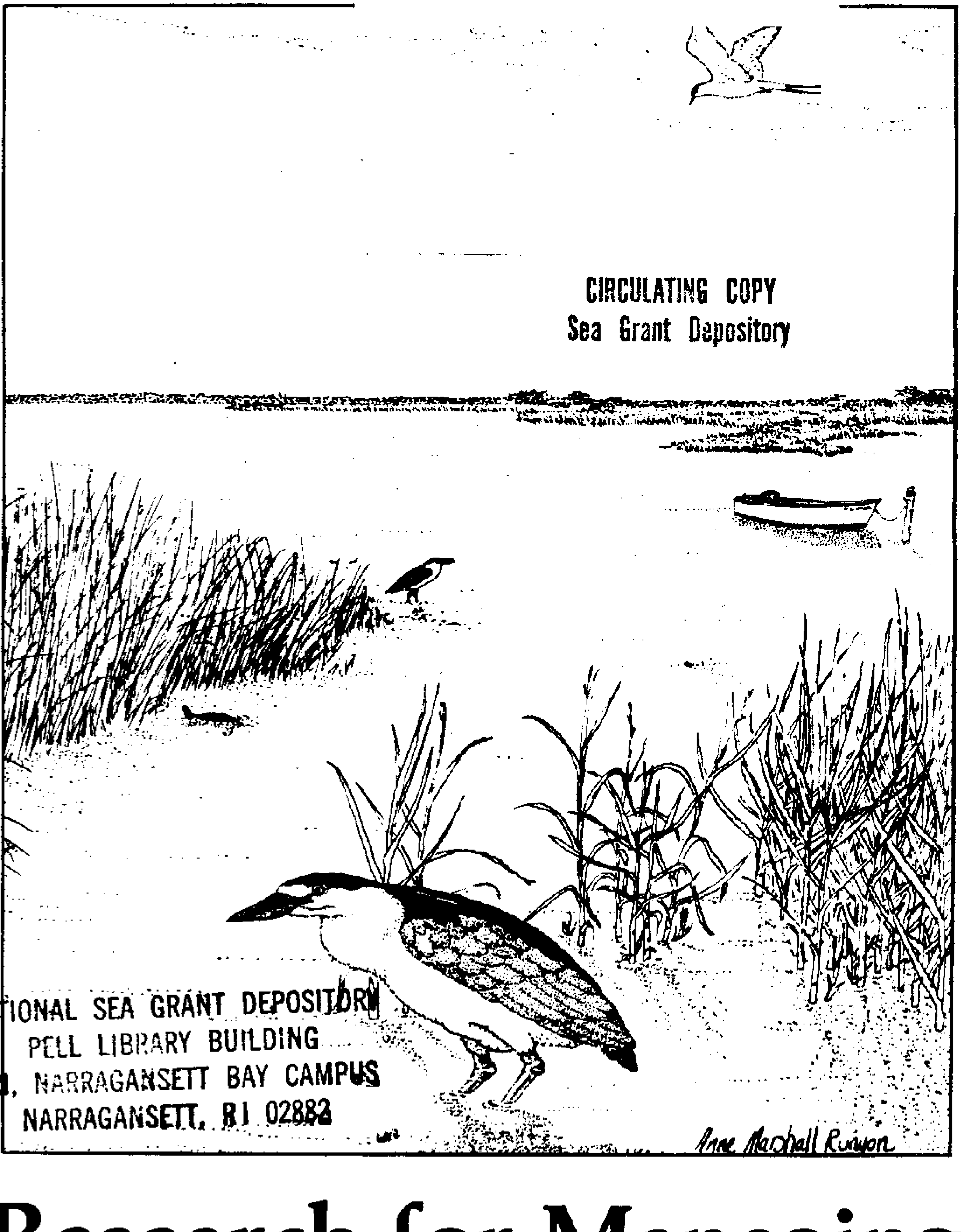

Anne Marshall Runyon

Research for Managing the Nation's Estuaries

RESEARCH FOR MANAGING THE NATION'S ESTUARIES: PROCEEDINGS OF A CONFERENCE IN RALEIGH, NORTH CAROLINA

March 13-15, 1984

Sponsored by the National Sea Grant College Program and
the National Marine Fisheries Service

Edited by:
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PREFACE

KEYNOTE ADDRESS

PREFACE

The nation's estuaries provide a valuable source for the economic development of our ocean and Great Lakes resources. Many of the commercially important fisheries species depend upon an estuarine habitat for at least a part of their life cycle. Estuaries lie at the end of rivers that drain vast land areas. Therefore, they serve as receptors of water, sediment, nutrients and whatever else might have reached the streams. Thus, it is in our vital interest to understand how basic processes function and to determine the best way to manage the milieu. This will require our best research efforts.

The purpose of this "national" symposium was to develop a research strategy needed to manage the nation's estuaries. The most capable researchers peered into the future and, based on the very latest scientific protocol, suggested those research directions necessary to better understand estuarine functions. Assessment of problematic needs resulted in five basic categories of research directions: water inflows, sediment inflows, nutrients and other chemicals, coupling of primary and secondary productivity, and fisheries habitats. Speakers accepted the challenges of addressing research needs, and the final chapter of the proceedings summarizes their recommendations. We hope that funding agencies will use these recommendations as a guide to future research programs.

The National Oceanic and Atmospheric Administration plays a prominent role in leading the necessary research efforts. Sea Grant and National Marine Fisheries Service are two components of NOAA with primary research responsibilities in estuaries. Therefore, they took the lead in planning and sponsoring the symposium. Appreciation is extended to those organizations for making this opportunity possible. The University of North Carolina Sea Grant College Program published the proceedings and is responsible for its distribution.

B.J. Copeland

ASSESSMENT OF ECOLOGICAL RISK

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INTRODUCTION

The evolution of terminology that we witness today, from "assessing the impact" to "assessing the risk," reflects a growing awareness of inherent uncertainties in the parameters of the models that we build. These uncertainties are both subjective, a result of our poor knowledge of the systems in question, and objective, the result of a true stochasticity that cannot be removed by additional data collection. The latter of these two has influenced a welcome change in terminology, which reflects the important underlying change in the perception of the problems that we face.

First of all, "risk" is by definition the probability of something undesirable happening. Being a probability, it is a hard concept to grasp. There are fundamental reasons why probabilities are hard to intuitively understand. Our vision, as well as our hearing and other senses, is distorted in many ways; our perception of randomness is severely distorted, too. I will address this subject of perception at the end of my talk. At present, let me state that there are interest groups in our society that would like to play the game of underestimating or overestimating ecological risks. The problem and the challenge for us is to objectively evaluate ecological risks and to defend this objective position in public forums.

Two types of theoreticians work in the field of mathematical ecology today. Let me conditionally divide them into "theorists " and "modelers." Theorists build simple and general models to advance our general understanding. Modelers build complex simulation models to describe concrete systems.

From the modeler's point of view, the theorist is someone who sits with his feet on the desk, never touches a computer, and develops insights that are valid for a variety of systems, but does not describe any of them because of too stringent assumptions. Modelers do not trust the Lotka-Volterra equations that say competing populations usually do not coexist, but sometimes they do, and it depends on four unmeasurable parameters.

The theorist views the modeler as someone who sits in front of a computer, frantically turning 100 knobs. Out comes the curve that finally fits a dozen data points. The model is calibrated!

"Can I trust your model," asks the theorist. "There are too many parameters in your model that we do not recognize from independent experiments."

"I performed the sensitivity analysis," answers the modeler, "and 98 out of 100 parameters are not that significant."

"Well," replies the theorist, "shouldn't you then build a two-dimensional model with parameters that matter?"

"The problem is that I did not know a priori which are those two important parameters," says the modeler. "Besides, to stand up to typical courtroom criticism, I need to demonstrate clearly what does, and does not, matter. The statement of insensitivity is, therefore, as important as the identification of the critical parameters."

This conversation can be continued indefinitely. Let me place myself in the middle of the two types that I have described. Although I began as a theorist, I have moved, step by step, towards the modeler's side. The dichotomy that I have created is certainly an artificial one.

One difficulty that modelers face is presenting their models in the one hour often allowed for presentation. The list of parameters and variables are frequently so long that just reading them would take up half the time.

I have, therefore, chosen a topic for this presentation that begins as purely theoretical, then moves closer to reality, step by step.

Let me see how far we can go. To define what sort of risk I am talking about, let us start, for simplicity's sake, with a one-dimensional model. Let us say we have a record of population size as a function of time. What is the risk that this population will go extinct? If asked for eternity, it is probably 1. Most of the species that have inhabited the earth are extinct now. When the same question is asked for a fixed, finite period of time, it becomes a more interesting, practical question. Let us address this question, using a sequence of models of increasing complexity.

DENSITY-INDEPENDENT GROWTH

The basic equations of the Malthusian model are either of the discrete-time type,

$$N(t + 1) = m(t)N(t),$$

where $N(t)$ is the population size at time t, $m(t)$ is the net growth rate at time t; or a continuous-time analog

$$\frac{dN}{dt} = r(t)N(t).$$

This model was studied by a number of authors (see references in Ginzburg et al. 1982).

In most work, $r(t)$ has the form

$$r(t) = r + \sigma\epsilon(t),$$

where r is the mean growth rate, $\epsilon(t)$ is the standardized white "noise," and σ characterizes the amplitude of the fluctuations.

Let us assume that the growth process starts with the population size N_o. We are interested in the chances of the population size crossing a given preassigned level, $N_c < N_o$, which is meant as a "critical level" corresponding to so-called quasiextinction. The answer is certainly time-dependent. Asymptotically for infinite time, these chances, P, are given by the simple expression

$$P = \left(\frac{N_c}{N_o}\right)^{2r/\sigma^2}$$

for positive r. For the negative and zero value of r, the probability is 1. Let us assume now that we will adopt this probability as the measure of persistence of our population and compare it with the same measure for the population being impacted. Assume, for simplicity, that the environmentally induced variance stays the same, but impact results in a new, lower value of the mean growth rate, r_{imp}. Let us define as the measure of our impact, I, the relative change in the probability of quasiextinction

$$P = \frac{P_{imp} - P}{P} .$$

We have

$$I = \left(\frac{N_c}{N_o}\right)^{2(r_{imp} - r)/\sigma^2} - 1.$$

Clearly, the greater the reduction in the growth rate, the larger is the value of our index, I. Interestingly, if the variance in the growth rate, $\sigma^2$is increasing, the index becomes less and less sensitive to the reduction in r. It is, therefore, absolutely insufficient to measure the impact in terms of the reduction of the average growth rate without considering the level of variability. How the critical level of quasiextinction, N_c, should be chosen constitutes another problem that should be discussed separately. I wish to show here the significance of the variance in the growth rate in reasonable criterion of the impact. In the case of striped bass in the Hudson River, the survival of the first-year fishes varies 50-fold, depending on the water temperature. Therefore a huge variance is produced in the year-to-year growth rate. A deterministic model of assessment is a misleading way to estimate the impact. As shown many times with different kinds of models, the mean behavior of the model does not correspond to the behavior of the mean model. This is always the case because the population trajectory is a nonlinear function of demographic parameters.

Another problem appears if we look at finite-time chances as opposed to asymptotic probability of quasiextinction. We have an exact impression for the density function for the first passage time at a prescribed level, N_c:

$$g\left(t, \frac{N_c}{N_o}\right) = \frac{\ln\left(\frac{N_c}{N_o}\right)}{\sigma\sqrt{2\pi}\sqrt{t^3}} \exp\left\{- \frac{\left[\ln\frac{N_c}{N_o} - rt\right]^2}{2\sigma^2 t}\right\}$$

This density adds up to the asymptotic probability given by the previous formula, $\int_0^\infty g(t) = p$. We are interested in the finite integral expressing the chances for the first passage to happen before time, T. With this we could compose an index of impact that will be time-dependent and determine the measure of the impact for a given length of time. Without calculations, the result will be strongly time-dependent for a relatively small T, tending to our asymptotic formula with $T \to \infty$. In cases when impact has a finite duration, this could be a reasonable approach to take. We can also calculate the expected level, its variance, and so on. All of these criteria, which are much harder to calculate than the simple deterministic criteria, seem more informative than the latter when assessing impact.

DENSITY-DEPENDENT GROWTH

Many people have worked on the logistic equation and its generalization. The standard form of the logistic equation is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right),$$

where K is the carrying capacity of the environment. In the best understood cases, it is assumed that the "noise" is concentrated in r, and K is a fixed constant. In this case, the equation can be transformed by introducing

$$x = \ln\frac{N}{1 - N/K}$$

to the simple form

$$\frac{dx}{dt} = r \ .$$

After that, the "noise" in r is introduced, and results are principally similar to the previous exponential growth model. From the standpoint of the probability of quasiextinction, the results can be obtained by replacing the ratio (N_c/N_o) with another expression involving carrying capacity

$$\frac{N_c\left(1-\frac{N_o}{K}\right)}{N_o\left(1-\frac{N_c}{K}\right)}$$

ILLUSTRATIVE EXAMPLE

Consider the simplest density-dependent growth model, the logistic equation

$$\frac{dN}{dt} = rN\left(1- \frac{N}{K}\right),$$

where we assume the carrying capacity, K, to be constant and the mean growth rate, r, subject to environmentally induced fluctuations described previously. An analytical expression for the probability, P, that a population started with initial size, N_o, will fall, at least once, below the actual level, N_c, in a time, T, is given by the integral

$$P = \int_0^T g(t)dt \ ,$$

where

$$g(t) = \frac{\left|\ln\left(\frac{N_c}{N_o}\,\frac{(1-N_o/K)}{(1-N_c/K)}\right)\right|}{\sigma\sqrt{2\pi}\,\sqrt{t^3}}$$

$$\times \exp\left\{-\frac{\left[\ln\left(\frac{N_c}{N_o}\,\frac{(1-N_o/K)}{(1-N_c/K)}\right)- rt\right]^2}{2\sigma^2 t}\right\}.$$

The answer to this problem is given in Ginzburg et al. (1982).

Let us examine graphically the probability distribution, P, numerically using the following assumptions:

$$\frac{N_o}{K} = \frac{1}{2},\ \frac{N_c}{K} = \frac{1}{10},$$

i.e., initially the population is at one-half of the carrying capacity and the critical level is chosen to be at 10 percent of the carrying capacity. We choose a range of $-0.06 \div 0.06$ (units 1/time) for the mean growth rate, r, and $0.10 \div 0.30$ as the range for variance of the growth rate, σ. Five periods of time---T=10, 50, 100, 10,000, ∞---are examined to see the time effect on the probability. (Figures 1-4).

As expected, the probability, P, of passing once below the critical level, N_c, increases with time for each fixed r and σ. The higher the variance, the less sensitive the probability, P, to a reduction in r. In 10 years (Figure 1) the effect could be insignificant. The longer the time, T, the more influential the effect of a given reduction, r.

For r negative we can observe a counterintuitive effect on the probability reduction with growing environmental variance. In reality, with negative r, a population will fall below the critical level given enough time. Stochasticity increases the chances of staying above the critical level. This effect is seen only for large periods of time, T, and strongly negative values of r. See Figure 2 with r = -0.06 for a demonstration of this effect.

AGE-STRUCTURED MODELS

Let us now move to a more realistic, age-structured approach. We start with the description of the underlying model. This is the standard Leslie matrix model that has been used in a variety of applications. The major difference is that we allow the elements of the matrix, which are fertilities and survivals for different age groups, to be stationary stochastic processes rather than constants as in the traditional model. To simplify our consideration, we assume the only stochastically varying parameter is juvenile survival. This assumption is reasonable for the

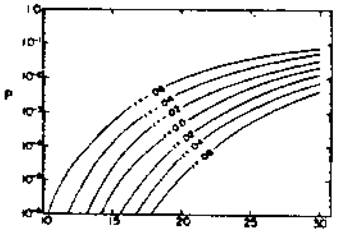

Fig. 1. The probability, P, of passing below the critical level, N_c, after 10 years.

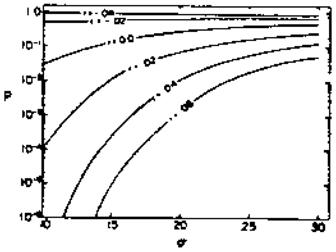

Fig. 3. The probability, P, of passing below the critical level, N_c, after 100 years.

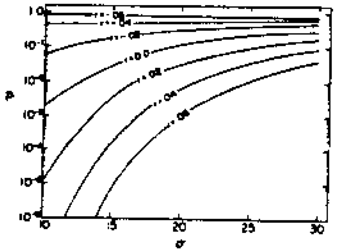

Fig. 2. The probability, P, of passing below the critical level, N_c, after 50 years.

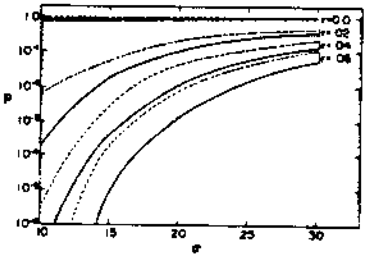

Fig. 4. The probability, P, of passing below the critical level, N_c, for 10,000 years (solid line) and the asymptotic probability (of ever passing the critical level, $T = \infty$ (broken line).

example that we will develop and is a biologically sound intermediate step between fully deterministic and fully stochastic life history description. Early stages of life are most vulnerable to environmental changes. Therefore the variability in juvenile survival is much greater than variability in fertility values of adult survival.

Consequently, the model is simply a recurrent system of linear equations

$$x_{t+1} = A_t x_t,$$

where t is the discrete time, t=0, 1, ...,

x_t is the vector of abundances of n different age groups $(x_{it}, \ldots, x_{nt})$,

A_t is the Leslie matrix of the form

$$A_t = \begin{vmatrix} 0 & f_2 & f_3 & \cdots & f_{n-1} & f_n \\ p_0(t) & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & 0 & \cdots & p_{n-1} & 0 \end{vmatrix}$$

where f_i represents fertilities of the females of the i-th age and p_i represents the survival between ages (i-1) and i. The only stochastically varying parameter in the matrix is p_0 (t). Let us note from the beginning that this assumption is not a limitation to the suggested method. The method will work with all the fertilities and survival being stochastic in an arbitrary covariation structure. We have chosen to work with this special model to simplify our formulations. In practice, the use of general models involving stochasticity in more, or even all, parameters is limited by the available data rather than mathematical technicalities. This does not mean that the problem is mathematically simple. However, most of the mathematical difficulties encountered are already contained in the simplified version. I feel the idea of our approach would only be obscured by overgeneralizations.

In applications, we are usually interested in a particular scalar variable, such as the abundance of adults, juveniles or any specific subgroup of a population. It may also be a biomass of a subgroup or any other variable of interest that is a linear combination of the original age group abundances. Let us denote this variable as N:

$$N(t) = (b, X_t) = \sum_{i=1}^{n} b_i x_{it}.$$

The choice of the vector, b, is dictated by purely practical consideration and has no relation to the population dynamics. If $b = (1, \ldots, 1)$, N(t) will represent the total population size at time, t. If $b = (0, 1, \ldots, 0)$, N(t) will be the abundance of juveniles.

Tuljapurkar (1981) established an important asymptotic property of the process, X_t using a set of biologically nonrestrictive assumptions about the parameters. Under this property, the asymptotically vector, X_t, is approximately lognormally distributed. In other words, there exist two constants, a and , such that

$$\frac{\ell n(b, X_t) - at}{\sigma\sqrt{t}} \to Y,$$

where Y is the standard normal variable with a zero mean and a variance equal to 1. The convergence is in distribution. It is particularly important that constants, a and σ, are independent of b. In other words, any variable of interest, N(t), with different vectors, b, is asymptotically equally and lognormally distributed.

This result gives us the possibility to evaluate the risks of the population variable, N(t), falling below a given critical level, N_c, at the time, t, as

$$\mathrm{Prob}\{N(t) < N_c\} \approx \Phi\left(\frac{\ell n N_c - at}{\sigma\sqrt{t}}\right),$$

where

$$\Phi(y) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{y} e^{-\frac{\zeta^2}{2}} d\zeta .$$

This formula is valid only if t is large enough. For one-dimensional models, this formula works for all t. Since we consider it as an approximation for a more complex multidimensional process, the actual time depends on the initial age distribution. Practically, a few generation times are sufficient for this formula to be accurate. Thus, in some sense, the problem of the long-term risk evaluation is resolved as long as we are able to evaluate parameters, a and σ. Formulas for the approximate evaluation of these two parameters were developed by Tuljapurkar (1981).

The more difficult, but practically more relevant, question is the evaluation of the probability that N(t) will cross the level, N_c, at least once in a given period of time, or

$$\mathrm{Prob}\{\min_{0 \leq \tau \leq t} N(\tau) < N_c\} .$$

This is the problem that we discuss next. We approach the problem in two steps. First, we build the one-dimensional "effective" model, which asymptotically simulates the behavior of the underlying age-structured model. Then, we consider a one-dimensional, first-passage time problem in terms of the variable, N(t).

THE "EFFECTIVE" ONE-DIMENSIONAL MODEL

The fundamental asymptotic property cited in the introduction and, particularly the independence of a and σ of the vector b, suggests that it might be possible to develop a one-dimensional model for the variable of interest, N(t), in the form

$$N_{t+1} = (a + \zeta_{t+1})N(t) ,$$

where ζ is a zero-mean stationary process with some autocorrelation structure. Although a and σ are independent of the vector, b, we will see that the autocorrelation structure will strongly depend on the choice of this vector. We therefore have different "effective" one-dimensional models for different definitions of the variable N. For every specific choice of b, however, the one-dimensional model behaves asymptotically as the underlying multidimensional process. We can attempt to use the simpler model to estimate desired probabilities. Note that the process, $\zeta(t)$, will be autocorrelated even if we assume the original process, $p_o(t)$, to be uncorrelated. The autocorrelation is borne by the underlying age-structured, multidimensional model. Nothing prevents us from assuming that environmental fluctuations, and therefore, the juvenile survival, $p_o(t)$, have a particular autocorrelation structure. The resulting autocorrelation function for $\zeta(t)$ will then depend on both, environmentally-induced historic influences, the Leslie matrix parameters and the choice of the variable of interest, b. In order to simplify notations, let us assume the environmental fluctuations to be of the "white noise" type, i.e., $p_o(t)$ is the process with zero autocorrelations. All the calculations can be generalized to include environmentally induced correlations if necessary. Details of the techniques for the suggested approach can be found in Ginzburg et al. (1984). Here, I will only present the results of our analysis as applied to the model of the Hudson River striped bass population.

To test our method, we have carried out extensive Monte Carlo simulations representing the "natural" behavior of the stochastic, age-structured growth process. We have estimated risks based on these simulations to generate the "true" values. Then we applied our method to the same problem to see whether the true results can be predicted analytically. A certain amount of numerical work is necessary to generate the theoretical prediction.

The other issue that should be discussed here is the choice of critical levels. In the density-independent model that we are considering, it is natural to choose critical levels in terms of a percentage of the initial level. In the age-structured context depending on the variable of interest, N(t), the effective initial level of

this variable should be assigned so that the critical levels are computed as its percentages.

The case of the Hudson River striped bass, which we used as a test case, is one of the hardest cases for the theory because the age distribution is very broad (bass live for at least 20 years), and asymptotic considerations require very long simulations. The value of the asymptotic rate of increase that results from the parameters is 1.0092, such that the population would remain almost stationary if driven by the mean matrix. Consequently, the probability of quasiextinction will be sensitive to the choice of the critical level.

Since we use these values only as an example for checking our methodology, the relevance of particular parameters to the actual population is a secondary issue. In general, for short-lived species, our approach will work better because more generations will be fitted into the same time period and the trajectory will be closer to its asymptotic behavior.

Let us review some of the results we obtained for the striped bass model. We have chosen $p_o(t)$ to be the logonormally and independently distributed random variable with CV = .5. The variable of interest, N(t), was defined as the overall number of adults (ages 5 through 20), such that b = (0,0,0,0,1, ..., 1).

First, in Figure 5, we show the simulated results versus the asymptotic expectation for the probability of falling below a certain level at time, t. The theoretical curve agrees with the simulated results quite well. For comparison, we also plotted the curve based on the purely "white noise" theory (disregarding the autocorrelation in the (t) process). The comparison demonstrates that we cannot ignore autocorrelation borne by the underlying age-structured process when we try to examine the population growth macroscopically in a one-dimensional process. At the same time, from the standpoint of risk calculation, the autocorrelated one-dimensional model catches the essence of the process well.

In practice, the decision of what should be the critical level is difficult. In any case, this

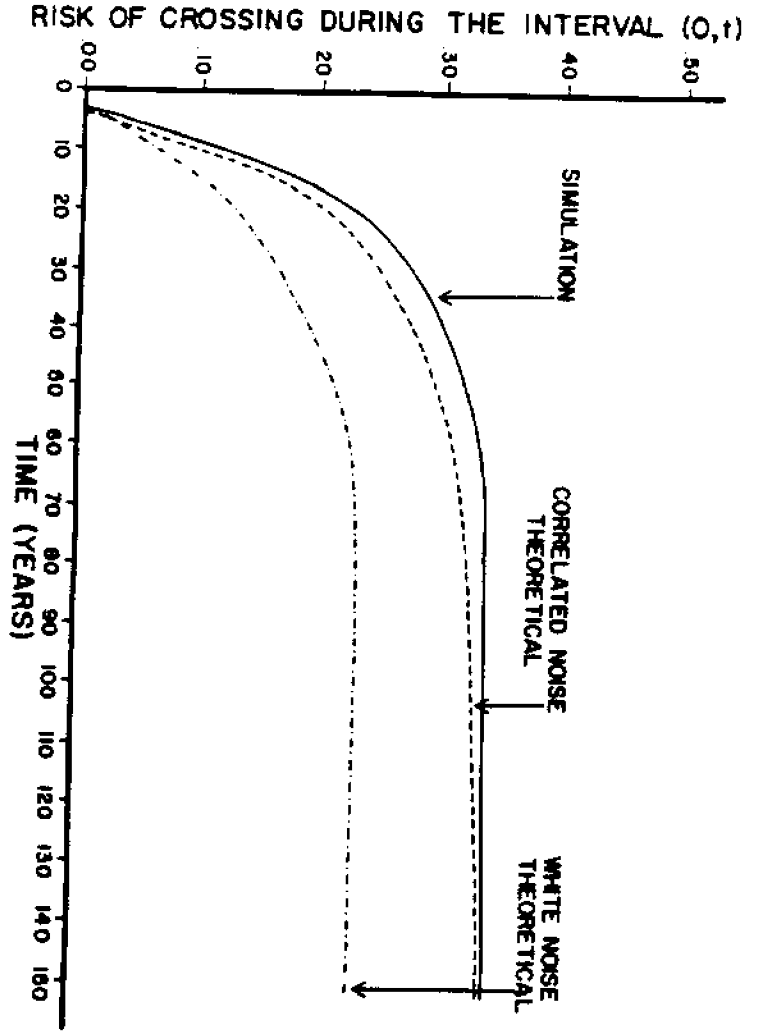

FIGURE 5

decision lies outside our method. We can only estimate risk given the level. It makes sense, therefore, to present results as a function of the critical level. Figure 6 gives results in this form. Again, we see close agreement between simulated and theoretically estimated results. In conclusion, the idea of one-dimensional approximation, which relegates all the complexity of a multidimensional process into the autocorrelation function for the growth rate, seems to work well. With shorter generation time, autocorrelation dies out quickly with the time lag, and the method works better. I can claim, therefore, that for a large variety of natural populations, we have a method of evaluating ecological risk, given their life-history characteristics and their levels of variability.

The next logical step is to take into account density dependence, or what industry calls more optimistically, "compensation." This is a very difficult problem and the difficulties are fundamental rather than merely mathematical. In most cases, we do not have sufficient empirical data to evaluate the shape or even the strength of density dependence. The results of risk evaluation will certainly depend on this critical information. There is one interesting statement that I can prove for a simple one-dimensional model and can predict to be correct for age-structured models also. Risks evaluated based on a nondensity-dependent model, which I discussed, are conservative estimates of risks evaluated on the basis of a wide class of density-dependent mechanisms. What we have, therefore, is a good conservative evaluation. If one needs to do better, the Monte Carlo simulations will work. That is the only method we have to address this problem today.

CONCLUSIONS

Finally, let me say a few words on the subject of people's perception of risks. As I have already mentioned, people have difficulty in intuitively evaluating random events. A variety of faults in the human perception of randomness have been identified by psychologists working in this area. I do not have the time to discuss their findings in detail here. What is interesting in relation

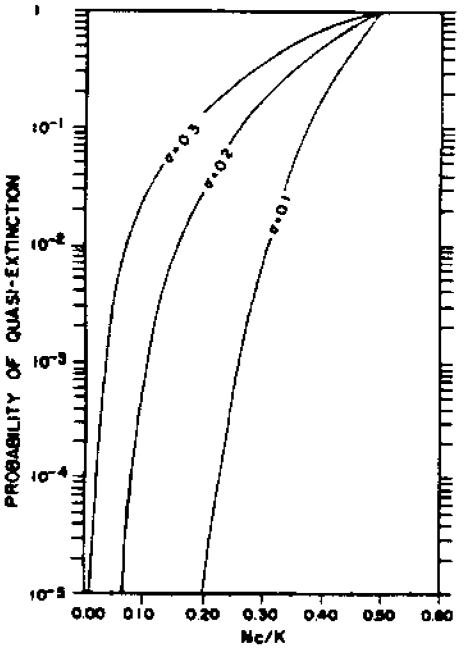

FIGURE 6

The probability, P, of passing below the critical level, N_c. The critical level divided by carrying capacity at time T=10 for a stable r=0 population.

to our topic is that these faults demonstrate themselves clearly in relation to random processes.

Here is an experiment that I performed recently with my undergraduate class (Figure 7).

I simulated five random processes on the computer, all with mean zero and a variance equal to one. The processes, however, have different values of the autocorrelation coefficient, r, which is assumed to be constant for any two consecutive values. The negatively autocorrelated process fluctuates more than the "white noise" (r=0) and the positively autocorrelated process fluctuates less. I asked the students in my undergraduate class to rank the five processes in order of randomness. All of the processes were random, but some were more random than others.

The results of my poll are given in Figure 7. Clearly, most people perceive the most negatively autocorrelated processes as most random and the most positively autocorrelated processes as least random. The most random process (graph D) was recognized as intermediately random.

This experiment shows that, even if we gather a large committee and vote on the risk of the outcomes of a random process based on the data presented, the faults in individual perception will not cancel each other out. There are definite general human biases in the ways that random events are evaluated. The committee is bound to be wrong.

The only way to approach the problems of risk evaluation, which we are going to face more and more often, is through careful, objective mathematical analysis and modeling. That is why the methods that I described today, combined with simulation modeling techniques, will be of greater importance in the future. We have no alternative but to create methods of clearly translating our doubts and uncertainties, both subjective and objective, into the language of risk, and to educate the public and the policymakers about the way it should be used to make decisions.

	r	"most" random	"least" random
A	-.2	3	4
B	.5	3	㉞
C	-.5	㉝	3
D	0	4	4
E	.2	4	2

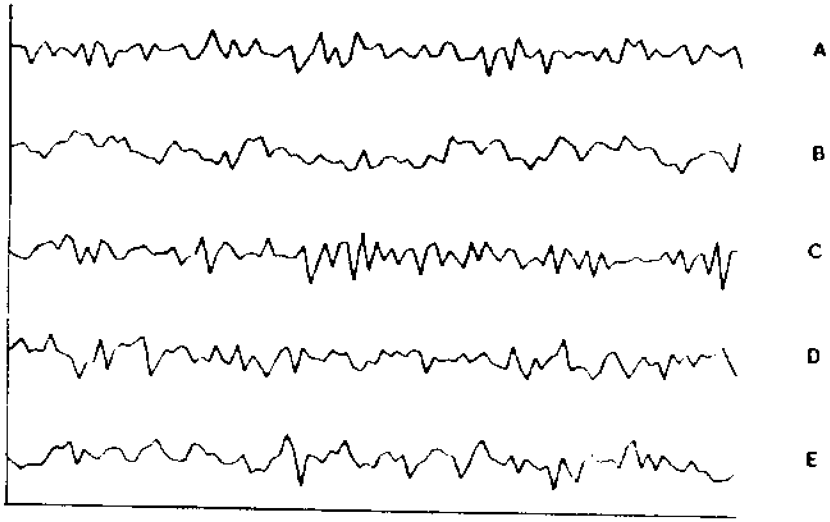

FIGURE 7

I would like to conclude with a picture (Figure 8) and some words from my colleague and friend, Dr. R.A. Goldstein:

The policymaker weighs the costs and benefits of alternative management policies. These include the benefits of additional research to reduce uncertainties and risks. The scales signify the importance of expressing quantitatively environmental effects, costs and risks. The policy judgment process is based on models and data supplied by scientists. The risks and uncertainties inherent in the process, models and data are indicated by the policymaker's position of unstable equilibrium. The sword represents the means of implementing or enforcing governmental policies and regulations.

Although it is desirable for justice to be blind, it would be preferable for the policymaker to see all the risks and uncertainties that make up the base on which she stands. A blindfolded person in a highly unstable position can raise tremendous havoc with a sword.

It is the scientist's responsibility to transmit clearly the information about the risks and uncertainties and hence remove the blindfold.

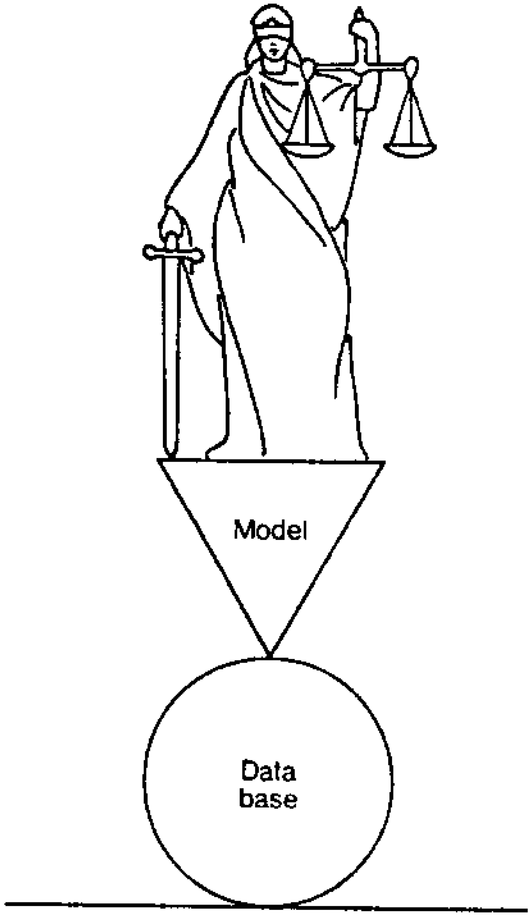

FIGURE 8

Ecological Risk Uncertainty Analysis. Printed with permission of the author, Robert A. Goldstein, Electric Power Research Institute, Palo Alto, CA.

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DISCUSSION

B. CHRISTIAN: Your models all dealt with an N_c that is less than N_o, namely an extinction type of thing. What we'll be talking about in the next couple of days is an N_c greater than N_o. Will that change anything qualitatively?

L. GINZBURG: Yes. I was recently talking to the pest control people for which the critical level is just on the other side of the initial level. They want the outbreaks to be below certain levels rather than above certain levels. Mathematically it's the same. I never worked with the models on that side. Not that the mathematics is different, but maybe something in reality is different that I should think about. I don't have experience in that. But I don't see any fundamental differences. I think the approach fundamentally is as applicable to the critical level above the initial level as below.

T. CLEMENTS: I'm with the North Carolina Division of Environmental Management. I am one of the persons with the unfortunate title of modeler, and I have some questions for you from a practical point of view.

You mentioned that you sometimes study on relationships where you have uncertainty. From my perspective, unfortunately, I feel that a lot of the uncertainty is system specific. Whether I'm dealing with an estuary that's dominated by lunar tides or one that's dominated by wind tides makes a difference. Yet, I have to make some management decisions that I would like to include uncertainty in. I feel that because it's system specific I'm having a great deal of difficulty in dealing with uncertainty. How do you handle that in terms of incorporating it into the decision-making process?

L. GINZBURG: You mean you want the decision for all systems together, not for one?

T. CLEMENTS: Sometimes we make across-the-board decisions or look at individual cases and make decisions. We deterministically use a model to reach an answer that I feel is unreasonable. I don't know how to incorporate the uncertainty because I can't make a statement according to the real relationships. They are different. They are specific. If they have to be estimated for a particular system, they may be different across systems. How do I handle uncertainty in the decision-making process with that in mind?

L. GINZBURG: That's pretty bad. If you have a number of systems that are all different, then you are forced to make decisions uniformly for all of them.

T. CLEMENTS: Maybe not necessarily, but you must deal with each system. I don't have the resources to measure and set up a data base.

L. GINZBURG: Usually one uses the bounding approach to be on the conservative side. Assume the worst. If you're talking about risk estimation, assume something that is definitely worse than it is.

WATER MANAGEMENT AND ESTUARINE PRODUCTIVITY

WATER MANAGEMENT AND ESTUARINE PRODUCTIVITY

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INTRODUCTION

Among the most pressing water resources questions today are those that concern the allocation of fresh water to bays and estuaries. In the lists of water uses, freshwater inflow to estuaries is a relative newcomer, but its importance is comparable to many of the highest priority uses. However, the procedures for determining the quantities and timing of water needs lag behind other uses, which quantities can be determined with precision and forecasted into the future. Such quantities must be calculated if freshwater inflows to estuaries are to gain and retain their proper status in water-use priorities.

Determining these inflows depends on our ability to understand how they govern the salinity regime, provide nutrients, couple primary and secondary productivity, and sustain habitats. The extent to which we can understand and quantify these functions and assess the amount of freshwater inflows needed will determine the success we will have in adopting inflow requirements.

WATER MANAGEMENT

To manage water means to use whatever means possible to provide water for beneficial uses. In a watershed, these uses can be many and varied. Conventional users include municipalities, industries, steam-electric power production, agriculture, mining, hydroelectric production, navigation, and recreation and tourism. Of these uses, hydroelectric production, navigation, and recreation and tourism are considered to be non-consumptive (i.e. no water is lost from the drainage basin because of them). However the other uses, particularly agricultural irrigation, results in substantial consumptive use. It is the consumptive use of water in the drainage basin that competes strongly with the bays and estuaries for water. To the upstream consumptive user, water "lost" to the bays and estuaries is also a consumptive use. Adding use of bays and estuaries to the list of legal water uses in a drainage basin creates an inherent conflict, which is larger than most others that develop. The usual recommended flows of fresh water to the bays and estuaries is the historic annual flows with natural seasonal variations. With such requirements at the lower end of the drainage basin, the water available for allocation upstream becomes limited, particularly in times of drought.

The agencies responsible for water management must allocate water among competing uses. Their allocation decisions must be based on the best information available about the amount of water needed and the timing for those uses. Municipal and industrial water supply demands can be easily estimated and projected. Agricultural demands are estimated and projected less easily. But these uses have a substantial data base on which to make their case. Allocation of water to bays and estuaries must be able to compete in the minds of those decision makers. The difficulties already encountered in establishing those required flows reflects the priority given to the allocations.

Water management includes water development, which is the reliable provision of water for various uses through the capture of surface water in reservoirs, the tapping of groundwater via wells, etc. Those who regulate water must allocate it among users based on priorities. In Texas, for example, the following priorities are used:

1. domestic and municipal uses,
2. industrial uses,
3. irrigation,
4. mining and recovery of minerals,
5. hydroelectric power,
6. navigation,
7. recreation and pleasure, and
8. other beneficial uses.

Such a list recognizes the preeminence of water supply as the highest use, the support of the industrial economic base second, and the value of food production through agriculture third. No specific provision is made for waters to bays and estuaries, although they could be included among

other beneficial uses. The Texas Water Code (Section 1.003) was amended in 1975 to recognize the importance of freshwater inflows to estuaries as follows:

> "It is the public policy of the state to provide for the conservation of the state's natural resources including: (6) the maintenance of a proper ecological environment of the bays and estuaries of Texas and the health of related living marine resources."

Also, state statutes require the Texas Department of Water Resources to consider the effects of upstream water resources development and new applications for water right permits on the bays and estuaries of Texas (Texas Water Code, Sections 11.147 and 16.051, as amended).

Such public policy and water allocation priority procedures bring problems, which have been recognized by the Texas Department of Water Resources (1982). To provide minimum freshwater inflows to certain Texas estuaries, it may be necessary to release more water at certain times from reservoir projects than would normally be released in accordance with the provisions of water right permits. When stream flows and effluent-return flows are insufficient to meet the minimum needs of certain estuaries, releases of water from reservoir storage would be needed to maintain specified water quality conditions. Releases of water would reduce the dependable yield of these projects during critical dry periods and raise the unit cost of water -- possibly to the point of making some projects economically infeasible. For existing projects, the loss of yield could mean less water to sell for revenue generation to pay for the project.

Such releases would compete with upstream uses such as irrigation. In the last session of the Texas legislature, a bill to update the Texas Water Plan was not allowed to pass out of committee because of the conflict between upstream water users and those wishing to allocate waters to the estuaries. The Texas Department of Water Resources had just updated its Water Plan (Texas Department of Water Resources 1983) and developed estimates of freshwater inflow needs to estuaries over the previous eight years. A better scientific basis for freshwater inflow needs in Texas was available. But the magnitudes of flows needed were questioned as were the priorities to be given to the estuaries.

Why not give the estuaries a low priority in the allocation of fresh water? How well are we able to determine freshwater inflow requirements? What should the basis be for these requirements -- salinity maintenance, productivity maintenance, habitat maintenance or other factors? Why should the estuaries be given higher or equal priority than municipal, industrial or agricultural uses? Who should pay the costs of water storage in upstream reservoir projects used for estuarine maintenance? Should population and water-intensive industrial growth be limited in river basins contributing fresh water to estuaries where significant, future reductions of fresh water could reduce their productivity.

These questions are being asked by those who set the priorities for freshwater allocation and by those who designate the amounts of flows to reach them. They are not unreasonable questions. If the allocation of fresh water to estuaries is incorrect, the economic damage to other users, present and future, can be great. At the same time, the damage to estuaries due to inadequate allocations can also be great.

What then should be the basis for allocation of fresh water to estuaries? Salinity maintenance and productivity (primary and/or secondary) have been suggested most often. Let us examine these two factors.

BASES FOR ALLOCATIONS OF FRESHWATER

Salinity

By definition, estuaries are coastal bodies of water measurably diluted with runoff from land drainage, (Pritchard 1967) and hence, are subject to management of water resources in their drainage basins. Freshwater inflows to estuaries determine their salinity regime, influence their mixing, impart nutrients, trigger organism migrations, and do many other important functions. To lose its inflow, alter its flood events, or modify it in almost any way, raises the specter of irreparable damage. Information presented at a recent conference on freshwater inflows to estuaries indicated that a 25 percent to 30 percent reduction in natural river inflow can result in disastrous ecological consequences to estuaries (Rozengurt and Haydock 1981). Rozengurt and Haydock say, "The early warning signs of excessive withdrawal are apparent in reduced productivity of fish and wildlife resources; changed biological structure of plankton, benthos, and fish communities; increased salinity intrusion affecting municipal and agricultural water supplies and the biota; and increased effects of pollution loads in progressively more stagnant waters." Clarke and Benson (1981) used this information to recommend a cessation of further consumptive depletion of natural freshwater inflow until it could be shown that additional depletion could be tolerated. They further recommended that the U.S. Water Resources Council include a criterion for evaluating adherence to such a standard as part of the president's proposed Independent Project Review Process.

Most of the early workers in estuaries recognized salinity as the most important factor in regulating organism distribution and survival (for example, Gunter 1956; 1961; and 1967). Others (e.g. Darnell 1981) saw such tolerance limits as key tools in estuarine management. Certainly it is recognized that maintenance of a regular, natural salinity regimen is desirable to minimize perturbations caused by floods, droughts and man-made alterations. The earliest federal water quality criteria contained recommendations for maintaining salinity variation in estuaries within about 10 percent of normal salinities (National Technical Advisory Committee 1968). During droughts, salinities increase and marine waters can be found in the mouths of rivers at the head of the estuary. Drastic changes in biota composition and population are found at the end of such a period when freshwater flows increase substantially (Hoese 1960). Reduced freshwater inflows during droughts also limit the quantity of organics imported to the estuary from the drainage basin and hamper detrital food chains dependent on that source (Copeland et al. 1972). At the other end of the spectrum, floods can decrease biotic populations by reducing salinities or flushing organisms out of the estuary (Matthews 1981; Kalke 1981). Flood flows do, in fact, reduce salinities and the populations of certain predators. Flint and Rabalais (1981) reported increased benthic production following such events.

Upstream water management can reduce the impact of droughts and floods by releasing water during droughts and retaining high flows during floods. The ability to manage freshwater flows implies an ability also to control salinities in the downstream estuary. For salinity, this ability to manage water for the benefit of the estuary may be the key to determining freshwater inflows. Indeed, Clark (1981) proposed that an optimal salinity regime be established for each estuary. He also suggested that maintenance of the optimal regime be the guiding objective for management. Clark recognized the oversimplification of doing so, but argued it was justified given the political nature of management and that other functions of the estuary fit in with it.

Productivity

It long has been thought that estuaries are more productive than most other ecological systems. The high productivity of estuaries has been well documented (Odum 1971 and many others). As Chapman (1973) summarizes:

> The productiveness of an estuarine system is an expression of its energy input. Whether that energy comes directly from solar radiation stimulation of photosynthesis or is from tidal flow, wind, rain, or tributary runoff, its conversion to other forms of energy such as food, is essential to the total life complex of the estuarine system. The energy from the gravitational forces of tide and river flow is controlled mostly by local and regional conditions whereas the direct energy of solar radiation depends mostly on latitude.
>
> Variations in an estuarine system relate directly to the sources and amounts of energy received; and the amount of energy available controls, to a large degree, the kind and variety of aquatic life present.

Chapman says that the mechanics of energy transfer are not well understood and cites the importance of vascular detritus from saltwater marshes to the food chains of estuarine organisms. He also points out the importance of nutrient recycling within the estuary. Finally, he concludes that "without tributary fresh water, this self-perpetuating system would cease to function."

How important is nutrient input to estuaries from freshwater inflow? Nixon (1981) addressed this question, noting four theories proposed in the literature about the importance of freshwater inflows to the nutrient regime of estuaries. These theories were: (1) fertilization by advection of deeper offshore waters, (2) fertilization by marshes, (3) fertilization by concentration - the nutrient trap, and (4) fertilization by rapid recycling. Although the first two mechanisms received much attention, they were discounted recently. Marsh systems, in particular, are now known to be importers and exporters of nutrients. Their role is to provide habitat not export nutrients. There is still controversy over the marsh's role and the importance of offshore waters. However for Texas estuaries, Armstrong (1982) showed the small role that marshes play in the nutrient regime. He calculated their contribution to be less than 5 percent of the total external inputs to any of the six major estuarine systems. In addition, he showed nutrients derived from exchange with offshore waters to be even less (in Wiersema et al. 1982) in Matagorda Bay, Texas.

Nixon (1981) explored the nutrient trap concept by examining a number of estuaries for their primary production characteristics, reasoning that the influx of nutrients with freshwater inflow should show up in the magnitude of the subsequent primary production. He was struck by the similarity of the levels measured and concluded that "some other, more constant feature of estuarine systems ... makes them so productive." He also explored the influence of freshwater inflows on secondary production. He examined production versus inflows on a year-to-year basis and on an estuary-to-estuary basis for systems with widely varying annual inflows. Several examples of positive and negative correlations of commercial finfish and shellfish landings, and freshwater inflows were [illegible], including Armstrong's (1973; 1982) plots of commercial shellfish landings versus freshwater renewal rates (inverse of residence time) for five Texas estuaries. The data used were limited by the accuracy of the data base and were rearranged from Copeland (1966). Since then, Armstrong (1982) used freshwater inflow, freshwater content of the estuary, and nutrient loadings on an areal basis for six Texas estuaries to show the relation between commercial finfish and shellfish landings, and nutrient flow to estuaries with fresh water. The relationships derived show the positive influence of freshwater inflow and associated nutrient loading on landings up to a point. Then a reduction is caused by too much fresh water. Others have developed complex multiple regression equations to relate seasonal freshwater inflow to commercial landings. These equations were used to develop the various levels of freshwater inflow requirements for Texas estuaries (Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b and 1981c). All of these previous works illustrate some relation between freshwater inflow and/or nutrient loading, and commercial landings, but the mechanism of that relationship is not clear.

Nixon (1981) supports the nutrient recycling theory about estuary production. He hypothesized that:

> . . . the high production of estuarine waters om general is brought about and maintained by the almost complete and rapid coupling of heterotrophic and autotrophic processes. Moreover, if the relative rates of organic synthesis and decomposition are considered, it seems likely that the upper limit of production is set, for the most part, by the slower rate of remineralization. If so, one of the important features of an estuary may be the relative importance of pelagic versus benthic remineralization, because the rate of these processes is quite different. The most rapid way to recycle nutrients is to put the organic matter through pelagic animals, such as microzooplankton.

Ward et al. (1982) came to similar conclusion in their study of Matagorda Bay, Texas. They calculated that external sources of nitrogen (primarily freshwater inflows) accounted for only 2 percent of the nitrogen fixed by producers

(primarily phytoplankton). And similarly, external sources of phosphorus (again primarily freshwater inflow) produced only 5 percent of the phosphorus fixed by the producers. It was concluded that most of the nutrients fixed were recycled through the pelagic or benthic system. Calculating secondary production based on measured primary production, it was estimated that the commercial catch of finfish and shellfish within Matagorda Bay accounted for only 2 percent of that theoretically available. This small amount, however, was similar to secondary production yield from primary production measured by Hellier (1962) in the Laguna Madre of Texas. But the large discrepancy between theoretical and actual yield is bothersome. Certainly some of the difference can be accounted for by emigration of organisms from the estuary to the ocean. Other possibilities are that primary production estimates are too high or that fisheries production is limited by factors other than food, such as habitat utilization, increased mortality rates at critical life-cycle stages and overfishing.

What is the coupling between freshwater inflows and primary and/or secondary production? Can much faith be placed in the relationships developed between freshwater inflows and secondary production represented by commercial landings either on a chronological basis for single estuaries or on regional basis for several estuaries? Are such relationships limited to one region of the country? If the nutrients brought to the estuary by freshwater inflows are so small compared to internal sources, how can they be related to production in the estuary - short term or long term? If freshwater inflows were cut off and the associated nutrient source lost to the estuary, would production be drastically affected in the short or long term? Will, on the other hand, internal cycling sustain high production in the absence of freshwater inflows as it does in the Laguna Madre of Texas (Odum 1967)?

RESEARCH NEEDS AND PRIORITIES

To answer the questions water managers are asking about the allocation of freshwater inflows to bays and estuaries, the following research is needed:

1. To determine the basis (salinity levels and gradients, productivity, and/or some other property or function of the estuary) to use to establish the amounts of inflows needed and the reliability of freshwater inflow estimates based on this property.

Will we find, as Clark (1981) believes, that salinity is the parameter to control and that other function indicators will fit in with salinity?

2. To establish the functional tie between nutrient inflows to the estuary with freshwater inflows and primary and/or secondary productivity as has been done between inflows and salinity.

Can we unravel the hazy link Nixon (1981) sees between nutrients brought into the estuary with freshwater inflow and secondary productivity?

3. To establish the role of the benthic system in nutrient recycling and the provision of food for higher trophic level organisms.

Is the benthic system the missing link between nutrients in inflows and secondary productivity as Flint and Rabalais (1981) propose? What are the major internal pathways of nutrients and the biota responsible for recycling?

4. To prepare nutrient budgets on other estuarine systems to show more clearly the roles of the freshwater inflows, marshes, benthic systems, coastal waters, precipitation and other sources, and to delineate the importance of each source in providing nutrients and recycling them.

Are freshwater inflows the major source of external nutrients and marshes a minor source as Armstrong (1981) and others have found? How do these external sources compare in magnitude to internal sources? If external sources are consistently small in comparison, what is their true importance?

