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An Analysis of Marine Microcosms Along an Environment Gradient

by

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1.0 Intent:

Complex marine ecosystems are often depicted in flow diagrams (Figure 1) as a simplified system of interconnected boxes. The behavior of the system is then interpreted in terms of the diversity levels in the ecosystem or the general flow characteristics of the system. The MERLIN project examines how the relative flow activities (defined in Methods Section 3.0) among the phytoplankton, zooplankton, and benthic populations affect the overall level and continuity of production within a marine ecosystem.

This report results from a preliminary run of the MERL Simulation and Flow Analysis system (MERLIN). MERLIN is based on data from the marine microcosms maintained at the Marine Ecosystem Research Laboratory, (MERL), at the University of Rhode Island's Graduate School of Oceanography.

This simulation/analysis exercise is intended only to investigate the adequacy and compatibility of the goals of the MERLIN project (W. Hahm, 1981) with the available MERL data sets. This report is based on the simulation and analysis of flows in the MERL microcosm over a two-day period (June 11-12). The report is intended to demonstrate:

i) the assumptions inherent in model,

ii) the experimental design applications and analysis utilities of the MERLIN output and,

iii) the problems associated with reconciling simulation and field observations. MERLIN is the product of considerable collaboration with the MERL scientific staff and is geared toward questions relevant to their ongoing studies.

2.0 The Case Study

2.1 The Environmental Gradient

There exists a pollution gradient strectching from the urban waters of upper Narrgansett Bay to the neritic conditions of Rhode Island Sound. To study this environmental gradient, nine MERL microcosms were set up the first week of August 1979.

The marine microcosms maintained at the MERL facility are 1.8 m in diameter and 5.5 m in height. Each holds 13.0 m^3 (13.3 tons) of Narragansett Bay water over a sediment pan holding .753 m^3 (1.1 tons) of marine sediments with the resident benthic communities. The turnover and circulation of water through the system mimicking Narragansett Bay is accomplished via peristaltic pumps. The water, from Narragansett Bay is heated or cooled through heat exchanges to keep the temperature within the seasonal temperature ranges.

The first three microcosms were installed with a sediment pan containing intact sediment communities from a Providence site. The second three microcosms were installed with sediment pans from Rhode Island Sound. The third set of microcosms was filled with a more intermediate type benthic community, from off North Jamestown, R.I. The MERL data sets generated by these microcosms resemble a series of snapshots of the standing stocks (phytoplankton, zooplankton, and benthos) and the profiles of dissolved nutrients, (NH_3, NO_x, PO_x, S_iO_x) and particulate matter in the water column and the underlying sediments. The findings of this report are based on the intensive sampling work carried out on June 11-12, 1980. This preliminary model is based

solely on measured observations (to minimize the assumptions and bias of the modeler). The compartments (Figure 2) support with MERL measurements include: x_1 = phytoplankton, x_2 = zooplankton, x_3 = the benthos, x_4 = dissolved nutrients, x_5 = suspended load, and x_6 = wall growth.

The complexity of the model will be increased when more detailed information is available or when it is desired to examine the consequences of hypothesized processes or compartments (i.e. microzooplankton or bacteria, see discussion in 5.0).

The phytoplankton biomass is based on Chl-A levels and an empirical 30 gC/gChl-A (Antia, et al., 1963). Zooplankton are sampled with a #20 mesh net and weighed. The dissolved nutrients (NH_3, NO_x, DON, DOP, PO_4, SiO_2) are siphoned from the tanks after a 15-minute mixing period. Particulates (Si, PO_4, Total) are filtered for analysis onto glass fibre filters. Primary production is based on oxygen production and ^{14}C incubations. The wall production is estimated through the increase of suspended load after the walls have been scrubbed. Benthic fluxes are obtained with an <u>in situ</u> chamber that encloses the entire sediment surface. The summary of MERL state measurements are given in Table 1.

The distribution of matter in the three systems is shown in Figure 3. The total suspended load decreases from the Providence microcosm to the Rhode Island Sound microcosm (Providence = $3.3 \times 10^3 \mu g/\ell$, Jamestown = $2.3 \times 10^3 \mu g/\ell$ and Rhode Island Sound = $2.0 \times 10^3 \mu g/\ell$).

The microcosms become increasingly phytoplankton dominated oceanward (4.9% of suspended matter in Providence, 6.0% in Jamestown, and 10.9% in the Rhode Island Sound microcosm).

The zooplankton dominance on the other hand decreases oceanward (2.7% of suspended load in Providence, 2.0% in Jamestown, and 1.9% in Rhode Island).

All microcosm water columns were dominated by detritus and suspended matter other than phytoplankton and zooplankton (Providence = 92.4%, Jamestown = 92.1% and Rhode Island Sound = 87.3%). Using the ratio of phytoplankton biomass to zooplankton biomass, as a measure of trophic dominance, the microcosms are increasingly phytoplankton dominated oceanward (P/Z_{Prov} = 1.85, P/Z_{JT} = 3.09, P/Z_{RIS} = 5.89).

2.2. The Carbon Flows Between Compartments

The data set described in Section 2.1, with the exception of intercompartmental flows is an almost complete description of the dynamics of the system. For an n-compartment system there are n^2 possible interactions. Let F(i,j) be the flow from the jth compartment to the ith compartment. Of the thirty-six possible compartmental flows, in a six compartment system, ten were included in this simulation study. With the exception of benthic fluxes, none of these flows can be directly measured.

MERLIN bases flow estimates on the time derivatives of compartmental changes. The assumption is made that time varying Redfield-type elemental ratios (C:N:P:Si) exist for the phytoplankton and zooplankton. The increase/decrease in biomass of these compartments then draws/releases on the appropriate donor/recipient compartments to meet the compartment's nutrient demands. MERLIN traces and analyzes the flows and recycling of carbon, nitrogen, phosphorus, and silica through the system. In this report, only the carbon flow will be examined. The major flows are illustrated in Figures 4a through 4c. The units of

these ten flows are in μg-at C/ℓ·day. The following sections list the equations and assumptions necessary to determine these flows.

2.2.1 The Fixation of Carbon F(1,4) and F(6,4)

The uptake of HCO_3 and CO_2 F(1,4)), from the dissolved nutrient pool x(4) by the phytoplankton x(1) is a consequence of primary production (see Section 2.3). ^{14}C methods seem to give net primary production estimates as opposed to O_2-method's gross primary production estimates. The MERL primary production estimates using both methods for June 11-12 however are very similar (Table 3). The PQ ratio (molar ratio O_2 release/$^{14}CO_2$ fixed) for the 24-hr period ranged from .99 for Jamestown to 1.43 for the Rhode Island Sound microcosm (Table 3). To bypass the problem of error associated with the PQ ratio, phytoplankton production is based on dawn-dawn ^{14}C incubations. Wall production was determined by measuring the increase in suspended load after wall cleaning in the Providence and Rhode Island Sound tanks. Production follows a sinusoidal curve with a maximum in the summer (J. Kelly et al., 1981) (Figure 5). As in phytoplankton carbon uptake, the carbon uptake by the wall community F(6,4), equals the production estimate.

2.2.2 The Accumulation of Particulate Carbon F(5,1), F(5,6), F(5,3)

In this model, the particulate pool contains the phytoplankton cells and fragments, plus the zooplankton and fecal pellets that are fed on by other zooplankton. The particulate pool is also in the process of decomposing or sedimenting to the bottom. The daily drops in the phytoplankton and zooplankton live biomass pools are assumed to have been eaten by zooplankton or to have died.

The MERL dataset (1979-1980) allows for the estimate of phytoplankton and zooplankton contributions to this particulate pool. There are unfortunately no estimates of water column bacterial or protozoan production and decomposition. Re-suspension, F(5,3) based on the Santschi (1979-1980) works are being investigated.

The total amount of POC available for a given day, is the initial standing stock of phytoplankton (based on Chl-A and the conversion factor $^{C}/\text{Chl-A} = 30$, Antia et al., 1963) plus the observed daytime primary production. The flow into the particulate carbon pool is based on the drop of phytoplankton carbon over the course of the day. Then:

$$F(5,1) = \frac{\{(\text{Chl-A}_1 * {}^{C}/\text{Chl-A}) + ({}^{14}\text{C-fixed Dawn-to-Dusk})\} - \{\text{Chl-A}_2 * {}^{C}/\text{Chl-A}\}}{12\ \mu\text{gC}/\mu\text{gatC}}$$

The wall growth's contribution to the particulate pool is based on MERL observations (Figure 5). It is assumed that the brushes are completely efficient.

2.2.3 Acccumulation of Dissolved Carbon F(4,1), F(4,2), F(4,3), F(4,5)

The inflows into the dissolved nutrient pool arise from excretion, benthic release, and decomposition of the particulate pool. The inflows due to excretion are estimated by the overnight drop in labelled ^{14}C. This involves subtracting the 24-hr $dawn_1$ through dusk. This loss is attributed in part to organic excretion (glycolate) by phytoplankton (J. Sharp, 1977; G. E. Fogg, 1977) which can under appropriate conditions be considerable (see Section 2.3). Then:

$$F(4,1) = \frac{(^{14}C\text{-Prod:Dawn}_1 \text{ to Dawn}) - (^{14}C\text{-Prod:Dawn}_1 \text{ to Dusk}^1)}{12\ \mu gatC/\mu gC}$$

No direct estimates of zooplankton excretion are available. The excretion was then simulated assuming that zooplankton respire a fraction of their biomass as a function of temperature. The general form of the flow equation is:

$$F(4,2) = RESP_o * \ell^{(Q_{10} \cdot t)} * X(2)$$

where $RESP_o$ = .1/day, and a doubling of rate every 10°C was assumed. X(2) = the standing stock of zooplankton.

The flow of carbon from the benthos was based on bottom respiration data (J. Kelly et al., 1980). The oxygen uptake of the sediment was taken as a measure of carbon metabolism. As suming a RQ = .7-1.0, (molar ratio of $\frac{CO_2 \text{ released}}{O_2 \text{ Consumed}}$) , the benthic flux contributes $F(4,3)=(O_2\text{-uptake})*(RQ)$ to the dissolved pool. Assuming only Redfield substances in the substance would set RQ = .768. MERL flux work has shown the metabolized material to be nitrogen poor.

The preliminary version of MERLIN does not include decomposition of the suspended matter. Future runs are being prepared to employ decomposition processes as observed by Otsuki and Hanya (1972).

$$F(4,5) = L_o.X(5).e^{-k_1 t} + R_o X(5).e^{-k_2 t}$$

L_o and R_o represent the labile and refractory fractions of the suspended particulate matter, (X(5)) and k_1 and k_2 are the relative decomposition rates.

2.2.4 Zooplankton Ingestion F(2,5) and F(5,2)

No direct measurements (Coulter Counter Methods, Heimle & Berman, 1978) were made since 1978. Inferences can be drawn from the zooplankton biomass. Zooplankton models (Kremer and Nixon, 1978) generally set up recipient controlled flows with Ivlev type capture efficiencies. Then:

$$R = X(5)*R_o*(\exp(Q_{10}*t) \quad R_o = .25 \qquad \text{Ivlev} = .007\ \ell/\mu gC$$

$$F(2,5) = R*(1.-\exp(-\text{Ivlev}.\text{Prey})) \qquad Q_{10} = 1.8$$

$$\text{where prey} = X(1)+X(2)$$

F(2,5) represents the ingestion by zooplankton. Flow (5,2) represents the unassimilated fraction of zooplankton ingestion, that returns to the particulate pool in the form of fecal pellets. If we assume .2 of ingestion is eliminated:

$$F(5,2) = F(2,5)\ *\text{ELIM} \quad \text{where ELIM} = 0.2$$

2.3 The Problems of Estimating Flows: they don't always balance

One of the implicit expectations in nutrient budgeting studies is that the net flows balance. The net compartmental flows into a compartment are a linear combination of the contributions of the other compartments. In the nonsteady state case, the compartment's time derivatives are non-zero. That is:

Biomass change = [Growth]-[Losses to other compartments] ± [import/export]

$$\frac{d\underset{\sim}{x}}{dt} = A\underset{\sim}{x} \text{ where } \begin{array}{l} \dot{x}_1 = \alpha_{11}\, x_1 + \alpha_{12}\, x_2 + \ldots + \alpha_{1n} x_n \\ \vdots \\ \dot{x}_n = \alpha_{n1}\, x_1 + \alpha_{n2}\, x_2 + \ldots + \alpha_{nn} x_n \end{array}$$

While this is intuitively straightforward, the task of obtaining balanced nutrient budgets in the field is difficult (C.A. Oviatt et al., 1980; Finn and Leschine, 1980; B.J. Peterson, 1980). The discrepancy between the researcher's expected and observed flows must be either rejected or accepted as real. The budget imbalances might be rejected on the grounds of instrumentation error or insufficient system measurements.

