Acta Científica 7(1-3):189-227, 1993

SIMULATION OF THE LAGUNA JOYUDA ECOSYSTEM IN WESTERN PUERTO RICO

Howard T. Odum
Environmental Engineering Sciences and Center for Wetlands
University of Florida, Gainesville, Florida 32611

and

Marty Munroe
Center for Energy and Environment Research
University of Puerto Rico, Mayagüez, Puerto Rico 00708
Present address: Water Resources Authority, Austin, Texas 78711

ABSTRACT

A microcomputer model is given that simulates variations in animal populations and ecosystem processes in Laguna Joyuda, a tropical lagoon in southwestern Puerto Rico. The model contains abiotic and biotic processes occurring in the lagoon including: hydrology, production, consumption, nutrient recycle, predation, import and export. Organic matter from mangroves and nutrient runoff are important inputs affecting the biological organization of the lagoon. Commercially harvested shrimp, crabs, and bony fish are significant exports controlling trophic flows within the system. Simulations showed complexity in the frequency and timing of lagoon animal populations while those components with longer time constants tended to prevail, stabilizing the oscillations of those with shorter time constants. High internal recycling of nutrients favored pelagic web compartments due to the imbalanced advantage of the pelagic primary producers to capture solar inputs. The similarity between the model system and the lagoon variables provides some systems basis for evaluating management alternatives using the existing hypotheses regarding the system's processes. Population patterns, including those of species valuable to man, were shown to be the result of a complex of system interactions rather than the interaction of a few, isolated components. Overall system performance, including frequently oscillating populations and high secondary productivity, were explicable by the model in terms of large energy subsidy to the lagoon unit in the landscape and the modifying influences of fish removal and larval imports. The model fulfilled the primary task of providing system overview with medium to large scale consideration of parts and processes.

INTRODUCTION

Understanding how dominant animal populations are related to the other components and processes in estuarine ecosystems is a basic objective of systems ecology. The spirit of the present research effort is to understand some of the structure and function of a representative mangrove lined tropical lagoon and, also, arrive at some insights for appropriate management. First a model was developed to represent in simplified form the concepts of interaction held by those studying the lagoon. Then simulation experiments were conducted on the model to determine responses and sensitivities. These were related to observed events and future management alternatives. In other words, study was made of a combination of difference equations designed to have output mimicking observed data of the lagoon. The model and its simulations, an artificial construct like any experiment, gives the mind some understanding of the phenomena it represents. Those interested in the phenomena of a smaller scale are forewarned that this approach favors retaining large scale interactions over the integrity of multiple small scale influences and individual organisms.

Although the main features and processes in estuarine ecosystems are well known, the way the physical, chemical and biological units operate together is still not understood well enough to account for observations over time. Studies of separate parts are not enough, because populations and concentrations depend on estuarine cycles, energy networks, and hierarchical patterns. By including these design features in computer models of medium complexity, main events of estuarine ecosystems may be simulated. Because self organization generates common features in network designs, models developed for a class of ecosystems may have considerable general applicability. Developing simulation models with generality is a frontier of systems ecology.

An important class of world ecosystems is the shallow tropical estuary which receives the runoff and wastes from land increasingly concentrated with nutrients and organic substances by rising populations and economic development. These lagoons are important nurseries essential to fisheries and protein production and at the same time are natural waste treatmentrecycle partners to the economy. Aguacultural management is often involved with varying degrees of intensity. These lagoons are linked to mangroves and their roles as green belts, aesthetic borders, and wood producers. A good example is the Laguna Joyuda in eastern Puerto Rico. The many studies that have been done provide an opportunity to develop general simulation models for overview understanding of shallow tropical estuaries.

In another article (Odum *et al.* 1993) short term behavior was studied with a simulation of diurnal and day-to-day changes in production, respiration, nutrients, and organic matter. In this article, after a simple overview model (LAGOONI) was used to relate production and consumer oscillations, a more complex model (LAGOONII) was used to overview seasonal, successional, and year-to-year events in the lagoon.

Once the model was generating the approximate levels of concentrations, populations, and flows and it was believed there were no errors remaining, fine tuning and experimentation could begin. As with a controlled experiment, simulation experiments were run which ask the question: "What if such and such were changed and everything else remained as originally aggregated and calibrated?" For the Laguna Joyuda and understanding of tropical estuaries, the following questions were included in the test runs.

What happens when inflows of the following were changed: inorganic nutrients, organic matter, population immigration, freshwater?
What changes affect the timing of the pulses of zooplankton, jellyfishes, and shrimp observed in the model and in the field?
What changes take place when there are large harvests of shrimp and fishes?
What changes occur if the mangrove inputs are removed?
What changes are produced if most of the light is used by plankton rather than by bottom producers?

Modeling Concepts

By quantitatively relating main features of hydrology, tides, nutrients, mangroves, producers and consumers, according to the mechanisms believed to be operating, tests of the consistency between hypotheses and data are arranged. Although models are much simpler than the natural system they represent, models can include what is found to be important by close study of nature. A medium complexity model may provide as much overview as human minds can understand in unified view. As one of the principal means of representing concept and fact, a working model that can represent main features of a system's behavior with time is a main objective of synthetic science.

The energy language systems diagram is a main feature of the study (see Figs. 1 to 5). By keeping the diagram in front and eventually memorized in the mind, parts and patterns are both dealt with in one motion. Mathematical terms are equivalent to configurations and may be written on the pathways for emphasis. Equations in the simulation program are readily read from the diagram by inspection and vice versa. Values of flows and storages are written on the diagram so they can be visualized. Because the diagram is hierarchical with small, rapid units on the left and larger slow units on the right, one may use common sense with inspection to make the whole make sense while writing numbers representing parts. The diagram is used to debug, by visualizing what response in a unit is to be expected. Then if it gets less when it should be more, one knows where to go in the program to look for an error.

Whereas modeling efforts sometimes start with the parts, later connecting them into an ecosystem, the top-down approach used here started with the whole pattern, introducing first the essential designs already known to exist in all ecosystems: the nutrient cycle, the food web, the hierarchy of dominant species with different turnover times, the main inflows, outflows, and sinks. Thus, a preliminary simple model was calibrated with appropriate values for the Laguna Joyuda. Some of the main observed events with time were simulated. This procedure helps show what properties emerge from the large scale features of structure and timing.

Next, the first model was disaggregated to show more of the detail, including the categories presently or previously studied. This included details of the water budgets, more of the prey-predator relationships, and separation of the benthic and plankton components. Since the modelling was intended to help communication among those measuring different quantities, each main item being studied was represented separately. A model of medium complexity resulted. More detail in the model generally produces more detail in the ups and downs of the simulation with time.

Simulating Small Fast Components Without Storage

The most important property of units in a dynamic model is the turnover time (called time constant in engineering). Position in hierarchy is indicated by the turnover time, with microbes having small values and Large fish having long turnover times. Care in calibration is required to keep turnover times of a species appropriate. If one changes a value of storage, without also changing the inflows and outflows, one inadvertently changes the turnover time. One changes characteristics of one size class to those of another.

One way to avoid such size-time errors is to diagram the storage and flows of a unit, writing the values on the diagram as shown in Figure 1. For calibration purposes inflows are set equal to outflow for an observed or average storage level Figure 1. This will be the level that variable will tend to develop or oscillate around.

Where one is considering short term phenomena like diurnal changes, fast turnover compartments such as nutrients, phytoplankton, and microphytobenthos are represented with storages. Their filling and discharging dominate the phenomena of production and consumption in the short range. Thus, these were included as storages in modelling diurnal variations (Odum and Odum 1993). However, for the longer period of interest considered in this chapter, if these are included as storages, one is simulating units of 3 or more orders of magnitude of turnover time. To do this without error requires that the time step be kept very small and a long time is required for a simulation. This is unnecessary if it is the larger items that are of interest, because the fluctuations of the small units are all filtered out so far as their effect on the larger consumers.

We developed a procedure of substituting "residual flow" as the state variable for the fast-tracking variables such as light, nutrients, and phytoplankton where longer times are being studied. When these storages are replaced with "residual flows," their values are instantaneously calculated without time delays. The details and mathematical justifications were given in SYSTEMS ECOLOGY (Odum 1983, p. 130). As a storage approaches zero, the differential equation for that storage approaches the equation for "residual flow." An example of "residual flow" method is given in Figure 1b for the light input of Figure 2. Many authors have inserted similar equivalent limiting factor mathematics, arriving at the same result empirically.

The practical result of using the "residual flow" method of representing fast turnover variables is to allow the program to be run 10 to 100 times faster and thus suitable for frequent testing on microcomputers. Whereas the real world simultaneously processes at many scales of time, microcomputer simulation to be useful should use a time window of only about two scales. The faster variables become instantaneous steady states just as long practiced by environmental chemists in using equilibrium calculations wherever the rates are much faster than the phenomena of interest. The variables that have longer period variations are those of larger systems in which the ecosystem is embedded. The very long period changes are the forcing function, input sources from the outside driven by long period changes in hydrology, climate, and economic development systems.

Background Studies

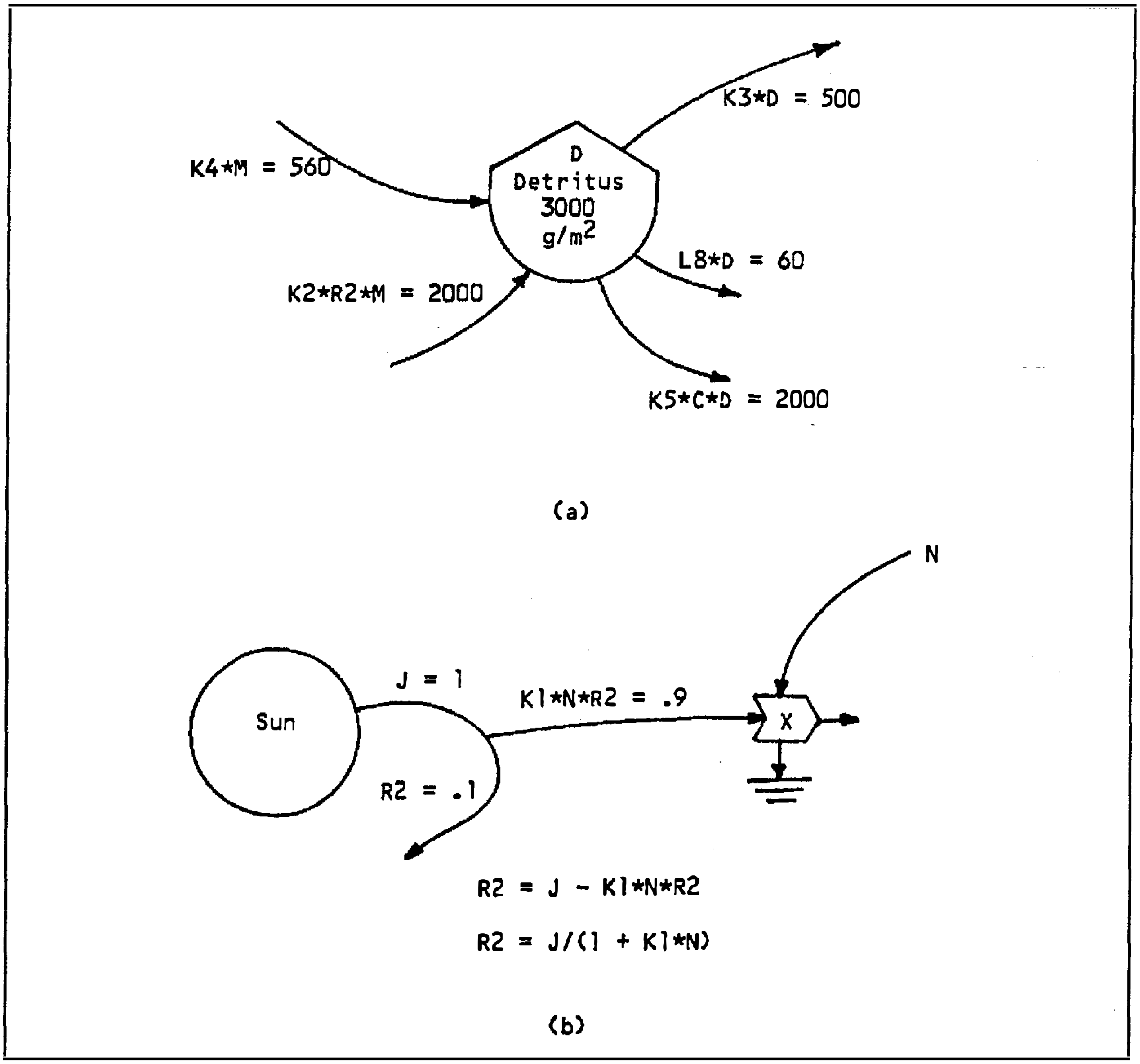
Even though recognition of detritus-based food webs of shallow, muddy estuaries with extensive plant communities is well over a decade old (Odum and Heald 1975, Odum and de la Cruz 1963, Odum 1963), little effort has been made to relate detailed studies of physical exchange, chemical cycles, and primary productivity to the consumer populations. Modelling efforts have usually focused on lower trophic relationships and have emphasized the influences of temperate factors in deep water phytoplankton based communities (Kremer and Nixon 1978). In the tropics, the shallow coastal lagoon surrounded by mangroves is an important class of ecosystem that has received little ecological study despite the heavy influence of agricultural waste runoff on these systems. A model of a subtropical estuary (Caperon 1975) recognized that understanding of higher trophic levels was necessary to understanding phytoplankton distribution in time and space. The importance of benthic-detrital pathways to higher consumers, however, was not explored. Attention to higher trophic levels of tropical lagoons has largely been descriptive (Yañez-Arancibia *et al.* 1980, Stoner 1986) with little evaluation of ecosystem dynamics. In this paper, a systems model of Laguna Joyuda, a small, shallow tropical lagoon in western Puerto Rico, was simulated to study effects and sensitivities of various mechanisms, magnitudes, and external impacts using a deterministic food web encompassing all trophic groups, albeit in aggregated form. Data and concepts from an ongoing research project were used to calibrate the aggregated model toward obtaining an overview of system responses to management alternatives.

A recent review of forested wetlands (Lugo *et al.* 1988) reports the high net primary productivity of salt-water forested wetlands balanced by a large export of organic carbon (198 g C $m^{-2}yr^{-1}$ the average of four studies, SE = 105). High quality detritus is defined as requiring shorter periods of microbial action before it is upgraded (lowering of the carbon to nitrogen, or C:N ratio) for use by higher trophic levels. A similar ratio, that of mass of litter fall to mass of nutrients in letter fall termed "the within stand nutrient efficiency" or WNE (Vitousek 1984), suggests high retranslocation of nutrients in the living plants if high. Emerging evidence indicates lower WNE ratios occur in forested wetlands not under oligotrophic stress (Twilley *et al.* 1986). Since nutrient conserving mechanisms are unnecessary in forests receiving nutrient laden waste water, the high quality detrital carbon subsidy (low C:N ratio), concomittent with a low WNE ratio, would be the rule for downstream systems in subtropical moist agricultural watersheds (*sensu* Holdridge 1967), such as Laguna Joyuda. Clearly, mangrove carbon plays an important role in the metabolism and dynamics of adjacent lagoons.

Laguna Joyuda

Laguna Joyuda is a small tropical estuary almost completely surrounded by mangroves, including the four species most prevalent in the Neotropics: red (*Rhizophora mangle*), black (*Avicennia germinans*), white (*Laguncularia racemosa*), and buttonbush (*Conocarpus erectus*). The 40 or so hectares of the mangrove forest band surrounds approximately 125 ha. of open lagoon waters whose shallow depth (1.3 m average, 2.5 maximum) gives the lagoon the aspect of an irregularly edged pancake (Kjerfve 1984) cut off from the sea by a sand bank deposited by littoral wave action on its western, seaward border (see Fig. 1). The low lying Sabana Alta ridge of hills in the east and northeast cuts the lagoon from regional drainage, creating a watershed only twice the area of the lagoon, limiting freshwater sources to being dominated by direct rainfall on the lagoon.