5. To delineate the value of a salinity as an indicator of freshwater inflow needs versus productivity or some other functional property of the estuary.

Can salinity be used as the only basis for freshwater inflow calculation? If so, what spatial and temporal salinity regime should be maintained? How reliable are freshwater inflow requirements based on salinity?

6. To determine the amount of freshwater inflow needed for the bays and estuaries on an annual basis, the amount of inflow needed on a seasonal or monthly basis, and the reliability of these estimates.

The bottom line is determining inflow requirements and their timing based on whatever criteria are developed in the research outlined above. What cause and effect relationships should be used? How should they be embodied in mathematical or conceptual models of the estuary and used to estimate inflow requirements?

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WATER MANAGEMENT IN THE EVERGLADES AND ESTUARINE PRODUCTIVITY

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INTRODUCTION

The Everglades differs significantly from most drainage and estuarine systems studied. There is no associated river with the upland marsh or estuary. The upland marsh is extensive, and the interface with the estuary is broad, extending nearly 80 miles. The slope of the marsh is approximately 1 inch per mile. Therefore water discharge into the coastal mangrove forests and shallow bays is diffuse. Tidal range in the estuary is less than 2 feet, and wave action is nearly nonexistent. The Everglades estuary is not a very dynamic physical system. But it has a well-known reputation as a sportfishing mecca and a nursery ground for several commercial fisheries.

Costello and Allen (1966) showed that the Everglades' pink shrimp, Penaeus duorarum, spend two months to six months in the mangrove estuaries and Florida Bay before migrating to the Tortugas shrimp grounds. In a recent study of spiny lobsters, Panulirus argus, Dodrill (in prep.) tagged juveniles in Florida Bay and recovered them from the Gulf of Mexico, the Florida Keys and Biscayne Bay. We also know adult populations of sport and commercial fish were abundant historically in the bays and mangrove creeks of the Everglades. Clearly, the Everglades estuary is an important site of biological production and contributes significantly to the shelf fisheries of Florida. Since the Everglades estuary is unlike most systems studied and is an important site of fishery production, it may serve as a proving ground for scientists' assumptions about how estuaries work.

WATER MANAGEMENT

The Everglades isn't just a national park. It's a much larger drainage system than most people imagine. It begins in the Kissimmee Valley with a cluster of lakes drained by the Kissimmee River, and it feeds into Lake Okeechobee. Lake Okeechobee historically overflowed its shallow banks into the saw grass marshes of the Everglades. But today it is contained by high levees and separated from the Everglades by a wide belt of agricultural land. Four canals connect the lake to the Everglades. The saw grass marsh, south of the agricultural zone, is divided into five water impoundment areas, a marginally developed region called the east Everglades, and a national park with a large estuary. The Everglades no longer functions as a flow-through system extending from Orlando to the Gulf of Mexico. It is divided into parts that are connected by canals, gates and pump stations.

The parts are heavily managed. Indeed, division of the Everglades allowed for some resolution in the conflicting uses of the system. Management uses of the Everglades include flood protection, agricultural and municipal water supply, coastal salinity control, nutrient uptake and recreation. However, the value of the Everglades to coastal fisheries and the health of the estuaries was one of the last important relationships to be recognized. Little regard was given to the Everglades estuary while designing the existing water management system. Each upstream use probably has a particular effect upon the Everglades estuary, and combined, the uses may dramatically alter some aspects of estuarine productivity.

Flood Control

The dominant design features of the Everglades water management system are the levees that contain high water and the canals that rapidly convey flood waters or drain wet areas. Flood control works reshaped the historical Everglades. The controls made it smaller, divided it into manageable pools, displaced its central axis, and redistributed its discharged waters. The Kissimmee River is now channelized, hastening drainage of its marshes. Lake Okeechobee, which formerly discharged only into the Everglades, now passes large volumes of water to the Atlantic by the St. Lucie Canal and to the Gulf of Mexico by

the Caloosahatchee. Four large canals (the West Palm Beach Canal, the Hillsborough Canal, the North New River Canal and the Miami Canal) cut through the Everglades to the Atlantic. Following storms, these drainage canals add immense volumes of fresh water to local estuaries. The canals were built to convey Everglades' waters rapidly through the coastal ridge to the Atlantic without flooding agricultural and residential areas. But the canals changed the relative discharge location of the Everglades. Now a larger proportion of the Everglades' surface-water runoff is discharged into the Atlantic Ocean and Biscayne Bay. Indeed, one minor canal discharged into Biscayne Bay during one year an amount of water equal to the mean annual volume delivered to Everglades National Park (Scheidt 1983). Not only has management shifted more water to the Atlantic and concentrated its effect at canal outfalls, but it may have changed the historic estuarine salinity regimes along the Atlantic coast, in Florida Bay and the Gulf of Mexico.

Water Supply

Early drainage excesses caused saltwater intrusion into the highly permeable limestone aquifer along Florida's southeast Atlantic coast. This forced water managers to control release of canal discharges and to construct impoundments within the Everglades to retard and store water for use in drier times. Municipal well fields were located adjacent to the larger canals, but relatively close to salt water. The well fields are recharged during the dry season by bringing stored water from the Everglades. Managers must use the contradictory practice of passing large volumes of water to the coast in dry times to keep well fields operating. The only way to gain water in the wells is to lose water to the coast. Confronted with this dilemma, water managers maximize the reserve water storage within the Everglades before the local dry season (December to May). Withholding water in the Everglades interior and allowing only conservative releases to coastal canals shifts estuarine salinity regimes in two ways. (1)It reduces the total discharge to the estuaries, accentuating early annual salinity increases; 2) it confines discharges in some areas to canal outfalls, causing extremely disproportionate longshore distribution of fresh water.

With the end of the dry season comes the hurricane season in south Florida, and stored water within the Everglades changes from an asset to a liability. An early storm can fill the impoundment areas quickly and damage the levees and gates. The beginning of June usually means an overnight shift from water-supply strategies to flood-control actions. Water is released from the impoundments; coastal canals are activated; and discharge gates to Everglades National Park are opened. Everglades water is lowered rapidly in anticipation of the wet season. This often has no relationship to current downstream conditions.

The modulation of the historical, hydrological system was altered effectively. Prior to canals and impoundment, the abundant water during wet season moved more slowly through the Everglades, releasing water to the estuary longer into the dry season. And, early wet season volumes took longer to reach the estuary. A phase shift in salinity levels occurred in several parts of the Everglades estuary.

CONSIDERATIONS FOR ALLOCATIONS OF FRESHWATER

Salinity

Salinity is the important organizer of estuarine biological communities. Salinity dictates what organisms will occur in a particular location, but not how productive they are. Productivity is determined by the availability of suitable nutrients. Within estuaries, an association may occur between salinity and nutrients. Increased freshwater discharge often accompanies increased transport of nutrients. Changes in nutrient levels, however, probably have a less dramatic effect upon estuarine communities than do changes in salinity.

Salinity organizes communities in several ways. It can limit or promote entry of organisms into the estuarine habitat, depending upon the physiological limitations of the species. At any one time, the current salinity level omits or discourages all but a physiological-tolerant set of species or life-cycle stages. We know salinity levels change with season, event or long-term climatic cycles. This fact, coupled with its action as a species and life-cycle filter, means salinity determines the progression of change in estuarine community assemblage. Salinity regimes act as clocks in estuaries, determining not only what organisms will occur in a particular location, but when.

Phase shifts in annual salinity regimes, such as occur in estuaries associated with altered drainage basins, may be of particular concern. Many organisms are cued to salinity levels at important points in their life cycles. Release of gametes and spawning may be associated with salinity. Settlement of larval invertebrates and fish may be determined by salinity. Depending upon the salinity, an appropriate settling habitat within the estuary may or may not be available to an organism. Phase shifts in salinity may upset the timing of many species' production cycles. Consequently the habitat may appear unproductive, even with adequate local nutrients.

A point must be raised regarding the relationship of upland discharge to salinity within tropical or semitropical estuaries. The relative importance of rainfall within the estuary and the added upland discharge needs consideration. In the tropics, rainfall within the estuary may significantly determine salinity levels. Depending upon where discharge measurements and nutrient counts are taken, it may be hard to separate the actual contribution of upland discharge from estuary rainfall. Moreover, rainfall levels normally have a seasonal cycle that reinforces the effects of upland runoff on estuarine salinity. In altered drainages, rainfall cycles may be asynchronous with altered discharge cycles. This asynchrony will complicate the interpretation, and perhaps the effects, of phase-shifted salinity regimes.

Just as timing of salinity levels is important within an estuary, magnitude variation in salinity also may have an ecological role. Rather than manage estuaries to avoid the impacts of upland floods and droughts on "regular" salinity regimes, it might be wise to allow salinity to reset the biological clock within the estuaries for ecological reasons. Productivity of ecosystems is often keyed to disturbance events. High productivity may follow the disruption and reestablishment of community assemblages. In managed estuaries, the trick is not to overly accentuate rate of change by increasing discharge too rapidly or initiating unduly long droughts by upstream retention. Also, repeated extreme perturbations never allow for the recovery that spurs higher productivity. Maintenance of the regularity of salinity regimes may have its own ecological pitfalls.

Productivity

If there is a connection between runoff and productivity in the Everglades estuary and productivity is determined by nutrient levels, then the probable source of nutrient contribution is the upland marsh, the mangrove forest or both. There is no river to transport mineral nutrients. Armstrong (1982) found that the marsh contributed only 5 percent of the external inputs to Texas estuaries, but that may be because those estuaries are dominated by rivers and the areal extent of the marshes are small compared to the total river basin. If the upland marsh contribution to the Everglades estuary is only 5 percent, then one would have to agree the marshes play a small role. However, the nutrient contributions to the Everglades estuary from upland marshes, mangrove forests, estuarine rainfall and offshore input is unknown. Since there is no river contribution, the source of nutrients becomes intriguing. The Everglades estuary exports great quantities of mangrove and sea grass detritus. Shrimp, lobster and some fish stocks move to the coastal shelf upon maturity. What replaces these losses in the nutrient budget?

Declines in fishery harvest in the Everglades during the 1970s accompanied reduced rainfall throughout south Florida. However, annual water deliveries to the park and its estuary during that time were maintained at historical mean levels. The overland deliveries to the park were based on the same historical period when fish production was high. Either delivery volumes in the 1970s were inadequate or rainfall within the estuary was insufficient. Perhaps local rainfall plays a more important role in the Everglades estuary than we considered. Also, heavy rainfall during storms, hurricanes or an unusually wet year may move nutrients from the marsh and mangrove forest to the estuary. The rainfall event may be more important at times than the maintenance of a regular regime.

The Everglades has not experienced a hurricane since the early 1960s. During the 1970s, storm events were quickly absorbed by a relatively dry upland or shunted to the coast rapidly by canals. Perhaps hurricanes and storms that occur in wet years provide the volume required to flush the Everglades and deposit nutrients in its estuary. Few studies have evaluated these kinds of events and their effects upon estuarine productivity. The events may disrupt estuarine productivity temporarily. Therefore the scientist and manager should examine a time-lagged cycle. Fish harvest within the Everglades estuary this year increased about 30 percent since the 1970s. Coincidentally, the park's annual delivery of water from October 1982 to October 1983 was nearly triple the historic mean. In addition, the rainfall within the park and in the estuary was significantly higher than other areas of south Florida. Heavy rainfall accompanied large water deliveries. Perhaps estuarine managers should examine mean salinity regimes more closely because their use may be too restrictive. Estuarine productivity may be coupled with runoff, but in a more complicated sequence than formerly thought.

MANAGEMENT OF ESTUARINE PRODUCTIVITY

Management of many estuaries would undoubtedly be indexed to the success of a few commercially important species. However, some caution should be used in how one approaches this kind of management. The success of any species usually involves the outcomes of other species and ecological processes. This network is so complicated that scientists and managers must reduce and simplify the issue to a handful of models for easier understanding. Models are important, but care must be exercised in their application to management. Management models currently in use discount the exceptional condition or disallow the importance of extreme conditions. Estuarine management models may be more appropriately regarded as the dials we watch to see how things are going, rather than tools to calculate management goals.

Selection of a few species, either as indexes of estuarine health or as the focus of production goals, presents inherent ecological problems. The temptation is to study the special species' ecological requirements and suggest which management actions will benefit them. The idea, or the hope, is that what's good for the species of interest will be good for the whole estuary. It's doubtful our models integrate enough environmental equations, account for sufficient species interactions, provide for alternative biological strategies, or adequately incorporate chance events. Unfortunately, those interested in estuaries and their protection are often defensive when justifying fair treatment of the estuary. Upstream users of the drainage often quantify their needs with confidence; i.e., projected per capita water consumption, acre feet of water needed to irrigate an agricultural field in order to maintain a specific root-zone moisture, etc. Ecosystem managers and scientists must avoid such simplification because their systems usually are not simple. We must recognize that the reductionists' power of scientific inquiry should be tempered with the humble admission that extrapolation of our findings to management action often oversimplifies the original problem.

CONCLUSION

Management of the Everglades and its estuary is a good example of oversimplification of a complex ecological process. Basing water allocations on a mean historical monthly schedule has not protected estuarine productivity. That productivity apparently needs more than overland allocation of water. We suggest that local rainfall in or near the estuary may be important. Also, some consideration must be given to the extreme events, especially floods, that move nutrients into the estuary. Whereas regular overland flow may not transport many nutrients, hurricanes and storms in wet years may provide sufficient momentum and the required volume. Even though nutrients are important to the estuary, we suggest it is the salinity regime between event periods that establishes what biological assemblage will use the available nutrients. Management that tampers with this salinity regime may make the estuary subtly unavailable to traditional species or life-cycle stages. We suggest that phase-shifted salinity regimes must be avoided to provide important reproductive and settlement cycles of estuarine species. In the Everglades, phase-shifted salinity regimes are likely to occur in estuaries because of the combination of upstream uses of Everglades water. Everglades managers retain water upland in the dry season, then rapidly release the water to the coast at the beginning of the rainy season. Not only has this changed modulation of upland hydrological cycles affected marsh communities, but it has also shifted salinity patterns in the estuaries. The Everglades is not a river-dominated system, so the mechanisms for salinity and nutrient maintenance in its estuary are likely to be different than those established in most studies. However, the Everglades and its estuary offer an exciting ecosystem for testing our assumptions about the interconnection of management actions and estuarine productivity.

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RESEARCH PERSPECTIVES ON ESTUARINE PRODUCTIVITY, NUTRIENT CYCLES, AND HYDROLOGIC REGIMES IN THE PACIFIC NORTHWEST

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INTRODUCTION

This paper addresses future estuarine research needs and priorities discussed by Armstrong (this symposium) It focuses on biological and chemical processes in the major freshwater-seawater interfaces of the Pacific Northwest estuaries. Specific topics include freshwater-seawater interactions, nutrient cycling and trophic dynamics within the region's estuaries. A description of the estuaries in the Pacific Northwest, with emphasis on the Columbia River, is followed by discussion of: (1) priority water uses and the importance of current and future hydrologic projects; and (2) major freshwater-seawater interfaces and their chemical and biological gradients, specifically turbidity maxima and salt marshes. The research community should recognize that the topics addressed comprise only some of the major research needs. Other equally important and relatively unknown components of estuaries in the Pacific coast should not be ignored (i.e., nutrient and trophic dynamics of tidal flats and eelgrass beds).

ESTUARIES OF WASHINGTON STATE

Washington State has the largest variety of streams and rivers in the continental United States. They range from the giant Columbia River, which drains most of the state and region, to coastal systems with short reaches of less than 200 kilometers from glacier to the ocean. These lotic systems connect 96 coastal and inland (Puget Sound) estuaries that are structurally, hydrologically, and biologically diverse. Major estuaries include those greater than 100 square kilometers (Columbia River estuary, Willapa Bay, Grays Harbor) and the numerous, small riverine estuaries of Puget Sound. Contemporary estuarine structure and dynamics reflect urban, industrial, recreational, miscellaneous developmental activities and past abuses (i.e., dredging, diking, logging, and road and dam construction).

The availability of estuarine habitats is extremely important to the maintenance of fisheries and fishery resources in the Pacific Northwest (Simenstad et al. 1982; Stevens and Armstrong, in press). For example, current landed value for Pacific salmon (five spp. of *Oncorhynchus*), which pass through and utilize estuarine habitats twice during their life histories, approaches $360 million per year. Dungeness crab (*Cancer magister*) populations, which use eelgrass (*Zostera marina*) beds and oyster and clam shell reefs for nursery habitats, sustain commercial landings between $26 million and $57 million per year. Oysters (principally *Crassostrea gigas*), which are grown and harvested almost exclusively in the region's estuaries, account for $25 million per year.

Undoubtedly, the most manipulated riverine system in the Pacific Northwest is the Columbia River, which is also the largest river entering the northeastern Pacific Ocean. Its extant average flow (about 7,280 m^3s^{-1}) contributes about 60 percent (winter) to 90 percent (summer) of the freshwater discharge to the ocean between San Francisco Bay and the Straits of Juan de Fuca (Barnes et al. 1972). Water removal and regulation due to hydroelectric power and irrigation projects began about 1840 (Depletions Task Force 1983). Most of the resulting flow modifications originate east of the Cascade Mountains (92 percent of the total drainage basin area but only 76 percent of the total discharge; Good and Jay 1978), where 13 major dams and over 100 minor dams have been constructed and approximately 32,000 square kilometers of land is under irrigation. The magnitude of the changes resulting from the construction of the dams was considerable (Jay et al. in prep.). The average spring freshet decreased by approximately 5,240 cubic meters per second. In contrast, average flows during the rest of the year increased. Minimum monthly average flows increased about 1,130 cubic meters per second during the normal low flow season in the late summer and early fall. Although the annual average flow depletion due to irrigation (approximately 280 and 425 m^3s^{-1}) was not included in these calculations, irrigation withdrawal, which is greatest in June and July, also reduces the spring freshet (approximately 1,130 m^3s^{-1} to 1,700 m^3s^{-1}).

As a result, modern river flows into the Columbia River estuary rarely exceed 17,000 cubic meters per second or decline below 3,000 cubic meters per second, compared to an extreme historical range (daily average) of approximately 1,000 cubic meters per second and 35,000 cubic meters per second.

In recent detailed studies of the Columbia River estuary by the Columbia River Estuary Data Development Program (CREDDP), scientists interpreted the anthropogenic changes in the structure and dynamics of the estuarine ecosystem (Jay et al. in prep.). The CREDDP studies showed that the effects of river flow regulation and withdrawal could not be easily separated from the effects of changes on the estuary itself (diking, filling, dredging, jetty construction). Simulation models (laterally averaged and time-dependent) of estuarine circulation prior to human modification of the river flow or the estuary indicated that many of the differences in the estuary's physical and ecological processes could be attributed to uniquely riverine influences (Hamilton 1984). Despite the decrease in low flow extremes, the residence time of the water in the river has increased, resulting in slower flushing times and higher summer water temperatures in the estuary. Extreme freshets (25,000 m^3s^{-1} to 35,000 m^3s^{-1}) no longer occur. Consequently, the energy level of the modern estuary is lower and less variable. This suggests that deposited sediments and endemic estuarine biota were flushed annually from the estuary during the highly energetic freshet and winter high flow periods. And maximum salinity intrusion probably declined to the lower minimum flows prior to the turn of the century.Because of anthropogenic changes in estuarine circulation processes, many ecological features undoubtedly changed over the last century. The mid-estuary accumulation of suspended material, called the "turbidity maximum," probably became more pronounced and less variable in its occurrence and spatial distribution. This is ecologically germane to the estuarine ecosystem because the turbidity maximum appears to be a sink for freshwater phytoplankton, where cells lyse upon encountering low salinities. This is particularly important to the modern estuary because the reservoirs behind the dams enhance the phytoplankton and zooplankton biomasses imported into the estuary. The turbidity maximum is also an area for detritus entrainment, maximum standing stocks of primary consumers (i.e., epitbenthic zooplankton and motile macroinvertebrates) and high demersal fish food consumption. Obviously, the changes in the spatial and temporal distribution and the variability of the turbidity maximum zone has important, though unknown, implications to the estuarine food web.

Similarly, the higher salinity intrusion in historic times indicated that salt marsh assemblages probably extended further upriver than in present time. Although the high discharge freshets may generate more chemically and physically unstable habitats for these assemblages. Historic alterations in emergent plant production within and phytoplankton import into the Columbia River estuary is important. These autotrophic components account for 38 percent and 58 percent of the modern, net primary production estimated annually (Jay et al. in press).

HYDROLOGIC PROJECTS

The previous review demonstrates that numerous Northwest estuaries are highly dependent upon the contemporary allocation of stream and river flow for established priority uses. Priority uses include: (1)domestic and municipal, (2)hyrdoelectric power, (3)irrigation and (4)industrial.

Of the above priority uses, freshwater allocations to hydroelectric power and irrigation become the only allocations that could redefine the development of freshwater inflow requirements for the region's estuaries. In other words, any inflow requirements must exist within the constraints of existing priorities. Hydroelectric allocation offers the greatest potential source of water regulation for estuaries because of its nonconsumptive use and provisions, which limit

impacts on migrating anadromous salmon. However, historical provisions have been primarily confined to low-flow periods or years and only provided for the maintenance of adequate flows for upriver migrations of returning adults.

Future research on water management and estuarine productivity in the Pacific Northwest should consider the current planning activities under the Pacific Northwest Electric Power Planning and Conservation Act of 1980 (P. L. 96-501; Northwest Power Planning Council 1983). Under the act, the Northwest Power Planning Council determines future electric power needs for Washington, Oregon, Montana and Idaho. The act includes "due consideration for environmental quality and the protection, utilization, and enhancement of fish and wildlife." The council's fish and wildlife plan contains a water budget for the Columbia and Snake rivers to provide adequate flows for migratory fish. Additional measures minimize the harmful effects of water level fluctuations and temperature control for specific dams. The plan also calls for a study to identify and rank potential hydropower development sites and potential risks to fish and wildlife within the riverine and estuarine ecosystems (Northwest Power Planning Council 1983).

ENVIRONMENTAL GRADIENTS AND FRESHWATER-SEAWATER INTERACTIONS

The definition of freshwater inflow requirements for Pacific Northwest estuaries might be best accomplished using an estuarine grid that portrays gradients of important environmental variables and biotic habitats encountered between upstream riverine and marine waters. Along these gradients, further definition can be made by examining relationships among select environmental variables, geochemical cycles, trophic dynamics (i.e., carbon and nutrient cycling), and community dynamics (i.e., plant and animal succession and production).

Turbidity Maximum

A simple example of environmental gradients are surface concentrations of salinity, suspended matter, and nutrients from the marine to freshwater reaches of an estuary. For instance, such gradients can be used to define the turbidity maximum. The magnitude of the turbidity maximum can be influenced by numerous factors, such as the concentrations of suspended matter in the river and tidal waters, settling velocities of different particle sizes, and estuarine circulation. As evidenced by the Columbia River estuary, its occurrence, location and behavior (e.g., landward-seaward excursion) is highly influenced by river discharge and spring neap tidal cycles.

The turbidity maximum and associated materials can be augmented continually by river and tidal flows, suspending and entraining material long enough to sustain considerable chemical and biological processing. For instance, associated low salinity depth profiles in DOC peaks and a decline in chlorophyll from upriver values could indicate abrupt osmotic and compositional changes as postulated for the Columbia River. Plasmolytic release by freshwater plankton of degradable dissolved organic material may support localized oxygen consumption by microbiota (Morris et al. 1978). Turbidity maxima also could behave like tidal fronts by concentrating phytoplankton and prey organisms for consumers (Hobson 1966; Pearcy and Mueller 1970; Bowman and Iverson 1978).

Such features provide dramatic examples of major questions that need considerable research. For example, is the major role of bacteria that of remineralizers, converting organic matter to inorganic matter and recycling it to primary producers (Mann 1982)? However, more detailed questions and examinations will be required. The high primary production and nutrient recycling capacities of estuaries, as noted by Armstrong (1984, this symposium), indicate that dynamic, complex trophic-nutrient pathways undoubtedly exist. Another major question is whether bacteria consumed by heterotrophic flagellates, which are in turn consumed by microzooplankton (i.e., ciliates), result in a "microbial loop," in which microconsumers represent at least three trophic levels that excrete minerals recycled to the phytoplankton (Azam et al. 1983). If so, do microbiota, which cover the same size range as most phytoplankton (<100 um), also comprise an additional, but unrecognized means, of

transferring energy to the conventional planktonic food?

The above discussion indicates that the chemically and biologically active turbidity maximum probably comprises a major estuarine interface because of the interacting influences of resuspension, entrainment and low salinities. These features will require greater attention and characterization than previously provided in estuarine investigations. The development of precise geochemical models for elemental cycling and a better definition of the oxygen models used for management are major subjects that would be enhanced by an increased understanding of turbidity maximum processes.

Future research on turbidity maximum would provide a logical, important extension of our knowledge of sources and contributions (organic and inorganic constituents) to the dissolved and particulate components of suspended matter in estuaries. Sources of particular interest are tidal circulation of marine matter, riverine inflows, shore erosion and biological production of estuarine habitats (primarily salt marshes, eelgrass beds, and tidal flats).

Salt marshes

An example of major estuarine habitats, which are extremely sensitive to variations in freshwater inflows, are intertidal marsh communities. Our emphasis on salt marshes is contrary to the impressions given by Armstrong (1984) that salt marshes are of minor importance in estuarine nutrient regimes. We expect that salt marshes act as the forested, riparian zones of streams and rivers by providing a buffering system against numerous watershed-riverine perturbations (i.e., erosion). Furthermore, these riverine-estuarine ecosystems not only play important roles as sources of organic matter (i.e., detritus) and as habitats for commercially important species, but their nutrient dynamics (i.e., storage) and hydrologic (i.e., groundwater) features may perform critical, long-term functions in estuarine development.

Salinity and elevation play important roles in controlling community composition (Burg et al. 1976; Ewing 1983; Kistritz et al. 1983). However, knowledge of the influences of salinity, elevation and other factors upon community composition and patterns is lacking for this region. Research needs to assess changes in community composition along environmental gradients for such factors as: (1) pore water salinity, (2) sediment structure (organic and nutrient content), (3) temperature, (4) redox potential, (5) site elevation, and (6) nearshore flow velocities (i.e., erosional, transport and depositional). Emphasis should be placed upon interactions of stressful environmental conditions, such as low redox potential, salinity levels and site deviations. Coupled with model development, such experiments would be able to predict the influences of freshwater and tidal flow variations upon below-ground saltwater intrusion and the resultant response of plant communities.

CONCLUSION

In conclusion, although turbidity maxima and salt marshes in Pacific Northwest estuaries serve as examples of regional research needs that are highly dependent upon hydrologic regimes, it should be emphasized that little information exists about most facets of Pacific estuaries. Past estuarine research has focused upon Atlantic and Gulf Coast estuaries because of extensive habitat area and pressures for urban and industrial developmental. The result is that our scientific knowledge of the functional and structural aspects of Pacific Coast estuaries lags behind that for East Coast systems. At present, Pacific Coast estuaries need considerable research attention due to the rapidly disappearing small, but diverse ecosystems. The need is especially critical given the current and projected urbanization and industrialization of coastal areas.

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WATER MANAGEMENT AND ESTUARINE PRODUCTIVITY: A FRESHWATER VIEW FROM THE GREAT LAKES

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INTRODUCTION

Armstrong's paper, "Water Management and Estuarine Productivity," offers a challenge to identify a functional property of estuaries that will provide a meaningful and operational guide to management.

Ideally this functional property should be common to most if not all estuaries are to have broad appeal and application. Danger exists in suggesting a single criterion to judge the integrity of an ecosystem and translate it into economically defensible and operationally feasible management objectives. Such a criterion may exist, however, if it is based on an integrated functional property such as productivity. Productivity is the bottom line of nature's ledger and reflects an integration of the whole. The question of its utility as a meaningful guide to estuarine management remains open for debate. From a Great Lakes perspective, productivity certainly has more utility than salinity.

The remainder of this paper will present a case for the use of productivity as a guide to estuarine management. The case is based on University of Wisconsin Sea Grant-supported research in an important estuary of the Great Lakes --- the bay of Green Bay, Lake Michigan. For that reason a brief description of Green Bay follows.

STUDY AREA

Green Bay can be characterized as a long, shallow bay of northwestern Lake Michigan (Figure 1). Morphometric statistics include: a length of 193 kilometers; a mean width of 22 kilometers; a mean depth of 15.8 meters; a water surface area of 4,520 square kilometers; and a volume of 67 cubic kilometers (Mortimer 1978).

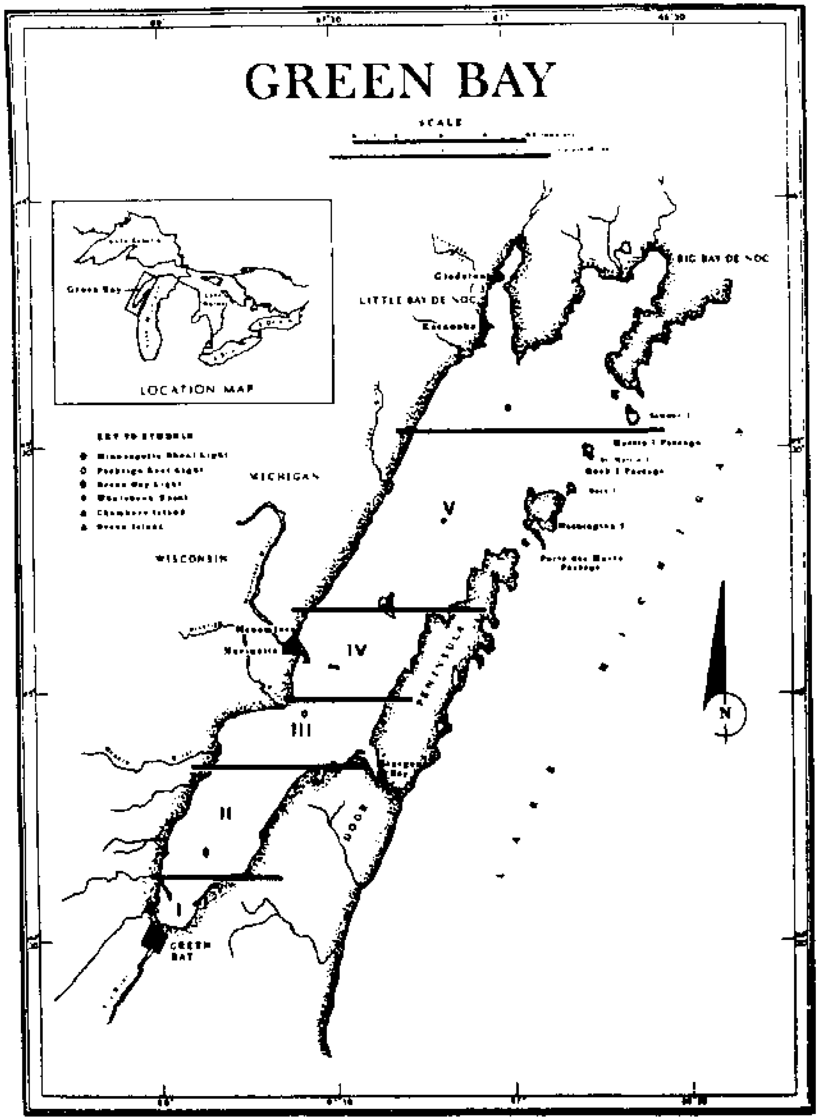

FIGURE 1

The bay of Green Bay showing five regions delineated on the basis of trophic characteristics map. Adapted from Brigham (1984).

Green Bay constitutes only 7.4 percent of the surface area of Lake Michigan, yet the land drainage area for the bay is about one-third of that for Lake Michigan, or 40,500 square kilometers. About one-third of the watershed is forested, with the remainder made up of rich agricultural land. A heavily industrialized area along the Lower Fox River has one of the largest concentrations of pulp and paper mills in the world (Harris et al. 1982). Mortimer (1978) estimated the total water supply for Green Bay amounts to about one quarter of the mean outflow of Lake Michigan through the Straits of Mackinac.

Of the six major tributaries, the Fox River is the largest, entering the bay at the south end with a mean flow of 118 cubic meters per second. The Fox is one of the most significant tributaries for the bay and for Lake Michigan because of its flow rate and load of dissolved and particulate substances (Sager and Wiersma 1972; Roznowski and Auer 1983). The transport and dispersion of these substances provide a basis for considering Green Bay and other Great Lakes bays as analogous to coastal estuaries (Ragotzkie et al. 1969). The tidal feature is practically missing, but surface seiches provide an analogous physical mechanism for water motion (Heaps et al. 1982).

The gradient in salinity or dissolved substances is reversed from that found in coastal estuaries. Specific conductance of the Fox River and lower bay is typically 1.5 to 2 times that of northern Green Bay waters (Ahrnsbrak and Ragotzkie 1970). Gradients in nutrients and algae production also are evident and have been utilized for comparative studies of uptake kinetics (Norman and Sager 1978; Vanderhoef et al. 1974).

Another estuarine feature is the morphology of the basin. The south end is shallow with mean depths of 2 meters to 3 meters; thermal stratification is rarely observed in summer. The deepest point in the bay (54 m) is in the north end approximately seven kilometers west northwest of Washington Island. The morphology gradient corresponds closely to the trophic conditions observed along the longitudinal axis of the bay.

RESPONSE

Armstrong (1984) has identified water quantity (freshwater inflow) as an important variable affecting the conditions of estuaries. In geographic areas of higher precipitation, water quality input may be as important to the integrity of the estuary as water quantity. However that may be, it is important to recognize that a common dimension between the two is nutrient loading to the estuary. The common denominator of estuarine management is management of watershed activities. While this observation does not provide the basis for a guide to estuarine management, it does recognize the importance of the coupling between watershed management and the receiving body of water.

From our experiences in Green Bay, we suggest that estuaries are highly responsive to nutrient subsidy, perhaps more so than land-locked lakes because of the continuous inflow feature. That response is reflected in the quantity and quality of primary and secondary production. For the first time, a data set on Green Bay, including physico-chemical parameters and major pelagial trophic levels (phytoplankton standing stock, species composition and productivity; zooplankton and fish standing stocks and composition), is available for analysis (Richman et al. 1983a; 1983b).

Physico-chemical gradients (south-to-north increases in mean depth, water volume and light penetration, and decreases in nutrient concentration and specific conductance) correlate with gradients in standing stock distributions of phytoplankton (numerical density, biovolume concentration, chlorophyll *a*), species composition and primary productivity (Sager et al. 1983; 1984). These parameters demonstrate a gradient in the bay from hypereutrophic conditions in the extreme southern end (i.e., summer average primary productivity = 586 mg C m^{-3} day^{-1}, chlorophyll *a* = 49.8 mg l^{-1}, phytoplankton biovolume = 12 parts per million, and phytoplankton density = 15,000 particles ml^{-1}) to mesotrophic/oligotrophic conditions in the upper bay (i.e., average primary productivity = 20.6 mg C m^{-3} day^{-1}, chlorophyll *a* = 2.1 mg l^{-1}, phytoplankton biovolume = 0.8 ppm, and phytoplankton density = 1500 particles ml^{-1}). Similar gradients were noted in algal species abundance and composition, especially in shifts from blue-green to green algae.

The distribution of zooplankton also shows a south-to-north trophic gradient in density, biovolume concentration and species composition. Total zooplankton biovolume concentrations drop from average summer values of 1.4 parts per million in the extreme southern region to 0.2 parts per million in the northern bay waters. These changes are due to distributional shifts in both rotifers and microcrustacea, and appear to be related to the influence of nutrient loadings on the food quality of the phytoplankton community.

A relationship between phytoplankton productivity, zooplankton production and fish yields has also been defined (Sager and Richman 1984; Richman et al. 1983b). The spatial distribution of fish yields in Green Bay correlates with mean depth, total phosphorus, phytoplankton biovolume, chlorophyll *a*, phytoplankton productivity and zooplankton production along the trophic gradient. Mean annual yields from 1972 to 1980 ranged from 313 mg C m^{-3} yr^{-1} (3.130 g m^{-3} fresh wt.) in the south to 3.47 in the north for major commercial species. Yield is highly correlated ($r > .90$) with each of the trophic variables.

While space does not permit a detailed discussion of the statistics presented above, we have tried to summarize the essence of our present understanding in Table 1. The data are presented as pooled averages for particular regions of the bay (Figure 1), which were delineated on the basis of similar physical, chemical and biological characteristics.

The data in Table 1 reveal interesting relationships between the trophic condition, basin morphometry and food chain efficiency of carbon transfer. Efficiency of carbon transfer from phytoplankton to fish yield is higher in the mesotrophic, middle bay region (0.66 percent) than in the hypereutrophic, lower bay (0.14 percent). The same pattern is observed for the efficiency of carbon transfer to zooplankton, suggesting important differences in the suitability of the phytoplankton production utilized by higher

TABLE 1

Trophic characteristics and food chain efficiencies (carbon transfer) of five regions of Green Bay (Figure 1). Efficiencies are calculated as ratios of production or yield for fish (FY), zooplankton (ZP) and phytoplankton (PP). TP = total phosphorus, chlor = chlorophyll a, z = mean depth. From Sager and Richman (1984).

	TP(gl^{-1})	CHLOR(gl^{-1})	Z	ZP/PP	FY/PP
I	190	49.8	2.9	2.3%	0.144%
II	76	8.4	7.6	8.3	0.588
III	45.5	5.8	8.9	5.9	0.664
IV	40	4.4	17.0	6.8	0.22
V	26.7	2.1	29.0	10.2	0.04

trophic levels in the regions of the bay. The proportion of the fish yield for the entire bay is highest in regions II and III, and species composition of the catch shifts dramatically along the trophic gradient (Table 2).

On the basis of carbon transfer efficiency and fish yield, the data suggest the existence of a region and an accompanying set of conditions where optimum carbon conversion to fish flesh occurs, at least in a quantitative sense.

The crux of the matter is this. We believe that production in the Green Bay estuary is driven by a nutrient influx (perturbation) introduced at the head. In region I, the influx constitutes a stress (with lowered transfer efficiencies and yield), while in region II and III it acts as a subsidy. Region IV and V are areas where the perturbation has little effect, neither subsidy nor stress.

This interpretation partly is based on the Odum et al. (1979) hypothetical performance curve for a perturbed ecosystem (Figure 2).

We suggest that production is a measure of the performance of an ecosystem. We also suggest there may be a consistent relationship between increased trophic transfer efficiency and fish yield. If so, it could provide some basis as a criterion for the management of estuaries, particularly if the market value of the production is used as a second component of the criterion. The utility of carbon transfer efficiency as a measure of effective management thus lies in its potential link to economic theory. In this regard, Farnworth et al. (1983) identifies the parallel in theoretical constructs between subsidy-stress ecological perturbation theory and economic production functions. They demonstrate the utility of these concepts for the management of a tropical forest, using market (priced) and non-market (unpriced) values.

Farnworth et al. (1983) argue that tropical forests, in addition to producing private goods, provide free or unpriced public goods and services to man that result from the integrated functioning of the forest system. They further suggest that both public and private values can be assured only

Fish yield* by region and trophic status in Green Bay.

Region	Trophic Status	Yield (x 10^6 Kg yr^{-1})	% Yield	Area (x 10^8 m^2)	% Area	Major Species
I	Hypereutrophic	1.575	16.2	1.755	9.5	Alewife (58%) Carp (30%) Perch (5%)
II	Eutrophic	3.779	38.9	3.679	20.0	Alewife (96%) Perch (2%)
III	Eutrophic/ Mesotrophic	3.102	31.9	4.243	23.0	Alewife (93%) Carp (3%)
IV	Mesotrophic	1.015	10.5	3.899	21.1	Alewife (94%) Whitefish(2%)
V	Meso/Oligo-trophic	0.229	2.4	4.839	26.3	Whitefish(87%
TOTALS		9.700 x 10^6 Kg/Yr		18.415 x 10^8 m^2		

*mean annual yield for major commercial species in the period 1972-1980. Records from Great Lakes Fishery Laboratory, Ann Arbor, Michigan.

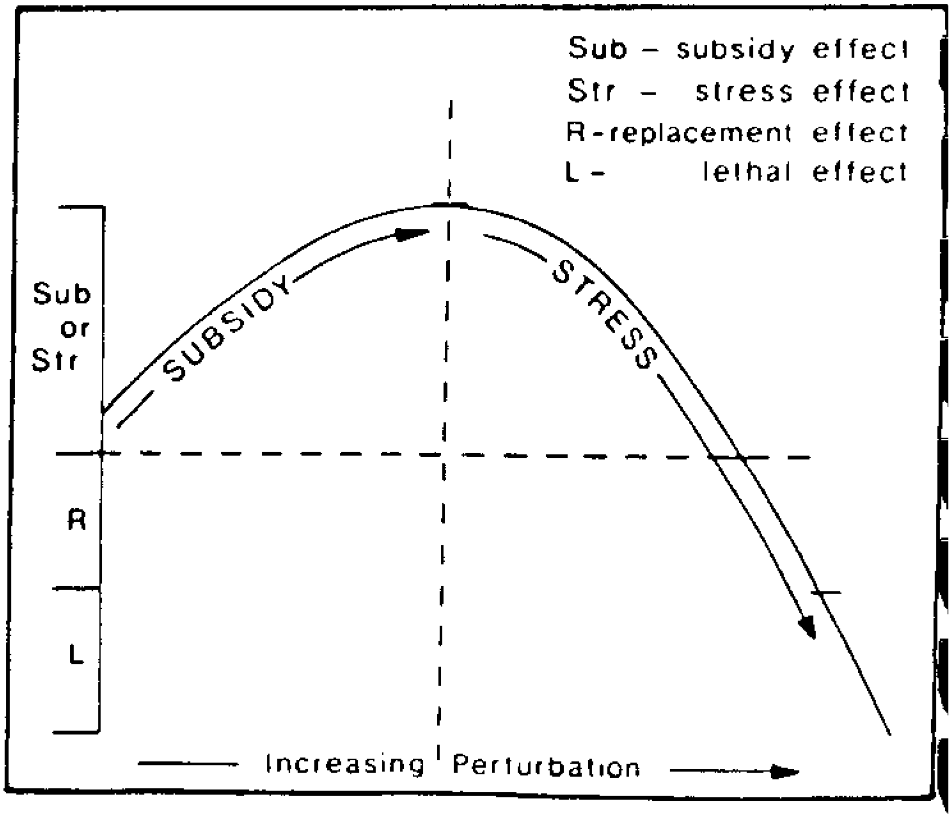

FIGURE 2

Hypothetical performance curve for a perturbed ecosystem subjected to two kinds of inputs (from Odum et al. 1979).

through the maintenance of an integrated functional system.

In this context the need for criterion to assess the overall performance (efficiency) of estuarine ecosystems becomes obvious. If the criterion is responsive to measurable, ecological subsidy-stress gradients, and if a good relationship exists between yield and the overall efficiency of the system, then the two can be used as measures of ecosystem output and be coupled in a production function model. The resulting model can be used as a management guide that integrates both economic and ecological values.

SUMMARY

In summary, the Green Bay estuary like all other estuaries is inextricably coupled to upstream, terrestrial ecosystems. Man's activities in the watershed, which are driven by economic market forces, are frequently reflected in estuaries as subsidies or stresses (e.g., sediments, nutrients and toxics) that produce measurable perturbations. When upstream watershed activities act as a subsidy to the estuary, there will be no loss of market or non-market values of the estuary. There likely could be an increase.

When watershed activities act as a stress on the estuary, non-market values (ecosystem processes) are likely to decline before market value (yield) is affected. The ecosystem dysfunction results from a failure of the economic system to maintain non-market values of the estuary. In order to assess dysfunction and prevent it from occurring, some measure of the overall performance of the estuary is needed that considers both market and non-market values. Market values clearly can be assessed through yield quantity and composition. We suggest that carbon transfer efficiency may be another criterion that can be used to account for losses of non-market values in estuaries. If so, it may provide the ecological/economic link to the externalities produced in upstream watersheds.

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DISCUSSION

R. BIGGS: Trying to specify an ideal salinity regime could get us into trouble. In Chesapeake Bay, for example, it has been proposed that we try to regulate the flow of the Susquehanna. If that were done, you could seriously affect the flushing of all of the tributaries of the upper Chesapeake Bay and enormously aggravate the water quality found within those tributaries. That variable is extremely important.

J. ZEDLER: I want to add to your list of research needs. We need to figure out how these systems respond or recover after you either impede or fall below the right salinity level. I think this is a property that differs by species and by functional group within the estuary. But it's extremely important to know the consequences, the long-term consequences, if we give it too much or too little fresh water.

N. ARMSTRONG: We have experienced that in the Texas estuaries in the drought of the 1950s in which freshwater inflows were reduced substantially. And, in fact, there were cases where full-strength sea water was found at the head of estuaries and river channels. Going from that case to one in the next year when there were large flood flows, the estuarine productivity changed drastically. But it was found that within three years, normal estuarine biota had returned to the estuaries.

The recovery process took a fairly short time. Dick Hoese and B.J. Copeland looked at this problem when it occurred in the Texas estuaries and would be able to comment in more detail on that. But it's one that had a short-term effect, and as far as I can tell, the long-term effects were nil.

In the Chesapeake Bay, it's different. I think the oyster problem there is one that's been very different from what we've seen on the Texas coast.

W. ODUM: Lumping carbon, nitrogen and phosphorus under the master title of "nutrients" can be a little misleading. Carbon, its sources and the way it behaves, might be different from the ways nitrogen and phosphorus behave. I think it's important to differentiate between the two when you talk about sources.

N. ARMSTRONG: I should have clarified that the carbon source I was talking about was particulate and dissolved organic carbon.

H. PAERL: I would like to underscore the earlier comment with regard to salinity modifications. We have many suggestions put forth in North Carolina that would affect the quality of freshwater systems feeding into estuaries and also create tremendous engineering feats and problems.

Secondly, I would like to emphasize some of the qualitative aspects of the productivity that is being discussed --- namely the quality of food and particulate matter that is coming from the freshwater environments into our estuaries. In North Carolina, we've had severe problems, particularly during drought years, with blue-green algal blooms and dinoflagellate blooms that may not be interpretable from a purely quantitative point of view. In other words, these organisms are not readily consumable by the food chain that is receiving them in the estuary.

C. SPENCER: I have a question for Bud Harris. You mentioned that carbon transfer efficiency was reduced in the stressed or hypertrophic end of Green Bay. Is this stress due to the dominance of the phytoplankton by blue-green algae? As a follow-up to Hans Paerl's question, should we be interested in total productivity? Or, should we concentrate on types of production and whether these are going to move up the trophic chain as efficiently?

H. HARRIS: Yes, it is dominated by blue-greens, particularly in the upstream region, and it falls off very rapidly from there to the next region. We see various shifts with the zooplankton population, because some can utilize blue-greens better than others. In effect, the abundance of blue-greens is reflected in actual shifts of the zooplankton.

It was brought up earlier that although we don't have a good handle on the benthos quantified in terms of biomass, it would appear that it is shifting from the grazing food chain to the detrital food chain, then to the microorganism food chain. So, production is simply going a different way. Consequently, the lower end of the chain is light-limited to a large extent. Of course, the blue-greens, which are able to utilize atmospheric nitrogen have some advantage.

N. ARMSTRONG: One of the issues I think we need to focus on, and one we see in Texas, is what criterion to use to allocate freshwater inflow. A couple of months from now we'll be at hearings to determine how much water will be required to be released from a reservoir near the coast to supply a downstream estuary with fresh water. The questions of which criteria to use and how much water to release have to be answered almost immediately.

Whether one uses salinity, productivity or some other factor is now the critical issue. One of the things we've discovered is that salinity and productivity are uncoupled in part.

Salinity reflects the freshwater inflows and tidal exchange in estuaries, making it a more direct indicator of freshwater inflows than most other parameters. Productivity, as suggested, is more of a function of recycling in the systems and is somewhat uncoupled with freshwater inflows.

We've seen in our mass balance calculations that freshwater inflows contribute small amounts of nutrients relative to what is being recycled in the system. How is that coupling achieved? How does one actually say that fresh water is related to secondary production? If one cannot make that connection very clearly, then is productivity a proper basis to use? Correlations between freshwater inflows and commercial harvests are fraught with all the problems of using commercial harvests based on effort, economics and so forth. But it's a tool that's available now. The question of whether it's the best tool is one that has to be debated.

Salinity may be the easier criterion to use. However, it is often assumed that there's a constant salinity throughout the year. But this is not the case.

determine requirements or estimates of freshwater needs to the estuaries in Texas, the Department of Water Resources, particularly Gary Powell, looked at salinity needs for the organisms using them. The department asked for examples, what are the salinity requirements for shellfish, primarily shrimp, using the estuary at various times of the year? Or what salinities need to be maintained in the estuary for the feeding and nursery grounds?

Once acquired, the salinity requirements were translated to freshwater inflows at that time of year. In this case, salinity was used as the basis to come up with monthly freshwater inflows. And, it turns out, that if those inflows require some fraction of the normal inflows there is a seasonal pattern to them. One constant salinity cannot be maintained throughout the year.

One of the questions I was hoping to get some guidance on is how does one judge the importance of salinity versus productivity as a measure of the freshwater inflow required?

J. SHARP: I think there's another aspect of river flow conditions to salinity that should be addressed. We have analyzed flood and drought data for the Delaware estuary over several decades. The extreme variances in salinity, largely from differences in river flow, are factors that I think push water managers toward the idea of regulation. What data like this does not show is the depth structure of salinity.

Throughout most of the year, the salinity structure is almost homogeneous from top to bottom. With spring flow, we get salinity differences as high as 15 parts per thousand from surface to bottom. This stratification sets up and persists with some intensity throughout the spring period. This is when we get much of the productivity of the year. From March to May, there is a pronounced chlorophyll maximum, pronounced productivity maximum, just below the turbidity maximum in the broad, lower parts of the open estuary. This is almost entirely because the photic depth is shallower due to stratification. If we were able to control the salinity and the water flow of this spring flush activity, control of the productivity of the estuary would be lost to a more homogeneous year-round flow.

Another aspect of this big spring flow is that its flushing activity may wash out some of the things in the estuary that are undesirable.

One of the major parameters in water quality has always been dissolved oxygen content. We have normalized dissolved oxygen concentrations in the Delaware by plotting it against salinity. The "apparent oxygen utilization" compares dissolved oxygen present with theoretical dissolved oxygen for each temperature and salinity measure. This gives you an idea about oxygen demand in a somewhat integrated manner. The total measurement of dissolved oxygen is difficult to evaluate, because the temperature and salinity greatly affect solubility. But by plotting dissolved oxygen against salinity and using AOU, we find that the Delaware has a consistently strong oxygen demand in the upper portion of the estuary where salinity is zero to five parts per thousand. Throughout most of the rest of the estuary there is near saturation and in some cases super-saturation of dissolved oxygen. Therefore, I think this may be a valuable parameter in evaluating water quality and stress.

D. BOESCH: One of the problems, with respect to making management decisions about freshwater inflow and anything else that's potentially manageable in these estuarine systems, is that we have a poor definition of the resources we're specifically trying to manage. Various discussions of overall productivity, primary productivity, species-specific management and other problems lead us to a sort of blind assumption that all of these sources have values that are completely compatible. We assume that if we target for some sort of simple good we will have all of these things.

The systems we're dealing with vary widely in their characteristics and potentials. Therefore, it seems to me that in the long run, we have to look at estuarine basins from the viewpoint of the resources we expect them to provide. Then we must try to develop our strategies on the basis of those resources, in terms of research and management strategies.

To give you an example, in Louisiana we have profuse estuarine drainage basins, where freshwater input varies widely from year to year. It seems that what is a good year for oysters is a bad year for shrimp. This is large freshwater inputs, or moderate freshwater inputs at least are good for oyster production because they prevent disease organisms and predators from encroaching on the oyster beds. But low flow conditions enhance the nursery ground habitat for shrimp. In addition, we have a very strong competing interest with management for waterfowl and for fur bearers.

My question, then, is how do we as scientists develop research strategies that couple the actual resources we should be managing with the process of learning how the system provides these resources? And how do we interact with social techniques to overcome the difficulties of erecting strategies for managing specific resources that may eliminate other resources people depend on in the system?