An alternative is to examine the role recycling, internal storages and metabolic pathways have in complicating the flow budgets.

Nutrient balances have generally been observed only under near steady state conditions in the central oligotrophic oceans (the Sargasso and the North Pacific gyre), (R.W. Eppley, 1980) or in laboratory chemostat studies, (J.J. McCarthy and J.C. Goldman, 1979). The problem with perceived imbalances increases as the time between samples increases. Sheldon and Sutcliff (1979) demonstrated that POC production can be seriously underestimated since carbon recycling runs on the order of hours. Between sampling measurements, atoms of scarce elements via repeated uptake and regeneration, can act like catalyst in the system generating more activity and production than would have been expected.

The discontinuity between nutrient uptake and anticipated primary production is further widened by the mounting evidence of decoupled subprocesses within carbon fixation (P.G. Falkowski, 1980). Carbon fixation can be broken down into three steps: energy fixation, nutrient uptake, and biosynthesis of cellular Redfield-type material. The energy fixing step involves the Hill and Calvin-Benson photosynthetic cycles. The Hill cycle involves the photolysis of H_2O to liberate high energy electrons. This chemical energy is then fixed into a more stable form via the reduction of carbon dioxide in the Calvin-Benson cycle. The reduced carbon (3 and 6 carbon chains) can be oxidized via the tricarboxylic acid (Krebs) cycle or modified for cellular biosynthetic development. Nitrogen, phosphorus, silica and other trace elements are brought into the cell through active membrane transport against a concentration gradient.

Apparent budget imbalances are encountered when primary production is assumed equal to C-fixation estimates based on ^{14}C uptake or O_2 production. These production measures actually measure the amount of carbon that is fixed primarily into three and 6-carbon chains. This first pool of reduced carbon is not necessarily fixed into the average Redfield type molecule (Redfield et al., 1963), but may be excreted, photorespired, or respired. Under low nutrient conditions, phytoplankton have been observed to excrete excess carbon in the form of glycolate (J. Myers, 1980). Under high light and high oxygen conditions, photorespiration "burns" up glycolates without ATP synthesis, (I. Morris, 1980; J.E. Burris, 1980). Considerable reserves of

reduced carbons are respired to generate the ATP necessary to take up nitrogen (Y. Collos and G. Slawyk, 1980), phosphorus (Stewart and Alexander, 1971), and silica (Coombs et al., 1967). The leakage and respiration of the initialy fixed carbons explains why N:P:Si uptake and fixation is much lower than would be expected, merely on the basis of oxygen production or ^{14}C based estimates of primary production. Marine phytoplankton plants tend to accumulate stores of reduced carbon and nutrients (N:P:Si) and combine them into tissue on seasonal cycles rather than on the mere basis of a Liebig-type rate limiter (K.H. Mann, 1980).

The findings that phytoplankton tissue approximates Redfield ratios only at maximum cellular growth rates (J.C. Goldman, 1980; J.C. Goldman et al., 1979; J.J. McCarthy et al., 1979) coupled with the fact that phytoplankton approximate Redfield ratios even under oligothrophic conditions (E.J. Carpenter and J.S. Lively, 1980) strongly suggest that primary production is an episodic phenomenon (W.G. Harrison, 1980). The assumptions of short-term steady state type nutrient balances (Redfield uptake of N:P:Si in proportion to C-fixation) is weak in the field. The modeling assumptions of flow analysis (Section 3.1) accept the excess or insufficient uptakes of nutrients over the short-term by assuming the existence of internal storages. It is then possible to determine the ecosystem nutrient and energy reserve levels. It is also possible then to assess when the system is especially susceptible to perturbations.

2.4 The Generalized Pattern of Flows

Section 2.1 compared the structure of the three sets of microcosms representing Providence, Jamestown, and Rhode Island Sound water columns. These three sets of microcosms generated three equally unique sets of flows (Figure 4a, 4b, and 4c).

In the presently simplified system, the primary flows are generated through primary production, benthic fluxes and zooplankton activity. Day long production based on ^{14}C incubations in the Rhode Island Sound microcosm was 2.6 times the Providence microcosm's production. The neritic microcosm was roughly twice as productive as the Jamestown microcosm (see Table 3). Primary production to no one's surprise was linked to phytoplankton standing stocks (see Table 3). The production to biomass ratios increase from Providence to Rhode Island Sound, (P/B_{Prov} = .62, P/B_{JT} = .89 and P/B_{RIS} = 1.09). This can be explained in part by the decreasing zooplankton (*Acartia clausi* with traces of *A. tonsa*) dominence along the oceanward gradient, (Prov = 77.5 μg/ℓ, JT = 44.3 μg/ℓ, RIS = 36.8 μg/ℓ, dry weight), resulting in less phytoplankton grazing in the mid bay and offshore.

In contrast to the phytoplankton production, fouling growth on the microcosm walls increased along an inshore direction, (wall growth: Prov = 300 gdw/tank, JT = 144 gdw/tank, and RIS = 100 gdw/tank). This has been attributed to the higher inshore benthic nutrient fluxes (J. Kelly et al., 1981). The benthic respiration (O_2 uptake) of Providence sediments is roughly 2.7 times the Jamestown and 2.6 times the Rhode Island sound levels of activity [see F(4,3), Figs. 4a, 4b, 4c)].

3.0 An Approriate Mode of Analysis

G.L. Swartzman (1979) noted the underlying similarities of ecosystem models describing systems as different as forest and marine ecosystem. The generality of ecosystem structure and dynamics prompted Patten, Bosserman, Finn and Cale (1976) to discuss the approach of identifying and comparing the general system properties of ecosystems.

The systems approach employed in MERLIN normalizes and quantifies such system concepts and properties such as "environmental gradients" and "resistent and resilient" communities through the use of system measures of activity and recycling on the whole system and compartmental level of organization.

E.P. Odum et al. (1979) spoke descriptively of a hyperbolic functional response of system productivity to energy or nutrient enrichment.

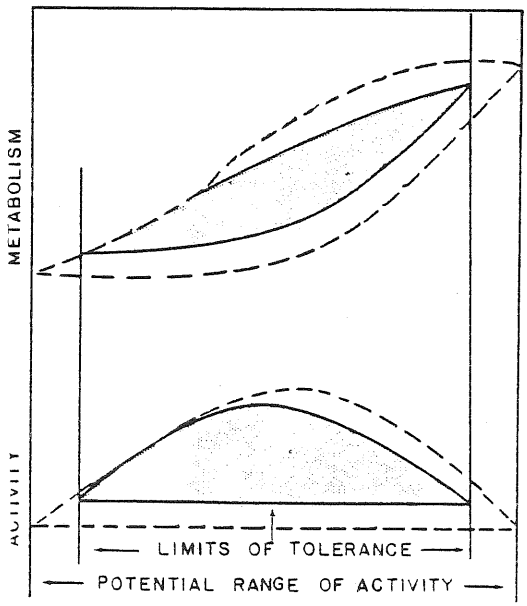


Fig. 10 Hyperbolic Production Response to Enrichment
from E.P. Odum, 1971

Whether the system is enriched with thermal energy, mineral nutrients on prey, there comes a level above which additional supplements to the system are deleterious. It is hypothesized that evolution works on the community level (M.J. Dunbar, 1960) and that there exist communities adapted to the level and frequency of inputs and perturbations, R. Levins (1968). Webster, Waide and Patten (1974) characterized the r-type and k-type communities (R. May, 1973) as being resilient and resistent, respectively. The mechanism that distinquished these communties was their ability to store and recycle scarce nutrients. The resilient r-type ecosystems specialize in the endpoint environments depicted in Figure 10 where nutrients are scarce relative to energy such as a new field, or eutrophic waters where energy is low - relative to the over abundant nutrients. Nutrient or energy pools are low and the stocks are maintained by high nutrient turnover rates and little recycling. The resistent, k-type ecosystems specialize in the optimum environs of Figure 10, characterized with high standing stock biomass, slow nutrient turnover and considerable nutrient recycling.

3.1 The Hypothesis to Test

The concept of stress gradients and the relationship of storage and recycling processes to system resistence are resilience are intuitively logical and attractive. These intuitions remain as hypotheses since most papers have analyzed only hypothetical ecosystems for these properties. The intent of MERLIN is to test these concepts directly on system observations. The MERL gradient experiment lends itself especially well to this task. Initially, the question is how Providence, Jamestown and Rhode Island Sound differ with respect to their mineral usage and recycling.

3.2 The Assumption and Methods

For simplicity the MERL microcosms are described by six compartments. (X_1 = phytoplankton, X_2 = zooplankton, X_3 = the benthos, X_4 = the dissolved nutrient pool, X_5 = the particulate pool, and X_6 = the wall growth). The flows between these compartments are described by the general equation:

$$d\underset{\sim}{X}/dt = A\underset{\sim}{X} \qquad \text{(eqn. 1)}$$

where dX/dt is the change of nutrient level in $\underset{\sim}{X}$. That is:

$$dx_i/dt = \sum_{j=1}^{n} (a_{i,j} * X_j) \qquad \text{(eqn. 2)}$$

There are n^2 linear combinations possible in this n-compartment system. Flow analysis examines the network of flows.

$$(f_{i,j} = a_{i,j} * X_j) \qquad \text{(eqn. 3)}$$

between compartments. By definition the throughflow of a compartment is the combination of incoming flows other compartments, the environment ($Z_{i,0}$) and internal storage ($\dot{\bar{X}}_i$). Throughflow, using the symbols of Figure 1, is:

$$T_i = \sum_{j=1}^{n} f_{i,j} \dot{\bar{X}}_i + Z_i \qquad \text{(eqn. 4)}$$

the flows ($f_{i,j}$) can be expressed in terms of fractions ($q_{i,j}$) of donor throughflow

$$(q_{i,j} = f_{i,j}/T_i) \qquad \text{(eqn. 5)}$$

Thus equation 4 in matrix form is

$$\underset{\sim}{T} = Q * \underset{\sim}{T} + (\dot{\bar{X}} + \underset{\sim}{Z}) \qquad \text{(eqn. 6)}$$

Solving for the throughflow vector we find:

$$\underset{\sim}{T} = (I-Q)^{-1} * (\underset{\sim}{X} + \underset{\sim}{Z}) \qquad \text{(eqn. 7)}$$

Intuitively, equation 7 solves for the dynamics of Figure 1. The throughflow (T_i) is a measure of the activity of the ith compartment. The inverse matrix $(I-Q)^{-1}$ is called the normalized matrix (N^{**}). In it, the activity of the ith compartment is apportioned among the inputs to the (n-1) other compartments and itself.

$$T_i = \sum_{j=1}^{n} (n^{**}_{i,j} * (\dot{\bar{x}}_i + Z_i)) \qquad \text{(eqn. 8)}$$

The elements of N^{**}, $n^{**}_{i,j}$ represent the apportioned throughflow caused by a unit input into the ith compartment. The compartmental recycling index is derived from this normalized matrix:

$$RE_i = (n^{**}_{ii} - 1)/n^{**}_{ii} \qquad \text{(eqn. 9)}$$

The cycling index in turn is,

$$CI = (\sum_{j=1}^{n} RE_i * T_i)/TST \qquad \text{(eqn. 10)}$$

The total system throughflow (TST) is the system equivalent of the T_i and is the sum of all the system's compartmental throughflows.

$$TST = \sum_{i=1}^{n} T_i \qquad \text{(eqn. 11)}$$

The flow coefficients are derived to quantify the microcosm's behavior over time and between experimental replicates for comparative and contrasting purposes. The input/output techniques are employed to take into account the simultaneous flows.

Requirements:

There are three steps to this project.

The first is to transform the MERL data into a time series of system time derivatives ($dX/dt = f(X_{i,t} - X_{i,t-1})$). Spline functions (IMSL Programs) will be used to draw smooth curves through the data points to facilitate the computation of time derivatives. One problem is that the microcosms change very quickly. By averaging over equivalent replicates, some estimate of the average behavior may be gained.

