \( x_9 \) is CSLPOM biomass,
- \( x_{10} \) is CFLPOM biomass.

Biomass update increment for CSLPOM

Biomass update increment for CFLPOM

Biomass update increment for SLPOM

Biomass update increment for FLFOM
where

- \( z_6 \) is fast-conditioned allochthonous input,
- \( g_{37} \) is decomposition of FLPOM,
- \( g_{38} \) is export of FLPOM,
- \( g_{45} \) is transfer of FLPOM to CFLPOM,
- \( x_{12} \) is FLPOM biomass.

\[
f_{13,13} = b_{33}x_{13}(1 - g_{35})(1 - g_{36}) + b_{35}z_5 - x_{13}
\]

where

- \( b_{33} = 0.895 \),
- \( b_{35} = 1.9 \),
- \( z_5 \) is slow-conditioned allochthonous input,
- \( g_{35} \) is decomposition of CSLPOM and SLPOM,
- \( g_{36} \) is export of CSLPOM and SLPOM,
- \( x_{13} \) is SLPOM conditioning gate.

\[
f_{14,14} = b_{34}x_{14}(1 - g_{37})(1 - g_{38}) + b_{36}z_6 - x_{14}
\]

where

- \( b_{34} = 0.56 \),
- \( b_{36} = 1.51 \),
- \( z_6 \) is fast-conditioned allochthonous input,
- \( g_{37} \) is decomposition of FLPOM and CFLPOM,
- \( g_{38} \) is export of FLPOM and CFLPOM,
- \( x_{14} \) is FLPOM conditioning gate.

(Programming note: In addition, \( f_{14,14} \) passes some information to the \( y \) functions (YCOMP) using labelled Common. The information is used in generating values of some plot variables.)
The following $y$ functions are used as plot variables for the analysis of process regulatory mechanisms. In calculating these variables, values of $x_i$ are values used to calculate the $f$ functions—not the current, updated state variable values.

$$ y_1 = \frac{(b_9 g_2 - g_1)}{x_2} $$

where

- $b_9 = 0.55$,
- $g_1$ is respiration associated with grazing,
- $g_2$ is grazing demand for periphyton,
- $x_2$ is the process biomass for grazing.

$$ y_{15} = (b_9 g_{51} - g_1)x_2 $$

where

- $b_9 = 0.55$,
- $g_1$ is respiration associated with grazing,
- $g_{51}$ is consumption of periphyton by grazing,
- $x_2$ is the process biomass for grazing.

$$ y_{16} = y_{15} - \frac{g_3}{x_2} $$

where

- $y_{15}$ is production (grazing),
- $g_3$ is emergence losses for grazing,
- $x_2$ is the process biomass for grazing.
\[ y_{17} = y_{16} - \left( \frac{g_{57}}{g_{57} + g_{58}} \right) \left( \frac{g_4}{x_2} \right) \]

where
- \( y_{16} \) is production (grazing) less emergence losses,
- \( g_4 \) is predation losses for grazing,
- \( g_{57} \) is consumption of primary consumers by invertebrate predation,
- \( g_{58} \) is consumption of primary consumers by vertebrate predation,
- \( x_2 \) is the process biomass for grazing.

\[ y_{18} = y_{16} - \frac{g_4}{x_2} \]

where
- \( g_4 \) is the predation losses for the process of grazing,
- \( y_{16} \) is production (grazing) minus losses to emergence and predation,
- \( x_2 \) is the process biomass for grazing.

\[ y_{19} = \left[ \left( \frac{b_{93}}{1 + b_{89}} \right) g_6 - g_5 \right] / x_3 \]

where
- \( b_{89} = 0.237 \)
- \( b_{93} = 0.18 \)
- \( g_5 \) is respiration associated with shredding,
- \( g_6 \) is shredding demand for LPOM,
- \( x_3 \) is the process biomass for shredding.

<table>
<thead>
<tr>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Production minus losses to emergence and invertebrate predation for grazing</td>
<td>g g^{-1}</td>
</tr>
<tr>
<td>Realized specific growth of the capacity for grazing</td>
<td>g g^{-1}</td>
</tr>
<tr>
<td>Potential to expand shredding process capacity</td>
<td>g g^{-1}</td>
</tr>
</tbody>
</table>
\[ y_{20} = \left[ \frac{b_{93}}{1 + b_{89}} \right] g_{52} - g_{5} \] / x_{3} 

where

\[ b_{89} = 0.237, \]
\[ b_{93} = 0.18, \]
\[ g_{5} \text{ is respiration associated with shredding,} \]
\[ g_{52} \text{ is consumption of LPOM by shredding,} \]
\[ x_{3} \text{ is the process biomass for shredding.} \]