N. ARMSTRONG: I think our management strategies should focus on what we want to get from the estuary. In Texas, commercial fishermen have the choice of dealing with shrimp or finfish. By increasing freshwater inflows in some estuaries, one can increase the harvest of the shrimp and decrease the harvest of finfish, and vice versa.

Water quality management embodies the questions we're raising. Based on the uses one wants to obtain from the estuary or any water body, criteria needed to support them must be decided. A research strategy should focus on the variety of uses possible for the water body.

Uses may change over time. We may change from wanting shrimp in this decade to wanting finfish in the next. Our strategy for managing the system should allow us to shift from one to the other. The research strategy has to be broad enough to encompass a variety of uses. It must incorporate, not limit us to only one use.

G. HENDRIX: We expect different estuaries to do different things. In my particular orientation, national parks, the mandate is to manage an estuary for its natural assemblage, natural progression of change and natural processes.

I do not believe, even in systems managed for harvest production, that we often know enough to take one species and work backwards to protect that particular production. Many factors need to be taken into account in making models for production. An understanding of the events, and of the phase shifts and various cycles and patterns is just now becoming available to us.

I think that management based upon production of a single species or of a few species is still a dangerous route to follow at this point. I would opt for a very conservative approach to managing estuaries and still try to stick with as many of the natural processes and natural progressions, as possible.

H. HARRIS: One of the problems is defining "we," and you've identified that. There is a sociological problem in trying to get some kind of consensus. You brought out the fact that estuarine systems have evolved and have received man's impact over time. So one of the things that's been driving the estuaries is the fact that they are used for their assimilative capacity. This has been the case with Green Bay.

Assimilative capacity of the estuaries for wastes is a legitimate use in every system. It is driven by market forces and those market values are easy to compute.

We need to do research in the area of non-market economics. That's a tough area, but the link there is some criteria or criterion that reflects the overall "health" of the ecosystem.

I am suggesting that productivity is a bottom line. The efficiency of any system represents a baseline upon which we may be able to measure the non-market values of those systems.

R. WISSMAR: The Columbia River is unique to the Northwest in that it has approximately 60 to 90 percent of the fresh water coming into that part of the Pacific Ocean between San Francisco and the Straits of Juan de Fuca. It's a high energy system, as far as flushing.

Because of this, the river is, and has been, considerably unproductive. With the construction of dams, it is probably more productive now than it ever has been. However, it is still a high energy system. Because of the dams, we do have a chance of managing this system by looking at the allocation of fresh water.

R. BIGGS: I think sometimes we believe we can manage these systems as we might manage chickens in a chickenhouse, controlling the organism or population from the cradle to the grave.

This is not true for estuarine systems. What we can hope to do, in terms of nutrients or fresh water, is control only the most fundamental aspects of the system. We're not going to control a 200-year flood, because we cannot build enough dams or impoundments to keep it from coming. We're not going to control next week's offshore forcing function that might dump a couple of billion cubic meters of salt water at the mouth of the Chesapeake Bay. These processes are on a scale that is not reducible, at least not unless we want to engineer such systems.

The best we can hope to do, at least in the foreseeable future, is try to define what we think will affect the overall health of individual systems. All processes and components stay within some reasonably defined bounds of system integrity. Therefore, we project that the system will provide the amenities and benefits we expect from it in the future.

I. VALIELA: Setting economic goals and ecological values in estuaries is not easy. Many of the kinds of problems that we're talking about are difficult to translate into economic terms. Although some non-market values have been pointed out, I don't see the overall strategy behind this. Even if you estimated an economic value, you would come up with a few thousand dollars, and that doesn't convince anyone. For example, there are places in New Jersey where one hectare of marshland is worth $200,000 for an industrial concern. This is not beneficial from an economic standpoint. If this idea succeeds, it is not going to do so in the arena of politics and economics where you want it to succeed.

H. HARRIS: In effect, what you're saying, is that the economic market has driven us to a point where we're trying to react, take account of the non-market values, and then use the same argument as the justification for management and the work of the system that we see as important. This can be a dangerous position, because it may lead to a lose-lose situation.

My response is that we are satisfied with the present system. And to say that we should not investigate those may mean we don't understand what some of the non-market values are.

J. WILLIAMS: I would like to address my question to Dr. Harris on the analysis of productivity and nutrient transport in the zones of Green Bay. I would also like to say that fisheries production and yield are not necessarily synonymous.

Did you look at any other methods, such as standardizing, in the different regions of Green Bay with some sort of estimate of production using Catch Per Unit Effort (CPUE)?

H. HARRIS: Actually, those data are not mine. That was done as another project, and I just pulled some of them together. There are a lot of assumptions. I don't think they computed Catch Per Unit Effort.

It is a variable, and we know, for example, that in the upper part of the bay we saw the yield falling off considerably in terms of whitefish. What we know about that area of the bay is that we're producing the whitefish in Michigan, and Wisconsin is harvesting them. Our yield bag, therefore, is biased by movement. So, there are some holes here.

W. ODUM: We ran into a problem about price a long time ago in Florida in dealing with mangrove swamps. There are acres in south Florida that are worth a half a million dollars for economic purposes.

We found an ideal solution to that. Some of you may have come to the same conclusion. That is, you simply establish the fact that wetlands are priceless. In other words, they cannot be replaced with anything else. They don't have a price; it cannot be calculated.

W. SEAMAN: In closing, I will state a few observations. Early in his presentation, Neal Armstrong listed users and uses of the estuarine system. Often, the users we deal with are in the public sector --- usually the ordinary citizen who buys a condominium and wants to live on the waterfront.

It is interesting that Florida's Department of Natural Resources recently commissioned an attitudes and education study of a coastal population and found that a significant majority of the public could not differentiate between a mangrove and a manatee. They had no real conception of the nursery function of estuarine systems.

In response to Don Boesch's second point about the socio-economic setting, we've got a tremendous education job to do in linking our scientific information to social understanding.

SEDIMENT MANAGEMENT AND ESTUARINE PRODUCTIVITY

MAN'S ACTIVITIES AND SEDIMENT INPUTS TO ESTUARIES

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INTRODUCTION

The topic I have been given is sediment management and estuarine productivity. My assignment is to present an overview of the subject and lay out some research priorities to provide needed knowledge for future management. At the outset, we need some definitions and some boundary conditions.

I shall restrict my discussion to fine-grained sediments, those sediments in the silt- and clay-size ranges (particles with diameters less than 62.5 μm). I shall use a broad definition of productivity. I do not restrict it to primary productivity, to secondary productivity or even to biological productivity. For the purposes of this paper, I define an estuary's productivity as a measure of the range and diversity of the estuary's uses upon which society places a high value. In other words, productivity is a measure of the extent to which an estuary meets society's expectations for it.

My role is that of a challenger; my assignment is to challenge. My dictionary defines the verb challenge as "to call, invite or summon to a contest, controversy, debate or similar affair; especially to invite to a duel." I would like to stop just short of a duel. But to make an effective challenge I feel obliged to make some rather blunt and unequivocal statements.

In this paper I shall concentrate on my assignment to lay out some research priorities to provide needed knowledge for future management.
I already have described in some detail estuarine sedimentation processes (Schubel 1983) and the effects of estuarine sediments on environmental quality (Schubel 1976; 1977; 1982). I shall deal with these topics only selectively and briefly here. In my discussion of research priorities, I shall draw heavily upon several papers and reports

that I have authored, coauthored, or edited, which deal with the subject at hand (Schubel et al. 1978; Schubel 1983; and Burns and Schubel 1983).

The most effective way to manage estuarine sediment is to reduce the amount of sediment that enters the estuary and to improve the quality (reduce its associated contaminant levels) of that which does. The most effective long-term strategy for reducing sediment inputs to an estuary is through proper soil conservation practices throughout its drainage basin. The most effective long-term strategy for improving sediment quality is through reduction of the inputs of contaminants at their sources.

Two of our management goals should be to reduce the amount of sediment released from the land (i.e., the sediment yields) through proper soil conservation practices and to reduce the inputs of contaminants to our nation's waterways. Reductions in either of these will have meliorative effects downstream in the estuary. But, even if we could achieve these goals in the extreme (if we could reduce sediment yields and contaminant inputs to zero, which we can not,) we still would have sediment management problems in many, probably most, of our major estuaries for several decades to a century. These are the time scales for movement of sediments from their sources in the drainage basins of major rivers down into the estuaries. While reduction of sediment inputs to estuaries may be desirable, reduction in the supplies of sediment to wetlands and deltas may be undesirable in actively subsiding areas, such as the Gulf Coast of the United States.

Little can be done to manage sediment while it is suspended within the waters of an estuary. Many of the more important effects are associated with sediment in suspension, but the opportunities for management are few. It's a little like trying to manage the path of a golf ball after it leaves the face of the club by applying "body English."

After sediment finds its way into the estuary, its only management occurs after it is deposited on the bottom. And the management often happens in conjunction with dredge-and-fill operations, which is associated with channel dredging and dredged-material disposal. It is my opinion that the management of this sediment and, more specifically, our activities to deal with it, could be improved substantially with a relatively modest investment. It is here where we should concentrate our sediment management efforts within the estuary.

I have grouped my research priorities into four general categories in decreasing order of payoff to management per unit cost of the research:

1) Development of estuary-wide dredging and dredged material management plans;

2) Documentation of estuarine sediment systems: sources of sediment, routes and rates of transport, sites and rates of accumulation, transformations of sediment composition between points of entry and sites of accumulation;

3) Characterization of the processes that control the adsorption and desorption of contaminants and other dissolved substances by fine-grained particles;

4) Characterization of the processes that control the particle-size distribution and degree of agglomeration of fine-grained particles within the water column and on the bottom and an assessment of how these processes affect bottom stability.

The ranking represents my subjective ensemble average across research priorities for improved sediment management within most of the large U.S. estuaries. For small estuaries and for component estuaries of large estuarine systems, the important classes of research questions and their rankings may vary significantly from those listed. In the sections that follow I discuss briefly each class of research activity and indicate what kinds of studies should be given high priority. First, I describe some of man's activities that affect the inputs of sediment to estuaries.

Particles are added to estuaries by rivers, by the atmosphere, by shore erosion, by biological activity within the estuary, by municipal and industrial discharges, and by the sea. The sources are external, internal and marginal. People's activities have affected the flow of particles into estuaries --- their quantity, their composition, their size distribution and the substances associated with them.

Regardless of the criteria one uses to measure environmental quality, the increased influxes of particulate matter into estuaries that result from man's activities have had a deleterious effect on many estuarine uses and salutary effect on few, if any. This is true whether the particles are suspended in the water column or deposited on the bottom. The most undesirable effects are associated with fine-grained materials and materials in the silt- and clay-size fractions. I shall restrict my attention to them. It probably is not an exaggeration to say that fine-grained particulate matter has a greater affect on environmental quality than any other single factor.

Although sediment in estuaries comes from many sources, the sources most affected by man are the rivers that carry sediment from upland areas into estuaries. This discussion focuses on the sediment loads of rivers that are increased by farming, mining, deforestation and urbanization; and are decreased by construction of reservoirs and other protective works.

People's activities have affected not only the amounts of suspended particulate matter added to estuaries, but also the size distribution and composition of these materials. There has been a shift to smaller particles and an increase in the amount of organic matter (Schubel 1976).

Man's Activities That Increase River Sediment Loads

Soil erosion is the ultimate source of most fluvial sediment. Ever since the first European settlers landed in North America, man has affected the amount of sediment in streams. The influence of man on sedimentation is well documented in the Chesapeake Bay region, where clearing of forests and wasteful farming practices (especially those used in raising tobacco) contributed enormous loads of sediment to the rivers. Clear streams became muddy and deep harbors at the heads of many Chesapeake Bay tributaries were filled rapidly with sediment (Gottschalk 1945). The Potomac River, whose waters were already turbid but still suitable for municipal use in 1853, had become so muddy by 1905 that the city of Washington had to install its first filtration plant. A comparison of the 1792 and 1947 shorelines of the upper Potomac shows that large areas of the Potomac near Washington had been filled with sediments stripped from farmland further upstream. The Lincoln and Jefferson Memorials now stand on what was described in 1711 as a harbor suitable for great merchant vessels. Even today, an average of about 2 million cubic meters of sediment is deposited every year near the head of tide in the Potomac; not all of this sediment is the result of agriculture. There are former seaport towns on the western shore of northern Chesapeake Bay where decaying docks are separated from navigable water by several kilometers of sediment-filled lowland. Streams that drain modern day farmlands in many of the Mid-Atlantic states carry about 10 times as much sediment as streams that drain equivalent areas of forestland. And this relationship is by no means unique. In the coastal plain of northern Mississippi, sediment yields from cultivated lands are 10 to 100 times the yields from equivalent areas of forestland (Gottschalk 1945; Trimble 1974). In two other areas where studies have been made, the Tobacco River Valley of Michigan and the Willamette Valley of Oregon, streams draining farmland carry two to four times as much sediment as streams draining equal area of forestland.

Mining is another activity that has increased the sediment loads of some rivers that flow into estuaries. San Francisco Bay, for example, contains nearly a billion cubic meters of sediment washed from the Sierra Nevada during the approximately 30 years of intensive hydraulic mining for gold in that range.

Even after the hydraulic processing was stopped in 1884, the mining debris continued to choke the valleys of the Sacramento River and some of its tributaries for many years. Gradually over the years the debris was deposited downriver in the marshes and shallow areas surrounding San Francisco Bay. The mining debris released in three decades is more than the total sediment from all other sources (including farmland) that the Sacramento River has carried in over 12 decades since 1850 (Gilbert 1917). It has been shown that this sediment had an important effect on the circulation of San Francisco Bay. The tidal prism was decreased, and the flushing regime changed significantly.

The high soil erosion rates prevalent in many unglaciated areas during the 19th and early 20th centuries now have been reduced by soil conservation practices and by reversion of uplands to pastures and woodlands (Meade 1980). But the effects of the earlier higher erosion rates are still being strongly felt downstream in the lower reaches of rivers and their estuaries. "Much of the soil material that was eroded off the uplands since 1700 is stored on hillslopes and on the floors of stream valleys," says Meade. Many alluvial valleys in the southern and mid-Atlantic piedmont of the United States are lined with a layer of sediment a meter or more in thickness that has accumulated since European settlers arrived (Costa 1975). Since upland erosion was curtailed by appropriate soil conservation practices, sediment has been supplied to streams from intermediate storage sites between the uplands and the river (Meade 1980; Meade and Trimble 1974; Trimble 1977). Trimble (1975) has estimated that more than 90 percent of the sediment eroded from the uplands of the southern piedmont of the United States since 1700 still remains above the fall line --- the boundary between the piedmont and the Atlantic coastal plain. The implication is that soil removed during an erosional episode can be released from intermediate storage sites over a period of decades to centuries and move downstream as a wave.

In glaciated areas, the influence of man on soil erosion rates has been less marked. (Gordon 1979; Meade 1980; Williams and George 1968). In a study of the Connecticut River valley, Gordon (1979) found little evidence that sediment yields had changed since precolonial days.

Urbanization is the most recent of man's activities to contribute large amounts of sediment to streams. Sediment loads derived from land being cleared or filled for the building of houses, roads and other facilities are best documented in the United States between Washington, D.C. and Baltimore, Md. During construction of housing developments, shopping centers and highways, the soil is disturbed and left exposed to wind and rain. The concentration of sediment in storm runoff from construction sites is 100 to 1,000 times what it would be if the soil had been left in a natural, vegetated state. Even though the soil is exposed to intense erosion for a short time, the amount of land cleared for new housing and ancillary uses in the Washington-Baltimore area was so great in recent years the contribution of sediment has been significantly large. Harold Guy of the U. S. Geological Survey has estimated that the Potomac River receives about a million tons of sediment per year from streams that drain the Washington area. This is about the same amount of sediment that the Potomac River brings into the Washington area from all its other upland sources.

In some areas of the world, lumbering has increased dramatically the sediment yields and sedimentation rates in rivers and estuaries. Large areas of forest have been stripped in southern Chile without replanting.

Another of man's activities that increases the sedimentation rates of estuaries is the discharge of dissolved phosphorus, nitrogen and other plant nutrients into rivers and estuaries. Municipal sewage effluents, including effluents that have received secondary treatment, the highest degree of conventional treatment, contain high nutrient concentrations. In some areas, agricultural runoff from fertilized croplands and animal feedlots also contributes nutrients to rivers and estuaries. These nutrients promote the growth of diatoms and other microscopic plants (phytoplankton) in the rivers and in the estuaries into which the rivers flow. The mineral structures formed by many of these organisms persist after the organisms die and become part of the sediment loads of rivers and the sedimentary deposits of estuaries. The U.S. Army Corps of

Engineers estimated, for example, that diatom frustules, produced in the Delaware River and the Delaware Bay, contribute about the same amount of sediment (a million-and-a-half tons per year) to the Delaware estuary as all upland river sources.

The effects of nutrient loading from municipal wastes on primary productivity are readily observable in the Potomac estuary, in the Baltimore Harbor and Back River estuaries (Maryland), in the Raritan Bay and Arthur Kill estuaries (New York/New Jersey), in the Hudson estuary (New York), in the Delaware estuary, in San Francisco Bay (California) and in many other estuaries around the United States and throughout the world. Stimulation of plant growth by nutrient-enriched runoff from agricultural areas is apparent in the upper Chesapeake Bay (Maryland) in the estuary of the Susquehanna River.

Man's Activities that Decrease River Sediment Loads

Reservoirs probably cause the most significant interruptions in the natural movement of sediment to estuaries by rivers. Reservoirs are built on rivers for a number of purposes: hydroelectric power generation, flood control, water supply and recreation. Regardless of their purpose or size, reservoirs trap sediment (Schubel and Meade 1977). For example, a reservoir that can hold only one percent of the annual inflow of river water is capable of trapping nearly half the river's total sediment load.

A reservoir whose capacity is 10 percent of the annual river water inflow can trap about 85 percent of the incoming sediment (Meade 1976; Meade and Trimble 1974). Although a river tends to erode its bed downstream of a reservoir to partly compensate for sediment it has lost, the net effect of the reservoir is to decrease the overall amount of sediment carried by the river. In the larger river basins of Georgia and the Carolinas, the sediment loads delivered to the estuaries are almost one-third of what they were about 1910, mainly because of the large number of reservoirs that have been built for hydroelectric power and, to a lesser extent, for flood control (Schubel and Meade 1977).

The trapping, however, cannot always be considered permanent, not even on time scales smaller than the life span of the reservoir. The sediment held behind some dams can be mobilized by extreme flood events (Meade 1980). Flooding of the Susquehanna River in Pennsylvania and Maryland following passage of tropical storm Agnes in June 1972 purged 10 to 20 years of sediment accumulation from reservoirs on the lower river (Schubel 1974; Zabawa and Schubel 1974; Gross et al. 1978).

On some rivers, settling basins and reservoirs have been built as sediment traps to improve the quality of water downstream. In 1951, three desilting basins were constructed on the Schuylkill River of Pennsylvania to remove the excessive sediment that resulted from anthracite coal mining in the upper river basin. The basins are dredged every few years, and the dredged material is placed away from the river out of flood reach. As a result of these basins, the sediment load carried by the Schuylkill into the Delaware estuary has been reduced from nearly a million tons per year to about 200,000 tons per year.

Return of cultivated lands to forests can significantly reduce sediment yields. In the last 50 years, the average suspended load of South African rivers has decreased by 50 percent largely because of the stabilization of river banks by vegetation (Rooseboom 1978).

Net Effect of Man's Activities on Sources of Sediment

The net effect of man's activities has been an increase in the sediment supplied to most estuaries, but we cannot say by how much. Although reservoirs and other controls have reduced the sediment in rivers in recent years, they have only partially offset the influences that caused the increases.

Added to this is the fact that sediment takes decades to move through a river system. Much of the sediment released by past mistakes, such as poor mining practices and poor agricultural soil conservation practices, is in transit storage between its sources and the estuaries. Even if the active supply of sediment to rivers were completely checked today, many decades would pass before the sediment loads would drop to natural levels.

The fight against erosion has been more successful in developed countries than in developing countries because of better land-use regulation. But, deterioration of water quality in coastal areas is a more serious problem in developed, industrialized countries than in most developing countries.

An Example of How Man Altered an Estuary's Circulation and Sedimentation Patterns By Altering Its Freshwater Input

Charleston Harbor is an interesting example of an estuary whose circulation and sedimentation were altered by changing the freshwater input to the estuary, and to a lesser extent, by changing its geometry. The Charleston Harbor estuary, located on the South Carolina coast (USA), is formed by the confluence of the Ashley, Cooper and Wando Rivers. The mouth of the estuary is restricted, and entrance from the Atlantic Ocean is gained through a single jettied channel. Prior to 1940, the total freshwater input was very small, averaging only about 2.8 cubic meters per second, and the harbor was between a vertically homogeneous and sectionally homogeneous estuary. Fine-grained suspended sediment moved slowly through the estuary to the ocean, and little dredging was necessary. The dredging required to maintain the main navigation channel at a depth of 9 meters was about 61,200 cubic meters at a cost of approximately $11,600 per year.

In late 1941, a dam was completed that diverted water from the Santee River into the upper Cooper River, which flows into Charleston Harbor. The average freshwater input to Charleston Harbor rose from only 2.8 cubic meters per second to about 425 cubic meters per second. The freshwater discharge increase shifted the circulation pattern from a very well-mixed estuary to a two-layered circulation pattern characteristic of a partially mixed estuary. Fine sedimentary particles, previously carried through the estuary to the ocean, were now entrapped in the estuary by the net upstream flow of the lower layer. They accumulated in the inner harbor, the upper reaches of the net non-tidal estuarine circulation regime. Shoaling became a serious problem. The dredging required to maintain the inner harbor channels increased to an average of approximately 1,758,000 cubic meters per year at a cost of about $380,000 per year between 1944 and 1952 (Schultz and Simmons 1957). Since 1952 the dredging rate has increased more; between 1960 and 1970 it averaged over 3,800,000 cubic meters per year at a cost of some $6 million per year. The increase in the shoaling rate resulted from the addition of new sediment sources, but the most important factor was the change in circulation produced by the increased river discharge. This was demonstrated conclusively by hydraulic-model studies.

Because of the enormous increased costs of dredging, the Charleston District of the U.S. Army Corps of Engineers developed a plan to redivert most of the Cooper River flow back into the Santee River. Implementation of that plan will cost of approximately $100 million.

SOME RESEARCH PRIORITIES

On the Need for Development of Estuarywide Dredging and Dredged-material Management Plans

The greatest single payoff to sediment management in most estuaries would come from the development of regional dredging and dredged-material management plans.

A dredging and dredged-material management plan should be developed for each estuary. The plan should be estuarywide and should ensure that maintenance dredging projects can be performed on schedule, and with predictable, acceptable impacts on public health, the environment, the biota and the economy. Each plan also should provide mechanisms for the timely and diagnostic evaluation of proposals for new work projects.

In maintenance dredging projects, the potential for adverse impacts is associated primarily with disposal and not with dredging. I believe most dredging experts would agree that we have sufficient knowledge to design and carry out maintenance dredging projects with predictable and acceptable impacts on public health, on the environment and on the living resources. The nature and extent of the impacts are set by the methods of dredging, especially by the medium within which disposal occurs, and by the methods and modes of disposal. To select an appropriate disposal strategy, planners must consider the quality of the material to be dredged (particularly the levels of associated contaminants) and assess the behavior and effects of the material and its associated contaminants for a variety of disposal options. Effects associated with the dredging can be limited in time and space to levels that do not pose significant threat.

In new work projects, the potential for adverse impacts is associated primarily with dredging and not disposal. The disposal of materials dredged for new work projects should pose little threat to human health, the environment or biota because the materials are primarily, or entirely, uncontaminated. We have sufficient knowledge to minimize potential adverse impacts associated with disposal through proper planning. In many cases, the material may be used for constructive purposes: beach replenishment, construction aggregate, landfill. In other words, material dredged for new work should be examined first as a resource and only after these possibilities have been exhausted should it be viewed as refuse.

The adverse effects of dredging in new work projects occurs not with the temporary effects associated with the act of dredging, but with persistent effects that may be produced by alterations of the circulation patterns, and as a result, alterations of the salinity distribution and sedimentation patterns. The magnitude of these alterations can be evaluated with appropriate models, particularly numerical models. The extent of the physical and geological changes associated with channel deepening and the environmental significance of these changes are highly site specific. They deserve careful consideration before major deepening projects are undertaken.

In the absence of any new work projects, nearly all major U.S. ports require periodic maintenance dredging. Often the volumes of material involved are large and the frequency of dredging relatively high. Environmental concerns and regulatory inefficiency sometimes cause prolonged, costly delays in maintenance dredging that could be avoided by proper planning and management.

An estuarywide dredging and dredged-material management plan should be developed for each estuary and should be based on a rigorous assessment of all plausible alternatives, including the "no dredge" alternative. Environmental and political pressure groups must not restrict the range of alternatives to be assessed. Imposition of the socio-political and economic "realities" should be constrained until the specific assessments have been completed. The plan should be based upon (1) a thorough characterization of the kinds and qualities of materials to be dredged, (2) a rigorous evaluation of the physical and chemical behavior of these materials on alternative disposal environments, and (3) an assessment of the resulting impacts of dredging and disposal on public health, the environment, the biota, other uses of that segment of the environment and the economy.

While there would not be unanimous agreement as to the range and magnitude of the specific environmental, ecological and human health impacts associated with each alternative, there almost certainly will be agreement among the experts as to the relative impacts associated with each alternative. That is, for a given kind (quality) and quantity of sediment, scientists could rank the disposal alternatives that are available for that port using a variety of criteria, and there would be agreement among them as to their relative acceptability. In other words, there would be general agreement that based on a number of criteria, alternative A is better than B, which is better than C. The plausible alternatives available will vary from port to port and, as a result, the relative ranking of a class of alternatives, or of any of its members, may vary from one port to the next even for the same kind (quality) and quantity of material. Alternative A may be the most acceptable alternative for Type C material for the Port of New York/New Jersey, but rank below other alternatives for the Port of Baltimore for the same kind of material. To put it simply, what's best for New York is not always what's best for Baltimore, Norfolk or Beaufort.

One probably can also rank with agreement the impacts --- public health, environmental, ecological and economic --- of disposal associated with various disposal options relative to the impacts associated with not dredging. The economic impacts of not dredging are often assessed or at least asserted. But there also are public health and environmental impacts of not dredging and only rarely are these assessed.

The first iteration of a portwide dredging and dredged-material management plan should be based entirely upon existing data and information. This procedure will highlight deficiencies in data and information and pinpoint areas where additional studies would contribute little to improved understanding or better management. A lot of time, effort and money have expended on unnecessary duplication of research, particularly on routine monitoring associated with maintenance dredging and disposal operations. At the same time, some important questions associated with the effects of these activities have never been addressed or have been addressed only feebly. It is only when one begins to summarize, synthesize and utilize the data, information and knowledge that exists to answer estuary-specific questions, that one can assess critically the adequacy of existing data, information and knowledge. We know more today about the effects of dredging and disposal than typically is incorporated into decisions affecting dredging and dredged-material management.

The preparation of a comprehensive dredging and dredged-material management plan for an estuary is a large undertaking that requires the skills of experts in a number of fields. Once prepared, however, the plan can be revised and updated easily to incorporate new information and advances in science and technology. Updating can be facilitated if information is incorporated into a computer-assisted decision-making system.

Once a plan is developed and endorsed, a full and rigorous assessment need not be completed every time a maintenance project is proposed. The quality of material accumulating in a channel normally varies little from year-to-year or over longer periods unless there is an accidental release of contaminants or a major natural event such as a flood or hurricane.

Spot analyses of material should be sufficient to determine whether that material falls within the normal range of materials for that project (channel). Additional bioassay and bioaccumulation tests may not be warranted, or if they are, the number should be small.

For each major estuary the appropriate agency should contract for the preparation of a draft regional dredging and dredged-material management plan. To be an effective management tool, the plan will require the review and endorsement of appropriate governmental agencies responsible for environmental matters and the participation by public interest groups during its development. Public participation will be most critical in the initial stages to identify objectives, goals and alternatives and in the final stages to review and endorse the plan.

Financial support for the development of regional dredging and dredged-material management plans could come from a reallocation of funds now used for routine monitoring of maintenance dredging projects. In many estuaries a major source of support for research on estuarine sedimentation comes from the U.S. Army Corps of Engineers in conjunction with monitoring of maintenance dredging projects. Much of this support, sometimes most of it, is wasted. All too often studies of the environmental effects of a particular dredging and disposal operation contribute little to our understanding of specific sedimentation processes or the sediment system of that particular estuary. Rarely do these programs affect the conduct of the operation they monitor or the design and conduct of future dredging/disposal operations, even those associated with that same project.

If one accepts that some support for research and monitoring is part of the price of carrying out a dredging project, then science, society and the environment could benefit from a different approach to the allocation and expenditure of those funds. The funds might be generated by a surtax on each dredging project set as a fixed percentage of the total cost of the operation or perhaps as a tax on each cubic yard of material dredged. These dollars could go into a fund to support research needed for development of a comprehensive dredging and dredged-material plan for that port or estuary. Such a practice could reduce, if not eliminate, significantly the practice of monitoring those properties that we can predict and measure and allow us to answer more important and more difficult questions.

In the first category I refer to such activities as monitoring the turbidity associated with dredging and disposal operations, the releases of contaminants during dredging and disposal, and the recolonization of sites following a dredging operation. In the latter category, I refer to processes such as the adsorption and desorption of contaminants under a range of environmental conditions and to studies of estuarine sediment systems that include the sources, routes and rates of transport and sites and rates of accumulation of fine-grained particles.

On the Need for Documentation of Estuarine Sediment Systems

Schubel et al. (1978) and Schubel (1983) have pointed out there are two different approaches to the study of estuarine sedimentation. One deals with specific processes such as the physical mechanisms that control the deposition and erosion of mud, the formation of composite particles (agglomerates) by biological and physico-chemico processes, the reworking and processing of sediments by benthic organisms and the consequent changes produced in the physical properties of the sediment, and the processes that control the uptake and release of dissolved substances by fine particles. The other approach deals with the characterization of the estuary as a sedimentary system.

Many studies of the first kind have been completed successfully. Others are just beginning --- the effects of benthic organisms on the physical characteristics of sediments and the processes that control the adsorption and desorption of contaminants by fine particles. The prospects for resolving questions of this kind are good as long as scientists find them exciting and as long as reasonable levels of support are provided through conventional funding mechanisms. But, studies of estuarine sedimentary systems hardly have been considered and when they have it has been in response to a crisis. One of the best examples is the work that explained the formation of the mud deposits in the Thames and the relationship of maintenance dredging of the shipping channels to the London docks (Inglis and Allen 1957). Two more recent examples of crisis studies resulted because of problems associated with Kepone (Nichols and Cutshall 1979) on the James River and its estuary from detection of high levels of PCBs in sediments, water and organisms (Olsen et al. 1978) on the Hudson River and its estuary. Studies of estuarine fine particle sediment systems are the key to improvement in our ability to manage sediment in estuaries.

The same biological, chemical, geochemical, geological and physical processes are at work in all estuaries, but the relative importance of these processes varies dramatically from one estuary to the next and among different segments of the same estuary at any given time. And there are large temporal variations within any segment of an estuary. One can learn a great deal about the mechanics of sediment transport and other sedimentary processes important in estuaries through laboratory flume experiments and isolated, short-term field studies. Unfortunately, these studies often provide little insight into the long-term manifestations of these processes in an estuary or the identification of the specific processes that control sedimentation in different parts of an estuary. Attainment of a level of understanding that is necessary for development of effective management strategies requires a holistic approach on an estuary-by-estuary basis that combines specific, short-term field and laboratory experiments with systemwide studies. It requires studies of estuarine fine particle systems.

Ideally, for each estuary we need to know: (1) the sources of sediment, their locations and strengths; (2) the character of the sediment introduced, its size distribution, composition and associated contaminants; (3) the routes and rates of sediment transport, including the transient repositories; (4) the sites of final accumulation within the estuary and the rates at which sediments are accumulating in each; (5) the exchange of sediment between the estuary and the ocean; and (6) the ways in which particle composition is modified between the points of entry and the final resting places.

Current knowledge permits acceptable forecasting of particle dispersion for short-term and near-field conditions. Advection and diffusion of particles within the water column is understood well enough to permit first-order estimates of initial dispersion from a source to the point of initial particle deposition. Complexities are introduced by the nonconservative behavior of the particles, the processes of biopackaging and, of primary importance, uncertainties about processes that control sediment resuspension from the sea floor. In each case, predictions are constrained primarily by a lack of site-specific rate information, rather than a lack of understanding of a basic process. There is a need to improve our understanding of resuspension processes. For management purposes, experts can adequately predict the resuspension of abiotic, coarser-grained sediment (sand) and empirical solutions for finer-grained sediment with site-specific information. This is another way of saying that for management purposes we need to understand an estuary's fine particle sediment system.

Schubel et al. (1978), Schubel and Hirschberg (1981) and Schubel (1983) have outlined different approaches to studying estuarine sediment systems.

On the Need for Characterization of the Processes That Control the Adsorption and Desorption of Contaminants by Fine-Grained Particles

The highest rates of contaminant removal (scavenging) from the water column are in estuaries, where progressively decreasing rates of removal occur as water moves seaward into open coastal and offshore waters. The rates of contaminant removal from the water column are increased by biological processes, specifically by primary production in the euphotic zone and by grazing and filter-feeding activities of animals at all depths.

Since initial partitioning of most contaminants introduced into natural waters is predominately from solution to fine suspended particles, knowledge of an estuary's fine particle sediment system is essential to, and sometimes is an acceptable premise for, making first-order predictions of the routes, rates and reservoirs of contaminants in that estuary. Local partitioning rates, however, may vary significantly from the calculated rates because of variations in grain size, particle composition, surface coatings and biological activity. Particle size plays a dominant role in determining partitioning between dissolved and particulate-adsorbed states. Small particles, regardless of their composition, adsorb more contaminant per unit mass than larger particles because of a higher surface area to mass (and volume) ratios and because of a ubiquitous coating. Some evidence exists for preferential affinities of contaminants among different kinds of particles in sewage sludge leading to pollutant separation. But the extent of control by particle surface chemistry under different environmental conditions needs further definition. This information is required for effective management of contaminated sediments.

Enough equilibrium partition coefficient (K_D) data are available to predict first order trends of pollutant-particle interactions for many classes of pollutants. Strongly adsorbed pollutants ($K_D > 10^6$) will follow particle transport pathways, while pollutants of intermediate K_D may be partially desorbed during transport. The lower the K_D, the more accurately one needs to know it for effective management. Further studies are needed on adsorption and desorption rates and on the rate of approach to sorption equilibrium under a range of environmental conditions.

One of the principal concerns with contaminated particles is determination of interactive time. This is the period of time that a contaminant is available for interaction with ambient biota. Interactive time is controlled largely by the recycling of bottom sediment by resuspension. Present knowledge of equilibrium partitioning coefficients for principal classes of contaminants permits prediction of first-order trends of sorption/desorption rates for resuspended particles. First approximations of remobilization rates are possible for many metals and bulk organic matter, but these are all conditioned by site-specific characteristics of resuspension and bioturbation. Without site-specific information, predictions of contaminant behavior cannot be accurate. For initial estimates, the principal vector for remobilization of contaminants from the bottom sediment may be taken as through the biota rather than by release from resuspended particles. Many classes of contaminants that re-enter the water column exhibit an aging effect. They also may be less bio-available than more recently introduced contaminants that have not been scavenged by particles, accumulated in bottom sediment, processed by organisms and recycled. Many contaminants become tightly bound with time, but the processes that control this are obscure. Research is needed on the bio-availability and sorption/desorption ratio of contaminants associated with sediments and pore waters. The effects of resuspension on these processes also need investigation. This information is required for development of effective management strategies for contaminated sediments.

On the Need for Characterization of the Processes that Control Particle-Size Distribution and Degree of Agglomeration of Fine-Grained Particles

The particle size distribution and the degree of agglomeration of fine-grained particles have a major affect on their physical behavior in the water column and on the bottom and, as a result, on the behavior and availability of their particle-associated contaminants. Stokes' Law or direct measurements are used to estimate particle settling velocity. This parameter is used to predict the transportation, deposition and erosion of sediments. Typically, the settling velocities used are for individual (primary) particles in samples that have been vigorously agitated to destroy any agglomerate particles. But, agglomeration is the rule rather than the exception for fine particles in estuaries.

The biological processes that control the agglomeration of fine-grained particles suspended in the water column need investigation. The removal rates of dissolved and particulate materials are related to primary production and the activities of filter-feeding zooplankton. The sequestering of pollutants in fecal pellets and subsequent removal to the benthos may be a removal mechanism for waste materials introduced in the open ocean. However, it is not known how effective this mechanism works in estuarine or shallow nearshore areas.

The degree of bio-availability of particle-associated contaminants ingested by organisms is dependent upon the nature of the particle, the phytoplankton species composition, the contaminant in question, and the species composition of the grazing organisms. Reliable application to specific disposal scenarios beyond first-order estimates is not possible with existing information.

Benthic ecologists have developed a time-dependent successional paradigm for the recolonization of sea floor areas that have been disturbed by storms, spoiling or other physical disturbances. The model is useful in sediment management, but needs tuning. This paradigm predicts the fate of particulate-associated contaminants within the biological benthic boundary layer is dependent upon the faunal successional state. While the biological foundation of the paradigm is well established, little information is available on how the physical sedimentary properties of the surficial deposits change with successional state or how these changes affect resuspension and mobilization of particle-associated contaminants.

The removal (burial) of particle-associated contaminants through biological packaging in benthic environments is a function of the rate and depth of mixing of the bottom sediments and the type of deposit feeders (shallow or deep). Research should focus on the character and durability of the biological packages and on the mechanisms of particle selectivity by deposit-feeding organisms. Agglomeration also affects bottom roughness, shear stress and erodibility of sediments. Erosion and resuspension of abiotic sediments can be predicted from such factors as the extent of sediment cohesion, roughness, particle size distribution and particle densities. Erosion rate models for noncohesive fine sediments and erosion rate measurements for sand exist, but a need exists for erosion rate models for cohesive and biologically-influenced, fine-grained sediments.

Aerobic degradation of organic pollutants, particularly by the aerating mechanisms of bioturbation and resuspension, is more efficient than anaerobic degradation and is dependent upon the successional stage of the benthos. The degradation potential of organics is higher in nearshore sedimentary environments than in offshore environments, particularly for petroleum hydrocarbons. Further research is needed on the factors regulating degradation of organic contaminants and the effects of chronic and acute loading of specific pollutants.

The efficacy of the practice of burial of PCB/DDT-laden sediments with 30 centimeters of cap needs testing.

The significance of detrital food chains in the transfer of pollutants through the biota needs substantiating. Available knowledge suggests that particle-associated pollutants remain in the sediments after deposition, particularly in areas with mature successional benthic communities that appear to enhance sediment column burden of pollutants through deep mixing and sequestering onto particles. The principal transport pathway for pollutant loss from sediments is through the food web, specifically areas with immature benthic successional stages. The extent of remobilization of pollutants needs to be evaluated for specific classes of pollutants and specific environmental scenarios, particularly for particle-associated organics.

SUMMARY AND CONCLUSIONS

Sediment, particularly fine-grained sediment, has had and continues to have, significant impacts on estuarine productivity. Problems result from increases in the sediment inputs produced by man's activities throughout estuarine drainage basins and from increases in the contaminant inputs, most of which become associated with fine-grained particles. The opportunities for effective management of estuarine sediment problems are restricted primarily to the two ends of the sedimentation process --- at the source and at the sink. Effective sediment management must come through (1) reducing sediment inputs throughout drainage basins by insistance upon proper soil conservation practices, (2) reducing contaminant inputs through proper source control, and (3) developing and implementing management strategies for sediment that is deposited in the estuary.

In terms of payoff to management of that sediment which reaches and is deposited within the estuary, the greatest benefits will be achieved by research that leads to:

(1) The development of a comprehensive estuarywide dredging and dredged-material management plan for each major estuary based upon an identification and analysis of the full range of alternatives.

(2) The development of a holistic and predictive model of the fine-particle sediment system of each major estuary.

(3) The development of a capability to predict, for a range of environmental conditions, the adsorption and desorption of different kinds of contaminants by fine-grained sediments.

(4) The development of a capability to predict, for a range of environmental conditions, the agglomeration of fine-grained particles within the water column and on the sea floor and how changes in the degree of agglomeration affect settling velocity, critical erosion velocity, and availability of particle-associated contaminants.

These research priorities are directed at management needs. My list of research priorities for significant scientific advances would be different.

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SEDIMENTATION AND ESTUARINE PRODUCTIVITY: RESEARCH PRIORITIES FOR MANAGEMENT

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J.R. Schubel's overview of research needs for the management of estuarine sedimentation focuses on major estuaries and fine particles. For California's major harbors, the problems of maintenance dredging, dredge disposal and water quality are of highest priority (R. Krone, U. C. Davis, pers. comm.), and we concur with Schubel's recommendations. But for most of the state's estuaries, these priorities need to be challenged because large estuaries are rare and fine sediments are not always the most problematic. Of California's 126 coastal wetlands (Fig. 1), only San Francisco Bay and San Pablo Bay are large. Ninety percent of the state's coastal wetlands are less than 2,000 acres (810 ha) in size. Most of these smaller systems are affected significantly by sand deposition along coastal sand bars and accumulation of materials from the watershed.

This paper will focus on the problems of smaller estuaries in California. Research leading to optimal habitat management is the most important priority for these estuaries. We need to understand the relationship between sedimentation and habitat types and the functioning of their respective ecosystems. At the same time, control measures and mitigation procedures must be developed to cope with sedimentation from coastal watersheds and dunes.

REGIONAL DIFFERENCES

There are several reasons why most California estuaries differ from those found in other regions. Physiography and hydrology combine to form estuaries that are small. In southern California, annual stream discharge into the Tijuana Estuary (Fig. 2) averages 16,882 acre-feet (20.5 million cubic meters) and occurs primarily between February and April. River valleys are

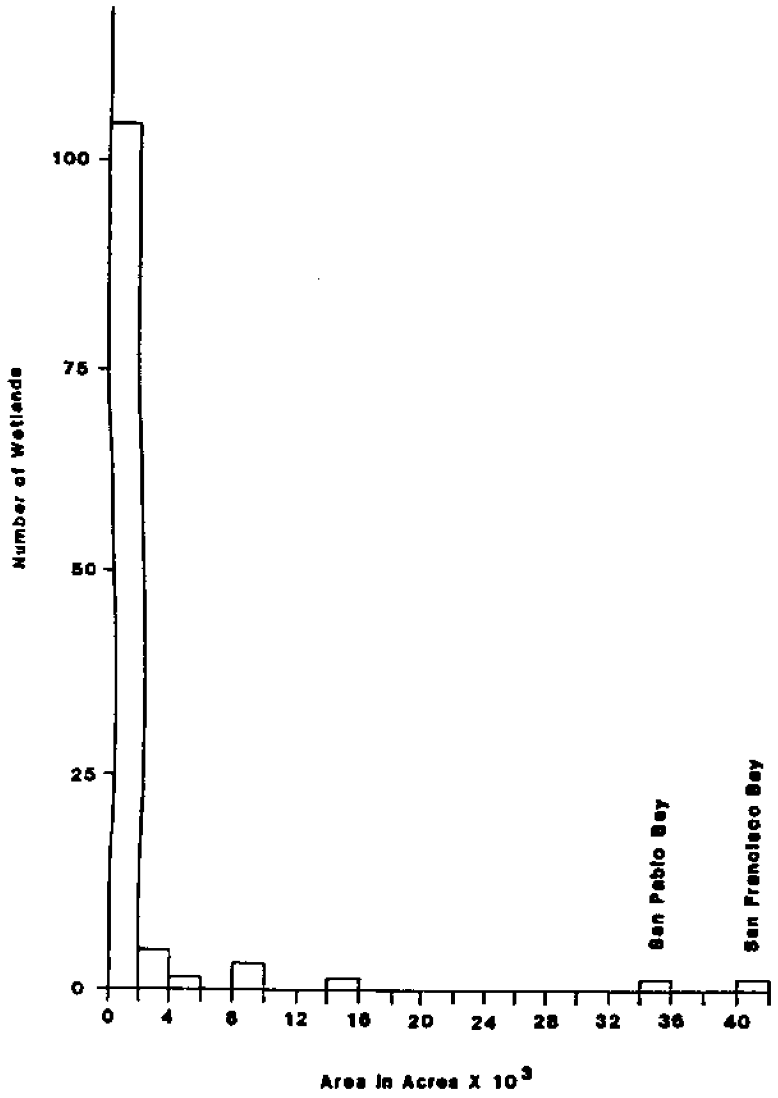

FIGURE 1

Size-frequency histogram for California coastal wetlands, developed from California Coastal Commission data. Note that acreages represent shallow-water habitats only and are conservative estimates for those systems with deeper estuarine habitats. For example, the whole of San Francisco Bay covers about 305,000 acres.

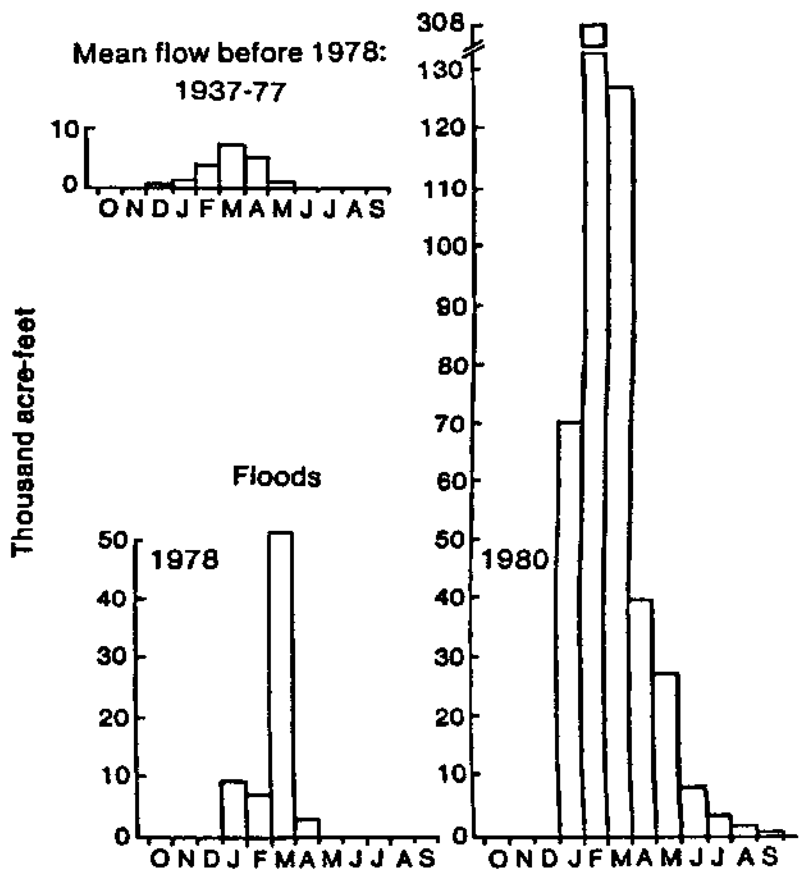

FIGURE 2

An example of intermittent streamflow: Tijuana River (USGS, Nestor Gage). Streamflow differed greatly in recent wet years. Floods in 1978 increased the annual streamflow four-fold; floods in 1980 increased annual streamflow about 30-fold over the 1937-77 average. Even before 1978, the coefficient of variation for annual streamflow was 327 percent (n=40 yr.).

narrow, so sediments have little space to spread out laterally. Delta formation is further restricted by a narrow continental shelf. Most estuaries, therefore, consist of a small lagoon basin, subtidal channels and intertidal creeks. Intertidal flats and salt marshes make up the majority of the habitat.

Variability of rainfall and stream flow is also an important feature of the region. Both droughts and catastrophic floods are likely to occur. Annual stream flow into Tijuana Estuary has a coefficient of variation of 327 percent. Recent floods illustrate the magnitude of change which that system undergoes (Fig. 2). During 1978 the annual flow was four times the 1937 to 1977 average, while in 1980 it was 28 times that average.

Variable stream flows result in variable sedimentation events. Harlin (1978) showed that sedimentation rates in fluvial systems are highly correlated with the coefficient of variation for annual rainfall in a watershed. We have few, perhaps no measurements of average sedimentation (those of Mundie and Byrne (1980) are based on single cores for each of five marshes studied). However, massive sedimentation events have been documented. In 1861, Goleta Harbor was filled with deposits from one flood. The resulting wetland, Goleta Slough, covered about 1,000 acres (Speth et al. 1970). More recently, Mugu Lagoon lost 40 percent of its low-tide volume as a result of cumulative sedimentation during the 1978 and 1980 floods (Onuf in press). Alluvial fans have developed in Carpinteria Marsh, Devereaux Lagoon, Los Penasquitos Lagoon and Tijuana Estuary. While some of these sedimentation events appear minor, each is significant in habitat alteration. As little as 6 inches (15 cm) of sediment can change one type of habitat to another. Covering as little as an acre can eliminate substantial portions of a small wetland, and if sediment covers endangered species habitat, it could eliminate entire populations.

Variable rainfall and stream flow can cause wide variation in estuarine salinities, particularly if the system is small. During drought years, the channels are dominated by marine waters most of the year. During flood years, fresh water may

dilute the entire estuary for several weeks. As a result, biological composition can change dramatically. For the most part, marine species dominate channels and embayments. Most are intolerant of long periods of fresh water influence, and large-scale changes occur following flooding. While salinity tolerances are not well known, coincidental data indicate that some species are affected by even brief periods of brackish conditions, and most fishes and invertebrates are eliminated by prolonged freshwater influence (Zedler and Koenigs 1984).

Public use of estuarine habitats differ for California. With an emphasis on recreation and nature appreciation, estuarine managers perceive different values for estuarine habitats. Shipping, industry and naval concerns appear to have precedence only in San Francisco Bay, Los Angeles harbor and San Diego Bay. Protection of natural resources and maintenance of biological productivity are specifically required by the California Coastal Act of 1976. Furthermore, the state takes a broad view of biological productivity, as indicated in the California Coastal Commission's (1981) Wetlands Interpretive Guideline, defining it not only as organic material produced per unit time, but also as the utilization of particular habitats by fish and wildlife species.

Estuaries disturbances may be similar in the United States, but their relative importance differs. Longshore currents deposit sand along beaches, and frequently block the ocean-lagoon entrance. The disturbances that augment sand bar formation include: 1) past filling for roads across wetlands that reduced tidal prisms to prevent sand accumulation at the lagoon mouth (cf. O'Brien 1969); 2) recreational use of coastal dunes by foot, horse and off-road vehicle traffic, causing vegetation denudation and erosion; and 3) sea storms that wash dunes into adjacent estuarine channels (e.g., Tijuana Estuary during winter 1983). Stevenson and Emery (1958) also discuss how the 1825 and 1861 floods caused sand spit formation at Newport Bay with sediments brought downstream by the Santa Ana River.

Disturbances within the watershed are also important. Construction projects on steep slopes accelerate erosion by releasing massive amounts of sediments to coastal streams following the heavy rains that can occur in this region. Because the estuarine sink is usually a small one, sedimentation from single flood events can be catastrophic. The central basin of Mugu Lagoon filled during the 1978 storms. Repeated flooding in 1980 added sediment throughout the lagoon, and the combined events reduced the lagoon's low-tide volume by 40 percent (Onuf in press).

Such impacts are not restricted to small estuaries, however. Historically, mining and the 1849 gold rush played an enormously important role in filling San Francisco Bay--an estuary that was once larger than Rhode Island (Atwater et al. 1979). Hydraulic mining was practiced between 1853 and 1884, resulting in "a few meters" of sedimentation filling the upper arms of the bay (Hedgpeth 1979) or about 1.146 billion yards deposited between 1849 and 1914 (Gilbert 1917, cited in Krone 1979). Since the gold rush, about 95 percent of the tidal marshes have been leveed or filled (Atwater et al. 1979). What was once the predominant habitat became a minor component of the estuary. Together, mining, diking and filling operations reduced the area of San Francisco Bay about 37 percent over the last century (Conomos 1979).