The second stage involves converting the smoothed time derivatives into the n^2 compartmental flows. The two assumptions made at this stage are that flows follow seasonal patterns shown in Figure 2. Second, it is assumed that the C:N:P:Si ratios in the seven compartments vary with time.

The third step involves the computation of the flow coefficients described in the methods section. Obviously the assumed linkages and the C:N:P:Si ratios will dictate the values of the derived flow analysis coefficients. The major task involves reconciling the results of this exercise with the working hypotheses. In an iterative manner, one can determine the time series assumptions of flow connections and C:N:P:Si ratios that best agree with the data. In modeling jargon the process of

fitting the model to the data is called system identification. This is an understandably controversial albeit unavoidable step in modeling. The outcome of the iterative process of comparing the implications of our working hypothesis with the field data is a refinement of our perceptions of the system.

4.0 Results

Figure 4 and section 2.4 depict the observed distributions and flows of carbon in three marine ecosystem. Comparisons can be made on individual bases (x_i vs. x_j, f_{ij} vs. f_{ik}) within and between system. Flow analysis is an approach for summarizing the relative size or importance of a compartment of flow taking into consideration the problem of system scale. Flow analysis produces for each ecosystem analyzed,

i. a set of flow coefficients and

ii. a series of normalized flow diagrams.

The flow coefficients allow for comparison between ecosystems. The normalized flow diagrams are useful for comparing the relative roles compartments play within a single ecosystem.

4.1 The Comparative Flow Coefficients

An ecosystem's total system throughflow, (TST), is a measure of that system's nutrient activity. Analogous to the GNP measure used by economist to compare national economic activity levels, TST increases with the magnitude of nutrient transfers between compartments.

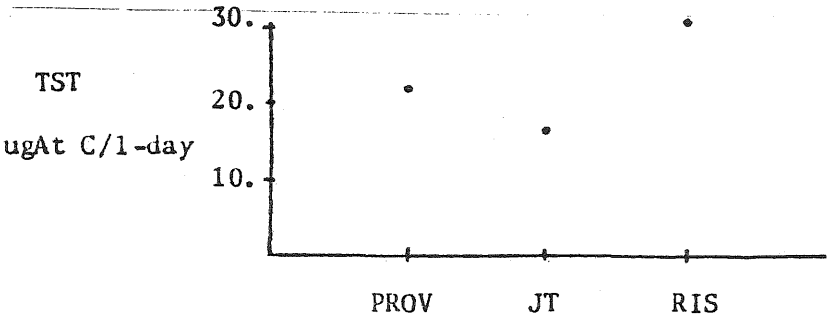


Fig.11 Total System Throughflow at Providence, Jamestown and Rhode Island Sound

The highest level of activity were observed in Providence and Rhode Island Sound. The Providence system was highly subsidized by the benthic sector. Rhode Island Sound's high carbon flow activity is in keeping with the fact that it had the highest phytoplankton and primary production levels. The TST is a measure that also allows the observer to normalize the other observed flows. Individual flows can than be interpreted in the context of the total activity of the system. For example, the regenerative flows (phyto- and zooplankton) into the dissolved pools of the Providence and Rhode Island Sound microcosms are both larger than Jamestown's flows. But within the perspective of total activity, Jamestown's regenerative activity is greater than either Providence or Rhode Island Sound, per unit of TST. This is shown by comparing the cycling indices of the three systems.

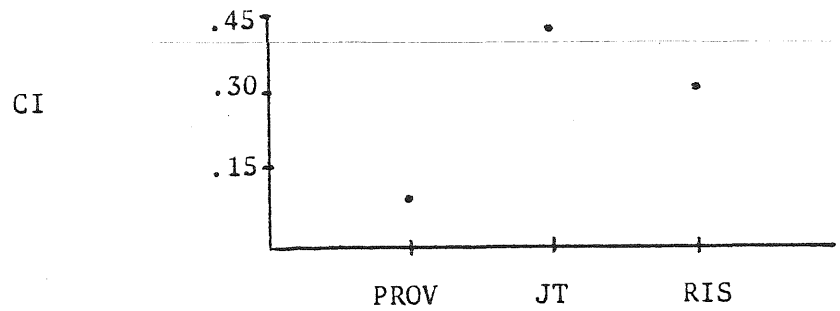


Fig.12 The Cycling Index at Providence, Jamestown and Rhode Island Sound

The cycling index, is the ratio of the portion of throughflow that recycles to the total throughflow of the system. CI ranges from 1 to zero. It is possible for a system with low total system activity to have a high cycling index when a greater portion of the nutrients are recycled.

This is analogous to the case of small country (Switzerland) having a higher currency recycling index than a larger country (Mexico) by virtue of having more intricate economic structure and recycling of currency. The cycling index is a measure of utility a system derives from a unit input of nutrient. The average path length (APL) represents the average number of compartments an injected atom of carbon would pass through before leaving the system. The respective APL for Providence, Jamestown and Rhode Island Sound are 3.713, 6.56 and 5.4

The compartment cycling index (RE_i) is a measure of the fraction of the nutrient flow that passes through the ith compartment that returns (Table 4). The relative magnitude of RE_i designates the sources and sinks of carbon in the system. Glancing at Table 4 reveals that the components do not play the

same roles in different ecosystems. In Providence the dissolved pool (X_4) and the walls (X_6) were the greatest recyclers, followed by the phytoplankton (X_1) and zooplankton (X_2). The relative sink of the system was the particulate matter's pool (X_5). Subsidized by the greatest benthic inputs, the production in the Providence water column was less dependent on recycling than the Jamestown and Rhode Island water columns. In the Jamestown water column, the zooplankton sector is shown to have the largest recycling index than either Providence or Rhode Island Sound. The other two microcosms recycle more through the phytoplankton than the zooplankton. The Rhode Island Sound microcosm is distinquished by retaining the carbon the longest in the zooplankton compartment.

4.2 Pulse Response Studies

The normalized flow diagrams (Figure 13) answer questions pertinent to the probable destinations of inputs (nutrient or equally soluable pollutants) to the system. Figure 13 describes the input responses of the Jamestown ecosystem. There are six normalized flow diagrams. Each represents the consequence of an input into one compartment at a time.

The numbers within each compartment represents the throughflow (in μgatC/ℓ) that can be expected in each compartment before all of the unit input, (1 μgatC/ℓ) exists from the system. The arrows represent the relative contributions of other compartments to this hypothesized compartmental throughflow. The fact that the compartmental throughflows are greater than 1.0 reflects the degree of recycling that is responsible for system activity.

Provided that the hypothesized flow mechanics (section 2.2) are correct, these normalized flow diagrams predict the consequences of enriching a specific compartment.

5.0 Summary and Conclusion

Through the simulation and analysis of the microcosm dynamics, it is possible to demonstrate some properties of ecosystems, (i.e. responses to enrichment gradients and the concepts of resistence and resilience) with real (data derived) system coefficients.

From the field data it was clear that Providence was a system whose internal flows were dominated by benthic nutrient fluxes. Rhode Island Sound was a more neritic water column dominant by phytoplankton. Jamestown was a more intermediate setting.

By normalizing the individual flows, F(i,j), with respect to total system throughflow, TST, the hyperbolic response of system production (defined in section 3.1) to enrichment was demonstrated. The general system properties of resistence and resilience, however, as defined by Webster, Waide and Patten (1974), have origins in terrestrial ecology, and are not entirely applicable to coastal marine ecosystems.

In this study the resilient r-type strategist are the Providence and Rhode Island Sound microcosms. They represent the end members of the hypothesized hyperbolic enrichment gradient (E.P. Odum et al., 1979). Their low cycling indices (CI) agree with the generalization that resilient ecosystems have characteristically low internal nutrient recycling. The more resistent k-strategist Jamestown ecosystem falls in line with the theory by having the highest cycling index (Figure 12).

In marine ecosystems, however, the more resistent systems are not necessarily distinguished by higher fixed biomass as in a forest. The more resistent marine systems tend on the contrary to retain nutrients and promote more production stability per mole of available nutrients through recycling. The Jamestown microcosm had the highest average path length of the three systems (APL_{PROV} = 3.7, APL_{JT} = 6.56 and APL_{RIS} = 5.4). In short, the Jamestown carbon atoms made more intercompartmental transfers before leaving the system. Although the Rhode Island Sound microcosm had a higher level of production, it can quantitatively be shown that the Jamestown system generated more activity per mole of carbon available than the Rhode Island Sound system. The normalized flow diagrams (Figure 13) discussed in section 4.2 describe how the nutrients are retained in the system. The normalized flow diagrams also show the relative distribution that would be obtained of tracers were injected into specific compartments.

The MERLIN simulation/analysis package has a potential of not only testing and refining our perceptions of ecosystem behavior in more quantitative terms, but of also acting as a tool in the design and analysis of MERL experiments such as the ^{14}C tracer studies in preparation. When the flow simulator is sufficiently refined, it might also be possible to predict the possible outcome of pollution events in urban, bay and coastal ecosystems.

The present study of the June 11-12 dynamics is just the tip of the iceberg. The analysis of the weekly data sets would pro-

vide insight into how the dynamics of the coastal ecosystem change through the annual cycle. A further elaboration would be the parallel analysis of the Nitrogen, Phosphorus and Silica cycles. Examination of the nutrient uptake depth profiles (Figure 9) indicate another order of complexity that must be considered.

Figures:

Fig.1 System view of the MERL microcosm

fig.2 The types of data available

Fig.3 Biomass distributions of standing stocks

Fig.4 Flows F(i,j) within the systems

Fig.5 Yealy Wall Production (Jack Kelly,MERL(1981))

Fig.6 Zooplankton time series

Fig.7 Phytoplankton time series

Fig.8 Nutrient time series

Fig.9 Uptake of nutrients:Depth Profiles

Fig.10 Hyperbolic Production Response to Enrichment

Fig.11 Total System Throughflow Plots

Fig.12 Cycling Indices

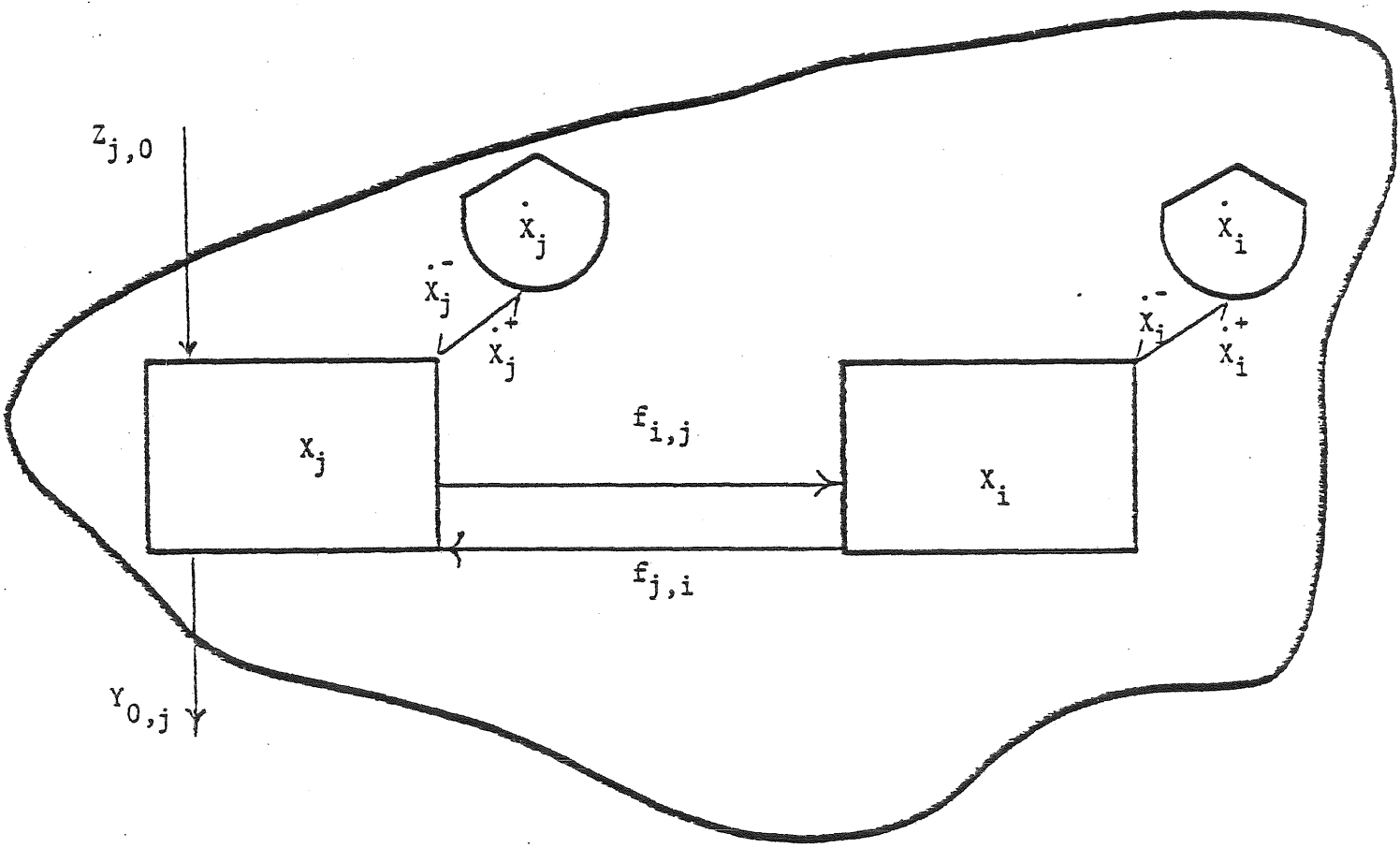
Fig.13 Normalized flow diagrams

Table 1 Data Summary

Table 2 F-Matrix

Table 3 Primary Production

Table 4 Compartmental Recycling Indices



Compartmental Model notation.

