1970

Aquatic Specialists' Meeting Idaho State University, Pocatello, Idaho September 9-10, 1970

U.S. International Biological Program

DESERT BIOME

US/IBP ANALYSIS OF ECOSYSTEMS

Aquatic Specialists' Meeting

IDAHO STATE UNIVERSITY

Pocatello, Idaho

September 9-10, 1970

IBP

Report on the

AQUATIC SPECIALISTS' MEETING

Idaho State University

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April 1971

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Report of the Desert Biome Aquatic Specialists' Meeting

9-10 September 1970

Idaho State University

Introduction

Prepared by G. Wayne Minshall

The second meeting of aquatic specialists in the Desert Biome was held in Pocatello, Idaho on September 9-10, 1970. The meeting was open to all interested persons and all of the aquatic investigators listed on the Biome's mailing list at the time were sent invitations to attend.

The purposes of the meeting were to explain the objectives and present status of the IBP Desert Aquatic Program to as many people as possible, to examine the work currently underway at each of the validation sites, and to develop an overall plan for the selection and scheduling of process studies. The agenda for the meeting is included below. It was found necessary to deviate from this schedule several times in order to complete our major objectives in the time available.

Agenda

1. Review of Desert Aquatic Program
2. Current status of funding for 1971
3. Objectives and research design for IBP Desert Biome
4. Modeling of aquatic systems -- an overview
5. Progress reports on the validation studies
6. Status of currently unfunded validation studies
7. Validation site operations after year 1
8. Reports on the data summaries:
   - Abiotic. . . . . Carpelan
   - Bacteria -- phytoplankton. . . Gorden
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   - Fish . . . . Kramer
9. Process studies:
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   - Rationale for previous selections
   - List of priorities for 1972 and subsequent years
   - Time schedule for phasing of aquatic process studies
   - Procedure and time table for submitting proposals for 1972
   - Selection of review panel
10. Problem areas
    - Modeling -- Bridges
    - Methodology

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Review of Desert Aquatic Program

G. Wayne Minshall

For all practical purposes, the development of our aquatic program began with the Organizational Meeting for the Desert Biome in Logan, Utah in February 1968. During that meeting, a comprehensive list of the aquatic habitats found in the desert was developed and the factors to be considered were outlined. This work provided the nucleus from which our present research design has developed. In February 1969, a description of goals and research plans was compiled and validation site coordinators received a copy of this document shortly thereafter. A revised version (June 1970) of this report is now available, which consolidates material covered in the more comprehensive Research Design and Research Proposal and provides a fairly concise review of our present status. Most of the emphasis up to the present has been on the validation studies and one purpose of this meeting is to begin work on a comparable design for the process studies.

In September 1969, a small group of aquatic specialists met in Logan, Utah in preparation for studies beginning in 1970 and as a preliminary to the present meeting. The report of the first meeting has already been distributed.

Actual operations were begun in 1970. The following sites have been activated under the direction of the coordinators listed:

Deep Creek	G. Wayne Minshall, Idaho State University
Locomotive Springs	John Neuhold, Utah State University
Jornada Playa.	Charles Ward, Texas Tech. University
Rattlesnake Springs (AEC funded)	Colbert Cushing, Battelle-Northwest

Progress reports on these studies will serve to bring our accomplishments up to date.

In a review of the Desert Aquatic Program it is also worthwhile to examine our overall goals. These will be covered in detail by Fred Wagner and Kim Bridges but I would like to offer a few introductory comments.

Very simply, we have set out to construct a predictive model of a series of rather common desert aquatic ecosystems, or at least to provide the information necessary for developing such a model (or set of models). We have chosen to do this for a complex of permanent springs and small streams, contrasting northern and southern desert conditions, and for temporary waters, represented by a playa and an intermittent stream. We intend to obtain as complete a description as possible of ecosystem dynamics in these important desert situations, to investigate the response of these systems to key environmental factors and, where feasible, to test the effects of manipulating certain components or conditions. Thus, the model we envision is not a static one simply describing conditions as they presently exist (although that in itself may be a considerable challenge). We propose to develop a dynamic model which will approximate the operation of an ecosystem with time and consequently provide us with a tool for predicting the effects of various disturbances, management procedures, etc.

This goal requires a fairly complete understanding of how each of the ecosystems is put together (structural elements) and its state at different points in time as well as a knowledge of the rates for critical operations (functions) within the system. These, in turn, determine how the system will respond to a given factor or set of factors. It is within the context of this goal that what each of us is doing takes meaning beyond that of simply conducting the studies as ends in themselves. And it is at this point that coordination and mutual understanding become essential, which, of course, explains why we are here.

The aquatic systems chosen for study within the Biome are as follows:

Springs (permanent)

Locomotive. . .Great Basin
Saratoga. . . .Mohave

Standing Water

Curlew Reservoir. .Great Basin
Jornada Playa . . .Chihuahuan

Streams

Rattlesnake Creek . . .Great Basin
Deep Creek. . . . . . .Great Basin
Sycamore Creek. . . . .Sonoran
Deep Canyon . . . . . .Sonoran

Rattlesnake Creek, at the Hanford site (Richland, Washington), lies at the northern extremity of the Great Basin. Locomotive Springs and Deep Creek are both in Curlew Valley on the Utah-Idaho border. Investigations are also proposed for Curlew Reservoir, a small reservoir used for irrigation water storage. Two springs at the Locomotive site are being studied: Sparks Spring, which is quite productive and filled with aquatic vegetation, and Off Spring, which is more open. Both are saline springs on the edge of the Great Salt Lake. Saratoga Spring, another saline spring, lies in Death Valley, California. Sycamore Creek, near Tempe, Arizona, has stretches of flowing water year-round, whereas the flow of Deep Canyon (near Riverside, California) is more intermittent, with only a few pools of water persisting through the summer. Jornada del Muerte, the site which contains the shallow playa, is located near Las Cruces, New Mexico.

Current Status of Funding

1970 was the first year of operation for the IBP Desert Biome studies. Funding was provided for the Locomotive Springs, Deep Creek, and Jornada Playa sites. These represent a total investment of about $100,000. Studies were also begun at Rattlesnake Creek, supported entirely by the Atomic Energy Commission. No studies of individual species or processes were implemented in 1970.

The proposal for 1971 was submitted to the National Science Foundation in June, 1970. Funding was requested for continuation of the three studies mentioned above, for initiation of full-scale operations on Saratoga Springs and Deep Canyon, for a biotic study of Sycamore Creek, and for eight process studies. NSF evaluated these proposals in August and provided a tentative estimate of the level of funding to be expected for 1971. As a result, the Deep Canyon study was postponed until 1972 and the process studies were reduced to five because of budgetary considerations. The funds estimated to be available for 1971 for aquatic studies are $50,000 for process studies and $126,000 for validation studies.

Bringing the aquatic program off successfully will require the most efficient expenditure of our efforts over the next few years. This implies a need to know the level of funding we might reasonably expect. Table 1 shows the proposed staging of the validation studies for the next few years. This is based on the assumption that continuation for a minimum of 5 years is highly desirable, but it is modified by the high degree of uncertainty existing after about 1975.

Table 1. Proposed Staging of Desert Aquatic Studies

	1970	1971	1972	1973	1974	1975	?
Curlew Valley							
Curlew Reservoir			?				
Deep Creek	____	....	....	....	....		
Locomotive Springs	____	....	....	....	....		
Death Valley							
Saratoga Springs		....	....	....	....	....	
Deep Canyon			....	....	....	....	
Jornada Playa	____	....	....	....	....		
Rattlesnake Creek*	____	....	....	....	....		
Sycamore Creek		1	....	....	....	....	

____ Funded
.... Proposed
? Uncertain

* AEC support
1 Biotic survey

There are at least 80 important species or higher taxa requiring study. For each of these a minimum of three to five functions need to be examined. Assuming that 5 process studies will be initiated in 1971, 8 to 10 in 1972, 9 to 12 in 1973 and 1974, and 15 to 20 in 1975, this gives a total of between 46 and 59 process studies over the next 5 years. It is obvious that a good deal of selectivity and intuition will be necessary to bridge the gap between number of studies needed and number likely to be funded.

