WHOI-79-29

Copy 2

Woods Hole Oceanographic Institution

1930

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY

by

Thomas M. Leschine

February 1979

TECHNICAL REPORT

Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant #04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

WOODS HOLE, MASSACHUSETTS 02543

WHOI-79-29

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY

By

Thomas M. Leschine

WOODS HOLE OCEANOGRAPHIC INSTITUTION
Woods Hole, Massachusetts 02543

February 1979

TECHNICAL REPORT

Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant #04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

Reproduction in whole or in part is permitted for any purpose of the United States Government.
This report should be cited as: Woods Hole Oceanographic Institution Technical Report WHOI-79-29.

Approved for Distribution Robert W. Morse

Dr. Robert W. Morse
Associate Director and Dean

ABSTRACT

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input - output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

FOREWORD

The author wishes to acknowledge the assistance of several people in the preparation of this report. Thomas E. Jordan of the Boston University Marine Program and James T. Morris of the Marine Biological Laboratory Ecosystems Center supplied unpublished data and aided in its interpretation. John Teal of Woods Hole Oceanographic Institution and Ivan Valiela of the Boston University Marine Program provided valuable comments and criticism. John T. Finn of the University of Massachusetts supplied his computer programs for the analysis which appears in the fourth section and in the appendix. He also aided in system programming and computation. Ann Martin of the Marine Policy Program provided editorial assistance and Lynda Davis did the typing.

The author acknowledges the permission of the Marine Technology Society and of co-author Leah J. Smith for the reprinting of the paper "Input-output analysis for salt marsh bioproductivity" as the appendix here. It appeared originally in the Proceedings of the MTS-IEEE meeting OCEANS 78.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The Great Sippewissett Marsh, located in Falmouth, Massachusetts, has been studied intensively by biologists from the Woods Hole scientific community since 1970, when a long-term program of fertilization of the marsh surface was begun. This research has emphasized the inputs and outputs of various forms of nitrogen with respect to the marsh, and the interconversions undergone by these forms as they pass through the marsh biotic system. This emphasis stems from the fact that nitrogen has been shown to be the limiting nutrient for the growth of the grasses which make up the great bulk of the biomass in New England salt marshes, as well as for growth in the coastal marine waters with which such marshes have tidal exchange.

The fertilizer, sown by hand onto 10 m diameter test plots throughout the growing season, is a commercial variety manufactured from sewage sludge and having a high nitrogen content. A significant portion of the research associated with the fertilization program has focused on the changes induced in fertilized areas compared to nearby control areas. For example, a central observation has been that the biomass of *Spartina* grass parts both above and below-ground increases significantly in the nutrient rich areas produced by fertilization (Valiela, Teal and Persson, 1976).

This kind of research generates many other types of questions to which the present experiment design can only suggest answers. Many of the spin-off policy questions deriving from marsh fertilization are of this nature. For example, if marshes like Great Sippewissett are used as disposal sites for secondarily treated sewage, what will be the effects of the resulting effluent discharge to the sea? The flow model explicated in this report is designed to deal with a question of this nature. Given that fertilization increases the biomass crop of marsh grass, and hence the production of detritus by the marsh, is the growth of marsh shellfish likely to be similarly enhanced? Can marshes be viewed as "open" aquaculture systems in which a desirable level of shellfish output can be achieved by manipulating the nutrient inflow in order to substantially increase the available food supply for filter feeding marine organisms?

Much of the mathematical analysis which allows for exploration of these questions is not presented in the body of this report. This material has already been published in the Proceedings of the MTS-IEEE meeting "Oceans 78" (Leschine and Smith, 1978). That paper, included here as an appendix, explains the analytic method used and develops, for Great Sippewissett, a tentative relationship between nitrogen inputs to marsh sediments and nitrogen outputs from the marsh in the form of net growth in shellfish.

The purpose of this report is to describe in detail the construction of a schematic model of nitrogen flow through Great Sippewissett Marsh (Figure 1), as well as to present analysis of the model which did not appear in the MTS paper. The model presented here as a diagram is not analytic in the sense that a simulation model is; rather, it presents a static "snapshot" view of the flow of nitrogen under conditions averaged over seasonal observations of the marsh, in many cases extrapolated to approximate annual activity. Thus all flows in the model are expressed in kg N per year, and a good deal of the main body of this report will be devoted to an exposition of the data sources and calculations which produced the values used in Figure 1. The "model" on which most of the analysis is based is represented by Equation 5 of the appendix and is adequately explained there.

The additional analysis alluded to above is of two types. On the one hand, an alternative set of values to the ones used in the paper is presented, with a discussion of the reasons why the second set may be more germane to the problem at hand. On the other hand further mathematical analysis which gives a more precisely defined link between fertilizer inputs to the marsh and shellfish outputs from it than that described in the MTS-IEEE paper is presented. This analysis is an application of a method devised by Jack Finn (1977). A corollary discussion outlines ways in which revisions in the diagram structure itself could build a stronger case for enhancement of shellfish production than would any reasonable changes in values assigned to flows in the present model. It is argued that such analysis can guide the direction of future biological research when applications such as shellfish growth enhancement are a goal.

How to read this report

The reader unfamiliar with this material, especially the mathematical methods used, should read the appendix before reading the main body of this report. The mathematical technique of input-output analysis is explained there and motivated by means of both an example from economics and a hypothetical ecosystem flow diagram. Also, more of the background of the enhanced bioproductivity problem from an aquaculture and economics point of view is presented.

The reader will note that most of the main part of the report is taken up by its third section, "Compartmental analysis of nitrogen flow." Those uninterested in how the values which appear in Figure 1 were generated can skip this section without loss of continuity. Those interested in only some of the values in the figure can quickly find the relevant material in the third section by noting that the subsection numbering corresponds to the numbering in the diagram. In each subsection flows entering the system to the compartment under discussion from the outside are termed 'inflows' while those leaving the system from it are termed 'outflows'. Intercompartmental flows are always discussed under the heading of the donor compartment. Thus the 65 units net growth shown at the bottom of Figure 1 is discussed as an outflow from compartment 5 in subsection 5, while the derivation of the value 1250, listed as resuspension in the center of the figure, is discussed in subsection 1 under the heading 'transfers to other compartments.' Each subsection is organized so that inputs and outputs of the corresponding compartment are discussed first, transfers to other compartments second.

GENERAL DESCRIPTION OF SIPPEWISSETT MARSH NITROGEN FLOWS

The processes by which nitrogen enters and leaves Great Sippewissett Marsh, and by which various organic and inorganic forms of nitrogen are transformed by the marsh nitrogen cycle, have been amply described elsewhere. In particular, work in the Great Sippewissett Marsh has generated more than 30 published papers since 1973. We do not attempt more than a brief summary of those nitrogen flows which are represented in Figure 1 here. None of the flows presently understood to be significant to the marsh's overall function have been omitted. More detailed discussions are contained in several of the papers listed in the references. Especially recommended are: Valiela, Teal and Sass, 1975; Valiela, Teal and Persson, 1976; Valiela and Teal, 1978; and Valiela, Teal, Volkmann, et.al., 1978. The last two named sources are especially relevant to the discussion immediately following.

The flow diagram shown in Figure 1 has five compartments: (1) shallow marsh sediments/pore water; (2) Spartina below-ground biomass; (3) Spartina above-ground biomass; (4) tidal water; and (5) shellfish. This organizational scheme reflects a view of the marsh in which the mainstream flow of nitrogen and other nutrients through it is roughly in the order indicated by the numbering of the compartments. That is to say, ground water and precipitation bring nitrogen into the sediment/pore water pool. Surface algae and bacteria associated with Spartina grass rhizomes fix free atmospheric nitrogen to make additional nitrogen available to plants. At the same time, denitrifying bacteria in sediments release a comparable amount of free nitrogen to the atmosphere. Spartina grasses, the chief biomass crop in the marsh, draw on the nitrogen pool in sediments via their root

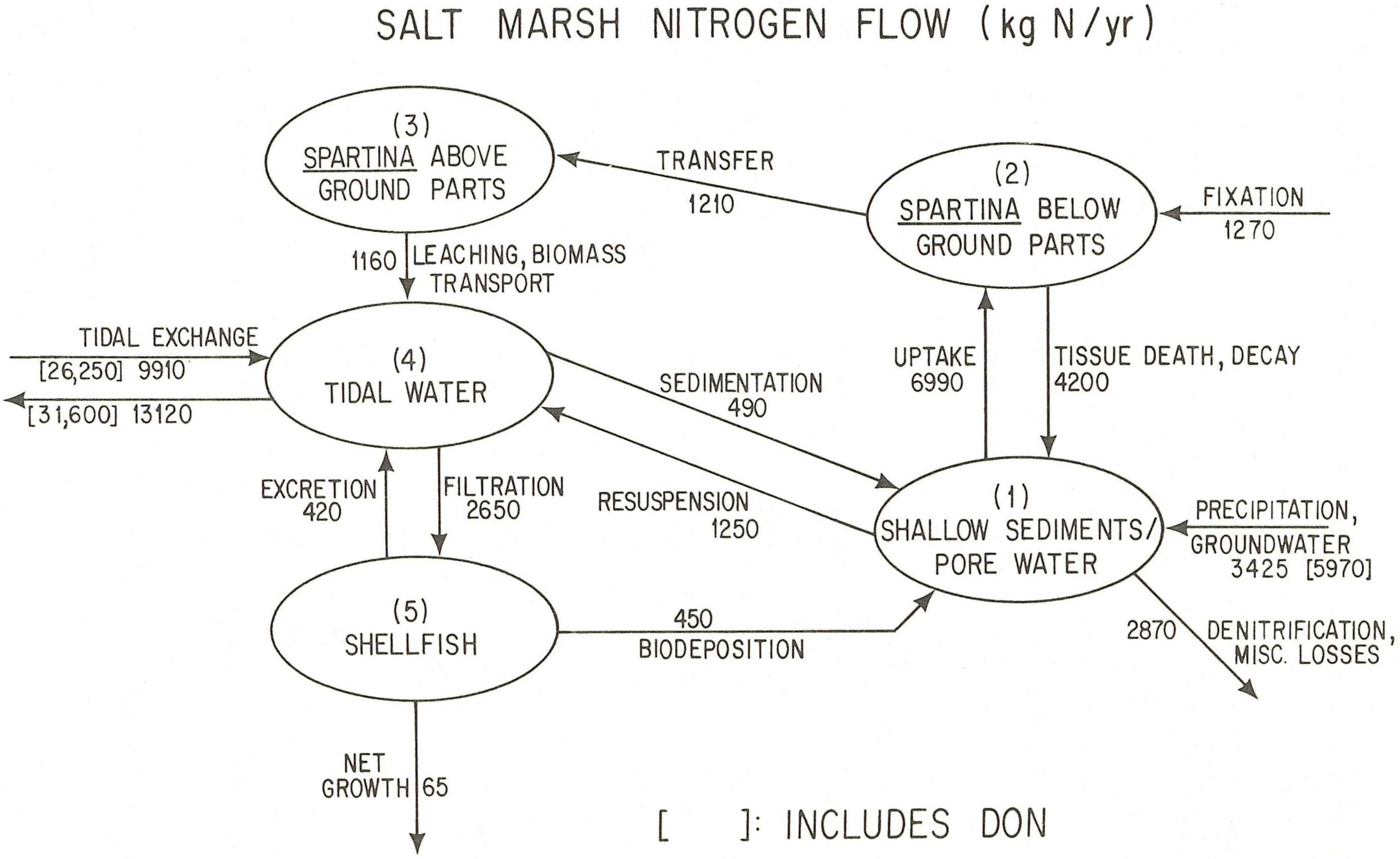

Figure 1. Annual exchanges of nitrogen among compartments in a schematic diagram of Great Sippewissett Marsh. See text for further description.

and rhizome systems. The nitrogen utilized by plants goes both to additional root and rhizome production and to production of above-ground stems and leaves. These above-ground parts, when they die or otherwise become separated from parent plants, form much of the detritus which floats in and out of the marsh on tides. Tidal action and decay and other biological agents break detrital matter into smaller and smaller particles which ultimately become potential food for shellfish and other marine organisms.