Hydrological modification is widespread in California (Cooper 1968). Sedimentation patterns have been disturbed by dams that reduce the seaward flow of particles and by importing water for irrigation, which increases the potential for erosion. Perhaps one of the most important modifications to be faced in future years is the conversion of intermittent streams to permanently flowing rivers, and associated changes in sedimentation.

Finally, background information on hydrology, sedimentation and estuarine ecology had lagged behind that on the East Coast. As a result, research needs that take priority elsewhere (e.g., effects of toxins on target species) must await identification of the resources that may be affected. Tijuana Estuary is currently receiving raw sewage from spills in Mexico. Determination of what fishes being damaged by toxins is hindered by the lack of quantitative records on what occurs

there. In many cases, fish and shellfish utilization of California's estuarine habitats is relatively unknown. Food chains are even less well understood.

Where some progress has been made, however, is in recognizing how species distributions differ in years of average and unusually heavy rainfall (Onuf and Quammen 1983; Onuf in press; Zedler and Onuf in press). Recent floods have eliminated many species of invertebrates and fishes, and recovery appears to be quite slow. Some of the changes are related to salinity, but sedimentation reduced habitat for water column fishes, and turbid water smothered large invertebrates at Mugu Lagoon. Therefore, research on sedimentation must not be restricted to "usual" conditions, because substantial effects occur during extreme events.

REGIONAL RESEARCH NEEDS

In addition to the research needs identified by major harbors (Schubel, this proceedings), we have identified six research priorities for sedimentation management in California's smaller estuaries. Specific research needs are provided as examples of what information managers must have to prevent or mitigate sedimentation problems. They are:

1) A relationship of estuarine physiography and habitat type to species composition and food chains.

a) A more thorough knowledge of biological resources is needed, along with the specific environmental conditions that control their distribution and abundance (Macdonald 1977; Zinn and Copeland 1982). Recent changes brought about by sedimentation indicate that 10 to 20 centimeter changes in elevation can shift one habitat type to another. At Mugu Lagoon, for example, a 19-centimeter deposit eliminated a subtidal eelgrass bed by raising the topography to an intertidal elevation (Onuf in press).

b) Substrate type is a well-known determinant of benthic community structure, but its influence on food chains is less well understood. Through experimentation, Quammen (1980) found that sand interfered with bird feeding by making it difficult to obtain benthic invertebrate prey. Fine sediments would favor surface-feeding shorebirds, while coarser substrate would favor larger shorebirds that can obtain prey from sand. Substrate type could thus determine bird use. Floods caused some habitats at Mugu Lagoon to become muddier and some to become sandier (Shaffer and Onuf 1983). Benthic metabolism was higher in fine than in coarse sediment, although gross productivity of benthic microalgae did not differ (ibid.). These studies begin to demonstrate the importance of sedimentation events on ecosystem functioning, but data are too few to make generalizations among habitats or ecosystems.

c) At a larger scale, the relationships among habitat types need to be understood, both within and between southern California wetlands. Our understanding of various species dependencies on coastal estuaries is poor. For example, various fishes use estuarine channels for spawning and feeding, but the extent to which estuaries add to their recruitment is not clear (Nordby 1982). Several bird species have become endangered as estuarine areas have diminished.
In order for populations to expand, there must be opportunities for dispersal into unoccupied habitats. This is true for animal (e.g., light-footed clapper rail) and plant (e.g., salt marsh bird's beak) species. At present, there is too little information on how the size, structure and proximity of habitats can facilitate such dispersal.

d) Regional restoration goals need to be established (Zedler et al. 1982). Research on habitat relationships is especially important because proposals for new developments along California's coastline include restoration proposals as mitigation for negative environmental impacts. Wetlands that have been degraded by diking, filling or other disturbances offer a wide range of possibilities for constructing artificial habitats. Yet we cannot plan habitat size and configuration without a better understanding of species-habitat dependence. While many restoration plans seek to enhance endangered species habitats, we need to develop whole-ecosystem management goals for biogeographic subregions within California (Zedler in press).

2) A dynamic nature of California's estuarine communities:

a) A better understanding is needed of how estuaries respond to unusual vs. common hydrological conditions. Recent investigations of San Francisco Bay, Mugu Lagoon and Tijuana Estuary under conditions of varying stream flow demonstrate that wide variation in species composition and abundance occur from season to season and year to year. Because stream flow is so variable, major changes occur in estuarine hydrology at several temporal scales. Annual winter rains control phytoplankton productivity in San Francisco Bay (e.g., Cloern et al. 1983). Unusual flood years stimulate salt marsh plant productivity (Zedler 1983). Major floods combined with disturbances in the watershed (e.g., increased erosion and reservoir drawdown) lead to major, large-scale changes in channel and intertidal marsh communities. Attempts to understand the relationship between estuarine productivity and sedimentation must consider a wide range of hydrological conditions. Such studies are few and do not begin to include all estuarine producers.

b) Research is needed on resilience and ecosystem recovery rates. Along with studies of how productivity changes with various types of sedimentation events, a need exists to understand how rapidly those populations recover. Long-term research at Mugu Lagoon suggests that five years is not enough time for water-column fishes to recover from sedimentation (Onuf and Quammen 1983). Vascular plants, on the other hand, returned to preflood conditions in the next growing season (Zedler 1983). The factors that prevent a rapid return to predisturbance conditions among fishes and invertebrates are poorly understood.

3) A maintenance of the estuary-ocean connection:

a) Better engineering designs are needed for self-maintaining lagoon mouths. Many estuaries in southern California close during part of the year (Gorsline 1967). Similar incidents of estuarine closure occur in other arid regions of the world. Jennings and Bird (1967) discuss the frequent closure of lagoons along the arid, high energy coastlines of Australia. These coastlines are typified by moderate to high tide ranges. In southern California, the arid climate favors the production of coarse, sandy sediments in streams, and the high wave energy produces a large longshore drift (Inman and Brush 1980). The tendency toward closure is countered by the flushing action of the tidal prism rather than stream flow. Any reduction in the tidal prism by fill, sedimentation or other sources may lead to closure of the estuary (O'Brien 1969), but a detailed understanding of the tidal prism necessary to maintain flushing is lacking.

b) Additional data are needed to understand shallow water sedimentation processes. Information on sediment concentrations and wave conditions in nearshore waters is inadequate for predicting sedimentation rates within intertidal marshes (Krone 1982). Goraline and Stewart (1962) suggest that the amount of erosion caused by wave attack on the ocean side of the shore adjacent to San Quintin Bay (Baja California) is equal to the sediment volume deposited within the bay. The role of mudflats in wave attenuation needs to be assessed (Krone 1982). We need to know the extent to which organisms resuspend sediments through burrowing and feeding activities, thereby counteracting the sedimentation process (Onuf, pers. comm.).

4) Methods controlling or mitigating sedimentation:

a) The control of sedimentation outside and within the estuary needs further study. Dredging has many impacts in the estuary. Turbidity increases, tidal circulation may be impaired, and primary productivity decreases (Johnston 1981). Whether such changes are negative or beneficial depends on individual estuarine situations. Krone (pers. comm.) indicated that low sediment turbidity (resulting from diversion of river flows into San Francisco Bay) can have a negative impact if it stimulates excessive phytoplankton productivity, which in turn causes anoxia of bay waters. In California, as on the East Coast, disposal of dredge spoil presents a continuing problem. As Schubel (these proceedings) points out, even if sediment loading of stresses were completely controlled, estuaries would continue to receive materials stored in streambeds for years thereafter. There would still be a need to manage sedimentation within the estuary.

b) For restoration projects, we need to predict how improved tidal flushing will alter sedimentation rates within estuaries. Will improved tidal flushing cause sediments to be remobilized, and where will they be redeposited? Attempts are being made to model the effects of renewed tidal flushing in Los Penasquitos Lagoon (H. B. Fischer, U. C.-Berkeley, unpub. analyses), a southern California wetland where roadbed filling has reduced the tidal prism. Historical sedimentation patterns will be predicted, and future deposition will be calculated for varying stream input.

c) New methods of small-scale sediment removal are desirable for small wetland systems. While dredging is generally recommended to maintain tidal circulation for habitat management, it does affect the wildlife for which habitat is being managed. New methods of low-impact dredging are needed. Inman and Nordstrom (1977) developed a sand-fluidization procedure, wherein water is added to stable sediments are carried away by the tides. Such small-scale hydraulic mining may effectively remove sediments without affecting sensitive species.

5) Changing freshwater flow regimes: a) Sediments are carried into estuaries by water, and research concerning water management is needed throughout California. The most ambitious water relocation scheme in the United States redirects water from northern California to the San Joaquin valley for agricultural use and to southern California for support of the growing populous. Stream flows to San Francisco Bay are modified in volume and periodicity. In the more arid coastal areas, most of the imported water is currently released offshore through sewage outfalls. However, proposals to treat sewage and release effluent within coastal watersheds would change intermittent streams to continuously flowing rivers. Not only would the entire hydrology change if such plans are implemented (Zedler and Koenigs 1984), but the patterns of sedimentation would also be altered. At present, there are no

studies to predict sedimentation with augmented stream flow into arid-region estuaries.

SUMMARY

We concur with Schubel's recommendations (these proceedings) for major estuaries: that dredging and dredge spoil management plans are necessary, that models of fine particle sediment systems should be developed, and that the relationships between sediments and toxic materials should be investigated. However, most of California's estuaries are small, and other research needs take priority for improving their management. Smaller size, more variable climate and hydrology, differences in disturbances and societal values, and less scientific information about California's estuaries are reasons why research needs differ from those of major estuaries elsewhere.

Research leading to improved habitat management has high priority for California. Most important for smaller estuaries is research that will improve our understanding of: the relationship between sediments and habitat type, the dynamic nature of estuarine communities, factors controlling the estuary-ocean connection, how to control or mitigate sedimentation, and how best to manage stream flow in arid coastal watersheds.

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BIOLOGICAL CONSEQENCES OF MANIPULATING SEDIMENT DELIVERY TO THE ESTUARY: A BLUEPRINT FOR RESEARCH

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INTRODUCTION TO THE PROBLEM

Identification of current sediment management problems and their implications for estuarine productivity requires input from at least two disciplines: sediment dynamics (geomorphology) and estuarine biology. Sediment dynamics can predict the long-term geomorphological consequences of manipulating sediment inputs. And estuarine biology is needed to understand the immediate influence of varying sediment delivery and the long-term impacts of potential geomorphological changes to the estuarine setting. Schubel (1984) reviews case studies of the geomorphological effects of increased sediment delivery and documents the geochemical roles that fine sediments play in estuarine systems.

I focus my comments on the biological consequences of varying sediment inputs to the estuary. In specific, I (1) identify a philosophical bias that underlies virtually all approaches to environmental management, (2) address some significant methodological problems in identifying the effects of varying sediment inputs, (3) explore the relationships between the geomorphology of the estuary and the role of sedimentation, (4) review evidence assessing the short-term biological effects of varying sediment inputs to the estuary, and (5) describe, in detail, the best available case history of the consequences of sedimentation on an estuarine system.

PHILOSOPHY AND ENVIRONMENTAL MANAGEMENT

A general philosophical schism exists among the public and scientists, separating those who believe that nature can be improved by the works of man (the "biotechnologists") from those who treasure and seek to preserve the biological and ecological status quo (the "bioconservatives"). This schism often injects substantial bias into testimony and recommendations offered by experts.

The literature on sediment management and its consequences for estuaries clearly shows this philosophical dichotomy. Engineers advocate intervention into natural systems --- the construction of dams, levees, dikes, catchment basins, groins and jetties to manage water flow and sedimentation. Frequently, the engineers' recommendation solves the immediate technological problem without assessing the consequences (especially the biological) and ramifications to the entire system. As illustration, I quote Besnier (1983):

> Coastal zones frequently raise problems as to their freshwater supply. On the other side, tidal estuaries on the Atlantic Coast, with backflows of sea water for tens of kilometers inland, and at the same time the settling of resuspended marine sediments which are deposited downstream of the tide, are the object of uninterrupted works in order to control both of these nuisances. The building of a dam on the estuary, as near as possible to the outlet into the sea, enables to solve all these problems: stopping the silt-loaded salt flow, and constitution of a freshwater reserve upstream.

In contrast to this myopic view of sediment management, biologists frequently demand no alteration of the natural systems. They implicitly assume the natural unmanaged system is optimal. Schubel (1984) shares this assumption. He argues that increased sediment erosion caused by development and poor agricultural practices within a drainage basin should be counteracted by construction of catchment basins or other structures to return sediment inputs to natural levels. I challenge this assumption. As I will discuss, sediment inputs into the estuary play vital roles in maintaining valuable biological functions (Benson 1981). I see no reason to believe that the natural rates of sediment delivery to estuaries are optimal. These rates have varied historically with short-term variances in weather and long-term climatic changes. Furthermore, many U.S. and world rivers have been

dammed, causing large reductions in their sediment transport and freshwater input to the estuaries (Day et al. 1977). Is further reduction necessary or even desirable? The best answer to most estuarine sediment management questions lies between the inaction or return to natural status demanded by the bioconservative and the manipulations advocated by the biotechnologist. If, as I argue later, sediment delivery to estuaries plays a significant role in biological productivity, what is the optimal level of sediment input for a given system? Future estuarine research should address such questions.

Even if we agreed that most effects of increased sediment delivery into estuaries diminish valuable system functions, sediment inputs will continue. Detailed and well-focused biological study is needed to assess the impact of varying sediment delivery rates (differing among estuaries and major estuarine functions). The study can anticipate effects and use rational biological criteria to assess the relative merits of alternative sediment or water management schemes. Most of the biology currently used to assess the impacts of proposed projects is in the form of untested models, which are used uncritically as if they represented well-supported generalizations or paradigms. This type of biological input to the decision-making process is naive, misleading and perhaps worse than no biological input at all because it creates false security. Biological models that predict the impact of sedimentation and various alternative management schemes require rigorous testing. That should be an important research priority.

COMPOUNDING OF FRESHWATER FLOW AND SEDIMENT DELIVERY

In any estuarine system, freshwater input and sediment delivery will be related positively over time within any period of unchanging utilization of the watershed. In dry years, river flows and sediment inputs are low; in flood years, increased freshwater flows carry a more than proportionate increase in sediment load. This normal confounding effects of fresh water and sediments is critical to recognize because it makes testing sediment delivery alone difficult. A biological comparison across estuarine systems that differ naturally in alluvium amounts but remain similar in total water flow (e.g., the Ganges with high concentrations of alluvium [1950 ppm] vs. the Mekong with little alluvium [20-500 ppm] [Pantulu 1975]) is not a controlled contrast. Other biological differences exist between estuarine systems, even between those that are close geographically, independent of alluvium differences.

If watershed usages remain similar over time within an estuary, temporal correlation represents a flawed method of assessing the effects of varying sediment delivery rates. Even though the sediment delivery rate probably does not change linearly with freshwater flow within most systems (but, rather, increases more rapidly as banks erode and soil becomes supersaturated, etc.), a multiple regression or partial correlation analysis will not identify whether fresh water or sediment causes variation in any dependent biological parameter. Although the shape of the biological-effects curve may resemble the sediment-delivery curve more than the water-flow curve, this does not imply that sediment caused the biological change. Perhaps the biological parameter in question responds non-linearly to water flow changes in just the same way as, but independent of, the sediment delivery rate.

The best, and maybe the only, analytical solution to this dilemma of confounded variables requires studies of replicate years before and after radical changes in watershed usage. Then we could study a different level of sediment delivery for a given flow rate within a single estuarine system. By altering the curve that relates sediment input to freshwater flow, the biological effects of sediment can be evaluated, unconfounded by changes in freshwater inputs. But this approach is not free of flaws. Biological parameters may vary temporally, independent of watershed changes. Nevertheless, this rigorous test of the biological effects of varying sediment inputs should be utilized in careful environmental research.

Although recognition of the natural confounding of freshwater flow and sediment delivery is necessary to test the factor individually, actual sediment management procedures differ in the degree to which they alter sediment inputs relative to freshwater flow. To predict environmental effects accurately, we must distinguish between sediment management procedures that alter sediment inputs alone without greatly changing freshwater flow and those that alter both simultaneously.

For many reasons it is difficult to disagree with inland soil conservation practices that retain topsoil while leaving freshwater flow largely unaltered. Everyone is served by contour farming on slopes, no-till planting, use of winter cover crops, maintenance or replanting of natural riparian vegetation along stream and river banks, and planting grass waterways on farms and in developed areas. However, the most commonly utilized construction methods of sediment management reduce freshwater inputs to the estuary (and alter the natural seasonal pattern of sediment and freshwater delivery). As Schubel (1984) correctly argues, engineering methods can reduce sediment loads without changing freshwater flows. Catchment basins selectively remove (coarse) sediments, while leaving total water flow rates largely unaltered. However, the multiple benefits commonly associated with dams make their construction the first solution suggested for sediment problems. A dam can provide a catchment basin for sediments, a freshwater reservoir, flood control, a recreational facility, a potential lake fishery and a means of hydroelectric power generation. Because a dam will affect freshwater delivery and sediment input into the estuary, assessment of the biological consequences of this sediment management method (and many others) must evaluate the joint impact of reducing fresh water and sediment. This requires a different biological data set from that required to assess a sediment management alternative that affects sediment delivery alone.

RELATIONSHIPS BETWEEN ESTUARINE GEOMORPHOLOGY AND SEDIMENTATION

The biological consequences of altering sediment delivery rates will vary geographically with the changing geomorphology, hydrology and human usage of the estuary and coastline. Knowledge of the geological processes acting on the coastline is critical for accurate prediction of the biological effects of varying sediment inputs. Increased sediment delivery implies increased estuarine and nearshore sedimentation. Coastal geology and sedimentology must tell us the consequences of increased sedimentation. Is sedimentation necessary to maintain a dynamic equilibrium between shoreline erosion and sedimentation? Or will increased sedimentation simply fill in the estuary and destroy estuarine habitat? These are critical questions that sediment dynamicists must answer before we begin altering sediment inputs.

Varying the rate of sedimentation in a fjord-like estuary along a once-glaciated coastline may have little negative impact. The depth of a fjord implies that little chance exists to significantly alter the estuarine volume or area by increasing sediment inputs from rivers. Furthermore, evidence suggests (e.g., Gordon 1979) that rivers and streams in glaciated areas do not carry increased sediment loads. Consequently, sediment management projects may not be needed in fjord-like estuaries.

Along subsiding coastlines, such as the Mississippi delta, varying the rate of sediment delivery has major impacts (Day et al. 1977). A continuous supply of sediments maintains salt marsh acreage and prevents it from becoming open water habitat. Human intervention reduced the flow and sediment delivery rate of the Mississippi River below previous historical levels. Transgression is evident and marsh habitat is rapidly disappearing. If we assume that salt marsh habitat is economically more important than equal areas of open water habitat because of its high primary productivity, then the decreased sediment delivery rate in the Mississippi River is negatively influencing biological productivity.

What may be worse than the transgression itself is the subsequent response of coastal communities. If the sediment input necessary to maintain the present position of shorelines is radically reduced by upstream sediment management and if substantial development of the coastline has occurred, then transgression may stimulate extensive building of dikes, levees and other structures designed to protect coastal investments (Pandian 1980). Maintenance of habitation along the estuary and coast at elevations progressively lower than sea level would effectively eliminate most estuarine habitat. Instead of a slowly sloping shoreline of intertidal habitat, we would find deep water immediately adjacent to "shore" (the dike).This scenario of sediment starvation is evident along the Mediterranean coast near the Nile River delta (Aleem 1972). If sea level rose substantially in response to the greenhouse effect, then this analysis of the sedimentation effects on a subsiding coastline would have broader applicability. In such systems, sedimentation can be an environmentally positive influence, enhancing or maintaining the economic values of the estuarine system.

On steep coastlines in Mediterranean climates, estuaries are few. They are small and run a serious risk of disappearing altogether from increased sedimentation. Although natural sedimentation processes rapidly fill these estuaries, any artificial increase in sedimentation rate can hasten the disppearance of estuarine habitat. In a small estuary, slight increases in net sedimentation can damage the system. The tidal prism is small and can be reduced to levels that are insufficient to maintain constant connection with the sea. Estuaries that intermittently connect to the sea lose most of their significant nursery and productivity functions. Consequently, sedimentation in this type of estuary is a critical problem (Onuf and Quammen 1983, Zedler and Onuf 1984).

In other areas, increased sediment delivery may imply increased estuarine sedimentation and potential reduction of estuarine habitat. Schubel (1984) reviews evidence of this process in various subestuaries of Chesapeake Bay and the Raritan and Delaware rivers. The potential reduction in estuarine area is the most serious negative effect of increased sediment delivery. Nonetheless, estuarine habitat also can be lost when dams control sediment inputs. Baxter (1977) discusses the conversion of marsh into pasture along the Peace River in Alberta. Damming reduced the usual spring floods that maintained the extensive marshes, substantially reducing hunting and fishing in the Peace estuary. Detailed studies of sediment dynamics in estuaries can evaluate proposed schemes to alter sediment and/or freshwater inputs and to predict how long-term effects of sediment manipulation will affect estuarine acreage.

SHORT-TERM EFFECTS OF SEDIMENT INFLUX ON ESTUARINE BIOTA

Although the long-term effects of increased sediment inputs into the estuary may be negative, many short-term biota responses are positive. Consequently, a prediction of the impact of varying sediment delivery in an estuary requires simultaneous examination of long- and short-term effects. We have learned enough about the natural variability in estuaries (e.g., Nixon 1980) to realize that each estuary may be unique in its response to varying sediment inputs. Thus, my brief review of the short-term consequences should be viewed as a set of reasonable hypotheses suitable for future testing.

Primary Producers

In general, more evidence is available to predict the effects of sedimentation on estuarine plants than on the fauna. Most of the evidence confounds the effects of sedimentation with water flow. This review is specifically applicable to sediment management schemes that affect the variables simultaneously.

Sedimentation during floods provides nutrients that make salt marsh plants highly productive. The floods also flush from the soils accumulated salts, which stimulate productivity in salt marsh plants (Zedler and Onuf 1984). This effect of sedimentation in the marsh is analogous to the classic fertilization by periodic floods of river bottom lands. The construction of the Aswan High Dam in Egypt illustrates the negative impact that flooding prevention can have on macrophyte productivity. Farmland along the Nile valley now requires fertilizing, which was unnecessary before dam construction (Baxter 1977).

The impact of sediments and the associated inorganic nutrients also provides a stimulus to estuarine and coastal phytoplankton productivity. After construction of the Aswan High Dam, the usual post-flood phytoplankton blooms disappeared, causing disasterous consequences to the economically important Sardinella fishery (Aleem 1972). Many estuaries suffer a nutrient overload from agricultural and industrial runoff and municipal sewage. The natural stimulus from nutrients associated with flood-borne fine sediments may not be needed. Estuarine nutrient levels need to be examined to assess the needs of each system for additional fertilization.

Sea grasses and macroalgae attached to the bottom suffer an initial decline in productivity during a flood due to the increased turbidity and decreased light penetration. In the deepest basins of shallow estuaries where sea grasses and macrophytes grow on the bottom, sedimentation from floods often causes burial and mortality of the plants. For those plants that survive, the input of new nutrients will stimulate higher productivity and growth.

Benthic microalgae show a similar response to sedimentation --- an initial reduction in productivity caused by turbidity followed by a large pulse of production stimulated by fertilization. The major effect from floods occurs via the alteration of estuarine sedimentary environments. The surface sediments will be enriched in fine particles, favoring those microalgae commonly associated with finer sediments. Is microalgal productivity in muds greater or less than its production in sands? The best available data reveal no significant variation in primary productivity of benthic microalgae with changing sediment grade (Shaffer and Onuf 1983). Nevertheless, this issue needs to be addressed with additional research.

Benthic Invertebrates

Research has assessed the impact of increased sedimentation on benthic invertebrates. Generally, suspension-feeding species in the benthos will suffer reduced growth and even mortality from increased inputs of fine sediments. The sediments clog their filtration apparatus (Rhoads and Young 1970). But deposit feeders benefit from the increase in fine sediments (Levinton 1972). And increased sediment inputs during floods can accentuate the stratification of the water column and enhance seasonal anoxia at the bottom of deeper estuaries (Copeland et al. 1974). The flood waters remain on top because fresh water is less dense than saline bottom waters. Increased turbidity reduces light penetration, and the consequent surface heating increases the temperature differential between surface and bottom, accentuating water-column stratification. This process increases the potential for widespread bottom anoxia in warm months in deeper estuaries. Bottom biological oxygen demand becomes greater than the resupply of oxygen from the stratified surface water (Tenore 1972). Fine sediments that settle during the floods increase the bottom biological oxygen demand more. The resulting anoxia, wherever it occurs, is widespread, meaning almost complete benthos mortality.

The drastic reduction in benthic invertebrate biomass is not necessarily detrimental to the estuary. After such a major disturbance, the bottom is quickly repopulated by dense settlements of opportunistic benthic species (McCall 1977). These opportunists may represent more abundant and available food supply for consumers than the long-lived "equilibrium" species they are replacing. The opportunists tend to be denser during early recolonization than the equilibrium populations. And as surface-dwellers, they do not have the protection from predators that depth of burial provides the equilibrium species (Rhoads et al. 1978). Furthermore, the opportunists allocate their energy toward rapid growth and reproduction rather than building structural or chemical defenses against predators (McCall 1977). The timing of floods, which usually occur in winter or spring, is also favorable for maintaining the valuable nursery functions of effected estuaries. Massive benthic mortality in winter or early spring leads to opportunist recolonization at a season (spring or summer) when juvenile predators are abundant in estuarine nursery grounds. This scenario of the impact of flood-borne sedimentation on benthos and the vital estuarine nursery functions needs rigorous testing in future research. But it is based upon the well-studied processes of benthic recolonization and succession.

Mobile Invertebrates and Vertebrates

We know very little about how increased estuarine sedimentation affects mobile invertebrates, such as crabs and shrimps. Multiple regression models of brown shrimp harvest in North Carolina suggest that heavy spring rains reduce brown shrimp catches (Frankenberg et al. 1980). Increased sediment delivery may be involved in this process. However, any reduction of freshwater flow, including methods designed to manage sediments, will induce saltwater intrusion farther up the estuary. And predators can penetrate farther into the estuarine nursery grounds, feeding on species such as brown shrimp that normally gain refuge by developing and growing in these low salinity areas. The best documented example of escape from predation is the increased survival of oysters in lower-salinity areas where its predator, the oyster drill (Urosalpinx), cannot survive.

We also cannot predict the effects of increased sedimentation on fishes and birds in the estuary. The negative effect of the Aswan High Dam on the catch of Sardinella (Aleem 1972) is obvious, but few other clear examples exist. One could argue that a reduction in turbidity would make feeding easier for a visually oriented predatory fish. But increased visibility would also help the fish's own enemies. Clearly, more research is needed to understand and predict the impact of varying sediment inputs on estuarine vertebrates. Because society places a high value on the fishes and birds of the estuary, research at this level is important.

THE CASE HISTORY OF MUGU LAGOON SEDIMENTATION

The work of Onuf (1984), Onuf and Quammen (1983) and Zedler and Onuf (1984) is the best case history for explaining how flood-borne sedimentation affects estuarine functions. This study of Mugu Lagoon is exemplary. Almost all estuarine biological components were studied simultaneously, and the study included two replicate flood events (in 1978 and 1980) with control years before and after each flood. The data on how flood-borne sedimentation affected birds and fishes is valuable in light of the dearth of similar information from other systems.

Rainfall data (Zedler and Onuf 1984) reveal extreme winters in 1978 and 1980 in Southern California. Rainfall levels recorded at the Mugu Lagoon weather station showed that the winter of 1978 was the second wettest in 113 years. Flow guages at Calleguas Creek showed correspondingly intense runoff during this winter and in 1980 winter. Because of a 1966 study into the morphology of Mugu Lagoon, Onuf (1984) was able to document the degree of sedimentation that occurred in these floods. In 1978, an average of 13 centimeters of fine sediments was deposited over the lagoon floor, and another 7 centimeters accumulated in the winter of 1980. The geomorphological consequence of this sedimentation reduced the low tide volume of water in the lagoon by 40 percent.

Onuf's (1984) data on plant productivity revealed a clear pattern. Microalgal productivity did not change after the storms, but chlorophyll pigment analyses suggested a taxonomic shift in favor of blue-green algae. The two predominant species of macroalgae, Ulva sp. and Enteromorpha sp., showed a large production increase after the storms. Salt marsh plants also exhibited a pulse of increased production during the growing season after the storms. Sea grasses suffered widespread mortality from burial, but subsequently regrew vigorously at new sites.

Several patterns were apparent in the benthic invertebrates reponses to the floods and sedimentation (Onuf 1984). The infauna, perhaps more intimately associated with sediments, responded to the storm and its sedimentation more than the epifaunal invertebrates. The smaller infaunal species were affected more than the larger ones. In the initial muddy lagoon areas, the infaunal community present before 1978 was replaced by opportunistic species (dominated by Pseudopolydora, Capitella and oligochaetes). The opportunists reached far higher densities than the original infauna. The benthos living along sandy bottoms was not greatly affected because the sediment did not remain at the surface long (Zedler and Onuf 1984). Higher current velocities over the sandy bottom and substantial reworking activities by abundant ghost shrimp, Callianassa californiensis, resuspended and buried the foreign sediments.

Beach seining at four sites every month for five years (Onuf and Quammen 1983) showed that total densities of fish and numbers of fish species were significantly lower in the major storm years than in preceding or succeeding years. With large changes in the surface sediments of Mugu Lagoon, one might expect the demersal fishes to decline more than the water-column species. But of the seven common demersal species, only one changed in abundance in a pattern consistent with this prediction. All three of the water-column species declined precipitously. Two factors contributed to this response: the 40 percent loss of water-column volume and the decline in sea grass.

Scientists monitored estuarine birds for five years at 24 sites every 20 days (Onuf 1984). The data was used to test the effects of the storms and sedimentation on the bird fauna (Onuf 1984). A total of 73 species was observed. During the five years that included the two major storms, the number of birds using Mugu Lagoon increased slightly. However, different guilds of birds reacted differently. Coots steadily declined by 59 percent over five years, while surface-feeding shorebirds increased by 96 percent. A redistribution of birds among the lagoon was evident. The central basin, which changed from open-water habitat to intertidal bottom, exhibited a four-fold increase in surface-feeding shorebirds. The shallower habitat created in the central basin also positively affected other guilds: the probing shorebirds, diving and wading fishers, mollusk-eating ducks, dabblers and coots.

In the eastern arm, the probing shorebirds and diving fishers showed significant population declines consistent with the decreases in invertebrates and fishes in that area. In summary, the geomorphological changes in the lagoon and the effects of sedimentation and storm floods on potential prey were important variables influencing the responses of estuarine birds.

SUMMARY RECOMMENDATIONS

This review concludes that the biological implications of varying sediment inputs into estuaries are not well-studied or easily predicted on the basis of available evidence. Many of the immediate effects of sediment delivery may enhance rather than harm the valuable functioning of the estuarine ecosystem. Studies of detailed sediment dynamics are necessary to predict, for each given estuary, whether increased sediment delivery increases sediment retention, causing the long-term filling and disappearance of estuarine habitat. Future efforts should identify the optimal balance between the long-term negative impacts of estuarine filling and the short-term positive stimulation of estuarine productivity. The optimum level of sediment input to estuaries is not necessarily the level that would prevail naturally. Varying coastal geomorphology and land use will cause the optimum to vary among estuaries. Identifying the optimal level of sediment input into an estuary will remain a challenge because of the confounding influences of freshwater flow. Nevertheless, the question is important for proper environmental management. The necessary interdisciplinary studies that meld sedimentology and estuarine biology should be a future research priority.

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DISCUSSION

W. GRAHAM: I would like to respond to Schubel's comment about national projects. Except for the greenhouse effect or projects where estuarine mixing is an important element, I think almost all environmental projects are local. They occur in a specific place. Whether it's New Bedford Harbor and PCB's or Times Beach, Mo., and dioxins.

I would argue that a national problem is nothing more than a collection of local projects. When they get to be large enough, people sit up, take notice and say, "We've got dioxins not only in Times Beach, but in a hundred local sites around the country." We've got PCB's in New Bedford Harbor, the Hudson estuary, or they say, Lake Michigan and other places. I think that the last people to perceive problems are the people in Washington. But they can perceive when a problem becomes nationwide because they get input from around the country.

Sea Grant research, NOAA research and other agency research will always be at some specific location addressed to some specific problem, because that's where the problem is. The question is how much of the research can you apply in other areas. And can we build on research rather than go reinvent the wheel for every site.

The question Peterson poses about an optimal sediment input is very important. A subquestion is: What is optimum sediment bypassing? The two are not necessarily the same. For example, an increase in sediment input to Chesapeake Bay would not measurably change the amount of sediment escaping the bay. But if you increase the sediment input to the Mississippi, you increase the amount that bypasses to the delta. It comes back to understanding an estuarine sediment system. You need to know if you change one part how it will affect the others.

I think the point is well taken about the Nile. I would add that we are making it habit around the world to eliminate or reduce the discharges of many rivers---small rivers in Indonesia to large rivers such as the Indus. The Indus now has an estuary only during the monsoon season. It has no discharge of fresh water to the Indian Ocean during the remainder of the year. And, as a result, they are losing about a hundred thousand hectares of mangroves every year. Their coastal fisheries have collapsed. Pollution problems in Kurachi and other ports have been aggravated seriously.

So, the right sediment input has many useful effects. And again, you have to understand the system. I think the questions that you asked are very good.

J. SHARP: I think that what has been said is correct and interesting. But I think there's another side of the sediment picture that hasn't been addressed here today. And, that is the effect of sediments on phytoplankton primary productivity in nutrient-rich estuaries. I would like to address them partly with the Delaware River estuary, but also with some of the concerns on the Chesapeake Bay.
There is a pronounced turbidity maximum in the Delaware estuary. This turbidity maximum is characterized by almost no primary productivity. There is productivity upstream and downstream. This is due to the fact that the attenuation of light is strongly related to the suspended sediment. There is a very pronounced relationship between suspended sediments in the Delaware and primary productivity.

One of the concerns in the Chesapeake Bay is that the bay is becoming more turbulent. This may have to do with the well-known reduction in overall primary productivity, in this case related to rooted aquatic vegetation.

My point is that suspended sediments in relatively nutrient-rich estuaries can have a dramatic effect upon primary productivity and productivity in the whole system. We do not have problems with the decline of rooted aquatic vegetation in the Delaware because the aquatic vegetation disappeared before recent recordings.

D. BOESCH: In your opinion, for the Delaware does turbidity result in a net decrease in the total system productivity or a shift of that productivity downstream?

J. SHARP: I think it's a shift at present. But what it is in the historical picture I don't know. We do not have hundreds of years of historical records to see if there is any decrease in productivity. Certainly there is a decrease in the number of things harvested from the Delaware and the Chesapeake. Whether this has anything to do with the decrease in primary productivity, I don't know.

H. PAERL: We can have two different situations, depending on the nature of the phytoplankton, that might respond to the sediment/nutrient-associated plumes. If the phytoplankton is buoyant, we could see situations, as in North Carolina, where phytoplankton responds positively to the nutrients carried by sediments. It turns out that those organisms are undesirable in a great many cases. So, I would argue that we should, at least in terms of research priorities, consider some of the biological ramifications before the engineering priorities. On dredging, for example, we have two different phytoplankton communities that respond differently to enhanced sedimentation and nutrient loading.

J. ZEDLER: I would like to challenge a responder and get a plug in for freshwater input research. Peterson talked about the stimulus vascular plants receive from sedimentation in Mugu Lagoon. I think some of the stimulus is due to sedimentation. But Chris Onuf and I have argued whether it's salinity changes or sediments that are responsible for the changes.

Experiments that we set up to desalinize the salt marsh soils in Southern California suggest that fresh water can cause the changes. The relief of stress in a hypersaline marsh sediment can stimulate productivity sufficiently. I don't think we need sediments and nutrients to cause the changes that occurred in Mugu.

C. PETERSON: I'll respond by apologizing to Joy for not mentioning that. All data from Mugu Lagoon, like all data sets one can find, confound the effects of sediment input and water delivery. Quite clearly, the desalinization of the soils is a stimulus to production of the halophytes. But it requires that experiments separate the confounding influences of fresh water and sediments/nutrient additions to identify what proportion of the effect can be ascribed to each variable.

I. VALIELA: We've done experiments in New England salt marshes to add nutrients over a number of growing seasons. Simultaneously in separate quadrants, we irrigated hectares of marsh with a nutrient solution in fresh water. For our experiments there was no effect of a freshwater addition by itself. The entire response was attributed to the nitrogen addition. The soil salinity was 32 parts per thousand, which may not be stressing the primary productivity.

J. ZEDLER: Our soils were more like 45 to 55 parts per thousand.

J. WEIS: I trust that the sediments washing into Mugu Lagoon are not contaminated. We had evidence of a storm event washing pesticides into an estuary, causing a reproduction failure in the fish populations we were studying. I trust there are no large amounts of agricultural development around Mugu Lagoon.

C. PETERSON: I was trying to pass that one off. Your trust may be misplaced. There's a tremendous amount of agriculture in the Oxnard Plain vicinity of Mugu Lagoon, where farmers cycle four crops a year through tremendous fertilizer use.

Some studies of toxicity and examinations of the sediment have been made in the Lagoon. There does not seem to be a large input of contaminants. But, I have not been involved in the study nor have I critically assessed the evidence. It could be a problem but the potential is certainly there.

N. ARMSTRONG: As sedimentation occurs, marsh habitat is created in open bay bottoms where, presumably, nutrient cycling is lost. Is this a net negative benefit or a net positive benefit?

C. PETERSON: I won't make a claim about that. I think that biological studies need to assess habitat management schemes. One can argue that the salt marsh is more important to maintain than other habitats. That has historically been argued, but it's been questioned recently for many reasons.

Data suggest that some algae are more utilizable, turn over more rapidly and do more for the higher trophic levels than the plants we protect in the salt marsh.

On the other hand, the salt marsh itself has high populations of benthic microalgae. The question of which is more important has not been answered to my satisfaction. I think shallow habitat is more useful for feeding shore birds than deep embayments. But I hesitate to argue which habitat is better or what the optimal mix of habitats might be in a system. I think that is an important area for future research to address.

J. SCHUBEL: If you look at most estuaries in this country, I think you would conclude that the net effects of man's activities have been to increase the sediment inputs, decrease the size and increase associated contaminants.

It is true that reservoirs, regardless of why they were constructed, trap sediment. For example, a reservoir that holds one percent of the annual river flow can trap up to 50 percent of the sediment that enters it, most of it in the bed load. A reservoir that holds 10 percent the annual river flow can trap up to 85 percent of the sediment that the river carries. A reservoir along the lower Susquehanna River accumulated sediment for decades. During Hurricane Agnes it purged about fifty years of sediment.

Over longer periods of time, it is clear that the activities of man increase sediment inputs to estuaries. And, as I mentioned before, we haven't seen what's to come. For example, it is estimated that 90 percent of the sediment released since 1700 in the Southern Piedmont is in storage above the fall line. It hasn't even gotten to the fall line yet, let alone into the estuaries. We will have many interesting problems confronting us.

Except for the Mississippi, most of us don't know what sediment loads are like in this country. I spent years studying the Susquehanna River, which is the largest river discharging into the Atlantic Ocean through the continental East Coast of the U.S. It discharges almost a million tons of sediment a year. Every day the Yangtze discharges as much sediment as the Susquehanna does in an entire year. The Yellow River discharges over a billion tons.

These estuaries were formed less than 10,000 years ago at the same time Chesapeake Bay and the Mississippi were formed. The Yellow no longer has an estuary. Even during the dry season, the river flow in the Yellow prevents sea water from encroaching into the basin.

During periods of low river flow, the Yangtze has an estuary several tens of kilometers long. That's how far salt water will penetrate. Now, the tidal effects in the Yangtze will go upstream 800 kilometers. About 2500 years ago, the Yangtze had a magnificant estuary--large, relatively deep and broad. It has been filled in over time with sediment. Is it good or bad? I don't know.

F. CHRISTHILF: This question is directed to Dr. Schubel. Much of the discussion about sediment seems to be related to man's activities, such as building dams and reservoirs. The Yangtze and Yellow River examples are in a country that is, in our estimation, underdeveloped. It seems to me that on the one hand we're saying what we're doing to estuaries causes problems. On the other hand, estuaries that have little interference from man have bigger problems. I just want to reconcile that in my mind.

J. SCHUBEL: The Chinese estuaries have large problems associated with sediment input. They also have serious problems associated with the contaminant inputs.

We talk about the depth of the euphotic zone and what levels of suspended sediment do to that. On a good day, when concentrations of suspended sediment in the Yangtze are low, the depth of the euphotic zone might be 10 centimeters.

I'm not sure how to answer your question, Frank. In developed countries we are doing a better job of controlling sediment inputs to estuaries than in developing countries. It is also true that levels of associated contaminants are higher in developed countries than they are in developing countries. That's not surprising. But those two things have to be kept in mind.

One other interesting situation is in Chili where they have magnificant estuaries. Their sediment inputs have been largely the result of deforestation without replanting. The coastline is near the Andes so the gradients are steep. If you release sediment, it moves down into the estuary in just a few years. As much as one meter of sediment per year accumulates in their estuaries because of deforestation. Many estuaries are almost gone, but there are still coastal embayments.

NUTRIENTS AND OTHER CHEMICAL INPUTS

NUTRIENTS IN ESTUARIES---RESEARCH DIRECTIONS AND PRIORITIES

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OUTLINE

1. We start with two observations:

   a) Most of the human population of the United States is concentrated around estuaries and along the coast. Projections are that by 1990, 75 percent of the populations of this country will live within 50 miles of the oceans or Great Lakes.

   b) There has been an exponential increase in the use of inorganic fertilizers in the United States since about 1880. Farmers are now putting about 1,000 times more nitrogen on their fields than they were 100 years ago. Compounding this trend has been the large-scale conversion of wetlands, which served as nutrient and sediment sinks, into agricultural land.

2. As a result of the above, we assumed that the amounts of inorganic, and perhaps organic, nitrogen and phosphorus carried by streams and rivers to the estuaries increased markedly. However, the lack of adequate long-term data makes it difficult to know if this is true or to make a quantitative assessment of the increase in loading over time. Moreover, the great costs of removing nutrients from sewage effluent and of controlling runoff from fields suggest that nutrients will continue to be a major anthropogenic input to estuaries and coastal waters.

3. Most of our knowledge of the effects of nutrient enrichment on marine ecosystems is based on laboratory studies of algal cultures or on short-term experiments involving nutrient additions to plankton communities. Nevertheless, it has been established that recycled nutrients supported much of the primary production of coastal systems, and that the role of the benthos in this cycling was

very important. We know little about how marine ecosystems respond to nutrient additions. How do recycling rates vary with the total amount of nutrients in a system? How do the standing crops of primary producers change in magnitude and variability of nutrient enrichment? How does the species composition (and size distribution, nutritional quality, etc.) of phytoplankton, microzooplankton and zooplankton change in more enriched systems? How is the enhanced primary production partitioned between pelagic and benthic communities? Is secondary production increased proportionally to primary production? Can nutrient additions alone increase total system metabolism to the point where anoxia develops? How does nutrient enrichment interact with organic toxins, heavy metals, etc.? How do plankton-based systems compare with macrophyte-based systems in regard to the above? None of these questions can be answered adequately with our present knowledge.

4. Field data can be helpful in addressing questions such as these. But problems of spatial and temporal variability; lack of control; and the inputs of fresh water, sediment and pollutants often associated with nutrients make it difficult to develop convincing evidence.

5. If marine ecology is to advance beyond quantitative natural history and provide information that is useful in protecting and exploiting coastal resources, it must develop ecosystem-level experiments involving microcosms, mesocosms and field manipulations. Marine science is behind limnology and terrestrial ecology in this regard, and we can learn from the experiences of others. Within marine ecology, three of the most exciting recent developments involved nutrient addition experiments to salt marshes, high salinity plankton-dominated mesocosm tanks, and shallow brackish ponds dominated by macrophytes. Experimental research of this kind can yield more information for a given investment than the traditional academic science based on individual isolated initiatives. The challenge to universities and researchers is to develop focused and

integrated multidisciplinary research programs to carry out ecosystem-level experiments while fostering, maintaining and rewarding individual creativity, independence and quality. The challenge to the funding agencies is to assemble a large enough support base to make such research practical and to provide the stability of funding for long-term study.

TOXIC CHEMICALS AND BIOLOGICAL DAMAGE IN ESTUARINE SYSTEMS: RESEARCH FINDINGS AND PERSPECTIVES

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INTRODUCTION

We agree with almost all of the positions taken by Scott Nixon, including his challenges to researchers and funding agencies. He has properly identified problems of estuarine viability as primarily "people" problems. Human populations around estuaries and along the coasts are increasing steadily and the attendant discharges of wastes and other activities will impose additional stresses on nearshore aquatic ecosystems.

Despite this general accord, we seriously disagree with Nixon on matters of emphasis. Certainly, increased inputs of nutrients in estuaries represent major concerns. However, a concept that nutrient loading is the predominant chemical perturber of estuaries is not defensible, in our view, with present knowledge. Yet an impression of the overriding, primary importance of nutrient loading certainly would be a salient point gained from Nixon's paper and from the title of this session. We see no challenges issued, for example, concerning the host of synthetic organic chemicals and metals that presently are found in estuaries; this is a serious omission.

In this presentation, I will make the point that several types of xenobiotics are of concern to estuarine viability, and I will discuss the implications and make recommendations.

ANTHROPOGENIC CHEMICALS IN ESTUARIES

Several published estimates suggest 70,000 synthetic chemicals are currently in commercial use and 1,000 new ones are synthesized each year.

Many of these chemicals eventually enter estuaries and other environments. Obviously it is not possible to analyze environmental samples for more than a fraction of the chemicals because of limited resources and limitations imposed by the state-of-the-art of analytical chemistry. Many persistent chemicals eventually wind up in bottom sediments, which may serve as long-term repositories or as sources for recycling. Numerous studies showed that sediments are major reservoirs for pollutants. For example, one sediment sample from the Hudson-Raritan Estuary in New York contained 180,000 parts per billion of aromatic hydrocarbons (AHs), including 5,600 parts per billion and 1,300 parts per billion of the carcinogens benz[a]anthracene and benz[a]pyrene (MacLeod et al. 1981). In other examples, the mean concentration of PCBs in sediments near a Los Angeles sewer outfall was 3,400 parts per billion (Young and McDermott 1976) and mean concentrations of lead, mercury and cadmium in Newark Bay sediments varied from 7,000 parts per billion to 400,000 parts per billion (Meyerson et al. 1981).

We have been investigating pollutants, their fates and effects in Puget Sound (Fig. 1), a major West Coast estuary, for about 10 years. Approximately 2 million people live in the greater Puget Sound area and the eastern shore is highly industrialized. Seattle, Tacoma and Everett are industrial centers. Commencement Bay (Tacoma) was designated by the U.S. Environmental Protection Agency as one of 10 most hazardous waste sites in the United States. In addition, health officials from three counties issued advisories warning against consumption of fish and shellfish from the most contaminated portions of Commencement Bay, Elliott Bay (Seattle) and Port Gardner (Everett).

As part of our studies, we extensively collected and chemically analyzed sediments and bottom-dwelling fish from various urban and non-urban embayments of Puget Sound (Fig. 1). Fish also were examined for grossly and microscopically visible abnormalities. Urban embayments investigated were Elliott Bay, Commencement Bay, Budd Inlet (Olympia), Sinclair Inlet (Bemerton) and Port Gardner. Non-urban reference areas studied were Case Inlet, Port Madison and Port Susan --- all within Puget Sound;

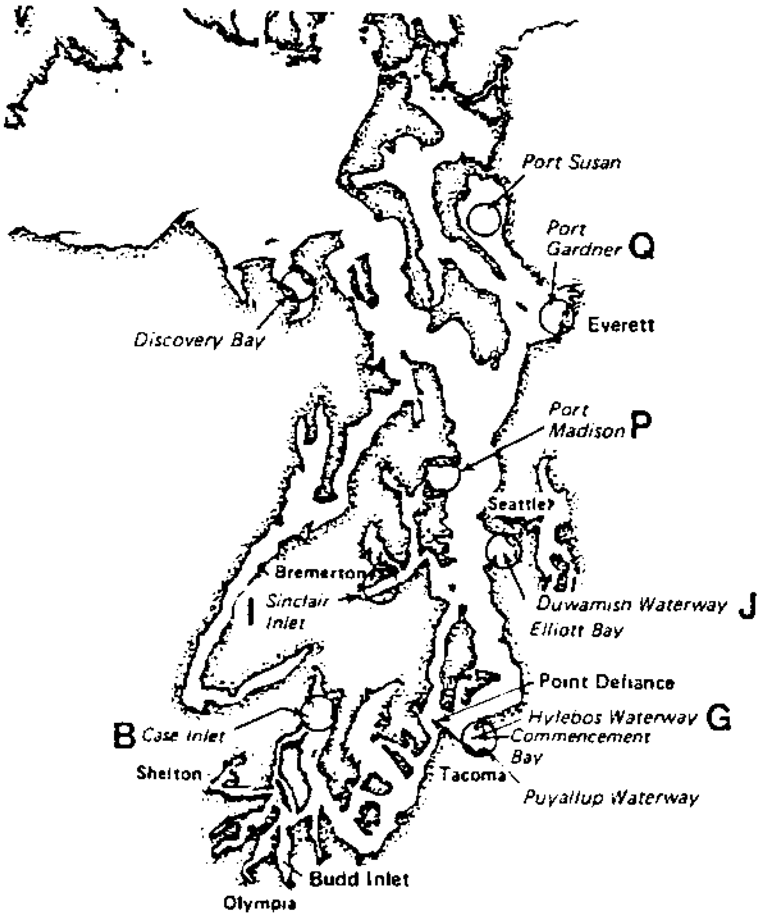


Figure 1: Map of Puget Sound, Washington, showing selected urban (G, I, J, Q) and non-urban (B, P) study areas.

and Discovery Bay --- just outside the northern entrance to the sound.

We found that a diversity of chemicals were present in Puget Sound sediments (Malins et al. 1982, 1984). For example, in Commencement Bay over 900 individual organic compounds were detected--more than 500 aromatic hydro, hundreds of chlorinated hydrocarbons, and various bromine-, sulfur-, nitrogen- and oxygen-containing compounds. The numbers and identities of these compounds have not been determined fully because of the complexity of the chemical mixtures. Mean concentrations of aromatic hydrocarbons in sediment of four of the major urban embayments (Fig.2) were as much as 46 times the mean concentration (280 ppb) of aromatic hydrocarbons in sediments from non-urban embayments. Within urban embayments the values varied greatly (e.g., 150 ppb to 63,000 ppb in Elliott Bay sediment samples). Sediments with the highest concentrations of aromatic hydrocarbons also had the highest concentrations of certain carcinogens, including benz[a]anthracene (7,600 ppb) and benzo[a]pyrene (2,400 ppb).

Chlorinated organic compounds --- including PCBs, hexachlorobenzene, and a number of chlorinated butadienes and pesticides --- were found in almost every sediment sample, with the concentrations usually higher in urban sediment samples (Fig.2). The concentrations of several metals with well-known toxic properties (e.g. arsenic) were consistently higher in urban than in non-urban areas. However, the concentrations of cadmium were similar in urban and non-urban embayments (Fig. 3).