Based on the points I have developed thus far and assuming a level of funding (per study or site) comparable to the 1971 level, it is possible to get some idea of the cost of the program for each year. The total funding for the entire Biome operation is expected to be $0.8 million in 1970, $1.3 million in

1970, $1.3 million in 1971, and $1.8 in 1972 and thereafter. Estimated funding for aquatic studies for the next several years is as follows:

	1970	1971	1972*	1973*	1974*	1975*
Validation Studies	96,000	126,000	145,000	130,000	130,000	70,000
Process Studies	none	50,000	80,000	95,000	95,000	155,000
Totals	96,000	176,000	225,000	225,000	225,000	225,000

* Reasonable estimates

These figures will have to be borne in mind in any further selection or discussion of validation and process studies.

Objectives and Research Design for IBP Desert Biome Studies

Frederic H. Wagner

The IBP was conceived in the early 1960's by the International Council of Biological Unions. IBP studies were initiated for the purpose of understanding the biological bases of productivity and human welfare.

The first U. S. meeting of the IBP organization was held in Williamstown, Massachusetts in 1966. Twelve committees were established at that time; two of these concerned with productivity of freshwater and productivity of terrestrial ecosystems. It became apparent that terrestrial areas with nearby aquatic systems required coordination. Out of this requirement, the biome concept developed with the intent of mounting integrated terrestrial-aquatic (hopefully discrete watershed) studies.

The goals of the Biome program are to analyze ecosystems and to develop simulation models of ecosystem structure and function. The Grassland Biome was the first of the biomes to be funded. The Pawnee site in eastern Colorado was selected as a general type.

David Goodall was appointed director for Desert Biome studies. The Desert Biome includes four desert types; the Great Basin, Mohave, Chihuahuan, and Sonoran deserts. Studies have involved different kinds of areas within each desert type rather than an extensive study of one site, as in the Grassland Biome.

The criteria for selecting desert study sites were proximity to manpower pools (such as near a university) and the existence of a substantial backlog of research.

No discrete watershed area, with interacting terrestrial and aquatic systems, has yet been found within the Biome (the Jornada Playa comes closest). Thus, some studies are of aquatic areas only, unaccompanied by a corresponding terrestrial study. The results obtained from studies of these generalized areas indicate that aquatic and terrestrial efforts need to be brought closer together. Initial steps to achieve this coordination have been taken.

The specific objectives of the IBP studies are: (1) to describe the flow of energy, carbon, phosphorus, nitrogen, and water through the ecosystem, and (2) to construct a model capable of predicting changes in the flow of these materials given perturbation in any part of the system.

The ecosystem may be described in terms of three entities:

1. Components -- Include energy plus materials such as carbon, nitrogen, phosphorous, and water organized in some form (e.g., living tissues or "abiotic component"). The "components" are the "boxes" in a flow diagram.

2. Processes -- Events or functions which alter the state of the components or move them about in the ecosystem. The "processes" correspond to the "conduits" between the "boxes" in a flow chart.

3. Factors -- Things which influence or affect the rate of the processes. The research design for the Desert Biome Program is divided into process studies, validation studies, and modeling efforts. Process studies are studies on individual species which indicate rates of exchange. The plant processes are:

(1) photosynthesis
(2) vegetative growth
(3) root growth
(4) flowering and fruiting
(5) foliar leaching
(6) transpiration
(7) nutrient uptake
(8) water uptake
(9) shedding of dead matter (mortality)

Animal processes may be listed as:

(1) food uptake
(2) assimilation
(3) metabolism
(4) Individual growth (production)
(5) reproduction
(6) mortality
(7) dispersal

Data from the process studies will be utilized in the construction of a computer model designed to predict future states of the ecosystem.

Validation studies are designed to check the accuracy of these predictions against measurements obtained in real-world sites.

--ooOoo--

Modeling Aquatic Systems

Kent W. Bridges

The past several months have been full of activity for the modeling group at Logan; we have had to gather a staff, upgrade specific technical talents, and plan a strategy for our modeling efforts. These efforts are being organizationally split between the terrestrial and aquatic studies, with attention being paid to the requirement of joining the two models. The personnel now involved directly with the modeling efforts include the student modelers; Mick Crawley, Jerry McRoberts, Mark Westaby, and Curtis Wilcott. Our mathematician is Jim Watson, and we have several undergraduate students who provide valuable programming support.

One of my overall fears regarding the modeling is that our group at Logan is going to be thought of as "The Modelers" and that everyone who is not a direct member of that group will not be involved in the modeling. We can aid such a separation by carrying out our operations using our special jargon so that even if you are interested, most of you will not be able to understand us. We will then have become a "high priest" category and, by my standards, will have failed in our attempt to create an interdisciplinary project. In a large measure, I will also consider the Biome efforts a failure.

It is my goal that we should work together as a team. The "Modeling Group" will serve in two capacities; we will coordinate all modeling activities, and we will be responsible for the actual computer implementation of the models. This later responsibility can be shared with any of you who feel you have the programming competence, or desire to gain it. Most biologists would rather not suffer the agonies of taking on a new set of machines, etc. Such a choice will not eliminate you from the modeling activities, however.

Let me illustrate this by showing you how I interpret modeling. This is certainly not the only interpretation, just mine.

Specific Modeling Tasks

Our charge as modelers is to synthesize all the knowledge of the components of the desert system and their interrelationships into a form which may be used for predictive purposes. There are several key ideas in such a charge. Synthesis involves the virtually simultaneous consideration of all the portions of the system. Since we are interested in the system quantitatively, speed of computation requires that a computer-based model be the end product of our efforts.

The original task in modeling is the accurate specification of the purpose of the model. This has yet to be done adequately for our Biome study. Steps are being taken to provide such a definition while we are doing some initial modeling based on our own intuition as to what the ultimate definition will be. This is an important area which should be discussed later.

After the definition is complete, several steps are taken in the building of complete ecosystem models. The entire ecosystem model needs to be divided into administrative unites so that work may proceed independently on multiple submodels. These are administrative, not necessarily biologically realistic subdivisions. Each submodel must then have the inputs and outputs specified. This specification generally requires the structural specification of the submodel. The development of each submodel may then proceed independently. This is the stage for implementation of the structural specifications into a quantitative, computer usable form. When each submodel is complete at least to some level, the model is available for use. These uses include further submodel development, sensitivity analyses, validation and, our original goal -- prediction.

Let me illustrate these procedures using the aquatic system as an example. This illustration will necessarily be incomplete because we, in fact, have not gotten very far in the aquatic modeling efforts. The following list of submodels was defined for the development of an aquatic model.

Abiotic processes
Primary producers
Herbivores
Carnivores
Decomposers

Submodel Resolution

Before discussing the details of any of the submodels, let me briefly describe the problem of submodel resolution. The degree of precision that is used in any particular submodel is obviously variable. At the one extreme, a simple linear equation may be used. In this case, perhaps little of the mechanistic biology is included. Such a submodel may provide a rough approximation over a rather limited range of environmental conditions. At the other extreme is the submodel which incorporates a very fine biological resolution with as much mechanistic biology as possible and which covers a broad range of environmental conditions.

Several such detailed submodels have been built; for example, Phil Miller's Mangrove Plant Growth Model and De Wit's Plant Physiological models. These are good models; detailed and robust, but they are expensive to run. An ecosystem model of this complexity would not be practical for the lengths of simulation time we expect to need. For the most part, therefore, we expect to build submodels which are intermediate. Where Miller calculates individual leaf angles for light interception, we will assume something like an exponential decay of light intensity with a plant canopy. The coarsest level model would probably neglect light decay within a canopy. Each level of resolution can be assigned a number; number 1 for the coarsest level of resolution, number 2 for the intermediate, and number 3 for the detailed. Each level has its important uses. Level 1 submodels are efficient to run and can be used while concentrating on the detailed development of another specific submodel. Level 2 will be used when a wider range of conditions needs to be met, or when the Level 1 model is not adequately working for some reason. The Level 3 models will be used only rarely; they are much to complex to be built in time to be very useful for the Biome. Moreover, they are, as mentioned before, too costly to run very often. Even the Level 2 models are costly. I would like to reemphasize that all three levels of submodels are interchangable. This is because the same submodel interfaces are used.

