A TUTORIAL AND TEACHING GUIDE FOR THE USE OF A LOTIC ECOSYSTEM MODEL

by

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PREFACE

The mathematical structures of the three versions of the stream ecosystem model described in this document evolved during a 25-year period. A periphyton model, which later became the Primary Production module of a stream ecosystem model, was programmed in MIMIC while I was on sabbitical leave in 1970-71 at the Center for Quantitative Science, University of Washington (Seattle, WA). The development of Version I of the McIntire and Colby Stream Model was supported mostly by funds from the Western Coniferous Biome, I.B.P., and most of the modeling was done between 1973 and 1976 at Oregon State University. The original mathematical documentation for Version I was prepared by J. A. Colby during the fall of 1976; this documentation was revised by Curtis White in October, 1977, and published as *Internal Report 165: Mathematical Documentation for a Lotic Ecosystem Model* (Coniferous Forest Biome, 1978). The Herbivory and Riparian Versions of the McIntire and Colby Stream Model were based on laboratory and field research conducted at Oregon State University between 1985 and the present. These versions of the model are modifications of Version I and were developed concurrently with an ongoing research program in stream ecology.

Model structure and parameter estimation were based on an enormous amount of information obtained from the literature and directly from an interdisciplinary group of stream ecologists. Among this group, I am particularly indebted to N. H. Anderson, L. R. Ashkenas, R. H. Boling, T. Bott, K. W. Cummins, C. E. Cushing, G. W. Fowler, E. Grafius, S. V. Gregory, J. D. Hall, G. A. Lamberti, G. W. Minshall, J. R. Sedell, A. D. Steinman, W. T. Summer, F. J. Triska, R. L. Vannote, and J. H. Wlosinski for their unselfish willingness to

share ideas and unpublished data. Very special thanks are due W. S. Overton for providing the theory upon which the three versions of the model are based and for his leadership in the development of the various versions of FLEX, a general model processor available at Oregon State University. I am also indebted to Brad Smith for programming the latest version of the FLEX model processor.

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INTRODUCTION

This tutorial provides the conceptual framework, descriptive information, and instructions necessary to run and examine the behavior of three versions of a lotic ecosystem model. Program and data files for these models are stored on the enclosed diskette. To use these files, an IBM or compatible PC with a math coprocessor is required. If the computer is equipped with a hard disk, the user can generate a complete set of output, which in this case, includes a screen display and print files for the simulation runs and the corresponding annual energy budgets. Without a hard disk, it is still possible to obtain the screen display and print files for each run.

The models described below are the McIntire and Colby stream ecosystem model (McIntire and Colby, 1978), henceforth referred to as the M & C Stream Model, and two modified versions of this model that were designed to investigate the process of herbivory and effects of irradiance, food quality, and nutrients on the processes of primary production and grazing. The files required to run these models include the three program files (STREAM.COM, HERB.COM, and RIPARIAN.COM) and a series of files that introduce the input variables; the other files on the diskette (e.g., BUDGET.COM, STRMTAB.COM, STRMTAB.CMD, HERBTAB.COM, HERBTAB.CMD, RIPARTAB.COM, and RIPARTAB.CMD) are required to calculate energy budgets for each simulation run. The three program files represent compiled versions of each model. With each version, the user can change the initial values for the state variables, the parameters, and the input tables (e.g., the irradiance, nutrient, temperature, and flow schedules, as well as the allochthonous introductions). The equations representing functional relationships among the system variables cannot be changed without an alteration of the Pascal procedure files and the generation of a new, compiled version of the model. Files required for this purpose are not included on the diskette. However, a complete mathematical documentation of the three versions of the model is included in the Appendices so the advanced user can reprogram the model with desired modifications in a programming language of choice.

Models and Modeling

From a scientific perspective, modeling is the process of putting structure on knowledge, and a model is some kind of statement of relationships. Therefore, all research scientists are modelers in the sense that they are involved in generating and updating conceptual models that evolve from field and laboratory studies. In some cases, it is useful to transform conceptual models into integrated numerical systems by mathematical formalization. In ecology, mathematical modeling is the translation of an ecological system into mathematical form and the subsequent investigation of the mathematical system, usually by computer simulation.