The food taken by mussels and other filter and detrital feeding bivalves can be assumed to include an unknown proportion of algae, phytoplankton and other sources of particulate nitrogen which may or may not originate in the marsh. Large amounts of nitrogen enter and leave the marsh in semidiurnal tides throughout the year, but it is very difficult to relate the material entering the marsh on any given flood tide to that which has left the marsh on previous ebb tides. The analysis makes no attempt to do this.

The picture drawn thus far is of a basically one-way flow of nitrogen through the marsh -- at best two-way when tides are taken into account. In part this is conceptual, but it may also be an artifact of the traditional view of marshes held by ecologists. Our conceptualization, a product of the problem at which this analysis is directed, attempts to ascribe a functional role to marshes as transformers of fertilizer inputs to marsh sediments into outputs in the form of net shellfish growth. The ecologist's view may be somewhat analogous, in that marshes often seem to be regarded primarily as processors of terrestrially originated nutrients intercepted on their way to the sea.

Nitrogen flowing through Great Sippewissett Marsh undergoes a significant amount of cycling as a result of mortality of living tissue, sedimentation and resuspension of particulate matter, and excretion and biodeposition by living organisms. These processes are explicitly considered in Figure 1. No doubt other phenomena not explicitly considered also have important effects on the retention and reuse of nutrients in the marsh. For example, microbial agents which drive decay processes are not disaggregated in the diagram; nor are pore water - sediment interactions considered. Data seem insufficient at this time to quantify annual exchanges of nitrogen via these routes. Future work may involve hypothesized linkages of this type, designed to determine whether the flow of nitrogen from fertilizer to shellfish is particularly sensitive to these kinds of processes and interactions.

The nitrogen considered to be in flux in the marsh can be in any of the forms generated by the marsh's nitrogen cycle. The major forms of nitrogen which must be distinguished are dissolved organic nitrogen (DON), particulate organic nitrogen (PON), and dissolved inorganic nitrogen (DIN), for which it may be important to distinguish further the flow of nitrite and nitrate from that of ammonia and ammonium. The availability of nitrogen for a given biological process depends in some cases on the form it is in. For example, the majority of all nitrogen entering and leaving Great Sippewissett Marsh annually is in the form of DON (57% of all inputs, 54% of all outputs (Valiela and Teal, 1978)). The function of this form of nitrogen in the marsh is uncertain (Ibid.), and it seems to play no role in shellfish feeding. Since inputs and outputs of DON nearly balance (total output is 98% of total input (Ibid.)), it makes sense to ignore DON completely in evaluating the nitrogen flow associated with shellfish growth. This we do in the alternative model below, with the result that the case for fertilizer-induced shellfish growth is strengthened.

COMPARTMENTAL ANALYSIS OF NITROGEN FLOW

As described in the introduction, the material in this section is arranged sequentially by the numbering scheme used in Figure 1. Each subsection is in turn arranged to consider first the inflow and/or outflow for the corresponding compartment, if any exist, followed by transfers to other compartments from the one under consideration.

(1) Shallow sediments/pore water.

This compartment represents the marsh surface on which marsh grasses grow. We consider this to include all marsh sediments down to the limit of penetration by grass roots, as well as the interstitial pore water which permeates these sediments. At Great Sippewissett about 98,000 m^2 are dominated by S. *alterniflora* while S. *patens* covers about 28,000 m^2. Roots generally penetrate to a depth of about 20 cm (Valiela, Teal and Persson, 1976).

Inflow.

Nitrogen is assumed to enter this compartment by four routes, summarized in the table below. Note that the values actually appearing in Figure 1 differ slightly in some cases due to rounding. Details of the sampling procedures by which data were collected and the integration techniques by which annual average values were generated are in the source papers listed. This applies to other values in this section wherever such information is not specifically given.

Nitrogen inflows to sediments and pore water, in kg N y^{-1}

	Total N	DON portion
Precipitation	180	90
Ground water	5470	2455
Algal fixation	140	____
Bacterial fixation (non-rhizomal)	175	____
Grand total	5965	
Total less DON	3420	

Table 1. Nitrogen inflows to Great Sippewissett Marsh sediments and pore water. Adapted from Valiela and Teal, 1978.

Outflow.

Almost all the export of nitrogen from the marsh system via sediments is by denitrification, a process which occurs in anoxic environments. 2830 kg N/yr are lost this way. An additional 25 kg are assumed lost to sediments below the plant root zone by sedimentation, and 10 kg are assumed lost by volatilization of NH_3 directly from the marsh surface. (Valiela and Teal, 1978). The total of these values was rounded to 2870 kg N/yr for use in the model.

Transfer to Spartina roots.

The key mechanism by which nitrogen enters the rich biological production system of the marsh is through uptake by roots and rhizomes of Spartina grasses. Nitrogen is fixed directly from the atmosphere by bacteria associated with plant rhizomes, and is removed from sediments and pore water by roots. The rate of uptake of nitrogen by roots apparently has never been directly measured in the field. Field conditions have been simulated, however, in experiments in which transplanted Spartina grasses were grown outdoors in controlled nutrient level hydroponic tanks. These experiments were conducted in 1977 by James T. Morris of the MBL Ecosystems Center, and the value we use is extrapolated from his unpublished data.

Morris (pers. comm.) has measured hourly uptake rates for plants grown at nutrient levels which approximate those in the unfertilized marsh. He believes that a fairly constant rate of 11 mg $N/m^2/hr$ can be applied to both S. alterniflora areas (98,000 m^2 at Great Sippewissett) and S. patens areas (28,000 m^2) for 24 hr activity over an entire seven month growing season. The annual uptake value derived from this calculation, 6990 kg N/yr, can be considered minimal if we assume that plants grown in oxygenated hydroponic environments are more efficient at utilizing available nitrogen than are their counterparts rooted in essentially anoxic marsh sediments.

Transfer to tidal water.

The cycle of sedimentation and resuspension, by which finely divided organic matter both settles out of tidal water into surface sediments and is drawn out of sediments into suspension by tidal currents, may be one of the most important processes in the marsh's nutrient cycle. Its effects are poorly understood, however, and the processes themselves very difficult to measure in the field. While sedimentation rates can be measured with sediment traps, there appears to be no satisfactory way to measure resuspension rates at present. At the suggestion of Thomas E. Jordan of the Boston University Marine Program, we estimated annual resuspension of PON at 1270 kg, to balance annual inflows and outflows with respect to the sediments/pore water compartment in the model of the appendix. In the alternative analysis which appears below we use a value of 1250 kg. However, the sensitivity of the shellfish growth questions posed in the introduction to variation in this value needs further exploration.

(2) *Spartina* root/rhizome biomass.

Roots and rhizomes are regarded in this analysis as simply translocators of nitrogen from sediments to above-ground production. It should be noted, however, that this below-ground tissue comprises a considerable biomass, and considerable nitrogen pool, in its own right. *Spartina* roots and rhizomes are perennial, with living and dead plant material occupying a large volume underground. Valiela and Teal (1978) estimate that at mid-summer the nitrogen pool in living roots and rhizomes is more than twice that in living above-ground plant tissue, and that the pool in accumulated dead underground tissue is nearly 30 times that in living stems and leaves.

Inflow.

We assume that the considerable quantity of nitrogen fixed by bacteria associated with Spartina rhizomes is all available to the plants themselves. Thus we list this quantity, 1270 kg N/yr, as an inflow to Spartina below-ground biomass. This value is as reported in Valiela and Teal, 1978.

Transfer to above-ground biomass.

The rate of transfer of nitrogen from below-ground to above-ground parts by Spartina grasses as photosynthesis proceeds during the course of a growing season has not been measured in the field. We again rely on the hydroponic experiments of James Morris for data on nitrogen uptake by this route. Table 2 is based on his unpublished data for mid-month to mid-month transfer, from April to December, for nutrient levels comparable to those in the unfertilized marsh. Using the acreage estimates for the two species reported above we calculate annual transfer to above-ground parts to be 1055 kg N/yr for S. alterniflora and 155 kg N/yr for S. patens. The data in Table 2 represent monthly averages of measured nitrogen content in plant leaf tissue. Thus the annual values were obtained by summing before multiplying by the acreage estimates. Details of sampling procedures and experimental conditions will appear shortly in Morris's Ph.D. thesis (pers. comm.).

Uptake by Spartina above-ground parts[1] (mg m^{-2})		
	S. alterniflora	S. patens[2]
April-May[3]	750	500
May-June[3]	1500	1000
June-July	2030	1410
July-August	2770	900
August-September	2070	990
September-October	1650	690
October-November	0	0
November-December	0	0

[1] Values rounded to three significant figures.
[2] Values for S. alterniflora grown at low nutrient levels were used as proxies for S. patens.
[3] Estimates.

Table 2. Mid-month to mid-month transfers of nitrogen from rhizomes to above ground parts. Source: J. Morris, pers.comm.

Transfer to shallow sediments/pore water.

We assume that all mortality of Spartina roots and rhizomes results in a return of nitrogen directly to marsh sediments, i.e., that none of this material enters tidal water directly as detritus. Valiela, Teal and Persson (1976) provide data on monthly biomass densities of dead material below ground over the course of a growing season. We interpret the change in their data from lowest to highest monthly density in the direction of the progress of the season as net annual death of roots and rhizomes, and assume this material to be 1% nitrogen by weight, after a suggestion of

Valiela (pers. comm.). We find net biomass change to be 4 kg/m^2 for low marsh (S. *alterniflora*) and 1 kg/m^2 for high marsh (S. *patens*) by this method. Multiplication by the nitrogen proportion and appropriate acreage figures lead to numbers which are added to produce the value of 4200 kg N/yr in Figure 1.

(3) *Spartina* above-ground biomass.

This compartment represents the annual production of plant stems and leaves both in low marsh areas dominated by S. *alterniflora* and in high marsh areas dominated by S. *patens*. Other species do occur in grass swards in the marsh, particularly in high marsh areas. Also, S. *alterniflora* has morphologically different tall and short forms, with the tall form occupying the wettest sites along creek banks. Valiela, Teal and Deuser (1978) report that fertilization can induce morphological changes in S. *alterniflora* as well. These complexities, as well as others, such as the high nitrogen demand plants have during periods of seed set, are ignored in the analysis.

Transfer to tidal water.

This important link in the marsh's nitrogen flow system is the one by which the marsh's large pool of primary productivity becomes available for secondary producers such as shellfish. Two mechanisms for the release of nitrogen to tidal water are considered. The first, the leaching of ammonia directly into tidal water during high tides, is assumed to account for 270 kg N/yr. This figure must be considered at best a rough estimate as efforts are only just getting under way to study the leaching process in

Great Sippewissett Marsh thoroughly. We arrive at this value by assuming that an average of 3 kg N/day is leached to tidal water over a period of three months at mid-summer. (I. Valiela, pers. comm.).