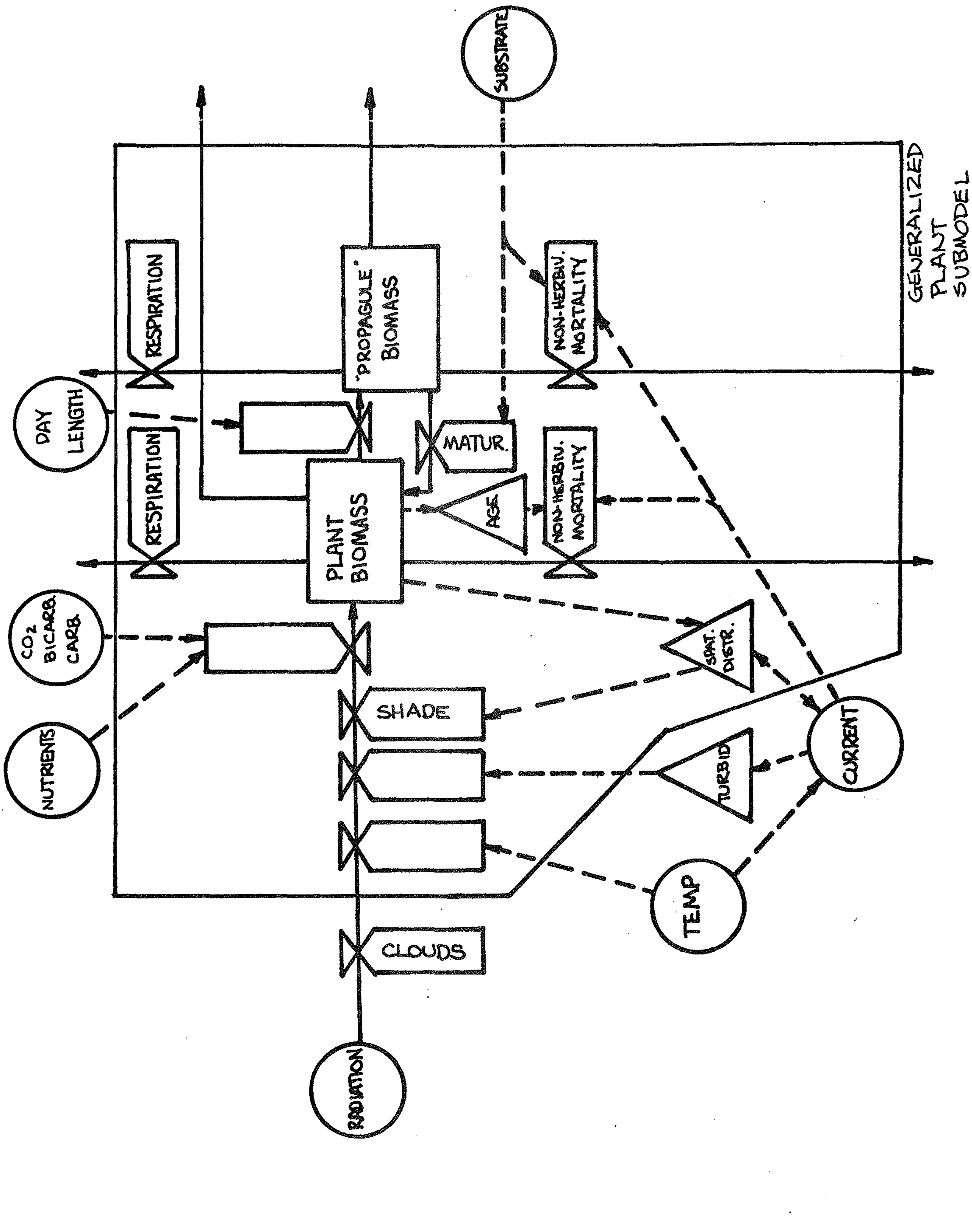
Implementation of the Model

Because ecosystem modeling is so new, there are several "schools," each developing techniques along somewhat different lines. Although there should probably be closer coordination between these efforts in order to avoid duplication, this separatism has resulted in the development of some substantially different techniques. I would like to mention just one of the differences, as I see it. One which I think is important because it directly involves you as potential modelers. Our submodels are based on algorithms; that is to say, a series of procedures, not just a set of equations. Our equations, as they occur in the algorithms, will tend to be simpler, if only because of their separation into small divisions. We hope that these algorithms are more intelligible to the non-mathematical biologists and that they display at least as much biological realism. I happen to think that this approach will generally display more realism. Of course, this is my own bias; others may feel the opposite.

Phase 1. Specific Submodels (Aquatic)

I would now like to present some specific sumbodels, developed at resolution Level 2. I have constructed "flow diagrams" to illustrate the structure of the submodels and these follow (pages 3.4.-9 through 3.4.-13). There is nothing very special about such diagrams; they represent an attempt to increase communication. They have forced me to be both concrete and complete. By presenting such diagrams, I am exposing my current knowledge of the system. Hopefully, this will help you to direct your criticism to specific problems without a lot of semantic difficulty. I will go through the models quickly to familiarize you with our notation and give you a quick overview of most of the aspects we are currently considering for inclusion in the aquatic model.

The plant submodel (page 3.4.-8) will illustrate the notation. A rectangle represents an accumulation of some material; the solid lines are the flows of materials; the "valves" regulate these flows; the dotted lines are information transfers. The triangles do not have a precise use; think of them as "comments" for the present.