Overall goals of model building are description and prediction. In particular, mathematical models can be used for simple forecasting (e.g., the weather) or for scientific purposes: (1) for hypothesis generation; (2) to synthesize the results of field and laboratory studies; (3) to evaluate a data base; and (4) to set priorities for future research. The process of model building usually includes the selection and classification of variables, equation writing and parameterization, simulation, and the comparison of model output with the behavior of the natural system under consideration (model testing). In this tutorial, we discuss the use of mathematical modeling for the scientific investigation of biological processes in lotic ecosystems.

The Role of Modeling in Stream Ecology

Lotic ecosystems have been investigated from the trophic level viewpoint (Odum, 1957; Warren et al., 1964) and more recently within the conceptual framework of functional groups (Cummins, 1974; Boling et al., 1975) or relevant dynamic processes (McIntire, 1983). The functional group approach involves the classification of taxonomic entities into groups of organisms considered to be similar to each other with respect to trophic position and function. Historically, the corresponding approach to analysis has been concerned with state variable dynamics, in this case with the biomass or numerical abundance of organisms in each functional group. In contrast, the process viewpoint is less concerned with taxonomic categories and places more emphasis on the capacity of a system or subsystem to process inputs. The stream models described in the following sections of this document are compatible with both the functional group and process viewpoints.

Functional groups of stream organisms do not live in isolation. Individual taxa experience complex interactions with abiotic and biotic components within the functional unit, and the group as a whole changes its structural and functional attributes in response to direct and indirect relationships with components outside the boundaries of the group. In the field or laboratory, experiments with functional groups of stream organisms are usually designed to examine effects of only one or at most, a few variables in systems that maintain the same environment with respect to the variables not under investigation. The role of modeling, as conceptualized in this tutorial, is to provide a context and coupling structure for the experimental work that will help optimize the relevancy of a particular experiment to the objective questions under consideration.

One approach to the study and modeling of lotic ecosystems includes: (1) identification of research goals and a set of corresponding specific objectives; (2) an initial system conceptualization, a process that involves the definition of system variables and their couplings, and the determination of appropriate levels of resolution relative to time and space; (3) translation of biological concepts into mathematical form and subsequent investigation of the mathematical model in relation to the objective questions under consideration; (4) validation of model behavior by the collection of observational data in the field; (5) generation of new hypotheses that are based on priorities revealed by modeling and field observations; (6) design and performance of experiments to examine new hypotheses; (7) modification of the mathematical model and system conceptualization based on the latest field observations and experimental results; and (8) reevaluation of specific objectives and research progress in relation to the level of understanding generated by the most recent round of experimental work and modeling. In summary, this approach is iterative and synthetic, and involves the careful interplay between modeling, field observation, experimentation, and a periodic update of specific objectives in relation to an overall research goal.

THE M&C STREAM MODEL: VERSION I

The structure and mathematical details of the M & C Stream Model were described by McIntire and Colby (1978). Model structure was based on the process point of view (McIntire, 1983) and current concepts of functional groups in stream ecology (McIntire, 1968, 1973; Cummins, 1974). In this case, ecosystems were conceptualized as hierarchical systems of biological processes with physical and chemical processes expressed as driving or control variables. Depending on the resolution levels of interest, various biological processes were the systems, subsystems, and suprasystems under consideration. This view of ecological systems is consistent with FLEX, a general ecosystem model paradigm developed by Overton (1972, 1975) and based on the general systems theory of Klir (1969). The original version of the model was developed for scientific purposes: to generate hypotheses, to synthesize the results of field and laboratory research, to evaluate a data base, and to set priorities for future research. More recently the model has been used for teaching purposes and for the generation of new hypotheses related to the processes of primary production and grazing in lotic ecosystems.