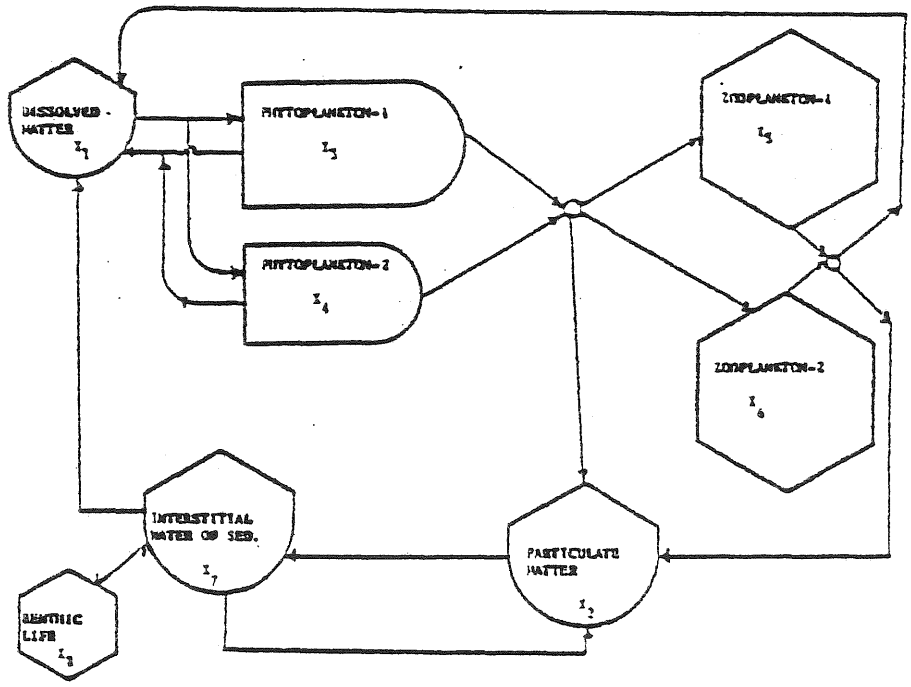


Figure 1. Generalized Flow Model

Figure 2. Data Available

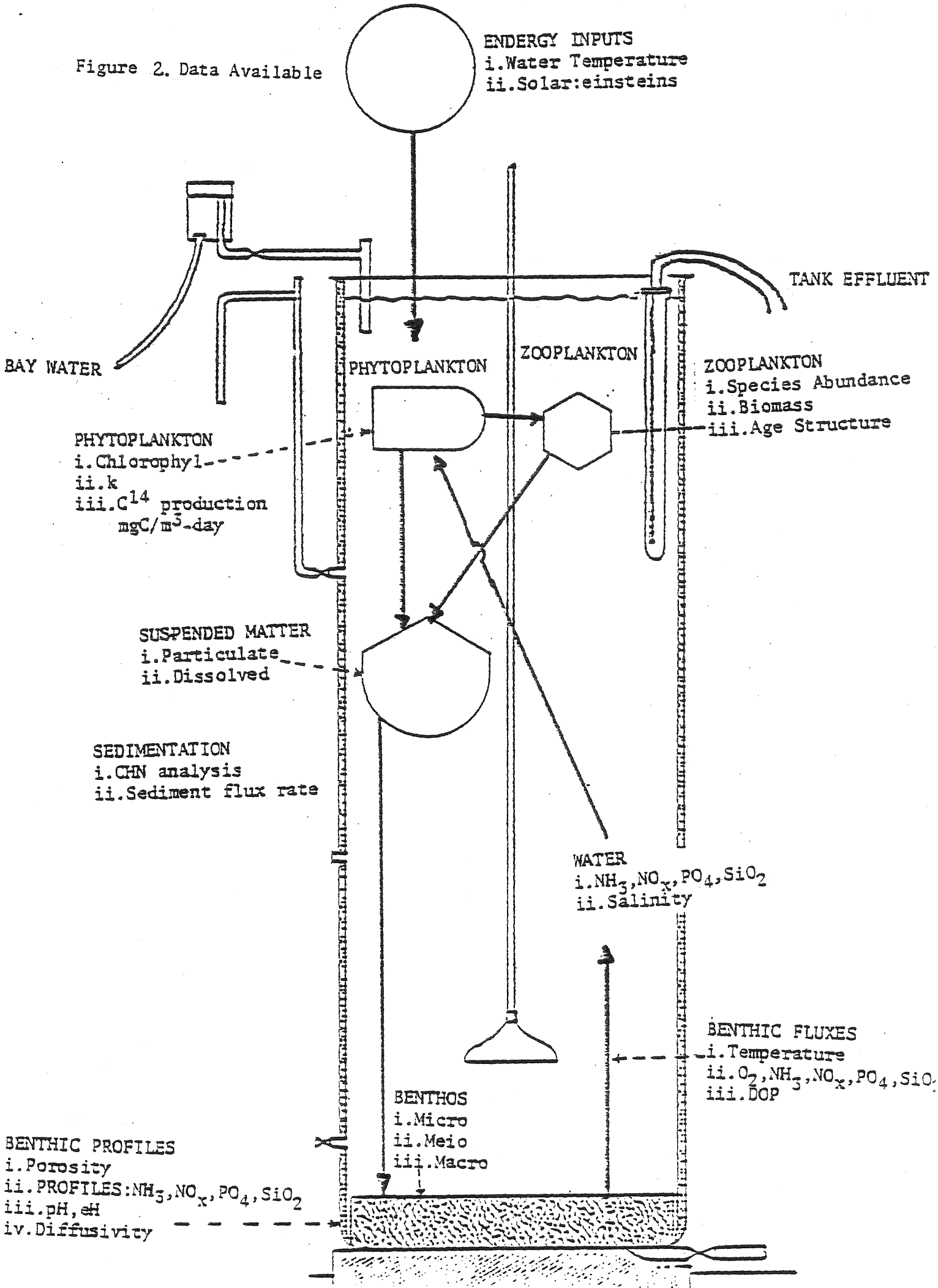


Figure 3. Particulate Biomass distributions

	PROV	JT	RIS	
%Phyto	4.8	5.9	10.9	
%Zoopl	2.7	1.9	1.8	
%Detritus	92.4	92.1	87.3	
P/Z	1.9	3.0	5.9	
Total Mass	3.3	2.3	2.0	$x10^3$ug/l

