NITROGEN-CYCLE DYNAMICS
OF
A WASTE RECYCLING OYSTER CULTURE SYSTEM

by

DIANE HOLBERT RIKER

Submitted in Partial Fulfillment
of the Requirements for the
Degree of Bachelor of Science
at the
MASSACHUSETTS INSTITUTE OF TECHNOLOGY
JANUARY, 1978

Signature redacted
Signature of Author..
Department of Mechanical Engineering, January 19, 1978

Certified by... Signature redacted ....
Thesis Supervisor

Accepted by.. Signature redacted ....
Chairman, Departmental Committee on Theses

NITROGEN-CYCLE DYNAMICS
OF
A WASTE RECYCLING OYSTER CULTURE SYSTEM

by

DIANE HOLBERT RIKER

Submitted to the Department of Mechanical Engineering on January 19, 1978 in partial fulfillment of the requirements for the Degree of Bachelor of Science.

ABSTRACT

A nitrogen-cycle model of a waste recycling oyster culture system was developed, simplified, and simulated to examine the influence of various parameters on maximization of oyster-protein yield in comparison to a pilot plant constructed at the Environmental Systems Laboratory at Woods Hole Oceanographic Institution. Simulation results indicate increases in oyster-protein with increases in algae ingestion rate, fluid flow rate, and initial algae content in the inflow water. Decreases in oyster nitrogen content coincide with increases in ammonia excretion rate and ingestion half-saturation coefficient. These results are consistent with the values reported by ESL. Further work on this model should include light intensity analysis and study of an appropriate set of consistent units easily measured by both biological and engineering teams.

Thesis Supervisor: Alician V. Quinlan
Title: Assistant Professor of Mechanical Engineering

ACKNOWLEDGMENTS

Roger Mann and John Ryther of ESL	-the original idea and supportive documentation
Rosalie Bright	-the solution to the respiration problem
Douglas White, Astrid Howard, and Anna Piccolo	-suggestions and inspiration
H.M. Paynter	-humor and DYSYS instruction
James Hutchison	-typing, editing and dinner
A.V. Quinlan	-solution to biological and psychological dilemmas and paper shortage

CONTENTS

FIGURES

INTRODUCTION

The Environmental Systems Laboratory (ESL) at Woods Hole Oceanographic Institution is devising a method for converting secondary sewage to high-quality protein. The proposed system saves treatment costs by use of a biological, rather than physical or chemical, sewage purification method which produces a marketable, nutritional protein foodstuff. As such the proposed method is economically attractive: a standard system would pay for a town's secondary plant operation and earn approximately $10,000 profit per year (Hugenin and Smith, 1975).

To test the feasibility of the proposed method, Roger Mann of ESL has created a pilot plant operation. Secondary effluent is fed to a culture of algae. The algae strip excess nutrient nitrogen from the effluent, and then are pumped into tanks of oyster beds where the oysters feed on the nitrogen-enriched algae.

The protein content of the oysters is determined by their nitrogen intake relative to their nitrogen excretion, and by the temperature, light intensity, salinity, and water flow-rate of their environment. By creating an optimal environment, the oyster's protein production is maximized.

The performance of two species is being evaluated: Crassostrea gigas (Thunberg), a Japanese oyster; and Ostrea edulis, a European oyster. C. gigas is the oyster harvested as a commercial food source. Four tanks were set up for each of four temperatures. Two hundred oysters were placed in each tank on plastic trays, twenty individuals per tray.

The food algae, Skeletonema costatum, were grown in outdoor ponds fed by secondary-treated sewage effluent in seawater. The algae and seawater were then pumped into the oyster tanks at a constant rate of 800 µl/min. and 8 L/min., respectively.

Over a period of nineteen weeks, the growth and excretion rates of the specimens were monitored (Tables 1 & 3). At biweekly intervals beginning with week 1, one tray of oysters per tank was sacrificed to determine their chemical composition. The results for C. gigas are shown in tables 1 and 3.

Mann's results indicate that maximum protein production occurs at or below 18° C. Higher temperatures stimulate the oyster's reproductive organs, diverting some of the protein-producing metabolism to carbohydrate consumption to aid in spawning ability.

Mann (1977) states that the major criteria for the optimal culture include "a marketable size product in a minimum time, a maximum conversion efficiency of food to end product, maximum nitrogen (and hence protein) production, or culturing an organism that has a large metabolic store of reserves with an accompanying ability to withstand any unforseen environmental stress."

Table 1. Growth and biochemical composition of *C. gigas* at temperatures of 12, 15, 18 and 21°C over a 19-week period. All data are expressed on a per individual basis W g, live weight; M mg, dry weight; S g, dry shell weight; C mg, carbon content of soft tissues; N mg, nitrogen content of soft tissues; CHO mg, carbohydrate content of soft tissues; ASH mg, ash content of soft tissues. (After: Mann, 1977).

Temp. °C	Parameter	Weeks										
		0	1	3	5	7	9	11	13	15	17	19
12	W g	5.2		6.2	7.2	8.0	9.4	10.4	12.8	14.3	16.5	23.5
	M mg	88.7		256.6	400.0	524.0	646.0	918.0	972.0	1141.0	1414.0	1736.0
	S g	2.48		3.13	3.56	3.86	5.38	5.76	6.76	7.06	8.15	11.37
	C mg	41.5		101.8	158.9	216.9	272.6	391.0	415.6	477.0	621.0	750.5
	N mg	10.8		18.9	30.2	40.6	47.9	52.1	61.6	70.5	96.9	113.0
	CHO mg	0.9		43.3	62.4	138.8	178.8	281.5	331.0	383.6	302.3	390.2
	ASH mg	27.1		38.4	72.0	53.0	46.7	86.2	87.8	86.4	106.8	119.2
15	W g		5.6	6.2	8.1	11.2	10.8	12.5	18.8	21.3	31.2	28.2
	M mg		131.5	228.7	462.0	718.0	696.0	844.0	1266.3	1614.0	2211.0	1253.0
	S g		2.67	3.21	3.7	5.71	5.74	6.74	8.8	9.78	14.85	14.29
	C mg		43.2	88.1	196.1	310.4	259.3	366.6	525.6	665.0	969.3	530.5
	N mg		10.1	17.5	36.9	55.1	44.1	53.8	78.9	101.0	168.7	93.7
	CHO mg		4.9	37.9	110.6	178.2	183.8	241.5	363.3	443.0	331.0	199.0
	ASH mg		37.7	35.8	43.1	65.1	64.7	58.6	140.6	198.2	275.9	109.5
18	W g		5.7	6.7	8.7	12.2	15.6	17.9	19.2	23.6	29.6	34.6
	M mg		94.0	270.0	491.0	641.7	851.0	751.0	888.0	1122.0	1425.0	1322.0
	S g		2.56	3.02	4.23	5.91	8.11	8.57	9.93	12.07	14.6	16.3
	C mg		32.6	110.0	202.4	273.6	341.2	305.1	352.9	442.6	593.2	525.9
	N mg		7.9	19.2	34.8	47.0	48.9	53.9	60.6	87.1	110.7	114.5
	CHO mg		4.9	39.9	60.3	166.3	200.7	144.7	167.4	178.4	186.7	133.1
	ASH mg		24.1	33.1	52.7	57.1	84.6	84.0	127.9	189.6	157.8	176.9
21	W g		5.6	7.5	10.6	12.4	18.3	22.5	19.6	25.2	29.8	38.7
	M mg		134.0	374.0	570.6	742.0	1145.0	1054.7	703.6	1136.0	1286.0	1219.0
	S g		2.67	3.77	5.04	6.38	9.35	9.65	10.12	12.72	15.25	18.97
	C mg		44.5	157.2	238.5	319.7	456.5	399.6	258.1	450.8	510.9	478.2
	N mg		10.4	30.4	45.6	67.8	75.7	89.2	60.9	100.2	102.0	102.3
	CHO mg		5.8	78.5	117.5	137.1	190.2	150.6	99.3	92.0	184.5	129.2
	ASH mg		36.1	60.6	56.8	65.8	119.0	136.3	156.4	89.8	117.7	160.2

Table 3. Ammonia excretion rate (µg NH_3-N/gm dry meat/hr) of *Crassostrea gigas* at temperatures of 12, 15, 18 and 21°C over a 19 week period. Each value gives the mean and standard error of 4-6 individual assays. (After: Mann, 1977).