Considerably more particulate nitrogen is released to tidal water when the marsh's annually produced sward of grasses dies, to be replaced by the next year's crop. This death of above-ground material does not occur all at once; nor is any one year's production completely removed from the marsh surface before the next year's crop appears. Nevertheless, since dead grass is not accumulating on the marsh surface over the long run, it appears reasonable to assume that average net annual above ground production is equal to average annual production of detritus by the marsh. This argument is analogous to one given by Valiela, Teal and Sass (1975) in estimating net annual above-ground production itself, which should be consulted for further justification.

We determine actual net annual production values from Table 2 of Valiela, Teal and Persson, 1976. Here the values listed for annual production in control plots are taken to be representative of the unfertilized marsh. It is assumed that the above-ground biomass is 1.5% nitrogen by weight. The values given for net annual biomass production are 423.7 gm/m^2 for low marsh and 631.8 gm/m^2 for high marsh. Appropriate multiplication and division result in an estimate of 59,200 kg detritus production annually for the marsh as a whole, or 890 kg N/yr.

(4) Tidal water.

Tidal water is regarded strictly as a transporter of dissolved and suspended particulate nitrogen in and out of the marsh. This transport has been measured directly at Great Sippewissett Marsh, where all exchange with nearby coastal waters occurs through a single tidal inlet. It should be emphasized that other marshes with other physical configurations could have a greatly different pattern of tidal exchange. This aspect of the analysis may be the one which exhibits the greatest variation across marshes in New England of all factors considered here.

Inflow and outflow.

Tidal exchange is the most significant of the forcing functions acting on the marsh's internal cycling of nitrogenous compounds. Tides import about 26,250 kg N/yr, of which 16,350 kg (62%) is DON, and export about 31, 660 kg N/yr, of which 18, 480 kg (58%) is DON. This DON is subtracted in the analysis presented below. Values are from Valiela and Teal (1978).

Transfer to surface sediments.

Sedimentation rates in tidal creeks at Great Sippewissett Marsh were measured by Thomas Jordan in 1976 (pers. comm.). Particulate nitrogen falling into sediment traps over the course of single tidal cycles amounted to 23 kg N per tidal cycle, on the average. Assuming this to be a process which continues uninterrupted over the nine ice-free months at Great Sippewissett, we calculate that 505 kg N/yr settles onto the marsh surface.

This value is based on an average of 1.87 tidal cycles per day at Great Sippewissett. A slightly lower value of 490 kg N/yr is used in Figure 1 and in model calculations.

Transfer to shellfish.

The removal of particulate nitrogen from sea water by the ribbed mussel (Modiolus demissus) population of Great Sippewissett was measured by Thomas Jordan in both 1976 and 1977. Jordan placed individual mussels in jars of sea water and measured nutrient concentrations in the water at the onset and at the end of flood tides. This method may significantly underestimate filtration rates (pers. comm.). Adjustments in the method used may account for a near doubling of the 1977 rates over observed 1976 values. The lower values are used in the appendix, the higher values in the Figure 1 and in the analysis below.

Filtration rates vary both seasonally and with the size of individuals tested. Jordan has measured midsummer filtration rates for a range of sizes of individuals and determined average rates to be 8.3 kg N/tidal cycle for the marsh's large (4.8 million) muddy creek bank population. Rates are known to be zero in early April and zero again by December. The curve in Figure 2 was averaged to determine a rate of 5.9 kg N/tidal cycle as representative of the seasonal activity of the muddy creek bank population. Multiplication of this value by 240 days at 1.87 tides/day yields the value 2650 used in Figure 1.

(5) Shellfish.[1]

Bivalue molluscs of several different species occur in Great Sippewissett Marsh. The greatest concentration of biomass in

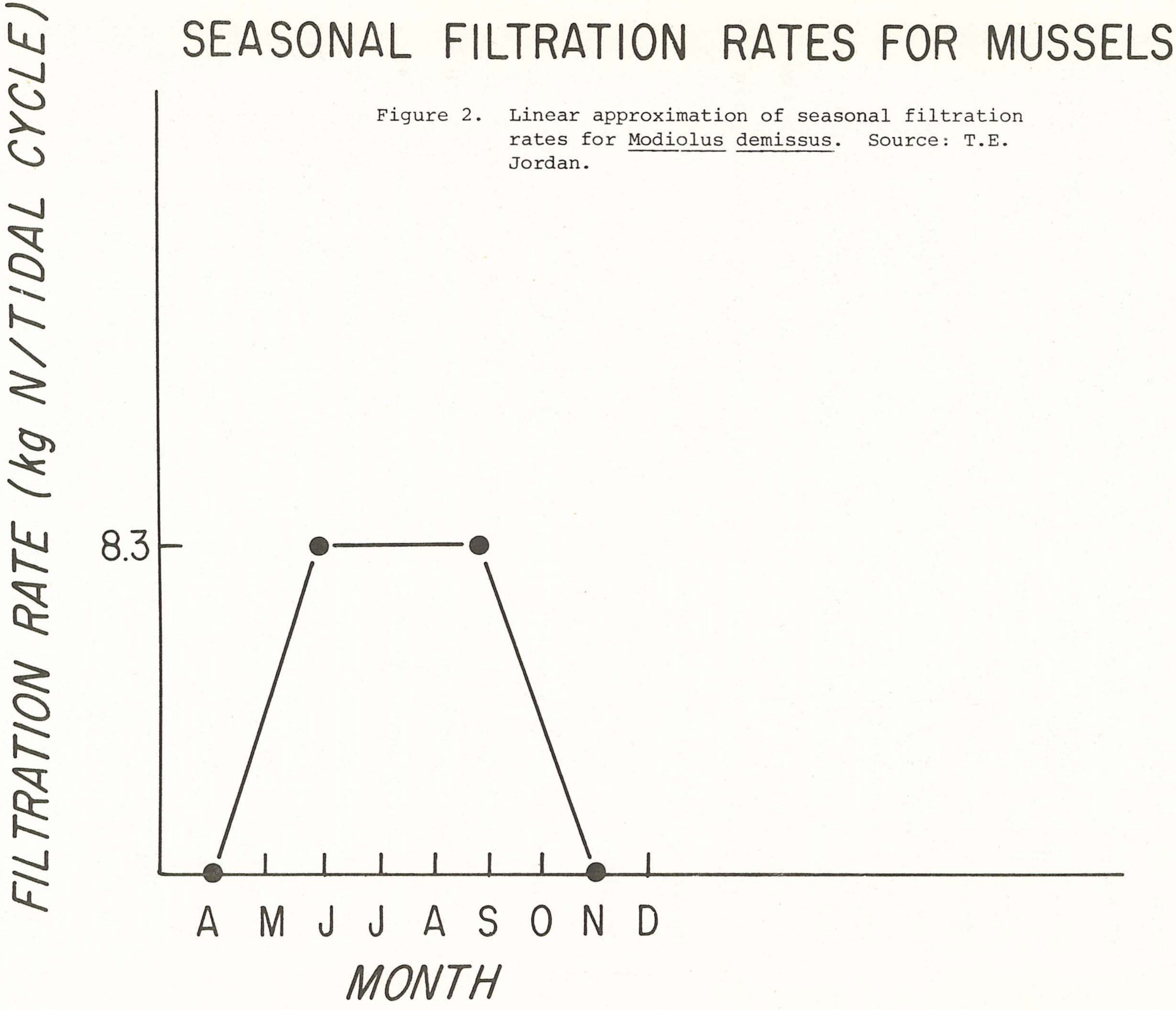

Figure 2. Linear approximation of seasonal filtration rates for Modiolus demissus. Source: T.E. Jordan.

this group, however, is in the marsh's population of ribbed mussels (Modiolus demissus), estimated to be about 7.2 million animals at present (Thomas Jordan, pers. comm.). Jordan has identified four distict habitat types over which this population is distributed: muddy or sandy creek banks, and tall or short form S. alterniflora surface areas. These four populations appear to differ from one another at least in terms of population densities and growth rates. By far the largest number (4.8 million) and greatest density ($454/m^2$) of animals occur in the muddy creek bank population, and this is the population upon which our analysis focuses.

Outflow.

We assume that very simple population dynamics govern the marsh's mussels. We assume no recruitment or mortality, but calculate instead an average net growth for individuals which we apply to the population as a whole. This net annual growth -- more specifically, the nitrogen content of mussel flesh added in a year's growth -- is interpreted as an outflow from the shellfish compartment in Figure 1. This approach was deemed most appropriate for the analysis at which this construction is directed. In other words, we assume that recruitment and mortality of mussels are events exogenous to both the normal transfers of nitrogen with respect to the marsh system and to the addition of nitrogen to the system via fertilization.[2]

The calculation of growth rates for the muddy creek bank mussel population is based on observed seasonal growth rates for individuals of "modal length", as determined below. Growth rates vary greatly with the size of the individual, but both the distribution of the population about the modal size and the distribution of growth rates about those measured for individuals of modal size made this approach to averaging growth rates feasible.

The growth rate calculation is as follows. In 1976 most mussels at Great Sippewissett were between 5 and 6 cm in length, and most growth occurred between the beginning of June and the end of September. Jordan has experimentally determined the following relationship between length and dry weight for the muddy creek bank population:

$$\text{gm dry wt.} = (6.244\text{x}10^{-6})(\text{mm length})^{2.748}.$$

This regression equation was used to estimate the change in dry weight associated with a 1 micron length increase for both a 50 mm and a 60 mm mussel. These values were then multiplied by the average daily length increase observed over the course of the June - October growing season for each size class. The resulting pair of daily growth rates was then averaged to obtain a rate applicable to the population as a whole. We used Jordan's estimate that mussel flesh is 10% N to convert this value to increase in nitrogen per day. Multiplication by the length of the growing season (120 days) and the total population size (4.8 million) yields an estimated seasonal increase of 66.2 kg in the pool of nitrogen stored in the flesh of the marsh's standing stock of mussels. The actual data used are summarized in Table 3.[3]

Data used to estimate average mussel growth rates

	mussel length 50mm	mussel length 60mm	how obtained
weight inc. per micron length inc. (gm)	1.6×10^{-5}	2.2×10^{-5}	regression
ave. daily length inc. (μ day^{-1})	85	40	direct obs.
ave. daily growth rate (mg day^{-1})	1.4	.9	multiplication
overall ave. growth rate (mg day^{-1})	1.15		

Table 3. Growth parameters associated with two size classes of the mussel Modiolus demissus. Source: T.E. Jordan, per. comm.

Transfer to tidal water and to shallow sediments/pore water.

The processes inferred by the above title, excretion and biodeposition, are treated together since they are calculated similarly. Both are assumed proportional to filtration as described in Subsection 4. Excretion is understood to represent the direct release of ammonia by mussels, while biodeposition refers to their production of feces and pseudofeces.

Our calculation of total annual filtration by Sippewissett mussels involved an extrapolation from midsummer filtration rates as measured by T.E. Jordan. In effect we calculate biodeposition and excretion the same way by setting up proportionality equations using Jordan's 1977 midsummer filtration rate (8.3 kg N/tidal cycle) and his independently measured rates for excretion (1.3 kg N/tidal cycle) and biodeposition (1.4 kg N/tidal cycle). The proportionality assumptions are, more specifically, that total excretion (biodeposition) is to the summer excretion (biodeposition) rate as total filtration is to the summer filtration rate. The equations used are thus

$$2650/8.3 = \text{total excretion}/1.3 = \text{total biodep.}/1.4.$$

The values obtained this way are

total excretion = 415

total biodeposition = 445

It should be noted that the values appearing in the appendix for these processes are, like the filtration value, based on 1976 estimates thought less reliable. The revised estimates are incorporated into the flow diagram in Figure 1.