SUBSTRATE
GENERALIZED PLANT SUBMODEL
RESPIRATION
"PROPAGULE" BIOMASS
NON-HERBIV. MORTALITY
DAY LENGTH
RESPIRATION
MATUR.
NON-HERBIV. MORTALITY
PLANT BIOMASS
AGE
CO_2 BICARB. CARB.
SPAT. DISTR.
NUTRIENTS
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TURBID
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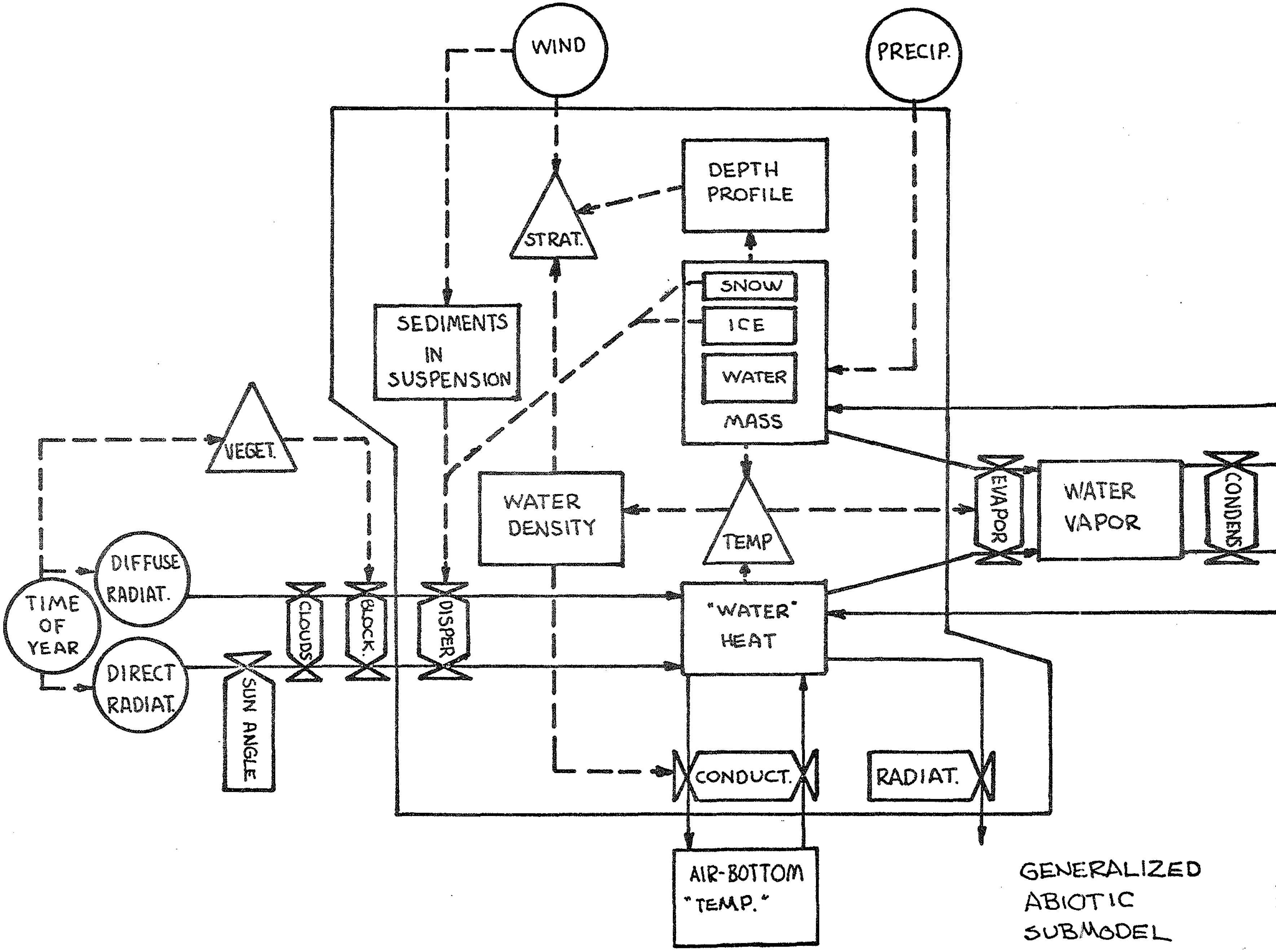
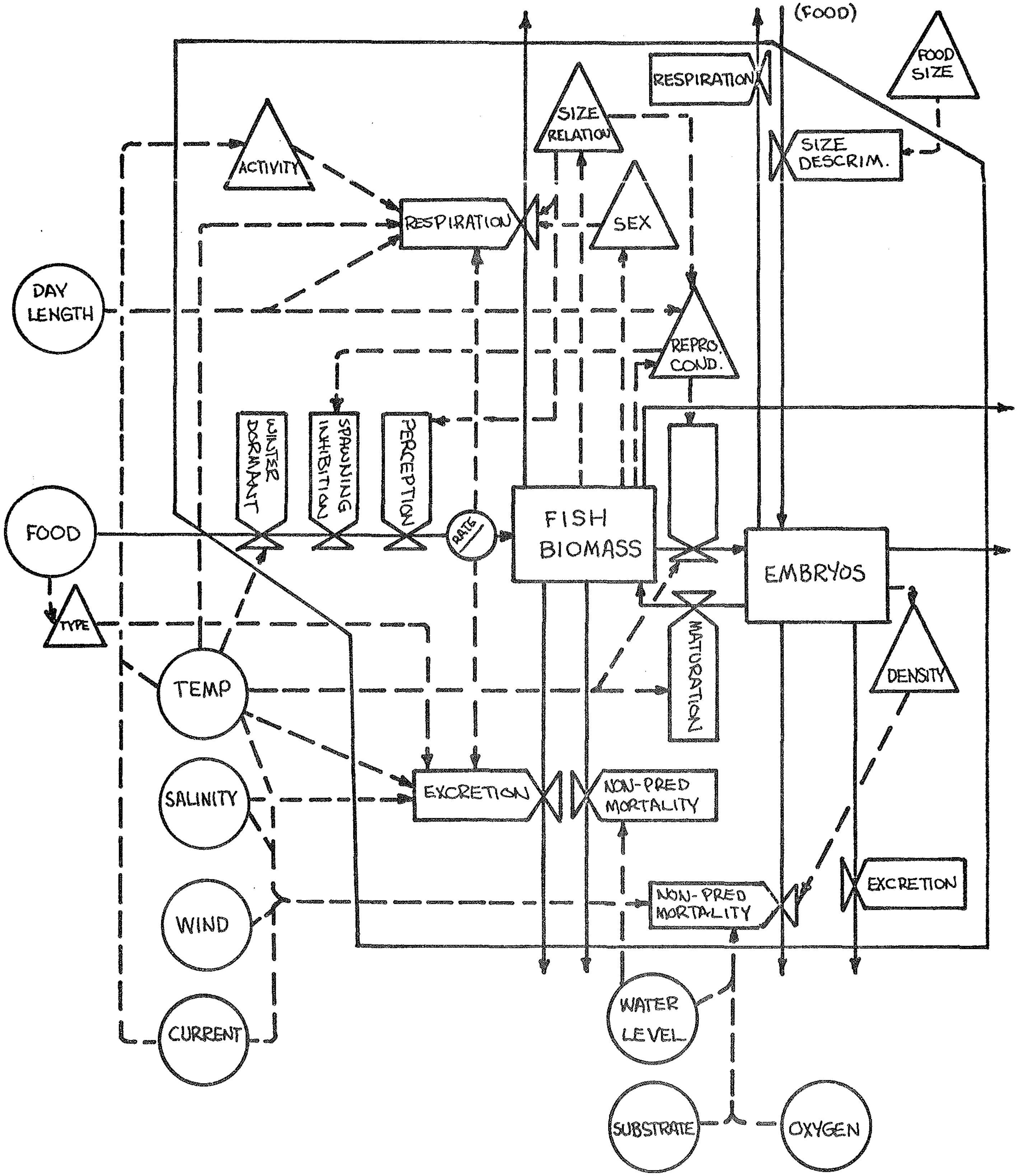
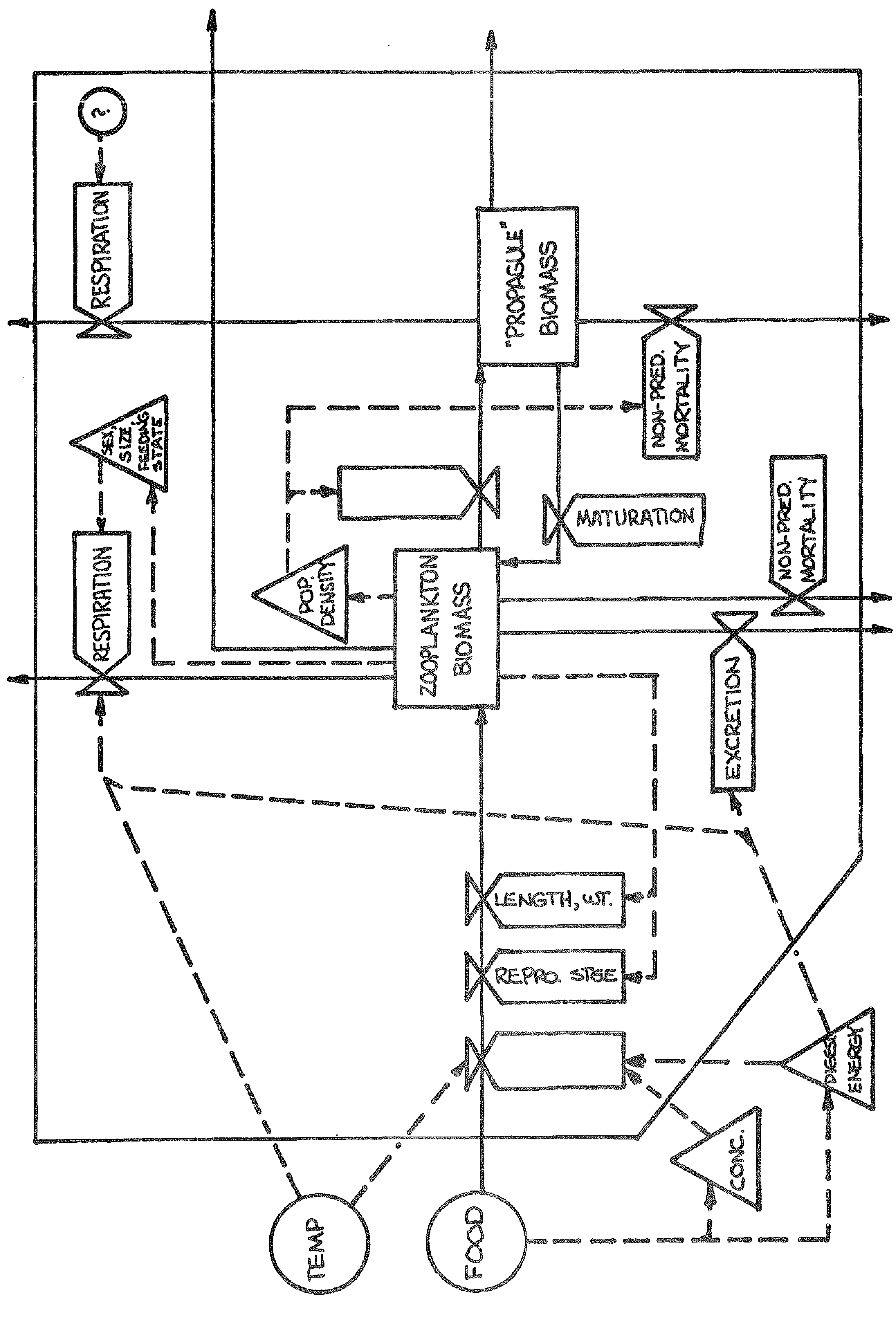
RADIATION