Temp. °C		Weeks										
		0	1	3	5	7	9	11	13	15	17	19
12°C	Mean	13.63		30.3	20.27	19.5	8.98	12.24	14.46	11.23	7.94	4.99
	S.E.	2.05		6.38	2.01	1.83	1.59	1.81	2.23	0.96	1.17	0.68
15°C	Mean		37.03	27.91	28.33	19.57	9.17	11.42	18.69	10.17	10.46	9.71
	S.E.		5.21	3.39	2.81	1.87	1.09	0.89	1.78	1.21	1.13	0.83
18°C	Mean		28.05	33.38	26.80	23.63	8.05	17.73	12.76	21.22	21.53	31.87
	S.E.		3.80	3.61	4.63	2.85	0.91	2.86	0.87	2.97	2.07	1.31
21°C	Mean		11.45	29.91	23.58	16.01	8.22	11.89	17.24	13.52	23.66	39.28
	S.E.		4.8	3.33	3.52	1.67	1.44	1.92	3.34	1.06	5.09	1.27

MODEL AND SIMPLIFICATIONS

A dynamic-systems model can be used to examine the influences of parameters on maximization of yield in Roger Mann's pilot plant at ESL.

The original model devised at M.I.T. represented a triangular cycle of nitrogen in the tank environment with appropriate inflows and outflows, as shown in Figure 1 below.

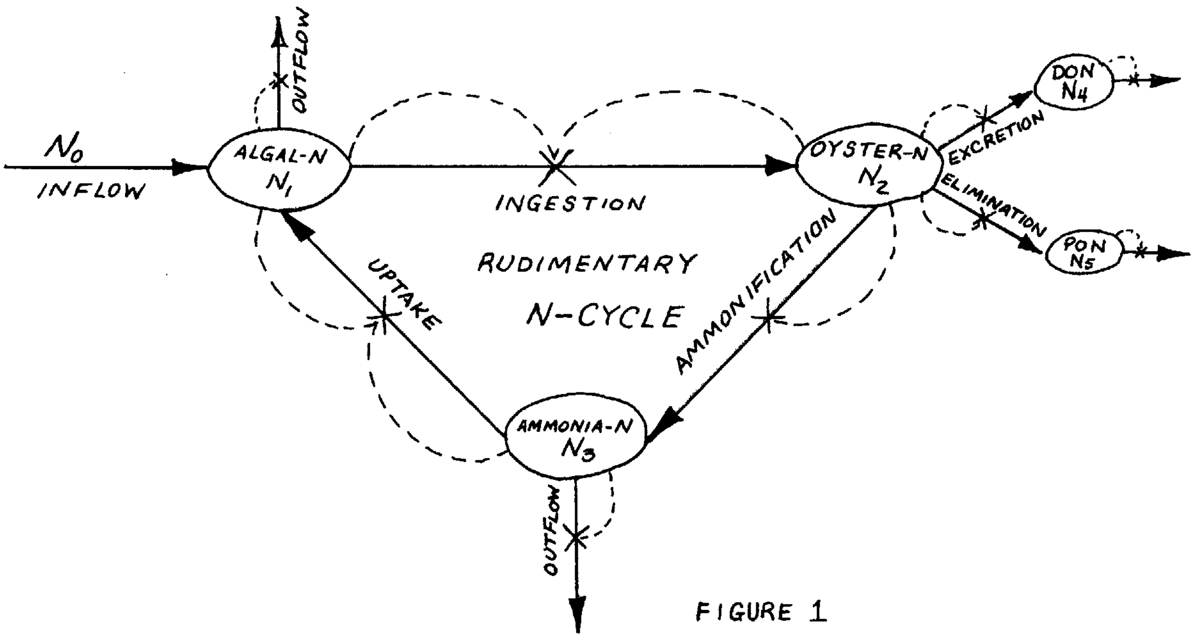


FIGURE 1

Each node represents an accumulation of nitrogen in a particular state. Each accumulation depends upon the inflows and outflows to that state. The flows are regulated by rate parameters including certain feedback terms: an example is oyster ingestion, which depends on the quantity of food available and on the level of ingestion saturation (satiation) that is already present in the oyster. A summary of the original model appears in Appendix 1.

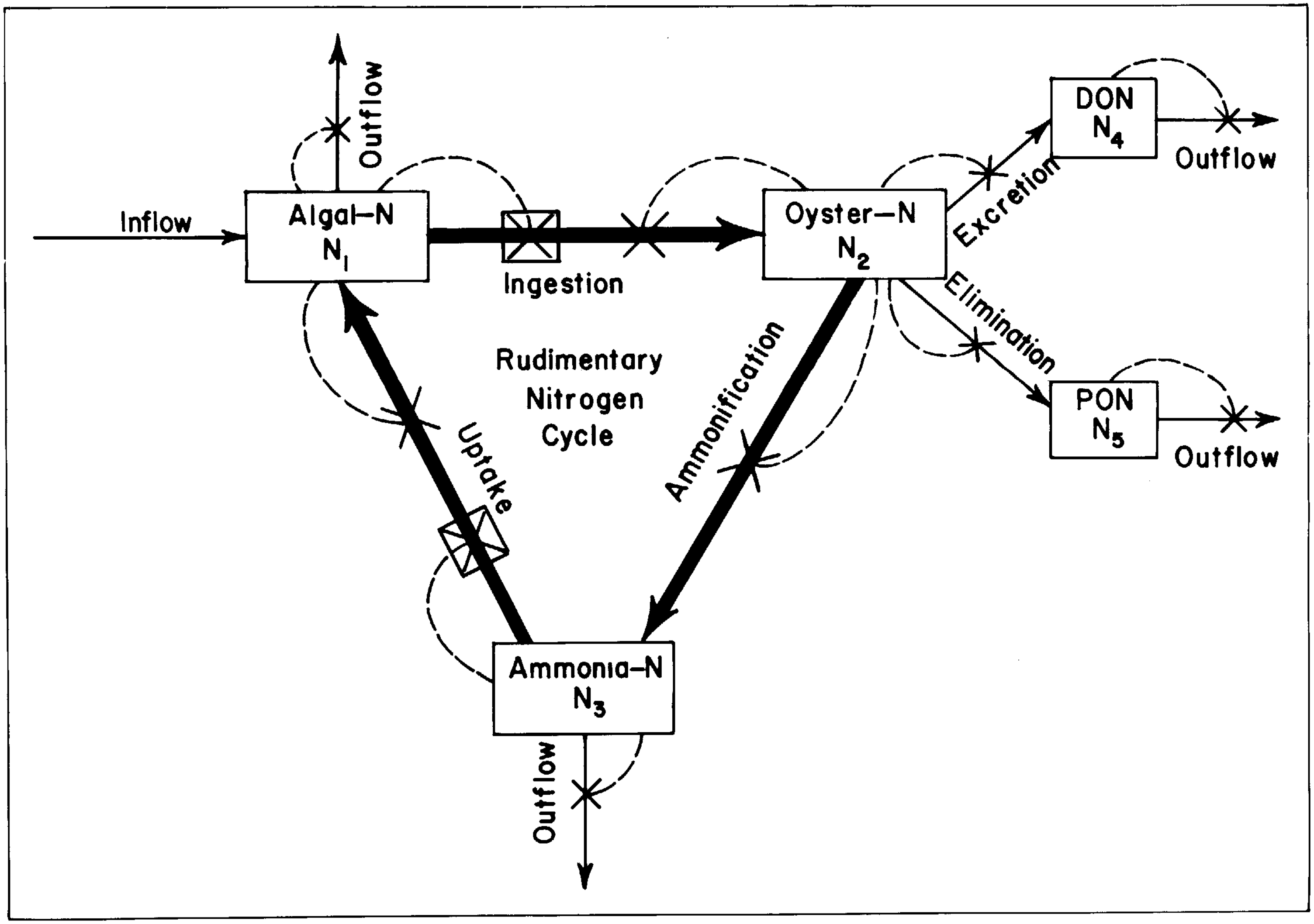


Figure 2. Complete Nitrogen Cycle Model

STATE VARIABLES

The concentration of algal-nitrogen actually present in the tank at any point is represented by the term N_1. Incoming N_1 may either be ingested by the oysters or may pass out of the system without being consumed. If the system is stagnant, N_1 may accumulate in the tank itself. N_1 is considered a state variable because it determines the effects of the regulatory mechanisms of the system.