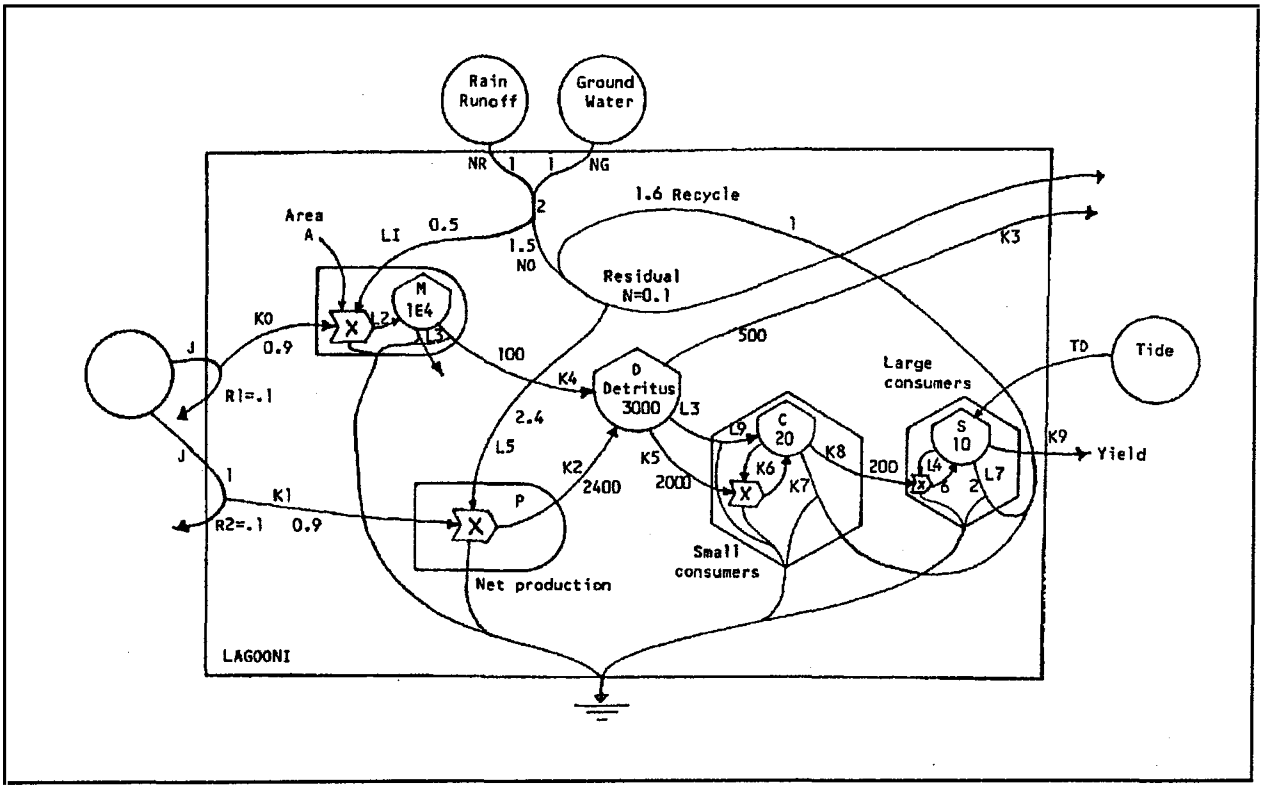
Figure 1. Examples of diagrams used to calibrate coefficients from Figure 2 of the minimodel LAGOONI. (a) Flows in and out of a storage, the detritus compartment; (b) use of "residual flow" to represent a very fast turnover variable, light input.



Groundwater studies were made in the immediate area in 1987 and they indicated that serpentinite rock underlies a substantial portion of the watershed.

The climate is typical of the leeward coast of tropical maritime islands with an annual rainfall averaging between 1 and 2 m (1575.8 mm reported for the lagoon in 1986, CEER unpublished data). Large scale wind influences on the western coast of Puerto Rico, trade winds and landsea breeze systems Figure 2 have less effect than the absence of mangrove forested wind row protection on the southeast; thus southeastern winds blow across a large fetch of lagoon water, mixing it thoroughly. Diurnal variation in temperature was greater than annual variation of monthly averages - 2.8 C vs. 9 C - as is typical of tropical regions (López *et al.* 1993). Mean annual air temperature was 26.1 C with May through October being the warmest months. Mean solar radiation was reported as 366.02 ± 28.81 cat cm^{-2}day^{-1}

Figure 2. Diagram of the very aggregated simulation minimodel LAGOONI of the Laguna Joyuda ecosystem with calibration values and letters designating flows and storages. See equations in Table 1 and calibrations in Table 2. The BASIC program for IBM PC is given as Table 5.



(Carvajal *et al.* 1980). Detailed information on climate, morphology, geology and soils is available in a report by López *et al.* (1993).

The surrounding uplands have been used for sugar cane and pineapple, but at the time of the study were under pasture with small amounts of coconut palms. Residential dwellings were increasing on the eastern slopes with new families. Perhaps the greatest threats to the lagoon were the expanding parking lots of seafood restaurants located on the western sand banks.

METHODS

The models of the lagoon ecosystem were developed diagrammatically with aid of comments of those studying the lagoons. Estimates were obtained for flows and storages. These were added to the diagram and adjusted to make inflows and outflows consistent. Equations were derived from the diagram (Tables 1 and 3) using the methodology in Odum (1983). With knowledge of lagoon hydrology a program in BASIC was written. Numerical estimates for storages and fluxes were written on the diagrams (Figs. 1, 2, 5, and 6; and in Tables 2 and 4). All organic storages were expressed in grams per square meter and associated flows in grams per square meter per year. Water flows and storage were in cubic meters. Some mangrove-associated flows were for the entire forest and thus multiplied or divided by area wherever needed to make units consistent.

The numbers were used to calculate coefficients (K's) of the equations (Tables 2 and 4), which were inserted in the program. Calibration calculations of coefficients were greatly simplified and errors reduced by setting them up on a spreadsheet. See LOTUS printouts in Tables 2 and 4). Sources, aver-

Table 1. Equations for minimodel LAGOONI in Figures 2 and 3. Coefficient values in Table 2.

Limiting Flows:	
Light: $R1 = J - KO*R1*NO$	Therefore $R1 = J/(1 + KO*A*NO)$
Light: $R2 = J - K1*N*R2$	Therefore $R2 = J/(1 + K1*N)$
Phosphorus:	$NO = NR + NG - L1*R1*A*NO$
	Therefore $NO = (WR+NG)/(1 + L1*A*R1)$
$N = NO + L6*C + N1*S - L5*R2*N$	Therefore $N = (NO + L6*C + N1*S)/(1 + L5*R2)$
Production:	$P = K2*R2*N$
Detritus:	$DD = K2*N*R2 - K3*D - K5*C*D + K4*M - L8*D$
Mangroves:	$DM = L2*A*R1*NO - L3*M$
Small consumers:	$DC = K6*D*C + L9*D - K7*C - K8*C*S$
Larger consumers:	$DS = L4*C*S + TD*L - L7*S - K9*S*TD$
Yield:	$Y = K9*S*TD$

age storages, average flows, and other parameters are set up in the first part of the spreadsheet (rows 1 through 48). The formulas for calculating each coefficient are labeled and printed out in the lower section of the table and placed into computation as part of the set-up of items in the final column. Adding a number into the first part of the table automatically makes a change in all the coefficients that utilize that number. Then the coefficients were typed into the BASIC program. The lotus program LAGOON.WK1 makes it easy for others to use the program, recalibrating after they have put other numbers on the systems diagram.

The program QUICK BASIC was used to speed up the hundreds of runs required in calibrating, debugging, and experimenting with the system. To facilitate the coefficient calibrations and to make it easy to recalibrate, a spreadsheet program was written for LOTUS. Changing one number automatically changes all the other coefficients affected. Because of the widespread use of spreadsheets, it is easy for others to use the same model for this or other estuaries. They can substitute numbers and copy the revised coefficients into the BASIC program.

The graphical simulations were obtained by inserting the disk, calling up BASIC, and then typing RUN "LAGOONII." Fourteen variables were usually plotted with the format given in Figure 7. By putting the variables in clusters, the program can be understood either in monochrome or color. There something was changed and runs repeated. If QUICK BASIC is on the same disk, the program runs much faster by being recompiled on each run. With computer in system mode (with A> prompt), type QB LAGOONII; then in sequence type ALT R. S. ENTER, and after compiling is complete and "OK" appears, type ENTER.

For different conditions scaling of the graph can be done by changing the scaling factors SO, GO, FO, etc (see program in appendix). To change the time scale represented, change TO. (TO = .1 is 32 years; TO = .01 is 3.2 years, etc.).

RESULTS

Included below are the simple and more complex Lagoon models in diagram form and in the form of equation tables, with calibration tables indicating the numerical values used. Then results of various simulation runs are given which generate some of the phenomena observed in the field, helping one understand their causality. The programs are in tables 5 and 6 and on diskettes available from the author for others to use.

Table 2. Sources, storages, flows, and coefficients for minimodel LAGOONI in Figures 2 and 3.

Item	Expression	Value	Units
Sources:			
Sunlight	J	1	unity (normalized)
Rain-runoff phosphorus	NR	1	g/m^2/yr
Ground water inflow	NG	1	g/m^2/yr
Tide inflow	TD	1	unity
Areas: water	A2	1.1 E6	m^2
mangroves	A1	0.46 E6	m^2
Storages:			
Mangrove biomass	M	1 jE4	g/m^2
Detritus	D	1000	g/m^2
Small consumers	C	20	g/m^2
Large consumers	S	10	g/m^2
Residual flows:			
Unused sun, mangroves	R1	0.1	10%
Unused sun, aquatic	R2	0.2	10%
Phosphorus inflow	NO	2	g/m^2/yr
Aquatic phosphorus	N	0.1	g/m^2

Item	Expression	Value		Coefficient	Value
Mangrove use of sun	K0*A*R*N	0.9		K0	45
Aquatic use of sun	K1*N*R2	0.9		K1	90
Aquatic net production	K2*N*R2	2000†	g/m^2/yr	K2	2 E5
Organic outflow	K3*D	500†	g/m^2/yr	K3	0.167
Detritus from mangroves	K4*M	560†	g/m^2/yr	K4	0.056
Consumer growth on detritus	K5*C*D	2000†	g/m^2/yr	K5	0.067
Consumer use of detritus	K6*C*D	500†	g/m^2/yr	K6	1.67 E-2
Small consumer respiration	K7*C	200†	g/m^2/yr	K7	10
Large consumer food use	K8*C*S	300†	g/m^2/yr	K8	1.5
Yield of larve consumers	K9*S	30†	g/m^2/yr	K9	0.33
Mangrove use of p.	L1*NO*A*R1	0.5†	g/m^2/yr	L1	50
Mangrove net growth	L2*NO*A*R1	100†	g/m^2/yr	L2	5E3
Mangrove respiration	L3*m	100†	g/m^2/yr	L3	0.01
Large consumer growth	L4*S*C	60†	g/m^2/yr	L4	0.3
Aquatic phosphorus use	L5*R2*N	2.4†	g/m^2/yr	L5	240
Small consumer recycle	L6*C	1.0†	g/m^2/yr	L6	0.05
Large consumer respiration	L7*S	30†	g/m^2/yr	L7	3
Detritus use, small consumer	L8*D	60†	g/m^2/yr	L8	0.02
Small consumer growth, detritus	L9*D	6†	g/m^2/yr	L9	0.002
Large consumer recycle	N1*S	0.15†	g/m^2/yr	N1	0.015

†g/m^2/yr

Table 3. Equations for LAGOONII in Figures 4 and 5. For coefficient values see Table 4.

Limiting Flows:

R1 = JS - K0*R1*NO/AM Therefore R1 = JS/(1 + K0*NO/AM)
R2 = JS - K1*N*R2 Therefore R2 = JS/(1 + K1*N)
R3 = R2 - M7*N*R3 Therefore R3 = R2/(1 + M7*N)
R4 = PH - V1*A*R4 Therefore R4 = PH/(1 + V1*A)
R5 = PB - V2*C*R5 -U3*G*R5 Therefore R5 = PB/(1 + V2*C + U3*G)

Water:

WR = RA*AL; WL = (W/AL)-Z; FL = W2*(TD - WL); EV = W8*WD*AL
If TD > WL then Y = 1: X = 0; If TD < WL then Y = 0: X = 1
DW = WR +WG +FL -W8*WD*AL - M6*M*AM

Phosphorus:

NO = WR*NR + WG+NG -L1*R1*AN*NO Therefore NO = (WR*NR +WG*NG)/(1 +L1*R1/AM)
N = NO/AL +Y*M1*NT*(FL/AL) +RC - X*L7*N*FL/AL -L5*R2*N -M8*R3*N
Therefore N = (NO/AL + Y*M1*NT*FL/AL +RC)/(1 +L5*R2 +M8*R3 +L7*FL/AL)

Production:

PH = K2*R2*N; PB = M9*R3*N; GP = PH + PB; RS = 200*RC
Detritus: DD = R4 +R5 +X*K3*(D/Z)*FL/AL -K5*C*D +K4*M*AM.AL -N4*D*A -L9&D + W4*WG*RG/AL
Benthos: DC =K6*D*C -K7*C -K8C*S -V3*R5*C -V4*C*B
Shrimp: DS = L4*C*S -X*M5*S -C9*S -W1*F*S +Y*M4*ST*FL/AL
YS = X*M2*S*FM
Mangroves: DM = L2*R1*NO/AM -L3*M -K4*M
Zooplankton: DA = N1*D*A -N2*A - N3*A*P -M3*A*J +U2*R4*A
Crazing fish: DG = U4*R5*G -N7*G -N8*G-Z5*G*F +Y*N9*GT*FLO/AL - U7*FH*G
Plankton fish: DP = Z1*A*P -Z2*P -W3*P -Z3*P*F +W9*PT*FL/AL -N5*FH*P
Bottom fish: DB = V5*C*B -V6*B -V7*B*F -U6*B +Y*U5*BT*FL/AL -N6*FH*B
Jellyplankton: DJ = W6*A*J -W7*J +Y*L8*JT*FL/Al +X*U1*(J/Z)*(FL/AL)

Higher consumers:

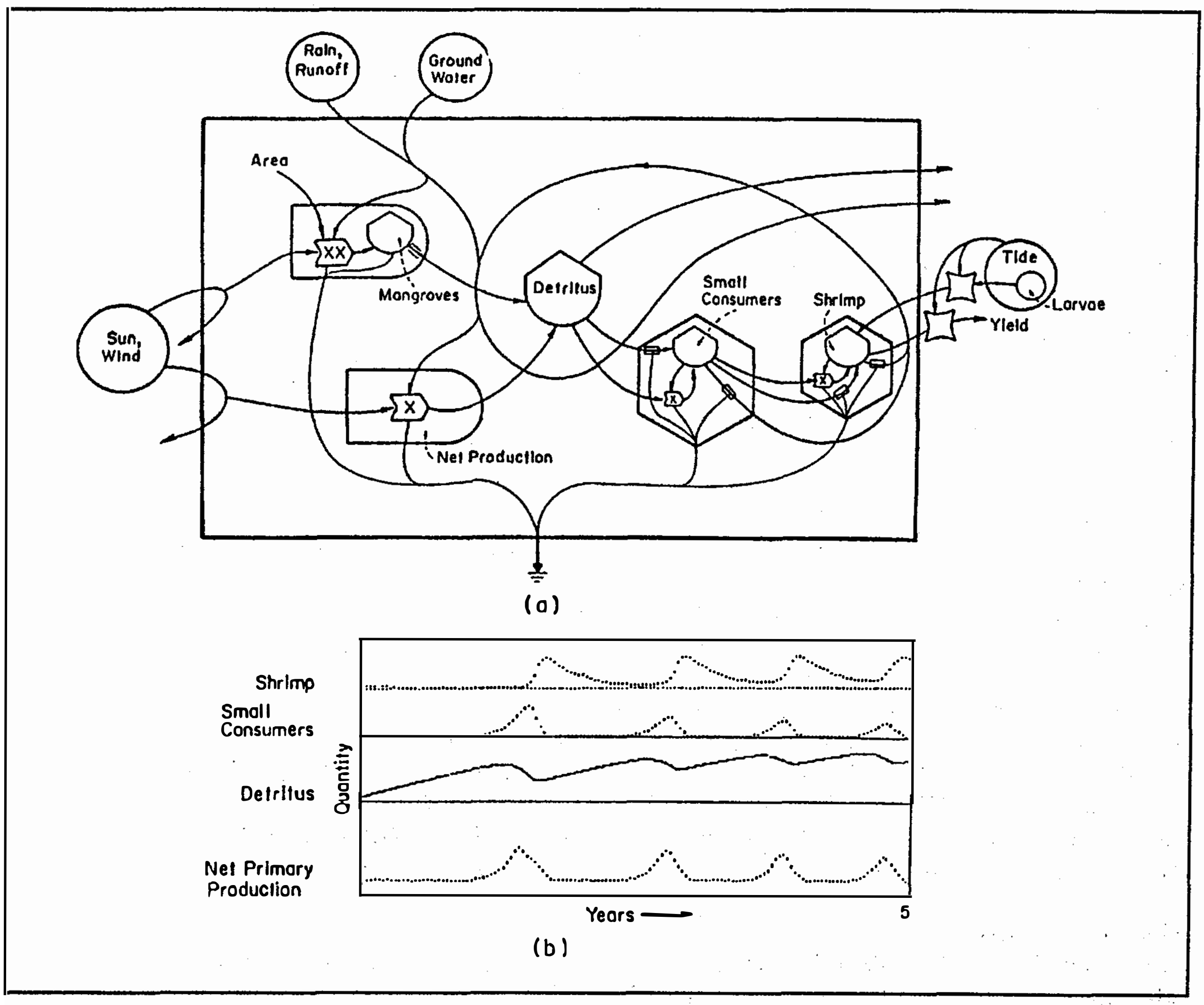
DF = Z4*S*F +Z7*P*F +Z8*G*F +V8*B*F -Z6*F -Z9*F -K9*FH*F +Y*L6*FT*FL/AL
Fishing: YF = K9*FH*F +N5*FH*P +N6*FH*B +U7*FH*G

Preliminary Minimodel LAGOONI

The simple preliminary minimodel LAGOONI is diagrammed in Figure 2 with equations in Table 1 and numbers used in calibration given in Table 2, On the left the sun is held steady. From the top the system is driven by the inflows of nutrients from rain and runoffs, held constant with different values for different runs. On the right nekton receive seeding from the outside Caribbean Sea and deliver yields. Available nutrients and available light are represented as "residual flows" and thus always at steady state with their inputs.