Fish and marine invertebrates accumulate many of the chemicals from polluted environments. Skeletal muscle of striped bass (Morone saxatilis) from the Hudson River contained 13,000 parts per billion to 54,000 parts per billion of PCBs (Meyerson et al. 1981) and bottom fish from near Los Angeles contained 3,200 parts per billion to 12,000 parts per billion PCBs and 78,000 parts per billion to 270,000 parts per billion DDE (Gossett et al. 1982). In our Puget Sound study, the mean concentration of PCBs in the muscle of English sole (Parophrys vetulus) from an industrial area of Elliott Bay was 4,800

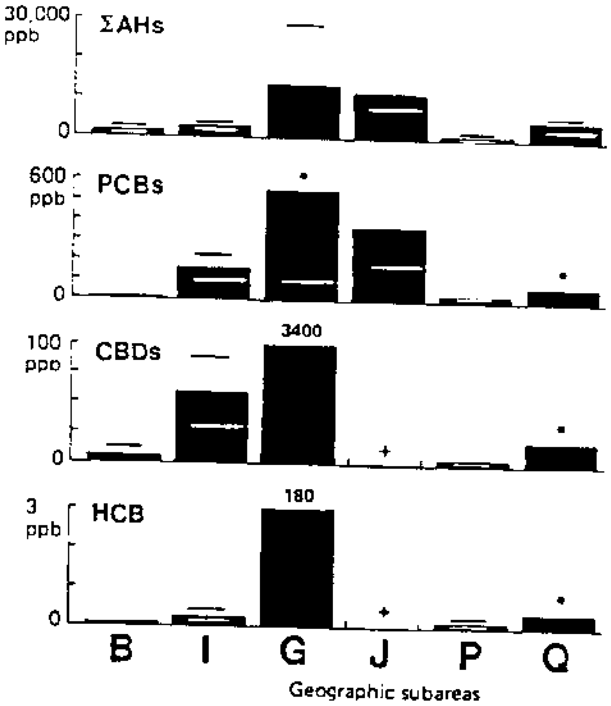


Figure 2: Concentrations of organic chemicals in sediment samples from selected urban and non-urban areas of Puget Sound. The term AHs represents the summed concentrations of 25 individual aromatic hydrocarbons. Concentrations below the limits of detection are denoted by "+". "*" denotes that PCBs were not quantified in certain sediments from Subarea G and Q because of interferences from other compounds. It is noteworthy that an especially large number of organic xenobiotics in extracts of Everett Harbor [Q] sediments could not be identified because they appeared in gas-chromatographs as myriad individual peaks super-imposed on a large unresolved envelope.

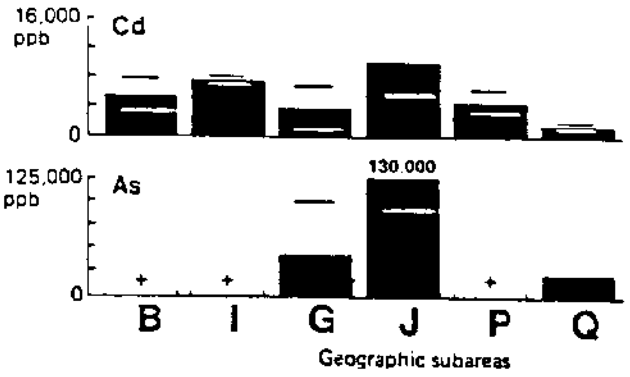


Figure 3: Concentrations of cadmium and arsenic in sediment samples from selected urban and non-urban areas of Puget Sound. Concentrations below the limits of detection are denoted by "+".

parts per billion (Malins et al. 1984). In contrast, studies in Southern California, New York and Puget Sound reported that metal concentrations generally were not elevated in demersal fish from urban compared to non-urban coastal marine environments (Young 1982, Sherwood 1982, Malins et al. 1984).

PATHOLOGICAL ABNORMALITIES IN BOTTOM-DWELLING FISH FROM POLLUTED ESTUARIES

Pathological conditions have been observed worldwide in marine fish from polluted coastal waters and estuaries. These apparently pollution-related conditions include (but are not restricted to) fin erosion (Sherwood and Mearns 1977) and a number of pathological conditions of the liver (e.g. hepatic neoplasms) (Falkmer et al. 1977; Pierce et al. 1978; Smith et al. 1979; Harshbarger 1981; Baumann 1982; McCain 1982; Black 1983).

In the Puget Sound studies (Malins et al. 1980, 1982, 1984) we examined three species of demersal fish for histopathological conditions: English sole, rock sole (<u>Lepidopsetta bilineata</u>) and Pacific staghorn sculpin (<u>Leptocottus armatus</u>). The organs of these fish with the greatest numbers of lesions were the liver, kidney and gills. Some lesions were apparently associated with infectious agents, whereas others had no such association and were of unknown cause (idiopathic). Idiopathic lesions (four major histopathological categories) were detected most frequently in the liver. Hepatic neoplasms were observed, with only a couple of exceptions, in fish from urban areas and not in fish from non-urban areas. The highest prevalences of hepatic neoplasms were in English sole from the Duwamish Waterway in Seattle, 8.2 percent (n=537), and from Everett Harbor, 12 percent (n=66). The major types of hepatic neoplasms were hepatocellular carcinomas and adenomas (Fig. 4).

RELATIONSHIPS BETWEEN POLLUTANTS AND ABNORMALITIES IN FISH

Two lines of indirect evidence suggest that the four major types of liver lesions in the three targeted demersal fish species from Puget Sound

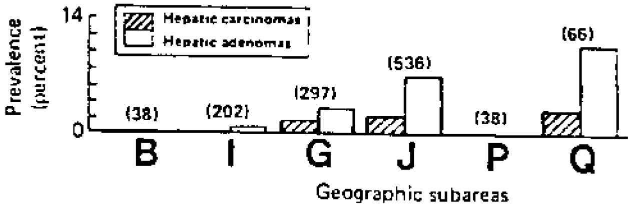


Figure 4: Prevalences of the major types of liver neoplasms in English sole from selected urban and non-urban areas of Puget Sound.

are causally related to xenobiotics. These are: (a) the highest prevalences of the lesions were found in the highly contaminated portions of the urban embayments and (b) these types of lesions occur in laboratory animals exposed to toxic and/or carcinogenic chemicals (Beliles 1975).

In an attempt to better explain relationships between chemicals and disease, we investigated whether certain groups of chemicals in sediments were correlated with prevalences of hepatic lesions in fish. We did not attempt a similar correlation analysis between tissue levels of chemicals and lesions. We and others have found that body burdens of certain organic chemicals do not directly reflect exposure, apparently because they are metabolized by the fish.

Table I illustrates the results of a representative mathematical/ statistical analysis we employed in comparing chemicals in sediments with lesion frequencies in English sole taken from the same areas as were the sediments. As indicated, the prevalences of hepatic neoplasms and various non-neoplastic liver disorders were positively correlated ($P \leq 0.003$) with sediment concentrations of aromatic hydrocarbons and metals (Malins et al. 1984). Surprisingly, statistically significant correlations were not obtained between chlorinated organic compounds and total hepatic lesions in this species.

CONCLUSIONS, IMPLICATIONS AND RECOMMENDATIONS

It is increasingly evident that urban-associated estuaries may contain thousands of anthropogenic chemicals. Evidence is also increasing that serious, pollutant-related pathological conditions, including neoplasia, exist in demersal fish species indigenous to these areas. These findings exemplify that the effects of chemical inputs into estuaries and coastal areas are important problems. The overall viability of an estuary is related to a host of variables, and it approaches absurdity to attempt to deal with any one in isolation. This point can hardly be overemphasized. In this context, J. W. Hedgpeth (1978) said that discussions of needs of marine ecosystem research "brought to mind the old story about the blind men trying to visualize an

TABLE I

Spearman's rank correlation coefficients (r_s) and significance levels for prevalences of hepatic lesions in English sole and concentrations of chemical groups in bottom sediment.[1,2]

Lesion Type	Chemical Group	r_s	Significance Level
Total hepatic lesions	AHs metals	0.58 0.54	0.001 0.001
Neoplasms	AHs	0.48	0.003
Megalocytic hepatosis	AHs	0.54	0.001

[1] Chemical groups were selected by factor analysis and the four principal groups were dominated by aromatic hydrocarbons, metals, selected metals plus PCBs, and chlorinated compounds, respectively. Tests were performed to detect all correlations between the lesion types and the four chemical groups; those not listed were not significant at the ≤0.003 level. A significance level of ≤0.003 was used in order to compensate for the number of bivariate statistical tests (16) performed for each comparison .

[2] Taken from Malins et al. 1984.

elephant from a disconnected set of tactile impressions." He summarized, "The lesson of the blind man and the elephant is that the whole is greater than its parts and that a complex, most improbable animal like the elephant cannot be visualized as a summary of its parts. Even with 20-20 vision, one cannot see all of the animal, especially what is going on inside." The analogy for marine ecosystems is not perfect. But it does illustrate the complexities involved and how we never will have in the foreseeable future the definitive answers some appear to be demanding by next Thursday.

In the face of these complexities and problems, what are truly viable research and managerial strategies? In managing marine environments, we have no alternative but to deal with individual, identifiable, manipulable parameters. At the same time, we should never lose sight of broader perspectives. Therefore, we need research strategies that account for important individual variables and the interactions of these variables. Optimizing the success of such an approach mandates use of interdisciplinary research and of appropriate computer-based model systems. We have diagrammed in Fig. 5 a protocol for relating marine xenobiotics to biological effects, which illustrates the approach we are attempting. An example of a relevant model system is shown in Fig. 6.

Obviously, all will not be made well in this imperfect world simply by following a certain protocol. Limitations of analytical chemistry, the horrendous variability in bioassay results and the inability to interpret or generalize the results, plus many other limitations and problems, tell us that more fundamental research also is needed.

In summary, and accepting the risk of banality, we reiterate premises that we and others have previously emphasized. These include: 1) that, for the present, environmental managers will have to base directions on mostly provisional data; 2) that the viability of marine ecosystems, and particularly those of estuaries, is modified by composite, variable parameters that include nutrient and xenobiotic inputs; and 3) that much

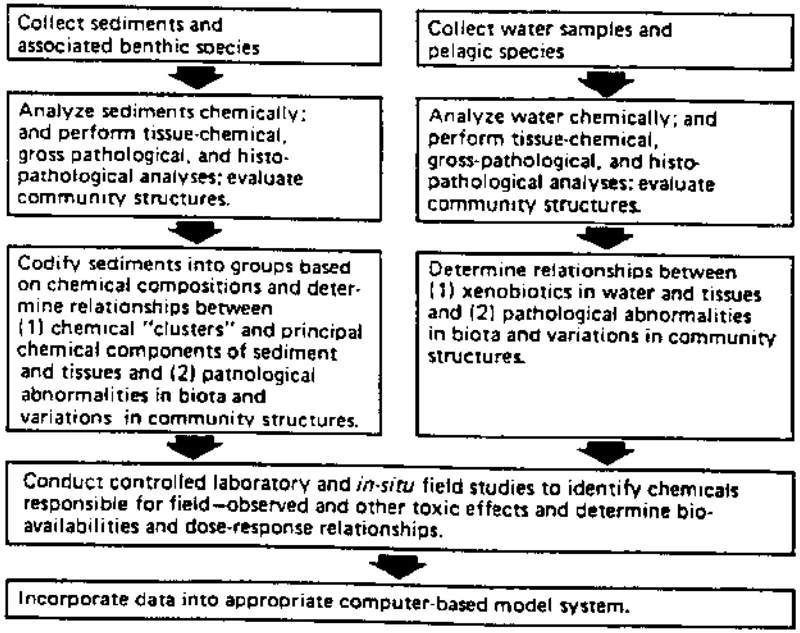
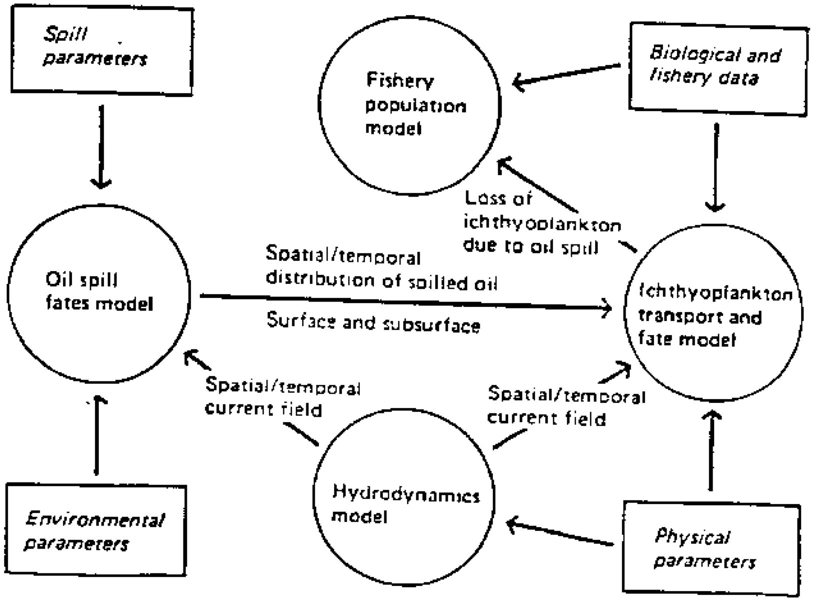


Figure 5: Protocol for relating marine xenobiotics to biological effects.



From Applied Science Associates, Inc., Wakefield, RI

Figure 6: An oil spill - fisheries impact model (Applied Science Associates, Inc. Wakefield, RI).

more needs to be done to advance methodology and enlarge credible data bases.

Nixon made telling points in his calling for "focused and truly integrated multidisciplinary research programs" rather than traditional science based on "individual isolated initiatives," and in his challenge to funding agencies to provide adequate, stable funding for "the long-term study that is needed." We completely concur.

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THE ROLE OF WETLANDS IN NUTRIENT CYCLING IN THE GREAT LAKES REGION

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INTRODUCTION

The Great Lakes coastal marshes are not true estuaries, but for purposes of this symposium they can be considered as analogs of estuaries appearing in these inland freshwater seas. They occur mostly as drowned river mouths or are associated with drowned river mouths. The marshlands are not subjected to significant daily tides, but effects are seen from the flushing action of seiches and episodic floodings. We have elected to discuss this topic because it relates to research on river systems that feed nutrients and chemicals to these marshes, research on artificial enrichment of aquatic systems, long-term data bases on the Great Lakes, and recent studies on the coastal marshes.

It is a curious human phenomenon that engulfs us when we come face to face with our peers to discuss what we know. Often we begin by admitting that we don't know all that much and that we lag behind related disciplines. In the challenge paper, Scott Nixon states that marine ecology must advance beyond quantitative natural history by carrying out ecosystem-level experiments, and that marine science is behind limnology in that regard. Actually, it is the reverse. We feel that we are just starting on coastal marsh studies that rival some of the salt marsh studies reported by marine ecologists. Nixon also made us a bit paranoid by the summary of his review of 20 years of research on salt marshes (Nixon 1980). He challenges us to maintain our credibility as scientists by paying close attention to the "minute particulars," and to be aware of self-deception. While we advance our knowledge by the "minute particulars," it is useful to step back at times, and see how much of the puzzle we have assembled. Thus the attempt here is to look at this subject from a few broad concepts, then see what pieces are still missing.

RESPONSE TO THE CHALLENGE

It is agreed that the input of nutrients and other chemicals to coastal marshes will continue to increase as do population and crop production. Attempts are being made to make fertilizer applications and irrigation more efficient (National Research Council 1982). However, at the same time, supplemental irrigation is increasing (Bartholic 1982). As more lands are brought into crop production, more fertilizer and chemicals will be used.

Adequate long-term data to document the above generalizations is not available. But in some cases, the historical data are available. Vannote (1961) established the annual input of nutrients by tributaries to the Red Cedar River. Municipal waste water treatment plants have improved, yet recent studies (Mattingly et al. 1981; Burton and King 1983) show similar nutrient loads in the Red Cedar River mainstream as in 1960. It appears that greater nutrient reductions by treatment plants have been offset by increased population and agricultural use of fertilizers (Burton and King 1983). Vannote's study should be repeated to address the speculation. Other situations like this must exist where early nutrient budget studies could be repeated to determine nutrient changes and causes of the changes.

More recent studies sponsored by the International Joint Commission (1978), verify the great input to the Great Lakes of phosphorus from cropland. In the case of Lake Michigan, cropland accounts for only about 12 percent of the watershed area, but contributes over 60 percent of the phosphorus load (Figure 1). Prior to upgrading our waste-water treatment plants to remove phosphorus, a much larger percentage of the phosphorus load came from urban areas (Waybrant 1971). Thus, as the challenge paper implies, we have made headway in controlling the point sources, but we still must contend with the non-point sources of nutrients.

Nutrient dynamics in coastal marshes have been and are being studied. Many questions posed in the challenge paper on nutrient cycling, response of these systems to nutrient additions, community

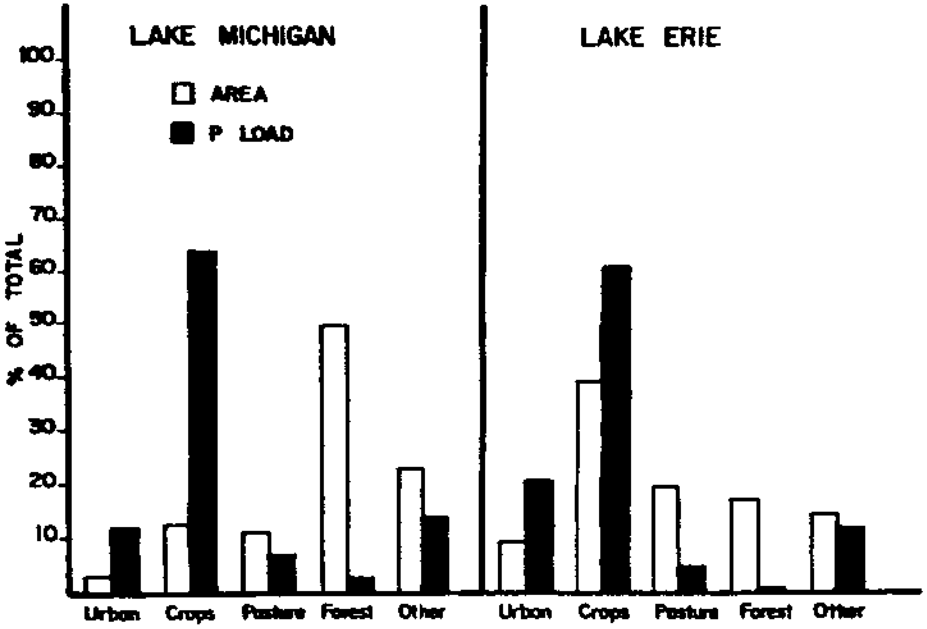

FIGURE 1

composition changes, primary-secondary productivity interactions, nutrient-metabolism responses and others have some answers in existing data. But much of it is in scattered, unrelated sources and awaits integration by motivated, broad-thinking ecologists. We need more integrative reports that pull together the "minute particulars" into meaningful concepts and principles.

CONCEPTS

Nixon (1980) reviewed many research publications and concluded that coastal marshes were not the great nutrient scrubbers and sinks that many of us would like to have protectionists believe. The reality is that episodic events, recycling patterns and equilibria situations, tend to be the dominant conditions.

In the early days of the Oak Ridge National Laboratory, a dam was constructed on White Oak Creek that received some liquid low-level radioactive wastes. The intention was that impounded waters would allow the radioisotopes to settle out, adsorbed to the sediments or taken up by aquatic vegetation. This was only partially accomplished since sediments eventually equilibrated with water concentrations, and radioisotopes incorporated in plant tissues were recycled. Most of the chemicals continued to flow over the dam.

Studies in the late 1950s and early 1960s on the Red Cedar River in south central Michigan revealed that floods were significant to nutrient loading and transport in the stream (Ball et al. 1968). The concentration of inorganic nitrogen increases dramatically (Figure 2) with the increase in stream discharge (Brehmer 1958). Thus, there is a multiplying effect on the transport of nitrogen. On an annual basis, the majority of the load moves downstream a small percentage of the time. In 1957 and 1958, three floods with a total duration of 31 days (Figure 3), transported about 45 percent of the total annual phosphorus load (Grezenda 1960). Kevern (1961) reported on phosphorus associated with drift of suspended particulate matter in the Red Cedar River. According to his report, 89 percent of the annual load of phosphorus incorporated is transported in

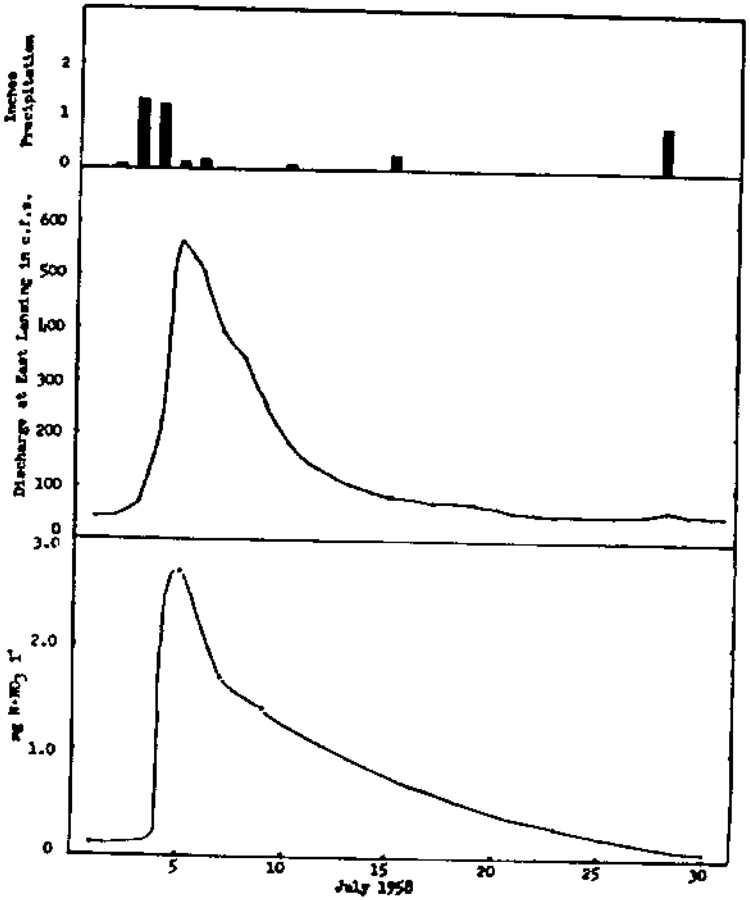

FIGURE 2

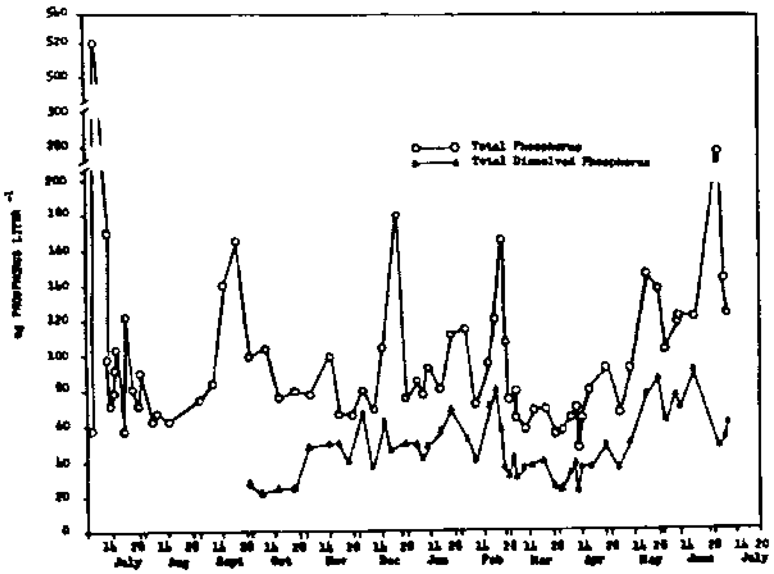

FIGURE 3

less than 60 days. Vannote (1961) studied the phosphorus-discharge relationship for non-urban tributaries of the Red Cedar River and found a strong positive correlation (Figure 4).

All of this indicates that a significant portion, if not the majority, of the nutrient load moves into and probably through the coastal marsh in a relatively short time. While flood waters slow when entering the coastal marsh and heavier sediments settle out, observation of great, dark plumes moving into the main lake body indicate that the majority of the material is passing through the marsh. In the Great Lakes region, peak stream and river discharges often occur in the spring due to snow melt and spring rains. At this time, vegetative cover in marshes and wetlands is reduced; therefore, spring runoff and its large sediment and nutrient load move rapidly through these systems. However, data collected from Pentwater Marsh, a coastal riverine marsh on Lake Michigan, indicate that during periods of high flows in mid-summer, suspended solids are effectively removed as the water moves through dense vegetation in the marsh. Also, during flow periods in the summer, the suspended solids output from the Pentwater Marsh is sometimes higher than the suspended solids input (Kelley and Burton unpublished data). This may result from export of algae or detritus produced in the marsh. Over the long-term, we have watched the Great Lakes gradually increase in total dissolved solids (Figure 5; Beeton 1969). Lake Michigan, in this instance, has a huge volume, and the increase in total dissolved solids represents a great input over the years. Either the marshes are not very good sinks or we need many more of them. The overall evidence is that our coastal Great Lakes marshes are not significant sinks, at least relative to the total sediment and nutrient loads that move or recycle through them.

NUTRIENTS AND WETLANDS --- GREAT LAKES REGION

Research on nutrient cycling and nutrient budgets in riverine marshes in the Midwest region is very limited (see review by Burton 1981). Conclusions drawn from these studies on the overall role of wetlands in nutrient removal are suspect, since they are based primarily on input-output concentrations unweighted for hydrologic inputs

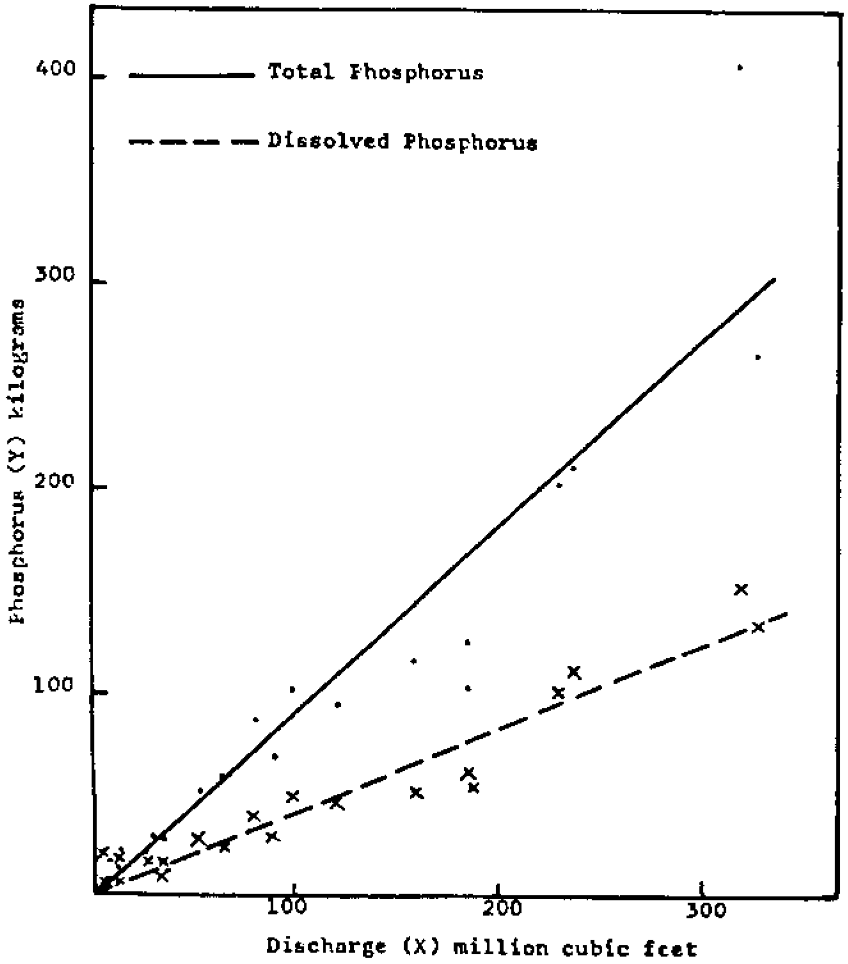

FIGURE 4

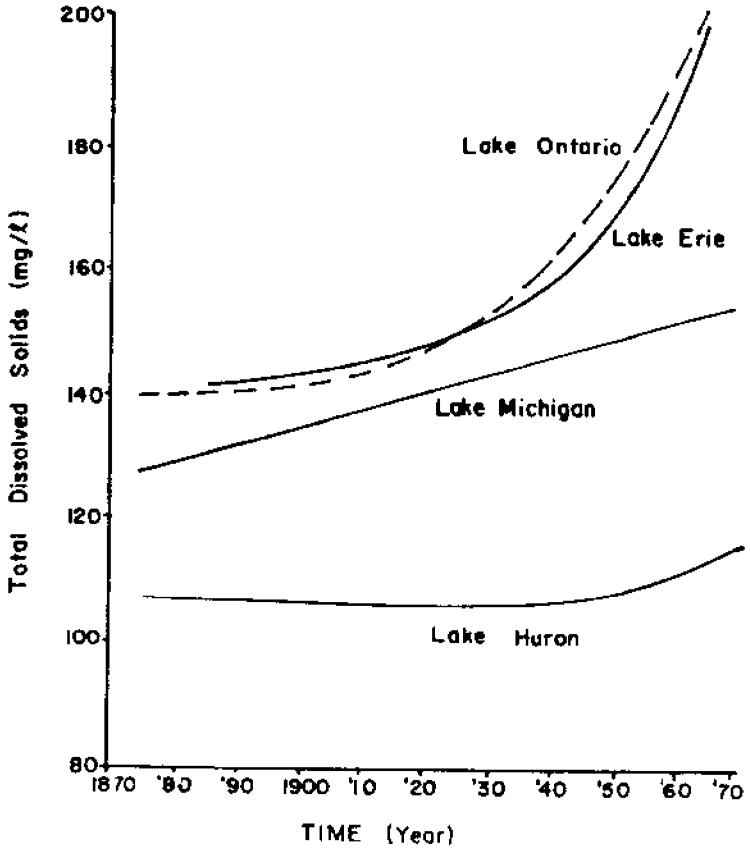

FIGURE 5

and outputs (Klopatek 1975, 1978; Lee et al. 1975; Petter et al. 1978). The general pattern in these studies is for nitrogen and phosphorus to be incorporated into the vegetation in summer, stored in the fall, then released from the wetlands during spring runoff (Burton 1981).

Currently, research is being conducted at Pentwater Marsh in Michigan by Tom Burton and his graduate students. This study may be the first attempt at a complete input-output sediment and nutrient budget for a riverine marsh in the Great Lakes region. Unfortunately, analysis of initial data from this project is not complete. Therefore no definite conclusions can be drawn at this time. Preliminary analyses suggest Pentwater Marsh has only subtle influences on the total nutrient and sediment load passing through the system. However, significant seasonal influences may occur (Kelley and Burton, unpublished data).

NITROGEN

It is generally believed that most wetlands serve as overall sinks for nitrogen and phosphorus. Wetlands serve as sinks for nitrogen by two basic means. Nitrogen may be deposited and buried in the sediments, or it may be transformed in the wetland resulting in nitrogen loss to the atmosphere (Figure 6). Wetlands also may contribute to nitrogen increases in aquatic ecosystems through nitrogen fixation. Nixon (1980) reviewed the salt marsh literature, and from the limited data available, it was difficult to determine the relative importance of nitrogen fixation, denitrification and burial in the nitrogen cycle. Conclusive data from freshwater wetlands are also lacking.

Although measurements of denitrification are scarce in wetland and estuarine literature, this pathway is commonly mentioned as a significant means of nitrogen loss. Another potentially important pathway for loss of nitrogen from aquatic systems is through ammonia volatilization to the atmosphere (Figure 6). This process has received little attention from either freshwater or marine scientists. Research conducted at the Water Quality Management Facility (WQMF) at Michigan State University over the last eight years provides evidence of significant losses of

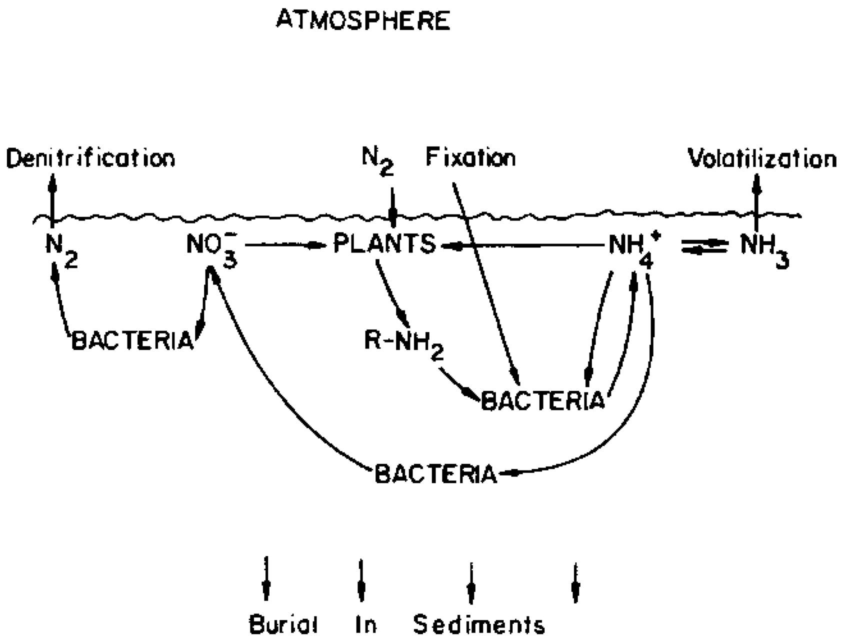

FIGURE 6

General nitrogen cycle in aquatic ecosystems.

nitrogen by ammonia volatilization from wetlands under certain conditions. The "wetlands" in this research consist of four interconnected shallow ponds (2 m deep), to which nutrient-rich secondary wastewater was added at a rate of 0.5 million gallons per day.

The average total nitrogen concentration of water as it flowed through the ponds is shown in Figure 7. As explained by King (1978), nitrogen is taken up by dense growths of submerged macrophytes and algae in the ponds and rapidly cycled through bacterial decay of plant biomass. This results in considerable ammonia production. Under elevated pH levels commonly maintained in these highly productive ponds, NH^+_4 is quickly converted to ammonia gas (NH_3) and lost to the atmosphere (equation 1). The pK of this equilibrium is about 9.2 at summer temperatures (Bates and Pinching 1950).

$$NH^+_4 \rightleftharpoons \overset{\text{ATMOSPHERE}}{\overset{\upharpoonleft\downharpoonright}{NH_3}} + H^+ \qquad \text{(equation 1)}$$

While the WQMF ponds received elevated nitrogen inputs in the influent water (Figure 8), there was production of high concentrations of ammonia from the deterioration and bacterial decay of a dense macrophyte and acriphyton standing crop in pond 4 (Spencer 1981). This ammonia would also be subject to volatilization losses.

Using mass balance data based on inputs and outputs of nitrogen, King (personal communication) calculated that 16.3 mg $N/m^2/hr$ was lost from pond 1 during August 1977. The pH of pond 1 ranged from 8.65 to 10.3 during this period. Galloway (1980) predicted a loss of 15.6 mg $N/m^2/hr$ over the same period due entirely to ammonia volatilization. His prediction was based on an empirical model considering pH, ammonia concentration, temperature and windspeed. Thus it appears that ammonia volatilization accounted for about 95 percent of the 16.3 mg $N/m^2/hr$ lost during this period.

Two other potential mechanisms involved in loss of nitrogen (Figure 6) are net accumulation of nitrogen in plant biomass and denitrification. During 1976, a vigorous plant harvesting program

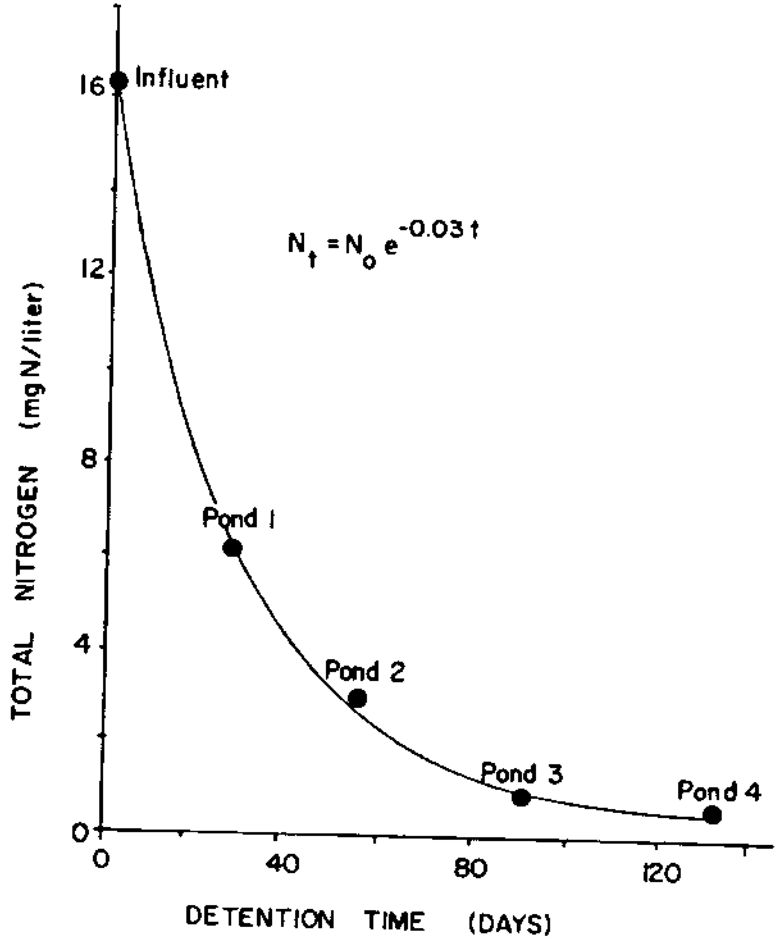

FIGURE 7

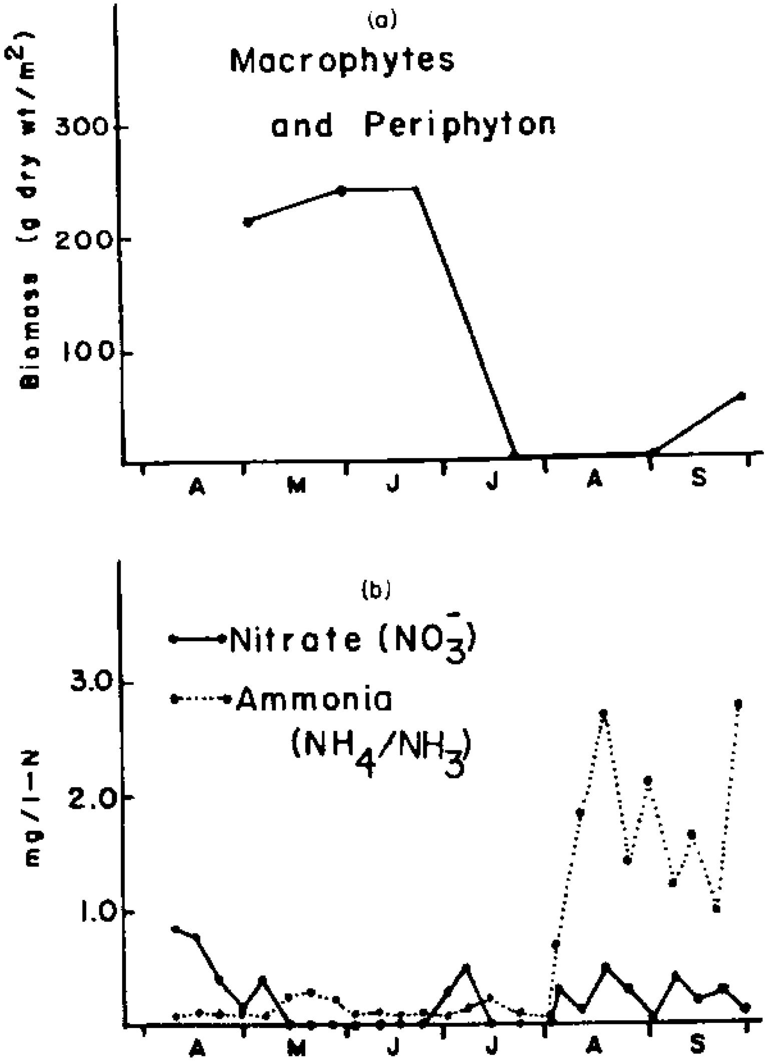

FIGURE 8

Time course measurements of (a) macrophyte and periphyton biomass and (b) nitrate and total ammonia concentrations in Pond 4 of the WQMF during 1980 (from Spencer, 1981).

was conducted in the four WQMF ponds using a large mechanical harvester. Plant harvest resulted in removal of only 9 percent of the total nitrogen removal (Burton et al. 1979a). During occasional periods of massive plant decay and oxygen depletion, denitrification may have resulted in nitrogen losses. However, the high pH and high O_2 levels maintained in these ponds throughout much of the growing season would tend to reduce the significance of denitrification in the overall nitrogen loss (King 1978).

Most wetlands and nearshore environments have lower pH levels than those occurring in the extremely productive WQMF ponds. As such, the potential for ammonia volatilization is reduced in these areas. This is particularly true in dense emergent macrophyte zones where reducing conditions often exist in the water and sediment. However, in shallow productive areas dominated by submerged plant and algae growth, higher pH levels would be expected. For example, the pH of much of the Pentwater Marsh system fluctuates around 8.0, but in some backwater areas dominated by submerged macrophytes, pH values in excess of 9.0 have been measured (Kelley and Burton, unpublished data). Ammonia produced in the more reducing emergent plants stands and transported to these areas of higher pH would be subject to volatilization losses. Other examples of areas with elevated pH values where ammonia losses might be expected come from nutrient rich, productive ecosystems discussed at this symposium. These include the Chowan River in North Carolina, where pH values up to 10.0 have been measured during algal blooms (Paerl, personal communication), Green Bay in Wisconsin (Harris, personal communication), and even in well-buffered salt water as evidenced by Nixon's highly nutrient enriched sea water mesocosms where pH values approaching 9.0 were measured (Nixon 1984). Galloway (1980) predicted that even at a pH of 8.5, one half of the total ammonia would be lost via volatilization in 41 days, at 25C, with a wind speed of 2m/sec, in a body of water 5 m deep. In areas less than 5 m deep, the rate of ammonia loss would be more rapid.

PHOSPHORUS

The movement and cycling of phosphorus through wetlands is simplified by the absence of a gaseous phase. The only mechanism for removal of phosphorus by wetlands is through a net accumulation of phosphorus in wetland sediments. This may occur through the deposition of phosphorus-containing sediments and organic detritus, or through incorporation of dissolved phosphorus into the wetland sediments through sorption or precipitation. We can address these processes through data collected at the WQMF at Michigan State University.

The shallow WQMF ponds initially served as effective phosphorus sinks (Figure 9) as shown by total phosphorus levels in the water system during the first year of operation (1976). The phosphorus concentration in pond 1, the most upstream pond, was initially reduced below influent concentrations. However, as the newly exposed bottom sediments became saturated with phosphorus, the phosphorus concentration in the water rapidly increased (Figure 9). As the sediments became saturated in the downstream ponds, the phosphorus concentration began to increase successively. In less than two years, the phosphorus concentration in pond 4 reached the maximum allowable discharge concentration of 1 mg P/l, and the discharge from this pond had to be diverted to a spray irrigation project. As King (1979) stated, "Thus it appears that pond systems will remove phosphorus just long enough for the designer and contractor to collect their fee and leave town."

Wetland sediments have the potential capacity to remove phosphorus from overlying waters. However, this capacity is highly dependent on sediment type, is finite, and is likely to be exhausted unless new sediments, that have been exposed to lower phosphorus concentrations than those found in the overlying water are deposited in the wetland. If the phosphorus concentration in water flowing through a wetland is increased, then additional phosphorus can be sorbed to the sediments until new equilibrium levels are established (the converse of this also is likely).

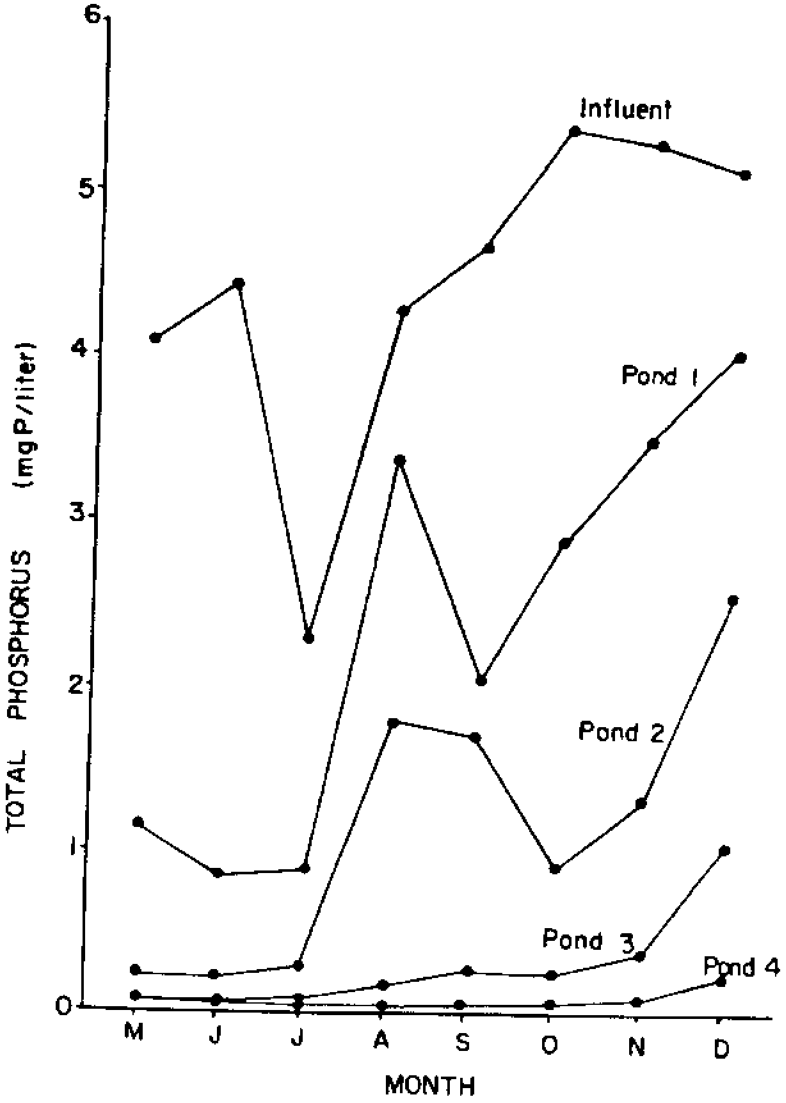

FIGURE 9

In addition to sorption, dissolved phosphates may also be deposited from water into the sediments through precipitation with calcium carbonate (Otsuki and Wetzel 1972). Biological activity may have a significant influence on this process (Figure 10). At elevated pH levels resulting from photosynthetic activity, the carbonate concentration increased causing a precipitation of phosphate. However, in July, the pH declined because of plant decomposition. This resulted in a substantial release of phosphate, alkalinity and hardness into the water, which was attributable to redissolving of precipitates of these materials in the sediments. Burton et al. (1979b), reported similar results from the WQMF ponds and concluded that "Long-term loss by physical-chemical precipitation does not appear to represent a significant sink for phosphorus in these lakes." The variability in the phosphorus concentration as controlled by biological activity (Figure 10) points to the importance of conducting longer term studies before conclusions are drawn concerning the potential removal of nutrients by wetlands.

SUMMARY AND RECOMMENDATIONS

We have tried to present some general concepts and some recent data that relate to the Great Lakes coastal marshes. Generally, we feel that the great majority of nutrients move into and through the marsh systems. Our feelings are supported by related stream studies, logic and intuition. More research is needed to substantiate the latter.

Phosphorus appears to move through marsh systems. If significant phosphorus deposits remain in the marsh, they must be sorbed or buried in the sediments. We need long-term research that documents the net accumulation of sediment in the marsh.

Nitrogen appears to be more complex. Much of the nitrogen moves through the system as does phosphorus. However, the action of photosynthesis and bacteria may cause considerable loss of nitrogen through denitrification or ammonia volatilization in highly productive systems. The loss of ammonia and nitrogen gas may be the only significant mechanisms for the true removal of nitrogen aside from the general dominant concepts of sedimentation, aquatic recycling and flow

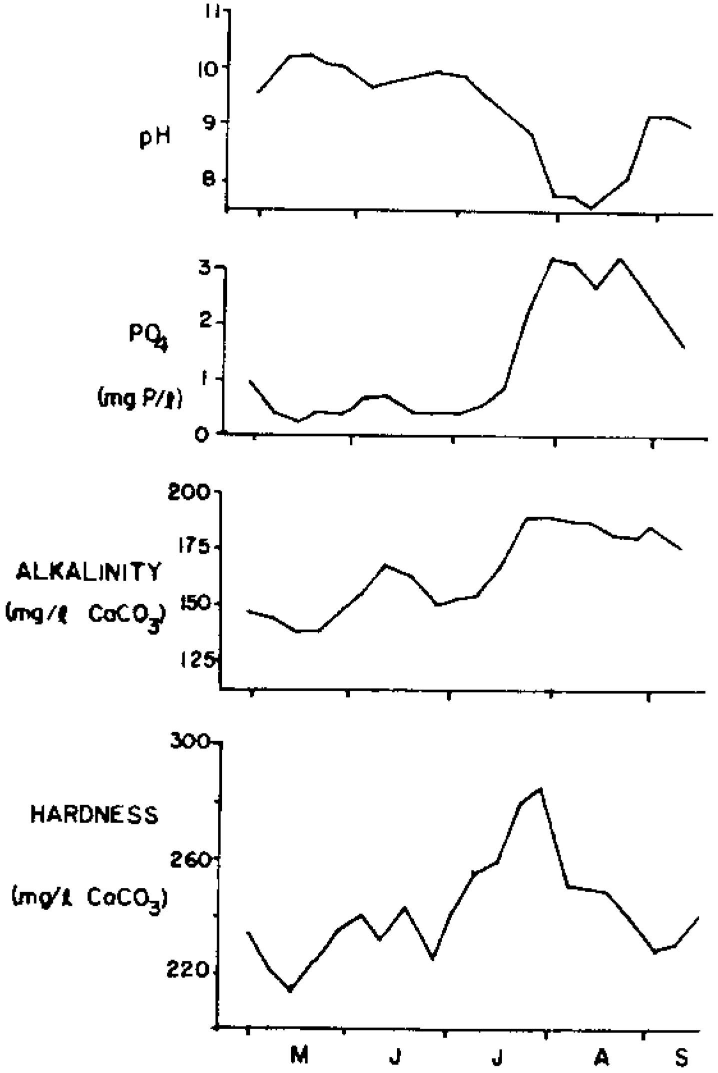

FIGURE 10

Time course measurements of pH, phosphate, total alkalinity, and hardness in Pond 1 of the WQMF during 1980.

through. To what extent do these marshes act as ammonia pumps or contribute to denitrification, thus reducing the nitrogen load to the Great Lakes? Is there a significant fixation of nitrogen by blue-green algae in the marshes that counters the nitrogen loss? Little or none of this ammonia loss or nitrogen fixation involves the emergent vegetation, so this research must focus on the submerged macrophytes, the phytoplankton and the periphyton. In comparison to the emergent plant communities, these plant components also have the greatest contact with the nutrient-laden water as it flows through the marshes.

In general, primary production in many lakes is phosphorus limited while estuaries and coastal oceans are commonly nitrogen limited. The mechanisms responsible for these different limitations have not been explained adequately. Howarth and Cole (1982), at the Marine Biology Lab at Woods Hole, are testing a hypothesis that these differences may be explained by lower rates of nitrogen fixation in saltwater systems than in fresh waters, due to reduced molybdenum availability. Data from our research at the WQMF show a significant lowering of the N:P ratio of water as it passes down through these productive systems. An alternative hypothesis to be studied, therefore, is that as water moves from nutrient-poor headwaters down through a variety of wetland, lake and river systems leading to estuaries and coastal oceans, and that nitrogen is lost more readily than phosphorus, particularly as these systems become nutrient enriched.