N_2 represents the concentration of nitrogen which remains in the oyster tissues after the ingestion and egestion processes (excretion, elimination, respiration, and ammonia production) occur. N_2 is specifically the nitrogen content related to the growth term of the ingestion equation. Increases in growth are reflected by an increase in total nitrogen content of tissue.

The concentration of ammonia-nitrogen in the system is represented by N_3. A water flow rate can be established such that all the excreted ammonia is not eliminated by the outflow. Accumulated nitrogen of this form may feed back into the algal consumption structure creating a higher potential algal-nitrogen outflow content to the oyster culture. The concentration of ammonia limits both potential outflow and uptake of N_3.

CONTROL VARIABLES

The concentration of algal-nitrogen pumped into the oyster tanks is represented by the term N_0. This concentration is controlled externally, and thus is considered a control variable of the system. N_0 is determined from the algal cell density entering the tank and the nitrogen content from a sample of algal cells. Multiplication of these two terms yields the total input algal-nitrogen concentration, N_0:

$$N_0 = \frac{\text{algal-N}}{\text{ml inflow}} = \frac{\text{algal-N}}{\text{algal cells}} \times \frac{\text{algal cells}}{\text{ml inflow}}$$

The temperature of the tank, T, determines the level of activity which the oyster exhibits. Certain values of T provide the correct environment for maximum protein production. Temperatures outside this range result in reduced protein production; in addition, higher temperatures result in activation of the reproductive systems of the oysters. This results in the conversion of metabolism from protein to lipid production with a subsequent decrease in the growth rate of the oysters. Temperature also aids in regulation of egestion rates.

Light intensity was not incorporated in the simplified model; however, it does play an important role. The photosynthetic processes of the phytoplankton (algae) are controlled by the amount of solar radiation available to aid in metabolic conversions. Light intensity also influences the activity of the oyster population. Mann (1977) notes the oysters may actually increase their feeding activity at night, indicating that the oysters may be nocturnal feeders. Another factor which may reduce daytime feeding rates is sensitivity to vibrations induced by daytime noise.

The volumetric flow of seawater and algae into and out of the system is labelled q. "q" is set externally and remains constant throughout the set of experiments performed at ESL.

The volume of the culture tank, $\forall$, represents the relative scale of the model. It can be used to determine the maximum potential oyster concentration for any particular tank size.

RATE VARIABLES

The inflow rate of algal-N is given by the expression

$$\left(\frac{q}{\forall}\right) N_0$$

which states that the rate is a function of the volumetric inflow rate divided by the volume of the tank times the concentration, in terms of concentration flowing in per unit time.

The expression

$$\left(\frac{q}{\forall}\right) N_1$$

is the outflow rate of algal-N in terms of the concentration of algal-N in the tank per unit time. It is calculated by the same method as inflow rate.

Similarly, the expression

$$(\frac{q}{V})N_3$$

is the outflow rate of ammonia-N.

The ingestion rate of algae by the oysters is determined by the amount of algae available, by the physical limitations on ingestion rates reflected by the value of the ingestion rate coefficient, i, and on the present satiation state of the oyster, I.

$$(\text{ingestion rate of algal-N}) \equiv i \cdot \frac{N_1}{I + N_1} \cdot N_2$$

This relation states that at high food concentrations (N_1) the ingestion rate saturates for food.

The ammonia uptake rate shows the same behavior as the ingestion rate:

$$(\text{uptake rate of ammonia-N}) \equiv u \cdot \frac{N_3}{U + N_3} \cdot N_1$$

The egestion rates: ammonification, excretion, and elimination are all linear functions of oyster-nitrogen, with respective temperature-dependent coefficients (a, d, and p).

RATE PARAMETERS

The ingestion rate coefficient, i, is determined by converting the published values of algal cells eaten per hour per oyster to algal-nitrogen consumed per hour per oyster. This value is then multiplied by the reciprocal of the algal-nitrogen fraction $(\frac{N_1}{I + N_1})$ to give the final algebraic solution for the ingestion rate coefficient as follows:

$$\frac{\text{algae ingestion rate}}{\text{oyster}} = \frac{\text{cells/hr}}{\text{oyster}}$$

$$\frac{\text{cells/hr}}{\text{oyster}} \text{ X } \frac{\text{algal-N}}{\text{cell}} = \frac{\text{algal-N/hr}}{\text{oyster}} = \frac{\text{nitrogen ingestion rate}}{\text{oyster}}$$

$$\frac{\text{nitrogen ingestion rate}}{\text{oyster}} \text{ X } \frac{\text{oyster}}{N_2} = i\left(\frac{N_1}{I + N_1}\right)$$

$$i = \frac{\text{nitrogen ingestion rate}}{N_2} \left(\frac{I + N_1}{N_1}\right)$$

A value of algae ingestion rate/oyster was taken from Walne, 1972, as shown in Figure 3 below. It corresponds to the maximum ingestion rate of Phaeodactylum algal cell consumption by oysters.

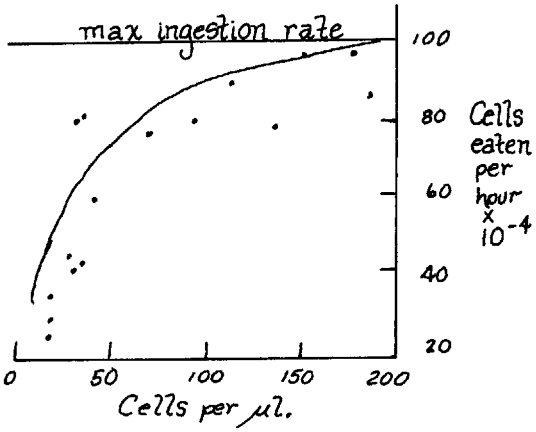


Figure 3.

Walne, 1972. Fig. 2f, page 350. FOOD CONSUMPTION RATE VERSUS FOOD CONCENTRATION. Maximum ingestion rate is superimposed.

Similar data was unavailable for S. costatum, which was used in the pilot plant studies. The parameter value derived from Figure 3 is assumed appropriate because Phaeodactylum are similar to S. costatum in size and nitrogen content. Further justification for this assumption comes from the use of S. costatum in the final ESL system; Phaeodactylum was used originally.

The ingestion half-saturation coefficient, I, is the value of the concentration of algal-nitrogen, N_1, which corresponds to an ingestion rate equal to $(i/2) \cdot N_2$. The ingestion rate coefficient is half its potential value. After appropriate unit conversions, a value for I can be estimated from Figure 3 by establishing a maximum value for ingestion rate on the curve and determining the value of N_1 which corresponds to the value of $(i/2) \cdot N_2$ (see Figure 4).

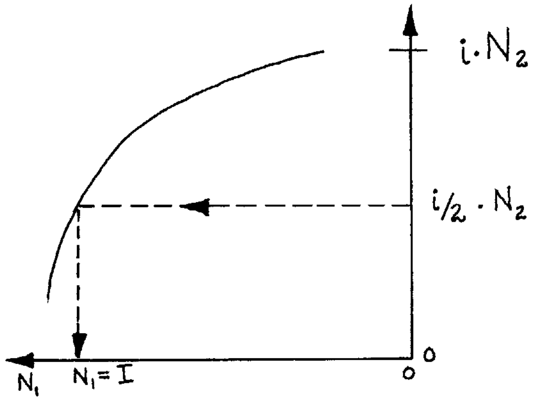


Figure 4.

METHOD FOR DEFINING I.

The uptake rate coefficient, u, and the uptake half-saturation coefficient, U, are estimated by a method similar to that used for the ingestion rate coefficients.