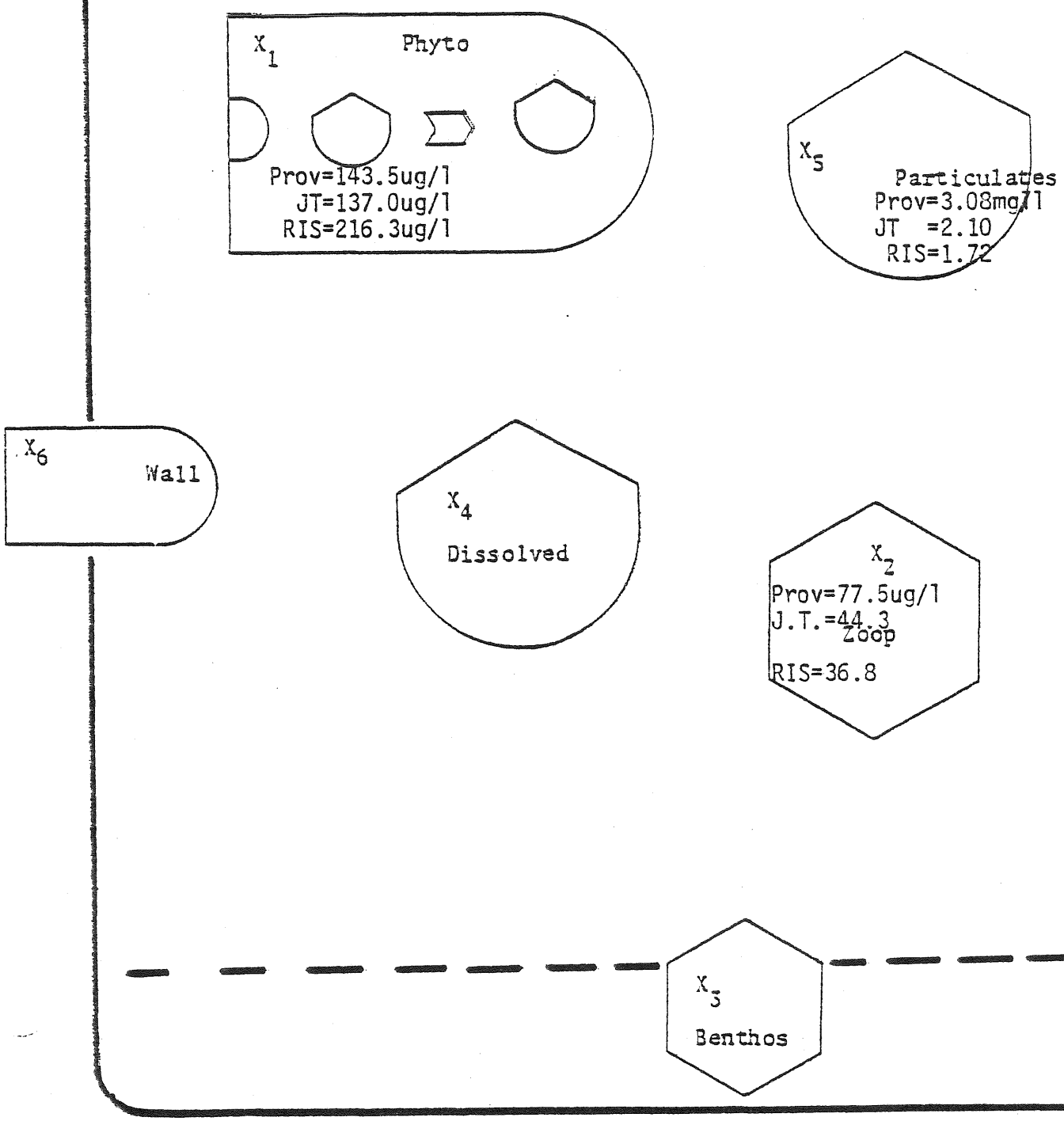


Figure 4a Nomenclature of Flows

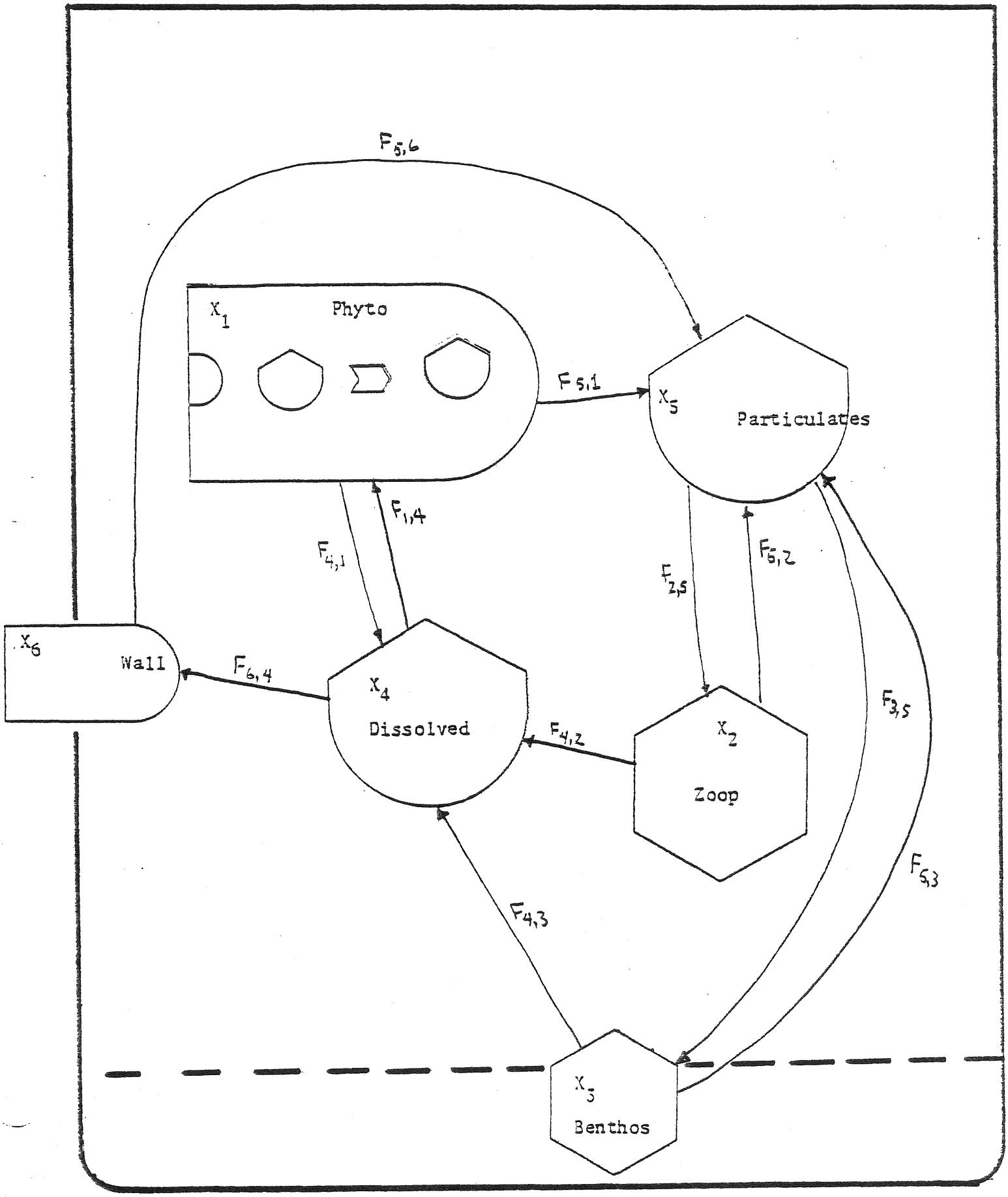
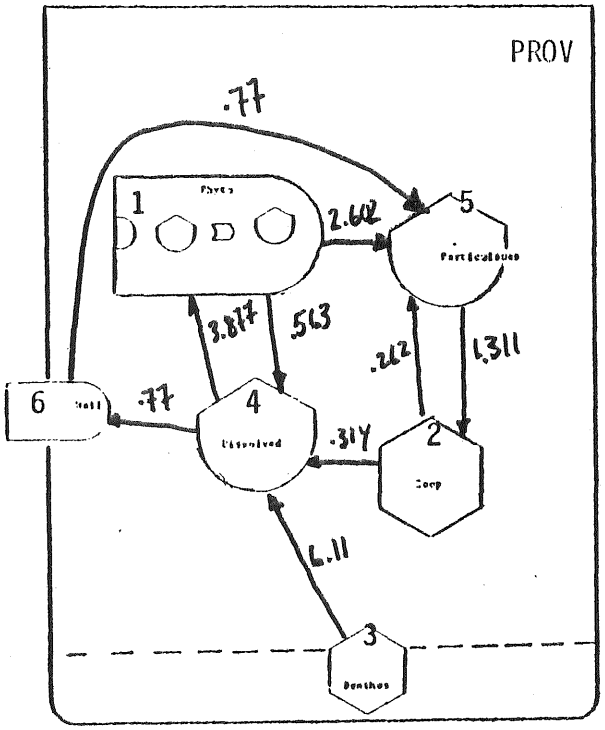
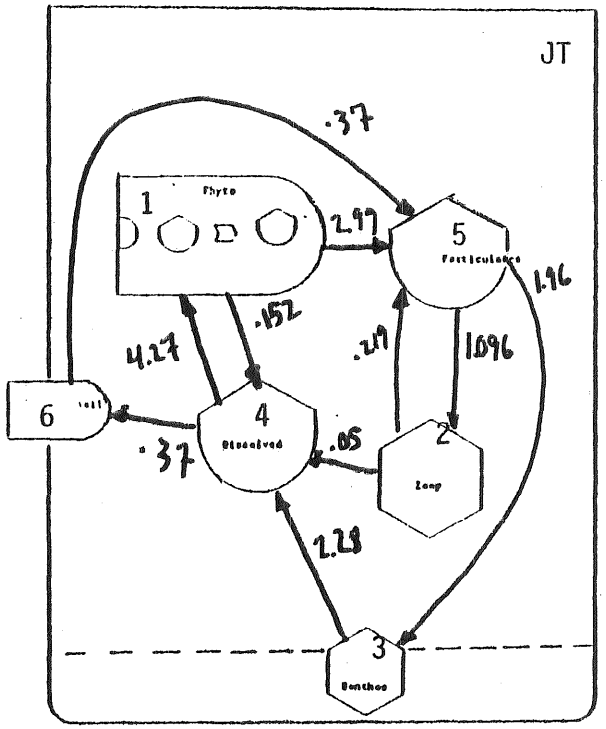
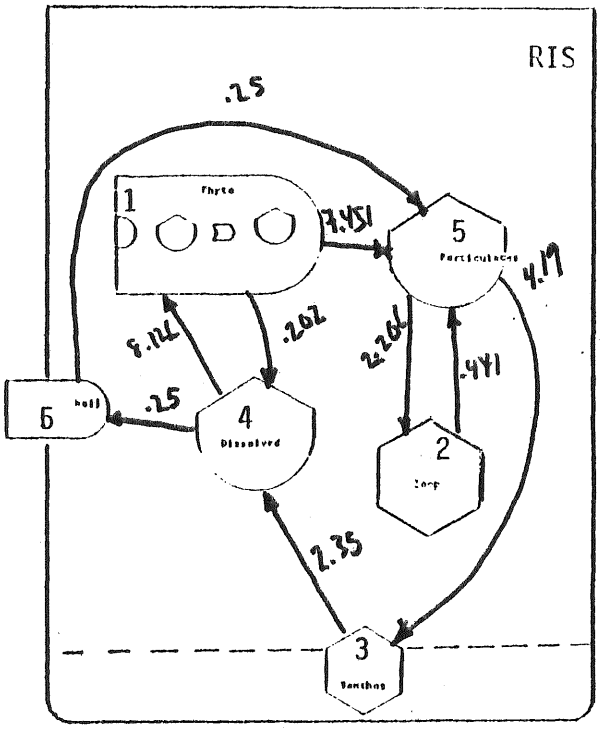


Figure 4b. Quantified Flows Unit= ugatC/l-day







Flow Coefficients

TST= 22.69ugatC/l-day
TSTS= 20.77 "
TSTC= 1.92 "