\[ y_{21} = y_{20} - \frac{g_{7}}{x_{3}} \]

where

\[ g_{7} \text{ is emergence losses associated with shredding,} \]
\[ y_{20} \text{ is production (shredding),} \]
\[ x_{3} \text{ is the process biomass for shredding.} \]

\[ y_{22} = y_{21} - \frac{g_{8}}{x_{3}} \]

where

\[ g_{8} \text{ is predation losses for shredding,} \]
\[ g_{57} \text{ is consumption of primary consumers by invertebrate predation,} \]
\[ g_{58} \text{ is consumption of primary consumers by vertebrate predation,} \]
\[ y_{21} \text{ is production minus emergence losses,} \]
\[ x_{3} \text{ is the process biomass for shredding.} \]
\[ y_{23} = y_{21} - \frac{g_{8}}{x_{3}} \]

where
- \( g_{8} \) is predation losses for shredding,
- \( y_{21} \) is production (shredding) minus emergence losses,
- \( x_{3} \) is the process biomass for shredding.

\[ y_{24} = \frac{(b_{94}g_{10} - g_{9})}{x_{4}} \]

where
- \( b_{94} = 0.21 \),
- \( g_{9} \) is respiration associated with collecting,
- \( g_{10} \) is collecting demand for FPOM,
- \( x_{4} \) is the process biomass for collecting.

\[ y_{25} = \frac{(b_{94}g_{53} - g_{9})}{x_{4}} \]

where
- \( b_{94} = 0.21 \),
- \( g_{9} \) is respiration associated with collecting,
- \( g_{53} \) is consumption of FPOM by collecting,
- \( x_{4} \) is the process biomass for collecting.

\[ y_{26} = y_{25} - \frac{g_{11}}{x_{4}} \]

where
- \( g_{11} \) is emergence losses associated with collecting,
- \( y_{25} \) is production (collecting),
- \( x_{4} \) is the process biomass for collecting.
\[ y_{27} = y_{26} - \left( \frac{g_{57}}{g_{57} + g_{58}} \right) g_{12} / x_4 \]

where
- \( g_{12} \) is predation losses for collecting,
- \( g_{57} \) is consumption of primary consumers by invertebrate predation,
- \( g_{58} \) is consumption of primary consumers by vertebrate predation,
- \( y_{26} \) is production minus emergence losses,
- \( x_4 \) is the process biomass for collecting.

\[ y_{28} = y_{26} - \frac{g_{12}}{x_4} \]

where
- \( g_{12} \) is predation losses for collecting,
- \( y_{26} \) is production (collecting) minus emergence losses,
- \( x_4 \) is the process biomass for collecting.

\[ y_{29} = (b_{58} g_{23} - g_{22})/x_6 \]

where
- \( b_{58} = 0.82 \),
- \( g_{22} \) is respiration associated with invertebrate predation,
- \( g_{23} \) is invertebrate predation demand for primary consumers,
- \( x_6 \) is the process biomass for invertebrate predation.

### Description
- **Production minus losses to emergence and invertebrate predation for collecting**

### Units
- \( g \text{ g}^{-1} \)

### Potential to expand the process capacity for invertebrate predation

### Realized specific growth of the capacity for collecting

### Units
- \( g \text{ g}^{-1} \)
\[ y_{30} = \frac{(b_{58} g_{57} - g_{22})}{x_6} \]

where
\[ b_{58} = 0.82, \]
\[ g_{22} \] is respiration associated with invertebrate predation,
\[ g_{57} \] is consumption of primary consumers by invertebrate predation,
\[ x_6 \] is the process biomass for invertebrate predation.

\[ y_{31} = y_{30} - \frac{g_{24}}{x_6} \]

where
\[ g_{24} \] is emergence losses associated with invertebrate predation,
\[ y_{30} \] is production (invertebrate predation),
\[ x_6 \] is the process biomass for invertebrate predation.

\[ y_{32} = y_{31} - \frac{g_{27}}{x_6} \]

where
\[ g_{27} \] is consumption of invertebrate predator biomass by vertebrate predation,
\[ y_{31} \] is production (invertebrate predation) minus emergence losses,
\[ x_6 \] is the process biomass for invertebrate predation.
\[ y_{33} = \frac{(b_{51}g_{26} - g_{25})}{x_5} \]

where
- \( b_{51} = 0.86 \)
- \( g_{25} \) is respiration and mortality (natural) losses associated with vertebrate predation,
- \( g_{26} \) is vertebrate predation demand for food,
- \( x_5 \) is the process biomass for vertebrate predation.