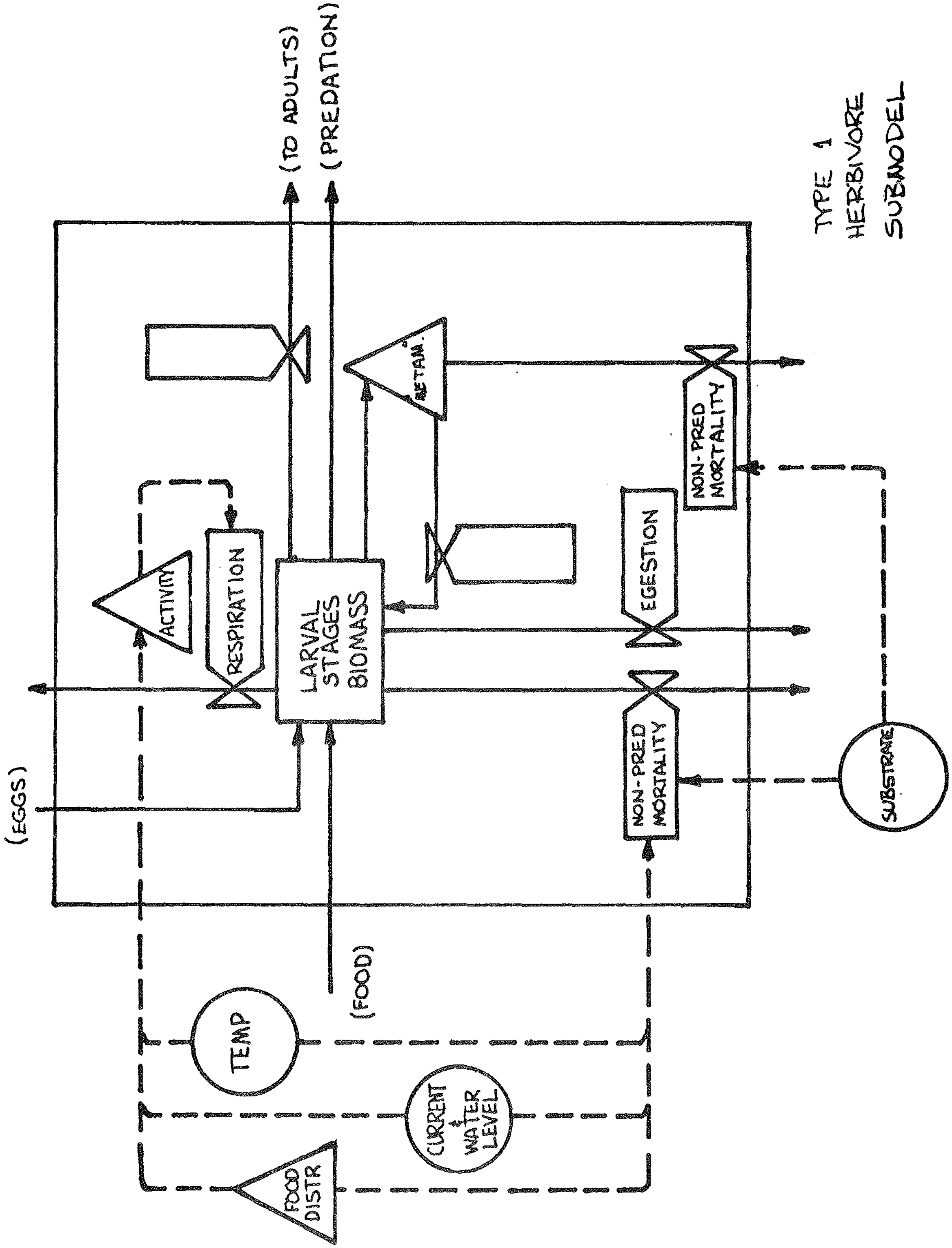
GENERALIZED ABIOTIC SUBMODEL



GENERALIZED
FISH
SUBMODEL



GENERALIZED ZOOPLANKTON SUBMODEL



TYPE 1 HERBIVORE SUBMODEL

The literature reviews have been invaluable in building these submodels. They were used to identify the structural relationships involved. Because each of these relationships is a function, the literature reviews will also help us approximate the rates determined from previous studies. It would be nearly impossible for us to progress rapidly, especially in these initial stages, without these reviews. This should be a substantial demonstration of how cooperative the modeling activities have to be.

Phase 2. Compression of Submodels

To carry you through the next phase of the modeling, let me illustrate how a submodel such as the plant submodel is "linearly" arranged. For the non-computer people, let me explain that all computer operations must be sequential and discrete. That is, this structure which implies that all processes may be concurrently operative, must be mapped into an approximately equivalent one in which each path (or rate) is calculated separately and in a serially discrete manner. The discrete time intervals may be made very small if desired, but this increases the cost of running the model. With large time increments, the problem of coincident events occurs. These are modeling problems and should not necessarily be the concern of the non-computer people.

Phase 3. Machine Compatible Coding

The next phase of the modeling is the conversion of this structure into actual machine compilable code, such as FORTRAN. At this point, actual relationships have to be specified.

Phase 4. Running the Models

Once the coding is complete, with the appropriate relationships between components specified, a complete set of starting values for the "size" of the components will have to be supplied. These are the state variable values. The model is then complete and can be executed for a specified period of time. Periodically, the model will report current values of selected state variables. These values are used to prepare a state history of the model.

The Relationship Between Modeling and the Research Design

Let me return to the overall project design and try to relate what I have said about the models to the validation and process studies.

Process Studies. Each rate involved in the model will have to have the appropriate quantitative function provided. To this point we have had to rely on literature reviews. These are not entirely satisfactory because all the factors important to the rate are not always included. Also, since our efforts are directed at the species level and many of the species found in our validation sites have not been studied.

All the factors listed for each of the rates (the dotted lines) must be included in the process studies over the range expected to be experienced in the validation sites.

Validation Studies. It was mentioned earlier that, in order to run a model, a complete set of state variables would be needed. These, ideally, need to be collected at the same time. In practice, this time should be as short as possible. Once these values are obtained and the model has been run (note that only one such set of values is required to run the model), the model output will provide a history of various state variables of the system. Periodic sampling of these variables on the validation sites will provide values by which we will attempt to validate the model. Unacceptable discrepancies will require revision of the model. By carefully examining the process, there will be indications as to which processes were in error. Performing additional process studies or confirming previous ones as necessary will, hopefully, make the model output conform more closely to the actual system as measured in the validation sites.

An important point to emphasize here is that the validation and process studies are independent. Otherwise, problems of confidence in the validation would arise. This is especially troublesome for the aquatic studies. In terrestrial studies, there is generally plenty of room adjacent to a validation site on which to perform process studies and thereby make reasonably sure of the independence of the validation and process data. In aquatic studies, where we are working with springs, for example, there are not always neighboring springs in which to do the process studies. Care and considerable ingenuity will thereofre have to be exercised.

The other observation I would like to make now is the periodicity with which we are going to need validation samples. The real problem for most species will be to provide the original state values. Hence, some experience in quantitative sampling is required. An analysis of the variance between samples should be made to determine the appropriate sample sizes.

The later samples which will be used to validate the model will be collected rather infrequently and will, in many cases, be samples of species which have been determined the best for model validation.

Samples which have been collected prior to the complete inventory will not be ignored. Some efforts will be made to run the model backwards from the time of the complete inventory.

Scope of the Modeling

Before we leave the topic of modeling, I would like to present a few of my ideas on the complexities of modeling to those of you who are new to such studies. The first consideration is the problem of spatial modeling and later I will mention an allied problem, individual variation. I think it is important to mention these problems now because as we progress into the actual details of the models, we will arrive at a point where these problems will block our ability to express, in modeling terms, those aspects which are so very obvious to us all.

We exist in a three-dimensional world in which we actively classify items based on spatial criteria. Yet we have developed only the crudest tools for spatially oriented descriptions. I have spent the past several years, for example, trying to quantitatively describe leaf shapes and leaves are relatively two dimensional. It is this mismatch between our abilities to recognize and describe that I am trying to emphasize. Spatial considerations abound in our biological systems. We recognize them, but are poor at describing them. We are working on this problem, but progress is not expected to be rapid. Hopefully, it won't completely frustrate us all. Since our models are descriptions, they too will be deficient in this area.