APL=3.713 compartments

CI=0.0845

Flow Coefficients

TST= 16.22
TSTS= 9.29
TSTC= 6.93

APL= 6.56

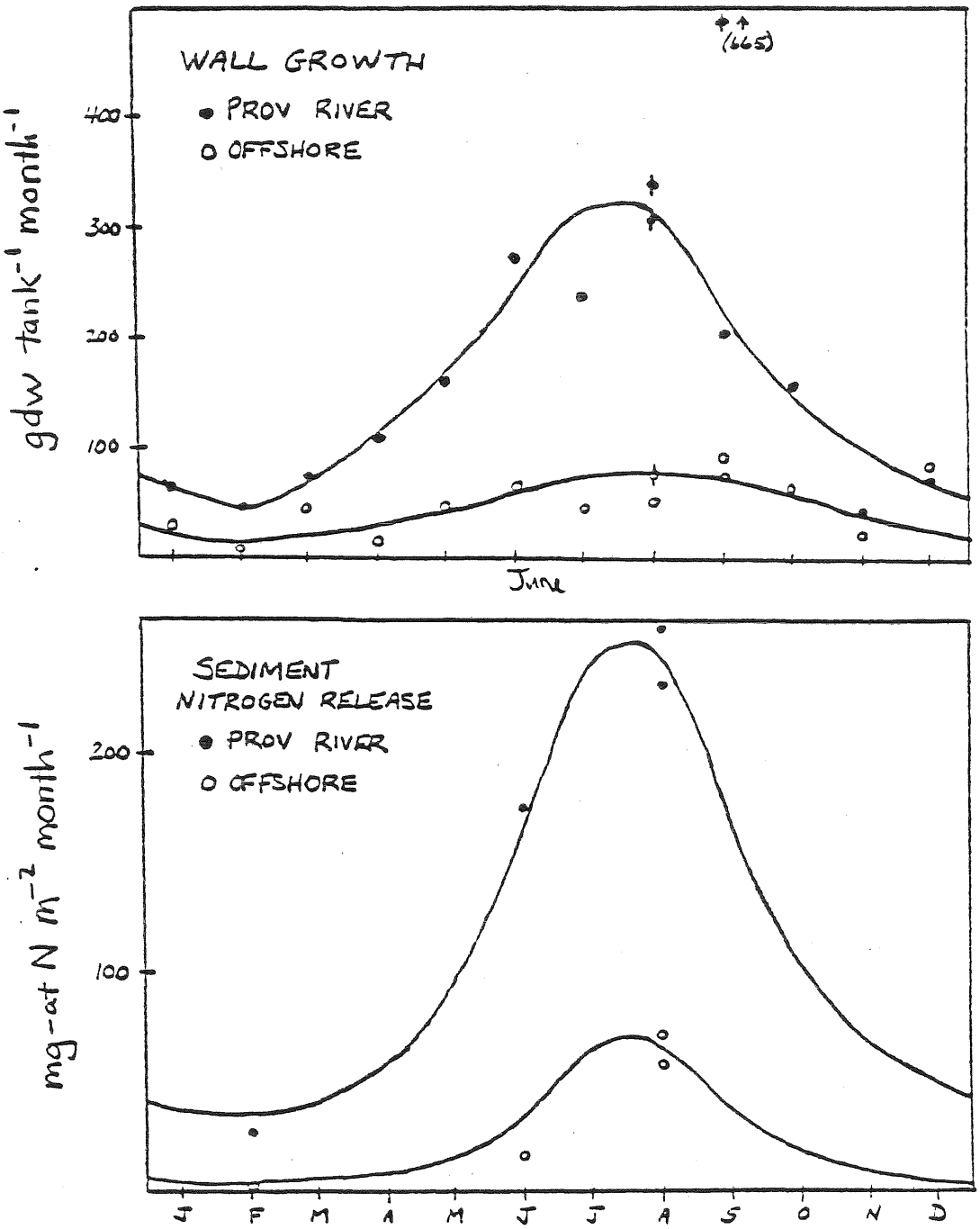
CI= 0.427

Flow Coefficients

TST= 31.29
TSTS= 22.17
TSTC= 9.12

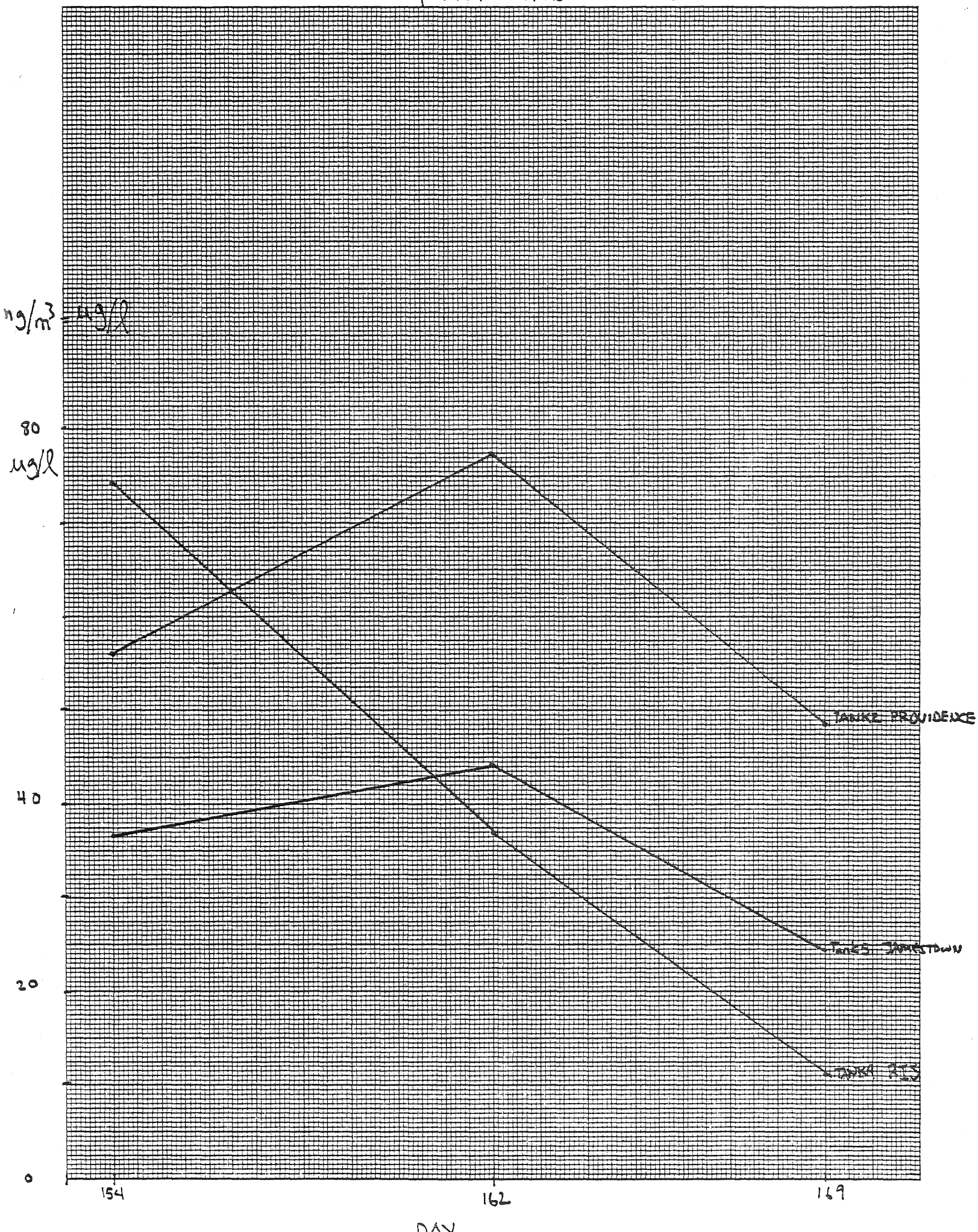
APL= 5.40

CI= 0.291



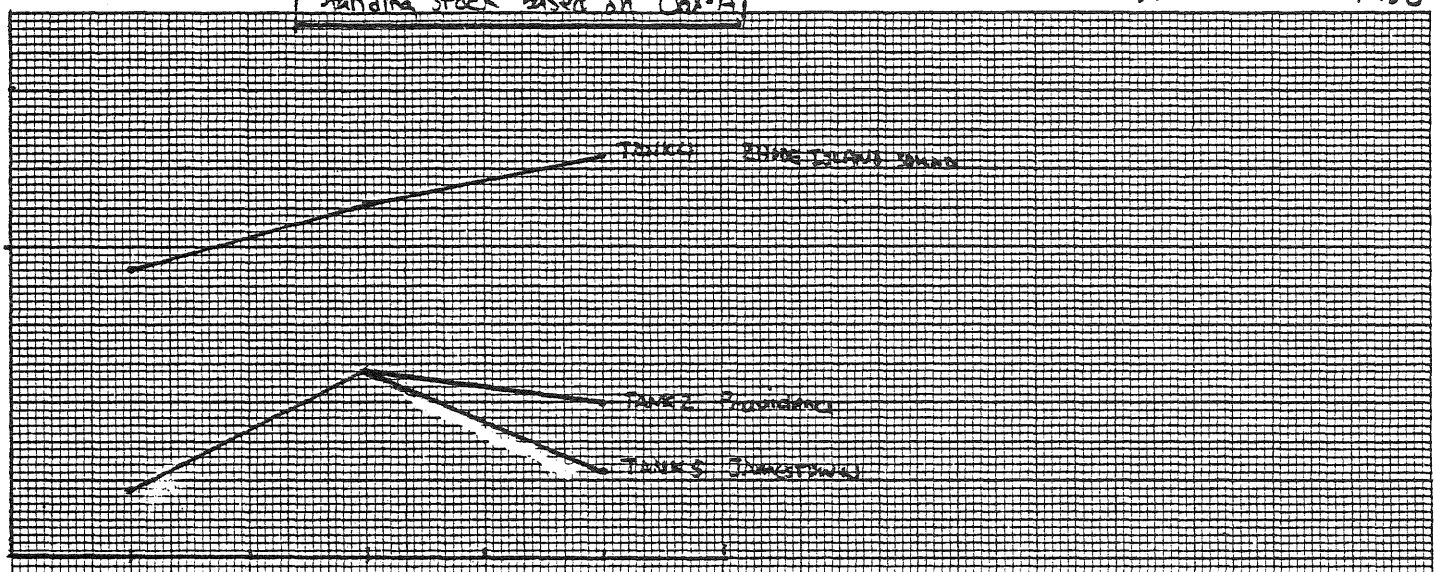
J. Kelly
MERL 1981

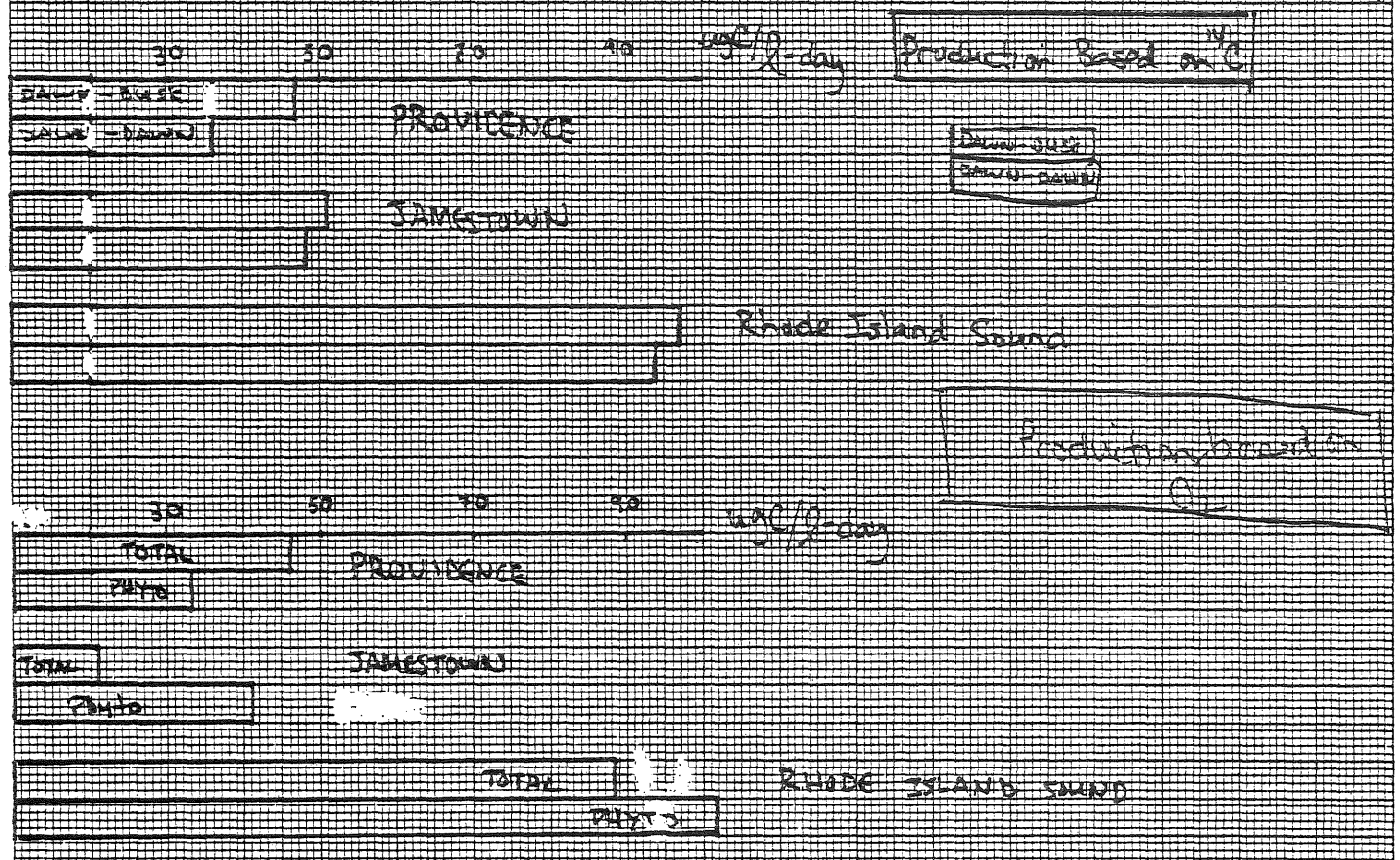
Zooplankton Biomass -vs- time



Standing Stock based on Chl-A