SUBTRACTING DON FROM THE FLOW

Elsewhere in this report we have discussed the domination of dissolved organic nitrogen in both the inputs and outputs to Great Sippewissett Marsh, although it does not appear to be a food source for shellfish and may pass through the marsh without being much affected by biological or physical processes while there. Dual sets of values are shown in Figure 1 for the two places where calculations include DON: fresh water inputs to the marsh and tidal exchange with the open ocean. This section presents an analysis of flows for the value set which results when DON is excluded, an exclusion which amounts to ignoring the values within brackets [ ] in Figure 1. Table 4 below is the matrix equivalent to Figure 1 for that set of values.[4]

Great Sippewissett Marsh nitrogen flow, by compartment

	From (1)	(2)	(3)	(4)	(5)	Inflows
To (1)	0	4200	0	490	450	3425
(2)	6990	0	0	0	0	1270
(3)	0	1210	0	0	0	0
(4)	1250	0	1160	0	420	9910
(5)	0	0	0	2650	0	0
Outflows	2870	0	0	13120	65	

Table 4. Flows matrix for Figure 1, with DON excluded. Compartment numbering is as in the figure and the text.

Table 4 should be compared with Table 2 of the appendix; its use here is identical to that to which Table 2 was put in the appendix. As before, the 5x5 central portion of Table 4 can be thought of as the central portion of a much larger matrix A which, after division by row totals, is subtracted from an identity matrix and inverted to form the matrix $(I-A)^{-1}$. This is consistent with the model presented in equations (3), (4) and (5) of the appendix. The matrix A generated by the computer program used (Finn, 1977) is actually 16x16 in this case, since it takes into account flows which must be added to balance the flow into and out of each of the compartments in Figure 1.[5] The 5x5 central portion of $(I-A)^{-1}$ is presented in Table 5, which corresponds to Figure 3 of the appendix.

Matrix inverse for Sippewissett Marsh intercompartmental flows

	(1)	(2)	(3)	(4)	(5)
(1)	1.50	.575	.00928	.130	.0640
(2)	1.27	1.49	.00785	.110	.0541
(3)	1.27	1.49	1.01	.110	.0541
(4)	.211	.154	.0745	1.04	.0355
(5)	.211	.154	.0745	1.04	1.04

Table 5. Central portion of the matrix $(I-A)^{-1}$, computed for the flows of Table 4.

DISCUSSION

As the discussion of the marsh fertilization question with regard to shellfish growth in the appendix indicates, the element in the (5,1) position in the matrix $(I-A)^{-1}$ gives a measure of how closely fertilizer inputs are linked to shellfish outputs in the schematic flow. That value, roughly the probability that nitrogen passing through compartment 5 (shellfish) has also been through compartment 1 (shallow sediments/pore water), was 10% in the flow analysis which included DON(appendix) and is 21% in the present analysis, in which DON is excluded. The strength of the linkage has doubled, but is this sufficient to indicate a significant response to marsh surface fertilization by tidal creek mussels? While it is inappropriate to use an input-output model to try to predict the effects of this changed input on the system, the prospect of a significant response to such a change does not appear promising.

It is not possible at this time to establish a "threshold" level in the strength of the linkages among compartments, above which responses to exogenous inputs like fertilization are guaranteed to propagate. The marsh's response to perturbations is generally not linear; nor do quantitative changes in one part of the system occur without inducing a host of quantitative and qualitative changes elsewhere in it. The steady state picture of the system we have drawn, simplified though it may be, nevertheless mirrors some of its important properties. Of central importance in this picture is the way the effects of closed loop cycling in a system like the marsh are made manifest, a phenomenon that is often neglected. This cycling is expressed in the model as a kind of multiplication and summation of the second and higher order effects which link various compartments through such cycles. The resulting set of "multipliers" are precisely those elements of the matrix $(I-A)^{-1}$ displayed in Table 5.

Our tentative conclusion that tidal creek mussels are unlikely to respond significantly to marsh fertilization is an inference from a more direct observation that compartments 1 and 5 in the model are neither linked directly via nitrogen flow nor linked indirectly in any significant way via cycled flow. The combined strength of the direct and indirect flow from compartment 1 to compartment 5 is what the (5,1) element in the matrix measures. This more precise statement of the nature of the inferences flow analysis of this type allows may permit us to place some bounds on the degree to which our results are predictive. For example, the elements in the (2,1) and (3,1) positions in Table

5 express inter-compartmental linkages which are significantly stronger than the sediments - shellfish linkage. These values, both 1.27, reflect the very strong connection experimentation has already shown to exist between marsh fertilization (applied to compartment 1 in the model) and the growth of both above and below-ground biomass of Spartina grasses (compartments 3 and 2 respectively). Essentially all of the nitrogen outflow of the latter two compartments can be thought of as having either originated in compartment 1 or passed through there due to return flow.[6] The dramatic responses of marsh grasses to fertilization discussed elsewhere in this report could have been predicted with confidence on the basis of this analysis for the unfertilized marsh.

The analysis presented above quantitatively relates the activity of one compartment, expressed in terms of the nitrogen flowing through it, to that of another. The further analysis shown schematically in Figures 3 and 4 is somewhat finer in terms of the problem at hand. Figure 3 shows the percentage contributions of the system inflows and of system compartments in deficit flow to an outflow of unit intensity from the shellfish compartment. The values inside the compartments correspond to the bottom row in Table 5, i.e., to the portions of the outflow of compartment 5 which have been through each of the other compartments. The outflows of each compartment add up to the value inside it, and the sum of all inflows and contributions from compartments in deficit flow is one.

This analysis shows that almost 64% of nitrogen in shellfish production is attributable to tidal influx, while only about

SOURCES OF A UNIT OUTFLOW OF SHELLFISH

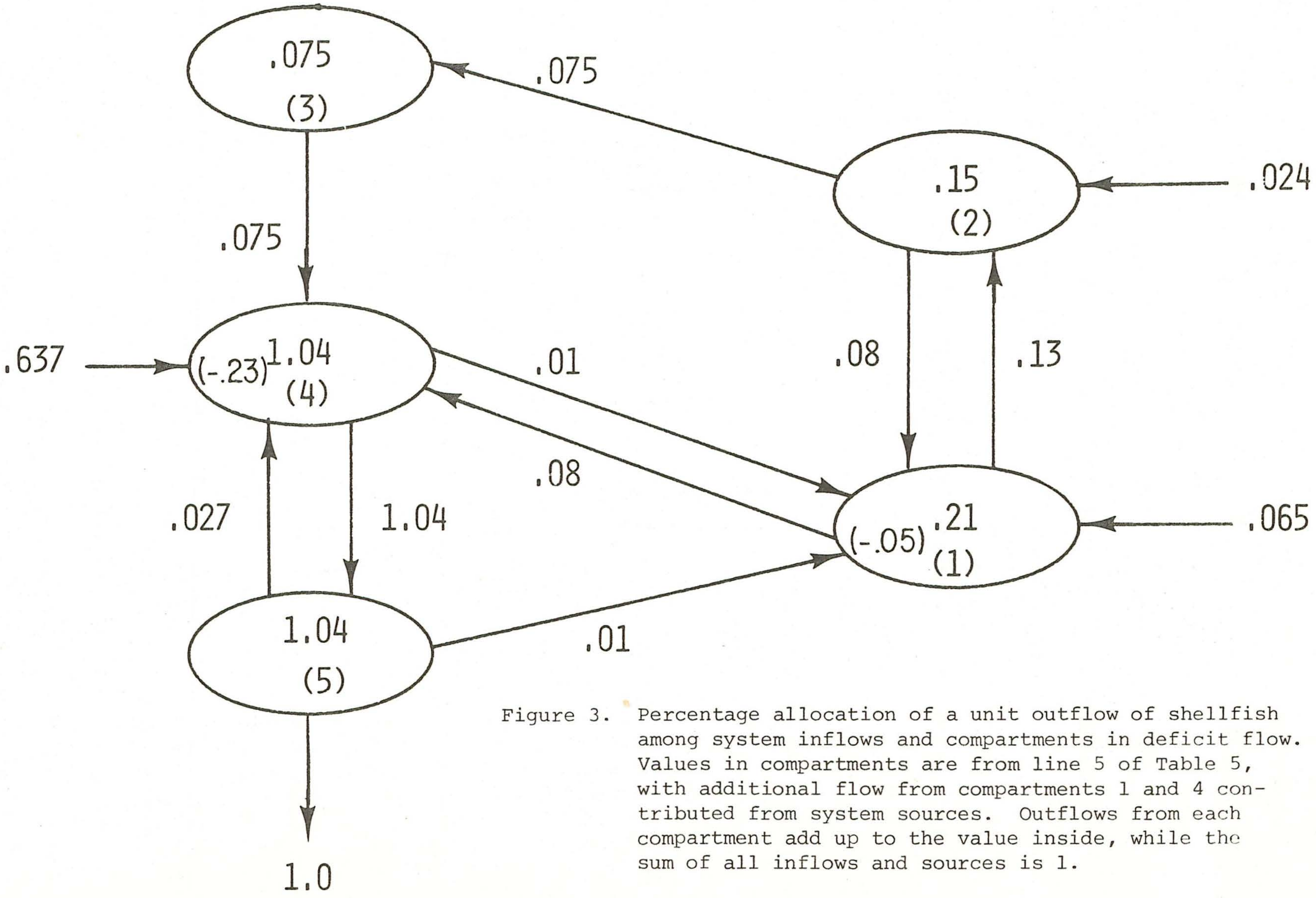

Figure 3. Percentage allocation of a unit outflow of shellfish among system inflows and compartments in deficit flow. Values in compartments are from line 5 of Table 5, with additional flow from compartments 1 and 4 contributed from system sources. Outflows from each compartment add up to the value inside, while the sum of all inflows and sources is 1.

6.5% is traceable to the inflow to marsh sediments. The tidal flux is so large in comparison to other flows in the system that the flow source in the tidal water compartment, added to correct for the imbalance between inflows and outflows there, is slightly larger than the total flow through compartment 1 (23% vs. 21%). The method used, and the variation on it which follows, is again due to Finn. Finn (1977) should be consulted for details.

Figure 3 was based on model equation 5 of the appendix, linking total system flow activity (vector $\overline{X}$) to intercompartmental flows (represented by the matrix A) and compartment outflows (vector $\overline{Y}$). Finn (1976) develops a dual formulation using a compartment inflows vector $\overline{Z}$ in place of the outflows vector. For the same system activity, this results in a different matrix of intercompartmental flows A' which solves the vector equation

$$\overline{X} = (I-A')^{-1}\overline{Z},$$

which has a derivation parallel to that of equation 5 of the appendix.