Briefly, the M & C Stream Model has a hierarchical structure and represents biological processes that are usually active in most lotic ecosystems. From this perspective, stream ecosystems are conceptualized as two coupled subsystems, the processes of primary consumption and predation (Fig. 1). Primary Consumption represents all processes associated with the direct consumption and decomposition of both autotrophic organisms and detritus, including the autochthonous production dynamics of the autotrophic organisms collectively. Predation includes processes related to the transfer of energy among primary, secondary, and tertiary macroconsumers. The subsystems of Predation are the processes of invertebrate and vertebrate predation, whereas Primary Consumption is represented by the processes of herbivory and detrtivory. Herbivory consists of all processes associated with the production and consumption of autotrophic organisms within the system, whereas Detritivory includes the consumption and decomposition of detrital inputs. The corresponding subsystems of

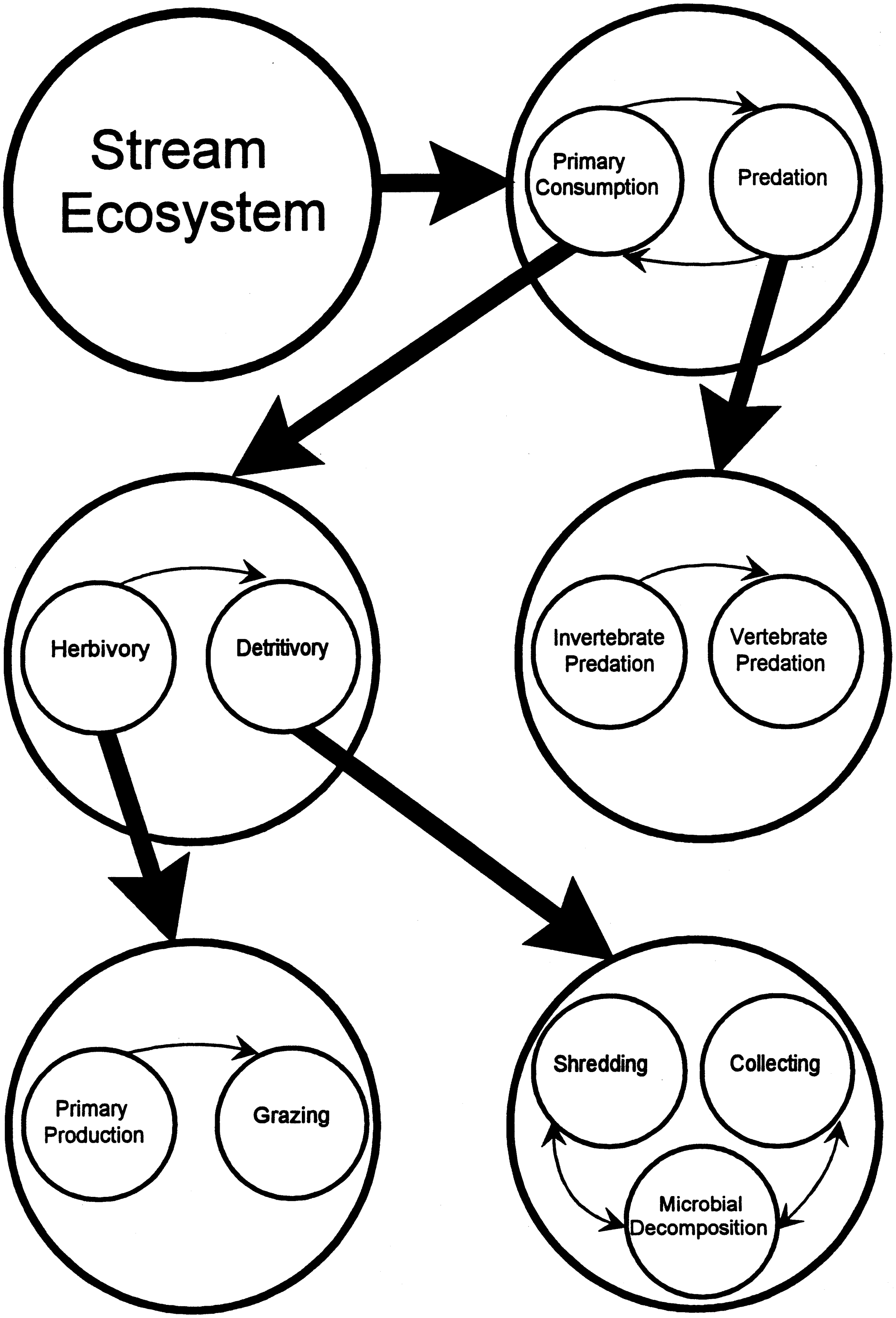

Figure 1. Schematic representation of a lotic ecosystem showing the hierarchical decomposition of the Primary Consumption and Predation subsystems. Arrows within processes indicate patterns of energy flow.