We see much data that documents the seasonal uptake and accumulation of nutrients by marsh vegetation and other data that reveal the breakdown and decay of vegetation and the subsequent release of nutrients. Many studies provide concentrations of nutrients but do not have detailed hydrologic information. The significance of the marshes as sources or sinks can only be answered by year-round, multi-year studies that document total nutrient movement, chemical concentrations and water and sediment volumes.

Finally, to satisfy our intellectual curiosity if nothing else, we should research the mechanisms that cause the transformation, recycling or movement of nutrients within these productive and dynamic systems.

Our coastal marshes are important features --- important habitats themselves and important to the Great Lakes. The questions raised in our summary and in the challenge paper focus on nutrients. To realize the overall importance of the marshes, we must follow the dynamics of the nutrients through organic production. Perhaps the greatest value of the marshes to the Great Lakes is their role as "manufacturing centers." Do the marshes contribute significant quantities of zooplankton and larval and juvenile fishes to the Great Lakes? These questions are modifications of those posed by Nixon in the challenge paper. We believe these questions need answers. We also believe a few ecosystem-level studies would help document the awaited integration of reported "minute particulars." Such ecosystem-level studies must involve teams of ecologists. To address problems of spatial and temporal variability, the studies would have to be large and long-term. In the Great Lakes area, we see at least one good mechanism to put together such integrated and coordinated studies. The collective Sea Grant programs in the Great Lakes states provides that possibility.

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NUTRIENTS IN ESTUARIES: RESEARCH NEEDS AND PRIORITIES

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INTRODUCTION

During the past decade, increased eutrophication in two North Carolina coastal rivers has led to recurring blue-green algal blooms. These blooms threaten the large and valuable estuaries at the rivers' mouths. Consequently, a research effort was developed to understand the bloom phenomenon and to construct management remedies with some guarantee of success. Below, we will describe some of the results of this research and discuss the insights this experience provided into research priorities and methodologies that are needed to study nutrients in estuaries. Although we will focus on North Carolina estuaries, most of the points are applicable to a large class of river-dominated estuaries on the U.S. East Coast.

Background

The occurrence of blue-green algal blooms in the lower Chowan and Neuse Rivers (Fig. 1) has become a serious water-quality problem in eastern North Carolina. The Chowan is a freshwater, tidal estuary extending from the confluence of the Nottoway, Blackwater and Meherrin rivers near the North Carolina-Virginia border to the western end of Albemarle Sound. Blooms of surface scum-forming blue-green algae (*Anabaena, Aphanizomenon* and *Microcystis*) began to appear in the early 1970s (NCDNRCD 1982). Further south in the lower Neuse River, *Microcystis aeruginosa* blooms developed in some, but not all, summers since the late 1970s between Goldsboro and New Bern, N.C. (Paerl 1983; NCDNRCD 1983).

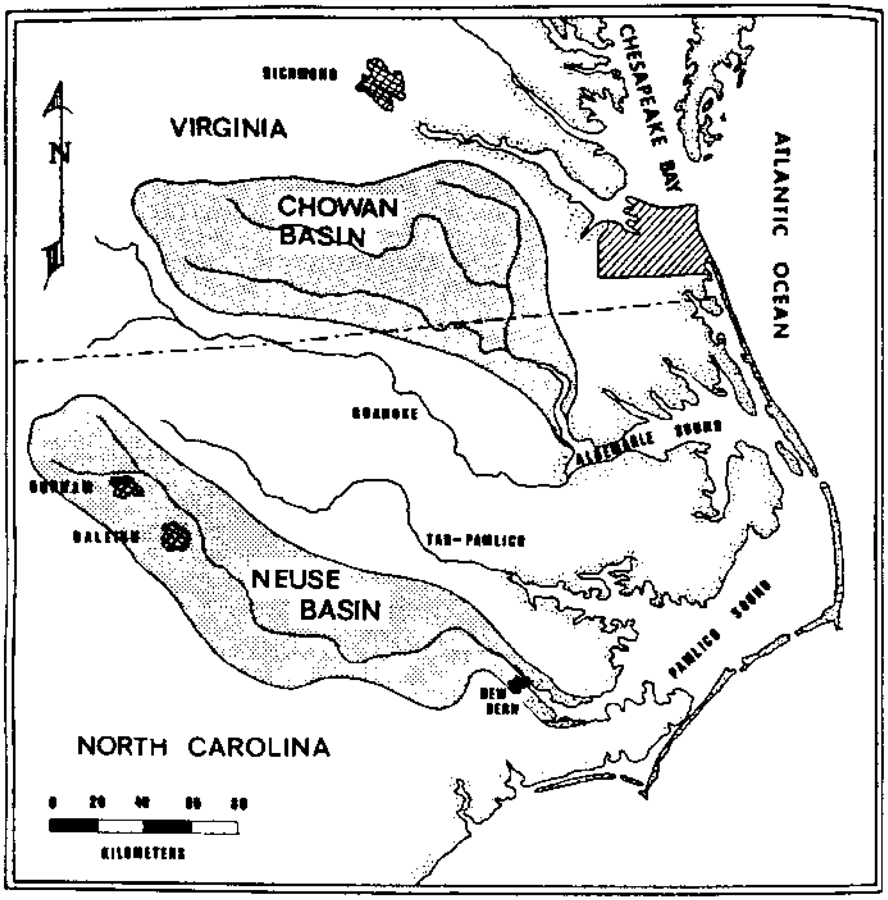

FIGURE 1

The Chowan and Neuse River basins in eastern North Carolina and southeastern Virginia.

Population growth, intensified agriculture and industrialization increased the quantities of nitrogen and phosphorous entering the Chowan and Neuse. This increased nutrient loading is the primary cause of the blue-green blooms (Stanley and Hobbie 1981; Kuenzler et al. 1982; Paerl 1983; NCDNRCD 1982). In the Neuse, upriver nutrient concentrations are high throughout the year. This is illustrated by Fig. 2, which summarizes four years of inorganic nitrogen and phosphorus data for 11 stations along a 400-kilometer stretch of the river and estuary. Of the three nutrient species considered, ammonium nitrogen (NH_4-N) levels were the least variable with respect to location in the river. Most stations averaged between 0.05 and 0.12 milligrams of nitrogen per liter. Peaks were largely associated with urban or industrial sources along the river. Nitrate nitrogen (NO_3-N) averaged about 0.4 milligrams per liter in the headwaters, but rose to around 1 milligram per liter to 1.5 milligram per liter in the Raleigh-Durham area, 200 kilometers to 280 kilometers above the river mouth at New Bern. The concentrations fell some, but remained relatively high (0.6 to 1 mg N/1) as far downriver as New Bern. There, at the freshwater-seawater interface, a steep decline began and continued through the length of the Neuse estuary. At the mouth, near Pamlico Sound, the NO_3-N average concentration was down to less than 0.1 milligrams per liter. This decline was caused largely by biological assimilation, and to a lesser extent, by seawater dilution (Stanley 1983). Phosphate phosphorus (PO_4-P) concentrations also peaked in the Raleigh-Durham area (Fig. 2). At the headwaters, phosphate averaged around 0.1 milligrams per liter, rose to as much as 1.0 milligrams per liter, and gradually fell to about 0.2 milligrams per liter in the New Bern vicinity.

ESTUARINE RESPONSE TO INCREASED NUTRIENT LOADING

The Neuse and Chowan studies provide some insight into how river-dominated estuaries may respond to excess nutrient loadings. But these studies also raise many questions.

1) Why have blue-green algal blooms developed above, but not below, the freshwater-seawater interface (FSI)?

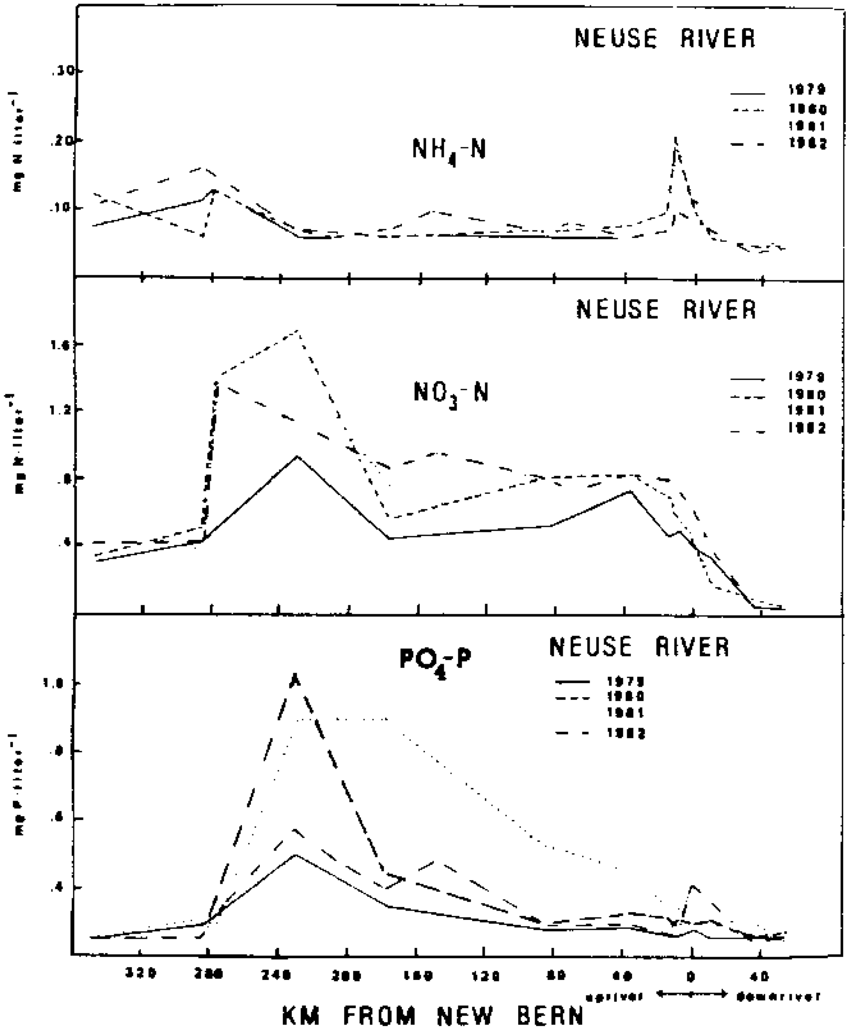

FIGURE 2

Mean annual dissolved inorganic nitrogen and phosphorus concentrations in the Neuse River, 1979-1982.

Upriver of the FSI in each estuary, the response to increased nutrients was a dramatic increase in primary productivity, in the form of intense summer blooms of blue-green algae. However, less obvious impacts were observed below the FSIs in the Neuse estuary and in Albemarle Sound.

During the 1983 summer bloom in the Neuse, over 90 percent of the algal biomass immediately above the FSI consisted of species of blue-green algae, primarily *Microcystis aeruginosa* (Fig. 3). At the same time, the phytoplankton at the New Bern station, 10 kilometers farther downstream and below the FSI (salinity = 5 ppt), consisted primarily of dinoflagellates. No blue-greens were observed there. However, algal diversity in this part of the estuary in 1983 was much less than in 1982, a non-bloom year (Fig. 3). Total algal biomass also decreased dramatically and rose again in this relatively short distance across the FSI.

Data such as these have been used as circumstantial evidence that salinity is the factor preventing the penetration of blue-green blooms into the estuaries. However, available experimental evidence is somewhat contradictory, especially with regard to the effects of low (0-5 ppt) salinities. Paerl (in press) showed that salinity treatments clearly inhibited *Microcystis* photosynthesis (^{14}C). Inhibition was observed at salinity concentrations as low as 0.5 parts per thousand. But in another experiment, the transfer of *Microcystis* to collected river water of various salinities did not result in a clear pattern of inhibition. Also, the decline in bloom biomass may actually occur in freshwater just above the FSI. Alternate hypotheses to explain the disappearance of the blue-greens include: 1)depletion of nutrients, especially NO_3-N, immediately above and in the oligohaline region of the estuary and 2)increased water turbulence as the river widens near the FSI. Such turbulence tends to break up surface scums of *Microcystis*. However, blue-greens do proliferate in sections of the Chowan above the FSI where the width is similar to the oligohaline Neuse below New Bern.

2)Is there potential for blooms of non-blue-green algae below the FSI in these

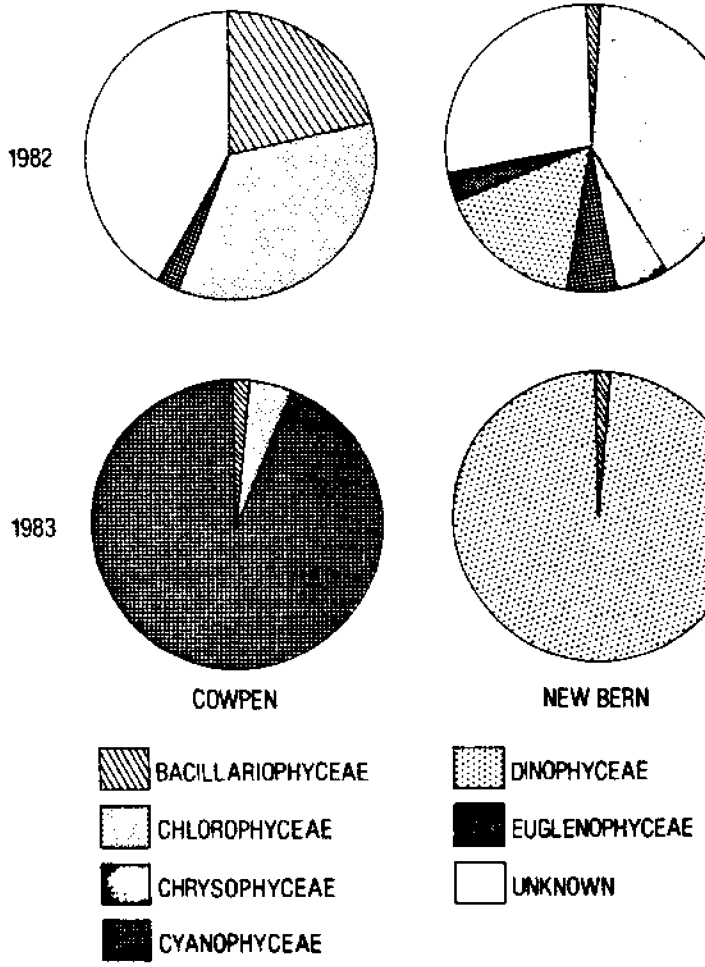

FIGURE 3

Phytoplankton biomass composition in the lower Neuse River Estuary during the summers of 1982 and 1983. Cowpen is a station located above the freshwater-seawater interface (FSI), and New Bern is a station located below the FSI. 1983 was a bloom year; 1982 was not.

estuaries, and if so, what would be the impact of such increased primary productivity?

Even if blue-greens do not penetrate the FSI, why do other more salt-tolerant algal species downriver from the FSI not reach biomass levels comparable to the blue-greens upstream. NO$_3$-N levels below the FSI are lower than upriver (Fig. 2). But based on the Chowan and Neuse nutrient studies of Stanley and Hobbie (1977) and Paerl (1983), it is doubtful that nitrogen or phosphorus limit phytoplankton growth in the upper reaches of these estuaries. In summers when blue-green algal blooms do not form, the high inorganic nutrient loads move directly into the upper estuary. Although substantial phytoplankton biomass develops there, it has never come close to that associated with the blue-green blooms. Perhaps other factors, such as light availability or zooplankton grazing pressure, regulate algal growth in the estuary.

These possibilities raise questions about how primary productivity in the estuary responds to increases in nutrient loading. Is there some loading threshold that must be reached before significant estuarine blooms can develop? Or have slow, subtle changes occurred in algal species composition and/or productivity that have gone unnoticed? Unfortunately, the year-to-year variability that occurs in phytoplankton productivity in the estuaries, combined with the lack of long-term monitoring data, make these questions impossible to answer.

3) Why have nuisance blue-green blooms not developed in most other river-dominated estuaries in this region?

The Tar-Pamlico River estuary watershed lies adjacent to the Neuse. And farther north, the Roanoke River empties into western Albemarle Sound close to the mouth of the Chowan. Neither the Tar-Pamlico nor the Roanoke experienced blue-green algal blooms. Why? Is it true, as has been postulated, that nutrient loadings to these systems are less than to the Neuse and Chowan? The data to support or refute this hypothesis have not been collected. Or, are there other hydrologic features that would explain the absence of blue-green blooms?

4) Why do blooms not develop every summer in the Chowan and Neuse?

Despite the persistence of high levels of growth-stimulating nutrients (Fig. 2), blue-green blooms do not develop in the Neuse or Chowan every summer. In the Neuse, strong blooms occurred in 1978, 1980 and 1983. There is circumstantial evidence that this inconsistent response may be related to variations in river flow (NCDNRCD 1982). At flows above 800 cubic feet per second (measured at Kinston, N. C.), there were only three out of 67 measurements made over a 4-year period when chlorophyll a in the lower Neuse River exceeded 10 ug/l. But as flows less than 800 cubic feet per second, the measured biomass values were usually 40 ug chlorophyll a per liter (Fig. 4). We believe that algal blooms are prevented from developing by intermediate to high flows because nutrient-rich water is carried to the estuary before algal densities can reach bloom levels. When flow is high, river water time-of-travel increases, water clarity decreases and turbulence increases. None of these conditions favor blue-green bloom development. The opposite is true when flow decreases. This hypothesis needs to be tested. If it proves acceptable, then high nutrient loading is not the only factor leading to severe eutrophication symptoms. Instead, the interaction between nutrients and other pertinent factors must be considered in assessing the potential impact on estuarine productivity.

5) What effects can excess nutrient loading of estuaries have on higher trophic levels?

The oxygen demands resulting from rapid decomposition of dying blue-green (or other algae) blooms can lead to kills or unusual migrations of fish or other animals. However in the Neuse, no serious fish kills have occurred, despite the apparent rapid die-off of blue-greens, resulting in a dissolved oxygen sag near the FSI. Chemical toxicity resulting from blooms of blue-green algae and some dinoflagellate algae is another possibility. A third possible impact is interruption of the normal estuarine food web. If eutrophication leads to algal species composition changes, then zooplankton and fish productivities may be altered. For example, there is a general

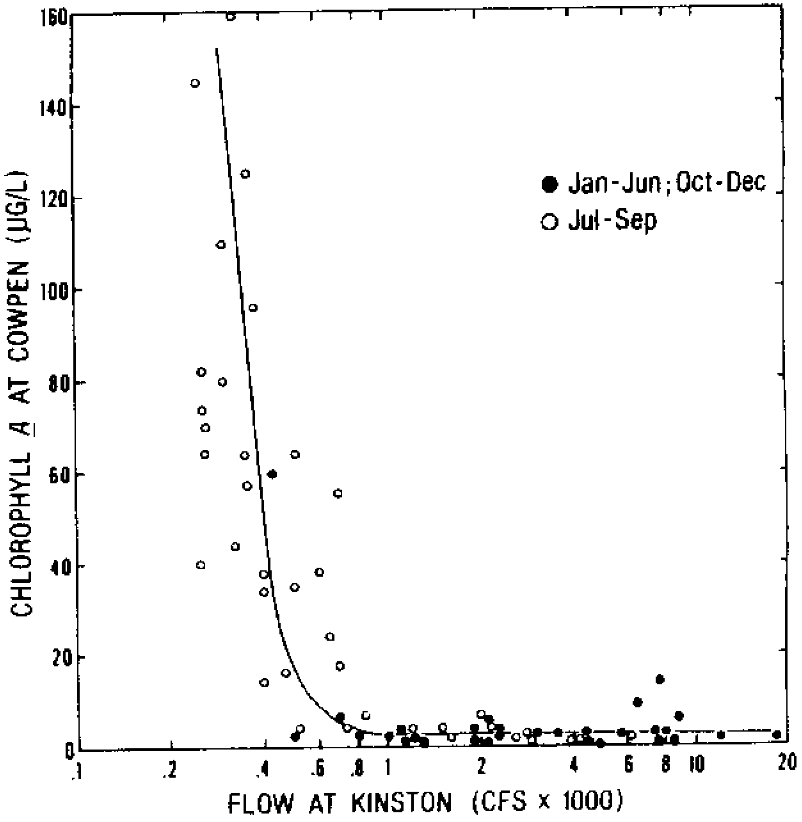

FIGURE 4

Chlorophyll a concentration (ug/liter) at Cowpen's Landing vs. river flow (cfs) at Kinston.

consensus that, relative to most other potential foods, blue-green algae are inadequate nutritional sources for zooplankton (Edmondson 1974; Porter 1977; Champ and Pourriot 1977).

RESEARCH METHODOLOGIES

In his challenge, Nixon emphasized the need for focused and truly integrated multidisciplinary research programs to carry out ecosystem-level experiments. We agree that this approach can be very efficient under some circumstances. In addition, however, we feel that other useful methodologies need to be discussed. We have focused on one: long-term, high-quality monitoring programs.

Nutrient-related water quality problems often require long-term monitoring because changes in loadings are usually gradual. A number of years of data are necessary to determine the actual trends and impacts. This fact has been demonstrated for a variety of aquatic ecosystems. For example, Likens (1983) showed that short-term measurements of nutrients in streams are often confusing or misleading. Similarly, Goldman (1981) found from long-term studies of Lake Tahoe that it took 15 years to demonstrate real changes in primary productivity. Another example comes from Lake Washington near Seattle, where long-term changes in the chemistry and biology occurred as the result of sewage disposal into the lake and later diversion of the sewage from the lake (unpublished data on W. T. Edmondson cited in Likens 1983). Without years of careful monitoring, the changes resulting from these activities could not have been determined. In Chesapeake Bay, the value of long-term monitoring of dissolved oxygen became apparent when Officer et al. (1984) showed the extent to which bottom water anoxia had increased over the past 40 years. Actually, the availability of long-term data for the Chesapeake resulted not from a planned, coordinated effort, but from the independent work of many researchers in laboratories around the bay. Unfortunately, few estuaries are researched by enough ecologists to generate long-term data in this haphazard fashion.

It is imperative that these monitoring programs be of highest possible quality. Likens (1983) discussed, in detail, a number of criteria that should be met for a successful program. The following points are based on his discussion and/or our own experiences:

1) In setting up the programs, careful thought should be given to the choice of variables that will be monitored, as well as the appropriate time and space scales. If the estuary already suffers from particular euthrophication symptoms, then the decisions will be easier than in cases where no visible disturbances occur. The temptation to monitor traditional variables must be avoided. As Likens (1983) points out, it is usually desirable to determine from preliminary studies what is the best frequency for samples in a time series. Some parameters may have to be sampled more frequently than others and at closer spatial intervals.

2) Analytical quality control must be maintained. It is important to standardize methods and procedures and to intercalibrate these with standard sources. Whenever a method is changed, care should be taken to avoid artificial trends in the data. In our own laboratory, we recently prepared several hundred replicate sets of NO_3-N, NH_4-N and PO_4-P standards from single stock batches. These ready-to-use 25 milliliter standards were ampoulated and then autoclaved. They will be stored for use over the next several years for biweekly analyses of nitrogen and phosphorus in a long-term monitoring program in the Pamlico River estuary (discussed later). This procedure should avoid the artificial trends that can result when errors occur in making up stock, intermediate and standard solutions for analyses of individual nutrient sample sets.

3)The raw data must not be warehoused, but made accessible to those who need it and analyzed to allow it to be useful in hypothesis formulation. Availability of large data sets generated in monitoring programs could be enhanced by storing the data in regional or national computer data banks accessible to a wide audience and by periodic preparation and dispersal of technical reports to university groups and state/federal agencies interested in the work. But even more important, those who generate the data must regularly review and assimilate the data with a goal of generating testable hypotheses. Indeed, if this is not done, then most of the potential benefits of monitoring will never be realized. Instead monitoring will become an end in itself. Those responsible for the program will become uninterested and uninspired to maintain the quality standards mentioned above.

Flemer et al. (1983) present a convincing argument to couple long-term monitoring with research for effective management of estuaries. First, observations generated by monitoring are frequently the basis for a hypothesis and often are used to formulate research programs. Next, the research can aid in the identification and evaluation of probable causes so that appropriate management actions can be made. Later, follow-up monitoring can determine if a management control action is effective. The results of research also often modify existing monitoring programs (i.e. change the variables measured or their time and space scales). Thus monitoring and research form a loop, each feeding or reinforcing the other to achieve better understanding of the estuary.

An example of coupling monitoring and research is provided by our experience with blue-green bloom problems in the Neuse and Chowan. As noted earlier, several years of monitoring data led to three observations: 1) nitrogen and phosphorus concentrations in the river are high every year at all times of the year, 2) bloom concentrations of algae do not develop in the rivers every year, and 3) periods when blooms develop coincide with periods of low flow. Based on these observations, we developed a hypothesis about the relationship between blooms, nutrients and river flow that offered a mechanism to explain the observations. The next step will be to conduct a research program over the next several years to test this hypothesis. The outcome of that research will, in turn, be incorporated into management strategies that must be devised to eliminate the bloom problem. Thus, monitoring can and should be an integral part of the scientific method in ecology.

4) Funding for long-term monitoring is difficult to obtain. A decade ago, the University of North Carolina Sea Grant College Program and the UNC Water Resources Research Institute funded the collection of one to two years of baseline nutrient data for three major estuaries in North Carolina (Hobbie 1974; Hobbie and Smith 1975; Bowden and Hobbie 1977). Since then, however, these agencies, like most others, emphasized basic and applied experimental research over monitoring. Consequently, the recent nutrient data available for comparison with the earlier measurements in the Chowan and Neuse were gathered coincidental to the research projects. This is not an ideal situation because sampling and analytical methods vary substantially from one project to another.

For the Pamlico River estuary there has been sustained funding for long-term monitoring of nitrogen and phosphorus, along with other basic hydrologic parameters. Since the late 1960s, a phosphate mining company located on the banks of the Pamlico has provided contract funds for biweekly monitoring of 20 stations in the estuary. The company's commitment to this effort stems from an agreement with the state of North Carolina. To receive permission to discharge wastewater into the estuary, the company was required conduct a monitoring program. The monitoring is carried out by universities within the state. The resulting data are turned over to the company and to state environmental management personnel. In addition, these data are available to other university researchers interested in the Pamlico. This arrangement has proven beneficial to all. The phosphate company enjoys the positive public relations generated from the program, the state monitors some aspects of water quality in the estuary at no cost, and university researchers can use the long-term data set to complement data collected in their short-term research projects. This industry-government-university partnership should be developed for more estuaries.

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DISCUSSION

H. PAERL: I would like to augment Stanley's talk while it's still fresh in our minds. He shows that there is a tremendous difference in these blooms as they develop in freshwater habitat, and disappear and presumably go into some kind of detrital food chain as they end up in the estuaries. But, I think one thing to keep in mind is that freshwater habitats, or even oligohaline habitats, which the blue-greens penetrate, are nursery and rearing grounds for many marine fish species important to commercial fisheries.

Therefore, we cannot isolate the events occurring in the more or less freshwater habitat from the economic benefits or detriments that are occurring downstream where we don't think we have a problem. There are indications that the food chains in these rearing grounds are erratically altered. The traditional zooplankton that normally feed on the algae in the oligohaline environments are faced with a food source they cannot readily utilize. It's decreasing the efficiency of transfer and increasing the number of links in the food chain.

So, we have some important ramifications in pure marine systems that need to be searched out in freshwater habitats where the problems originate.

D. FLEMER: I would like to see data from a little further into the Neuse estuary because I assume it has a turbidity maximum (or a null zone) since you have salinity intrusion. The physics of the system may explain if you have particles accumulating. Phytoplankton might behave the same way. If you look at the literature for some estuaries along the East Coast, you will find that you tend to get low concentrations, typically in the summer, in tidal fresh water relative to a system which has a turbidity maximum in it.

It will be difficult for a senior technical person in a research agency not to go back with a story. It's going to be hard to ignore all of this, particularly Don Malins' story. Frankly, that scares me. And I expect one of these days it's going to hit the news. I don't see how that cannot be information to provide guidance on some further research that has some rather significant management implications.

M. KJELSON: I want to emphasize that I appreciate Malins' comments on the linkage we need between research and management. And although I'm a hesitant to say this, I think a lot of the things said in the last few days were purely from the habitat standpoint. I think we need more of a linkage between the habitat biologists and the stock biologists, if I may use that term, because stock is really what we're trying to protect. That by no means negates the feeling that we have to protect the system so we can protect the stock. We have all sorts of aesthetic things we're concerned about.

In California we've found a similar relationship between hydraulic residence time and chlorophyll levels. In our system we've been looking at it in the (tidally influenced) portion of the system rather than simply in the river. We see the same relationship in the river. We ought to look at the hydrodynamic processes that are occurring in the estuaries. They become very complex with tidal influence on top of river flow, and so forth. We find that as residence time increases, blooms are initiated. The duration and the magnitude of the blooms are not only influenced by flow, but also by nutrient depletions and other things.

Scott Nixon seemed to refer to residence-time issues in his talk. I would like for him to add if he has any evidence of that occurring in the estuarine brackish water area.

S. NIXON: I think in dealing with whole estuary systems we're hampered for a number of reasons. First, the hydraulic residence time is a very difficult thing to know for any estuary, and it's not been adequately described for most, if any of them. And the significance of it is not totally clear because it varies at every point in the estuary, and it varies for every substance that's discharged into it. It's not a simple number that we can drag off the shelf. That's the kind number we would like to have, but the physicists aren't going to give us a number like that.

I think it certainly makes a big difference when you're comparing a system like south San Francisco Bay where the water stays for a long period versus the mouth of the Hudson River where it stays for only a matter of days. In most estuaries, I suspect that it's not going to be as important as we would like to believe in separating systems where the residence time is long relative to biological and chemical rate processes. In that case, those are going to be more important things that dominates what goes on in the estuary.

C. SPENCER: I would like to add one thing on retention time with ammonia loss. The longer the water was in our pond systems, the more nitrogen was lost. If retention time had been less in the four ponds, then it would have resulted in less ammonia loss. If ammonia loss was occurring in a river system, however, the retention time would be an important consideration.

J. Weis: Having listened to three papers on nutrient input and one paper on chemical inputs and coming from a state (New Jersey) where other chemicals are really important, I suspect that those areas of Puget Sound might seem pristine when compared to some areas in New Jersey. We're left with the impression that agricultural runoff gives nutrients and industrial/urban runoff gives other toxic substances. I would like to encourage people who are studying agricultural runoff to remember that in with all those fertilizers and nutrients you might be getting a whole host of pesticides. Think about the interactions that might occur.

D. MALINS: What Judy Weis says is correct. I think these interactions are tremendously important. And, I think the problem is in all of these systems and it's tremendously difficult to differentiate the effect of one sort of perturbation from that of another. I can certainly speak for Puget Sound where it's a continual quest to try to understand whether it's a problem of human sewage, pesticides or industrial activity. How we're going to differentiate, I don't know. But it certainly is a factor, and I agree with all the possibilities for interaction.

J. SHARP: We should reference the chemical tool that's used to understand concentration of nutrients and their behaviors in estuaries. This is the concept of the property salinity plot that geochemists use. You try to look at the dilution of any property in an estuary. You can do this with any dissolved chemical, but it's used frequently with nutrients. If you have strictly dilution as you go down the gradient of salinity, concentrations fall on a straight line. If there's net removal, the line curves downward. If there is net input, the line curves upward.

You can use this technique to generalize for a lot of estuaries. As you get a slope from that line, plot the slope against the maximum upward-end number concentration. I've done this with data from the Delaware, the Tamar in England, San Francisco Bay, the Zaire in Africa, the Magdalena in South America, the Columbia and the Dutch Wadden Sea. You get a fairly good relationship. All of these show, for the most part, a very similar, conservative type of behavior for a nutrient such as nitrate. Phosphorus behaves much differently. Using the same technique for the estuaries listed above, we find that phosphorus stays at about the same concentration down the gradient. In other words, it does not behave conservatively. One practical conclusion from this type of generalization is that if management reduces phosphates input, there's likely to be little effect.

R. BIGGS: I wanted to make a comment about toxic substances and the tidal approach that Scott Nixon used for nutrients. EPA funded his study of fourteen estuaries and the nutrient loading system. They also initiated a companion study that dealt with toxic substances that I worked on. They decided, however, that they had more pressing needs in the Chesapeake Bay and took us off that project. We began working on something else. Therefore, the companion study of the relationship between toxic loading, primary productivity and chlorophyll, was not completed.

J. BROWDER: In our first session, we were looking for mechanism by which changes in freshwater flow affected an estuary. Don Stanley, in his presentation, showed the possibility that blue-green algae blooms might be linked to periods of low water flow in the river. Although that is a perfectly natural situation, it points out how

changing the flow of a river might create a condition like this that didn't exist before.

R. CHRISTIAN: I thought the inter-systems comparison Scott Nixon made were interesting. The question for you is twofold. Do you think comparisons have been pushed as far as they can, given the limitations of data? And if so, what would Sea Grant's role be in developing the data to allow this kind of thing to be done more reliably?

S. NIXON: That's a tall order. I don't think we've gone as far as we can go with existing data in the sense that I think we need to engage constantly in that comparative exercise. In other words, put the data from one system next to another, and test the ideas that we develop in one estuary against the phenomena that we observe elsewhere.

A lot of us tend to be parochial, and we try to figure out how estuary X is working. We elaborate fancy hypotheses about what went on. But we don't usually go through the exercise of trying to say, "If that's true, how does it fit in with what's going on in the Potomac River or the Neuse?" And we ought to do that more, and we ought to have a chance to get at each other's data and try those things out. Certainly agencies like Sea Grant and EPA can help with that.

Don Stanley's point about data sets not being allowed to accumulate in some professor's archives where he guards them like a lion, but having them out there for others to use, is very important.

I think part of the trouble is how we collect and analyze the data that we're going to use. In most of the ecological work, we've been unimaginative in the way we treat our data. We go out and report concentrations from a given point in time, and that's the way we run our data collection.

Trying to deal with the data in the simple format of integrating the hydrography and the biogeochemical processes with mixing plots is a useful way to go. What I try to do in comparing systems is use volume-weighted concentration data. Since estuaries get deeper and wider toward the mouth, the low concentrations you find there represent dilution by a much larger body of water. One of the troubles is that almost no one reports their data that way. And when you start to work with most estuaries, trying to get the basic histographic information on the system becomes very difficult.

We tend in this business not do our homework very well. Therefore, many of the basic first steps are whisked over and breezed by. A lot of the hard-core building blocks are often missing---what the estuary looks like, where it is. You read paper after paper, and people don't even tell you what part of the estuary they're talking about. The sizes reported for estuaries vary by 15 or 20 percent depending on whose paper you read. San Francisco Bay, for example, is reported as all different sizes.

J. SAUBER: I'm one of the regulators that Don Malins was talking about. It's not surprising to find elevated concentrations of synthetic organic chemicals and metals building up in our estuaries. The threat of increasing eutrophic conditions in our estuaries seems to be a common theme among Southeast estuaries. Given the public pressures to develop our coastal areas for agricultural, industrial and population centers, the picture of these trends seems to be developing in a scary fashion. Nonetheless, we're left with the challenge of trying to manage that situation.

Don Stanley referred to the necessity of coordinating monitoring, research and management. And, as Lev Ginzberg pointed out in his keynote address, the manager preferred definite answers, even though they weren't necessarily correct, to the more uncertain answers. This is because we are hand-tied via historical requirements of the standard engineering "you have to meet a number" criteria. We are replacing that with biological interpretations, but we're far behind where we need to be in that respect. This paints a pretty gloomy picture for us in terms of implementing a management process.

I think Harris' point about developing non-market values for estuaries is probably the only course of action we can take to compete with the benefits of the economic development of our coastal areas.

D. STANLEY: Being a bit cynical, I would argue that there are a lot of millionaires who have won by shooting from the hip. You win some, you lose some. What seems like a good management plan today may need revision next year or in the following decade. I think maybe the best policy is to make the best judgment you can today. Put it right up front, and make it very clear that you are making that decision on the best available information. It may need to be revised five or ten years from now. I don't see that you have any other choice except to go ahead.

D. MALINS: I understand what you're saying, and I've heard it many times before. It's a legitimate pressing problem. But I'm afraid the reality of the situation is that we're always looking for direct answers, and we should. But we never seem prepared to expand the basis of understanding. That's always something that comes dribbling along with whatever funds we might have or that we can spare. That's a very serious mistake in the stewardship of estuaries and other coastal areas.

In my view at least, the ability to adjudicate these problems is about as good as the data base. If the data base is inadequate, then the decisions will be too. We have serious problems, not only in terms of understanding effects on organisms, but even in understanding the length and breadth of the problem of toxic chemicals. We can talk about a thousand here and a hundred there, but in many areas one can conservatively propose that we might be dealing with ten to fifteen thousand compounds, considering transformation derivatives. We must take the responsibility, as rapidly as possible, to expand our understanding in what we're dealing with. We've got to know the territory.

L. GINZBURG: I hear a gloomy picture of the future, with 75 percent of the population living on the coast and increased loading on nutrients and carcinogens. I would like to point out the importance of educating the general public.

The recent best seller, <u>Megatrends</u>, points out an interesting trend --- a trend from representative to participatory democracy,. In other words, people begin not to trust the representatives and want to make decisions themselves. We have seen that happen to nuclear power. It will start happening with respect to our coastal environments, I think, if that percentage of an expanding population is going to live there.

Unfortunately, the general public receives information mostly through television and, to a lesser extent, through newspapers. I think that educational journals could be a way people can get information.

Scientists are not making decisions. Managers and representatives are not going to make decisions. General referenda, that is what will happen. If we don't educate the general public through some means, we are not going to get the right picture and we'll be faced with wrong decisions all the time.

L. CROWDER: I agree with Lev Ginzburg's comment. I think it's critically important to do that, and Sea Grant's advisory services role is an area that can be very helpful.

Let's go back to the question of the management people and their management problem. In addition to needing data to make proper management decisions, we also need to make stronger efforts to follow the management actions we take. When we implement a management strategy, does it in fact do what we intend it to do?

The people at the University of Washington (Crawford Holling's group), who are talking about adaptive management strategies, are, in my opinion, onto some interesting approaches. They don't believe in setting management strategies in stone and defending them over and over.

Let's suggest management strategies based on the best data available and make projections about what we think ought to happen when we implement this management strategy. Then follow it up and see if it works. In other words, use management as a hypothesis-testing strategy. In fact, that's what it is. We don't know enough to make management edicts set in stone. Therefore, I encourage additional efforts to gather appropriate data to make good management decisions. In addition, consider following up those management strategies with appropriate kinds of monitoring to make sure that things are going in the direction we intended.

F. CHRISTHILF: This conference is, in part, about a dialogue between scientists and managers. It seems from what I've heard that researchers are finding out all kinds of things over a period of time, albeit not all they want to find out. Then they're faced with getting managers to accept that information and make better decisions.

I wonder about turning that around. Go to managers and ask them what their problems are. Then orient monitoring and research toward the questions those managers face.

S. NIXON: People don't usually come to us with questions about long-term trends and nutrient enrichment or fish. Management questions usually turn on whether someone can build his dock 10 feet long or 8 feet long, it's hard to respond to these very site-specific questions.

My impression is that very few people manage the environment. What they do is permit the environment. It is frustrating for lawyers and politicians making the decisions rather than technicians. Politically appointed boards have a variety of interests and spend little time in taking the initiative to modify the environment or restore it.

In other cases we just don't know enough. Somebody will come and want to know if he can put a housing development on a certain lagoon. Or, what are the nutrients going to do when they get into that lagoon? And we don't know.

COUPLING OF PRIMARY AND SECONDARY PRODUCTIVITY

ESTUARINE PRODUCTIVITY: UNRESOLVED QUESTIONS CONCERNING THE COUPLING OF PRIMARY AND SECONDARY PRODUCTION

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INTRODUCTION

Estuarine ecosystems are characterized by intrinsic high levels of primary production (e.g. Petersen 1918; Odum 1961; Teal 1962; Marinucci 1982). Whitaker and Likens (1975) estimated a mean annual primary production of 1,500 grams/square meter/year (dry matter) for estuaries, compared to values of 125 for the open ocean, 360 for continental shelf waters, 400 for lakes and streams, and 650 for cultivated land.

Accompanying these well-documented estimates of estuarine primary production are apparent high levels of secondary production. While quantitative estimates of secondary estuarine production are generally lacking, high yields of fishes (McHugh 1967), birds (Stewart 1962), and fur-bearing mammals (Chabreck 1979) offer compelling evidence. In fact, estuarine waters are classified, along with oceanic upwellings, as the most productive fisheries habitat on the earth's surface (Ryther 1969).

The connection between high primary production and high secondary production remains an enigma for estuarine ecologists. While a theoretical relationship exists between the two, documentation of the pathways and satisfactory clarification of the relative importance and ecological efficiencies of individual pathways remains an unresolved problem.

After 50 years of research, the sources of fixed organic carbon in estuaries are fairly well known (Fig. 1). But it is not clear how the carbon sources are utilized by consumers and what degree of importance is attached to various sources.

Hypotheses to answer these questions fall into two general categories. In the first category,

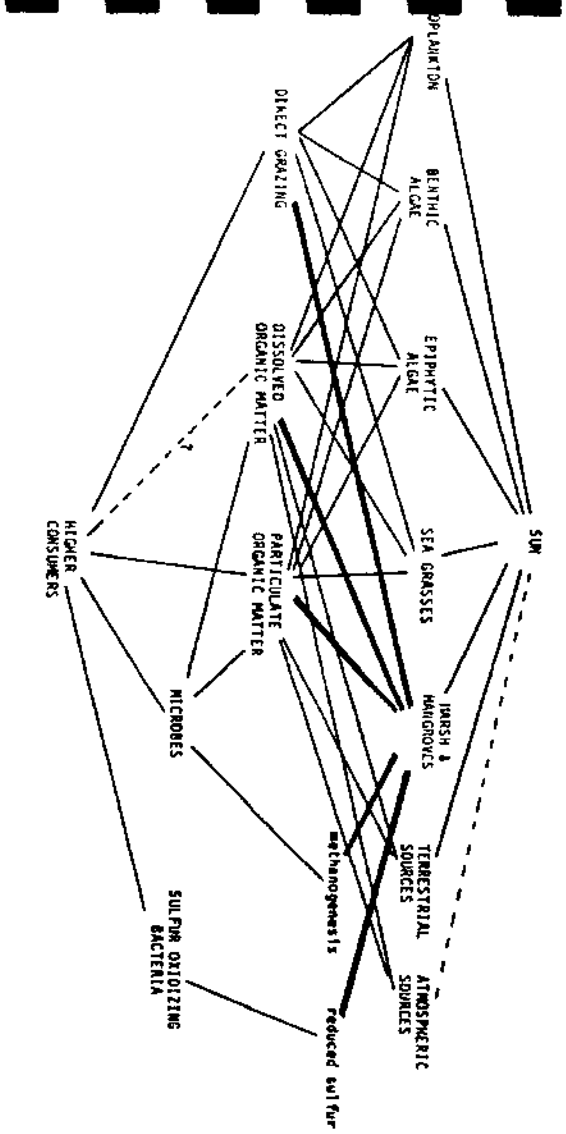

FIGURE 1

Potential pathways of energy flow in estuarine ecosystems. Not all possible pathways have been drawn; for example, methanogenesis and sulfur reduction could originate from any of the sources of organic matter. Mangrove and marsh pathways are enhanced for emphasis and do not imply relative importance. Modified from Odum et al. (1982).

vascular plant detritus, originating from marsh grasses, sea grasses, and mangroves, serves as a major energy source for marsh and estuarine consumers. This argument has been advanced by Petersen (1918), Odum (1961), Teal (1962), Darnell (1967), Mann (1972), de la Cruz (1973), Day et al. (1973), Nixon and Oviatt (1973), and Odum and Heald (1975) among others. The second category of hypotheses suggests that the importance of vascular plant detritus as an energy source has been overemphasized and that phytoplankton and benthic algae are more important (e.g., Correll 1978; Haines 1976, 1977).

ASSUMPTIONS AND BASIC QUESTIONS

This paper will examine the question of basic energy sources for estuarine primary production. This reduces to a debate over the contributions of different types of primary producers. I will argue that the quintessential question concerns the importance of vascular plant detritus. In the following paragraph I make several basic assumptions.

If these assumptions are acceptable, then the onus of proof is shifted to the vascular plant detritus/consumer question.

Assumptions

(1) Most estuaries are sites of high annual production of phytoplankton, benthic microalgae and benthic macroalgae. There are exceptions, such as highly turbid estuaries with muddy shorelines. But even these have appreciable benthic microalgal production.

(2) Most organic material of algal origin (a) provides an adequate food value, (b) is digestable, (c) can be assimilated, and (d) supports consumer growth and reproduction. There are, of course, exceptions (e.g. filamentous blue-green algae, certain macroalgae, etc.).

These points are supported by a vast amount of research too extensive to review in this paper. It is possible to argue about exceptions, but the weight of the evidence supports the generality of the assumptions. What remains to be better understood about algal-based food chains are the relative assimilation efficiencies of various types of algal diets by different consumers.

Basic Questions

Assuming that algal production is an important estuarine energy source, we question the importance of vascular plant detritus. I have broken this large question into a series of smaller questions.

(1) Is there a significant input of vascular plant detritus from marsh grasses, terrestrial plants, mangroves and sea grasses into estuaries?

The answer to this question is unquestionably positive (see reviews by Mann 1972; Odum et al. 1973; Thayer et al. 1979; Zieman 1982; etc.). But the magnitude of the inputs to specific estuaries remains unresolved. The methodological problems in measuring organic detrital flux are complex (see Odum et al. 1979; Nixon 1980). Although we may not know the exact amount of vascular plant detritus arriving in a particular estuary from a particular source, in most cases we can determine relative significance. For example, mangrove detritus inputs are high in the tidal rivers of the Everglades estuary in southern Florida (Odum and Heald 1975) and that marsh grass detritus inputs are high in the Louisiana estuaries (Day et al. 1973).

If we accept that vascular plant detritus inputs are high in many estuaries, the following questions become pivotal.

(1) Are there significant amounts of consumers that ingest vascular plant detrital material?

(2) Can these consumers assimilate any part of the detritus complex (substrate, microbes, microbial exudates) and grow on a vascular plant detritus diet?

(3) Assuming ingestion, assimilation and growth, how important is detritus to primary consumers in comparison with algal sources?

(4) Is there indirect evidence to suggest that vascular plant detritus provides much of the energy base for inshore or nearshore fishery organisms?

Examination of the available evidence on these unresolved questions reveals conflicting field data and experimental results. I have classified this evidence into two categories: (1) primary evidence that provides direct information about the first three questions and (2) secondary evidence that relates to the fourth question. The secondary evidence is more thought-provoking and worthy of further study than the primary evidence.

PRIMARY EVIDENCE

Digestive Tract Content Analyses

Investigators examined the digestive tract contents of estuarine primary consumers. In many cases significant quantities of vascular plant detritus have been found. For example, Darnell (1958, 1961) reported plant detritus in the stomach contents of salt marsh fishes and invertebrates. Odum and Heald (1972, 1975) reported similar findings from organisms in a Florida mangrove swamp. Other examples include plant detritus in the digestive tracts of mullet (Odum 1970a), grass shrimp (Welsh 1975), fiddler crabs (Montague 1980) and estuarine fishes (Carr and Adams 1973). And phytoplankton and other algae also are found in the tracts of estuarine fishes and invertebrates (e.g. June and Carlson 1971; Odum 1970a; and many others).

This data tells us that estuarine primary consumers ingest vascular plant detritus and algae in large quantities. Unfortunately, it leaves many unanswered questions. For example, it doesn't reveal the degree to which the organism utilizes the potential food substrate. What percentage is assimilated by the consumer, and what percentage is excreted? It is possible that digestive tract material passes through the animal without being assimilated. And delicate algal cells may be digested more quickly than vascular plant detritus. Such differential digestive rates can lead to extremely misleading conclusions.

In summary, digestive tract content information can establish preliminary information about consumption of detritus and algae. But this information cannot be extrapolated too far in drawing definitive, final conclusions about assimilation and growth.

Detritus Enrichment

Extensive literature is available on the nutritive change that occurs in decaying plant detritus (summarized by Tenore and Rice 1980). Depending on a number of factors (original composition of the plant material, nitrogen content, crude fiber content, content of water soluble compounds, presence of phenolic residues, etc.), vascular plant detritus may be a more nutritious substrate during the early decomposition stages (e.g. Waksman and Tenney 1928; Odum and de la Cruz 1967; Fenchel 1969). The increase in potential food value, often expressed as an absolute increase in total nitrogen, has been attributed to microbial colonization, growth and mobilization of nutrients from the water column (Fenchel 1969; Odum 1970b; Mann 1972).

The increased nutritional quality of aging vascular plant detritus has been used as an argument for the importance of the detritus-microbe complex in aquatic food webs (de la Cruz 1965; Odum 1970b; Mann 1972; Cummins 1974; and others). But the issue is not that simple. Potential food value does not necessarily translate to actual food value. The increased total nitrogen content in decaying detritus may not represent usable or digestable nitrogen, but quantities of refractive, metabolically unavailable, non-protein nitrogen compounds (Odum et al. 1979). Moreover, this nitrogen increase may be due to accumulation of extracellular, organic nitrogen in the form of microbial exudates (Rice 1979; Hobbie and Lee 1980).

In summary, the literature on the aging and nutritional changes of vascular plant detritus suggests that it is potentially nutritional to many primary estuarine consumers. But this information must be interpreted cautiously, with thought given to the exact chemical composition and change in composition of the decaying substrate. Much important research remains to be done in this area.

Feeding Studies Utilizing Plant Detritus

Attempts to experimentally feed detritus to consumers reveal a tangle of conflicting results. Some confusion results from using different detrital substrates with different nutritional composition. More confusion results from the criteria utilized; some investigators have monitored for simple assimilation, but others have followed subsequent growth. Govoni et al. (1982) pointed out many technological difficulties in attempting to estimate rates of assimilation.

In general, it seems that most experimental results suggest that:

(1) Detrital substrates, which are low in nitrogen and high in refractive carbohydrates (such as detritus originating from the marsh grass, Spartina alterniflora, are not assimilated to any great extent by consumers (Johannes and Satomi 1967; Prinslow et al. 1974; Kirby-Smith 1976; Wetzel 1975; Williams 1981).

(2) Detrital substrates, which are high in nitrogen and low in refractive carbohydrates (such as marine macroalgae and tidal freshwater plants including arrow-arrum, Peltandra virginica), may be assimilated directly by detritivores (Newell 1982; Findlay and Tenore 1982; Bowen 1980).

(3) The attached microorganisms (and microbial exudates) on both types of detritus can be assimilated by detritivores (Newell 1965; Johannes and Satomi 1967; and many others).

(4) Coprophagy, or reingestion of fecal matter, plays an important role in allowing bacterial recolonization to enhance the nutritional value of decaying detritus (Newell 1965; Frankenberg and Smith 1967).

(5) Many feeding and stomach-content studies suggest that detritivores ingest a mixture of detritus and living algal material (Odum 1968; Odum 1970b; Odum and Heald 1975; Kirby-Smith 1976).

This last point is exceedingly important. It suggests that a diet limited to only detritus is unnatural and insufficient. Virtually all filter- and deposit-feeding detritivores feed in a way that guarantees detritus and algal particles will be ingested. Therefore, studies that limit an animal's diet to detritus and then conclude it is not a useful food source may be misleading.

Equally misleading are laboratory experiments that utilize artificially produced (or artificially collected) detritus. This material may or may not reflect what is available in the real world or what an organism will consume in the real world. Odum (1968) has shown the striped mullet, *Mugil cephalus*, is highly selective about what it eats, utilizing an elaborate filtering device to reject unsuitable detritus particles.

Feeding studies have uncovered considerable information, but we should be careful in our interpretation of this information. The diets of detritivores are extremely complex, often including some animal material. Attempts to draw conclusions about the importance of the detrital substrate, attached microbes, microbial exudates and algal material are probably premature at this time. Recent evidence (Peters and Lewis 1984) suggests that supposedly unassimilatable substrates, such as *Spartina* detritus, may be assimilated by consumers such as menhaden, which have some cellulase activity in their digestive tracts.