6/11 - 6/12 1980



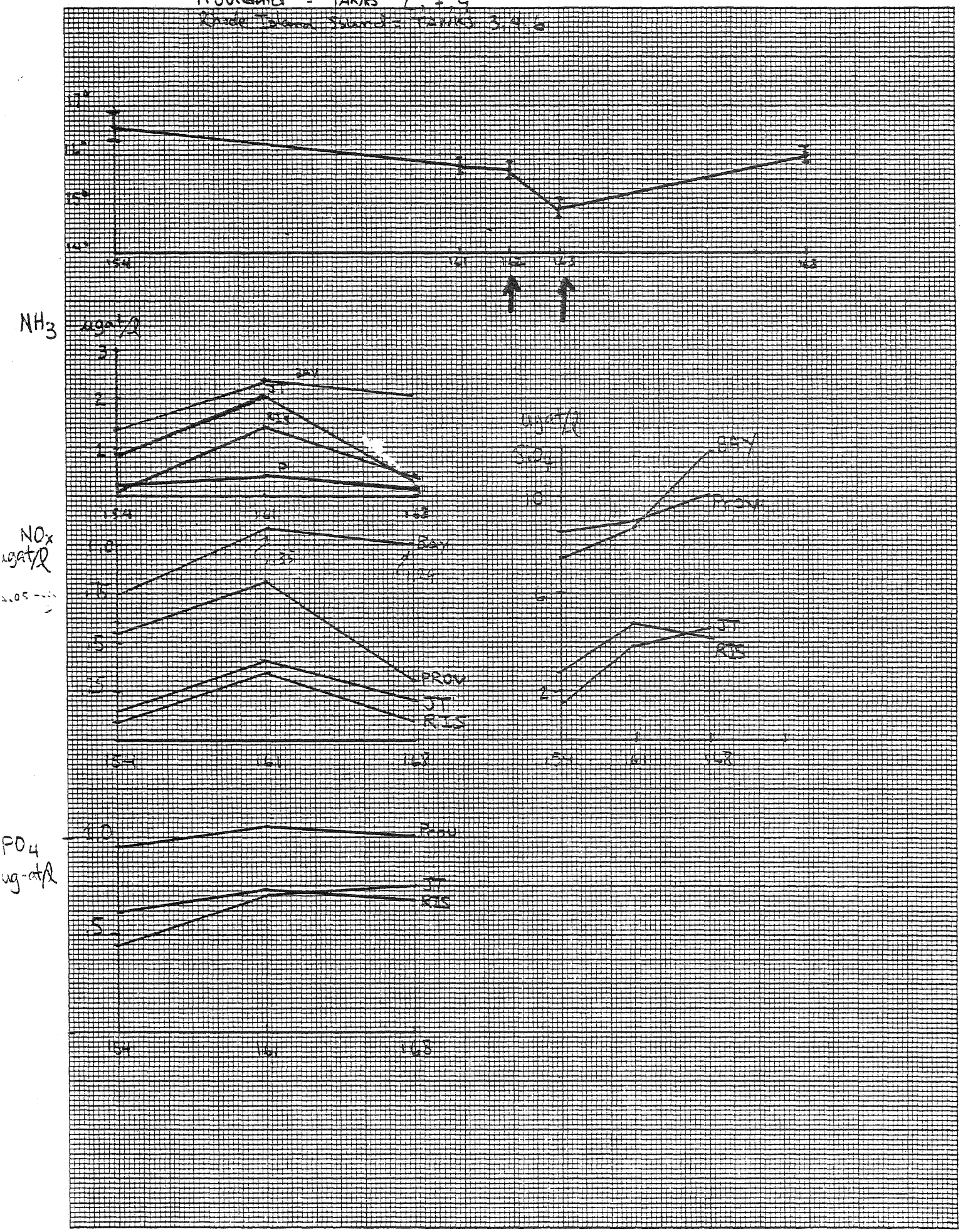


CONTROL (JAMESTOWN) = TANKS 1, 5, 8

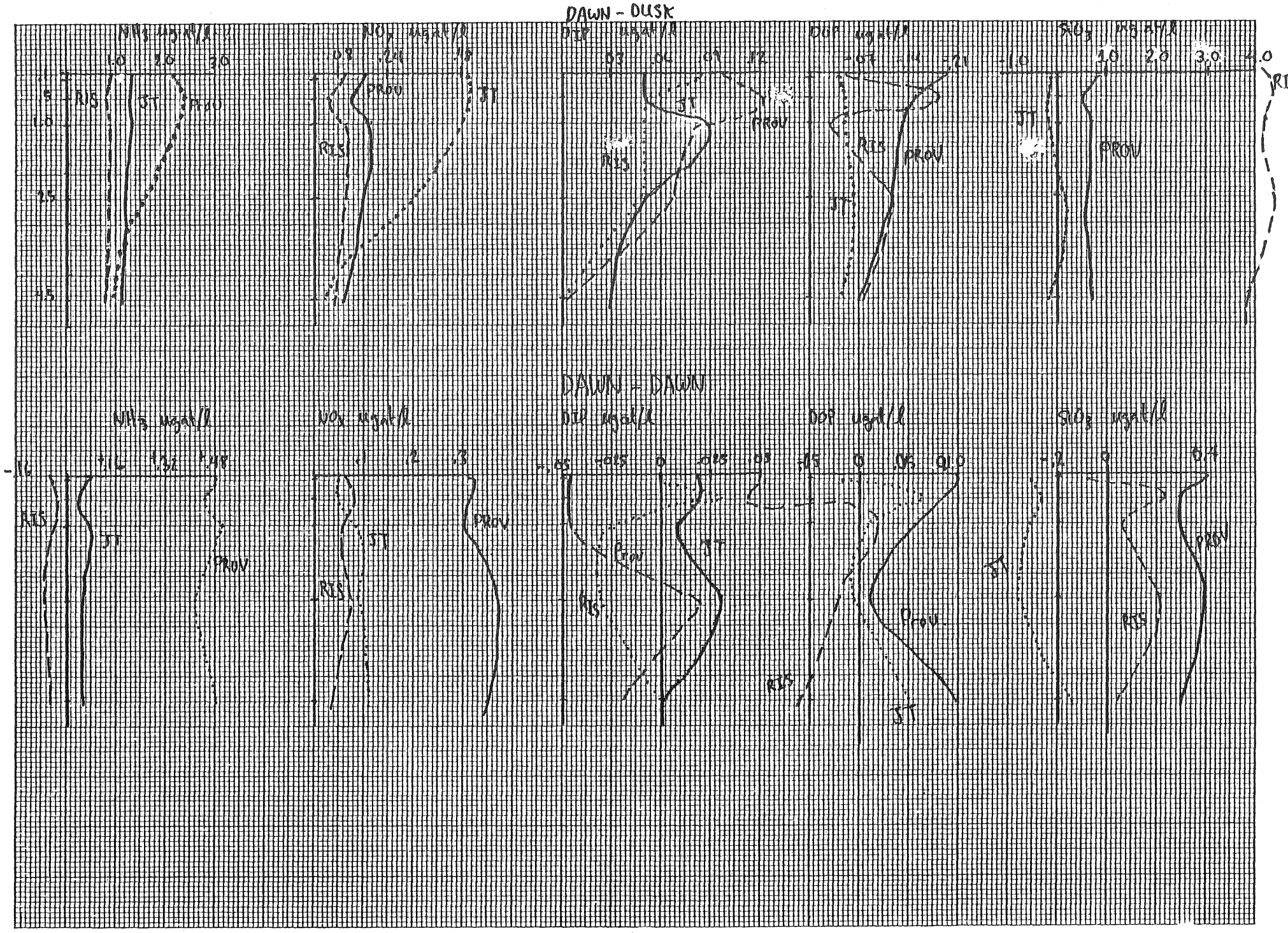
Providence = TANKS 2, 7, 9

Rhode Island Sound = TANKS 3, 4, 6

Environmental Data



UPTAKE



TANK 1 | Providence Sediments | Jamestown | Rhode Island Sound |

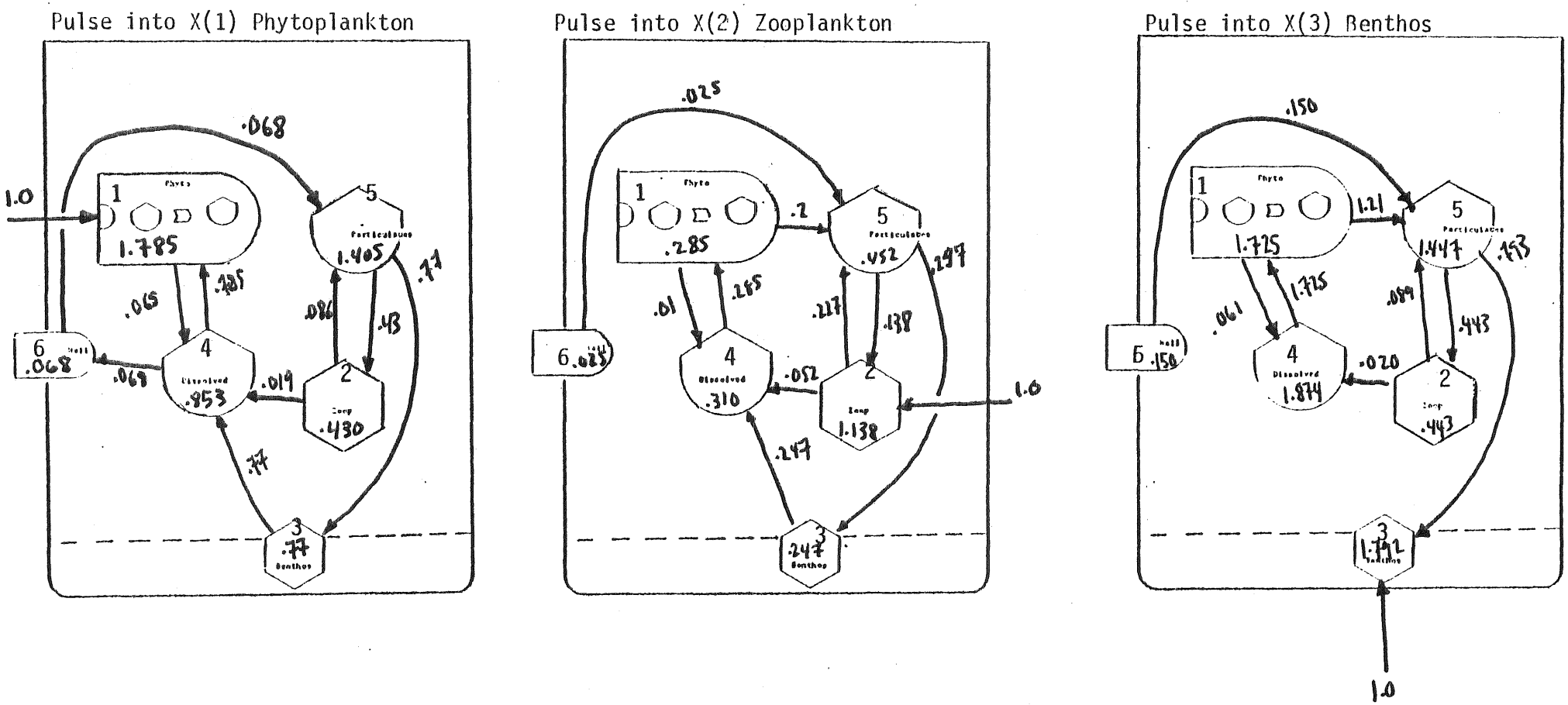
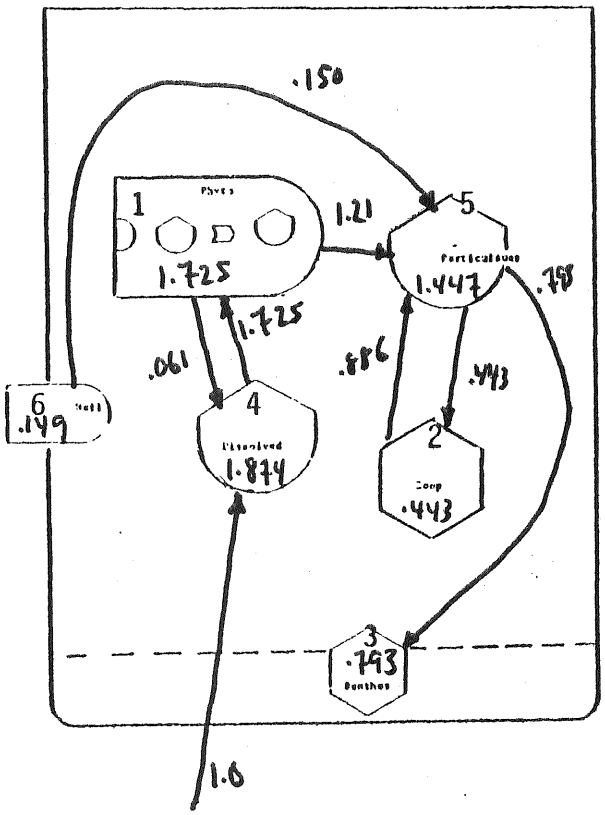
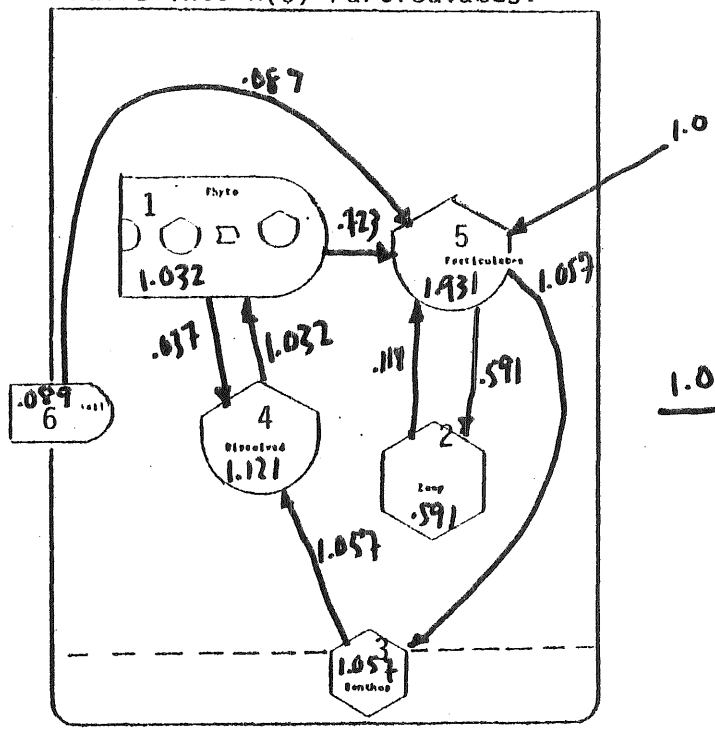