The other consideration is that of the heterogeneity of individuals. I suspect that much of the stability in ecosystems comes from the relative competitiveness of the individuals in each population. This is most pronounced in hierarchical social structures where the dominant always receives his ration, even when there is relatively scarce food. Susceptability to predation also increases downward in these social hierarchies. In non-hierarchical populations, there are also individual variations, if only related to genetic differences. I do not think that we can always ignore this aspect. It constitutes a problem, however, when we try to represent it within our models.

I have tried to go through the various modeling procedures very quickly, primarily to give an overall view of what we are trying to do. I hope that you aquatic specialists can see your niche in the whole scheme. If not, bear with us, for I hope that it will soon become clear.

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Progress Reports on Aquatic Studies

Reports were presented by the site coordinators concerning the current status of investigations at Locomotive Springs, Rattlesnake Creek, and Jornada Playa. Due to a shortage of time, the report for Deep Creek was not given. Since this information is already, or will soon be, available as a part of the reports section of the annual grant proposal, it is not included herein. The presentations served to inform the other participants of what was currently being done and to identify a number of problem areas. Considerable discussion ensued, particularly in reference to what constitutes validation data and process data and the necessity of keeping the two discrete. This discussion was led by Fred Wagner and Kim Bridges.

The main question on which the discussion turned was the distinction between process and validation studies, and the problem of circularity. The process studies are concerned with the measurement of rates: photosynthetic, growth, reproductive, etc. In this context, a project on production would be a process study except that the research design has called for separate studies of the processes which together make up the production process.

The model will be constructed from these rate studies. Given initial state-of-system values in terms of energy, nitrogen, or phosphorus content, it will simulate the changes over time in these state variables.

Validation measurements are periodic standing-crop measurements which check, at specified times, the continuous simulation of the system by the model.

It is true that process and validation measurements are different aspects of the same phenomenon;

Aquatic Specialists' Meeting - continued

the one the dynamic aspect and the other the instantaneous points in the continuous phenomenon. One can take two standing crop measurements, and the difference between them when expressed relative to time, is the production rate. It is here where the risk of circularity enters. One could program the model with the production rate thus derived and the first of the two standing-crop measurements, and unerringly predict the second value in this somewhat facetiously oversimplified example. The operation would be a boot-strap one.

But the principle is valid. The rate measurements from which the model is constructed must come from entirely different data, and preferably different systems, than the initial state-of-the system measurement and the subsequent standing-crop estimates which check the predictions of the model. For this reason, situations should be sought in which process studies can be carried out in one (or more, if desirable replication is possible) pond while validation measurements are made in near-by ponds. Or, process studies could be carried out in one stretch of a stream while validation measurements were made in another.

In theory, the separation could be temporal rather than spatial, i.e. process studies could span one series of years while validation measurements on the same site could span another time period. This is not practical in the Biome program since it is likely to continue only 4 to 6 more years and several years are likely to be needed each for process and validation studies.

Data Summaries

Copies of the recently completed aquatic literature reviews were distributed to all participants. However, the formal reports prepared by each of the reviewers and the hoped-for discussion had to be deleted because of lack of time. Also, many problems of methodology (of immediate concern to many of the participants) were not discussed formally for the same reason. It is hoped that these shortcomings can be rectified in the near future.

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Process Studies

G. Wayne Minshall

Introduction

Most of the second day was spent discussing process studies and selecting the species and functions for which studies will be needed during 1972.

The purpose of the process studies is to provide measurements of critical rates for key species (or other subsystems) found in the validation sites and to determine the effects of important environmental factors on these rates. Ideally, one would set up preliminary studies to determine which functions should be included, based on their overall importance in the system. As there is not time for this approach, we must instead make some educated guesses as to the important functions and be prepared to add or delete them as more information becomes available.

Rationale for Previous Selections

The first aquatic process studies are those proposed for 1971. It should be noted that the actual selection of the species and functions for study was done in the fall of 1969, consequently there is a considerable time lag between selection and completion. A principal criterion for the selection of the first set of studies was that the species occur at one or more of the validation sites expected to be operational in 1970 and that the species be of obvious importance. Furthermore, it was decided at the aquatic meetings in September 1969 that, due to likely limitations of money and manpower, initial emphasis should be placed on those rate functions related to energy flow and nutrient cycling and that consideration of other important factors, such as those dealing with population dynamics, be postponed.

Thus, the important rate functions for plants are:

a. Net photosynthesis in response to a variety of factors (temperature, light, mineral nutrition, etc.).

b. Growth

c. Nutrient uptake (as influenced by such things as nutrient supply and temperature).

For animals, the important critical rates include:

a. Ingestion

b. Assimilation

c. Respiration

d. Growth

as functions of temperature, food quantity and composition, population density, etc.

Following the establishment of criteria for the selection of process study topics, a request for research proposals was circulated to the entire mailing list. Although a number of replies were received, only eight dealt with topics or species named. These eventually became incorporated in the Biome proposal for 1971 and five of them will receive funding. One of these, directed by W. G. Bradley, will determine the primary productivity of marsh vegetation at Saratoga Springs, California. Productivity measurements will involve the aquatic macrophytes Ceratophyllum demersum and Ruppia maritima, and several semi-aquatic macrophytes. Net photosynthesis, growth rate, and rates of litter fall and decay will be determined. A second study will be directed by Arden R. Gaufin and will deal with the dynamics and productivity of desert benthos. Three species will be studied; Enallagma anna, Hydropsyche occidentalis, and Hyalella azteca. Respiration rates will be measured in relation to temperature, current velocity, andoxygen content. Growth rate as a function of body size will also be studied.

Robert H. Kramer will study the respiration of the Utah chub. The effects of water temperature, size, sex, starvation, season, and time of day in relation to respiration will be measured. Another objective of this study is to describe the food habits of Utah chub at Locomotive Springs in relation to size and season. A fourth study, directed by T. C. Bjornn and R. L. Wallace, deals with the assimilation, metabolism, and growth of the Utah chub. Information on consumption, food utilization, excretion, and growth will be obtained. The fifth study will concern the food utilization of Cyprinodon nevadensis in relation to age, season, and availability of food. This study, to be directed by James Deacon, will also involve determination of types of food eaten, rate of assimilation, and feeding periodicity.

Establishment of Priorities for 1972

As mentioned previously, the anticipated levels of funding and the number of the studies likely to be supported dictate that careful consideration be given to the selection of topics for 1972.

Based upon information from the validation site coordinators, a list of taxa thought to account for 60 to 90% of the energy flow at each of the validation sites was compiled prior to the meeting (Table 2). In several instances the list is still extremely speculative and too often the species involved are still not known. Nevertheless, it is the best available and we must begin immediately to set priorities for 1972. Altogether there are about 79 taxa which, at the rate of 2 to 5 functions each, could yield an impractical number of process studies if taken individually. Obviously, consolidation as well as a high degree of selection is necesarry. For 1972, we can probably initiate 8 to 10 new studies. These will couple with the 5 scheduled for 1971 and should fill in gaps identified by the data summaries.

Table 2. List of taxa which cumulatively account for 60 to 90% of the energy flow at each of the validation sites.