As shown in the simulation result in Figure 3, the two levels of consumers provide a simple prey-predator oscillation that causes the nutrients and productivity to oscillate. The time constants of the consumers supply the timing of the internal oscillation. The first consumer compartment represents

Figure 3. Microcomputer simulation of the model LAGOONS in which internal oscillations of higher, long-period consumers cause the whole system to pulse including nutrients and phytoplankton components. (a) Energy systems diagram without numbers and letters; (b) simulation graph with external sources constant.



smaller faster components like the copepods and small bottom capitellid worms. The second consumer compartment represents the fishes and shrimp dependent on the smaller components. Since occasional pulses of these components occur, there is some reality in the behavior. The model is a dramatic demonstration that higher consumers can control the timing of nutrients and production even though their own processing of nutrients is small. Their control is through the generating of the oscillation of the smaller units whose nutrient recycle flux is the main source of nutrients to plant production.

If one starts the model with low nutrients, a successional accumulation of nutrients and increase of production occurs as in nature. In other words, the recycle design with embedded food web self organizes for higher energy processing by building up its recycle of nutrients.

Simulation of the Minimodel LAGOONS

A simulation of the minimodel of Figure 2 is given in Figure 3 showing what the simple structure causes. Various pulses of growth by the *Acartia* and/

or the capitellids were followed by a predator surge of jellyfish or shrimp, the same kind of pattern observed in the simpler model. Nutrient and productivity variations were generated by the consumer oscillations. In runs of a few months mangroves were little affected. These and the detritus pool provided considerable stability.

In the absence of variations applied to external sources, changes were driven by the consumer growth pulses. As *Acartia* or capitellids went into a pulse of consumption raising the total respiration, detritus decreased, nutrients rose, production was stimulated but less than the respiration. The pulse of the smaller, fast consumers was terminated by rise in their consumers (shrimp or jellyfish) which then decreased. With detritus less, and nutrients now higher, gross production was slightly greater than respiration for a period until detritus rose and caused another round of pulses. As time passed, the fish stocks increased, dampening out some of the pulsing.

The simulation suggests a way for producers and consumers to be nearly simultaneous and still be a pulsed alternation of production and consumption that can favor overall maximum system performance and continuation. The consumers by their timing release the production that facilitates their own system basis. With consumption in short pulses, photosynthetic production is given longer periods with which to favor solar energy capture with adequate nutrients. The model suggested the need to study data to see if nutrients and photosynthesis were being correlated by consumer action instead of the traditional way of thinking that consumers track and lag production.

A More Complex Model LAGOONII

The diagram in Figure 4 represents the more complex simulation model LAGOONII that has more features of the food chain. It has the main parts and processes of the ecosystem according to the concepts developed by the Joyuda project group from field studies. The way the symbols are defined, material balances, mathematical relationships, and energetics are represented. Equations are given in Table 3. Values used for calibrations are given in Figure 5 with enlargement details in Figure 6. Calibration inputs and resulting coefficients are given in the Lotus print-out in Table 4. The following paragraphs describe some of these relationships.

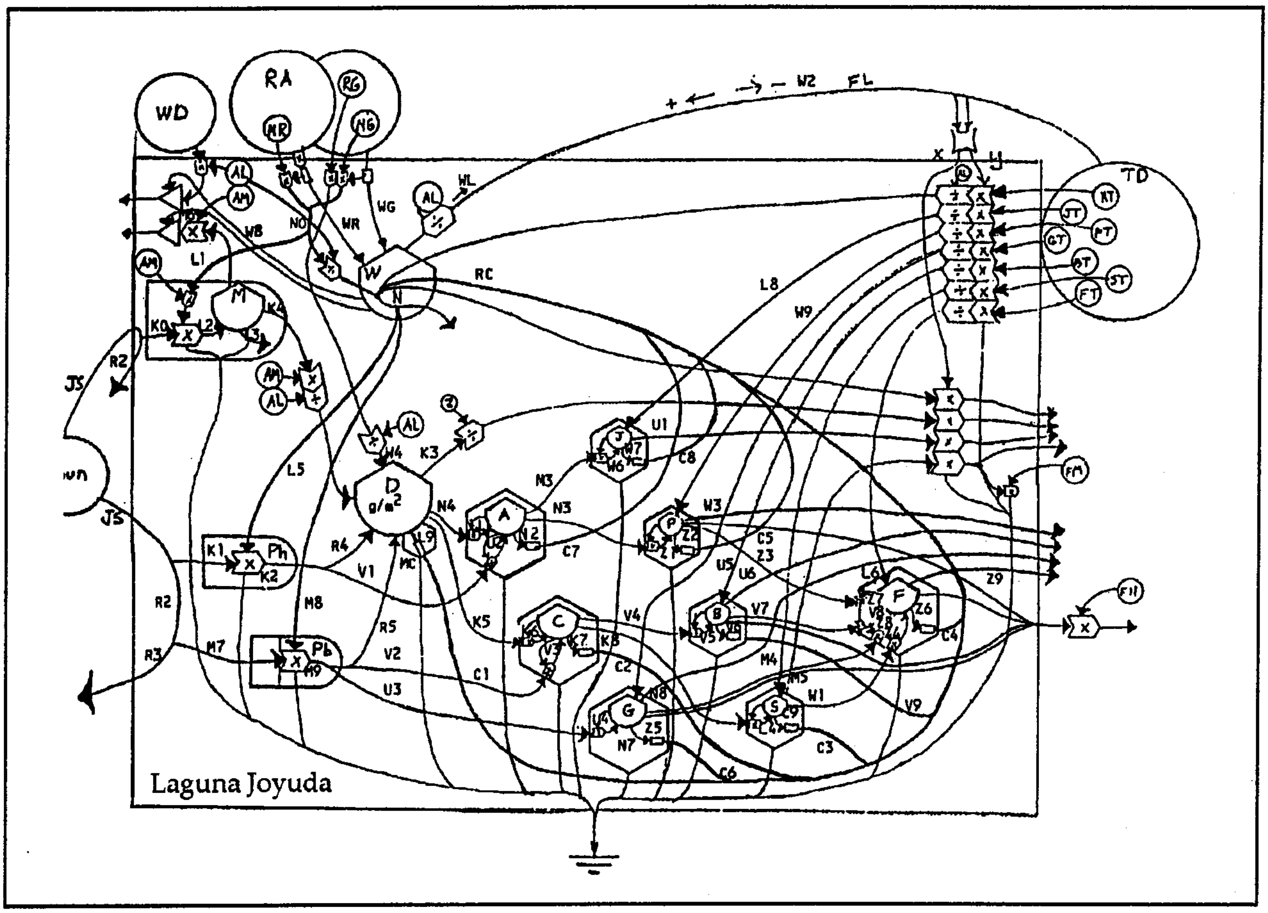
Producers included the mangroves, phytoplankton, and benthic plants that contribute to the detritus pool. In the very shallow system with strong sea breezes, detritus was often stirred up from the bottom. Detritus consumers represented as separate compartments were the zooplankton (*Acartia*, etc.), benthos (small benthic animals such as capitellids, etc.), and the microorganisms. Zooplankton were consumed by the jellyfish and plankton-eating fish. Benthos were consumed by bottom-eating fish and by shrimp. The plant production of the bottom were consumed by benthos and by "grazing fish" such as mullet. A compartment of top carnivores to include blue crabs was shown as consumer of all the other fish compartments.

In most of the runs light per day was held constant. The same light per area was provided to the mangroves, there multiplied by mangrove area to get total mangrove production. Residual light available to phytobenthos was that remaining after much was used by phytoplankton.

Water budget W received the outside inflow (surface and groundwaters), direct rain, and tidal water when the outside water level was higher than the level in the lagoon. Most of the time the outside water level was lower and the canal was flowing out. Waters were evapotranspired by the fringe of mangroves and evaporated from the surface.

A tidal regime was simulated with two superimposed sine waves, one representing the daily swings of the tide, the other representing the increase and decrease in tidal amplitude from neap to spring tide periods. When waters were outflowing, detritus, nutrients, and jellyfish were moved out in proportion; when waters were inflowing, nutrients, and seeding of the larger species were swept in representing larvae and juveniles as well as some swimming of larger members. Harvest of larger fish and shrimp by fishermen were included.

Figure 4. Energy systems diagram of the model LAGOONII including letters designating storages, flow variables, and coefficients. See equations in Table 3 and calibrations in Table 4. The BASIC program for IBM PC is given as Table 6.



The nutrient pool was calibrated with phosphorus. As the diagram in Figure 5 and 6 show, phosphorus flows in from rain and run-in, a little from tidal inflow, and most from recycle derived from all the consumers. Included in the recycle is the outside phosphorus that comes in with mangrove detritus and organic matter inflows from the landscape.

Most of the compartments were represented in grams per square meter and their respective flows in grams per square meter per year. However, water and water flows were in cubic meters for the whole lagoon. Thus, a number of the flows involving water and other compartments were multiplied or divided by area or depth to keep units correct. These were also diagrammed in Figures 4 and 5.

Simulation of the More Complex Model LAGOONII

Simulations of the LAGOONII are given in Figures 8 to 14. First horizontal yellow lines marked off 5 panels, with several simulation graphs within each, according to the key in Figure 7. The top graph in red was the tide rising and falling twice a day and with amplitude varying with neap and spring tidal regimes. Most of the time the tide was lower than the mean level of the lagoon, which is the reference horizontal line near the top. The green graph is the nutrient concentration per unit area (in water and available ooze).

The second panel had gross production within the lagoon (not mangroves) in yellow plotting up

Table 4. Lotus print-out of sources, storages, and flows and calibration of coefficients for LAGOONII (Figures 4 and 5).

Item	Expression	Value Units
	Storages for Calibration	
Mangrove biomass	M	1.00E+04 g/m^2
Labile detritus	D	3.00E+03 g/m^2
Nutrient phosphorus	N	3.30E-02 g/m^2
Zooplankton	A	1.00E-01 g/m^2
Benthos, capitellids, etc.	C	3.00 E-01 g/m^2
Jellyplankton	J	1.00E-01 g/m^2
Grazing fish, mullet	G	3.00E+00 g/m^2
Plankton fish	P	2.00E+00 g/m^2
Benthic fish	B	1.00E+00 g/m^2
Shrimp	S	1.00E+00 g/m^2
Higher consumer	F	1.00E-01 g/m^2
Water in lagoon	W	1.50E+06 m^3
	Sources for Calibration	
Sunlight	JS	2.20E+06 J/m^2/y
Unused sunlight, mangroves	R1	2.00E+05 J/m^2/y
Unused sunlight, middle	R2	1.20E+06 J/m^2/y
Unused sunlight, deeper	R3	2.00E+05 J/m^2/y
Ungrazed phytoproduction	R4	3.00E+02 g/m^2
Ungrazed benthic production	R5	1.20E+02 g/m^2
Direct rain	RA	1.50E+00 m^3/m^2/y
Water inflow	WG	5.98E+06 g/m^2
Tide level	TD	- 3.00E-01 m
Sea nutrient	NT	1.60E-02 g/m^2
Grazing fish in sea	GT	1.00E-01 g/m^2
Plankton fish in sea	PT	1.00E-01 g/m^2
Bottom fish in sea	BT	1.00E-01 g/m^2
Shrimp at sea	ST	1.00E-01 g/m^2
Carnivores in sea	FT	1.00E-01 g/m^2
Shrimping effort	FM	1.50E_03 hr/y
Mangrove area	AM	1.10E+05 g/m^2
Area of lagoon	AL	1.17E+06 m^2
Depth	Z	1.30E+00 m
Evaporation rate	E	1.80E+00 m^3/m^2/y
Detritus inflow	RG	+ 6.90E+01 g/m^3
Phosphorus in inflow	NG	1.00E-01 g/m^3
Phosphorus in rain	NR	1.00E-01 g/m^2 •
Wind	WO	5.00E+00 mph
Phosphorus inflow	NO	5.40E+05 g/y

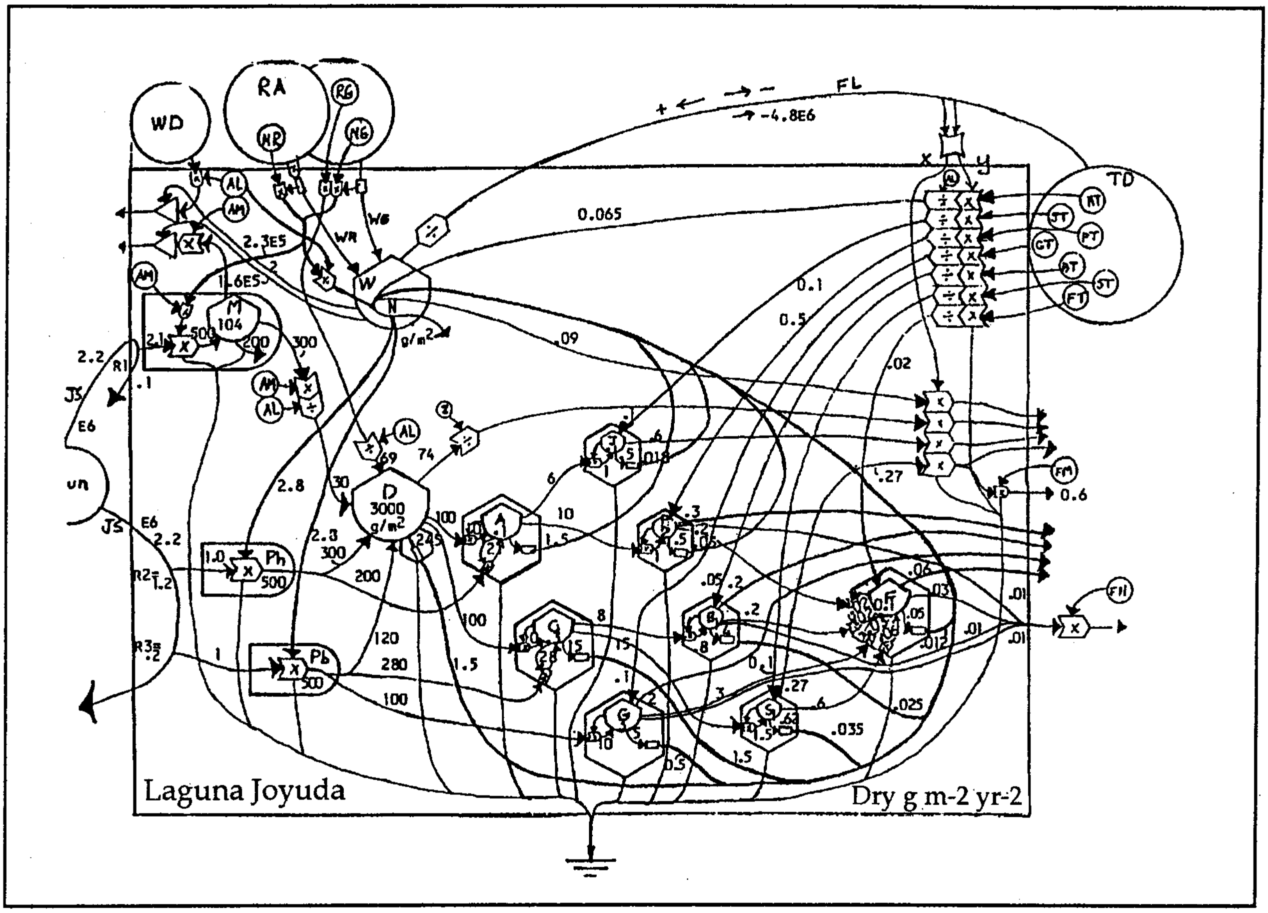
Table 4. (continued).