\[ y_{34} = \frac{b_{51}[(1 - b_{25})g_{26} + g_{54}] - g_{25}}{x_5} \]

where
- \( b_{25} = 0.5 \)
- \( b_{51} = 0.86 \)
- \( g_{25} \) is respiration and natural mortality losses for vertebrate predation,
- \( g_{26} \) is vertebrate predation demand for food,
- \( g_{54} \) is consumption of drift by vertebrate predation,
- \( x_5 \) is the process biomass for vertebrate predation.

\[ y_{35} = \frac{b_{51}(g_{48} + g_{54} + g_{27}) - g_{25}}{x_5} \]

where
- \( b_{51} = 0.86 \)
- \( g_{25} \) is respiration and natural mortality losses for vertebrate predation,
- \( g_{26} \) is consumption of invertebrate predator biomass by vertebrate predation,
- \( g_{27} \) is consumption of invertebrate predator biomass by vertebrate predation.

**Description** | **Units**
--- | ---
Potential to expand the process capacity for vertebrate predation | \( \text{g g}^{-1} \)
Potential to expand the process capacity for vertebrate predation when a fraction of the demand \((b_{25})\) must be satisfied by drift feeding or left unsatisfied | \( \text{g g}^{-1} \)
Production per unit of biomass (minus natural mortality) for vertebrate predation in the absence of competition with invertebrate predation | \( \text{g g}^{-1} \)
$y_{36} = b_{51}(g_{58} + g_{54} + g_{27}) - g_{25}$

where $b_{51} = 0.86,$
$g_{25}$ is respiration and natural mortality losses for vertebrate predation,
$g_{27}$ is consumption of invertebrate predator biomass by vertebrate predation,
$g_{54}$ is consumption of drift by vertebrate predation,
$g_{58}$ is the consumption of primary consumers by vertebrate predation,
$x_5$ is the process biomass for vertebrate predation.

$y_{37} = \left( \frac{g_{30}}{g_{14} g_{15}} \right) - g_{29}$

where $g_{14}$ is the nutrient limiting coefficient,
$g_{15}$ is the light limiting coefficient,
$g_{29}$ is periphyton respiration,
$g_{30}$ is periphyton primary production,
$x_7$ is the periphyton biomass.
\[ y_{38} = \frac{g_{30} - g_{29}}{x_7} \]

where
- \( g_{29} \) is periphyton respiration,
- \( g_{30} \) is periphyton primary production,
- \( x_7 \) is the periphyton biomass.

\[ y_{39} = y_{38} - \frac{g_{32} + g_{33}}{x_7} \]

where
- \( g_{32} \) is the fine particle export of periphyton,
- \( g_{33} \) is the large particle export of periphyton,
- \( y_{38} \) is the realized net periphyton community production,
- \( x_7 \) is the periphyton biomass.

\[ y_{40} = y_{39} - \frac{g_{60}}{x_7} \]

where
- \( y_{39} \) is realized net periphyton production minus particulate export,
- \( g_{60} \) is export of dissolved organic matter from periphyton,
- \( x_7 \) is the periphyton biomass.

\[ y_{41} = y_{40} - \frac{g_{51}}{x_7} \]

where
- \( y_{40} \) is the realized net periphyton community production minus export,
- \( g_{51} \) is consumption of periphyton by grazing,
- \( x_7 \) is the periphyton biomass.

**Description**

<table>
<thead>
<tr>
<th>Units</th>
<th>Realized net periphyton community production per unit biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g \cdot g^{-1} )</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Units</th>
<th>Realized net periphyton community production minus particulate export (( &gt;0.45 \mu m ) export)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g \cdot g^{-1} )</td>
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</table>

<table>
<thead>
<tr>
<th>Units</th>
<th>Realized net periphyton community production minus total export (including dissolved organic matter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g \cdot g^{-1} )</td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Units</th>
<th>Realized specific growth of periphyton biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g \cdot g^{-1} )</td>
<td></td>
</tr>
</tbody>
</table>
6. **Special Functions:**

\[ s_1(k, \text{NAME}, \alpha, \beta) = \text{NAME}(i_1 + 1) \]

\[ + \frac{s_2(k, \alpha) - i_1 \beta}{\beta} [\text{NAME}(i_2) - \text{NAME}(i_1 + 1)] \]

where \text{NAME} is an array of data for \( \alpha \) days at \( \beta \) time resolution, 
\( i_1 = \text{integer} \left[ \frac{s_2(k, \alpha)}{\beta} \right] \), the greatest integer function, 
\( i_1 + 1 \) is the array index corresponding to time \( k \), 
\( i_2 = \begin{cases} 1 & \text{if } \alpha < (i_1 + 2)\beta \\ i_1 + 2 & \text{otherwise} \end{cases} \), the array index after \( i_1 + 1 \) 
\( s_2 \) is the modulo function.

\[ s_2(k, \alpha) = k \mod \alpha \]

The modulo function varies with \text{NAME}.