SECONDARY EVIDENCE

The direct evidence concerning the trophic value of vascular plant detritus is extensive, but contradictory. Worse yet, the prospects of untangling the conflicting data in the near future are not promising. We can conclude that many primary consumers ingest quantities of detritus (along with algae). But determining how much is assimilated, what is assimilated, and how this contributes to long-term growth and reproduction, when compared to algal sources, is an exceedingly complex research question.

These primary sources of evidence are really a reductionist approach to the problem. Like any reductionist methodology in science, they offer precision, but at a great time cost. While we're waiting for the reductionist answers to accumulate so that fundamental questions can be answered (and it may not occur in our lifetime), it is interesting to take a holistic look at the question through indirect pieces of evidence. As with any holistic approach, the danger lies in over-simplification and generation of superficial information that may be misleading.

Proximity of Major Fisheries to Sources of Detritus

Many of the world's major inshore fisheries for shrimp, crabs and fish lie in geographical proximity to regions that produce copious quantities of vascular plant detritus (i.e. mangrove swamps, coastal marshes, sea grass lagoons). Examples along the United States coast include the fish and penaeid shrimp fisheries adjacent to (a) the coastal *Spartina* marshes of the southeastern Atlantic and Louisiana coasts, (b) the mangrove-dominated Everglades estuary of southern Florida, and (c) the sea grass beds of Laguna Madre in Texas. Other examples can be cited, including the shrimp fisheries off the mangrove areas of Central America, Africa and Southeast Asia.

This apparent relationship may be misleading. Enhanced fishery production could be related to habitat value and protection offered by the features that produce detritus---marsh grasses, sea grasses and mangroves. And the examples above (*Spartina* marshes, Everglades mangrove swamps, etc.) also are affected by significant quantities of inflowing fresh water containing high concentrations of dissolved nutrients. It is possible that high fisheries production in these areas can be traced to high algal production caused by freshwater inputs of nutrients.

Correlations of Fisheries Production and Wetlands Area

Turner's (1977) paper correlated average annual commercial yields of penaeid shrimp with the area of intertidal wetland vegetation. He found a strong positive correlation (P = 0.01). On a regional basis, inshore shrimp yields correlated highly with the area of wetland vegetation, but they had little or no positive correlation with the area, average depth or volume of estuarine water.

Although this is intriguing evidence, correlations tell us nothing about cause and effect. It is possible that this high correlation resulted from another related factor. For example, shrimp may utilize intertidal marsh grasses for their habitat value---as protection from predators. Then areas with large expanses of marsh grass would provide favorable shrimp habitat, but not necessarily a food source. Schaaf and Peters (1982) pointed out the problems these studies have in defining system boundaries. Where does one functional nursery area or fishing region stop and the next begin?

In a later paper, Turner et al. (1979) suggested that offshore (continental shelf) primary and secondary production are more or less directly coupled to estuarine primary production. Yoder et al. (1981) agreed in respect to the inner continental shelf, but felt that primary and secondary production on the outer continental shelf depends on open ocean physical processes such as ocean upwellings.

Declines in Fisheries Catches in Response to Wetland Destruction

Fisheries catches fluctuate over time in response to a variety of density-dependent and density-independent factors. Odum (in press) mentions several cases in which catastrophic declines in fisheries yields appear to coincide with extensive wetland degradation. But these cases are not numerous or well documented.

As an example, Krishnamurthy and Jeyaseelan (1980) report prawn production from a partially protected Indian mangrove swamp to be 110 kilograms/hectare/year; fish production was 150 kilograms/hectare/year. In a nearby estuary where the mangroves were damaged or removed by man, prawn production was 20 kilograms/hectare/year and fish production 100 kilograms/hectare/year.

This is highly circumstantial evidence. Secondary production in the areas may never have been comparable. Declines in the altered areas may have been caused by siltation, lack of suitable habitat and other factors unrelated to detritus as a food supply.

A similar example, equally flawed by possible multiple causality, was reported by Woodburn (1961). He compared commercial fisheries catches from Lake Worth in Palm Beach County, Fla., before and after a dredge-and-fill operation obliterated large tracts of mangroves and sea grasses. In comparing catches before (1950) and after (1956) the dredging and filling, he found dramatic declines. Channel bass declined from an annual catch of 25,148 to 300; spotted sea trout dropped from 336,936 to 1,258; and snook slipped from 21,445 to 8,989.

A multiplicity of factors is involved in a dramatic drop in fisheries yield (e.g. loss of habitat, possible increased turbidity and pollutant concentrations). The role of detrital loss in secondary production is not clear. A few well-documented studies before and after the destruction of a major detritus-producing area might give us a better idea of how reduced detrital input quantitatively affects secondary production. This would be particularly useful if detailed trophic studies could be incorporated into the experiment.

Stable Isotope Data

Beginning in the 1960s, stable carbon isotopes were used to unravel marine food chains (Parker 1964; Smith and Epstein 1970; Nissenbaum and Kaplan 1972; Eadie and Jeffrey 1973; Haines 1976, 1977; Thayer et al. 1977; Haines and Montague 1979; Fry 1981; Schell 1983). The delta-13 carbon of an organism may reflect the stable isotope ratio of its trophic carbon source. Using this technique, Haines (1976, 1977) concluded that phytoplankton and other algal sources were the most important energy sources in Georgia estuaries and that detritus originating from the marsh grass (Spartina alterniflora) was less important.

Recent evidence has suggested that Haines's conclusions may have been premature and incorrect. Peterson et al. (1981) showed microorganisms associated with decaying Spartina may have a different delta-13 carbon signature from their marsh grass substrate. They hypothesized that this might be due in part to bacterial use of energy-rich reduced inorganic sulfur compounds to fix carbon from marsh waters. Therefore if a detritivore assimilates a small quantity of these attached bacteria, its stable carbon signature could be significantly altered.

Examination of the stable carbon literature shows that the method works best when the consumer obtains its carbon from a single source with a single signature (i.e. phytoplankton). If the consumer assimilates materials from a variety of sources (i.e. phytoplankton, benthic algae, vascular plant detritus originating from terrestrial, sea grass, mangrove, or marsh grass sources, sulfur oxidizing bacteria), as is the case with many estuarine primary consumers (Odum and Heald 1972), then the results of stable carbon analyses become extremely difficult to interpret.

If an organism feeds on carbon substrates with widely separated carbon signatures (i.e. mangrove detritus and seagrass detritus) and on nothing with intermediate carbon signatures, then it may be possible to reach rational conclusions concerning the importance of the carbon sources.

Since most estuarine consumers feed on many materials with a variety of carbon signatures, the use of a single isotope is probably not valid. Zieman et al. (in press) have suggested that multiple isotope techniques offer a more powerful tool. For example, Macko (1981) demonstrated that stable isotopes of nitrogen can be used like isotopes of carbon to trace ecological and geochemical pathways. Sulfur isotopes may offer the same potential (Macko, personal communication).

The combination of these three isotopes and possibly the D/L amino acid ratio (Zieman et al. in press) offers a powerful tool to understand the complex trophic relationships found among estuarine consumers. For this reason, most of the conclusions from early stable carbon research, particularly in reference to the relative importance of algae and vascular plant detritus to estuarine consumers (e.g. Haines 1976, 1977), should be viewed with skepticism.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

The following points can be drawn from the preceeding discussion.

(1) Algal sources provide a significant food source and growth impetus for estuarine consumers.

(2) Direct analytical and experimental evidence suggests that vascular plant detritus is (a) ingested, (b) partially assimilated and (c) can support some growth of estuarine consumers. Significant questions remain to be resolved about the portion of the detritus complex that is assimilated and the degree to which a mixed diet of algae and detritus provides the best growth.

(3) Indirect, circumstantial evidence suggests a close relationship exists between the magnitude of detritus production from marsh grasses, mangroves and sea grasses, and nearby fisheries production. Although much of this evidence is indirect and correlational, the recent work of Zieman et al. (in press) suggests that pink shrimp (Penaeus duorarum) have a carbon signature that approximates either mangroves or sea grasses, depending on their nursery area.

In summary, the most important questions concerning estuarine productivity revolve around the comparative trophic importance of vascular plant detritus versus algae. Related to this question is the degree to which coastal fisheries organisms utilize detritus as an energy source and the impact of removing large tracts of detritus-producing swamps, marshes, and sea grass beds.

Research Priorities

Given this set of questions, the following research priorities appear to be important:

(1) Utilization of multiple isotopes (stable carbon, nitrogen and sulfur ratios) and other techniques to identify indirectly the apparent source of organic carbon for estuarine primary consumers.

(2) Studies (with an emphasis on new techniques such as D/L amino acid analysis) to determine the chemical composition and nutritional status of: (a) detritus of different origins such as mangrove, sea grass, and marsh grass; (b) different components of the detritus complex (e.g. amino acid content of detritus-associated microbes versus microbial exudates on the particle surface); and (c) detritus complexes of different age and particle size.

(3) Laboratory feeding experiments to ascertain details about the utilization of vascular plant detritus by consumers. This would include studies of: (a) degree of assimilation of total detrital nitrogen and carbon; (b) comparative assimilation of different components of the detritus complex (i.e. substrate, microbes, microbial exudates, etc.); and (c) the relative ability to digest and assimilate the detritus complex versus algal material.

(4) Growth and ecological efficiency studies in large tanks or small ponds to investigate consumer diets of: (a) detritus of various types and chemical composition, and (b) detritus and algae in various ratios ranging from pure detritus to pure algae.

(5) Controlled field experiments in ponds to see if detritus aquaculture is feasible. This would involve attempts to grow organisms such as freshwater crayfish, mullet and others in pond systems that receive inputs of properly conditioned vascular plant detritus.

(6) Carefully planned before-and-after studies to investigate the local impact of marsh, mangrove, or sea grass removal on fisheries organisms. Projects would have to be coordinated with previously approved grandfather clause development of coastal areas. The research project would be designed to separate the effects of trophic alterations (i.e. decreasing detritus input or increasing algal productivity) other effects such as direct habitat destruction.

(7) Field investigations and laboratory experiments to investigate the potential and realized importance of hypothetical reduced-sulfur food webs. This might include direct examination and immunological studies to test for the presence of sulfur oxidizing bacteria in consumer diets.

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ESTUARINE PRODUCTIVITY: RELATING TROPHIC ECOLOGY TO FISHERIES

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The marsh, estuarine and nearshore ecosystems of the southeastern United States provide about half of the nation's total recreational and commercial fishery landings. Unfortunately, the quantity and environmental quality of these shallow habitats are being degraded by coastal development, with an implied risk to fisheries. Success in maintaining and enhancing their yield will depend in part on our knowledge of factors affecting fish production. While many kinds of information are desired, one of the most important is a clear understanding of the coupling between primary and secondary production. Broadly defined, this coupling includes nearly all food web interactions. However, its common use refers to consumption of plants.

Most of the recent efforts to describe this coupling involve reductionist attempts to demonstrate that detritus is an important food source. Because the preceding presentation (Odum 1984) reviewed the main research areas, this paper will be more limited. We will briefly discuss some of the conceptual and methodological problems that may have limited promise. The main focus is on the approaches, conclusions and hypotheses that are part of an ongoing effort to describe the role of detritivory in fishery production.

From the previous paper (Odum 1984), it appears that recent research has not resulted in any notable advancements. This is probably due to a variety of reasons, including lack of direction. If the approaches tried or suggested by various investigators are equally relevant, then current fact-gathering may be a nearly random activity. The problems encountered in unraveling the complex coupling between primary and secondary production might seem intractable. However, our progress will be more rapid if research is appropriately directed. Other hindrances to an understanding of trophic relationships include narrow individual perspectives and a less than optimum mix of reductionist and holistic approaches.

A shift in emphasis from the general topic of this group of papers (linking primary and secondary production) to a more specific and practical topic (linking primary production and fishery yield), has several advantages. One practical advantage is that it encourages consideration of the same ecological processes, but in a more relevant context. Understandably, society and funding agencies have little concern about the vague concept of secondary production, yet readily appreciate the value of fisheries. Concentrating on the fishery aspects will also focus attention on the potential relevance of any information gained. For example, the presence of a direct link from vascular plant detritus to fish is considerably relevant to the habitat manager's argument that sea grass meadows and marshes should be preserved. In addition, fishery managers can use knowledge of trophic pathways supporting a multispecies fishery to help them predict how some populations of important species may be affected by the harvesting strategies for others.

Scientific reasons for stressing the trophic links to fish, while more abstract, are at least as important as the need to retain relevancy. An understanding of the coupling between primary and secondary production requires information about processes operating at higher trophic levels. For example, fish are as important as primary production and detritus, though the latter seem to receive more attention. Contemplation of fish's roles serves two purposes. First, it encourages a more holistic approach. Second, it focuses attention on the vast body of fishery data that is frequently ignored by ecologists, including food habits, biomass, production and harvest rates of many ecologically important species.

The general idea that detritus utilization represents a major pathway in estuarine energy flow is supported by various observations, but it can never be proven. In fact, according to Sir Karl Popper's logic, we can never prove a general statement from specific ones (Dolby 1982). Our inability to verify any general idea would not change even if the idea were stated as a specific, testable hypothesis. We accept or reject hypotheses rather than prove them. Just as the theory of evolution required thorough examination before it was accepted as a biological law (Futuyma 1983), the generalization that detritus is a major estuarine food must undergo considerable scrutiny. It is clear from the preceding paper (Odum 1984) that investigators disagree about the relative importance of detritus. Perhaps the easiest way to reconcile the relevant observations, through the logic of Occam's razor, is to accept an important trophic role for detritus while explicating apparent contradictions.

It is difficult to reach a concensus about the importance of detritus as a major food source because: (1) the term "detritus" is used in different ways --- usually without an explicit definition, (2) the experimental methods used are frequently artificial and questionable and (3) the animals examined are frequently of only minor importance in overall estuarine energy flow.

In many instances, the term "detritus" seems to refer to visually recognizable vascular plant fragments. However, such fragments may be of little relevance if the major pathway of detrital utilization is through "amorphous aggregates" (Bowen in press).

Because it is difficult to collect natural detritus in the same way a detritivore does, most experiments depend on simulated detritus. If caution is exercised in experimentation, the difference between natural and simulated detritus may be small and unimportant. However, the difference is frequently substantial, unacknowledged and probably important. Even if the detritus is adequate, the results may be misinterpreted if it is offered as an unnatural fraction of the diet. Another frequently ignored, but potential problem is that a natural dietary item may appear indigestable if it is presented as a sudden dietary change. The potential for digestive enzyme induction should not be ignored. Although well designed research may show which types of detritus a species can utilize, the information will be of limited value in substantiating the importance of estuarine detritus if the species is not abundant and widely distributed.

Menhaden are particularly attractive candidates for studies of detrital utilization because of: (1) their abundance, (2) ubiquitous distribution in both Atlantic and Gulf Coast estuaries, (3) the presence of extensive fishery data bases and (4) reports of detritus being found in their stomachs (Darnell 1958 and 1964). These fish, so abundant that their harvest constitutes about half of the total United States fishery landings, are also a major link in the food chain of predators such as striped bass, bluefish and mackerel. Documenting that detritus as a major food of such a dominant species may substantiate its importance in estuarine food chains.

Recent efforts to determine the role of detritus in trophic ecology of juvenile Atlantic menhaden have included measures of feeding selectivity, visual and chemical analysis of stomach contents, deterministic models of energy flow, measurements of digestibility and enzyme assays. While each data set and technique has its shortcomings, in total they strongly support the view that juvenile Atlantic menhaden eat and digest large quantities of detritus. To place this inference in proper perspective, the conclusions and some criticisms of these studies will be presented in near chronological order.

The results of a laboratory feeding experiment, using both algae and detritus (estuarine particulate matter that settled to the bottom of a holding tank), indicated that menhaden readily eat both foods, but select the larger of two available sizes (Peters 1972). This observation of detrital ingestion may be questioned as an artifact of laboratory conditions.

Visual analysis revealed that nearly three-fourths of the stomach content of juvenile fish that had ted in an estuary (Peters and Kjelson 1975) was detritus (primarily amorphous material of unrecognizable origin). Later observations (unpublished) indicated that juveniles, throughout much, but not all of the range (Florida to New York, but not New England), had similar diets. These indications of detrital ingestion are questioned on two grounds: (1) the unidentified

material could be easily ruptured cells rather than amorphous detritus, and (2) the material might have been accidentally eaten while the fish were searching for algae.

Seeing no immediate or easy solution to the problem of describing juvenile menhaden's diet via field or laboratory studies, we decided to examine other information for clues about their role in the systems trophic ecology (Peters and Schaaf 1981). Our goal, to estimate energy flow through the population, was accomplished with reasonable accuracy because the species is so economically important that it has been heavily studied for many years. The substantial information base allowed us to calculate and compare several independent estimates of population size and food requirements, thus permitting us to reject any data or techniques that seemed biased. Estimates of the food required by the juvenile population during late summer were about the same as estimates of the average annual phytoplankton production rate. Assuming there were other competitors for this phytoplankton, we proposed that an alternative energy source, such as detritus, is necessary. Since this conclusion is based on indirect evidence, it is open to the criticism that it is an oversimplification and raises the reasonable possibility of a phytoplankton shortage.

A subsequent effort that described material flow through a multispecies fishery in estuarine and coastal waters (Schaaf and Peters 1982; Peters and Schaaf 1983 and unpublished manuscript) related commercial and recreational fishery harvests back through the food chain to primary production. The amount of food required by the trophic chains supporting the fishery yield was calculated by using intermediate trophic levels based on dietary studies of yield species. From our calculators, it appears that (1) menhaden require about one-third of the total energy needed by the food webs supporting all the yield, and (2) an organic subsidy (e.g. vascular plant detritus) is needed as a supplement to algal production.

If menhaden and other fishery food chains depend on detritus as an energy source, vascular plants are its most likely origin. To determine the source and composition of the "detrital-like material" in menhaden stomachs, additional visual and chemical analyses were performed (Lewis and Peters unpublished manuscript). Direct counts and volumetric estimates indicated that bacteria, meiofauna, zooplankton and unruptured algae were not substantial dietary components, and that the "detritus" was once again of undiscernible origin. As revealed by a chemical analysis, protein constituted about one-half the organic material. This can be explained by the presence of ruptured algae, bacterial byproducts and the reaggregation of dissolved amino acids. Further measurements showed that about one-fifth of the organic matter was cellulose. Therefore, vascular plants were implicated as a substantial source of amorphous detritus. Clearly the presence of this cellulose needs verification.

We next studied, by experimentation, whether menhaden could digest the vascular plant materials they consumed. We settled on ground Spartina as an appropriate experimental food because we could not collect the natural amorphous material in the same way as menhaden collect it, and because Spartina is the probable source of the cellulose we found in the fish's stomachs. Fish were brought into the laboratory, conditioned on similar food for several weeks, then fed the ground Spartina. We found that the carbon, organic matter and cellulose it contained were readily digested (i.e. with 75% efficiency). The results of dietary studies, and our inference that an additional nonalgal food source was needed to sustain the population, had led us to expect this result. However, these high digestibilities were contrary to expectations based on feeding studies in which different techniques and species were used. Because of this contradiction, independent verification may not bring acceptance unless the data are accompanied by a description of digestive physiology involved.

In preliminary studies to verify the digestibility of Spartina, we found that juvenile menhaden possess enzymes in the gut capable of partially digesting cellulose. We assumed they contained B-1,4 glucan cellobiohydrolase and cellobiase (Berghem and Petterson 1973) since extracts from their digestive tracts hydrolyzed carboxymethyl cellulose to reducing sugars.

Whether menhaden have any additional enzymes that may be required to digest the cellulose they consume is uncertain. Speculation that cellulase may be endogenously produced is supported by the preliminary observation that enzyme activities are greater in extracts from the pancreas and intestine than in extracts from more anterior portions of the digestive tract. We have no basis for further speculations of whether such enzymes might be produced by the fish or by symbiotic microorganisms.

From the studies of menhaden and their role in estuarine ecology, we conclude that these fish ingest and utilize large quantities of detritus. The same information also supports the more general statement that detritus represents a major pathway in estuarine energy flow. The fact that science cannot verify such statements should be of little concern. A more important consideration is whether the evidence is clear enough to assist society in making more reasonable management decisions.

One of the prime justifications given for preservation or rehabilitation of marshes, swamps and sea grass beds is that the detritus they produce is extremely important to fishery food chains. Since the food chain information is incomplete, it is difficult to determine how particular habitat modifications or rehabilitations would affect fisheries.
We suggest three research areas that may provide information useful in the evaluation of food chain impacts:

1. We need to describe the role of nonyield forage fish. What is the diet of the species eaten by predatory fish? How much food do they consume? What fraction of their mortality is consumed by yield species?

2. The species that are abundant and consume large quantities of detritus warrant study to determine the source and composition of the detritus and its digestibility.

3. Detrital formation processes need to be described better. Particular emphasis

is needed on the energetic efficiency, sources and mechanisms of amorphous aggregate formation.

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MECHANISMS LINKING PRODUCERS AND CONSUMERS IN SALT MARSH ESTUARINE ECOSYSTEMS

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SOME TYPES OF MECHANISMS LINKING PRODUCERS AND CONSUMERS

In estuaries, as in other ecosystems, consumers and producers are coupled by feeding relationships. Producers significantly affect consumers. The amount of consumable biomass may be important to consumers, but the chemical quality of the organic matter produced may be of greater importance than the amount produced. Food quality largely determines palatability and assimilability.

In turn, consumers affect producers. Evidence shows that consumption by animals restricts the abundance of producers in various habitats. Further, consumption can lead to marked changes in the species composition of producers.

There are other interactive mechanisms between producers and consumers that are not so obvious. One important class of such non-feeding interactions concerns the fact that producer-consumer interactions occur in an arena. The physical architecture of the arena has major effects on the outcome of the producer-consumer interaction.

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Producer-consumer interactions have evolutionary dimensions --- an area of current interest but beyond the scope of this brief review. This paper is limited to an examination of some trophic interactions between producers and consumers, and of producer architecture on consumption, in salt marsh estuary ecosystems.

EFFECTS OF PRODUCERS ON CONSUMERS

Herbivorous consumers seldom eat the entire crop of producers in coastal ecosystems. The data vary on how much of annual primary production is eaten by grazers (Table 1), but suggest that grazing on phytoplankton tends to be more intense than grazing on vascular plants. The one high value for North Carolina salt marshes is the result of an anomalously large gathering of snow geese. Although not shown in Table 1, macroalgae lie, as a group, somewhere between phytoplankton and vascular plants.

These differences in susceptibility to grazing stem from differences in nutritive quality, particularly nitrogen content, and from the presence or absence of anti-herbivore compounds.

The microalgae found in plankton and benthos tend to have lower carbon (C) to nitrogen (N) ratios than macroalgae or vascular plants (Table 2). If C/N is a rough indicator of nutritive value, it is evident that one-celled algae are nutritionally better than macroalgae and vascular plants, and might therefore be consumed more readily.

An example of the importance to grazers of plants containing nitrogen comes from our work on experimentally enriched salt marsh plots (Valiela et al. 1975; 1982). In these field plots, nitrogen addition led to a threefold increase in biomass (Fig. 1, top; Valiela and Teal 1974). The increased amount of biomass was not sufficient to account for the increase in grazers. The sevenfold to eightfold increase in insect herbivores (Fig. 1, bottom) was attributable to growth prompted by the increased nitrogen (Fig. 1, middle; Vince et al. 1981) of the plants within the enriched plots. Note that the differences in nitrogen content are seemingly small, yet they decisively affect herbivores. The importance of

TABLE 1

Percent of primary production by estuarine and coastal plants and phytoplankton consumed by herbivores.

Vegetation Type	% of primary production consumed by herbivores	References
Vascular plants		
Eelgrass, North Sea	4	Nienhuis & Van Ierland (1978)
Salt marsh, Georgia	4.6	Teal (1962)
Salt marsh, N. Carolina	58	Smith & Odum (1981)
Mangrove swamp, Florida	9-27	Onuf et. al. (1977)
Phytoplankton		
Long Island Sound	73	Riley (1956)
Narragansett Bay	0-30	Martin (1968)
Cochin Backwater, India	10-40	Qasim (1979)
Off California	23 (7-52)	Beers & Stewart (1971)
Peruvian Upwelling	92, 54-61	Walsh(1975) Whitledge (1978)

TABLE 2

Approximate carbon to nitrogen ratios in some marine producers. Data adapted from compilation in Valiela (1984) from various sources.

Vegetation Type	C/N
Microalgae	
Diatoms	6.5
Greens	6
Blue-greens	6.3
Peridineans	11
Bacteria	5.7
Fungi	10
Marine macroalgae	
Browns (*Fucus*, *Laminaria*)	16-68
Greens	10-60
Reds	20
Marine vascular plants	
Zostera marina	17-70
Spartina alterniflora	24-45
Spartina patens	37-41

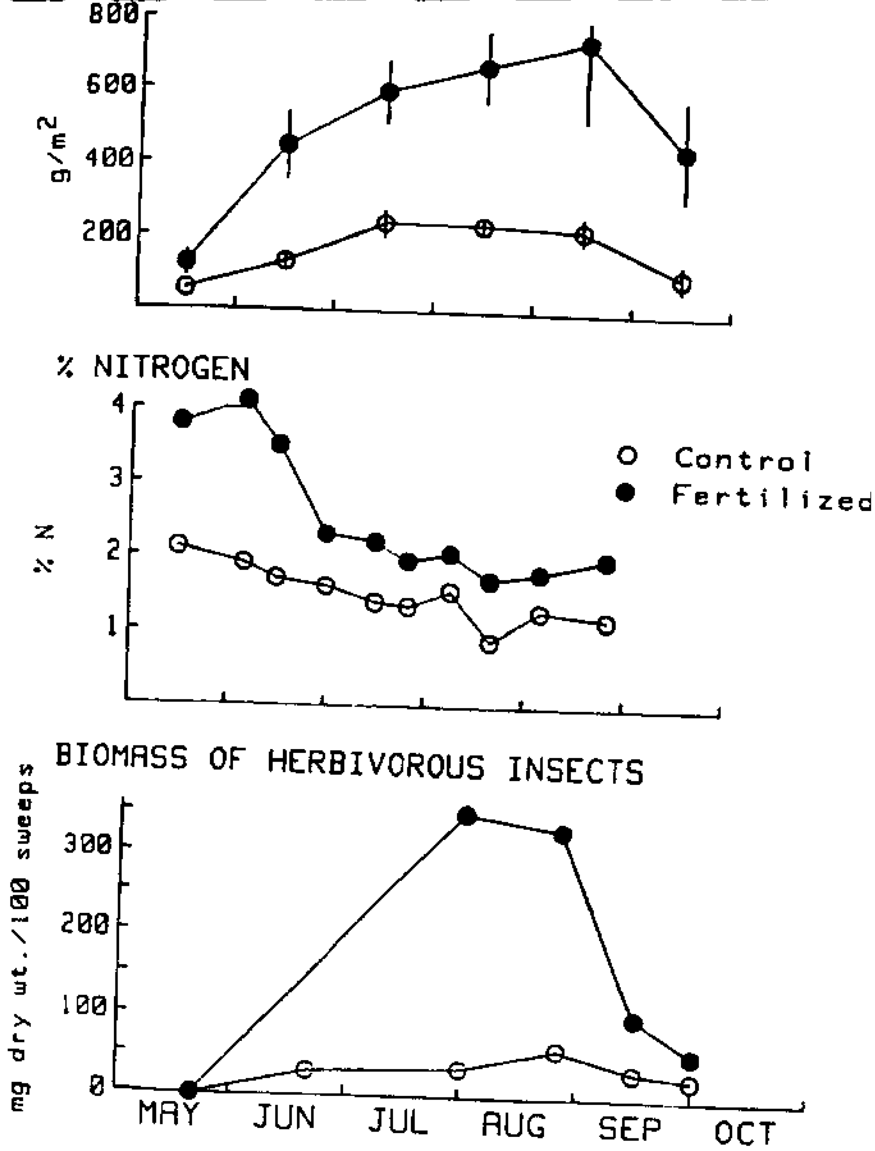

FIGURE 1

Biomass and percent nitrogen in *Spartina alterniflora* and biomass of herbivorous insects in canopy of *S. alterniflora*. Measurements taken in experimentally fertilized and control plots. Data of I. Valiela and S. Vince.

small differences in nitrogen content to susceptibility to grazers seems to be a general phenomenon (Mattson 1980).

Consumption by herbivores does not often lead to disappearance of the vegetation (Table 1), even in nitrogen-enriched vegetation. Current research (reviewed by Swain 1977; Rosenthal and Janzen 1979; Norris and Fenical 1982; for example) demonstrates that many secondary metabolites in plants reduce grazing pressure by lowering palatability and assimilability. Feeding by Canada geese on salt marsh vegetation, for example, is inhibited by certain concentrations of ferulic acid, one of the two most common cinnamic acids in *Spartina alterniflora* (Buchsbaum et al. 1981). In fact for geese, the palatability of several species of marsh plants was largely determined by the concentration of such phenolic acids rather than by nitrogen content (R. Buchsbaum, WHOI, unpublished data).

The assimilation of plant biomass by grazers also is affected by secondary metabolites. For instance, the assimilation of organic compounds and proteins by Canada geese is negatively related to the content of phenolic compounds associated with cell walls, and the lignin concentration of the grasses (R. Buchsbaum, unpublished data), respectively.

The chemical composition of organic matter produced by plants is also important to organisms other than herbivores. Herbivores consume only a small portion of the annual production of coastal producers, especially in the case of vascular plants (Table 1). The result is that most of producer biomass in coastal waters enters the detrital food web, and estuarine consumer species often feed on the abundant detritus.

Feeding on dead organic matter, however, is a trade-off between the high abundance of detritus and its low nutritional quality. Not only are some nutritionally valuable soluble compounds of live plants lost by leaching soon after death of the plant, but some of the secondary metabolites still remain in detritus.

Feeding in detritus, regardless of its abundance, has several drawbacks: low palatability, low assimilation, and consequently, low growth. We can show, for instance, that the higher the content of ferulic and p-coumaric acids in detritus, the lower the palatability to salt marsh snails and amphipods (Valiela et al. 1979; Valiela and Rietsma, in prep.). In contrast to the hierarchy observed with geese, the nitrogen content of detritus is more important than that of ferulic acid as a cue to feeding. The snail *Melampus bidentatus* prefers to feed on detritus with enhanced nitrogen content (Fig. 2, left histogram). At low nitrogen contents usually found in relatively new detritus (two weeks or so in age), the presence of ferulic acid in high quantities deters feeding (Fig. 2, middle histogram). If, however, nitrogen content is high (comparable to that found in detritus eight months to nine months in age), the effect of ferulic acid is eliminated (Fig. 2, right histogram). Palatability is thus affected by both cues, and if nitrogen is sufficiently high, it overwhelms the effect of ferulic acid.

The efficiency of assimilation of detritus is generally lower than that achieved with live producers or animals as food (Fig. 3). Carnivores have a modal assimilation efficiency of 80 percent to 100 percent, herbivores about 60 percent to 80 percent. Detritivores, on the other hand, have a modal assimilation efficiency of 0 to 20 percent. The low assimilation efficiency is not a feature of the species of consumers involved but rather of detritus as a food. For instance, amphipods, polychaetes, and holothurians have assimilation efficiencies from 7 percent to 22 percent when feeding on dead organic matter. The assimilation efficiencies of these consumers rise to 40 percent to 83 percent when microalgae or microbes are eaten (Hargrave 1980; Cammen 1980; Yingst, 1976).

The result of low palatability and assimilation of detritus is low growth on detrital diets. We reared *Fundulus heteroclitus*, a fish that ingests large amounts of detritus (Daiber 1982), on detrital and other diets (Prinslow et al. 1974). No growth was recorded when the diet consisted of detritus. In more recent but similar work, an age 0 fish showed no growth on a purely detrital diet (Table 3, top). The detritus eaten included the microbes and meiofauna attached to detritus. Growth was measured as the change in

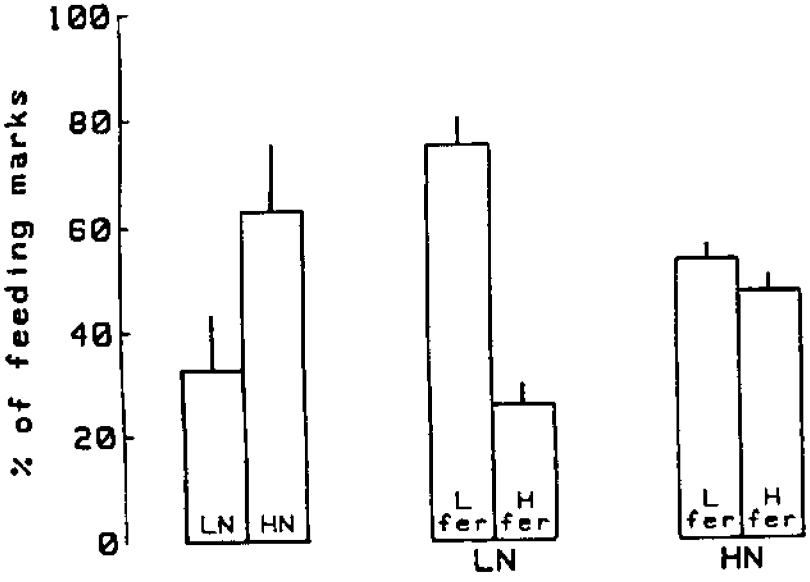

FIGURE 2

Feeding preference tests in <u>Melampus bidentatus</u>. These choice experiments were done by counting feeding marks on the surface of agar suspension of detritus (Valiela et al. 1979) to which albumin (a nitrogen source) (shown as HN) or ferulic acid (shown as Hfer) were added. The natural concentrations of nitrogen and ferulic acid in nine-month-old detritus are shown as LN and Lfer. Adapted from Valiela and Rietsma, in prep.

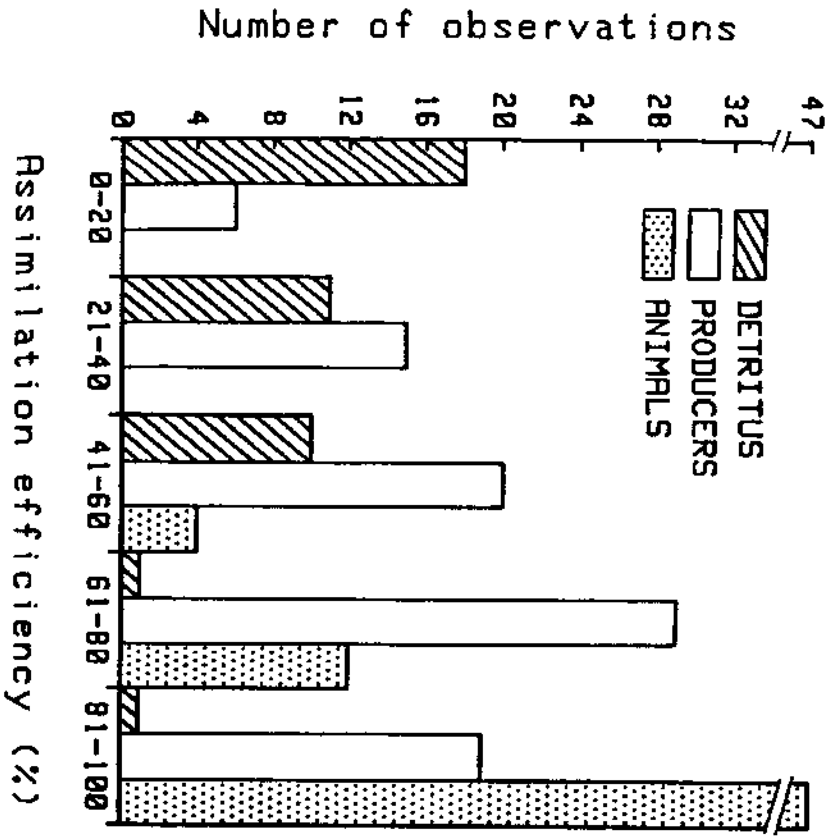

FIGURE 3

Distribution of assimilation efficiencies in a wide variety of consumers that fed on detritus, live producers or animals. Adapted from Valiela (1984).

TABLE 3

Results of laboratory experiments in which *F. heteroclitus* of age classes 0 and 1 were fed on three different diets [small invertebrates (age 0) or mussel flesh (age 1), filamentous algae or *Ulva*, and detritus from creeks]. Data are std. error (unless otherwise specified); for 0 class fish after nine days of incubation; for 1-year-old fish, representative data for a 1-month experiment. Data courtesy of Charlene D'Avanzo, Mark Abad and David White.

AGE 0 FISH

Diets	Chi^2 value final vs. initial size distribution	% Mortality	Condition factor (wt. x 10^{-5}/ length)
Animal	5.5*	6	135±12
Algal	9.4**	93	107
Detrital	3.9 N.S.	60	91±5

AGE 1 FISH

Diets	Daily wt change (g day^{-1})	% Mortality	O_2 consumption (nmol O_2 g^{-1} min^{-1})
Animal	3.7±1.1	0	564±42
Algal	-4.9±1.4	77	
Detrital	-9.5±1.7	54	821±78

the size distribution of 15 fish over a nine-day period. Mortality of the fish fed on detritus was high, and their conditions were poor. Fish of the same age that fed on algae grew, but suffered high mortality. High growth, low mortality and best condition were achieved on an animal diet.

Similar results were obtained in an experiment with one-year-old fish (Table 3, bottom). Growth and low mortality were possible on an animal diet, but not on a detrital (or algal) diet. The respiration rate of fish on detrital diets was high [as it is for copepods (Chervin 1978)], suggesting that detritivory requires high energy expenditures, perhaps due to metabolism of resistant compounds.

Similar effects of detritus feeding on growth may be common for other marsh estuary species (Fig. 4). Werme (1981) performed gut analyses on common fish in Great Sippewissett Marsh, Cape Cod, Maine, and measured growth of the fish over time. Her data on gut contents can be compiled into three categories (animal, algal and detrital) for each species of fish. The faster growth rates are associated only with high contents of animal foods (Fig. 4). This pattern is striking even if animal foods are digested faster than other foods.

The poor performance of detritivores must be related to the chemical composition of detritus. Carol Rietsma has done growth experiments with *Melampus bidentatus*, a detritivorous salt marsh snail, that highlighted how chemistry of detritus affected growth rate.

M. bidentatus fed a diet of new (2-week-old) detritus low in nitrogen and containing moderate amounts of lignin (Valiela et al. in press) grew slowly (Fig. 5, open circles). Snails grew faster when fed older detritus (8-month-old, open triangles), richer in nitrogen but about equal in lignin (Valiela et al. in press). Thus, the additional nitrogen may have prompted the higher growth.

Snails fed on new detritus from nitrogen-fertilized plots (black circles) grew faster than on young control detritus. This was most likely the result of the enhanced nitrogen of detritus from fertilized plots (Fig. 1, middle).

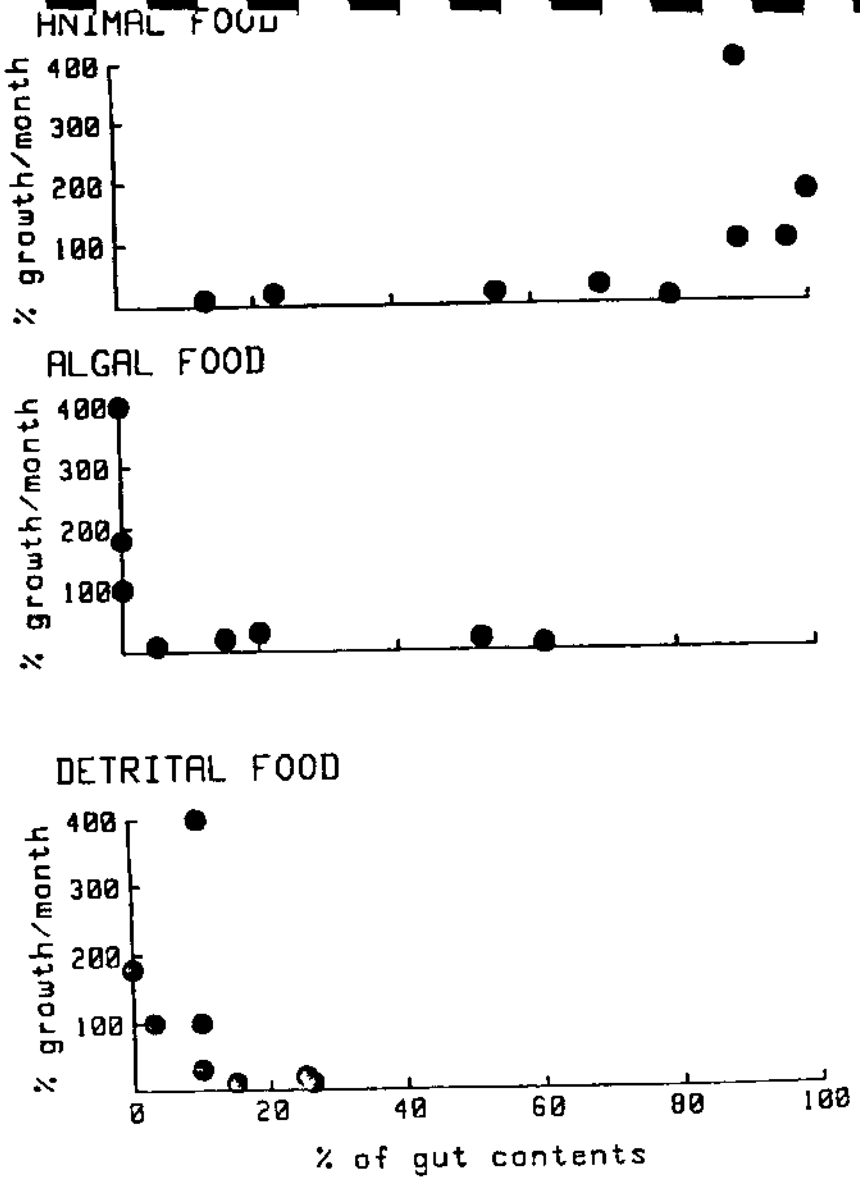

FIGURE 4

Relation of growth rate (calculated as increase in length of fish per month) to diet as shown by gut contents in nine species of estuarine fish. Adapted from data in Werme (1981). Note that each species appears in each of the three graphs, since these species fed on the three kinds of food.

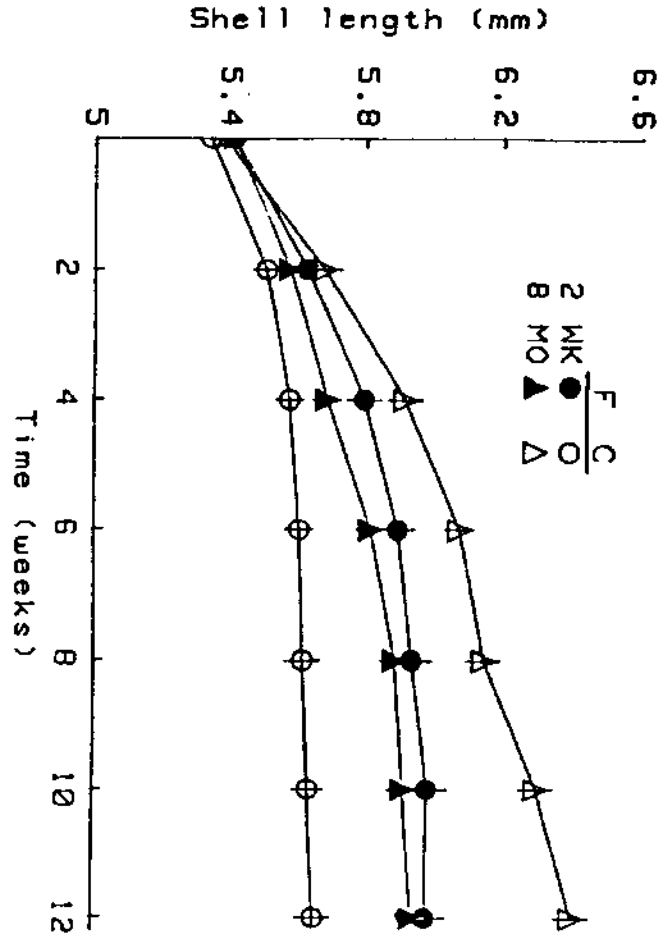

FIGURE 5

Growth of *Melampus bidentatus* on detritus of different chemical composition. Snails were reared on four types of detritus: young (2-week-old) and old (8-month-old) litter collected from control (C) and experimentally fertilized (F) salt marsh plots. Data courtesy of Carol Rietsma.

Intriguingly, snails fed on old fertilized detritus (black triangles), where age and fertilization combined to furnish the highest nitrogen (Valiela et al. in prep.). This detritus did not provide faster growth than young, fertilized detritus. The enrichment led to an increased degradation of labile compounds, so that lignins --- the major refractory compounds left --- were in highest concentration (Wilson et al. in prep.). Complex phenolic compounds, such as lignins, bind protein and make its nitrogen unavailable to consumers (Van Sumere et al. 1975; Robinson 1983; Rice 1982). It seems reasonable that the higher the concentration of lignin, the larger the proportion of nitrogen that will be bound and hence unavailable to consumers.

These results suggest that nitrogen and phenolics are important to detritivores. More significantly, the data imply that nitrogen may be present in two pools --- one available for consumers and another bound in forms unavailable to consumers. Future work on the nature of detritivory needs to address the relative sizes of these pools and their dynamics.

It is thus clear the detritivores face the problem of obtaining sufficient nitrogen. This dilemma can also be demonstrated by a different line of evidence. The maintenance ration of C to N needed by consumers is thought to be 17/1. The C/N of plankton detritus is not far from the 17/1, but vascular plants produce much higher C/N ratios (Table 2). Since some of the nitrogen may not be easily available, detritivores have a nitrogen-deficit problem.

The second dilemma of detritivores is that detritus furnishes low amounts of assimilable carbon compounds and energy. *Nereis*, for example, assimilates only about 20 percent of its carbon needs from detritus (Cammen 1980), and often no growth is recorded for animals on detrital diets. Yet, detritivores are common in estuaries and elsewhere. These animals are abundant; it might be that we are missing something in our understanding of detritivory. Some areas in which further research might show the way out of the detritivore quandary include:

1) Perhaps we have not appropriately measured total microbial contributions to detritus. Fungal nitrogen has seldom been measured. New ways have been proposed to measure fungal biomass that lead to much higher estimates than observed earlier. In litter of *S. alterniflora*, 12 percent to 22 percent of the nitrogen may be fungal (Marinucci et al. 1983) and available to consumers that can eat fungi.

2) Detritivores may be facultative predators, supplementing their diet with occasional prey, and thus increasing their nitrogen ratio.

3) Detritivores may use microbial exudates (Hobbie and Lee 1980). These exoenzymes and mucopolysaccharides may be released in great quantities by microbes and may be high in nitrogen, carbon and energy.

4) Some detritivores may have microbial symbionts that use the reduced sulfur compounds abundant in marsh estuaries as energy sources (C. Cavanaugh, in prep.).

5) Maybe detritivores select nitrogen-rich fractions of detritus (Odum et al. 1979; Bowen 1980). Amorphous aggregates of previously dissolved organic matter are abundant, may be particularly suitable and enriched, and may be preferentially eaten.

6) Detritivores may have adaptations in their digestive tracts to foster dissociation of proteins bound to phenolics. Insects that feed on refractory plant and detrital material show alkaline sectors of guts (Feeny 1970; Berenbaum 1980; Martin et al. 1980). Certain herbivorous (Lobel 1981) and detritivorous (Payne 1978; Bowen 1980) fish, including estuarine species such as killifish and mullet, also have relatively basic portions of gut.

These alternatives require further study and represent potentially interesting research directions.

EFFECTS OF CONSUMERS ON PRODUCERS

Many studies in coastal environments demonstrate that grazing can determine the abundance of producers and the species composition of the assemblage of producers (see review in Valiela 1984, Chap. 8). The quantitative effect of grazers depends on the relative susceptibility of producers to grazers. Single-celled algae tend to be grazed more intensively (Table 1). Grazers on salt marsh bottoms may remove more than 75 percent to 85 percent of the biomass of benthic microalgae relative to that inside cages where grazers had no access (K. Foreman, unpubl. data). Grazers feeding on vascular plants (Table 4, control data) are less impressive; only when nitrogen content increased under eutrophic conditions did losses due to grazers increase to substantial proportions of the stands of plants.

Grazers can also determine what species are present in an assemblage of producers. One example is provided by the changes in vegetation that took place in our long-term studies where we experimentally eutrophied salt marsh plots. In certain sections of our plots within the low marsh, the vegetation is made up largely of short and tall forms of _S. alterniflora_, the salt marsh cordgrass. In untreated plots over the course of different years, there are small shifts in abundance, in which 50 percent to 70 percent of the sward are short _S. alterniflora_ (Fig. 6, open circles). In experimentally fertilized plots, however, marked changes occur. The grass grows taller, and particular patches are attacked by grazers (Valiela et al. in press). Grazing can create bare patches, which are colonized by the opportunist grasswort, _Salicornia europaea_ (Fig. 6, black circles). At some point, however, the abundance of _S. europaea_ is sharply reduced, primarily by the grazing activity of a herbivorous beetle (_Corynephala maritima_, C. Cogswell unpubl. data). In a few growing seasons the stand reverts to _S. alterniflora_, but the grasses grow as the tall form. This latter conversion is due to the simulation of growth of _S. alterniflora_ by the chronic fertilization during the period of study.

This example shows that feeding by grazers can result in replacement of some species by others, thus altering the course of succession and defining what species of plants remain in a particular site. In the case of _S. europaea_ and _S. alterniflora_, the glasswort is shaded

TABLE 4

Mean percent of stems/m^2 (+ s.e.) that were damaged by herbivores in three treatments (C: control; LF: experimentally fertilized plot where 7.5 g m^{-2} wk^{-1} of a mixed NPK fertilizer were applied chronically; and HF, where 22.5 g m^{-2} wk^{-1} were applied).

Animal Grazer	Control	LF	HF
Voles (_Microtus pennsylvanicus_)[a]	1.8±0.7	18.5±8.2	29.1±0.3
Insects (various fly larvae)	7.5±3.5	8±2.5	4.9±4.4
Total	9.6±4.6	26.9±6.2	34.2±5

[a] Voles consumed only a small proportion of each plant that they damaged. The bulk of the plant became detritus. From 77 percent to 83 percent of the stems damaged by voles died, however, perhaps because of waterlogging of the internal air ducts in damaged plants.

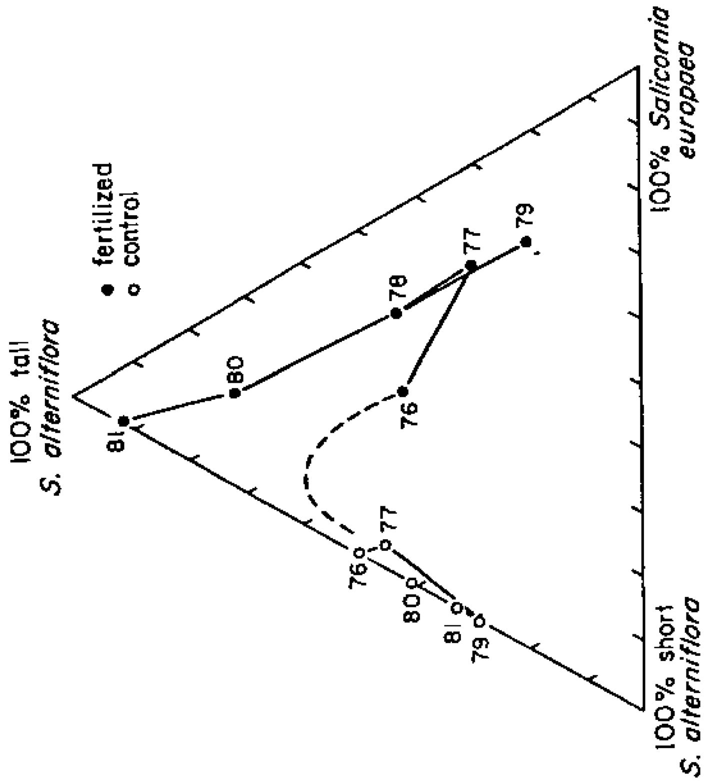

FIGURE 6

Percent cover in low marsh areas typically dominated by the short and tall form of S. alterniflora, in control and experimentally fertilized salt marsh plots, for 1976 to 1981. Note the appearance and disappearance of the glasswort Salicornia europaea in fertilized plots. From Valiela et al., in press.

and replaced by the grass. The beetle merely hastens the disappearance of the glasswort. The data of Fig. 6 demonstrate, nonetheless, the intimate relation of grazing to quality of producer biomass (and to eutrophication). Grazing is far more successful as an agent of change when producer tissues have improved nitrogen content. Lastly, the data of Fig. 6 show that long-term studies are essential if we are to understand the consequences of eutrophication. Consider, for example, that the changes of Fig. 6 took place over several years, and that there have been further changes in vegetation in our plots since 1981. These are not trivial changes in species composition of interest only to the plant taxonomist; the alterations resulted in major changes in amounts and quality of the live biomass bulk and detritus produced in the environment. Future work should focus on long-term effects --- a point to be made to funding agencies.