Item	Expression	Value Units		
Water inflow (when Y=1)	FL	8.00E+05 m^3/y		
Fishing effort	FH	1.50E+03 Hr/y		
Sea jellyplankton	JT	1.00E-01		
Water flow out (X=1)	FL	4.80+06		
Sun use by mangroves	k0*R1*NO/AM	2.00E+06 J/m^2/hr	K0	2.04E+00
Sun used, phytoplankton	k1*R2*N	1.00E+06 J/m^2/hr	K1	2.53E+01
Net production, phytoplankton	k2*R2*N	5.00E+02 g/m^2/y	K2	1.26E-02
Detritus outflow	X*K3*0*FL/AL	7.40E+01 g/m^2/y	K3	6.01E-03
Mangrove litter in	K4*M*AM/AL	3.00E+01 g/m^2/y	K4	3.19E-02
Detritus to benthos	K5*C*D	1.00E+02 g/m^2/y	K5	1.11E-01
Benthos growth, from detritus	K6*C*D	1.00E+01 g/m^2/y	K6	1.11E-02
Benthos respiration	K7*C	1.50E+01 g/m^2/y	K7	5.00E+01
Benthos to shrimp	K8*C*S	1.50E+01 g/m^2/y	K8	5.00E+01
Higher fish caught	K9*FH*F	3.00E-02 g/m^2/y	K9	2.00E-04
Nutrient to mangroves	L1*R1*NO/AM	2.30E+05 g/m^2/y	L1	1.94E-11
Mangrove production	L2*R1*NO/AM	5.00E+02 g/m2/y	L2	5.09E-04
Mangrove respiration	L3*M	2.00E+02 g/m2/y	L3	2.00E-02
Shrimp production	L4*C*S	1.50E+00 g/m^2/y	L4	5.00E+00
Phosphorus to phytoplankton	L5*R2*N	2.75E+00 g/m^2/y	L5	6.94E-05
Consumers from sea	Y*L6*FT*FL/AL	2.00E-02 g/m^2/y	L6	2.93E-01
Phosphorus outflow	X*L7*N*FL/AL	1.30E-01 g/m^2/y	L7	3.17E-06
Jellyplankton in	Y*L8*JT*FL/AL	1.00E-01 g/m^2/y	L8	1.46E+00
Detritus to microbes	L9*D	2.45E+02 g/m^2/y	L9	8.17E-02
Phosphorus from sea	Y*M1*NT*FL/AL	6.00E-02 g/m^2/y	M1	5.48E+00
Shrimp caught	X*M2*S*FM	2.00E-01 g/m^2/y	M2	1.33E-04
Acartia to jellyfish	M3*A*J	6.00E+00 g/m^2/y	M3	6.00E+02
Shrimp juveniles in	Y*M4*ST*FL/AL	1.00E-02 g/m^2/y	M4	1.46E-01
Shrimp out pass	X*M5*S	2.70E-01 g/m^2/y	M5	2.70E-01
Mangrove transpiration	M6*M*AM	1.60E+05 g/m^2/y	M6	1.45E-04
Botton plant light use	M7*R3*N	1.00E+06 g/m^2/y	M7	1.52E+02
Bottom plants phosphorus use	M8*R3*N	2.75E+00 g/m^2/y	M8	4.17E-04
Bottom plants to detritus	M9*R3*N	5.00E=02 g/m^2/y	M9	7.58E-02
Detritus to zooplankton	N1*O*A	1.00E+01 g/m^2/y	N1	3.33E-02
Zooplankton respiration	N2*A	2.50E+01 g/m^2/y	N2	1.50E+02
Zooplankton to plankton fish	N3*A*P	1.00E+01 g/m^2/y	N3	5.00E+01
Detritus to zooplankton	N4*D*A	1.00E+02 g/m^2/y	N4	3.33E+02
Plankton fish caught	N5*P*FH	1.00E-02 g/m^2/y	N5	3.33E-06
Bottom fish caught	N6*B*FH	1.00E-02 g/m^2/y	N6	6.67E-06
Grazing fish respiration	N7*G	5.00E+00 g/m^2/y	N7	1.67+00
Grazing fish out	N8*GG	2.00E+00 g/m^2/y	N8	6.67E-01
Grazing fish in	Y*N9*GT*FL/AL	1.00E-01 g/m^2/y	N9	1.46E+00
Microbe recycle	C1*D	1.50E+00 g/m^2/y	C1	5.00E-04

Table 4. (continued).

Item	Expression	Value Units		
Benthos recycle	C2*C	2.00E-01 g/m^2/y	C2	6.67E-01
Shrimp recycle	C3*S	3.50E-02 g/m^2/y	C3	3.50E-02
High consumer recycle	C4*F	1.20E-02 g/m^2/y	C4	1.20E-01
Plankton fish recycle	C5*P	5.00E-02 g/m^2/y	C5	2.50E-02
Grazing fish recycle	C6*G	5.00E-01 g/m^2/y	C6	1.67E-01
Zooplankton recycle	C7*A	1.50E+00 g/m^2/y	C7	1.50E+01
Jellyplankton recycle	C8*J	1.80E-02 g/m^2/y	C8	1.80E-01
Shrimp respiration	C9*S	6.20E-01 g/m^2/y	C9	6.20E-01
Shrimp to high consumers	W1*S*F	6.00E-02 g/m^2/y	W1	6.00E+00
Water out	W2*(TD-(W/AL)-1	-4.80E+06 m^3/y	W2	1.70E+07
Plankton fish out	W3*P	3.00E-01 g/m^2/y	W3	1.50E-01
Detritus inflow	W4*WG*DG/AL	6.90+01 g/m^2/y	W4	1.96E-01
Jellyfish production	W6*A*J	00E+00 g/m^2/y	W6	1.00E+02
Jellyplankton respiration	W7*J	5.00E-01 g/m^2/y	W7	5.00E+00
Evaporation	W8*WD*AL	2.10E+06 m^3/y	W8	3.59E-01
Plankton fish in	Y*W9*PT*FL/AL	5.00E-02 g/m^2/y	W9	7.31E-01
Plankton fish production	Z1*A*P	1.00E+00 g/m^2/y	Z1	5.00E+00
Plankton fish respiration	Z2*P	5.00E-01 g/m^2/y	Z2	2.50E-01
Plankton fish to high consumers	Z3*P*F	2.00E-01 g/m^2/y	23	1.00E+00
High consumers on shrimp	Z4*S*F	6.00E-02 g/m^2/y	Z4	6.00E-01
Grazing fish to high consumers	Z5*G*F	3.00E+00 g/m^2/y	Z5	1.00E+01
High consumer respiration	Z6*F	5.00E-02 g/m^2/y	Z6	5.00E-01
High cons. on plankton fish	Z7*P*F	2.00E-02 g/m^2/y	Z7	1.00E-01
High cons. on grazing fish	Z8*G*F	3.00E-02 g/m^2/y	Z8	1.00E-01
High consumers out	Z9*F	6.00E-02 g/m^2/y	Z9	6.00E-01
Phytoplankton to zooplankton	V1*R4*A	2.00E+02 g/m^2/y	V1	6.67E+00
Phytobenthos to benthos	V2*R5*C	2.80E+02 g/m^2/y	V2	7.78E+00
Benthos on Phytobenthos	V3*R5*C	2.80+01 g/m^2/y	V3	7.78E-01
Benthos to bottom fish	V4*C*B	8.00+00 g/m^2/y	V4	2.67E+01
Benthic fish on Benthos	V5*C*B	8.00E-01 g/m^2/y	V5	2.67E+00
Bottom fish respiration	V6*B	4.00E-01 g/m$_2$/y	V6	4.00E-01
Benthic fish to high consumers	V7*B*F	2.00E-01 g/m^2/y	V7	2.00E+00
High consumers on benthic fish	V8*B*F	2.00E-02 g/m^2/y	V8	2.00E-01
Benthic fish recycle	V9*B	2.50E-02 g/m^2/y	V9	2.50E-02
Jellyplankton out	U1*J	6.00E-01 g/m^2/y	U1	6.00E+00
Zooplankton on phytoplankton	U2*R4*A	2.10E+01 g/m^2/y	U2	7.00E-01
Phytobenthos to grazing fish	U3*R5*G	1.00E+02 g/m^2/y	U3	2.78E-01
Grazing fish on phytobenthos	U4*R5*G	1.00E+01 g/m^2/y	U4	2.78E-02
Bottom fish from sea	Y*U5*BT*FL/AL	5.00E-02 g/m^2/y	U5	7.31E-01
Benthic fish out	U6*B	2.00E-01 g/m^2/y	U6	1.73E-03

Figure 5. Energy system diagram of the model LAGOONII including numerical values of flows and storages used in initial calibration. See enlarged details in Figure 6 and spreadsheet calculations reported in Table 4.



and total respiration within the lagoon waters in red plotting downward with the same scale. The reference line was zero. Thus, it is easy to see how the two complementary processes were varying. In the middle panel were three graphs: detritus in red, grazing fish in yellow, and top carnivores in green. In the fourth panel down, the three graphs were: zooplankton in red, jellyfish plankton in yellow, and plankton fish in green. In the bottom panel, there were 3 graphs: benthos in red, shrimp in yellow, and bottom fish in green.

Simulation with Initial States Similar to Calibration States

Figures 8 and 9 have simulation runs with most of the initial conditions with the values used in calibration. In other words, the simulation represents an ecosystem already near steady state. Most of the light is taken by the plankton part of the food chain, causing a rapid increase in plankton fish.

Figure 8 is a run with a small time scale of a month so that the sinusoidal rise and fall of the tides and the neap and spring tides is shown in the top graph. The water flows into the lagoon from the sea when high spring tides exceed the reference line 5 in Figure 7. By increasing TO further, the time scale is compressed to cover more years (3 years in Figure 9). There was a large initial development of temporary displacement of bottom components which returned later along with larger consumers. These simulations started with most variables, including nutrients and detritus, at moderately high steady state

Table 5. Basic program LAGOONI for IBM PC microcomputer.

```
B>2 REM IBM
3 REM LAGOONI
4 CLS
5 SCREEN 1,0: COLOR 0,0
6 LINE (0,0)-(320, 180), 3, B
7 LINE (0,30)-(320, 30)
8 LINE (0, 100)-320, 100)
9 LINE (0, 60)-(320, 60)
20  REM SCALING FACTORS
21 I = .01
23 T0 = .019
27 C0 = 5
30 P0 = 100
35 D0 = 100
40 Y0 = .5
45 N0 = .2
47 N = .1
50 S0 = 5
52 L = .1
55 NG = 1
60 NR = 1
65 J = 1
66 A = .1
67 M = 10001
68 D = 100
69 C = 2
70 S = 2
100 REM COEFFICIENTS
110 K0 = 45
120 K1 = 90
130 K2 = 2000001
140 K3 = .167
150 K4 = .056
155 K5 = .067
157 K6 = .0167
160 K7 = 10
165 K8 = 1.5
168 K9 = .33
170 L1 = 50
```

Table 5. (continued).

```
175 L2 = 50001
178 L3 = .01
180 L4 = .3
190 L5 = 240
195 L6 = .05
197 L7 = 3
198 L8 = .02
199 L9 = .002
200 REM PLOTTING
230 PSET (T / T0, 180 - P / P0), 1
250 PSET (T / T0 100 - D / D0), 2
285 PSET (T / T0, 30 - Y / Y0), 3
290 PSET (T / T0, 60 - C / C0), 1
300 REM EQUATIONS
301 TD - TD + 1
302 IF TD = 2 THEN TD = 0
305 R1 = J / (1 + K0 * A * N0)
310 R2 = J / (1 + K1 * N)
317 N0 = (NR + NG) / (1 + L1 * A * R1)
320 N = (N0 + L6
320 N = (NO + L6 * C) / (1 + L5 * R2)
325 IF N < .00001 THEN N = .00001
330 P = K2 * R2 * N
340 Y = K9 * S * TD
350 REM NEW VALUES OF STORAGES
352 DD = K2 * N * R2 - K3 * D - K5 * C * D + K4 * M - L8 * D
355 DC = KG * D * C = K7 * C - K8 * C * S + L9 * D
360 DS = L4 * C * S - K9 * S - L7 * S + L * TD
365 DM = L2 * A * N0 * R1 - L3 * M
370 D = D + DD * I
375 C = C + DC * I
377 IF C < .0001 THEN C = 0001
380 S = S + DS * I
390 M = M + DM * I
392 T = T + I
395 REM GO BACK AND REPEAT FOR THE NEXT TIME INTERVAL
400 IF T / T0 < 320 GOTO 200
500 END
```

Figure 6. Diagrams containing those numerical values and mathematical terms for flows used to calibrate each storage (variable) unit of LAGOONII. These are enlargements of sections of the whole ecosystem diagram in Figure 5 and listed in Table 4.

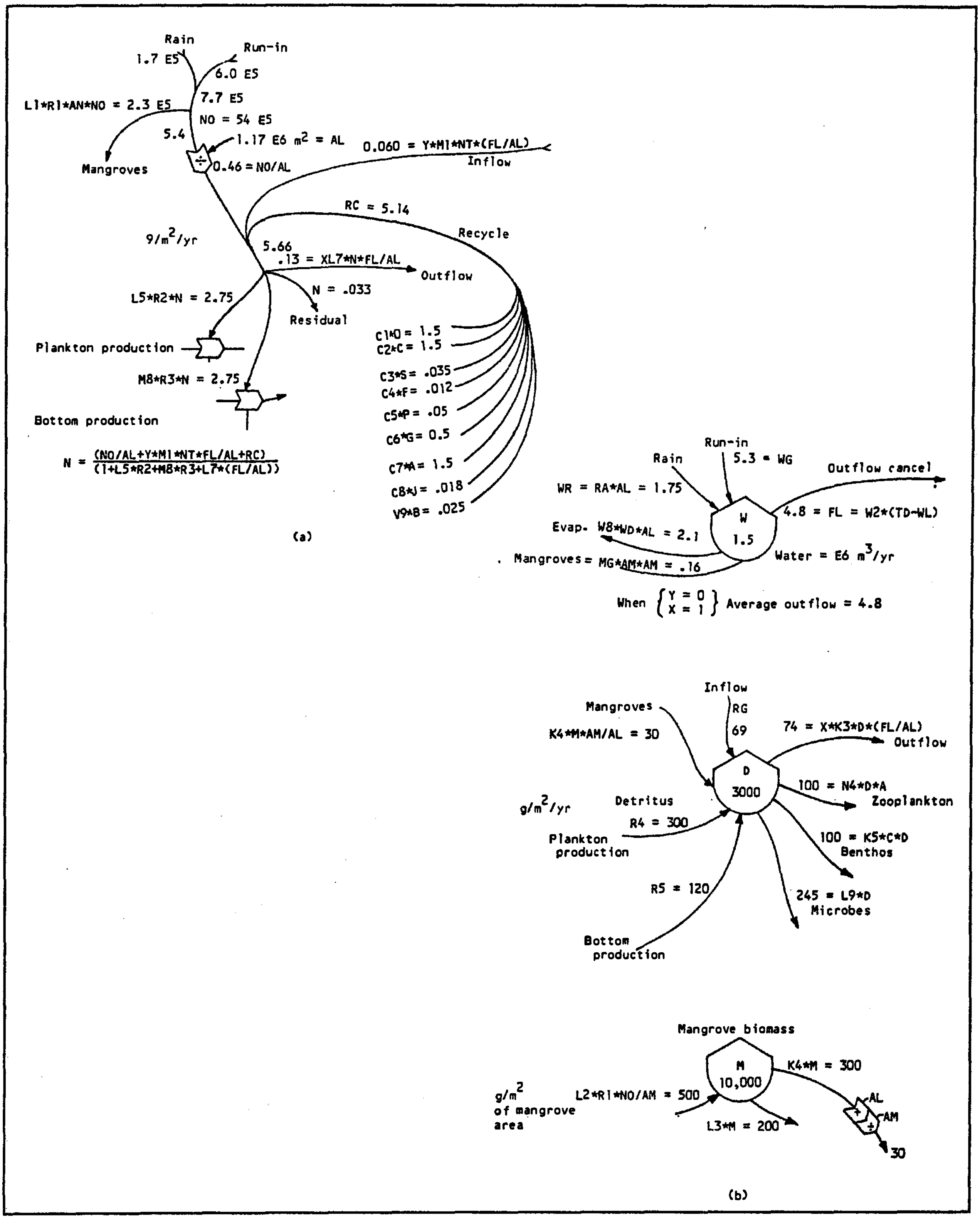


Figure 6. (continued).