7. **B Parameters:**

<table>
<thead>
<tr>
<th>List</th>
<th>Value</th>
<th>Description</th>
<th>In Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>( b_1 )</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>( b_2 )</td>
<td>1.39 ( \times 10^{-2} )</td>
<td>Channel slope</td>
<td>( z_{13}, z_{15} )</td>
</tr>
<tr>
<td>( b_3 )</td>
<td>5.7 ( \times 10^{-2} )</td>
<td>Current effect parameter</td>
<td>( z_{14} )</td>
</tr>
<tr>
<td>( b_4 )</td>
<td>12</td>
<td>Mean annual temperature</td>
<td>( z_1 )</td>
</tr>
<tr>
<td>( b_5 )</td>
<td>6</td>
<td>One-half the temperature range</td>
<td>( z_1 )</td>
</tr>
<tr>
<td>( b_6 )</td>
<td>0.114</td>
<td>Channel depth parameter</td>
<td>( z_{10} )</td>
</tr>
<tr>
<td>( b_7 )</td>
<td>0.581</td>
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<td>( z_{10} )</td>
</tr>
<tr>
<td>( b_8 )</td>
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<td>Suspended load parameter</td>
<td>( z_{7} )</td>
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<tr>
<td>( b_9 )</td>
<td>94.4</td>
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<td>( z_{7} )</td>
</tr>
<tr>
<td>( b_{10} )</td>
<td>9.42 ( \times 10^{3} )</td>
<td>Suspended load parameter</td>
<td>( z_{7} )</td>
</tr>
<tr>
<td>( b_{11} )</td>
<td>1.08 ( \times 10^{3} )</td>
<td>Suspended load parameter</td>
<td>( z_{7} )</td>
</tr>
<tr>
<td>List</td>
<td>Value</td>
<td>Description</td>
<td>In Function</td>
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<td>-------</td>
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<tr>
<td>$b_{12}$</td>
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<td>$z_{8}$</td>
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<tr>
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<td>Roughness parameter</td>
<td>$z_{8}$</td>
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<tr>
<td>$b_{14}$</td>
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<td>Channel width parameter</td>
<td>$z_{11}$</td>
</tr>
<tr>
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<td>Channel width parameter</td>
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</tr>
<tr>
<td>$b_{16}$</td>
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<tr>
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<td>Cross sectional area parameter</td>
<td>$z_{9}$</td>
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<td>Food density limiting rate parameter (vertebrate predation)</td>
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</tr>
<tr>
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<td>$1.6 \times 10^{2}$</td>
<td>Food density limiting rate parameter (vertebrate predation)</td>
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<tr>
<td>$b_{21}$</td>
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<td>Food density limiting rate parameter (grazing)</td>
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<td>$b_{22}$</td>
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<td>Emergence index parameter for drift feeding</td>
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<td>$b_{25}$</td>
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<td>List</td>
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<td>Description</td>
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<td>-------</td>
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<tr>
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<td>f_{13,13}</td>
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<td>Refuge parameter for invertebrate predation</td>
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<td></td>
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### 8. R Parameters

- $r_1 = 4.46 \times 10^{-3}$: Respiration parameter for grazing
- $r_2 = 4.46 \times 10^{-3}$: Respiration parameter for shredding
- $r_3 = 4.46 \times 10^{-3}$: Respiration parameter for collecting
- $r_4 = -1$: Constant allochthonous input (fast conditioned)
- $r_5 = 1.44 \times 10^{-4}$: Respiration parameter for vertebrate predation
- $r_6 = 0$: Respiration parameter for invertebrate predation
- $r_7 = 5.85 \times 10^{-2}$: Periphyton respiration parameter
- $r_8 = 9.11 \times 10^{-4}$: Decomposition parameter for CSLPOM and SLPOM
- $r_9 = 1.99 \times 10^{-4}$: Decomposition parameter for CFLPOM and FLPOM
- $r_{10} = 5.85 \times 10^{-2}$: Decomposition parameter for FPOM
- $r_{11} = -1$: Constant nutrient input
- $r_{12} = -1$: Constant stream flow
- $r_{13} = -1$: Constant light input
- $r_{14} = -1$: Constant allochthonous input (slow conditioned)
9. **Initial Conditions**

These initial values correspond to the parameters and input tables for Version I of the Standard Run. For additional information, see McIntire and Colby (1978).