	Locomotive Springs	Saratoga Springs	Rattlesnake Creek	Deep Creek	Sycamore Creek	Deep Canyon	Jornada Playa
Decomposers	?	?	?	?	?	?	?
Phytoplankton	x	?	-	-	-	-	?
Bacillariophyceae	x						
Periphyton	x	-	x	x	x	x	?
Chlorophyta	x		x	x	x	x	
Filamentous	x		x	x	x	x	
Cladophora	x			x			
Spirogyra	x		x	?			
Chrysophyta			x	x	x		
Vaucheria			x				
Bacillariophyceae			x	x	x		
Cyanophyta						x	
Filamentous						x	

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Table 2. - continued

	Locomotive Springs	Saratoga Springs	Rattlesnake Creek	Deep Creek	Sycamore Creek	Deep Canyon	Jornada Playa
Macrophytes	x	x	x	x	-	x	x
Chara				x		x	
Ceratophyllum demersum		x					
Distichilis spicata		x					
Eleocharis macrostachya							
Hilaria mutica							x
Lemna			x				
Nitrophila occidentalis	x						
Panicum obtusum							x
Phragmites communis		x					
Potamageton pectinatus	x			x			
Rorripa nasturtium-aquaticum			x	x			
Ruppia maritima	x						
Scirpus olneyi		x					
Typha			x				
Zooplankton	x	?	-	-	-	?	?
Rotifera						?	?
Copepoda	x					?	?
Cladocera							?
Benthic Invertebrates (includ.assoc.w/sub. plants)	x	x	x	x	x	x	x
Mollusca	x	x	x	x	-	?	-
Gastropoda	x	x					
Fontelicella		x					
Physa	x						
Tryonia		x					
Pelecypoda				x			
Pisidium				x			
Annelida	x	-	-	x	-	?	-
Oligochaeta	x						
Tubificidae							
Hirudinea				x			
Helobdella				x			
Arthropoda							
Crusteacea							
Branchiopoda							x
Anostraca							x
Streptocephalus							x
Thamnocephalus							x
Notodtraca							x
Triops (Apus)							x
Conchostraca							x
Eulimnadia							x
Ostracoda			x		x		
Amphipoda	x		x	x			
Hyalella azteca	x	?		x			
Gammarus							
Decapoda				x			
Pacifastacus				x			
Insecta	x	x	x	x	x	x	x
Ephemeroptera			x	x			
Baetis			x	x	x		
Tricarythodes							

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Table 2. - continued

	Locomotive Springs	Saratoga Springs	Rattlesnake Creek	Deep Creek	Sycamore Creek	Deep Canyon	Jornada Playa
Odonata		x	x	x	x		
Anisoptera		x		x			
Ophiogomphus				x			
Pantala		?					
Tarnetrum		?					
Zygoptera			x	x			
Archilestes			x				
Argia				x			
Enallagama				x			
Hemiptera		x	x		x	?	
Belostomatidae		x					
Belostoma		x					
Lethocerus		x					
Corixidae		x	x		x		x
Trichocorixa		x					
Gerridae			x				
Gerris			x				
Naucoridae		x					
Ambrysus		x					
Pelocoris		x					
Notonectidae		x	x				x
Notonecta		x	x				
Coleoptera		x	x	x	x	?	x
Dytiscidae		x	x				x
Agabetes			x				
Cybister		x					
Dytiscus		x					
Eretes							x
Hydaticus			x				
Oreodytes			x				
Thermonectes							x
Elmidae							
Dubiraphia				x			
Optioservus				x			
Hydrophilidae							x
Hydrophilus							x
Trichoptera		x	x				
Hesperophylax		x					
Hydropsyche			x				
Leptoceridae		x					
Diptera	x	x	x	x		x	x
Chironomidae	x	x	x	x		x	x
Simulium			x				
Fish	x	x	-	x	x	-	-
Agosia chrysogaster					x		
Cyprinodon nevadensis		x					
Cyprinus carpio	x						
Gila atraria	x						
Rhinichthys osculus				x			
Amphibians	x	-	-	-	-	x	-
Bufo punctatus						x	
Hyla arenicolor						x	
Rana pipiens	x						
Scaphiopus hammondi							x
Scaphiopus couchi							x

x= important (but known only to level shown)
?= probably important but not known at present
-= not important

Aquatic Specialists' Meeting - continued

After considerable discussion, the following taxa were chosen for study:

Periphyton
- Filamentous Chlorophyta
  - preferably *Cladophora* and *Spirogyra*
- Bacillariophyceae

Benthic Invertebrates
- Tubficidae
- Anostraca
  - preferably *Streptocephalus* and *Thamnocephalus*
- Notostraca
  - preferably *Triops* *(Apus)*
- Conchostraca
  - preferably *Eulimnadia*
  - *Hyalella azteca*

Insecta
- *Baetis* (Ephemeroptera)
- *Hydropsyche* (Trichoptera)
- Dytiscidae (Coleoptera)
  - preferably one or more of the following: *Agabetes*, *Cybister*, *Dytiscus*, *Eretes*, *Hydaticus*, *Oreodytes*, *Thermonectes*
- Chironomidae (Diptera)
  - preferably at least one herbivore and one carnivore

In all cases the *species* preferred are those occurring at the validation sites.

The processes selected for emphasis in 1972 are listed below in order of importance:

Periphyton
1. Net photosynthesis.
2. Respiration.
3. Nutrient uptake and excretion of carbon, nitrogen, and phosphorus.
4. Mortality (detritus input).

Benthic Invertebrates
1. Ingestion
2. Assimilation
3. Excretion
4. Non-predatory mortality
5. Movement
6. Respiration

In addition, the need to develop a series of "Technique Studies" dealing with detritus and bacterial-fungal decomposers was identified. The information required is listed below:

Detritus
1. Nutrient output.
2. Biomass of output.
3. Factors involved in determining 1 and 2.
4. Whether the variations in the rate or the proportion (of 1 to 2) depends on the species makeup of the microflora present.
5. Factors affecting the rate of nutrient input.
6. Factors affecting the rate of biomass input.

Decomposers (bacteria and fungi), greater than .45 μ in size.
1. Nutrient output.
2. Biomass of output
3. Factors involved in determining 1 and 2
4. Whether the variations in the rate or the proportion (of 1 to 2) depends on the species makeup of the microflora present.

APPENDICES

Included here are the reports of two meetings attended by representatives of the Desert Biome. It is hoped that this method of presentation will serve to facilitate communication within the Biome.

APPENDIX I

Report on the IBP Aquatic Microbiologists Meeting

June 1970
Pittsburgh, Pennsylvania

prepared by Robert W. Gorden

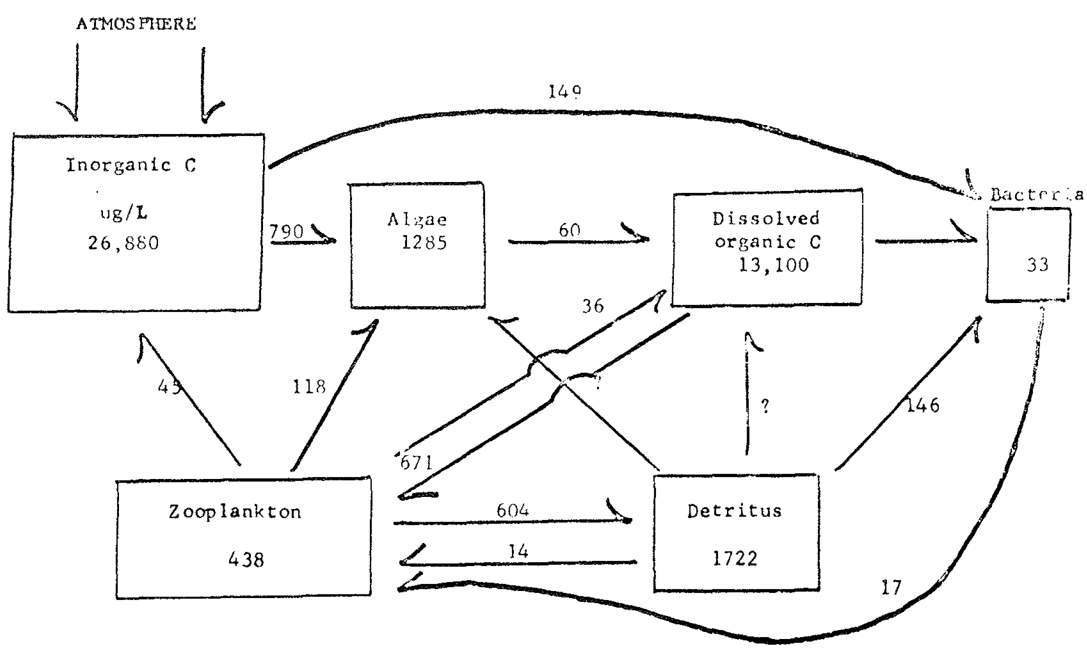
Papers describing methods useful to IBP work were presented by Dr. George Saunders and Dr. Harold Allen. Both presentations offered approaches and data of specific interest to the other participants attending the meeting.

Saunders' talk, "Methods of measuring carbon flux in aquatic systems" summarized years of research during which he and his group have looked at control mechanisms operating in the aquatic system. Basically, his approach is to separate the major components of the ecosystem and allow them to assimilate radioactive substrates. The components are selected by filtration and antibiotics and placed in 5 gal. carboys. Labeled substrates are added and the incubation process takes place in the lake. Following incubation, the organisms are killed, filtered, and radioactivity is counted. Various other measurements (dissolved organic carbon, particulate carbon, etc.) are also made of each component.