We do not present the details of this dual formulation which is oriented to inflows, but Figure 4 is related to it in the same way that Figure 3 relates to equation 5 of the appendix. Figure 4 shows how a unit inflow to marsh sediments is allocated among compartments accumulating excess flow and system outflows. The values displayed in it have similar interpretations to those in Figure 3. Thirty nine percent of this inflow is lost through processes occurring in sediments, 25% through tidal export; only .1% is transformed into shellfish growth.[7]

FATE OF A UNIT INFLOW TO SEDIMENTS

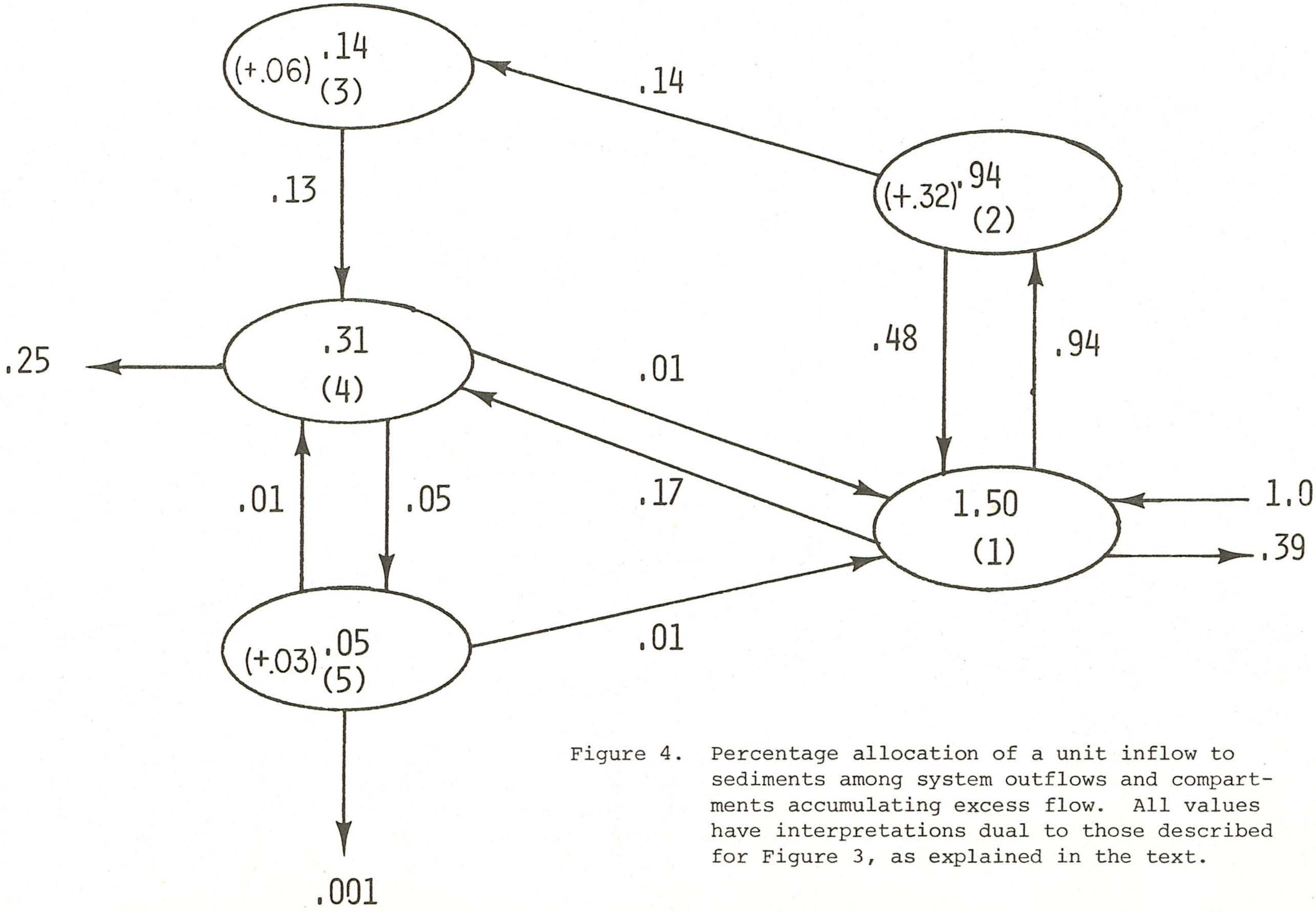

Figure 4. Percentage allocation of a unit inflow to sediments among system outflows and compartments accumulating excess flow. All values have interpretations dual to those described for Figure 3, as explained in the text.

* * *

Figure 5 shows a schematic of experimental plots in Great Sippewissett Marsh, where the response of the marsh's ecology to various levels of fertilization has been used as a gauge for measuring the nature of fundamental processes in on-going experiments. We include it to emphasize the scale of the experimentation compared to the scale of the processes relevant to shellfish growth in the marsh's tidal creeks. The present level of fertilization is insufficient to provide a direct test of the downstream effects of fertilizer applied to the marsh surface. A significant portion of a tidal creek will have to be directly impacted by the effects of fertilization before a definitive test of this question can be made.[8]

The flow diagram in Figure 1 was constructed on the assumption that the only nitrogen available to shellfish is in the water that covers them during semidiurnal periods of tidal inundation. This is reflected in the very high value, 1.04, in the (5,4) position of the matrix in Table 5, which links shellfish to tidal water. Figure 6 displays data from Valiela, Banus and Teal (1974) showing a shift in the size distribution of a marsh surface population of _M_. _demissus_ in fertilized plots. The authors report a 1 cm increase in modal shell height for these mussels after four seasons of fertilization, while mussels in unfertilized control plots showed no significant increase over the same period. These data, while possibly equivocal since differential mortality could produce the same result, suggest that mussels do indeed respond to fertilization in the right circumstances.

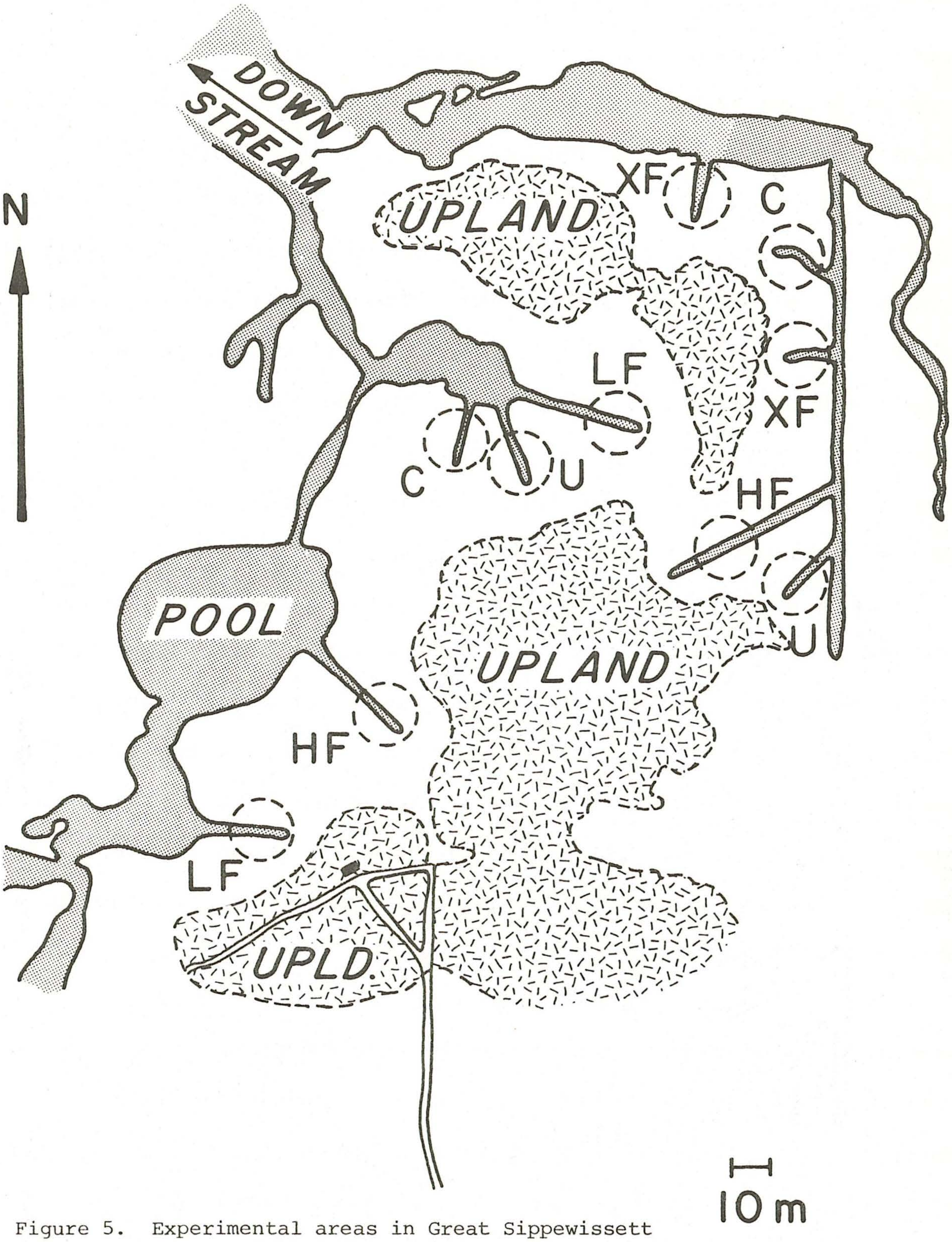

Figure 5. Experimental areas in Great Sippewissett Marsh. Lettering indicates test plots to which fertilizer is applied at various densities. Source: Ivan Valiela