Figure 13. Normalized Flow Diagrams for Jamestown Microcosm Site

Pulse into X(4) Dissolved Nutrients



Pulse into X(5) Particulates



Pulse into X(6) Wall Community

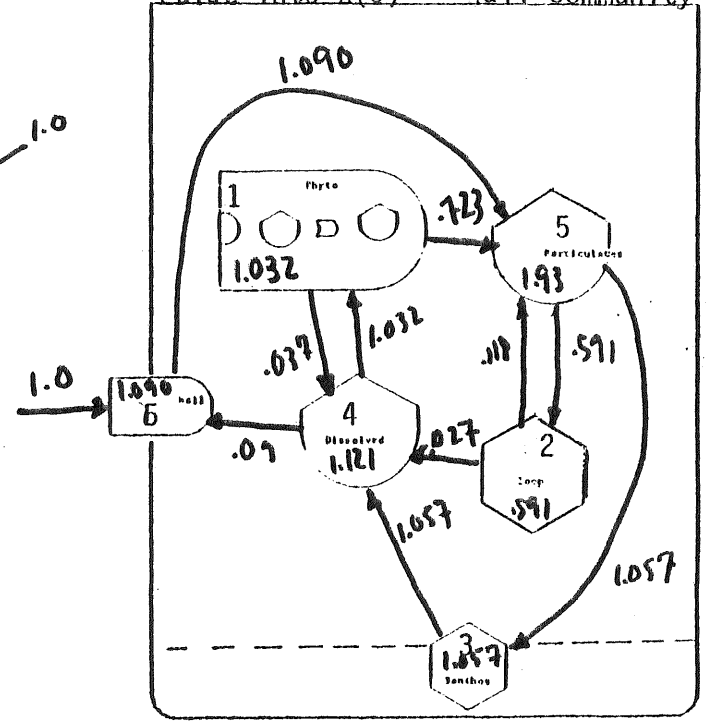


Figure 13 Continued

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(Batch)?

DAY 162: morn
163: morn

		Providence				Mid Bay				
		Dawn	Dusk TANK 2	Dawn	Dusk	Dusk TANK 5	Dawn	Dawn	Dusk TANK 7	Dawn
Experiments	NH_4, ugat/l	3.32	2.08	1.91	1.31	0.12	0.20	0.54	0	0.03
	NO_2+NO_3 ugat/l	1.30	1.58	1.49	.78	.55	.65	0.26	0.22	0.25
	DON	22.5	22.1	20.9	15.0	12.0	11.5	10.0	[illegible]	18.5
TABLE-1	TOTN	27.12	25.76	24.3	17.07	13.27	12.35	11.7	[illegible]	15.78
	DIP ugat P/l	.95	.90	.95	.55	.52	.55	0.06/0.01	0.61	0.61
	DOP ugat P/l	.49	.62	.56	.50	.56	.46	0.59	0.58	0.58
	Part-Phos									
	SiO_4 ugat/l	12.1	11.5	19.0	6.51	6.34	6.75	7.74	[illegible]	[illegible]
Experiments	Part-SiO_3 ugat/l	2.41	3.65	[illegible]	3.74	2.95	3.01	3.6	3.8	5.07
	Part-Total mg/l	1.92±.49	3.17±.19	4.5 ±.23	2.05±.47	2.44 ±.12	2.36±.27	1.8 ±.08	1.95 ± [illegible]	2.15 ± [illegible]
	Chl-A mg/l	1.63	2.14	1.97	1.63	2.14	1.71	2.58	2.85	3.22
Fluxes	Flux O_2 mg O_2/m²h	54.7 mgO₂/m²h	137.8 mgO₂/m	1.06×10^{-2} mgO₂/l-h	20.4 mgO₂/m²h	51.4 mgO₂/hr	3.95×10^{-3} mgO₂/l-h	21.0 mgO₂/m²h	52.7 mgO₂/m	4.07 $\times10^{-3}$ mgO₂/l-
	Flux NH_3 ugat/m²h	217.4 ugat/m²h	547.8 ugat/hr	4.21×10^{-3} ugat/l-h	66.7 ugat/m²h	168.1 ugat/hr	1.29×10^{-2} ugat/l-h	13.5 ugat/m²h	46.6 ugat/m	3.58 $\times10^{-3}$ ugat/l-
	Flux NOx ugat/m²	26.3 "	66.3 "	5.10×10^{-3} "	13.5 "	34.0 "	2.62×10^{-3} "	4.6 "	11.6 "	3.12×10^{-3}
TABLE-2	DIP ugat/m²	14.2 "	35.8 "	2.75×10^{-3} "	5.9 "	14.9 "	1.15×10^{-3} "	2.6 "	6.6 "	5.08×10^{-4}
	DOP ugat/m²	5.4 "	21.2 "	1.63×10^{-3} "	1.2 "	3.0 "	2.31×10^{-4} "	-7.1 "	-17.9 "	-1.38×10^{-3}
	SiO_3 ugat/m²	69.0 "	173.9 "	1.34×10^{-2} "	62.0 "	156.2 "	1.2×10^{-2} "	-28.0 "	-70.6 "	-5.43×10^{-3}
	DON ugat/m²	182 "	458.6 "	3.53×10^{-2} "	17.6 "	44.4 "	3.42×10^{-3} "	-148 "	-373 "	-2.87×10^{-2}
TABLE-3	^{14}C Dawn-Dusk	230 mgC/m²			253 mgC/m²			482 mgC/m²		
	^{14}C Dawn-Dawn	178 "			241 "			408 "		
Net metabolism	Total O_2 Δ/Δt	.72 mgO₂/m²h	6.07×10^{-3} mgO₂/l-h		0.34 mgO₂/m²h	2.87×10^{-3} ← mgO₂/l-h		1.37 mgO₂/m²h	11.51 $\times10^{-3}$ mgO₂/l-h	
	Phys Δ/Δt	.52 "	4.38×10^{-3} "		2.64 "	5.31×10^{-3}		1.7 "	15.11 $\times10^{-3}$	
	Alk meq/l	2.0	1.95	1.95	2.0	1.99	1.99	2.04	2.05	2.05
	CO_3 mgC/l	23.0496	22.8144	22.8144	23.4036	23.2848	23.6400	22.8144	23.0496	23.0496
	corrected by	betty for dilution?								
		Tank 2	Tank 5	Tank 4	(mgat O/l-hr)					
	Total O_2 Δ/Δt mgat O_2				= (Xg/hr-m²)·(2.63 m²) / mgat O (X)*(12.64)					

Table 3. Primary Production

	PROV	JT	RIS		
Phyto Biomass	57.4	54.8	86.5		
^{14}C Prod	46.5	51.2	97.5	Dawn-Dusk	ugC/l
	36.01	48.76	94.7	Dusk-dusk	"
O_2based Prod	33.42	41.12	115.06		
PQ	1.098	0.9958	1.43		

Table 4. Compartmental Recycling Indices RE_i

Compartment	PROV	JT	RIS
x(1)	0.176	0.440	0.302
x(2)	0.143	0.122	0.080
x(3)	0.0	0.442	0.289
x(4)	0.189	0.466	0.309
x(5)	0.143	0.482	0.330
x(6)	0.189	0.082	0.013

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Final Bottle Concentration

Table 4

		Dawn-Dusk NH3 ug/l	NOx ug/l	DIP ug/l	DOP ug/l	SiO2 ug/l	Dusk→Dawn NH3 ug/l	NOx ug/l	DIP	DOP	SiO
Tank 2	0.1m	1.08	1.14	.85	.58	11.3	1.6	1.26	[illegible]	0.52	11.[illegible]
Prov	0.5m	0.93	1.17	.82	.67	11.6	1.63	1.88	[illegible]	[illegible]	11.[illegible]
	1.0m	1.05	1.12	.90	.62	11.4	1.55	1.28	[illegible]	[illegible]	11.[illegible]
	2.5m	1.52	1.14	.88	.61	11.5	1.66	1.21	[illegible]	[illegible]	11.[illegible]
	4.5m	2.41	1.20	.95	.56	11.4	1.60	1.23	[illegible]	[illegible]	11.[illegible]
Tank 5	0.1m	0.00	0.28	0.50	0.54	6.52	0.05	0.50	[illegible]	[illegible]	6.[illegible]
Mid Bay	0.5m	0.06	0.28	0.50	0.49	6.61	0.02	0.50	[illegible]	[illegible]	6.[illegible]
	1.0m	0.0	0.30	0.46	0.55	6.63	0.04	0.46	[illegible]	[illegible]	6.[illegible]
	2.5m	0.06	0.45	0.50	0.56	6.42	0.06	0.46	[illegible]	[illegible]	6.[illegible]
	4.5m	0.24	0.74	0.52	0.55	7.31	0.06	0.44	[illegible]	[illegible]	6.[illegible]
Tank 4	0.1m	0.00	0.17	0.58	0.54	3.48	0.04	0.16	0.61	0.61	3.7[illegible]
R.I.S.	0.5m	0.02	0.21	0.61	0.78	3.43	0.02	0.14	0.58	0.71	3.7[illegible]
	1.0m	0.00	0.16	0.61	0.62	3.46	0.04	0.16	0.64	0.55	3.7[illegible]
	2.5m	0.00	0.16	0.61	0.71	3.38	0.07	0.14	0.64	0.62	3.[illegible]
	4.5m	0.00	0.21	0.66	0.66	3.86	0.06	0.18	0.61	0.65	3.[illegible]

Table 5

		Dawn concentration - final concentration CONSUMPTION					Dusk concentration - Final concentration				
		Dusk→Dawn NH3 ug/l	NOx ug/l	DIP ug/l	DOP ug/l	SiO2 ug/l	Dusk→Dawn NH3	NOx	DIP	DOP	SiO
	0.1	2.24	.16	0.1	-.19	0.8	0.48	.32	-.05	.16	0.[illegible]
	0.5	2.39	.13	0.13	-.15	0.5	0.45	-.30	-.05	-2.05	0.[illegible]
TANK 2	1.0	2.24	.18	0.05	-.13	0.7	0.53	.30	-.05	.06	0.[illegible]
PROV	2.5	1.50	.16	0.07	-.12	0.6	0.42	.37	.02	.01	0.[illegible]
	4.5	0.91	.10	0.0	-.07	0.7	0.48	.35	-.02	.10	0.[illegible]
initial concent. →		(init=2.32)	(init=1.3)	(init=.95)	(init=.49)	(init=12.1)	(2.08)	(1.58)	(.90)	(.[illegible]2)	(11.[illegible]
	0.1	1.31	0.5	0.05	-.04	-.07	.07	.05	.02	-.03	-.[illegible]
	0.5	1.25	0.5	0.05	.01	-.10	.04	.05	.02	.07	-.[illegible]
TANK 5	1.0	1.31	0.48	0.09	-.05	-.12	.08	.09	.01	.02	-.[illegible]
MID BAY	2.5	1.25	0.33	0.05	-.06	.09	.06	.09	.03	-.01	-.[illegible]
	4.5	1.07	0.04	0.03	-.05	-.80	.06	.11	.06	.05	-.[illegible]
initial concent →		(1.31)	(.78)	(.55)	(.50)	(6.51)	(.12)	(.55)	(.22)	(.[illegible])	(6.[illegible]
	0.1	.84	.09	.08	.05	4.26	-.04	.06	0.0	-.1	-.0[illegible]
	0.5	.81	.05	.05	-.19	4.31	-.02	.08	.03	-.13	.0[illegible]
TANK 4	1.0	.84	.1	.05	-.03	4.28	-.04	.06	-.03	.03	.0[illegible]
R.I.S.	2.5	.84	.1	.05	-.12	4.36	-.07	.08	-.03	-.04	.[illegible]
	4.5	.84	.05	.00	-.07	3.88	-.06	.04	.0	-.07	.0[illegible]
initial concent →		(.84)	(.26)	(.66)	(.52)	(7.74)	(0.[illegible])	(0.22)	(0.61)	(0.53)	(3[illegible]

(c DIP [illegible]

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