The coefficients describing the functions of egestion are ammonification rate, a; DON (dissolved organic nitrogen) excretion rate, d; and PON (particulate organic nitrogen) elimination rate, p. Since Roger Mann only gives values for "excretion rate", this rate coefficient will be used instead of the aggregate egestion coefficient (equalling the sum of a, d, and p) such that:

$$e \cdot N_2 = (a + d + p) \cdot N_2$$

Values for e can be derived from Table 3, page 9.

ACCUMULATION RATES

There are three accumulation rates, $\dot{N}_1$, $\dot{N}_2$, and $\dot{N}_3$. Their units are in terms of concentration per unit time. They are governed by the same rules as are followed by node-branch models.

The rates of accumulation ($\dot{N}_1$, $\dot{N}_2$, and $\dot{N}_3$) depend on the sum of the inflows and outflows to each node with the appropriate sign conventions. Figure 5 below shows the "word model" describing the accumulation terms for this Nitrogen Cycle Model. Following this is a mathematical model which substitutes the quantitative relations for their word equivalents.

Figure 5: NITROGEN CYCLE MODEL

Word Model - Rate Conservation

Algal Accumulation = (inflow - outflow) + uptake - ingestion

Oyster Accumulation = ingestion - (ammonification + excretion + elimination)

Ammonia Production = ammonification - uptake - outflow

Mathematical Model

$$\dot{N}_1 = \frac{q}{V}(N_0 - N_1) + u \cdot \frac{N_3}{U + N_3} N_1 - i \cdot \frac{N_1}{I + N_1} N_2$$

$$\dot{N}_2 = i \cdot \frac{N_1}{I + N_1} N_2 - [a + d + p] \cdot N_2$$

$$\dot{N}_3 = a \cdot N_2 - u \cdot \frac{N_3}{U + N_3} N_1 - \frac{q}{V} \cdot N_3$$

Simplification of this model leads to a second-order damped system with limited exponential growth. The ammonia-N (N_3) branch of the system was eliminated because Roger Mann observed no accumulation of N_3 due to the high flow rate of the system (Personal Communication, Roger Mann, 1977).

Measurements of light intensity and elimination, respiration, and uptake were unavailable; therefore they were not accounted for in the numerical model. The rate parameters dealt with were i, I, and e, using values calculated by the method described in the previous section.

The accumulation rate of N_1, $\dot{N}_1$, is assumed to equal the sum of inflowing algal-nitrogen minus the outflow minus the ingestion rate of algal-nitrogen.

$$\dot{N}_1 = \frac{q}{V}(N_0 - N_1) - i\cdot(\frac{N_1}{I + N_1})\cdot N_2$$

The expression for the accumulation rate of N_2, $\dot{N}_2$, is simplified by elimination of the sum of parameters a, d, and p. The parameter e has been substituted.

$$\dot{N}_2 = i\cdot(\frac{N_1}{I + N_1})\cdot N_2 - e\cdot N_2$$

The accumulation rate of N_3, $\dot{N}_3$, depends upon the oyster excretion rate, the uptake rate of N_3 by the algal culture, and the outflow rate of ammonia-N. $\dot{N}_3$ is not considered in this model because high outflow rates dominate any potential accumulation rates (Mann, 1977).

A summary of the simplified model appears in Appendix 2.

MODEL BEHAVIOR

THE SIMULATION

The original model was run on the CE/ME Joint Computer Facility (JCF) using DYSYS, Dynamic System Simulation, with predesignated values of the Quinlan / Paynter run, 1976. Results are shown in Figure 6.

The simplified model was then constructed with values derived from Roger Mann's experimental data. Any values that were unavailable from Mann but well-documented in other work were used to supplement the known quantities.

The results of the simplified model appear in Figure 7, page 22. All curves show the expected limited exponential growth of oyster-nitrogen with a corresponding decrease in algal-nitrogen. Sensitivity analyses were performed to examine the changes in final steady state values of N_1 and N_2 with 10% increases in each of the following quantities: i, I, e, q', and N_0, where q' is defined as $\frac{q}{V}$.

Curve B in Figure 7 shows that the solution for the values of N_2 in the original simplified model are virtually indistinguishable from the curve solutions for sensitivity analyses of i and I. The same result applies to the curves for sensitivities of q' and N_0 as can be seen in Curve A. Curve C shows the results of increased e. As expected, the increase in excretion rate causes a decrease in the total amount of oyster-nitrogen converted to protein. Curve D shows the decrease in algal-nitrogen which results from increase in oyster-N.