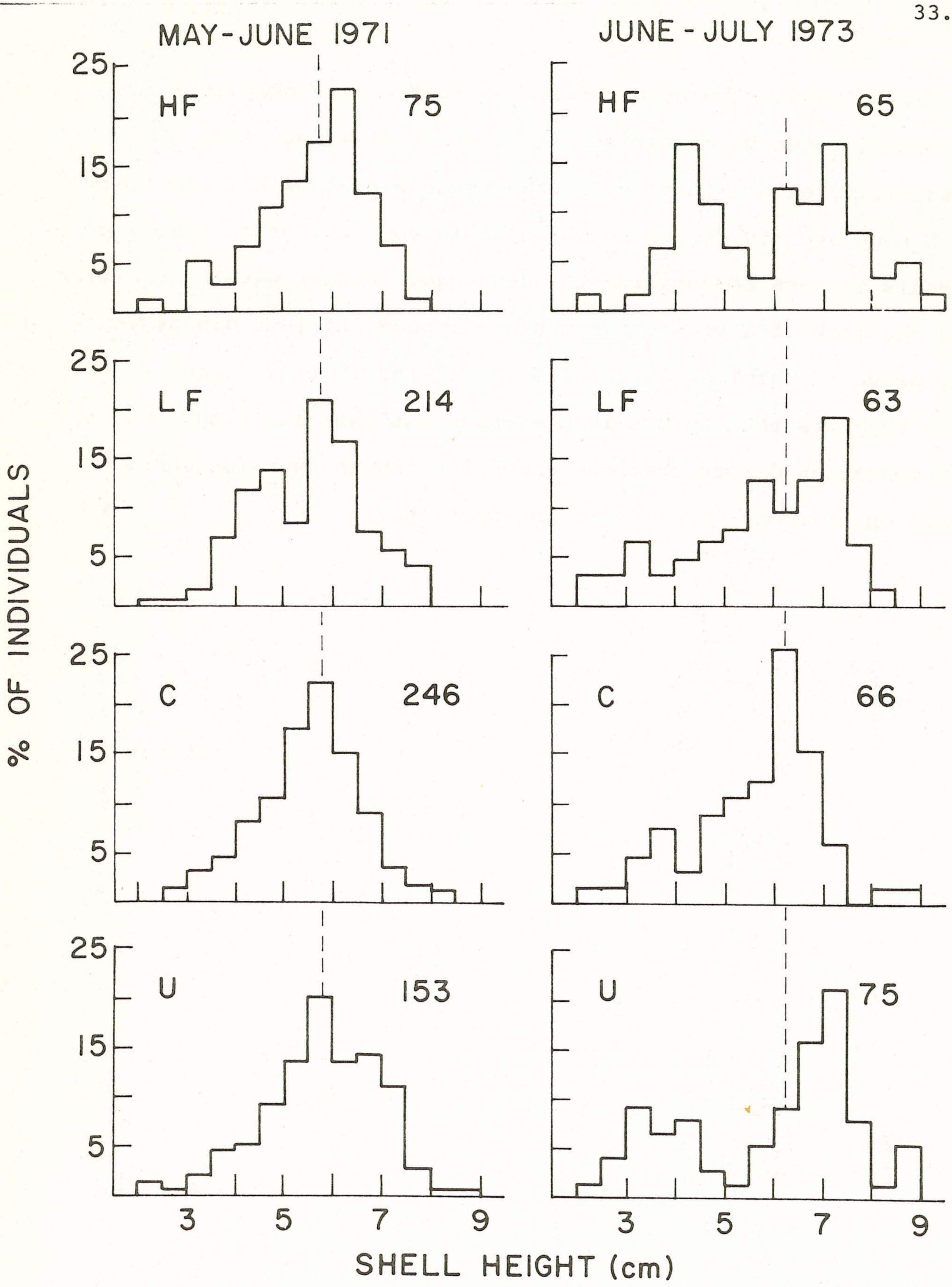

Figure 6. Distribution of shell heights for M. demissus in test plots at Great Sippewissett Marsh, before and after fertilization. Source: Valiela, Banus and Teal (1974).

If we retain the hypothesis that mussels are only able to ingest nitrogen by filtering it out of tidal water, then the possibility exists that fertilizer forms a shallow but nutrient-rich soup over the areas to which it is applied, which nearby mussels in turn can utilize to advantage. Higher water velocities and the lack of a vegetative mass to impede nutrient dispersion may prevent a similar effect from occurring in tidal creeks. This suggests that future input-output analysis and future experimentation directed at the shellfish growth question should focus on sediment-tidal water interactions.

NOTES

1. The values reported in this section generally differ from those used in the paper in the appendix. This is due to T. E. Jordan's revision of the estimates he originally supplied. No DON is assumed to be involved in any of the calculations for flows associated with the shellfish compartment.

2. Valiela, Banus and Teal, (1974) discuss the problem of shellfish mortality associated with additions of fertilizer laden with heavy metal contamination. They also provide some data on mussel growth associated with fertilizer enrichment which will be discussed in the last section of this report.

3. Jordan, using 1977 data, has since recomputed growth rates by a more direct method. He obtains practically the same result: 64.6 kg N seasonal increase in the nitrogen pool. (pers. comm.)

4. The calculations to follow will parallel those made in the appendix. The reader will note that the set of values determined from Figure 1 by including DON does not coincide with those appearing in the appendix for reasons explained in note 1 above. We omit the revised calculations which would reflect these minor alterations since they do not materially affect the model computations of greatest interest.

5. The reader should note that none of the compartments in Figure 1 have balanced flows, i.e., total inputs do not equal total outputs for any compartment. The matrix inversion process developed by Finn (1977) begins by expanding the 5x5 core portion shown in Table 4 by in effect adding one additional row for each of the three outflows shown in the table and one additional column for each of the three inflows. These additions are then balanced by adding, respectively, the same number of columns and rows of zeros. The whole procedure is then repeated for the balancing flows required for each of the five compartments, sinks being added as rows, and sources as columns. See Note 7.

6. Values greater than 1 for multipliers are the result of multiple counting; some of the flow through a recipient compartment passes on to another compartment which ultimately passes it back again, possibly through intermediary compartments. Such multiple counting is not only desirable but the very point of any input-output analysis.

7. The signed numbers in parentheses in Figures 3 and 4 are relative measures of how badly the compartments in the model are out of balance with respect to their inputs and outputs. These values are substantial in some cases and indicate the extent to which present data fails to describe important processes governing the transformation of nitrogen in the marsh. The very large relative imbalance in the shellfish compartment may stem from failure to consider the entire marsh shellfish biota, as well as the overly simple way in which mussels are assumed to process nitrogen in the model. It is doubtful that a more balanced model would substantially alter the results of analysis discussed in this section.

8. As this report is being prepared, planning is underway to begin large scale fertilization at Great Sippewissett. It is hoped that an entire 2.5 acre site can be fertilized so that questions such as that of shellfish response to fertilizer can be studied. The cost estimates in the appendix are based largely on estimates developed for this expanded fertilization program.

REFERENCES

1. Finn, J.T. 1976. Measures of ecosystem structure and function derived from analysis of flows. The Journal of Theoretical Biology 56: 363-380.

2. Finn, J.T. 1977. Flow analysis: a method for tracing flows through ecosystem models. Unpublished Ph.D. dissertation, University of Georgia, Athens.

3. Leschine, T.M. and L.J. Smith. 1978. Input-output analysis for salt marsh bioproductivity. MTS-IEEE OCEANS 78 Proceedings: 285-293. (Also the appendix of this report)

4. Valiela, I., M.D. Banus and J.M. Teal. 1974. Response of salt marsh bivalves to enrichment with metal-containing sewage sludge and retention of lead, zinc and cadmium by marsh sediments. Environmental Pollution. 7: 149-157.

5. Valiela, I., and J.M. Teal. 1978. Inputs, outputs and interconversions of nitrogen in a salt marsh ecosystem. In R.K. Jefferies and A.J. Davy (eds.), Ecological Processes in Coastal Environments. British Ecological Society Symposium, Blackwell.

6. Valiela, I., J.M. Teal and W.G. Deuser. 1978. The nature of growth forms in the salt marsh grass Spartina alterniflora. American Naturalist. 112: 461-470.

7. Valiela, I., J.M. Teal and N.Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Below ground biomass. Limnology and Oceanography. 21: 245-252.

8. Valiela, I., J.M. Teal and W.J. Sass. 1975. Production and dynamics of salt marsh vegetation and the effects of sewage contamination. Biomass, production and species composition. Journal of Applied Ecology. 12: 973-982.

9. Valiela, I., J.M. Teal, S. Volkmann, et.al. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: Tidal exchanges and inputs by precipitation and groundwater. Limnology and Oceanography. 23: 798-812.

APPENDIX

MTS/IEEE OCEANS 78
SEPT 6-8, 1978 CAT
NO 78 CHD134 7 OEC

INPUT-OUTPUT ANALYSIS FOR SALT MARSH BIOPRODUCTIVITY *

Thomas M. Leschine
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02543

Leah J. Smith
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02543

Abstract

Input-output analysis is applied to a salt marsh system to describe possible bio-economic effects of adding nitrogen fertilizer. A simple model is developed to trace exchanges of nitrogen among five compartments of the marsh model: sediments, Spartina root/rhizome biomass, Spartina aboveground biomass, tidal water and shellfish. The resulting matrix can be used to show relationships in the system among controllable inputs and outputs with potential economic value. Some costs of fertilizing an experimental plot are given, but no direct comparison can yet be made between costs and likely economic benefits.

1. Introduction

Recent research on salt marshes at Woods Hole has emphasized both qualitative and quantitative aspects of the flow and interconversion of nitrogen as it passes among the various biological compartments of salt marsh systems. It has been established that the artificial addition of nitrogen-based fertilizer can enhance the productivity of biological systems within such salt marshes (10), although the possible bio-economic benefits of salt marsh fertilization - enhanced fish and shellfish production - are relatively far removed from initial perturbations on the system such as fertilization. The structure of this small-scale bio-economic system is in many ways similar to that of economic systems which have been described with input-output analysis. Other economic approaches have been used to describe production in manufacturing or agricultural systems. Production functions of various kinds either describe such systems in engineering terms or make assumptions about the contribution and substitutability of various factors of production (principally labor and capital). Most of these systems, however, assume a high degree of control over all inputs and outputs. In a salt marsh used as a site for enhanced productivity, many of the assumptions underlying standard economic production functions do not hold. In addition, the complex and vital roles of biological interactions require different treatment than a standard manufacturing system. The input-output approach enables us to combine some of the important biological interactions with the total input requirements and potential economic outputs of the system.

In a sense, nitrogen is the "currency" being passed back and forth among tidal water, grasses, herbivores and other compartments in the marsh as biological activity takes place. Much ecosystem analysis over the past 20 years has focused on the flow of energy and nutrients through similar biological systems (among frequently cited energy flow models are H.T. Odum (6) and J.M. Teal (9)). Several recent authors have noted the similarity of these flows to the flow of money through a national economy, and a mathematical theory of flows in ecosystems equivalent to the economic input-output analysis of W. Leontief (5) has been developed (Hannon (3) and Finn(1)). Gosselink et al (2) have used this analogy directly in placing a dollar value on an acre of salt marsh, determined by measuring annual net primary productivity, a proxy for annual energy flow, and converting energy units to dollars. Our goal is to link the costs of marsh fertilization to the potential harvest of fish and shellfish relatively far removed in position in the food web from these initial nutrient inputs, and it is natural for us to use an input-output format.

Productivity of the grasses which comprise the major component of the tidally borne detritus in these marshes, mainly two species of Spartina, is enhanced by fertilization. This detritus in turn is the basic food source for the marsh's food webs. Primary production both in salt marshes (10) and in coastal waters (7) is nitrogen limited. A good deal of research on the flow of nitrogen through marsh food webs has been done in Great Sippewissett Marsh of Falmouth, Massachusetts, and in Buzzard's Bay, with which the marsh has tidal exchange. A complete annual budget of nitrogen inputs and outputs to and from Great Sippewissett has been prepared (10).

---

*Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant #04-7-158-44104, and the Marine Policy and Ocean Management Program of the Woods Hole Oceanographic Institution.

The salt marsh performs an important "conversion" activity on the nitrogen which enters it. The marsh intercepts a flow of ground water rich in dissolved nitrates, its principal natural nutrient source, and converts it to a mixture of particulate nitrogen and disssolved organic and inorganic nitrogen compounds, comprising a net annual export to the Bay. The particulate nitrogen is mostly grass detritus while a large portion of the dissolved nitrogen export is ammonium. The effect of the marsh is thus to manufacture particulate nitrogen food for harvestable shellfish which is then available to man, and for small mollusks and other benthic creatures available in turn to commercially valuable fish. All are dependent on the tidally innundated habitat the marsh provides. Were the marsh not there, the impact of the nitrogen from the groundwater would be primarily on the phytoplankton in the Bay, and through them on the grazing food webs less directly tied to resources harvestable by man.

The effects of nitrogen-based fertilizer applications on the biomass yield of Spartina alterniflora, the dominant grass in the marsh, can be dramatic: an application of 8.4 g/m^2/week, done biweekly over a seven month period, was shown to double net annual aboveground production of S. alterniflora in experimental plots, while an application of 25.2 g/m^2/week resulted in a near tripling of biomass yield (11). Thus, the simple application of fertilizer can increase the food supply for marine organisms, making it tempting to regard fertilized salt marshes as open aquaculture systems and to view salt marsh fertilization in economic terms.