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APPENDIX - Input Tables

These input tables correspond to Version I of the Standard Run. For additional information, see McIntire and Colby (1978). Read each row from left to right for correct chronological order.

1. Table: EXLITE

Unit: ft-c

Description: Light intensity values for one year at 2-day resolution.

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Unit: mg l\(^{-1}\)
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Unit: cfs
Description: Stream flow input data for one year at 1-day resolution.
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4. **Table: SALLOC**  
   **Unit:** g m\(^{-2}\)  
   **Description:** Slow-conditioned allochthonous input for one year at 5-day resolution.  
   **Values:**  
   \[
   \begin{array}{cccccccc}
   0.8060 & 0.7700 & 0.7400 & 0.7150 & 0.6958 & 0.6850 \\
   0.6752 & 0.6690 & 0.6810 & 0.6960 & 0.7110 & 0.7260 \\
   0.7412 & 0.7552 & 0.7356 & 0.7050 & 0.6794 & 0.6696 \\
   0.6602 & 0.6598 & 0.6646 & 0.6624 & 0.6374 & 0.6102 \\
   0.5862 & 0.5776 & 0.5706 & 0.5692 & 0.6582 & 0.7776 \\
   0.9182 & 1.0576 & 1.1146 & 1.1670 & 1.2194 & 1.2682 \\
   1.2502 & 1.1716 & 1.0870 & 1.0024 & 0.9180 & 0.8300 \\
   0.7308 & 0.6356 & 0.6242 & 0.6404 & 0.6566 & 0.7048 \\
   0.9610 & 1.2502 & 1.5370 & 1.8172 & 1.9644 & 1.9134 \\
   1.8628 & 1.8116 & 1.7612 & 1.7394 & 1.9032 & 2.0972 \\
   2.2908 & 2.4840 & 2.6780 & 2.7616 & 2.5048 & 2.1848 \\
   1.8640 & 1.5432 & 1.2228 & 0.9982 & 0.8860 & 0.8480 \\
   \end{array}
   \]

5. **Table: FALLOC**  
   **Unit:** g m\(^{-2}\)  
   **Description:** Fast-conditioned allochthonous input for one year at 5-day resolution.  
   **Values:**  
   \[
   \begin{array}{cccccccc}
   0.1669 & 0.1584 & 0.1501 & 0.1423 & 0.1393 & 0.1436 \\
   0.1478 & 0.1522 & 0.1579 & 0.1618 & 0.1596 & 0.1570 \\
   0.1545 & 0.1517 & 0.1459 & 0.1390 & 0.1346 & 0.1375 \\
   0.1408 & 0.1455 & 0.1512 & 0.1540 & 0.1485 & 0.1425 \\
   0.1367 & 0.1319 & 0.1275 & 0.1238 & 0.1376 & 0.1571 \\
   0.1711 & 0.1838 & 0.1798 & 0.1748 & 0.1698 & 0.1648 \\
   0.1587 & 0.1463 & 0.1329 & 0.1195 & 0.1061 & 0.0927 \\
   0.0797 & 0.0677 & 0.0759 & 0.0907 & 0.1056 & 0.1208 \\
   0.1381 & 0.1558 & 0.1694 & 0.1708 & 0.1751 & 0.1849 \\
   0.1947 & 0.2045 & 0.2142 & 0.2320 & 0.3003 & 0.3766 \\
   0.4529 & 0.5292 & 0.6055 & 0.6595 & 0.6054 & 0.5242 \\
   0.4430 & 0.3618 & 0.2806 & 0.2303 & 0.2184 & 0.2334 \\
   \end{array}
   \]
6. **Table: GEMER**  
units: \( g \, m^{-2} \)  
Description: Grazing 15-day emergence totals for one year at 15-day resolution.  
Values:

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7. **Table: SEMER**  
units: \( g \, m^{-2} \)  
Description: Shredding 15-day emergence totals for one year at 15-day resolution.  
Values:

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8. **Table: CEMER**  
units: \( g \, m^{-2} \)  
Description: Collecting 15-day emergence totals for one year at 15-day resolution.  
Values:

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9. **Table: PEMER**  
units: \( g \, m^{-2} \)  
Description: Invertebrate predation 15-day emergence totals for one year at 15-day resolution.  
Values:

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