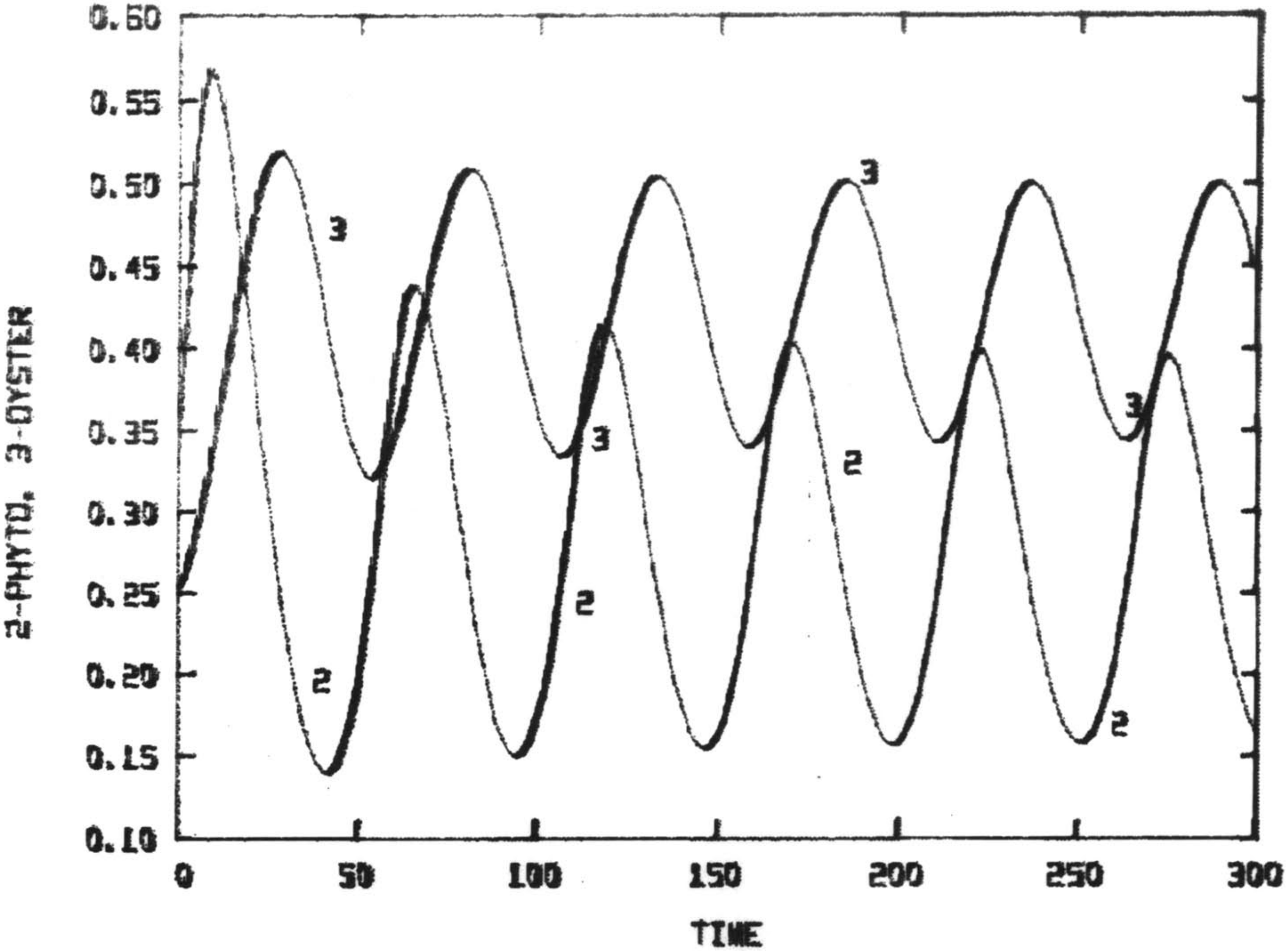


Figure 6: Quinlan / Paynter Results

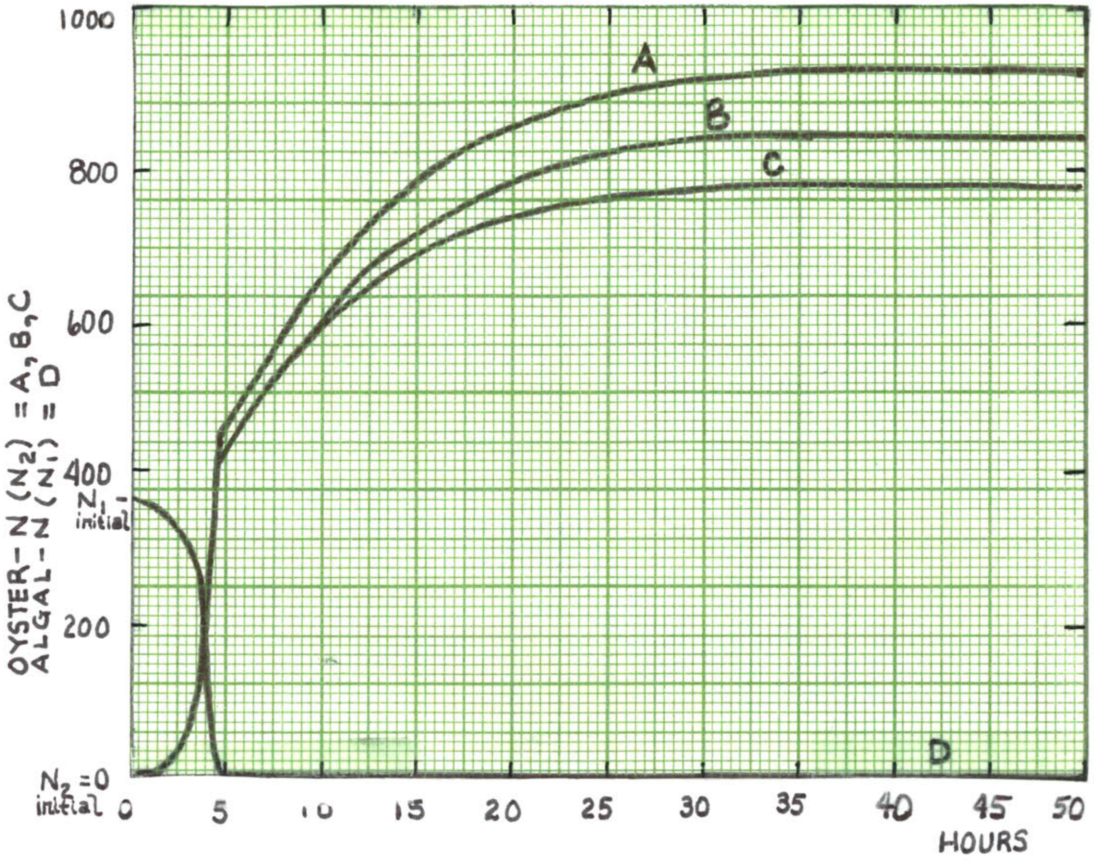


Figure 7 . NITROGEN CONCENTRATION VERSUS TIME

Curve A: N_2 sensitivity results for 10% increases in q' and N_0.

Curve B: Original simplified model for N_2, and N_2 sensitivity results for 10% increases in i and I.

Curve C: N_2 sensitivity results for 10% increase in e.

Curve D: N_1 results for all models.

Inspection of the computer calculations of final maxima and minima (corresponding to steady state values for N_1 and N_2) shows the slight increases and decreases that are not resolvable by the CRT screen of the JCF machinery and thus are not visible in Figure 7. Figure 8, below, gives the predicted and actual results of the steady-state sensitivity analyses in percent difference from the original simplified model solution. A positive percentage represents an increase in total nitrogen. A negative percentage represents a decrease. In analyses of q' and N_0 the values of results for N_1 did not differ from their original values.

PARAMETER SENSITIVITY STEADY-STATE SOLUTIONS

Parameter +10%	Results-N_1*		Results-N_2*	
	Predicted	Actual	Predicted	Actual
i	-9.8	-10	+.08	+.1
I	+10	+10	-.08	-.1
e	+10.8	+11	-9.2	-9
q'	-	-	+10	+10
N_0	-	-	+10.1	+10

Figure 8.

The predictions are computed according to the method shown in Appendix 3.

*Predicted: Results of Steady-State Analysis
Actual: Results of Computer Simulation

Derivation of the steady-state equations for N_1 and N_2 and governing equations for the parameter sensitivity analyses can be found in Appendix 3. The steady-state solutions for the differential equations of $\dot{N}_1$ and $\dot{N}_2$ are solved; then sensitivity is determined by establishing the partial derivative solutions for N_1 and N_2 with respect to each of the parameters tested. These equations show the governing relations for changes in N_1 and N_2 with respect to changes in parameter values. Stability analyses of the region bounding steady-state shows that the system is always stable and does not oscillate. This is because the real portion of the quadratic solution for the linearized system is always negative. The imaginary portion of the solution is always positive $(\alpha^2-4\beta\gamma)$ so the system does not oscillate. Appendix 4 derives the equations of the linearized perturbed system, describes the conditions for stability in the neighborhood of steady-state, gives a sample solution for the original simplified model, and gives comparative values of α, β, and γ for the various changed values of i, I, e, q', and N_0 used in the sensitivity analysis.

DISCUSSION AND CONCLUSIONS

The simplified model does sxhibit the growth form given by results from ESL (see Figure 9). The original simplified model shows unlimited exponential growth with a break at 5 time units corresponding to the effects of limiting factors on exponential growth; however, the time scale of the model is incorrect. All rates were calculated in terms of hours: the model system is in saturation after 50 hours. The ESL system responds over a longer time scale.

Sensitivity analyses and simulation were performed to show the effects of changes in the system parameters and the results these changes have on the final values of oyster-nitrogen and algal-nitrogen. Figure 8, page 23, shows how the steady-state nitrogen contents are influenced by 10% increases in the parameters i, I, e, q', and N_0. This information is useful in pilot plant operation for at least two reasons: first, parameter uncertainty can be accounted for; and second, the sensitivity analyses show which of the control variables can be most effectively increased or decreased to maximize oyster meat content.

The model suggests that i and I would not make good control parameters. Results also suggest that the model is relatively insensitive to uncertainty in values assigned to i and I.

In contrast to changing i or I, a 10% change in e, q', or N_0 will produce nearly an equal percentage change in