It is unlikely that commercial aquaculture based on salt marsh fertilization would be practical, since little control can be exerted over the natural biological processes in a marsh. On the other hand, lack of controllability is a virtue in that the costs incurred in maintaining a salt marsh as an open aquaculture system are low. This is especially true if we adopt the viewpoint that fertilization, if it proves practical, should be conducted locally by towns for the benefit of local residents and in-shore fishermen who harvest marsh-dependent fish and shellfish. The explicit costs are thus limited to maintenance of the fertilization program if harvesting is assumed free. It is possible that secondarily treated sewage effluent could be used as fertilizer in some areas, reducing costs even further and providing an additional tertiary sewage treatment benefit (8). Though the market value of the potential increase in harvest may be small, an important component of its total value is recreational and difficult to quantify.

We will show how "biomass flow" through the marsh can be indirectly charted by an analysis of the flows of nitrogen which result as initial nitrogen inputs are converted biologically into higher organisms. In the sections that follow we describe our input-output methodology in more detail and develop some cost estimates for marsh fertilization. We show how it is possible by "back calculation" through a flow model to estimate the nitrogen requirements of meeting a desired level of demand for marsh outputs expressed in terms of biomass output of fish or shellfish. This gives a way of estimating the feasibility of marsh fertilization for the purpose of enhancing bioproduction as well as the probable costs of fertilization. The method is general and can be applied in any situation in which an appropriate flow model is available.

2. A Linear Model for Bioproduction

If a national or regional economy is composed of n sectors i = 1,...,n, then the total cash flow through sector j (i.e. the value of j's total production) can be expressed as the sum of the cash flows to all other sectors from j (the value of sales made by j to other sectors for the purposes of their production) and the value of sales to consumers by j (final demand). Letting x_j be the value of j's total production, x_{ij} be the value of sales to i by j for production by i, and y_j be the final demand for j's production, we can express this formally as

$$(1) \quad x_j = \sum_i x_{ij} + y_j .$$

If we assume further that x_{ij} is proportional to x_i, then Equation (1) can be written

$$(2) \quad X_j = \sum_i a_{ij} x_i + y_j , \text{ or}$$

$$(3) \quad \overline{X} = \overline{X}A + \overline{Y}$$

in vector notation, where $\overline{X}$ and $\overline{Y}$ are n dimensional row vectors and A is an nxn matrix of coefficients.

The equations above are derived from the usual assumptions of economic input-output analysis. Replacement of the economic sectors with compartments in an ecosystem model and the cash flows with flows of energy or nutrients generates the equivalent interpretations of Hannon (3) and Finn (1). In the specific example we will present below, Equation (1) will be interpretable as a statement that the total nitrogen flow through compartment j is equal to the sum of the direct flows from j to all other compartments and the flow from j out of the system, after Finn. It is not necessary to assume that the system modeled is conservative (i.e. that the inputs balance the outputs for each compartment), though in a technical sense the computations require that inputs and outputs do balance. It is easy enough, however, to balance the flows artificially by the addition of sources and sinks without changing the nature of the basic result. It should also be noted that the substitution used to derive Equation (2) assumes that a change in total compartment flow leads to proportional changes in the flows which enter that compartment from other compartments. Were the methods of Isard (4) to be cast in this framework, then the flows could be thought of as flows of goods or materials directly, rather than of the nutrients or energy stored in such materials.

The model described by Equation (3) has two simple equivalent forms of interest:

(4) $\overline{X}(I-A) = \overline{Y}$, and

(5) $\overline{X} = \overline{Y}(I-A)^{-1}$,

where Equation (5) is understood to mean the equality holds given that $(I-A)^{-1}$ exists. The first form expresses the outflow from the various compartments in terms of the total flow through them, while the second makes it possible to solve for the total flow necessary for the system to produce an outflow of a given intensity. This latter interpretation is the one of greatest interest to us and also the formulation of greatest use in input-output economics. In our system we will consider marsh shellfish production (measured as nitrogen content in average annual mussel growth) as an outflow from the model's shellfish compartment. By expressing the total nitrogen flow through the compartment to which fertilizer is an input (marsh sediments) as a function of its nitrogen input, we can then estimate the increase required in nitrogen inflow (and hence the required fertilization rate) to support an increase of a given size in shellfish production.

In the economic literature the quantity $(I-A)^{-1}$ is called the Leontief inverse of the matrix A. In a sense, it expresses the multiplier effect that a change in final demand for one sector's goods will have on the other sectors, as a result of the direct and indirect cash flows which that sector's changed production will induce throughout the economy. This is easy to see in the simple one-dimensional case: If we replace Y by $Y + \Delta Y$ in Equation (5) and solve for the new level of total cash flow X' which will result, we find

$$X' = (Y+\Delta Y)(1-A)^{-1} = Y(1-A)^{-1} + \Delta Y(1-A)^{-1} =$$

$$X + \Delta Y(1-A)^{-1}$$

In the special case in which $\Delta Y = \$1$, $X' = X + (1-A)^{-1}$, so that $(1-A)^{-1}$ represents exactly the total new cash flows required to sustain the new level of production. In the nitrogen flow model elements of the nxn matrix $(1-A)^{-1}$ essentially total the direct and indirect outflows coupling the compartments at the row and column headings which result when a unit change is made in the outflow from the compartment at the row heading. Specifically, the element in the (i,j) position represents the portion of outflow from i which has been through j.

3. A Flow Model for the Great Sippewissett Marsh

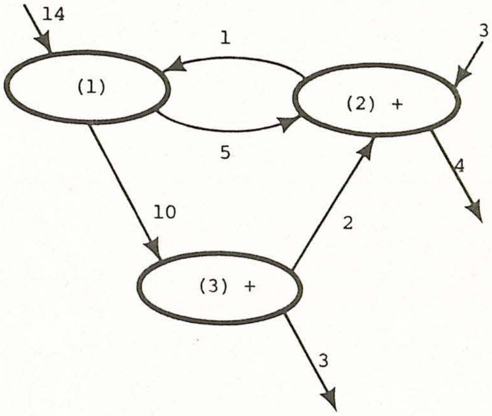

Figure 1

A three compartment ecosystem with flows. Plus signs indicate compartments which are accumulating excess flow.

Figure 1 below illustrates a hypothetical three-compartment ecosystem with intercompartmental flows, inflows and outflows of specified magnitude. Note that the flow in the figure is unbalanced and that compartments two and three are each accumulating an excess of five units of flow. The system's flows are summarized in input-output form in Table 1. Here each column represents the outflows from the compartment at its heading, both to the compartments at the row headings and out of the system completely. Sinks are added to the appropriate columns so that total inflows and outflows balance. Rows provide similar information with respect to inflows for compartments at their headings.

	(1)	(2)	(3)	Sources	Inflows	Total
(1)	0	1	0	0	14	15
(2)	5	0	2	0	3	10
(3)	10	0	0	0	0	10
Sinks	0	5	5		0	
Outflows	0	4	3	10		
Total	15	10	10	10		

Table 1

Flows matrix for the system in Figure 1.

The 4x4 matrix A, consisting of the intercompartmental and balancing flows of Table 1 after division by the row totals, is shown in Figure 2, along with the corresponding $(I-A)^{-1}$ matrix. Direct calculation via Equation (5) shows that if the outflows vector $\overline{Y}$ is replaced by $\overline{Y}' = (0,4,6,10)$, in which the outflow from compartment 3 is doubled, a total flow requirement from compartment 1 of about 18 units results, a 20% increase in the 15 units total flow it supplies to the rest of the system in Figure 1. If intercompartmental flows in the system are proportional to flows into the donor compartments, then an appropriate manipulation of the magnitude 14 inflow to compartment 1 could produce the desired total requirement from that compartment.

$$A: \begin{bmatrix} 0 & .07 & 0 & 0 \\ .5 & 0 & .2 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & .5 & .5 & 0 \end{bmatrix}$$

$$(I-A)^{-1}: \begin{bmatrix} 1.05 & .0736 & .0147 & 0 \\ .735 & 1.06 & .210 & 0 \\ 1.05 & .0736 & 1.015 & 0 \\ .893 & .563 & .612 & 1 \end{bmatrix}$$

Figure 2.
Normalized matrix of flows A and corresponding matrix $(I-A)^{-1}$ for the system of Figure 1.

The detailed marsh model, together with its application to the problem of linking shellfish production to marsh grass fertilization, is quite similar to the example above. The model traces the annual exchanges of nitrogen (in units of kg N yr^{-1}) among five compartments in a schematic flow model of the marsh. The compartments are (1) Sediments, (2) Spartina root/rhizome biomass, (3) Spartina aboveground biomass, (4) Tidal water, and (5) Shellfish. The path of a nitrogen input via fertilization would be roughly through the five compartments in the order listed, though there is a fair amount of internal cycling and flow to and from the outside environment in the model. The nitrogen in all major forms of nitrogen found in the marsh (particulate organic, dissolved organic, dissolved inorganic) is included. Inputs to the system from outside include the nitrogen in groundwater, precipitation and tidal inflow, and bacterial, algal and rhizomal fixation. Outputs include the nitrogen in tidal outflow, denitrification, volatilization, and losses to deep sediments. All are summed over a year. In most cases data used are averages of several years. Details of how various values were calculated are omitted here, but are available upon request.

Fertilization, the nitrogen in groundwater and precipitation and that fixed by surface bacteria and algae are lumped into a single exogenous inflow to compartment 1. The inflow value used in the model excludes fertilization values, however, so that the model actually describes the marsh in its natural state. Fertilization is thus viewed as a manipulation of this inflow similar to that described for the input to compartment 1 in the hypothetical system. Likewise, the nitrogen in net annual average growth of shellfish, as estimated for the marsh's natural population of ribbed mussels (Modiolus demissus), is listed as the sole exogenous output from compartment 5. This is done in an attempt to approximate a potential sustained yield harvest. This figure, 70 kg N yr^{-1}, corresponds to roughly 8500 kg mussel meat production, wet weight. Flows in the marsh are summarized in Table 2 below, in the format used for Table 1. The flow diagram is omitted, but it can be easily drawn from the information in the table.

	(1)	(2)	(3)	(4)	(5)	In-flows
(1)	0	4200	0	490	470	5970
(2)	6990	0	0	0	0	1270
(3)	0	1210	0	0	0	0
(4)	1270	0	1160	0	70	26250
(5)	0	0	0	730	0	0
Out-flows	2870	0	0	31600	70	

Table 2

Annual nitrogen flows for Great Sippewissett Marsh in kg N yr^{-1}, summed over the nitrogen in all major forms found in the marsh. Balancing flows are omitted. Compartments are: (1) Sediments, (2) Belowground biomass (3) Aboveground biomass (4) Tidal water (5) Shellfish.

The central portion of the matrix $(I-A)^{-1}$ is presented in Figure 3 below. As explained above, the elements of this matrix summarize the intercompartmental transfers which lead to the various outflows from the system. This kind of information can provide important clues about the specific relationships between flows in the system. With respect to the problem we have posed, the element in the (5,1) position is especially significant. It tells us that, given an outflow of a specified magnitude from compartment 5, only about 10% of that outflow has been through compartment 1. This stands in marked contrast to the situation in our hypothetical example, in which no flow could enter compartment 3 without first passing through compartment 1 (See Figure 1). Thus, based on the model, it would be difficult, for example, to double shellfish production in the marsh (outflow from compartment 5) by fertilization alone (i.e. by increasing the magnitude of the inflow to compartment 1).