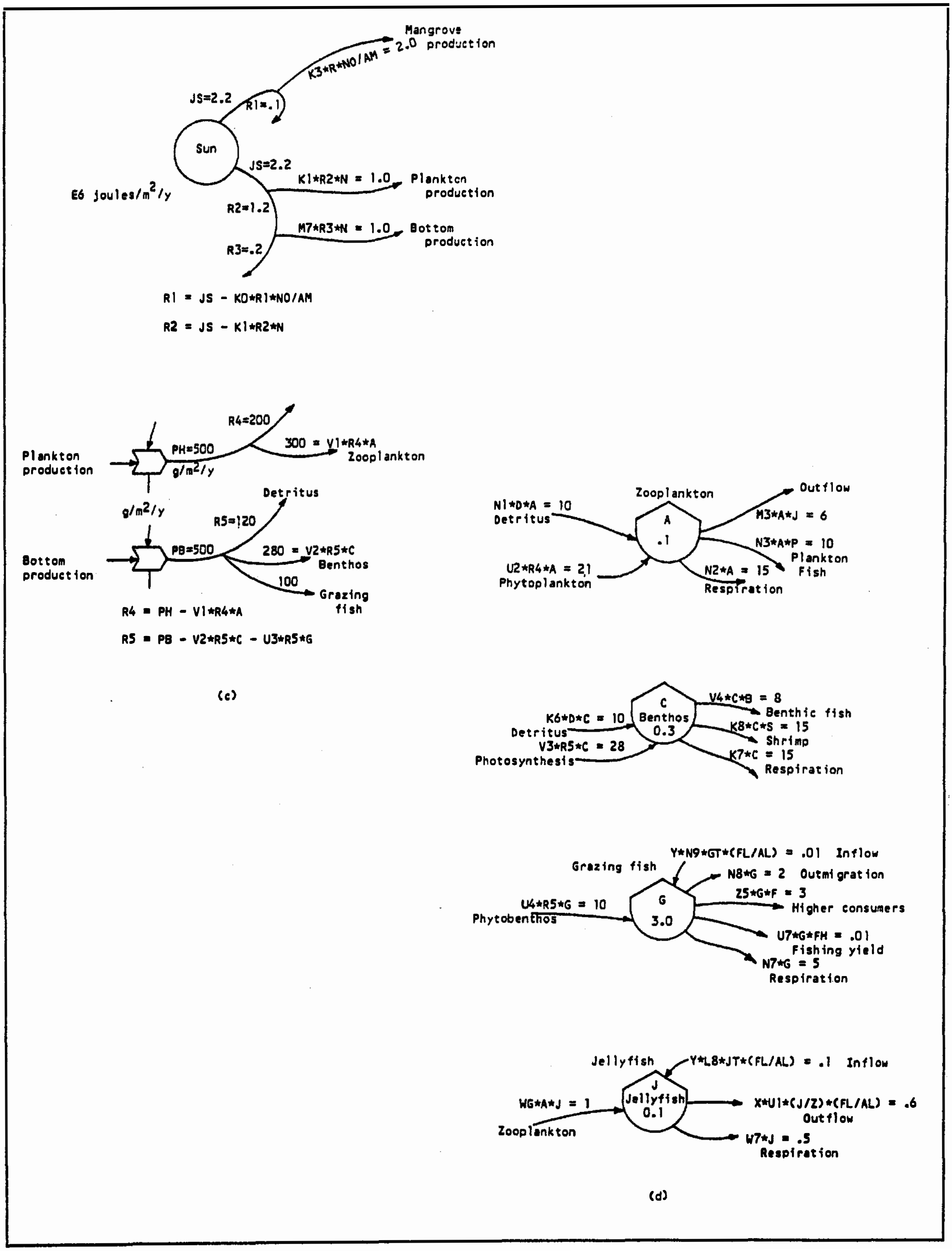
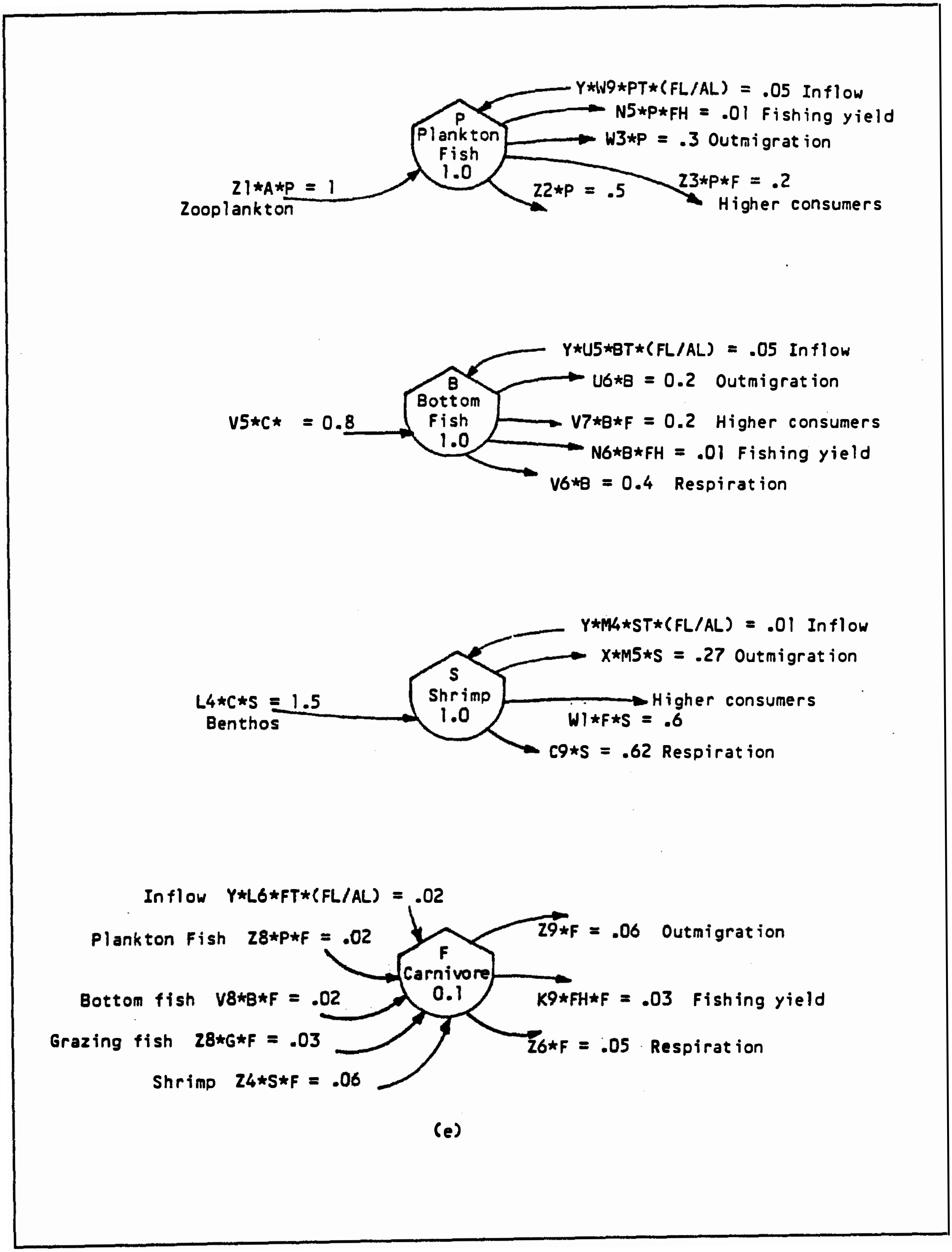


Figure 6. (continued).



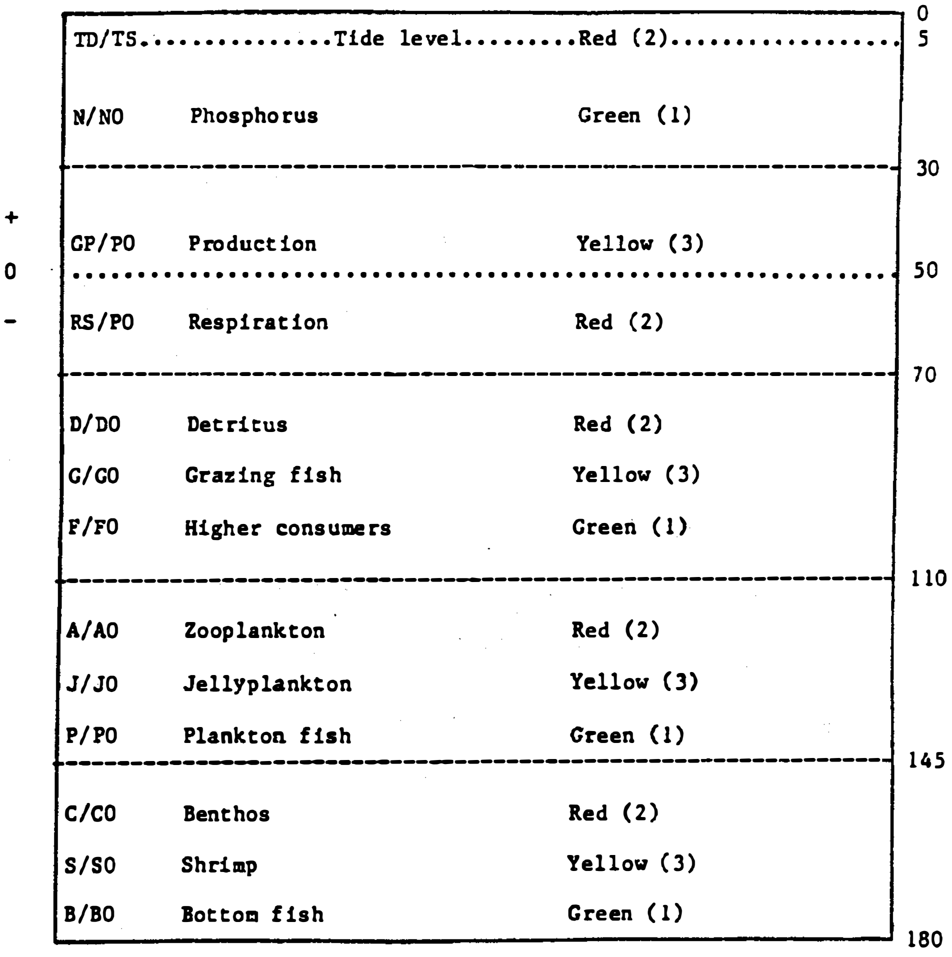
levels. There were few preypredator oscillations under these conditions. Frost nutrients were bound up in the detritus and stocks. Some kind of regulator process resulted.

Simulation with Most Initial States Small, as in Succession

The simulation run in Figure 10 was begun with low values so that the output graph showed growth and successional changes. With low nutrients initially, the pattern was oligotrophic, and more light passed to the deeper benthic plant production. With less detritus initially, a time passed before the oscillations began that were dependent on the benthic food availability. At first, the consumers with fast time constants burst into abundance. The zooplankton, small consumers, and jellyfish soon developed a prey-predator type of oscillation between the smaller prey and the fishes. Grazing fish oscillations were damped by increase in higher consumers. Most variables were near steady state or oscillating about a stable mean after 10 years.

Although the inflow of nutrients was small, nutrients were recycled well, surging when the small consumers developed pulses. But the levels maintained available were low, characteristic of oligotrophic conditions. However, high photosynthetic production was maintained, divided between plank-

Figure 7. Key to the graphs plotted by the model LAGOONII.



				0
	TD/TS	..............Tide level.........	Red (2).................	5
	N/NO	Phosphorus	Green (1)	
				30
+	GP/PO	Production	Yellow (3)	
0				50
-	RS/PO	Respiration	Red (2)	
				70
	D/DO	Detritus	Red (2)	
	G/GO	Grazing fish	Yellow (3)	
	F/FO	Higher consumers	Green (1)	
				110
	A/AO	Zooplankton	Red (2)	
	J/JO	Jellyplankton	Yellow (3)	
	P/PO	Plankton fish	Green (1)	
				145
	C/CO	Benthos	Red (2)	
	S/SO	Shrimp	Yellow (3)	
	B/BO	Bottom fish	Green (1)	
				180

Figure 8. Simulation of conditions near steady state with expanded time scale (one month) showing the tidal output.

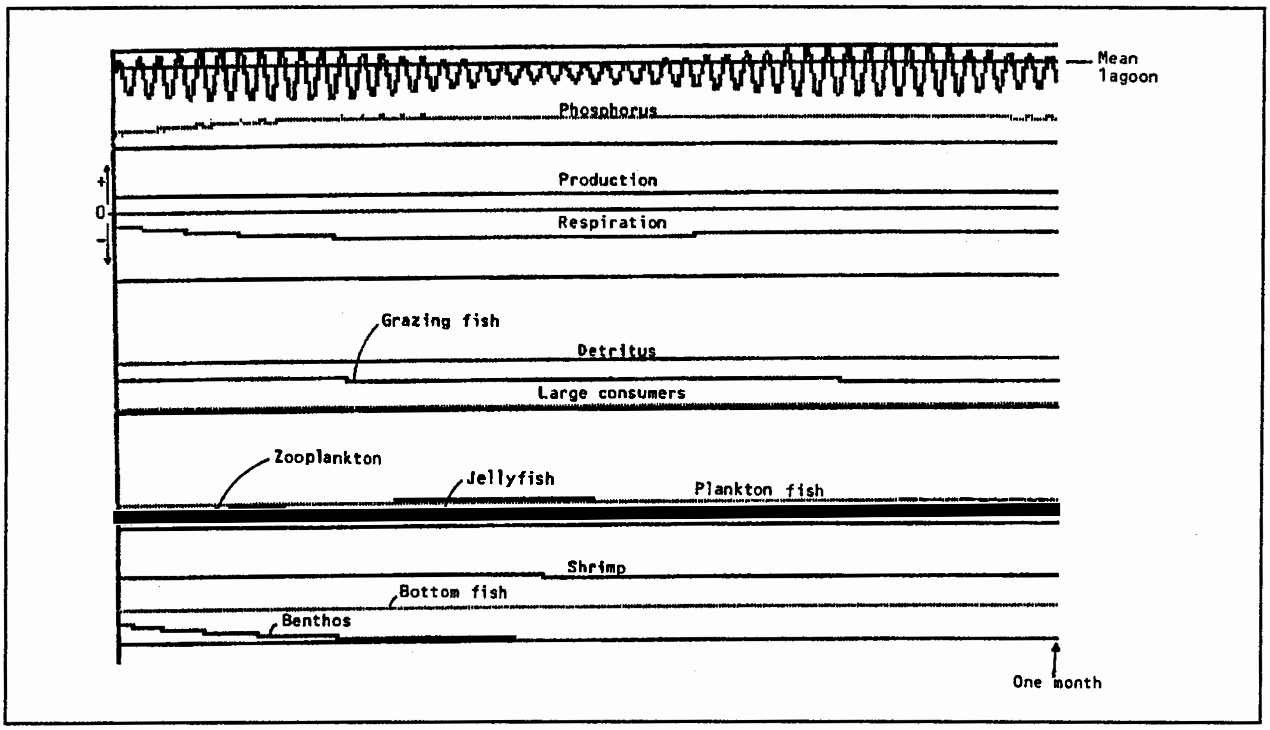


Figure 9. Simulation of conditions near steady state with six year time scale.