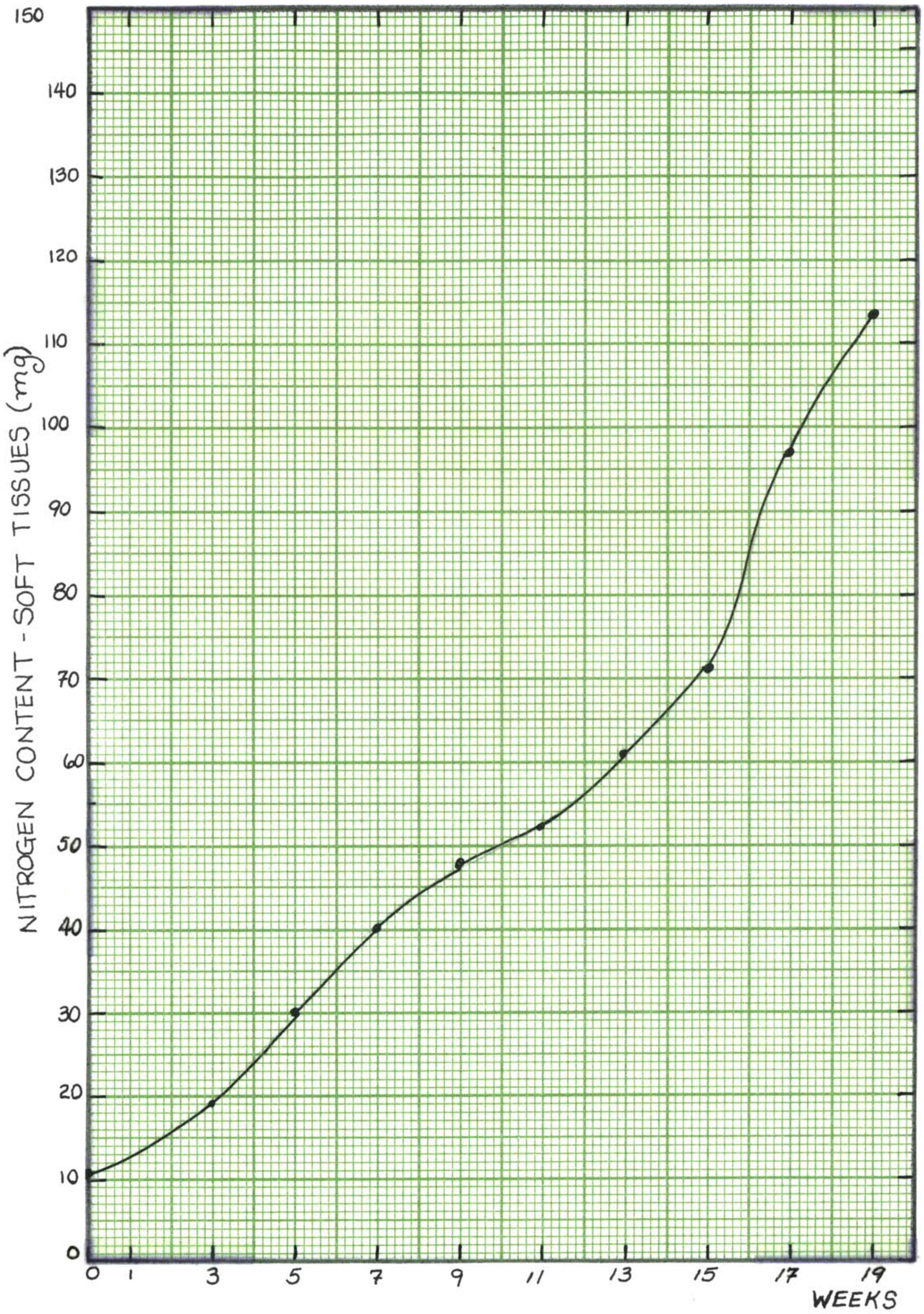


Figure 9: Results from Mann, Table 1:
NITROGEN DATA AT 12°C.

oyster-nitrogen content at steady-state. Uncertainty in these three parameters will produce an equivalent uncertainty in the steady-state oyster-nitrogen values.

The ESL system can expect limited exponential growth of its oyster population. Increases in the volumetric flow rate of seawater and algae, and increases in the algal-nitrogen concentration of the inflow, will cause the greatest increases in oyster-nitrogen growth. In general, 10% increases in q' or N_0 should result in 10% increases in N_2. The marketable oyster-protein content can be increased by monitoring the system temperature, flow rate, tank level, and algal feed concentration.

RECOMMENDATIONS

1) Incorporate light intensity.

2) Attempt to establish some system for consistent measurement units.

3) Attempt to duplicate the species used in other work. This tends to help in verification of results and comparison of various chemical assays.

4) Identify values for all outflows experimentally.

5) Run the model at a slower flow rate to allow feedback of ammonia-N to the algal culture and monitor the effects. Compare and contrast results to those of the original model proposed in this paper.

6) In particular, care must be taken to reduce or report uncertainty in parameter values because this uncertainty hinders quantitative analysis.

REFERENCES

Ali, R.M., "The Influence of Suspension Density and Temperature on the Filtration Rate of Hiatella arctica," Marine Biology 6, 291-302, 1970, pg. 297.

Fogg, G.F., Algal Cultures and Phytoplankton Ecology, Madison: The University of Wisconsin Press, 1966, pp. 39-40.

Goldman, J.C., "Temperature effects on phytoplankton growth in laboratory cultures, Note to Limnology and Oceanography," WHOI Annual Report, 1976, Figure 2, Skeletonema costatum, 1.2-1.7 g/ million cells.

Hugenin, John E. and Smith, Leah J., "The Economics of Wastewater-Aquaculture Systems," IEEE Ocean '75, pp. 285-293.

Mann, Roger, "Some Biochemical and Physiological Aspects of Growth and Gametogenesis in Crassostrea gigas (Thunberg) and Ostrea edulis L. Grown at Sustained Elevated Temperatures," First Draft for publication in J. Mar. Biol. Ass. U.K., Contribution No. 4040 from WHOI, Woods Hole, Mass.

Quinlan, Alician V., "Linearization of Nonlinear Systems About Singular Points," (unpublished).

Quinlan, A.V., Mann, Roger, and Ryther, John, "Nitrogen-Cycle Dynamics of a Waste Recycling Oyster Culture System," Proposal for Joint Research Seed Funds; Submitted to M.I.T.-WHOI Joint Program in Oceanography, January, 1977.

Quinlan, A.V. and Paynter, H.M., "Some Simple Nonlinear Dynamic Models of Interacting Element Cycles in Aquatic Ecosystems," J. Dynamic Systems, Measurement and Control, A.S.M.E. Transactions, Series G, 98: 9-16, 1976.

Ryther, John H., "Bivalve mollusc culture in a waste recycling aquaculture system," Sea Grant Proposal R/A 1, February 1, 1972.

Walne, P.R., Culture of Bivalve Molluscs, Surrey, England: Fishing News (Books) Ltd., 1974.

Walne, P.R., "Growth rates and nitrogen and carbohydrate contents of juvenile clams, Saxidomus giganteus, fed three species of algae," J. Fish. Res. Board Can., 30: 1825-1830.

REFERENCES

Walne, P.R., "The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves," J. Mar. Biol., U.K., 1972, 52: 345-374.

Walne, P.R., "Observation on the influence of food supply and temperature on the feeding and growth of the larvae of Ostrea edulis L.," Fisheries Investigations, Series II, Volume XXIV, Number 1, 1965.

Walne, P.R., "Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera Ostrea, Crassostrea, Mercenaria, and Mytilus," Fisheries Investigations, Series II, Volume XXVI, Number 5, 1970.

PERSONAL COMMUNICATIONS

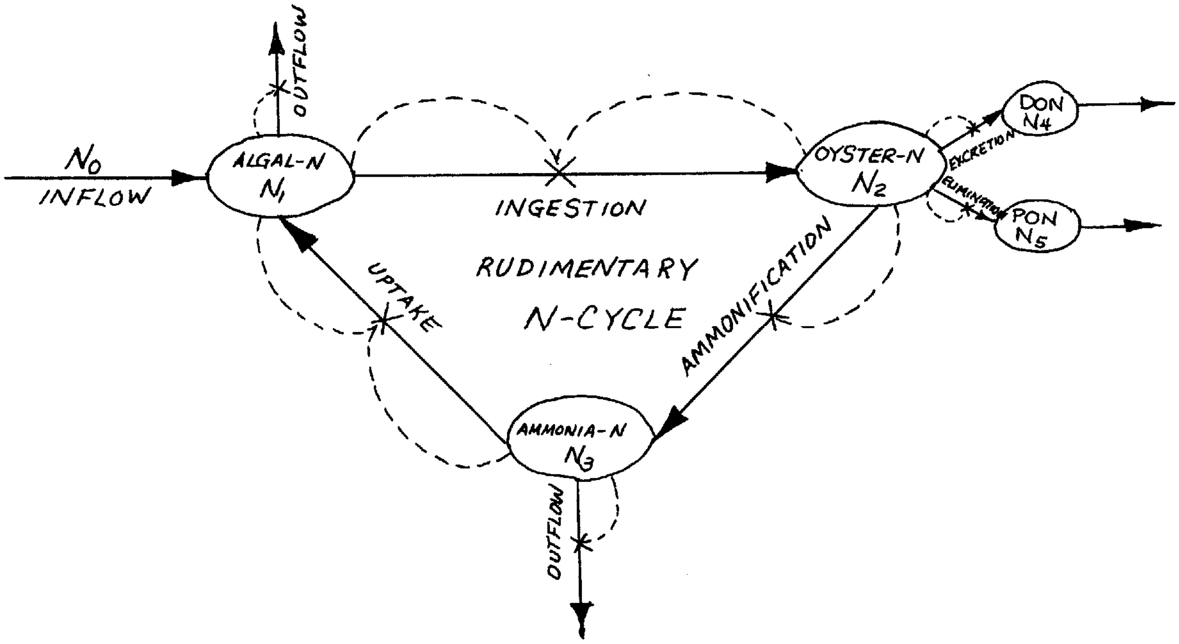
Mann, Roger, 1977, ESL, WHOI, Woods Hole, Mass.