Herbivory are Primary Production and Grazing, and those of Detritivory include Shredding, Collecting, and Microbial Decomposition (Fig. 1).

The M & C Stream Model is programmed in Pascal as a series of procedure files that were cocompiled with FLEXPC.COM, a model processor that is compatible with the FLEX paradigm. Instructions for running Version I of the model include a short introduction to the Standard Run and the more detailed, step by step, procedure for producing various kinds of output from the Standard Run. In addition, the procedures for modifying the Standard Run are outlined. Such modifications can be introduced by changing the input tables, parameters, and initial conditions. A complete mathematical documentation of Version I of the M & C Stream Model is presented in Appendix I (page 146).

The Standard Run for Version I

The Standard Run for Version I of the M & C Stream Model simulates the process dynamics of a small, low-order stream that is shaded in the summer by a dense canopy of riparian vegetation and receives annual allochthonous organic inputs of 473 g m^{-2}. If the input tables are not changed, this run generates the state variable trajectories illustrated by McIntire and Colby (1978, Fig. 4). This version of the model has 11 state variables that represent biomasses associated with the processes of grazing (x_2), shredding (x_3), collecting (x_4), vertebrate predation (x_5), invertebrate predation (x_6), and primary production (x_7); and biomasses associated with the decomposition of fine particulate organic matter (x_8) and four categories of large particulate organic matter (x_9, x_{10}, x_{11}, and x_{12}). In addition, two other state variables (x_{13} and x_{14}) are used as dummy variables to introduce lag times for the microbial conditioning of the allochthonous organic inputs. The variable x_1 is not used in Version I of the model.

The files that introduce the input variables for the Standard Run are:

File	Variable
EXLITE	daily mean illumination expressed as ft-c;
XNUTR	limiting nutrient concentration (mg l^{-1}), NO_3^- in this case;
STRFLOW	stream flow (cfs);
SALLOC	slow-conditioned allochthonous daily input (g m^{-2});
FALLOC	fast-conditioned allochthonous daily input (g m^{-2});
GEMER	daily emergence losses (g m^{-2}) for grazers;
SEMER	daily emergence losses (g m^{-2}) for shredders;
CEMER	daily emergence losses (g m^{-2}) for collectors;
PEMER	daily emergence losses (g m^{-2}) for invertebrate predators;
STRTEMP	daily mean water temperature (°C);
PHOTPER	number of daylight hours per day (hr day^{-1}).

Each file consists of a table of 360 values representing the daily inputs for a one-year simulation run based on 12 30-day months. Schedules of illumination and allochthonous inputs (Appendix II) were obtained from direct measurements at sites on Berry Creek, a small stream near Corvallis, Oregon, and Watershed 10, a research area at the H. J. Andrews Experimental Forest, approximately 60 mi east of Eugene, Oregon. Patterns of these inputs are illustrated in Figures 2A and 2B, whereas hydrologic properties generated by the stream flow schedule (**STRFLOW**) are tabulated in Table 1. For more detail, the user can plot the values in each table and examine listings of the tables in Appendix II..