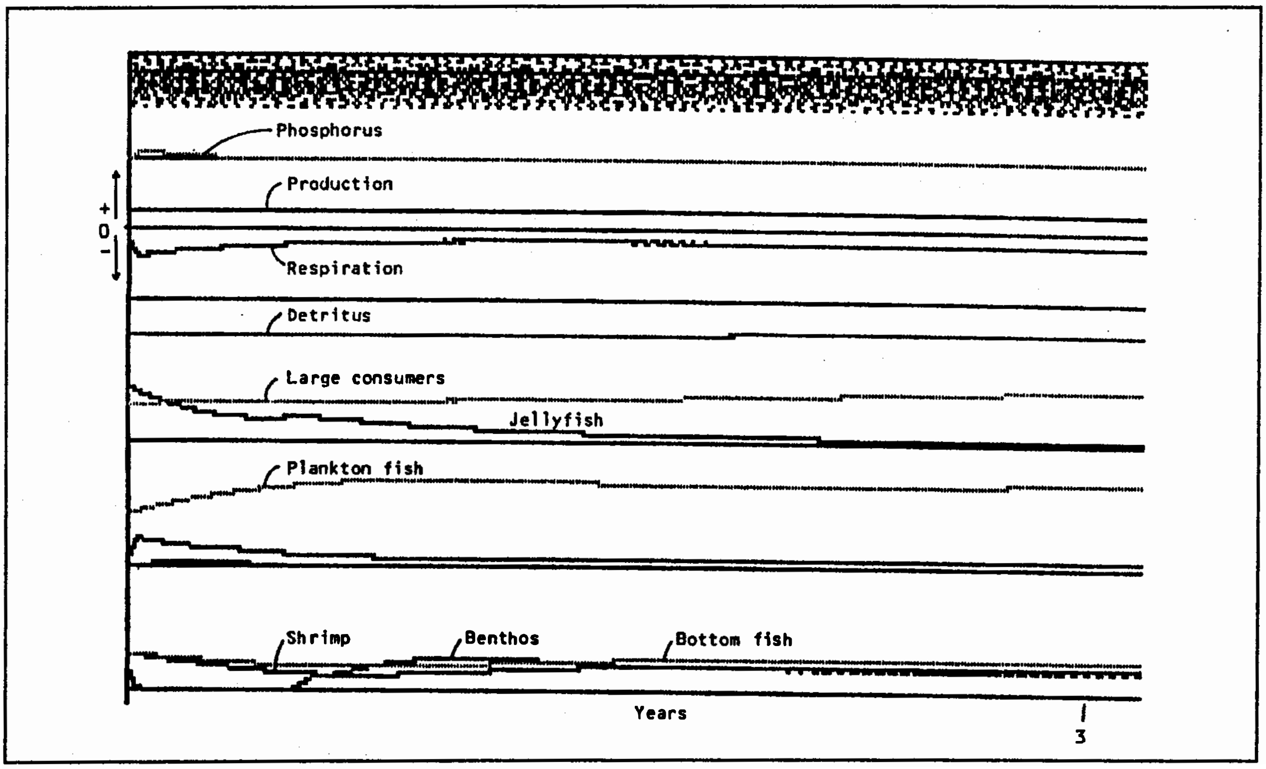
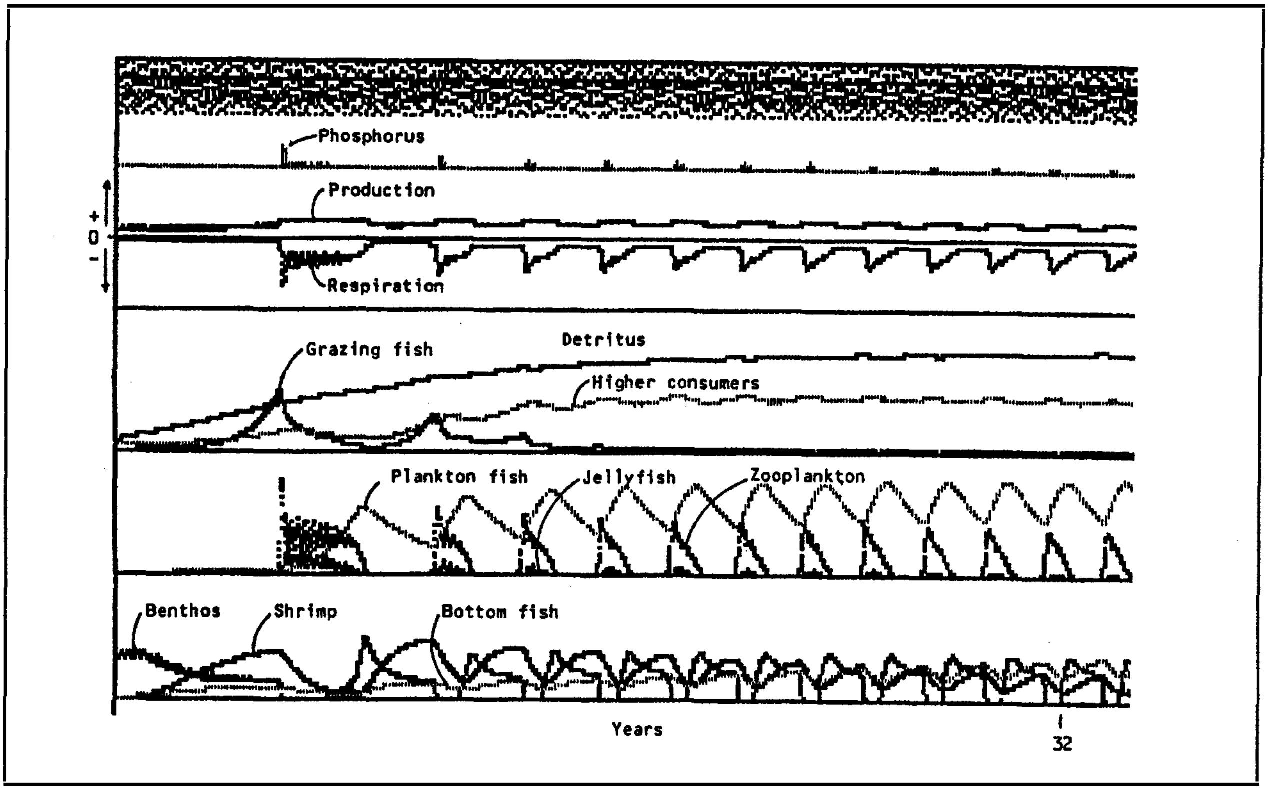


Figure 10. Simulation of succession starting with low levels of detritus, nutrients, and populations.



ton and bottom, with the characteristics of morphometric eutrophy.

Effect of Changed Detritus

The relationship of different initial levels of detritus to population dynamics were tested. Figure 11 is one of these runs with detritus at high levels, 30,000 g/m^2, over 12 years. After a couple of years there was incredible pulsing of benthos, shrimp and benthic fish, and levels of nutrient phosphorus were high and pulsing, as was the respiration. Production was steady, but heavily pelagic. Crazing fish were only present for a short period early on. By half way to two thirds one can see that jellyplankton and zooplankton had been reduced a great deal from early high non-pulsing levels, whereas pelagic fish rose as always. Lastly, a great pulse of higher consumers occurred in the simulation with an exponential decline of detritus.

Simulation of Higher Organic Matter with a Flood

A simulation in Figure 12 increased the detritus inflow from outside as with flood from torrential rains. The simulation was done with the system in near steady state. The sudden increase in organic detritus caused larger and more rapid oscillations Figure 12 which were soon dampened. Field studies in the period following large floods found pulsing populations.

Simulation of Nutrient Eutrophy

When a simulation was run with higher levels of inflow of nutrient phosphorus, Figure 13 resulted. Higher levels of available nutrients were maintained, production exceeded respiration, and detritus accumulated rapidly. With more intense phytoplankton photosynthesis, less light penetration reached the bottom and the benthic growths and oscillations were delayed, and zooplankton plankton fish and their

Figure 11. Simulation of large amounts of initial detritus in the lagoon.

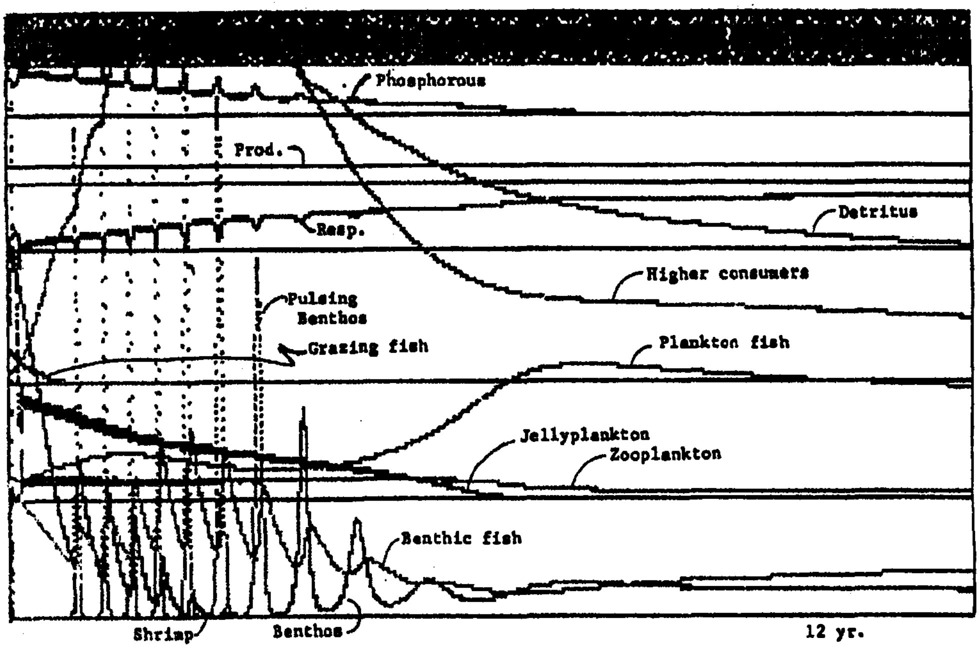
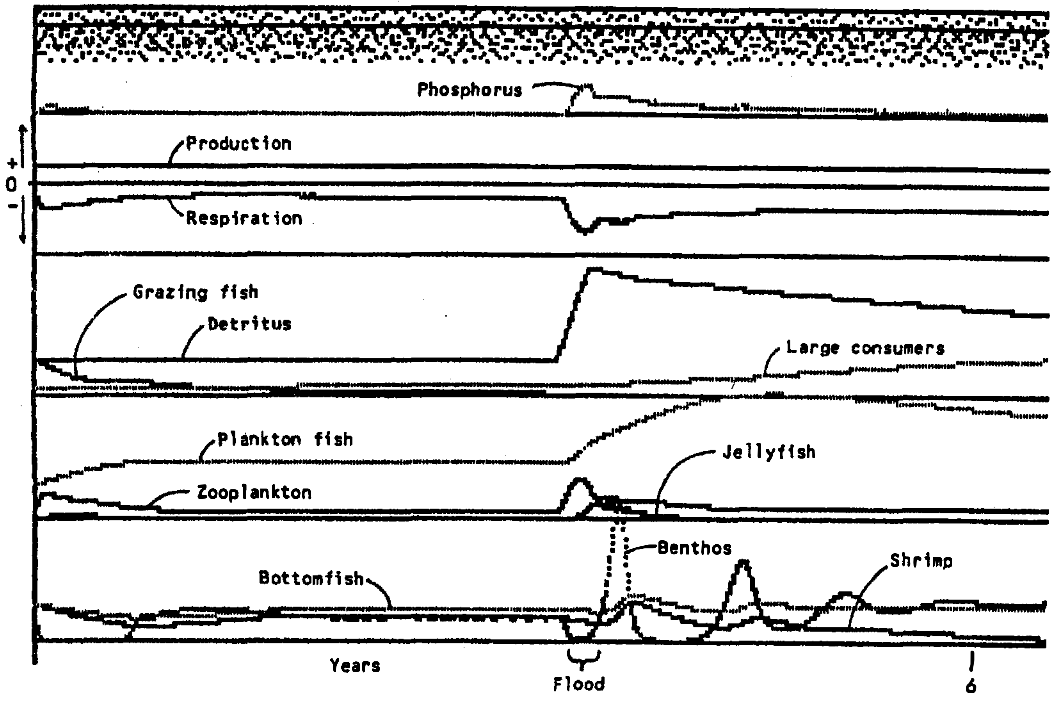


Figure 12. Simulation of a flood that sharply increases organic matter.



consumers predominated. However, when the detritus accumulation reached a higher level, the oscillations of the benthos, shrimp, and bottom fish started.

Fisheries Management

For a look at what might happen if the fishermen were to catch pelagic fish with smaller nets, the large number of anchovies were removed in the middle of a 12 year run, Figure 14, with the inputs at the original level of Figure 9. The rest of the pelagic web, zooplankton and jellyfish, developed higher levels after removal of the pelagic fish. Nutrients were higher, as was respiration, but the benthic food web diminished very little. Detritus was less than before. Higher carnivores began to decrease also, after this time.

Simulation of Heavy Harvesting of All Fish from within the Lagoon

The simulations described above had little fishing of larger species included. When all the fish were suddenly harvested after 3 years (large FH, Figure 15), zooplankton and benthos jumped to higher levels. When this was done in an oscillatory run like Figure 10, many oscillations stopped.

Effect of Changed Food Chain Relationships

In order to re-examine assumptions about flow of primary production and mangrove detritus into pools or direct consumption, coefficients were recalibrated for a much larger proportion of primary benthic production into detritus and from detritus into zooplankton and benthos. Thus, the importance

Figure 13. Simulation of eutrophic conditions with high inflow of inorganic phosphorus.

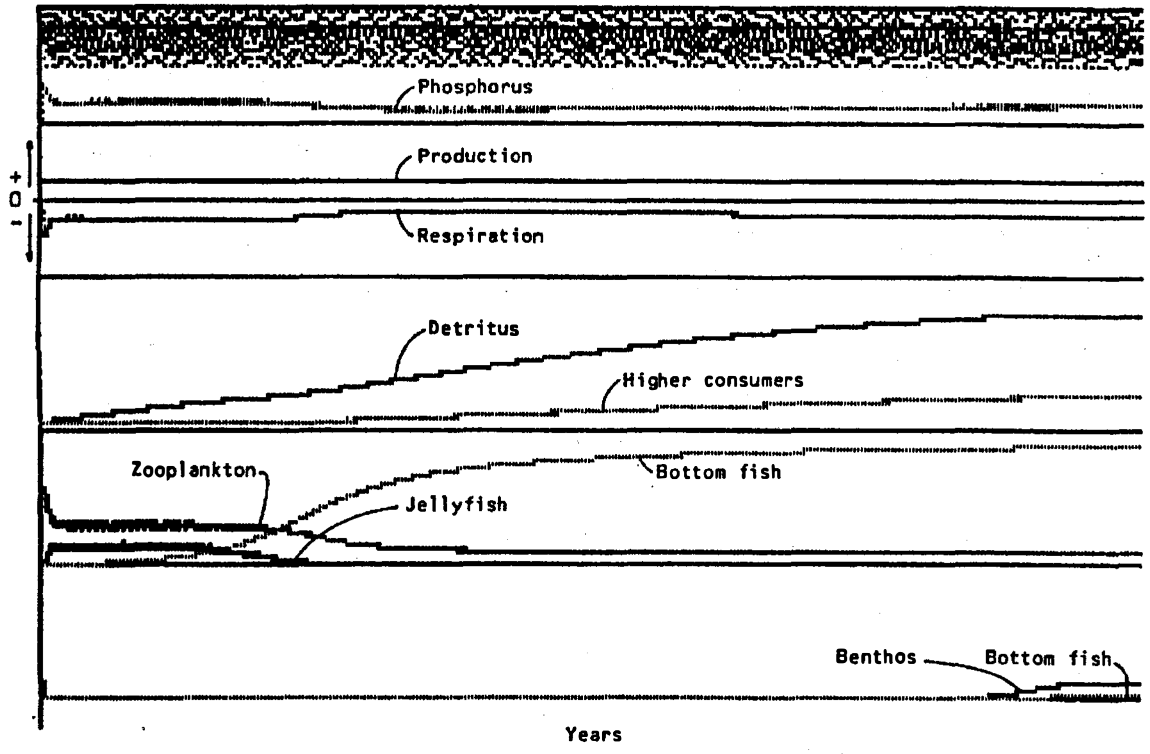
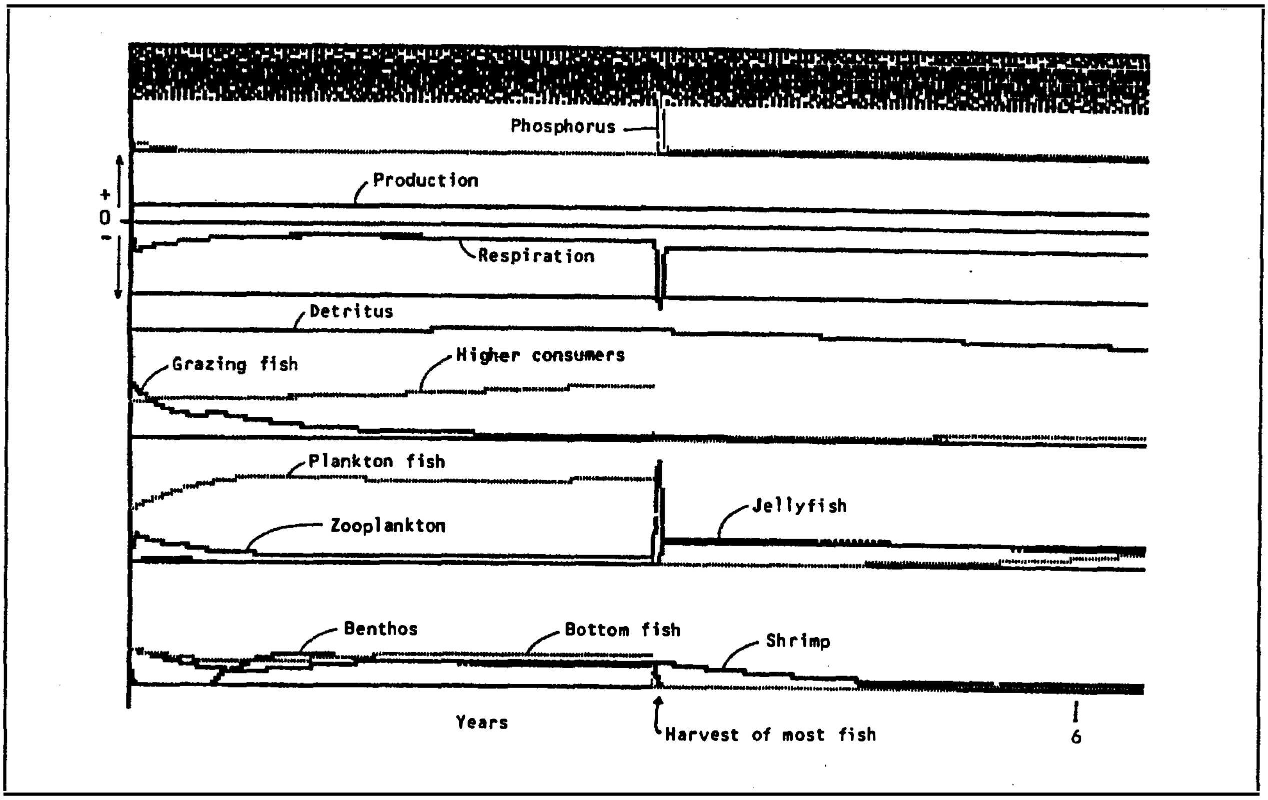


Figure 14. Simulation with removal of small plankton fish from the lagoon after six years.



of a communal detritus pool of primary carbon sources with a faster turnover time is reflected in Figure 16.