Paynter, H.M., 1977, Department of Mechanical Engineering, M.I.T.: DYSYS.

Quinlan, A.V., 1977, Department of Mechanical Engineering, M.I.T.: Steady-State Solutions, Parameter Sensitivity Analysis, System Linearization, and Stability Analysis.

APPENDIX 1

A. ECODYNAMIC DESCRIPTION OF SYSTEM



State Variables

N_1 = concentration of algal-nitrogen in culture tank

N_2 = concentration of oyster-nitrogen in culture tank

N_3 = concentration of ammonia-nitrogen in culture tank

Control Variables

q = volume rate of inflow and outflow

N_0 = concentration of algal-nitrogen in inflow

T = temperature of culture tank

L = light intensity in culture tank

V = volume of culture tank

Rate Variables

inflow of algal-N = $[q/\forall] \cdot N_0$

outflow of algal-N = $[q/\forall] \cdot N_1$

outflow of ammonia-N = $[q/\forall] \cdot N_3$

ingestion of algal-N = $i \cdot \dfrac{N_1}{I + N_1} \cdot N_2$

ammonification of oyster-N = $a \cdot N_2$

excretion of oyster-N = $d \cdot N_2$

elimination of oyster-N = $p \cdot N_2$

uptake of ammonia-N = $u \cdot \dfrac{N_3}{U + N_3} \cdot N_1$

Rate Parameters

$i = i(T,L)$ = ingestion rate coefficient; may depend on temperature and light

$I = I(T,L)$ = ingestion half-saturation coefficient

$u = u(T,L)$ = uptake rate coefficient

$U = U(T,L)$ = uptake half-saturation coefficient

$a = a(T)$ = ammonification rate coefficient

$d = d(T)$ = dissolved organic nitrogen (DON) excretion rate coefficient

$p = p(T)$ = particulate organic nitrogen (PON) elimination rate coefficient

B. NITROGEN-CYCLE MODEL

Word Model

Algal Accumulation = (inflow - outflow) + uptake - ingestion

Oyster Accumulation = ingestion - (ammonification + excretion + elimination)

Ammonia Production = ammonification - uptake - outflow

Mathematical Model

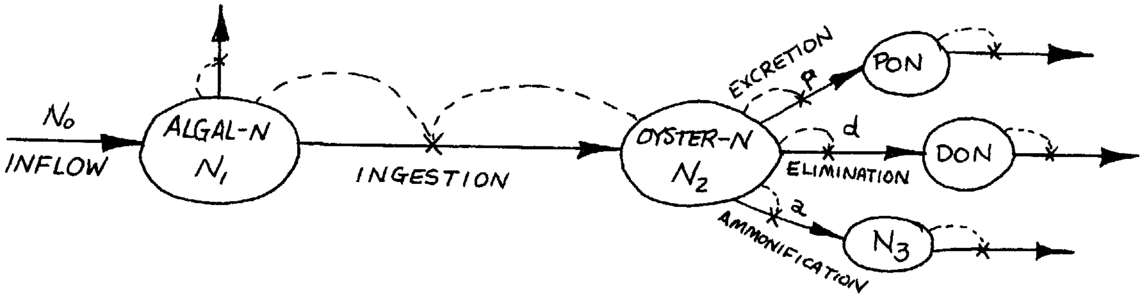
$$\dot{N}_1 = \frac{q}{\forall}(N_0 - N_1) + u\cdot \frac{N_3}{U + N_3} N_1 - i\cdot \frac{N_1}{I + N_1} N_2$$

$$\dot{N}_2 = i\cdot \frac{N_1}{I + N_1} N_2 - [a + d + p]\cdot N_2$$

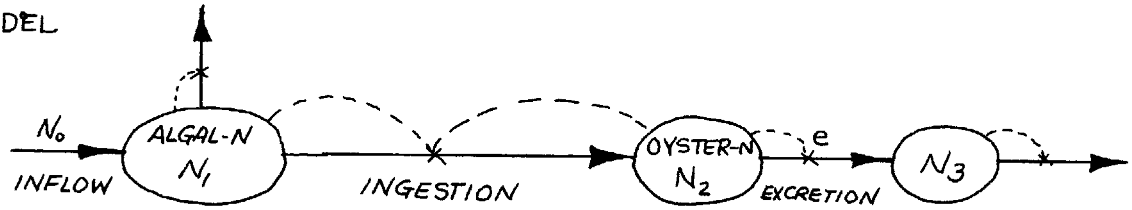
$$\dot{N}_3 = a\cdot N_2 - u\cdot \frac{N_3}{U + N_3} N_1 - \frac{q}{\forall}\cdot N_3$$

APPENDIX 2

SIMPLIFIED MODEL



FINAL MODEL



<u>State Variables</u>

N_1 = concentration of algal-nitrogen in culture tank

N_2 = concentration of oyster-nitrogen in culture tank

N_3 = concentration of ammonia-nitrogen in culture tank

<u>Control Variables</u>

q = volume rate of inflow and outflow

N_0 = concentration of algal-nitrogen in inflow

T = temperature of culture tank

V = volume of culture tank

Rate Variables

inflow algal-N = $[q/\forall] \cdot N_0$

outflow algal-N = $[q/\forall] \cdot N_1$

outflow ammonia-N = $[q/\forall] \cdot N_3$

ingestion of algal-N = $i \cdot \left(\frac{N_1}{I + N_1}\right) \cdot N_2$

excretion of oyster-N = $e \cdot N_2$

Rate Parameters

$i = i(T,L)$ = ingestion rate coefficient; may depend on temperature and light

$I = I(T,L)$ = ingestion half-saturation coefficient

$e = e(T)$ = excretion rate coefficient

NITROGEN-CYCLE MODEL (SIMPLIFIED)

Word Model

algal-N accumulation rate = (inflow - outflow)- ingestion

oyster-N accumulation rate = ingestion - excretion

Mathematical Model

$$\dot{N}_1 = \frac{q}{\forall}(N_0 - N_1) - i \cdot \frac{N_1}{I + N_1} N_2$$

$$\dot{N}_2 = i \cdot \frac{N_1}{I + N_1} N_2 - e \cdot N_2$$

OBJECTIVE

identify values of control variables (q, N_0, T, and $\forall$) which maximize accumulation rate of oyster-N, $\dot{N}_2$.