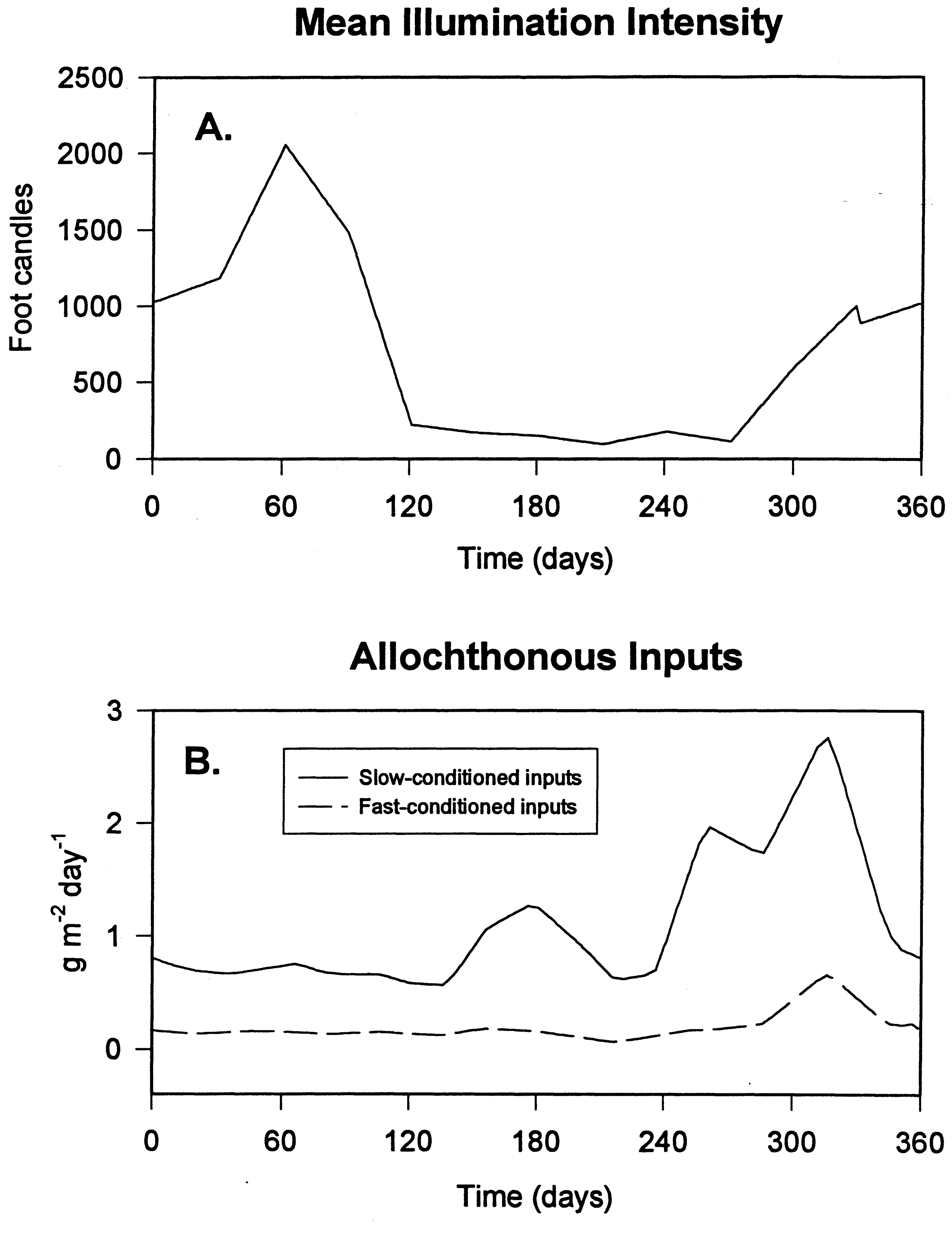

Figure 2. Schedules of illumination (A) and allochthonous inputs (B) for the Standard Run of Version I of the M & C Stream Model. Data were obtained from Berry Creek and Watershed 10 (see text).

Table 1. Hydrologic properties associated with the Standard Run of Version I of the M & C Stream Model. Maximum, minimum, and mean values correspond to output from a 1-year simulation run at a time resolution of one day. Parameters for the equations and the mean channel slope are based on data for Oak Creek, near Corvallis, Oregon.

Property	Units	Maximum	Minimum	Mean
Flow	cm s^{-1}	3540	22	221
Current Velocity	cm s^{-1}	231	20	50
Suspended Load	mg l^{-1}	330	1	14
Roughness Coefficient	none	0.075	0.048	0.054
Channel Width	m	3.17	3.12	3.13
Channel Depth	m	0.58	0.03	0.09
Cross-sectional Area	m^2	6.95	0.28	0.94
Channel slope	%	-	-	1.4

Simulation Procedures

This section describes the procedures for (1) generating output from the Standard Run; (2) changing the screen output display; (3) changing parameter values; (4) creating files for printing or plotting; and (5) generating an annual energy budget. The commands that the user must supply are indicated in bold type.

If your computer has a hard disk (assumed here to be the C drive), type

```
C:\>md model                                  (return)

C:\>cd model                                  (return)

C:\MODEL>md stand                             (return)

C:\MODEL>cd stand                             (return)

C:\MODEL\STAND>copy a:\stand\*.*              (return)
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