The most conspicuous difference between this simulation and Figure 9 is greater frequency and irregularity of pulsing. Respiration fluctuates significantly higher and lower than production. The nutrients again follow respiration but are often lower than previous simulations. The benthic chain shows highly irregular pulses with some smoothing of the cycles of shrimp and benthic fish. The chaotic pulsing is manifest in the zooplankton but the jellyfish populations are still obscured by the pelagic fish dominance of the chain. However, the pelagic fish show an oscillation around their higher level not evident in earlier simulations. The most noticeable difference with respect to previous simulations is the surge of grazing fish without a change in the amount of flow given to them in the calibrations. This probably results from more consistent phytobenthic production (less nutrients in water column = more bottom lighting) and less dependence of benthos on the algae.

Sensitivity to Inputs

The runs reported here were made with constant source inputs, sunlight, water flow, etc., and the output was not sensitive to small changes except where organic storages were around the threshold for the oscillations. No effort has been made to exactly duplicate a time series by introducing observed time series for the external variables. How precise a model of this aggregation can be in generating detailed fluctuations with exact timing remains to be seen.

DISCUSSION

Often models in the literature report only the results, leaving colleagues to wonder over equations and finer choices of the models' construction. Here the equations are available in the pro-

Figure 15. Simulation with extensive harvesting of all fish from the lagoon.

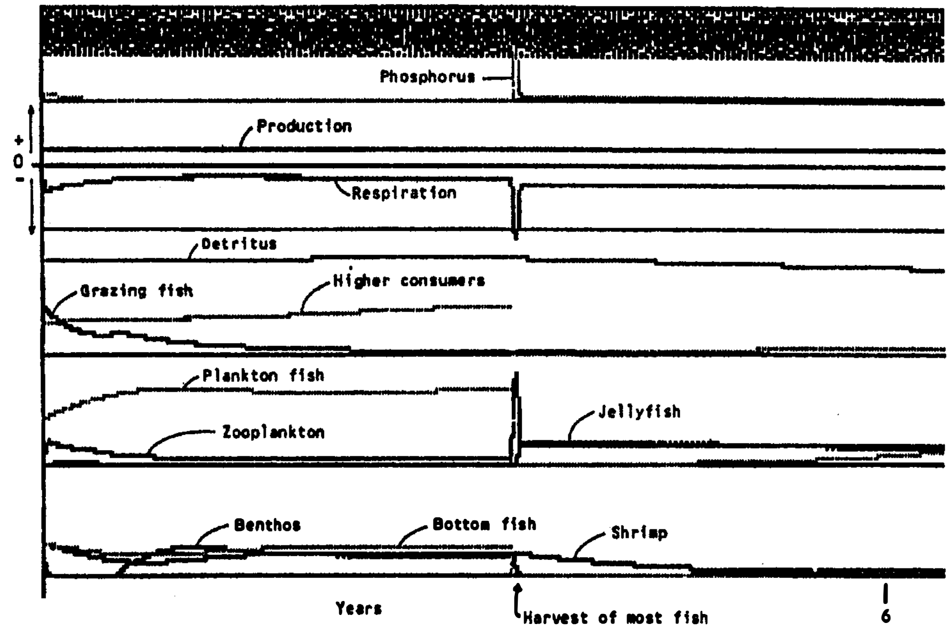


Figure 16. Simulation of recalibrated primary carbon flows so that detritus is primary food source of benthic organisms and zooplankton.

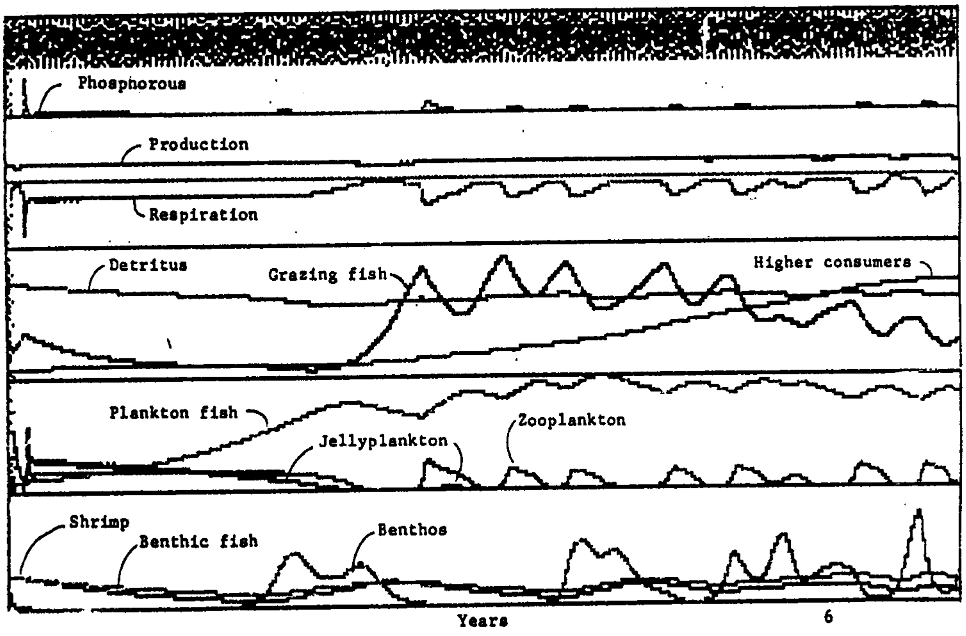


Table 6. BASIC Program LAGOONII for IBM PC Microcomputer.

```
3 REM LAGOON4A on IBM PC
5 CLS
30 REM JOYUDA LAGOON PUERTO RICO, H.T. Odum and Marty Munror, 1988.
40 SCREEH I,0: COLOR 6,1
50 LIHE (0,0)-(320,200),3,B
60 LINE (O,5)-(320,5),2
70 LINE (O 30)-(320,30) 3
80 LINE (0.50)-(320, 50), 2
90 UNE (O,70) (320,70) 3
100 LINE (0110)-(320 liO) 3
110 LIHE (0 115)-(320115) 3
120 LINE (0,100)-(320,180),3
130 REM SCALING FACTORS
140 FO = .01
150 TS = .1
160 NS = 1!
170 DT = .01
180 TO = .1
185 BO = .15
190 CO = .05
200 GO = .15
210 DO = 100
220 YO = .05
230 PO = 200
240 SO = .01
250 AO = .03
260 JO = .04
270 MO = 500
280 MP = 30
290 REM INITIAL STORAGES
300 N = .1
310 NO = 1!
320 AM = 110000!
320 AL = 1170000!
340 M = 10000
350 D = 300
355 B = .01
360 C = .03
370 S = .01
380 J = .01
390 A = .01
400 G = .03
410 P = .02
420 F = .02
430 W = 1500000!
```

Table 6. (continued).

```
440 REM OUTSIDE SOURCES
450 NG = 0
460 NR = .1
470 RG = 69
480 S = 2200000!
490 RA = 1.5
500 WG = 5980000!
510 TD = - .3
520 NT = .016
525 BT =.1
530 GT = .1
540 JT = .1
550 PT = .1
560 FT = .1
570 ST = .1
580 FM = 1500
590 AAM = 110000!
600 AL = 1170000!
610 Z = 1.3
620 V = Z * AL
630 WD = 5
640 FH = 1
650 REM COEFFICIENTS
660 KO - 2!
670 K1 = 25.3
680 K2 = 0126
690 K3 = .00601
700 K4 = 0319
710 K5 = .111
720 K6 = 0111
730 K7 = 50!
740 K8 = 50!
750 K9 = .0002
760 L1 = 1.94E-11
770 L2 = 000509
780 L3 = .02
790 L4 = 5
800 L5 = 0000694
810 L6 = .293
820 L7 = 0!
830 LB = 1.46
840 L9 = .0817
850 M1 = 5.48
860 M2 = .000133
870 M3 = 600!
```

Table 6. (continued).

```
880 M4 = .146
890 M5 = .27
900 M6 = .000145
910 M7 = 156
920 M8 = .0000417
930 M9 = .0758
940 N1 = .0333
950 N2 = 150!960 N3 = 50
970 N4 = .333
1000 N7 = 1.676
1010 N8 = .6666
1020 N9 = 1.46
1030 C1 = .0005
1040 C2 = .667
1050 C3 = .035
1070 C5 = .025
1080 C6 = .167
1090 C7 = 15!
1100 C8 = .18
1110 C9 = .62
1120 W1 = 6
1130 W2 = 1.7E+07
1140 W3 = .15
1150 W4 = .196
1160 W5 = 100!
1170 W6 = 100!
1180 W7 - 5
1190 W8 = 359
1200 W9 = .73
1210 Z1 = 5
1220 Z2 = .25
1230 Z3 = 1
1240 Z4 = .6
1250 Z5 = 10
1260 Z6 = .5
1270 Z7 = .1
1280 Z8 = .1
1290 Z9 = .6
1291 U1 = 6
1292 U2 = .7
1293 U3 = .27
1294 U4 = 0278
1295 U5 = .731
1296 U6 = .2
1297 U7 = .2
```

Table 6. (continued).

```
1298 U1 = 6.67
1299 U2 = 7.77
1300 V3 = .778
1302 V4 = 26.7
1304 V4 = 26.7
1305 V5 = 2.67
1306 V6 = .4
1307 V7 = 2
1308 V8 = .2
1309 V9 = .025
1310 REM PLOTTING
1320 PSET (T/0,50 + RS/PO), 2
1330 PSET (T/TO,50 - GP/PO), 3
1340 PSET (T.TO,5 - TD/TS), 2
1345 PSET (T/TO,30 - N/NS), 1
1350 PSET (T/TO,110 - D/DO0, 2
1360 PSET (T/TO,110 - G/GO), 3
1370 PSET (T/TO,180 - S/SO), 3
1380 PSET (T/TO,180 - C/CO), 2
1390 PSET (T/TO,110 - F/FO), 1
1400 PSET (T/TO, 145 - A/AO), 2
1410 PSET (T/TO, 145 - P/GO), 1
1420 PSET (T/TO, 145 - J/JO), 3
1427 PSET (T/TO, 180 -B/BO), 1
1430 REM EQUATIONS
1500 R1 = JS / (1 + KO*NO/AM)
1510 R2 = JS / (1, + K1*N)
1520 R3 = R2 / (1 + M7*N)
1530 NO = (WR*NR + WG*NG) / (1 + L1*R1*AM)
1540 PH = K2*R2*N
1550 PB = M9*R3*N
1552 R4 = PH/(1 +V1*A)
1555 R5 = PB/(1+V2*C+U3*G)
1560 PM = L2*R1*NO/AM
1570 GP = PH + PB: REM GROSS PRODUCTION IN WATER
1580 RS = 200*RC
1590 TZ = .5 + .25 * SIN (T/.00654)
1600 TD = - .3 + TZ * SIN (T/.000218)
1610 EV = W8*WD*AL
1615 IF TD >WL THEN Y = 1: X=0
1616 IF TD <WL THEN Y = : X=1
1620 MC = L9*D
1630 WR = RA*AL
1640 REM WATER LEVEL MEASURED FROM AVERAGE LEVEL OF JOYUDA LAGOON
1650 WL = (W/AL) - 1.3
```

Table 6. (continued).

```
1660 FL = W2*(TD - WL)
1670 RC = C1*D + C2*C + C3*S + C4*F + CS*P + C6*G + C7*A + C8*J+V9*B
1680 N = (NO/AL) + RC + X*L7*(N/Z)*(FL/AL) - Y*M1*NT*FL/AL)/(1, + L5*R2 + M8*R3
+L7*FL/AL)
1690 IF N <.00001 THEN N = .00001
1700 REM CHARGES IN STORAGES
1710 DD = R4 + R5 + X*K3*(D/Z)*FL/AL - K5*C*D + K4*M*AM/AAL - N4*D*A - L9*D +
W4*WG*RG/AL
1720 DC = K6*D*C - K7*C - K8*C*S +V3*R5*C -V4*C*B
1730 DS = L4*C*S - X*M5*S - C9*S - W1*F*S + Y*M4*ST*FL/AL
1740 DM = L2*R1*NO/AM - L3*M - K4*M
1750 DA = N1*D*A - N2*A - N3*A*P - M3*A*J +U2*R4*A
1760 IF A < .00001 THEN A - .00001
1770 DG =U4*R5*G - N7*G - N8*G - Z5*G*F + Y*N9*GT*FL/AL
1780 DG = Z1*A*P - Z2*P - W3*P - Z3*P*F + Y*W9*PT*FL/AL
1985 DB = V5*C*B -V7*B*F -U6*B + Y*U5*BT*FL/AL
1790 DF = Z4*S*F + Z7*P*F + Z8*G*F - Z6*F - Z9*F + Y*LG*FT*FL/AL -K9*FH*F
+V8*B*F
1800 DJ = W6*A*J - W7*J + Y*L8JT*FL/AL + XU1*(J/Z)*(FL/AL)
1810 DW = WR + WG + FL - W8*WD*AL - M6*M*AM
1820 REM NEW VALUES OF STORAGES
1830 A = A + DA*DT
1840 IF A <.0001 THEN A = .0001
1845 B = B + DB*DT
1850 G = + DG*DT
1860 IF G < .001 THEN G = .001
1870 D = D + DD*DT
1880 IF D < .1 THEN D = .1
1890 P = P + DP*DT
1900 IF P < .001 THEN P = .001
1910 C = C + DC*DT
1920 IF C < .0001 THEN C = .0001
1930 F = F + DF*DT
1940 IF F <.001 THEN F = .001
1950 S = S + DS*DT
1960 IF S < .001 THEN S = .001
1970 YS = X*M2*S*FM
1980 J = J + DJ*DT
1990 IF J < .0001 THEN J = .0001
2000 M = M + DM*DT
2010 IF M < 1 THEN M = 1
2020 W = W + DW*DT
2030 IF W < 1 THEN W = 1
2040 WL = (W/AL) - 1.3
2050 T = T + DT
```

Table 6. (continued).

```
2060 IF T/TO <320 THEN GOTO 1310
2080 END
2100 PRINT “Rl = “Rl
2110 PRINT “R2 = “R2
2120 PRINT “R3 = “R3
2140 PRINT “M = “M
2150 PRINT “D = “D
2160 PRINT *W = *W* : WL = *WL* X = *X
2170 PRINT “A = “A
2180 PRINT “C = “C
2190 PRINT “J = “J
2200 PRINT “G = “G
2205 PRINT “B = “B
2210 PRINT “P = “P
2220 PRINT “F = “F
2230 PRINT “S = “S
2240 PRINT “YS = “YS
2260 PRINT “N = “N
2270 PRINT “GP = “GP” : RS = “Rs
2280 PRINT “PH = “PH
2290 PRINT “PB = “PB
2300 PRINT “PM = “PM
2310 PRINT “RC = “RC
2320 PRINT “T = “T
```

gram in Table 6. Or with a copy of the Systems Ecology text (Odum 1983) one can use the methods for deriving the equations directly from the diagram in Figure 3 and use the numerical values of flows and storages in Figure 4 to reconstruct the model and coefficients completely.