APPENDIX 3 (QUINLAN, 1978)

SYSTEM

$$\dot{N}_1 = q'(N_0 - N_1) - i\left[\frac{N_1}{I + N_1}\right] N_2 \qquad q' = q/V$$

$$\dot{N}_2 = i\left[\frac{N_1}{I + N_1}\right] N_2 - e N_2$$

STEADY STATE

$$\dot{N}_1 = 0 \qquad N_1 = \hat{N}_1 = \left[\frac{1}{(i/e) - 1}\right] I$$

$$\dot{N}_2 = 0 \qquad N_2 = \hat{N}_2 = \left[q'/e\right)\left[N_0 - \left(\frac{1}{(i/e)-1}\right) I\right] = q'/e\left(N_0 - \hat{N}_1\right)$$

$$\uparrow i \longrightarrow \downarrow \hat{N}_1 \longrightarrow \uparrow \hat{N}_2$$

$$\uparrow e \longrightarrow \uparrow \hat{N}_1 \longrightarrow \downarrow \hat{N}_2$$

$$\uparrow I \longrightarrow \uparrow \hat{N}_1 \longrightarrow \downarrow \hat{N}_2$$

$$\uparrow q' \longrightarrow \qquad \uparrow \hat{N}_2$$

$$\uparrow N_0 \longrightarrow \qquad \uparrow \hat{N}_2$$

CONSTRAINTS ON PARAMETER VALUES

$i > e$

$N_0 > \hat{N}_1$

EQUATIONS GOVERNING PARAMETER SENSITIVITY OF $\hat{N}_1$

$$\hat{N}_1 = [e/(i-e)]\, I$$

$$\partial \hat{N}_1/\partial e = i\, I/(i-e)^2 = +(i/e^2 I)\, \hat{N}_1^{\,2} \qquad > 0$$

$$\partial \hat{N}_1/\partial i = -e I/(i-e)^2 = -(1/e I)\, \hat{N}_1^{\,2} \qquad < 0$$

$$\partial \hat{N}_1/\partial I = +e/(i-e) = +(1/I)\, \hat{N}_1 \qquad > 0$$

$$\partial \hat{N}_1/\partial q' = 0$$

$$\partial \hat{N}_1/\partial N_0 = 0$$

FOR 10% INCREASE OF PARAMETER:

$\uparrow e$ BY 10% $\longrightarrow \Delta \hat{N}_1 \approx +(.1\, i/e I)\, \hat{N}_1^{\,2}$

$\uparrow i$ BY 10% $\longrightarrow \Delta \hat{N}_1 \approx -(.1\, i/e I)\, \hat{N}_1^{\,2}$

$\uparrow I$ BY 10% $\longrightarrow \Delta \hat{N}_1 \approx +.1\, \hat{N}_1$

EQUATIONS GOVERNING PARAMETER SENSITIVITY OF $\hat{N}_2$

$$\hat{N}_2 = q'_k e^{-1} (N_0 - \hat{N}_1)$$

$$\partial \hat{N}_2 / \partial e = -[(1/e) \hat{N}_2 + (i q'_k / e^3 I) \hat{N}_1^{2}] \quad < 0$$

$$\partial \hat{N}_2 / \partial i = +(q'_k / e^2 I) \hat{N}_1^{2} \quad > 0$$

$$\partial \hat{N}_2 / \partial I = -(q'_k / e I) \hat{N}_1 \quad < 0$$

$$\partial \hat{N}_2 / \partial q'_k = +(1 / q'_k) \hat{N}_2 \quad > 0$$

$$\partial \hat{N}_2 / \partial N_0 = +(q'_k / e) \quad > 0$$

FOR 10% INCREASE IN PARAMETER:

$$e \longrightarrow \downarrow \Delta \hat{N}_2 \approx -[.1 \hat{N}_2 + (.1 i q'_k / e^2 I) \hat{N}_1^{2}]$$

$$i \longrightarrow \uparrow \Delta \hat{N}_2 \approx +(.1 i q'_k / e^2 I) \hat{N}_1^{2}$$

$$I \longrightarrow \downarrow \Delta \hat{N}_2 \approx -(.1 q'_k / e) \hat{N}_1$$

$$q'_k \longrightarrow \uparrow \Delta \hat{N}_2 \approx .1 \hat{N}_2$$

$$N_0 \longrightarrow \uparrow \Delta \hat{N}_2 \approx .1 i q'_k / e$$

PARAMETER SENSITIVITY OF $\hat{N}_1$ AND $\hat{N}_2$

$$\text{FOR} \left\{ \begin{array}{l} i = 1.59 \\ I = 36.25 \\ e = .12 \\ q' = 0.284 \\ N_0 = 363.0 \end{array} \right\}$$

$\hat{N}_1 = 2.96$

$\hat{N}_2 = 852.01$

	$\hat{N}_1$	$\hat{N}_2$
10% ↑ i	9.8% ↓	.08% ↑
10% ↑ I	10.0% ↑	.08% ↓
10% ↑ e	10.8% ↑	9.2% ↓
10% ↑ q	↔	10.0% ↑
10% ↑ N_0	↔	10.1% ↑

APPENDIX 4 (QUINLAN, 1978)

LINEARIZED PERTURBED SYSTEM

$$\eta_1 = N_1 - \hat{N}_1$$
$$\eta_2 = N_2 - \hat{N}_2$$

$$\left[\begin{array}{c} \dot{\eta}_1 \\ \hline \dot{\eta}_2 \end{array}\right] = \left[\begin{array}{c|c} -\alpha & -\beta \\ \hline \gamma & \delta \end{array}\right] \left[\begin{array}{c} \eta_1 \\ \hline \eta_2 \end{array}\right]$$

$$-\alpha = \partial \dot{N}_1 / \partial N_1 = -[q_r' + i\, I\, \hat{N}_2 / (I + \hat{N}_1)^2] < 0$$

$$-\beta = \partial \dot{N}_1 / \partial N_2 = -e \qquad < 0$$

$$\gamma = \partial \dot{N}_2 / \partial N_1 = +i\, I\, \hat{N}_2 / (I + \hat{N}_1)^2 \qquad > 0$$

$$\delta = \partial \dot{N}_2 / \partial N_2 = 0 \qquad = 0$$

$$\therefore \left[\begin{array}{c} \dot{\eta}_1 \\ \hline \dot{\eta}_2 \end{array}\right] = \left[\begin{array}{c|c} -\alpha & -\beta \\ \hline \gamma & 0 \end{array}\right] \left[\begin{array}{c} \eta_1 \\ \hline \eta_2 \end{array}\right]$$

STABILITY IN THE NEIGHBORHOOD OF STEADY STATE

LET $$\left[\begin{array}{c|c} -\alpha-\lambda & -\beta \\ \hline \gamma & -\lambda \end{array}\right] = 0$$

$$\lambda^2 + \alpha\lambda + \beta\gamma = 0$$

$$\lambda = -.5\alpha \pm .5(\alpha^2 - 4\beta\gamma)^{1/2}$$

SYSTEM **ALWAYS STABLE**

- BECAUSE $Re(\lambda) < 0$ FOR ALL PARAMETER VALUES

SYSTEM **MAY OSCILLATE**

- IF $Im(\lambda) \neq 0$
- *ie*, IF $4\beta\gamma > \alpha^2$

STABILITY SAMPLE CALCULATION

$$\text{FOR} \left\{ \begin{array}{l} i = 1.59 \\ I = 36.25 \\ e = .12 \\ q' = 0.284 \\ N_0 = 363.0 \end{array} \right\} \qquad \begin{array}{l} \hat{N}_1 = 2.96 \\ \hat{N}_2 \quad 852.01 \end{array}$$

$\alpha = 32.18$

$\beta = .12$

$\gamma = 31.90$

$\lambda = -16.09 \pm 15.97 = \left\{ \begin{array}{l} -.12 \\ -32.06 \end{array} \right\}$

$Re(\lambda) = \left\{ \begin{array}{l} -.12 \\ -32.06 \end{array} \right\} < 0 \Rightarrow$ SYSTEM STABLY DAMPED

$\tau_{1/2}$ = DAMPING HALF-LIFE

$$A_0 \exp\left(\left\{ \begin{array}{l} -.12 \\ -32.06 \end{array} \right\} \tau_{1/2} \right) = .5 A_0$$

DAMPING $\tau_{1/2} = 5.78$

SOLUTION IS OF THE FORM:

$$X = C_1 e^{-.12t} + C_2 e^{-32.06t}$$

CALCULATIONS - α, β, γ

FOR ORIGINAL SIMPLIFIED MODEL
AND SENSITIVITY ANALYSES

SYSTEM	α	β	γ
original	32.18	.12	31.90
$i = 1.75$	35.95	.12	35.67
$I = 40.0$	29.17	.12	28.88
$e = .132$	28.82	.132	28.54
$q' = .312$	35.39	.12	35.08
$N_0 = 399.0$	35.37	.12	35.08

FOR THESE PARAMETER VALUES:

$4\beta\gamma$ is never $> \alpha^2$

$\alpha^2 - 4\beta\gamma > 0$

$\therefore$ SYSTEM DOES NOT OSCILLATE