The entire process is crude and represents a probing attempt to determine flux rates and activities. The processes within the system are complex and the procedures described are extremely time consuming. The interesting thing is that "after you run it, you find out it is trivial because it won't tell you anything except that it describes what is happening."

The following diagram illustrates the procedures described by Dr. Saunders. In order to quickly obtain simple first order kinetics, the blocks were isolated. However, other interactions quickly developed and it became apparent within a few hours that the simple, first order kinetics analysis was not sufficient.

DIAGRAM OF MODEL OF A LAKE - 24 hr rates in ug/liter/day.



On the diagram (page 3.4.-21), the numbers in the squares signify the initial conditions while those on the arrows indicate rate of transport from one compartment to another within a 24-hr period. In the upper zone, the algae dominate the system and there is more gross photosynthesis, as opposed to respiration.

Dr. Saunders continued with details about methodology and discussed future research plans. His data for this study was collected over a period of four months by four members of his group. It was his opinion that this particular experiment could be run at one level of the lake 25 times a year by 35 people. He suggested that a more feasible approach would be to select specific components for study using similar methods.

Dr. Allen's presentation included one aspect which was of particular interest. He enclosed macrophytes in a Saran Wrap chamber and added $^{14}CO_2$. He then observed the uptake of the radioactive label by the plant, and the subsequent movement to epiphytes. His procedure and results follow:

Procedure

1. Surround the plant with Saran Wrap, tying both ends to the plant.
2. Inject $Ba^{14}CO_2$ into the chamber.
3. Add known amount of HCl into the chamber; evolve $^{14}CO_2$ at 3.5% of total air volume in the chamber.
4. Where has all the label gone?

Results

1. After 3 minutes, much of the label was found outside the stem of the plant.
2. After checking epiphytes (after 5 hours) and also measuring uptake on sectioned pieces of the plant, 70 to 80% of the CPM were associated with the bacteria.
3. Changes in the concentrations of dissolved organics ranged as much as 300% in a few hours time (in the lake).

Another procedure (and results) used in Dr. Allen's laboratory and reported by him was:

Procedure

1. Plants were labeled and placed in the center of a three-part chamber of which each part was separated by G. S. Millipore filters previously washed with 60 ml of 0.1 N HCl as a cleaner to remove all dissolved organics.
2. Cultures of bacteria isolated from the plant were placed in the chambers to see (a) if they could live on the excreted organics, and (b) if they would take up the radioactive label.

Results

1. The bacterial isolates did take up material released from the plants. Algae did, as well.
2. Algae and bacteria together took up more when combined than additive amounts.
3. Algal uptake was increased in the presence of bacteria.
4. Some form of ^{14}C was passed from the macrophyte to the algae -- directly or indirectly.

Talks by others at the meeting involved the more classical approaches to the study of microbial activities.

Francisco's method of epifluoresence is similar but more expensive than the better known acridine orange method of Strugger and Woods. It is no more precise.

Staley's field measurements of in situ bacterial growth consisted of submerging a microscope and carefully transferring a suspended slide to the stage for viewing. By observing the slide hourly, or at least regularly, he determined growth rates of specific colonies. The method is not practical for IBP work, I think, and has the surface-bottle effect of only observing growth of surface bacteria.

Decomposition studies suggested tubes in which leaf sections can be enclosed; separated by filters of various sizes or by screens. These are especially effective for fast currents and are probably better than the litter bag method which we have used at Jornado. Less detritus would be collected on the leaves, etc. A more accurate measurement would result.

Much discussion resulted in not a single recommended method.

APPENDIX II

Report on the Deciduous Forest Biome Workshop on Aquatic Primary Productivity

November 19-20, 1970
Wisconsin Center, Madison Wisconsin

prepared by Fred L. Rose

Aquatic specialists from the Lake Wingra, Lake George, and Oak Ridge study sites of the Deciduous Forest Biome met in Madison to review the current status of their work and to discuss at some length the common problems faced by investigators at their respective sites.

Speaking as an observer only, it was my impression that a major problem faced by investigators in the Deciduous Forest and Desert Biomes is one of communication and agreement of objectives between people conducting the work and the modelers. At this workshop certainly, a significant portion of the time was spent in an attempt to agree upon specific objectives in the measurement of primary productivity as process studies. The obvious necessity for such agreement and the close cooperation between modelers and investigators appears to be one of the stumbling blocks which must be overcome before meaningful work can be undertaken and the broader objectives of IBP attained.

After a brief introduction including a description of the study sites and the process studies both planned and underway, the first topic considered was one of objectives. It was the view of modeler Mac McCormick that general IBP objectives were too vague to use in constructing a model for primary productivity. He suggested that a more specific approach needs to be taken and that the model must be constructed in terms of nutrient and energy flow. To accomplish this, it appears necessary to identify the components of primary production and then develop submodels for each of the components. Ed Dettman noted that at present, no model exists for primary productivity and indicated that before one could be constructed the participants must reach agreement of specific objectives. Although considerable discussion followed, no list of such objectives was forthcoming for the three major categories of aquatic plant life until the final portion of the workshop.

Dr. Robert G. Wetzel, participating in the workshop as consultant to the Biome, noted that it is necessary to agree upon the resolution of models and that it would be impractical to attempt the same resolution for all species. Operating under the assumption that nutrient requirements or uptake characteristics of nutrients are limiting to algal growth, several of the investigators proposed the use of Michaelis-Menten kinetics studies. Such work, if successful, would disclose rate limiting factors and would be a powerful tool in the prediction of algal growth. Bob Wetzel suggested that studies on algal metabolism will be meaningful only if conducted in situ. He further stated that if a range of values for metabolic parameters could be obtained under perturbed conditions, it would provide an excellent basis for future predictive capabilities. The complexities of nutrient studies, in particular carbon, nitrogen, and phosphorus, were discussed and it was pointed out that measurements of the nutrient pool cannot be equated with algal growth. In the case of carbon studies, turnover rates of labile organic carbon and ratios of labile to refractory organic carbon must be known. Other parameters in use in modeling primary productivity including light, temperature, current velocity, and turbidity were not discussed in great detail.

Biomass estimates, although a poor indicator of primary productivity, are being made at the Lake Wingra study site, particularly in relation to macrophyte production. Since it is impossible to assess macrophyte production throughout the entire lake, a quadrat analysis with sampling by skin divers has been used. An attempt is being made to obtain gross biomass estimates through comparison of the vegetation distribution and abundance from aerial photographs. Biomass estimates for phytoplankton have been made by hypothesizing cell volume and subsequently making cell counts.

Investigators from all study sites indicated a preference for the ^{14}C uptake technique in the measurement of algal photosynthesis. However, numerous problems associated with this technique may result in the introduction of serious error and complicate its use. Among those problems considered were:

1. Calculation of available carbon
2. Extrapolation of the results from 4 hr incubation periods to a 24 hr basis.
3. A "Bottle Effect" due to changes in bacterial populations.
4. Excretion of organic carbon during periods of incubation.

Michael Adams, APP Process Coordinator, indicated his intent to use ^{14}C uptake studies on Myriophyllum on Lake Wingra on an annual basis. An attempt will be made to correlate these data with biomass measurements in the hope of obtaining annual primary productivity.

Near the close of the workshop, agreement was reached regarding specific objectives to be used in the construction of models for primary productivity. These appear below in the tabular form developed at the workshop:

Parameter	Phytoplankton	Macrophytes	Periphyton
Biomass (M)	Biomass by size distribution	Biomass	Biomass by species composition
Carbon uptake dM/dt	A problem area, ^{14}C technique to be used but cannot model nutrient interaction at present time; light and temperature influences to be followed.		
Time	Nutrients to be measured weekly for 2 hr periods.		
Grazing	Size dependent Removal by zooplankton		
Looses	Excreted orgnic matter		
Nutrients	Characteristics of nutrient replenishment		

In summary, it was my impression that APP process studies in the Deciduous Forest Biome will reflect the abilities and talents of the greater number of specialists participating in these studies. Indeed, it represents an impressive strength of the Biome. Moreover, when compared to aquatic studies in the desert, they have the added advantage of already possessing a considerable wealth of background information regarding the study sites which we are striving to obtain through validation studies. It would appear that greater inter-biome communication, particularly with regard to process studies, would benefit all investigators. This is especially true in light of budgetary limitations and the necessity of avoiding duplication.