Still, a large grey area remains regarding the framework of the model and its relation to the real world ecosystem it is supposed to represent. Especially important is the thinking that went into choices of aggregation when moving from perceptions of the real world to the model system. Although a detailed presentation of the evolutionary development of discussion and thought that went into the present model would be too lengthy, enough written explanation of the model is given so that readers can appreciate the appropriateness of the limited complexity of the model.

Plankton Web

The pelagic food web was considered to be relatively simple in the early trophic levels. Pesante's (1978) one year study of zooplankton, suggests that the domination of the macrozooplankton by the calanoid copepod *Acartia tonsa* and its drastic fluctuations is likely due to the pulsing ctenophore *Mnemiopsis gardeni*. In a later study a large pulse by the styphozoan *Phyllorhiza punctata*, the other dominant jellyplankter in the lagoon, was concurrent with a rapid decline in the numbers and biomass of zooplankton (García 1993, García and López 1987). García (1993) also observed a complete dominance by *A. tonsa* of the non-gelatinous zooplankton. Both authors reported abundant decapod larvae but they are not so different trophically to be grouped separately from the main zooplankter variable, A, with *A. tonsa*.

Also highly abundant in the pelagic waters are the anchovies (Engraulidae), *Anchoa hepsetus, Centengraulis edentulus,* and others. These are also zooplankton predators. Unlike the jellyplankton these are a link between zooplankton biomass and higher trophic levels as prey to piscivorous fishes (García 1984, 1993).

The pelagic piscivorous fishes in the higher trophic level include many species especially *Sphyraena barracuda, Bairdiella ronchus,* and Centropomidae (snook) and Elopidae (ladyfish and tarpon) (García 1993).

At the base of the pelagic food web, one encounters dispute over the ability of zooplankton to use vascular plant detritus as carbon source. In the model (Figure 5) production by phytoplankton is routed as a direct source to zooplankton, but can also be an indirect detritus source along with mangrove carbon. Thus the question is left somewhat open. Stable isotope ratios from Pesante (1978) suggest up to 50t of *A. tonsa's* carbon requirements are being met by mangrove carbon. Lugo and Musa (1993) estimate inputs from 10 to 51% of lagoon net primary productivity coming from the surrounding fringe and basin mangroves. Basin mangrove detrital inputs were highly decomposed, whereas those from fringe mangroves were little-decomposed dead leaves. *A. tonsa,* however, can ingest detritus directly or through the bacteria ciliate link because of its feeding habits (Román 1977, Heinle *et al.* 1977).

Benthic Web

The benthic web consists of both invertebrates and vertebrates. The primary consumer invertebrates are the most aggregated group of the model (variable C). Mullet (*Mugil curema*) was the sole species in group G because they were thought to require a higher quality fuel, such as filamentous algae, than is provided by detritus in order to maintain high levels of activity (Stoner, *personal communication*) in contrast with reports in the literature (Odum and Heald 1972). In the model it was more interesting to separate this group of "grazing fish" from the numerous invertebrate amphipods and isopods dwelling in the sediments differing most importantly in their longer turnover time. The food web within in the sediments was very complex including multiple carbon pathways from detritus and algae through associated bacteria and protozoans, that eventually reached capitellids and oligochaetes, and nereids - the most numerous macrobenthos (Stoner 1984). For simplification purposes the model sidesteps the multiple flow possibilities by growing a combined macroinfauna variable, C, directly cn detritus levels, while keeping the microorganismal consumption of detritus for mass balance and nutrient remineralization purposes. The importance of bacteria and other microorganisms for food quality of the macrobenthic organisms was recognized by the model even though not diagrammed directly.

The highest invertebrate predators in the lagoon were the paneid shrimp (*Peneus* spp.) and the swimming crabs (*Callinectes* spp.). The three species of shrimp were grouped as variable S because of similar life history and because they derived primary sustenance from the capitellids and oligochaetes of the benthos (Stoner 1984, Stoner *et al.* 1993). The crabs were grouped with the higher carnivores because they consumed the shrimp which elevated them one trophic level despite being non-selective deposit feeders. Thus the model forced convergence of the lagoon food web into one category of higher carnivores to focus on the behavior of like trophic groups with similar time constants.

For the many bony fishes that have a primarily dermersal feeding habit of consuming benthic infauna, mojarras (*Gerres cinereus and Eucinostomus gula*) and lined sole (*A. lineatus*) have been observed in abundance (García 1984, 1993; Stoner 1986; Stoner *et al.* 1993). *Diapterus plumieri* and *D. rhombeus* also occur as demersal fish in this category. These are diagrammed separately from shrimp, as B. but with the same trophic position (source: benthos and predators: large carnivores) even though it is pelagic larger fish that consume them and not crabs as with the shrimp. The reason for this artificial trophic division was an earlier interest in shrimp yields only.

Benthic Pelagic Metabolism and Nutrient Recycle

The interaction between benthic and pelagic webs revolved around nutrients available for planktonic photosynthesis by algae and the common use of detritus. When nutrients were at low levels, planktonic photosynthesis absorbed most of the light. The less phytobenthic production caused benthos to diminish rapidly. Later lower nutrients allowed more light to reach the bottom, resulting in pulses in the web of benthos, shrimp and benthic fish (Fig. 9). Pelagic fish, anchovies, often very abundant in the lagoon, dominated the pelagic web in the model despite increasing levels of detritus and higher consumers. Thus, a predator prey equilibrium was only evident between zooplankton and jellyplankton when zooplanktivorous bony fish were absent.

Human Effects on Lagoon Populations

Although the lagoon is a natural shrimp pond supplying local fishermen with substantial catch, shrimp harvest had little effect on the lagoon populations of juvenile shrimp because they were seined passively as they migrated out through the channel. Effect of depletion of offshore adult spawning population on larval reseeding of the lagoon was not tested by the model. Local fishermen removed large amounts of the higher consumer category (García 1987), but many other groups of the nekton were removed as well, except the mullet. The simulation in Figure 14 explored possible impacts of removing only the abundant smaller pelagic fish. The immediate release and higher levels of nutrients were due to zooplankton blooming, which in turn favored the phytoplankton and pelagic web over the benthic organisms. Under these conditions the blooming of the jellyplankton kept the zooplankton at a low level.

This graph also shows the condition of fewer when higher carnivores. Their decline was precipitated by the loss of light to the benthic chain and the loss of the smaller pelagic fish as a food source. The consequent increase in the other plankton groups, zooplankton and jellyfish, due to lowered competition from pelagic fish, caused nutrient regeneration by respiring zooplankton suppressing the benthic web.

Cascading Influence of Detritus Subsidy

The wild pulsing of benthos, shrimp, and benthic fish in Figure 11 suggests that the oscillating behavior observed in the benthic web may not be restricted to high phytobenthic primary production, but can be induced by substantial detrital loading even though the pathway in this model favors the phytobenthos as the primary food items for macrobenthic infauna (Fig. 5). Low phytobenthic production resulted from high nutrient levels because high nutrient levels caused the phytoplankton to use most of the incoming light and available phosphorous. With less bottom algae, grazing fish (mullet) quickly became less. Perhaps the ephemeral occurrence of demersal herbivorous fishes may be due to the lack of consistent bottom primary production when nutrients from land or organic matter from the mangrove wetlands flood the lagoon during times of high rainfall. In Figure 11 a large amount of detritus was associated with one large pulse of the higher consumers. This simulation demonstrated filtering of the smaller scale's pulses by the organisms with larger time constants. It also demonstrated dramatically how secondary production of resources valuable to man such as the blue crabs and large fish are influenced by the metabolic gifts from the surrounding low-respiring mangroves.

What may be surprising is the small effect of high levels of detritus on shrimp. In this model intermediate levels of detritus and removal of higher predators were necessary to maintain a shrimp output from the lagoon. With the distribution of flows assumed in this model, the pathways supporting higher carnivores passing around the shrimp can lead to levels of predators high enough to reduce the shrimp. Perhaps there is a general principle regarding intermediate units of webs that first diverge and then converge again.

Mangrove Detrital Subsidy of Secondary Productivity

An important question to the Joyuda project team concerned the nature of the mangrove dead leaf material as an energy subsidy to the lagoon proper, sustaining high levels of secondary production. Insofar as the model is a representation, in sum, of the processes believed to be operating, the model behavior may help resolve the issue of the dynamics of secondary production as being influenced by detrital energy flows. In anticipation of the issue, the model was configured to distinguish growth of both zooplankton (*Acartia* mostly) and benthos (mostly capitellids) primarily. These consumers differ regarding consumption of live production, phytoplankton or phytobenthos, respectively, and that of detrital pools including mangrove detritus, the food value of which was affected by microbial action over time and therefore expected to be different.

Looking at Figure 5, one can imagine increased secondary production along either chain, benthic or pelagic, from the mangrove leaf-rain reaching the upper sediments either as a direct food source or as a nutrient supply, looping through microbial remineralization to support high primary productivity in situ. The meanings of symbols and flow lines convey this as well as do the calibration of flow values. The lack of a microbe arrow to primary consumer groups does not mean they do not supply nutritional value to them, only that it is taken into account in the pathway of detrital flow to the primary consumers and their growth on it.

Without inferring the magnitude of secondary production, the simulations indicate the observed predator-prey oscillations in the benthic food chain are dependent on the detrital subsidy because of the necessary higher levels of detrital storage needed to induce the oscillations in Figures 8, 9, 10, 12, and 13. The pelagic chain appears less influenced by nutrient level, which may be more consistent with C14 data and gut analysis indicating its independence.

Jellyfish as Quick Carnivore

In the absence of competing plankton-eating fish, jellyfish developed rapidly but were displaced by slower-growing fishes later. Displacement of jellyfish by plankton fish may be an example of the longer time constant components prevailing in succession. The model gives insights on jellyfish blooms. Perhaps they occur whenever something removes plankton fishes such as fishing, migration, ontogenic changes in consumer food uses, pollution, etc.

Summarizing Remarks

Many of the patterns observed in the Laguna Joyuda seem to be occurring in the simulation model due to the interplay of recycle and prey-predator oscillations. General levels of production, respiration, and population categories were maintained. To the extent that there are general patterns of similarity, the model helps justify existing hypotheses about how the system is working.

Many rates and variable time series that were not directly measured but that are part of the model may now be inferred by graphing of printing from the model during simulation. In this way new hypotheses are given quantitative expression. The model may have some predictive uses for determining what types of responses are to be expected for large changes in initial conditions, forcing functions, or coefficients. Thus, the model is possibly state-of-the art, useful for its primary purpose, helping to make hypotheses quantitative enough for testing and developing principles.

The chaotic behavior of system variables in the simulations and the higher frequency of oscillations over the six year time period were reminiscent of observations of populations in the lagoon. In the simulation, Figure 16, more variables were maintained at levels observed in the lagoon. The grazing fish and the entire benthic chain were at higher levels and oscillating. This suggests the real system may be heavily influenced by detritus; or, conversely, the populations that maintain themselves are the ones that can take advantage of the detrital subsidy directly, or indirectly through predation on those that do.

ACKNOWLEDGEMENTS

This paper is one of a series on the Laguna Joyuda Ecosystem, the results of a project of the Center for Energy and Environment of the University of Puerto Rico from 1980 to 1990. The program began with Dr. L.J. Tilly and was completed under coordination of Dr. José López, Department of Marine Sciences, UPR, Mayagüez. Among the purposes of the project was understanding the basic processes of tropical lagoons, evaluating potentials

of estuarine lagoons for fisheries, capacities of lagoons for absorbing runoff substances, estuarine processing of serpentine chemical contributions, developing models to help relate the knowledge about species and metabolism, and training tropical marine scientists in systems ecology. It may be appropriate to start the series with simulation models that raise questions and hypotheses about how the ecosystem may work. Financial support for this project was provided by the Marine Ecology Program, Center for Energy and Environment Research, University of Puerto Rico, Mayagüez, Puerto Rico; the US Department of Energy; EPSCOR program of the National Science Foundation; and the University of Puerto Rico. Javier Colley, José López, and Allen Stoner helped with the construction and understanding of the model system by providing relevant data, experiences in and discussion of the lagoon system. José Figueroa assisted field investigations with an early reconnaissance of the lagoon, providing insights into lagoon metabolism. Simulation work was aided by Mark Brown and April Lander.

LITERATURE CITED

Caperon, J. 1975. A trophic level ecosystem model analysis of the plankton community in a shallow-water subtropical estuarine embayment. *In* L.E. Cronin, editor. Estuarine Research, I. Academic Press, New York. 738 p.

Carvajal, J.R., M.A. Pérez, and G. Cintrón. 1980. Estudio de la Laguna Joyuda: un ecosistema marino. Departamento de Recursos Naturales, Programa de Zona Costanera de Puerto Rico. Sección 306. 94 p.

García, J.R. 1984. Some ecological aspects of the community of fishes in Joyuda Lagoon. A.W. Stoner and J.M. López, editors. Pages 46-54 *in* Cycling and transport processes in a tropical estuarine lagoon. Center for Energy and Environment Research publication. Mayagüez, P.R.

García, J.R. 1993. Zooplankton and pelagic fish communities of Laguna Joyuda. Acta Científica 7(1-3):105-136.

García, J.R. and J.M. López. 1987. Influence of zooplankton abundance on the phytoplankton productivity of Laguna Joyuda. Proceedings 22th European Marine Biology Symposium, Barcelona, Spain.

Heinle, D.R., R.P. Harris, J.F. Utack, and D.A. Flemer. 1977. Detritus as food for estuarine copepods. Marine Biology 40:341-353.

Holdridge, L.R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Kjerfve, B. 1984. Hydrodynamic Considerations in the study of a tropical lagoon. Pages 10-14 *in* A.W. Stoner and J.M. López, editors. Cycling and transport processes in a tropical estuarine lagoon. Center For Energy and Environment Research Publication, Mayagüez, P.R.

Kremer, J.N. and S.W. Nixon. 1978. A coastal marine ecosystem: simulation and analysis. Ecological Studies 24. Springer-Verlag, New York. 218 p.

López, J.M., C. Goenaga, I. García, and R. Almodóvar. 1993. Introduction to Laguna Joyuda ecosystems studies. Manuscripts available from CEER, Mayagüez.

Lugo, A.E., S. Brown, and M.M. Brinson. 1988. Forested wetlands in freshwater and saltwater environments. Limnology Oceanography 33:894-909.

Lugo, A.E. and J.C. Musa. 1993. The mangroves of Laguna Joyuda. Acta Científica 7(1-3):67-90.

Odum, E.P. 1963. Primary and secondary energy flow in relation to ecosystem structure. Proceedings 16th International Congress Zoology 4:336-338.

Odum, E.P. and A.A. de la Cruz. 1963. Detritus as a major component of ecosystems. AIBS Bulletin (now BioScience) 13:39-40.

Odum, H.T. 1983. Systems Ecology. Wiley and Sons environmental series. New York, N.Y.

Odum, H.T., J.M. López, and E.C. Odum. 1993. Simulation of diurnal variation in Laguna Joyuda, Puerto Rico. Acta Científica 7(1-3):91-103.

Odum, W.E. and E.J. Heald. 1972. Trophic analyses of an estuarine mangrove community. Bulletin Marine Science 22:671-738.

Odum, W.E. and E.J. Heald. 1975. The detritus based food web of an estuarine mangrove community. *In* L.E. Cronin, editor. Estuarine research, I. Academic Press, New York. 738 p.

Pesante, D. 1978. A study of the plankton in Laguna Joyuda, a tropical lagoon on the west coast of Puerto Rico. Thesis, University of Puerto Rico, Mayagüez. 106 p.

Román, M.R. 1977. Feeding of the copepod *Azartia tonsa* on the diatoms *Nitzchia closteria* and brown algae (*Fucus vesiculosus*) detritus. Marine Biology 42:69-84.

Stoner, A.W. 1986. Community structure of the demersal fish species of Laguna Joyuda. Estuaries 9(2):142-151.

Stoner, A.W. 1984. Macrobenthic consumers in Joyuda Lagoon: residents and transients. Pages 34-45 *in* A.W. Stoner and J.M. López, editors. Cycling transport processes in a tropical estuarine lagoon. Center for Energy and Environment Research publication. Mayagüez, P.R.

Stoner, A.W., B.A. Buchanan, and C. Acevedo. 1993. Ecology of the demersal communities in Laguna Joyuda. Acta Científica 7(1-3):145-188.

Twilley, R.R., A.F. Lugo, and C. Patterson-Zucca. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. Ecology 67:670-683.

Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285-298.

Yañez-Arancibia, A., F. Amezcua-Linares, and J.W. Day, Jr. 1980. Fish community structure and function in Terminos Lagoon, a tropical estuary in the southern Gulf of Mexico, Pages 465-482 *in* U.S. Kennedy, editor. Estuarine perspectives. Academic Press, N.Y.