	(1)	(2)	(3)	(4)	(5)
(1)	1.48	.564	.005	.128	.063
(2)	1.25	1.48	.004	.108	.053
(3)	1.25	1.48	1.00	.108	.053
(4)	.102	.074	.036	1.01	.006
(5)	.102	.074	.036	1.01	1.01

Figure 3

The central portion of the matrix $(I-A)^{-1}$, as computed for Great Sippewissett Marsh nitrogen flows.

This result is not surprising in terms of the nitrogen flow model we have presented. Inspection of Table 2 shows, for example, that no flow can enter the shellfish compartment without first passing through compartment 4, tidal water. This compartment in turn is strongly driven by the large annual tidal exchanges it has with nearby coastal waters, signified by the large inflows and outflows shown for this compartment in the table. A related factor which must be considered is the fact that dissolved organic nitrogen (DON), whose function is not well understood in the marsh, makes up a significant portion of the inflows and outflows in our model. In fact DON makes up 62% of tidal inflows, 58% of tidal outflows, 45% of groundwater flow, and more than half of the total inputs and outputs to and from the marsh (10). DON apparently plays no role in shellfish feeding and in fact may pass through the marsh with very little interconversion, since total inputs and outputs of this species very nearly balance (10). The model presented here must be regarded as a first pass attempt at analytical assessment of the potential for enhanced shellfish production via marsh fertilization. A fairer test would probably involve a model in which all DON is subtracted from the flows. Final judgement on the ultimate practicability of marsh fertilization must thus be withheld until further analysis is made.

4. Costs of Fertilization

Estimating the cost of nitrogen fertilization of a salt marsh is difficult because the equipment for applying the fertilizer is not standard. Rather than provide engineering cost estimates of large - scale systems, we will indicate the approximate cost of the system now used to fertilize a 2 to 3 ha section of marsh. This system pumps the fertilizer through spray irrigation pipes to all sections of the plot. The capital cost of the system is approximately $29,000, excluding design costs. Depending on remoteness, type of foundation required and other site - specific factors, this cost could be reduced by $5,000 or more. Vandalism has been a problem in maintaining the equipment, so a ten-year life is estimated. Assuming that the operator of the system can check it during periodic visits to the marsh for other purposes, and that approximately the present level of vandalism continues, annual maintenance cost is estimated to be $3,000 per year or less.[1] The operating costs are then labor and fertilizer. If fertilizer is applied for six months of the year, labor requirement will be about one-half time during that six months ($3,000 if annual full-time salary rate is $12,000) to apply fertilizer daily and check the equipment. Commercial fertilizer containing 45% nitrogen is estimated to cost $1,000 per year(25kg N/ha/week for 25 weeks = 650 kg of nitrogen in fertilizer). This is the high-level application rate; researchers feel most of the increase in growth of Spartina could be obtained with only one-third as much fertilizer[2]. This would decrease fertilizer cost but not labor and capital upkeep costs.

The alternative of obtaining nitrogen from secondarily treated sewage effluent would depend on acceptance by the local community as well as on the presence of a nearby sewage treatment plant. Under these circumstances, the nitrogen itself could be provided free of charge to the marsh, but the labor and capital costs would be higher to handle the greater volume required. In contrast to the 45% nitrogen content of some commercial fertilizers, secondarily sewage effluent has only about 15 parts per million of nitrogen, and an application rate comparable in nitrogen content would be 1.25 million liters per week per hectare (instead of 25 kg N/ha/week of commercial fertilizer). The feasibility of using this source of nitrogen is clearly very dependent on particular characteristics of the site.

5. Summary and Conclusions

Input-output analysis can be a useful tool for assessing the economic potential of biological systems over which man can exert little control. It makes possible the linkage of controllable inputs to outputs of potential economic value, while allowing for explicit consideration of the complex biological processes which ultimately govern the system's output of such commodities. This seems particularly true of salt marshes, where research has shown that fertilization can lead to dramatically increased yields of marsh grass biomass, and hence grass detritus which is potential food for shellfish.

We have used an input-output format to describe nitrogen flow through a New England salt marsh which has been intensively studied by biologists over the past few years. While much has been written about the use of input-output analysis to integrate environmental and economic concerns, attempts to do so are often limited by the lack of a detailed data base for the analysis. We believe the problem of linking a marsh's biomass yield of fish and shellfish to fertilization presents a valuable opportunity to test in detail this extended input-output methodology in a setting in which all links in the system being considered are under active study.

The input-output model presented here represents a distillation of data collected in field and laboratory studies. While the present model is far from definitive in answering the questions we have presented, it illustrates a method which can be used to examine other similar ecological-economic interactions. Future work should lead to detailed analysis of the fate of the various flows in the marsh system and provide some strong indications of the extent to which similar systems lend themselves to this type of analysis.

Acknowledgements

Several people must be acknowledged for helpful criticisms and access to unpublished data used in the preparation of this paper. These include Ivan Valiela and Thomas Jordan of the Boston University Marine Program, Jim Morris of the Marine Biological Laboratory Ecosystems Center, John Teal and Peter Kallio of Woods Hole Oceanographic Institution. Special thanks go to Jack Finn of the MBL Ecosystems Center for his assistance in the computer analysis of our results.

---

[1] Peter Kallio, personal communication, June 1978.

[2] John Teal, personal communication, June 1978.

References

1. Finn, J.T., "Measures of ecosystem structure and function derived from analysis of flows," The Journal of Theoretical Biology, Vol. 56, 1976, pp. 363-380.
2. Gosselink, J.G., E.P. Odum and R.M. Pope, "The value of the tidal marsh," The Center for Wetland Resources, La. State University, Baton Rouge, 1973, SG-74-03.
3. Hannon, B., "The structure of ecosystems," The Journal of Theoretical Biology, Vol. 41, 1973, pp. 535-546.
4. Isard, W., Ecologic-Economic Analysis for Regional Development, The Free Press, New York, 1972.
5. Leontief, W., "Quantitative input-output relations in the economic system of the United States," The Review of Economics and Statistics, Vol. 18, 1936. pp. 105-125.
6. Odum, H.T., "Trophic structure and productivity of Silver Springs, Florida", Ecological Monographs, Vol. 27, 1957, pp. 55-112.
7. Ryther, J.H. and W.M. Dunstan, "Nitrogen, phosphorus, and eutrophication in the coastal marine environment," Science, Vol. 171, pp. 1003-1013.
8. Smith, L.J. and J.E. Huguenin, "The economics of waste water - aquaculture systems," IEEE OCEAN '75 Proceedings, 1975, pp. 285-293.
9. Teal, J.M., "Energy flow in the salt marsh ecosystem of Georgia," Ecology, Vol. 43, 1962, pp. 614-624.
10. Valiela, I. and J.M. Teal, "Inputs, outputs and interconversions of nitrogen in a salt marsh ecosystem," Paper presented at the First European Ecological Symposium, Ecological Processes in Coastal Environments, Norwich, U.K., 1977.
11. Valiela, I., J.M. Teal and W. Sass, "Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge," The Journal of Applied Ecology, Vol. 12, 1975, pp. 973-982.

BIBLIOGRAPHIC DATA SHEET

1. Report No.
WHOI-79-29

2.

3. Recipient's Accession No.

4. Title and Subtitle
SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY

5. Report Date
February 1979

6.

7. Author(s)
Thomas M. Leschine

8. Performing Organization Rept. No.

9. Performing Organization Name and Address
Woods Hole Oceanographic Institution
Woods Hole, MA 02543

10. Project/Task/Work Unit No.

11. Contract/Grant No.
04-8-M01-149

12. Sponsoring Organization Name and Address
Pew Memorial Trust, Department of Commerce (NOAA)

13. Type of Report & Period Covered
Technical

14.

15. Supplementary Notes

16. Abstracts

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input-output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way, the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh (Cont. **

17. Key Words and Document Analysis. 17a. Descriptors

1. Salt marsh productivity
2. Salt marsh fertilization
3. Nitrogen flow analysis

** tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

17b. Identifiers/Open-Ended Terms

17c. COSATI Field/Group

18. Availability Statement

19. Security Class (This Report)
UNCLASSIFIED

20. Security Class (This Page
UNCLASSIFIED

21. No. of Pages
47

22. Price

Woods Hole Oceanographic Institution
WHOI-79-29

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY by Thomas M. Leschine. 47 pages. February 1979. Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant 04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input-output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way, the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

1. Salt marsh productivity
2. Salt marsh fertilization
3. Nitrogen flow analysis

I. Leschine, Thomas M.
II. Pew Memorial Trust
III. 04-8-M01-149 (Sea Grant)
IV. Marine Policy and Ocean Management Program

This card is UNCLASSIFIED

Woods Hole Oceanographic Institution
WHOI-79-29

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY by Thomas M. Leschine. 47 pages. February 1979. Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant 04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input-output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way, the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

1. Salt marsh productivity
2. Salt marsh fertilization
3. Nitrogen flow analysis

I. Leschine, Thomas M.
II. Pew Memorial Trust
III. 04-8-M01-149 (Sea Grant)
IV. Marine Policy and Ocean Management Program

This card is UNCLASSIFIED

Woods Hole Oceanographic Institution
WHOI-79-29

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY by Thomas M. Leschine. 47 pages. February 1979. Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant 04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input-output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way, the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

1. Salt marsh productivity
2. Salt marsh fertilization
3. Nitrogen flow analysis

I. Leschine, Thomas M.
II. Pew Memorial Trust
III. 04-8-M01-149 (Sea Grant)
IV. Marine Policy and Ocean Management Program

This card is UNCLASSIFIED

Woods Hole Oceanographic Institution
WHOI-79-29

SALT MARSH NITROGEN ANALYSIS: FERTILIZATION AND THE ALLOCATION OF BIOLOGICAL PRODUCTIVITY by Thomas M. Leschine. 47 pages. February 1979. Prepared with funds from the Pew Memorial Trust and by the Department of Commerce, NOAA Office of Sea Grant under Grant 04-8-M01-149 and the Institution's Marine Policy and Ocean Management Program.

A five compartment schematic model of the flow of nitrogen through Great Sippewissett Marsh is presented. Flows are described in terms of annual inputs, outputs and intercompartmental transfers of nitrogen. The nitrogen in all forms occurring in the marsh is considered, though dissolved organic nitrogen is disaggregated from the total flow.

A computer aided input-output analysis is performed on the model to assess the degree to which nitrogen inputs to the marsh surface are linked to nitrogen outputs in the form of net growth in marsh shellfish. In this way, the effects of both direct and indirect flows linking the two compartments involved are considered. The analysis is done to assess the likelihood that a large scale application of fertilizer to the marsh surface will significantly enhance shellfish growth in marsh tidal creeks. While no definitive answer to this question can be given, it is argued that the present level of understanding of the marsh nitrogen cycle does not support an expectation that shellfish growth will be enhanced. This argument is supported by a comparative analysis which shows a strong likelihood that Spartina growth is enhanced by fertilization, an effect which has already been observed.

1. Salt marsh productivity
2. Salt marsh fertilization
3. Nitrogen flow analysis

I. Leschine, Thomas M.
II. Pew Memorial Trust
III. 04-8-M01-149 (Sea Grant)
IV. Marine Policy and Ocean Management Program

This card is UNCLASSIFIED