EFFECT OF PRODUCER ARCHITECTURE ON CONSUMERS

The relative complexity of the architecture of an environment influences foraging by consumers, as pointed out by Huffaker (1958). In salt marsh estuaries, much of the physical structure is provided by plants.

One example of the potential importance of habitat architecture provided by vegetation is documented by Vince et al. (1976). The canopy Spartina patens is more complex than that of S. alterniflora, and S. patens stems occur much more closely together than those of S. alterniflora (Valiela et al. 1978). Fundulus heteroclitus feed on the marsh surface during high tide, seeking prey within the plant canopies. Laboratory experiments showed that the number of prey eaten per unit time was larger in the simpler, less dense S. alterniflora canopy. Field samples showed that fish found it easier to find prey of the most appropriate size in the S. alterniflora canopy (Vince et al. 1976).

It is not certain that such effects occur in other marshes (Kneib 1982). Results of experiments in eelgrass beds, however, uniformly show reduced impact of predation in vegetated habitats compared to bare sediments (Peterson 1979). Further work is needed on the importance of habitat architecture, especially that furnished by vegetation, on consumer activity.

EUTROPHICATION, PRODUCERS, CONSUMERS, ARCHITECTURE: COMPLEX INTERACTIONS

The mechanisms we discussed above do not exert their influence on their own. Rather, their effect is meshed in a complex set of relationships, which can be illustrated by some results of experiments we did to assess the importance of eutrophication and predation in salt marsh estuaries.

In habitats where marsh grasses grow on the sediments, experimental eutrophication increases the abundance of detritus-feeding invertebrates (Fig. 7, top). Carnivores and herbivores add only a trivial amount of biomass to the data of Fig. 7 (top) and are not included. Note that predators --- principally fish --- had access to these habitats. Animals from vegetated sediments were extracted with Tullgren funnels, and the smallest animals sampled were mites and springtails.

The results from experiments in vegetated sediments contrast to those from experiments done on bare sediments (Fig. 7, bottom). The macrofauna from bare sediments were collected by sieving through 500-um sieves, and provided animals of about the same size range as those collected from vegetated sediments.

In the control and experimentally fertilized bare sediments, the biomass of macrofauna quickly decreased after June (Fig. 7, bottom). Evidence suggests that predation by fish is the most likely cause of the decrease. First, there is an inverse relation of numbers of macroinvertebrates in creek sediments and fish throughout the year (Fig. 8) in untreated areas. And, guts of the fish involved, mainly *F. heteroclitus*, frequently contain species found in sediments. Second, the growth rate of the fish is about one-third higher during June and July than it is during August and September (Valiela et al. 1977). This agrees with the pattern of prey abundance seen in Fig. 6 (bottom).

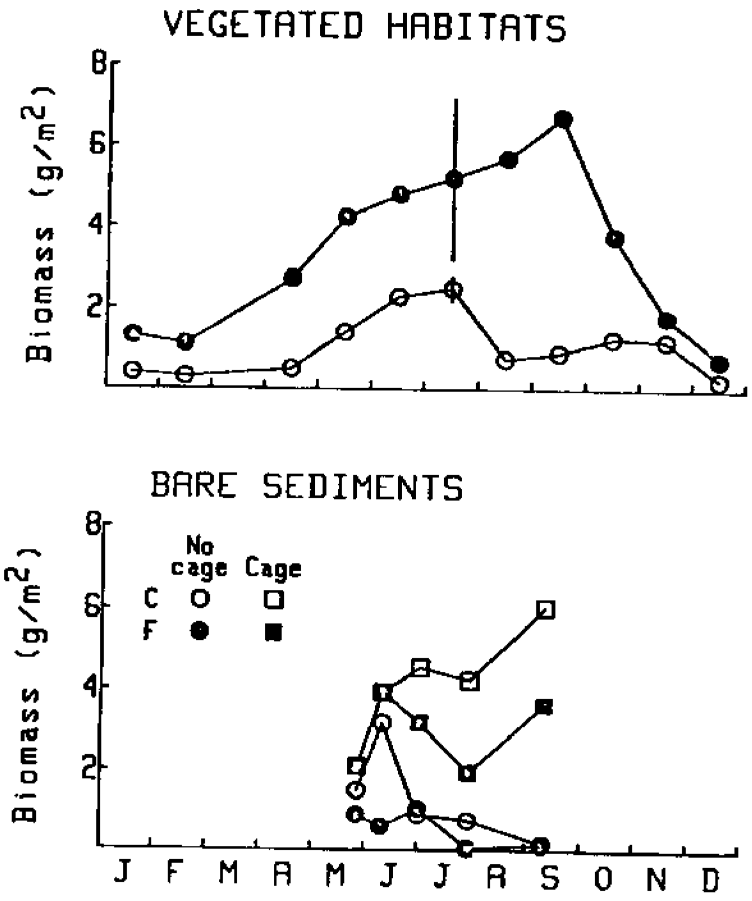

FIGURE 7

Top: Biomass of detritivorous macroinvertebrates on vegetated sediments of control (C) and experimentally fertilized (F) salt marsh plots. Average of five years of data. The error bars on July dots represent average standard errors for the whole data set. Bottom: Biomass of macroinvertebrates from bare sediments in salt marsh creeks within control and fertilized plots (both not protected by cages). In addition, data from sediments from these two treatments where cages were protecting invertebrates from predation are also included. Data courtesy of Wendy Wiltse and Ken Foreman.

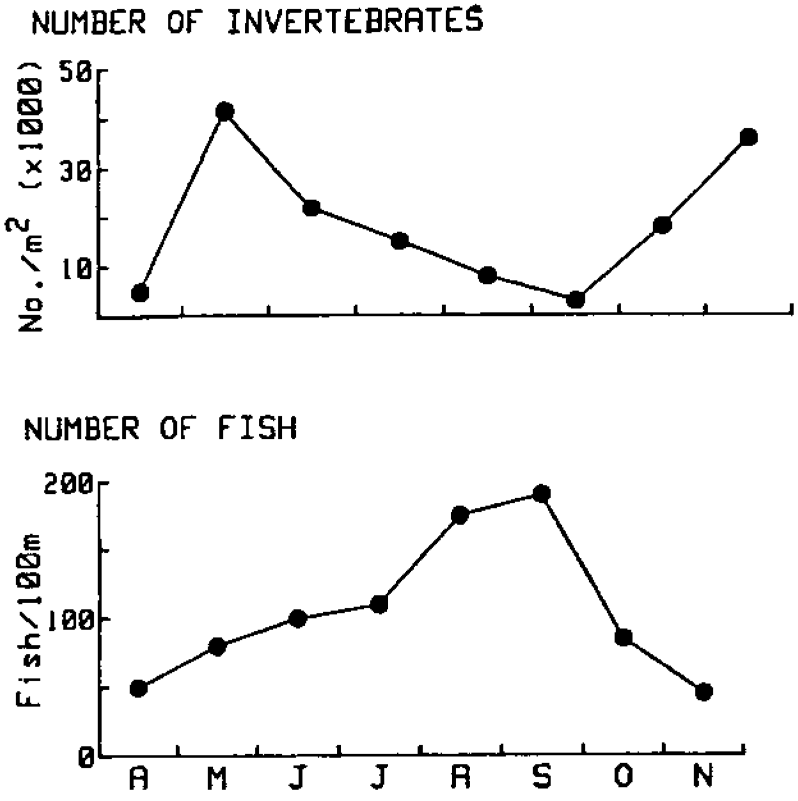

FIGURE 8

Top: Number of invertebrates in samples of macroinvertebrates from surface of marsh creeks over time. Bottom: Number of fish per 100 meters of shoreline along tidal creeks over time. Data of Werme (1981).

Kenneth Foreman and Wendy Wiltse also carried out experiments in which they placed plastic mesh cages in the bare creek sediments to exclude and evaluate the effect of predators (Fig. 6, bottom). The macroinvertebrates within these cages increased in abundance, in striking contrast to invertebrate abundance in sediments not protected by cages. Predators thus have major effects on fauna in bare sediments.

The seasonal pattern of abundance in the vegetated sediments (Fig. 6, top) resembled that inside caged bare sediments, as if the vegetation conferred some protection from predators. Although some predation takes place in the grass-covered habitats, as discussed earlier, it seems likely that the presence of any vegetation makes prey-seeking more difficult, and hence protects prey.

The effect of plant architecture is not the only non-feeding mechanism operating. Note, for instance, that the invertebrate biomass from vegetated fertilized plots (Fig. 6, top) exceeds that of control plots. In contrast, the invertebrate biomass from cages in fertilized bare sediments is less than that of cages in control bare sediments (Fig 6 bottom). The reduction of predation pressure allows the expression of the influence of other factors. At least two explanations are possible. Perhaps some detrimental effect of the fertilizer reduces the maximum growth of invertebrates in bare sediments. On the other hand, the changes prompted by the experimental eutrophication on the sediments may be responsible. Fertilization tends to oxidize vegetated sediments because the stimulated plant growth leads to greater oxidation of sediments on which plants grow (Howes et al. 1981). In bare sediments, fertilization increases microbial activity (Valiela et al. in prep.), thus leading to increased chemical reduction of sediments. Macroinvertebrates may therefore do better in the more oxidized sediments in eutrophied vegetated plots, and less well in the more reduced bare sediments. It is not clear what the explanation is, but the suggestion is that properties of the sediment --- nitrogen content and redox --- are intimately linked to consumer abundance.

CONCLUSIONS

I have identified a series of first-order mechanisms---involving feeding---that potentially might couple producers and consumers. It seems clear that differences in the chemical composition of the organic matter manufactured by producers confer differential susceptibility to consumption by animals. Single-celled algae seem most susceptible to consumers, since they appear to lack the chemical defenses often found in macroalgae and vascular plants.

The chemical composition of vascular plants and their detritus prompts low palatability, assimilation efficiency and growth for consumers. The specific mechanisms involved seem most likely to be a supply of available nitrogen and secondary metabolites, especially phenolic compounds.

There are second-order effects that might also play prominent roles in relations between producers and consumers. These include the impact of the habitat architecture provided by vegetation, of consequence to foraging consumers.

None of the mechanisms discussed above acts separately. In fact, we have speculated that sediment properties (redox, nutrient supply) change chemical composition and architecture of producers. The latter properties of producers, in turn, interact with consumers and their predators. What we see taking place in the field is the net result of these four-level interactions.

The interrelationships described in this paper are potentially important, but their impact in the field or on the ecosystem has not been identified. This is a priority for future work.

The complexity of the interactions is evident, and so should be the difficulty in attributing causes. Correlational or descriptive studies are not going to provide the needed insight into the processes involved. Experimental approaches such as those reviewed above seem to offer the best opportunity to assign causality and to unravel the complexity.

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COUPLING OF PRIMARY AND SECONDARY PRODUCTION: A GREAT LAKES PERSPECTIVE

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What are the limits to food chain dynamics in the Great Lakes? It is important to understand what factors control the population density and production of important species. Research addressed questions about the abundance of forage fish and about whether pressures from stocked salmonids will deplete the forage fish base. But unlike ocean research (Ryther 1970), scientists have not utilized data on primary production to estimate the potential harvest of Great Lakes fisheries, despite the availability of annual rates of production (Vollenweider et al. 1974).

The Great Lakes are managed for two important resource uses. The first is to preserve water quality. The Great Lakes are a source of drinking water for millions of people in Canada and the United States. Management efforts limited phosphorus inputs to control eutrophication and regulated inputs of toxics substances. Efforts to maintain water quality should be beneficial to long-term management objectives for fisheries. However, the hypothesis that decreased standing crops of algae benefit the quality of fisheries production has not been tested. Qualitative changes in the food base could have effects on fisheries production, and changes in algal species composition result from anthropogenic increases in nutrient loading.

HISTORICAL CHANGES IN FISH POPULATIONS

Fish population records for the Great Lakes, which were obtained mainly from commercial fisheries catches, oscillated widely in the last 150 years (Beeton 1969). Many species that were once important commercially, such as the Atlantic salmon in Lake Ontario, have become extinct. Populations fluctuated or became extinct because of one or more reasons: 1) overfishing for commercial species, 2) invasion of the parasitic sea lamprey, 3) destruction of spawning habitat,

4) eutrophication and other types of pollution, and 5) competition from exotic species including alewives and smelt (Smith 1972).

Because natural reproduction of large carnivores failed, predators were stocked to fill this niche. In one interesting experiment, Pacific salmon were stocked in Lake Michigan to provide a sports fishery and a predator for alewife. Alewives were underutilized and dying in numbers large enough to create nuisances on beaches. The stocking program has been successful to the extent that now concern exists about the adequacy of the forage fish base.

DIFFERENCES BETWEEN THE GREAT LAKES AND SHALLOW TURBID ESTUARIES

In contrast to the type of estuaries discussed in the challenge paper, the Great Lakes are not estuarine because of their low salt content. In addition, vascular detritus is a source of organic material in only small areas of the Great Lakes. Nutrient loading and biological enrichment of nearshore areas, bays and harbors, and subsequent transport of these materials to offshore waters is analogous to the transport and mixing of estuarine waters with coastal and offshore waters. Standing crops of chlorophyll, for example, can be greater in nearshore areas or bays than in adjacent offshore waters.

One would expect food chains in the Great Lakes to be simpler because the major source of primary production is phytoplankton. Although relationships have not been worked out quantitatively, this conclusion seems obvious because of the depth and long residence time of waters in the lakes and because the water surface area represents about 25 percent of the drainage basin.

In contrast to shallow mixed estuaries, most of the surface area of the Great Lakes is nutrient limited. Phytoplankton are phosphorus limited. But excessive phosphorus inputs can induce secondary nutrient limitation, in which silica limits diatom growth and, in extreme cases, inorganic nitrogen limits algae growth except nitrogen-fixing blue-greens (Schelske 1979).

From the standpoint of biological resource management, fish are the only organisms of importance. Almost no commercial or sport interest exists for invertebrates.

In much of the system there is spatial separation and structure in food chains. In the oligotrophic and mesotrophic parts of the Great Lakes (Lake Superior, Lake Michigan and Lake Huron), where waters are clear, primary production occurs in an upper mixed layer of the water column that is nutrient-limited and in deeper layers where light becomes limiting when waters are thermally stratified (Dugdale 1967; Moll and Stoermer 1982). During significant periods of the annual thermal cycle, the water column is mixed convectively. Therefore, phytoplankton populations that appear to be mixed from top to bottom are light-limited during much of this time (Stoermer 1978). Due to this spatial structure, autrotrophic- and hetrotrophic-based food chains will be separated spatially in the water column. Some detrital materials will be processed in the trophogenic zone, and some living phytoplankton will settle into the tropholytic zone. One means of detritus supply to the benthic environment is fecal pellets, which may be a major source of detrital materials (Bathelt and Schelske 1983).

But portions of the Great Lakes are more like estuaries estuaries than lakes. Ketchum devised methods to study estuarine flushing in Saginaw Bay (Beeton et al. 1967) and Green Bay (Modlin and Beeton 1970). In the western basin of Lake Erie, Saginaw Bay and southern Green Bay, waters may be turbid and phytoplankton may be light-limited because of inorganic turbidity or shelf-shading. Due to the shallow waters, vertical structure in producer communities will be insignificant. In addition, vascular plant detritus has greater importance in areas adjacent to freshwater marshes.

TOP-DOWN VS. BOTTOM-UP CONTROL IN ECOSYSTEMS

The Great Lakes are ideal for studying how community structure in ecosystems are controlled. A broad range of trophic characteristics are present there (Vollenweider et al. 1974; Dobson et al. 1974). Comparison of these systems should provide insight into how community structure is affected by bottom-up control of food chain dynamics from different levels of phosphorus enrichment. Large-scale stocking of predators can be used to study how community structure and food chains are altered from the top down.

The combined effects of eutrophication affected community structure from the bottom up by changing the qualitative character of primary producer communities. In their pristine state, diatoms dominated phytoplankton assemblages in all of the Great Lakes. But as phosphorus inputs increase, silica-limited diatom production occurs seasonally in three lakes --- Lake Ontario, Lake Erie and Lake Michigan (Schelske et al. 1983). In Lake Huron and Lake Superior, diatom production is at its highest level in over 200 years because of increased phosphorus loadings. Phosphorus loading has not great enough to induce silica limitation. Qualitative changes in diatom communities in Lake Huron and Lake Superior probably resulted from increased phosphorus enrichment (Stoermer 1978). How this has affected coupling between primary and secondary production is not known.

Evidence shows the effect of nutrient enrichment on the qualitative composition of phytoplankton communities. Empirical evidence that relates total phosphorus concentrations and minimum silica and nitrate nitrogen concentrations among the Great Lakes shows silica and nitrogen limitation result from increased phosphorus concentrations (Dobson et al. 1974). Silica limitation in the water column would shift the species composition of phytoplankton. The proportion of diatoms would decrease with a concommitant increase in the proportion of green and blue-green algae (Schelske et al. 1983). Nitrate limitation would provide a competitive advantage for species that can fix free nitrogen---blue-green algae. These secondary nutrient limitations for silica and nitrogen produce extreme changes in the phytoplankton food base and affect the coupling between primary and secondary production (Stoermer 1978).

Two other consequences of increased anthropogenic nutrient loading on phytoplankton species composition should be mentioned. The first is the effects of conservative ions on the quality of phytoplankton. Conservative substances, in particular sodium and chloride, increase with nutrient enrichment, causing changes in phytoplankton quality (Stoermer 1978). The second consequence is from accessory growth promoting substances. The three categories of these substances that have been studied include vitamins, trace metals and chelating agents. Microgram and nanogram concentrations of these substances, in combination with phosphorus enrichments, produce large changes in standing crops and species composition compared to treatments in which they were absent (Schelske 1979). In experiments, these trace additions have increased standing crops by a factor of two and changed the species dominant in the phytoplankton assemblage (Stoermer et al. 1978).

Field studies showed that nutrient enrichment does not alter the food base under all conditions. Stoermer (1978) reviewed this evidence for the Great Lakes and concluded that moderate enrichment did not affect the qualitative composition of the primary producers. He provides evidence which shows that, in addition to phosphorus loading, these changes may be affected by such factors as secondary nutrient limitation, accessory growth substances and conservative ions. Empirical and experimental evidence point to the unimportant role of nitrogen, except for secondary nutrient limitation (Schelske 1979; Stoermer et al. 1978).

This discussion points to ways that ecosystem function could be controlled by qualitative and quantitative changes in primary producers. If qualitative changes are important, then present strategies to limit phosphorus inputs should have long-term benefits for fishery management. Little research has been done on how bottom-up control affects secondary production or fisheries.

Top-down control of ecosystem function can be illustrated using Lake Michigan as an example. A dramatic change in this system can be attributed to the stocking of predators, primarily Pacific salmon.

The state began stocking these large predators in 1966 for two reasons. Pacific salmon replaced indigenous fisheries that had collapsed for one reason or another. And the fish were ideally suited for sport fishing, which provides more economic benefits to the region than commercial fishing. By this time, the commercial fishery for lake trout, one of the most important large predators, was dependent on stocking. Consequently alewife populations in Lake Michigan exploded, providing a forage food base that was not utilized.

The stocking program initiated in 1966 and 1967 produced changes in the system. First, it reduced the alewife population, which peaked in 1966 and crashed in 1967. After the crash and for most of the 1970s, alewife populations were maintained at large levels. In 1982, populations decreased. By 1983 they were about 12 percent of the 1981 level (Crowder 1984; Evans in prep.).

In a second change described by Crowder (1984), the decline in the planktivorous alewife decreased grazing pressure on larger sizes of zooplankton. Evans (in prep.) documented this change in the zooplankton community structure from 1972 to 1983. From 1972 to 1981, Daphnia retrocurva and D. galeafa mendotae were the dominant daphnids. However, in 1982 when the alewife population decreased, a form of Daphnia pulex first became an important part of the zooplankton community. By 1983, this daphnid comprised more than 90 percent of the numerical standing stock of the summer Daphnia community.

Thirdly, water clarity in Lake Michigan increased with the growth of larger daphnid populations (Scavia et al. in prep). Presumably this increase resulted from the greater filtering efficiency of the larger Daphnia. Evans (in prep.) shows that the average body length of the Daphnia pulex is about twice as large as the formerly dominant species.

In a fourth change discussed by Crowder (1984), populations of bloater chubs increased as the population of alewives decreased. Why this potential forage food source is not being utilized by predators is unresolved. However, it appears that the increase in bloater chubs can be attributed to lack of competition from alewives and that the reported decrease in the size of salmon can be attributed to reduced availability of forage fish.

It is interesting and, perhaps facetious to note, that the end result of stocking salmon may be an improvement in water quality. It is reasonable to conclude that increased water clarity is the result of decreased standing crops of phytoplankton. The decrease probably occurred not only because of declines in nutrient concentrations but because of the increased filtering efficiency of the larger Daphnia (Scavia et al. in prep.). The change in zooplankton community structure would be expected based on a similar change found by Wells (1970) after the alewife declines in 1967, which were attributed to size-selective predation by alewife.

RESEARCH FOR THE FUTURE

If we are to have self-sustaining fish populations in the Great Lakes, more information is needed on what factors are important in the early life histories of these species. Is reproduction limited because of toxic substances in the environment? Are historical spawning areas unsuitable? Have qualitative changes in planktonic communities affected the recruitment of larval fish? Can management actions provide better environmental conditions in the future?

What are the links in food chains between primary and secondary production and ultimately to economically important species? What is the optimum level of stocking for predators in large systems? Will stocking pressure ultimately produce a more diverse and stable forage fish base? To answer these questions, we must obtain data about the magnitude of primary production and about the factors that control energy transfer to higher trophic levels. We need to find how changes in zooplankton and fish community structure, described earlier, affect primary and secondary production? Has the level of primary production changed with the reduction in the standing crop of algae, or has there been an increase in turnover rates to compensate for the lower standing crop? Data from Green Bay indicates that energy transfer from primary to secondary producers is affected along the trophic gradient in this part of the Great Lakes.

In the Great Lakes, scientists can study the partitioning of primary production through the pelagic or planktonic food chain and the benthic food chain. Planktonic food chains would be based largely on autotrophic production, but a greater proportion of the energy for benthic food chains would have a detrital origin. The importance of the planktonic and benthic food chains could be determined from a study that combined measurements of primary production in the trophogenic zone with fluxes of organic material out of this zone. Fluxes of carbon out of the euphotic zone could be determined with sediment traps.

Results of recent experiments with sediment traps show how this type of study might be applied to the problem of interest. Lorenzen and Welschmeyer (1983) showed that the vertical phaeopigment flux was conservative and that there was no significant loss of the combined total of pigments (chlorophyll and phaeopigment) enroute to the benthic environment. Because phaeopigments are forms of chlorophyll that are degraded by grazing zooplankton, quantities of chlorophyll that are grazed and sedimented can be estimated and separated from chlorophyll that has not been grazed. Therefore, the flux of these materials at different depths in the water column can be used to study the dynamics of organic matter transport. This transport in the marine environment is enhanced by zooplankton fecal pellets that may sink 100 meters per day (Lorenzen and Welschmeyer 1983). In the Great Lakes, sinking rates can be almost that fast (Bathelt and Schelske 1983).

Sediment trap studies of biogenic silica are another means of estimating the flux of biogenic particles to the benthic environment in the Great Lakes, especially Lake Michigan. Biogenic silica produced primarily by diatoms is transported quantitatively to the benthic environment (Schelske et al. 1984). This transport is mediated by zooplankton grazing and fecal pellet production. Given data on production of organic carbon in the trophogenic zone and the flux of organic carbon out of this zone, an estimate can be made on the potential flux of carbon, primarily detrital carbon, to the bottom. In studies of this type, the effects of resuspension should be considered.

Sediment trap studies can be used to explain food chain dynamics and coupling between primary and different types of secondary producers. How much energy for deep-water benthic communities originates from phytoplankton directly? How much originates from different detrital sources, including grazed phytoplankton? Does the carbon-to-nitrogen ratio of settling organic matter change with the depth of the water column? The ratio should increase if detrital carbon is relatively poor in nitrogen. How is detrital carbon enriched with nitrogen? How does the qualitative character of organic matter change with depth as it is being degraded by different processes (see Meyers et al. 1984)?

Questions about how different ecosystem changes have affected coupling between primary and secondary production and ultimately fisheries yields are complicated in the Great Lakes because of many interacting factors. However, some changes, such as the increased stocking of predators in Lake Michigan, can be used to study associated effects in the system. This type of a change is an experimental manipulation. Historic changes in important biological characteristics of these systems are not well-known. Therefore it is not possible to relate fisheries yields to lower levels in the food chains. However, it is likely that paleolimnological studies will provide insight into some of the causes for these changes. For example, several recent studies showed that phytoplankton assemblages in Lake Erie and Lake Ontario were affected by nutrient enrichment before 1880 (see Schelske et al. 1983). These changes may be significant because effects of eutrophication had not been considered important at such an early date.

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DISCUSSION

S. NIXON: I attempted to make an empirical link between the fisheries yield of several coastal and oceanic marine systems and the purported primary productivity data for these systems. To my knowledge, this has not been done before. I published the information at the U.S. Fish and Wildlife Symposium on Freshwater Inflow to Estuaries, held in San Antonio, Texas, in 1981. It turns out that you can get some rough empirical relationships. For many large, temperate lakes, the fisheries yield seems to be 10 times to 20 times lower than for the comparable regression for estuaries. I wonder if Claire Schelske might comment on why we see a difference like that.

C. SCHELSKE: I really don't have an explanation. It could be that many harvested marine species are at much lower levels in the food chain. In most of the freshwater systems, we're dealing with top carnivores. Therefore, you might expect at least an order of magnitude difference based on that.

C. PETERSON: I'd like to take Bill Odum's bait here and add something to the litany of problems in doing gut-content analysis. That is, the differing rates of digestibility of alternative prey one might find in the gut. If you have, for instance, a piscivorous fish--something high on the food chain--and you find in its gut one fish or another, you don't have a terrible problem. But as you go down the food chain (in other words, looking at the level of coupling primary and secondary production), I think the problem becomes a great deal worse. If you compare, for instance, the assimilation rate in the gut of dissolved organic matter, bacteria, a green flagellate and juncus detritus, there's a tremendous range in the rate at which those things may disappear. Consequently, in the extreme, I'll be provocative and argue that gut contents might tell you what is not important in the diet rather than what is.

W. ODUM: You're right. I agree with you one hundred percent.

S. NIXON: Delaware Bay has plenty of salt marshes, but it has fairly low phytoplankton production.

Delaware Bay also has very low fisheries yields and always has had as far as we know, at least back into the late 1800s. I don't think it's something that we can blame on the city of Philadelphia or on toxins or something exotic like that. The fisheries yields from Delaware Bay are about 20 kilograms per hectare, which is very low for an estuarine region.

If these marshes are so important, one is compelled to ask why Delaware Bay's fisheries yields aren't higher. But one thing they don't have is a lot of phytoplankton production. It's just a piece of anecdotal information.

L. CROWDER: I was interested in a comment that Claire Schelske made regarding apparent changes in water quality in the Great Lakes. Most of you are probably aware of research that's been done in freshwater systems, mostly in smaller lakes, looking at what controls food chain interactions. In other words, is eutrophication in lakes a result of nutrients inputs, or does it have something to do with the food chain effects at the top? Several researchers studied how those food chain interactions affect what we perceive as water quality or enrichment.

I'm fairly new to the estuarine scene, and I'm wondering if people are seriously testing those alternate hypotheses in estuaries. In other words, how important are nutrient inputs relative to controls from the top end of the food chain, which may influence the number of critters in the estuary that consume production?

I. VALIELA: There's almost no data that can make that kind of comparison. The people who study lakes and pounds are able to manipulate small enclosed bodies of water. They can, in fact, make statements about a density attendant to some fish population and so forth. There's almost nothing like that for estuaries.

W. ODUM: This is a question for Dave Peters. I think Dave has some data here that, if it's true (and I won't judge that at this point in time), has profound significance. I think most of you let that wash by you. If it's true that menhaden can metabolize that sort of refracted material and you really think the data is that good, it has incredible implications. Do you want to comment on that?

D. PETERS: I suspect it's true that they're utilizing it. It's easy for me to believe that they would. There has to be some reason they eat it. One thing that we didn't talk about much is that detritus is a lot of different things. The detritus that menhaden eat looks like mucus. I don't know what it is or why it has cellulose in it. More than likely it's reaggregated organic matter that's dissolved. Maybe that explains why it has such a high nitrogen content.

Probably it's reaggregated. If it's a physical-chemical process, it's probably very efficient. I could easily understand that the system could be working on vascular plant production. It certainly is on detritus, but the extent of vascular plants is not clear.

I. VALIELA: I also was struck by 75 percent assimilation efficiency of cellulose. I find it hard to believe that an animal without the help of bacteria can do that. Maybe it's true. However, some of my colleagues found that a lot of cellulose is cleaved to individual elements of a polymer. Then, reaglutination makes amorphous gorp often found in guts. In that case, the whole idea might differ because the individual sugars may assimilate at different rates than cellulose as a compound.

One other comment. I would like to reiterate a point that Scott Nixon made that I think went by without much attention. John Teal and I have been doing long-term experiments in salt marsh plots for ten years. We've been chronically adding materials similar to the kinds of dosages that you add in the MERL tanks.

We have been looking at the vegetation during this intervening ten years. Even now, we are still seeing significant changes in the vegetation structure of those plots. They are major shifts in the major species. Your interpretation is not going to be addressed by having one- or two-year projects. And we can give very strong evidence that even 10 years after this set of plots was started, we're getting major shifts which need to be examined.

D. PETERS: Maybe I was misinterpreted. I did not mean to say that bacteria didn't have any role in detritus utilization. I don't know how menhaden accomplish it. I don't know how the material gets to be where it is. I have no evidence to prove that there aren't bacteria in the gut that have some role. I was saying that the stuff they ingest has cellulose in it, and it doesn't come out the other end.

L. DEEGAN: We have evidence from studies in Louisiana that menhaden have enzymes in their digestive tract that are strongly cellulolytic. The origin of the enzyme may be a yeast very common in salt marshes. It may be that they ingest it and hold it in their intestines, culture it and use it to break down Spartina. This evidence corroborates what David Peters said about menhaden's ability and may also account for the relatively high assimilation rates. It seems to be mediated through a yeast that specializes in breaking down Spartina.

B. CHRISTIAN: I'd like to come back to the vascular material that Bill Odum mentioned. In looking at water samples from Sapelo, I saw it very rarely. The question that always comes to mind is how many times has this material passed through a gut when we actually look at it? What is the turnover time for an average particle between the water and the gut and out again?

W. ODUM: You have a good point. When you look at this suspended material it is mostly suspended flox. To answer your question, I think there is continual breaking down and reformation of these flox materials. So it's very hard to say how many times any particular piece of material has been through a gut. It could be a great many times. It must be broken down to few micrometers or smaller, then reformed into flox of 100 or 200 microns across and broken down again.

R. BIGGS: We've done an estimate such as you're talking about not in terms of organic matter, but in terms of the total material in suspension.

We've measured the standing crops of zooplankton in Delaware Bay and major benthic filter feeders in open water Delaware Bay. By weighting for seasonal temperatures, etc., it turns out that total suspended sediment in Delaware Bay recycles about 200 times a year through the filter feeders.

Delaware Bay has a zooplankton standing crop about an order of a magnitude lower than Chesapeake Bay, Long Island Sound or most other East Coast estuaries. Therefore, I would expect that the numbers are similar.

Of course, all this means is that most of the total suspended material of an estuary is due to resuspension. It's resuspended every tidal cycle or so, and something filters it out and uses it.

J. MILLER: In order for Scott Nixon to obtain the tight couplings between yield and primary production for lakes, he had to severely constrain the types of lakes used. He used large lakes. In some cases small lakes don't fit. They used lakes that are intensively fished because lakes that aren't don't fit. Are there similar constraints on the type of estuary where you may or may not expect to see this type coupling versus others?

W. ODUM: Scott Nixon and I wrote a review paper in which we independently suggested that there are a number of factors about morphology in an estuary --- the tidal range, the shape of the basin, the freshwater inflow and the relative amount of sediment flowing in. I think freshwater flow is probably one of the biggest factors.

Anyway, there's a whole list of possible variables that could, on one extreme, create an estuary which is phytoplankton-based. On the other extreme, it could probably produce an estuary that is largely detritus-based. And there are probably estuaries in between.

We've all proposed those things, but we haven't tested them with statistics. Getting information to test is a little more difficult. I have no doubt in my mind that there's a tremendous range in different estuaries. And you can see that there's a bias depending on where we work.

Obviously, I think there's a tremendous variation between estuaries, and we haven't done a good job of going past the first sort of descriptive state. That's the only aspect I can really comment on.

J. MILLER: I think it would make an interesting comparison if, for example, there certain estuaries are more detritus-based than phytoplankton-based. What we've heard today suggests that there might be at least one extra food link in there. If we believe ecological theory, there should be some difference between the response of the system in a systematic sort of way.

W. ODUM: I don't think there are ever any absolutes. I don't feel that there's any system, unless it's a cave somewhere, that's totally detritus-based or one that's totally phytoplankton. Therefore, there are mixtures between the two, and that is the only question.

D. FLEMER: I think the problem is extremely complicated when we consider estuaries. As we all know, they are characterized as gradient systems. If you work in the tidal tributaries such as the Patuxent, you will have a different bias about the role of detritus than if you work in the mouth of the Chesapeake where detritus is insignificant.

FISHERY HABITAT REQUIREMENTS

ESTUARINE FISHERY HABITAT REQUIREMENTS

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INTRODUCTION

Estuaries throughout the world are valuable nursery areas for many commercially and recreationally important species of fish (Gunter 1967; McHugh 1967; Tyler 1971; Bayly 1975; de Sylva 1975; Wallace and van der Elst 1975; Lenanton 1977; Warburton 1979; Weinstein 1979; Bozeman and Dean 1980; Chubb et al. 1981; Pollard 1981; Dovel 1981; Lenanton 1982; Deegan and Thompson in press). However, some estuaries support more fish than others. For example, Albemarle Sound represents 26 percent of the estuarine area in North Carolina, yet it produces only 7 percent of the commercial catch. Pamlico Sound produces 67 percent of the catch with only 56 percent of the state estuarine area (Copeland et al. 1983). This paper will evaluate to what degree and why nekton use estuaries as habitat and what characteristics make one estuary better habitat than another. We will review the life-history patterns of fish that use estuaries. And we will examine the three major reasons often proposed for why fish use estuaries: (1) food availability, (2) protection from predators, and (3) physical and chemical suitability.

TO WHAT DEGREE DO FISH USE ESTUARIES?

Different species of nekton evolved various life-history strategies for using estuaries. Based on aspects of their ecology, including spawning location, feeding and salinity tolerance, the nekton's use of the estuary can be divided into five major life-history patterns (McHugh 1967; Tyler 1971; Wallace and van der Elst 1975; Day et al. 1981; Deegan and Thompson in press).

(1) Fresh water - Primarily freshwater species spawn in salinities less than 0.5 parts per thousand and have slight to moderate salinity tolerances. Typical species include largemouth bass, bluegill and some catfish.

(2) Estuarine - True estuarine residents spawn and complete their life cycle in estuaries. They generally have wide salinity and temperature tolerances. Finfish in this group are rarely of commercial or recreational importance, although shellfish often are. Typical species include hogchoker, sea catfish and oysters.

(3) Estuarine/marine - These species are found in estuaries primarily as juveniles. They spawn in nearshore or offshore waters and have wide salinity tolerances. These species are referred to as "estuarine-dependent" because they reside in the estuary during the early, critical stages of their life cycles. Examples of typical estuarine/marine species are shrimp and menhaden. The former is the top value species in the U. S. fishery; the latter is top in weight. Estuarine/marine species make up more than 88 percent (by weight and by ex-vessel dollar value) of the total fishery landings in the southwest region of the United States (Lindall et al. 1979). Oecause of the large commercial and recreational value of these species in Atlantic and Gulf of Mexico estuaries, considerable efforts have been made to analyze and quantify the importance of estuarine habitat to these species.

(4) Marine - These species spend most of their lives in nearshore or offshore marine habitat and are generally intolerant of low salinity conditions. They spawn in marine habitat and invade estuaries with intrusions of high salinity waters. The bluefish is an example of a marine species on the Atlantic coast.

(5) Diadromous - These fish migrate between the sea and fresh water. Anadromous species spend most of their lives in the sea and migrate to freshwater for breeding. Juveniles spend varying amounts of time in estuaries. The most spectacular examples of these fish are salmon and shad. Catadromous species migrate from fresh water to the sea to spawn. The most well-known examples of this type are American and European eels.

Historically, work on the relationship of fish and estuaries in the United States was centered on the South Atlantic coast. Because the fish populations in these estuaries are dominated by estuarine/marine species, this life-history pattern became the archetypical "life history" of an estuarine-dependent fish. Although this pattern is widespread along the Atlantic and Gulf coasts, we now know that it is not the dominant pattern in all estuaries. For example, estuaries along the Pacific and North Atlantic coasts are typified by more marine and diadromous species.

The widespread use of estuaries by many larval and juvenile species has led to the concept of estuarine dependence, implying that the estuary is required for part of the life cycle of these organisms. Because over geologic time any particular estuary is short-lived (less than several thousand years), controversy exists about their essential nature (Walford 1966; Schubel and Hirschberg 1978). Schubel and Hirshberg argued that the value of estuaries in supporting fisheries species has been overstated because of the ephemeral nature of particular estuaries and because during geological time estuaries have been small and rare. This is misleading for two reasons. Although a particular estuary is short-lived, the estuarine environment has existed continuously during the evolution of commercially important estuarine-dependent species. It is probable that certain life-history patterns have been more prevalent during different stands of sea level (i.e. diadromous species during periods of low sea level). Second, the interest in estuarine dependence is motivated by the desire to manage and conserve fishery stocks. The time span that most management plans cover is only decades at most. Fish abundance cycles that span several thousand years, although scientifically interesting, are not important from a management standpoint.

Part of the controversy stems from an imprecise definition of estuarine dependent. Is a salmon, which needs the brackish transition of the estuary to complete the smoltification process, any less dependent than menhaden, whose juvenile stage is never found anywhere else? In the past, finding a critical stage (usually juvenile or larvae) exclusively in estuarine areas qualified a species for estuarine dependent status. Is this sufficient criteria? Can alternative habitats be used by these species if estuaries did not exist? For example, a survey of the Blackwood River estuary, Australia, and adjacent marine embayments (Lenanton 1982) revealed that three of the 16 species encountered were found exclusively in the estuary. These species were regarded as estuarine-dependent. The remaining 13 species also used the marine embayments, but were not considered estuarine dependent. In New England, juvenile winter flounders are abundant in estuaries and nearshore coastal habitats, yet this species often is referred to as estuarine-dependent (Pearcy 1962).

LOCATIONS OF CRITICAL IMPORTANCE AS NURSERY AREAS

Because attributes of nursery areas are difficult to define, they are determined empirically by estimates of the abundance of larvae and juveniles. Several workers (Weinstein 1979; Bozeman and Dean 1980; Shenker and Dean 1979; Day et al. 1982; Weinstein and Brooks 1983) demonstrated that shallow tidal creeks and marsh shoals harbor dense populations of juvenile marine species such as spot, mullet, flounder and menhaden. Some fish, for example Atlantic croaker, also use open deeper water near the head of the estuary (Weinstein 1979). Sea grass meadows are another distinct and important nursery area (Thayer et al. 1975; Adams 1976; Heck and Orth 1980) for species such as spot, blue crab, pin fish and sea trout. Nursery areas tend to be situated in shallow areas along shorelines and contain high levels of organic matter and nutrients.

The distribution of juvenile fishes within primary nursery areas has been related to many factors, including temperature (Joseph 1973), salinity (Gunter 1961), turbidity (Blaber and Blaber 1980), calm water (Blaber and Whitfield 1977), food availability (Lasker 1975; Laurence 1977; Whitfield 1980a,b) and predation pressure (Blaber ad Blaber 1980; Weinstein and Walters 1981). Physiochemical parameters, which affect individual tolerances, govern broad spatial distributions within the estuary. But species interactions fine tune spatial distributions. Some factors, such as salinity or turbidity, may influence distribution secondarily by controlling the distribution of predators (Joseph 1973; Blaber and Blaber 1980).

How specific is the selection for a nursery habitat? Within a single estuary, some species are found as larvae and juveniles in grass beds and marshes. What is the relative value of these habitats? Are growth, feeding and survivorship different? For species that use multiple areas, what is the contribution to the total stock from the different nursery areas? For some species, the area used as a nursery differs among estuaries. In North Carolina, Atlantic croaker reportedly use the deeper open water oligohaline regions in greater abundance than shallow marsh creeks (Weinstein 1979). However, in the Gulf States, young croaker use marsh creeks and shallows extensively (Herke 1977; Yakupzack et al. 1977). What causes this difference? In North Carolina, Miller et al. (1984) suggest that currents are the primary determinant of larval distribution and determine use of an area as a nursery ground.

The distribution of species is also life-stage dependent. Most species use different habitats in a predictable sequence. For example, menhaden spend the first four to six months of their stay in estuarine tidal creeks, then move into open bay waters for three to four months before moving offshore (Reintjes and Pacheco 1966; Hinchee 1977). What are the relative values of these two habitats? A recent study of gulf menhaden suggested that marsh creeks may be important for feeding and protection from predators at early stages. But open water is important for growth and lipid storage before the fall immigration (Deegan and Thompson 1983). We do not know, however, the cueing mechanisms that initiate and guide these movements. Attainment of a specific size (Yakupzack et al. 1977), depletion of food resources (Miller and Dunn 1980; Levin 1980) and environmental changes (Herke 1977) have been proposed.

We need answers to questions as basic as when, at what size and why do species migrate? How long does an individual of each species stay in a nursery? What are the effects of environmental variations on survival, growth and movements?

IMPORTANCE OF PREDATOR PROTECTION

One of the primary reasons cited for use of marshes and grass beds as nursery areas is protection from predators. Evidence from empirical studies indicate few predators in these areas (Herke 1977; Bozeman and Dean 1980; Weinstein and Walters 1981). Recent grass bed work correlated greater species number and abundance with greater habitat complexity, as measured by above ground biomass (Heck and Wetstone 1977; Heck and Orth 1980). The relationship appears to increase protection from predators and increase living space. Food seems less important for some species because favorite food items are more abundant in other habitats (Heck and Wetstone 1977; Holt et al. 1983). Experimental studies that tested this hypothesis demonstrated reduced predator efficiency in grass beds and greater protection from denser vegetation.

It is difficult to postulate similar hypotheses for salt marshes. Fish do not live among grass stems but in adjacent, shallow marsh creeks. However, the physical nature of these shallow creeks may limit predators. The large fluctuations of temperature and salinity in shallow marsh creeks may be beyond the tolerance level of predators (which tend to be adults), but not juveniles (Cushing 1975; Hyatt 1979; Heck and Orth 1980). Weistein and Walters (1981) reported that mortality of spot (Leiostomus xanthurus) was significantly higher in polyhaline creeks than in other portions of the estuary. The difference was attributed to the greater numbers of stenohaline marine predators seasonally occupying polyhaline marshes. Tidal creeks are also characterized by high turbidity levels that may provide protection from predators. Although many senses are involved in feeding, sight is important for capture success (Nikolsky 1963; Hyatt 1979). High turbidity could also lower the foraging efficiency of juveniles, but this cost may be offset by increased survivorship? Zimmerman and Minello (1984) learned that a number of species were found in the marsh during high tide.

IMPORTANCE OF FOOD AVAILABILITY AND SOURCE

Scientists believe coastal fishery production in intertidal areas is dependent on primary production in estuaries and wetlands. Correlative studies of fisheries yield and estuarine production provide evidence for this theory. The importance of food to fish production can be divided into two components--quantity and quality.

The question of fish food limitation is central to the relationship between fish and food. Can we increase fishery productivity by increasing available food? Evidence linking increased fish production to increased food is found in the relationships of fish yields and river discharge. Scientists correlated increased fishery productivity with river discharge. Similar correlations were made for estuaries in Texas, Mexico, Louisiana, Mississippi, Alabama, Florida and California. Freshwater discharge stimulates the productivity of the estuary, increasing the food available to larval fish during their first few months, a highly crucial time in their development. Nixon (1982) and Bahr et al. (1982) show a correlation between coastal fisheries and estuarine primary productivity. Nixon correlated estuarine fisheries yield per area with the primary production per unit area of the estuary. Similarly, Bahr et al. demonstrated a quantitative relationship between gross primary production and secondary production of fishery species. These studies point to a relationship between primary productivity and fisheries yield, but they are simple correlative analyses that do not show the possible mechanism. We need more information to define the mechanisms involved and to verify that these correlations show a dependence. In these correlative studies, no consistent treatment is given to what is defined as fisheries yield or to what the yield is correlated with. Some studies adjust everything to a per unit area basis, others correlate totals and others look at ratios of water to wetland. Often the relationship derived for one species is different from the same type of analysis developed for the entire fish community in the same estuary. A careful analysis of these studies needs to determine if any basic relationships exist.

Several studies comparing food availability with fish food requirements suggest that food supplies potentially are limiting in estuaries (Peters and Kjelson 1975; Laurence 1977; Weinstein 1979; Bahr et al. 1982). Many fish with similar food requirements exhibit temporal or spatial segregation in nursery areas. Some researchers proposed fish may be food limited in estuaries (Weinstein 1979). Polgar (1982) suggests that food availability is the cause of differential mortality in Potomac River striped bass larvae. Peters and Schaaf (1981) calculated the food requirements of Atlantic menhaden. They found that observed phytoplankton production was not sufficient to support the population, leading them to conclude that menhaden also must use detritus and zooplankton. Other scientists attributed the movements of fish in estuaries to depletion of food supplies (Levin 1980). Experiments excluding fish from areas showed that fish can deplete food organisms in a local area quickly (Virnstein 1977, 1978, 1979; Peterson 1979; Holland et al. 1980; Fitzhugh 1982), leading to locally limiting food resources.

Another important question is the effect of food sources on fishery composition and production. For many years, organic detritus derived from fringing wetlands was considered a major food source in estuaries (Darnell 1961; McHugh 1967; Odum and Heald 1975). The original concept of salt marshes supporting fisheries production was based on food web analyses showing detritus as an important food source. The studies of Darnell (1961) and Odum and Heald (1975) indicated direct consumption of detritus as an important food source. Recent studies suggest that fishes previously thought to be detritivores may be carnivores. These fish may consume detritus indirectly in the capture of food items. Many scientists assumed that detritus was still the base of the food web, but it passed through one or more trophic levels before reaching fish.

Other studies, using stable carbon isotope ratios as tracers of primary production in food webs, questioned the role of organic detritus in estuarine trophic structure. Haines and Montegue (1979) reported that most estuarine animals in a Georgia estuary have stable carbon isotope rations more similar to phytoplankton than to marsh grass. Thayer et al. (1978) found animals in a North Carolina sea grass bed that had ratios indicating phytoplankton or microalgae and sea grasses were important carbon sources. Fry (1981) found carbon isotope ratios of brown shrimp correlated with the habitat in which it fed or was captured.

Just as there are problems with interpreting gut contents to construct a food web, there are problems when using isotope ratio's to trace primary production. A single stable carbon isotope ratio is not a unique number and can be derived from several different combinations of food types (Hughes and Sherr 1983). Ratios are also known to shift between trophic levels, and different tissues in animals often exhibit different isotope ratios (Rau et al. 1983).

Current evidence indicates that estuarine food webs are a mixture of detrital-and phytoplankton-based pathways, and that the importance of these primary producers varies among estuaries. In a study of eight Gulf of Mexico estuaries (Deegan et al. 1983), the following contributed to the total primary production: phytoplankton 16 percent to 53 percent, marshes 0 to 72 percent, sea grasses 0 to 80 percent and mangroves 0 to 60 percent. These estuaries also support varied fisheries. What is the relative importance of these producer types? Chesapeake Bay has high fishery yield, primarily due to the planktivore Atlantic menhaden. But it has a low-marsh-open-to-water ratio (Nixon 1980). Perhaps it should not surprise us that the fishery is an estuary with a large, productive open water area is dominated by a pelagic planktivore. Patterns of production utilization and export also depend on the dominant sources of primary production. Thus macrophyte or marsh production and decomposition results in high amounts of detritus with long residence times. On the other hand, phytoplankton production is characterized by rapid turnover and utilization. What are the consequences of shifting the production base to phytoplankton by dredging and filling salt marshes, mangroves or sea grasses? Will a phytoplankton-based fishery necessarily invade the area? To what extent do these different producer types substitute for each other as habitat and food sources?

IMPORTANCE OF THE PHYSICAL AND CHEMICAL CHARACTERISTICS

The importance of hydrology in determining the relative fish productivity of estuarine habitats often has been overlooked. However, current evidence indicates hydrology may be important in determining entrance and use of estuarine habitats. The importance of tidal currents at estuarine mouths in determining the entrance of larval and post-larval marine-spawned species (Weinstein 1979; Miller et al. 1984) is documented. Less understood is the relationship between wind-driven currents and fish entrance in estuaries with small tidal amplitudes, such as those in the Gulf of Mexico. Current studies (Thompson et al. in prep) indicate frontal passages may be important in creating current flows that favor immigration into estuaries in winter or early spring. Herke (1977) showed semi-impoundment of marsh creeks with weirs diminished nursery use by some migratory estuarine-marine species, increased use by other species and changed growth patterns.

These studies indicate the importance of an ecosystem's configuration to fisheries production. However we are far from understanding the complete mix of physiographic features that make these estuaries so productive. Some of the questions still unanswered are basic. If shallow seems to be better, what is shallow? What is the optimum depth for good nekton use? Does it vary from species to species? How much wetland relative to creek area is optimum? How much open water is needed relative to marsh and creeks? How many of each species does each hectare of a nursery send back to the sea? How much does the environment of a marsh creek depend on the adjacent marsh? Is fish space limited? Can we enhance fish production by creating more creek or marsh edge? Some studies show increased fish production with ditching for mosquito control (Resh and Balling 1983), but dredging oil and gas canals seems detrimental to fish production (Day et al. 1982).

The two most studied physics-chemical parameters of nursery areas are salinity and temperature. Because nursery areas are brackish, scientists once thought low salinity was needed for complete species development. For example, menhaden's transformation from zooplankton picker to filter feeder was believed to require low salinity (Reintjes and Pacheco 1966). However, laboratory experiments showed this transformation can occur in full-strength sea water. Perhaps the transformation in low salinity waters is a matter of simultaneous occurrence? With menhaden, the transformation occurs when the larvae are 60 days old, and it takes 60 days from spawning for menhaden to reach brackish areas. Some species are more stenohaline than others. Use of estuarine areas may be limited by salinity tolerances. Yields of brown shrimp in Louisiana have been correlated with the mean salinity of estuaries during their stay in the nursery grounds (Turner 1977). To explain the correlation of high shrimp yields with high salinities, scientists found that more estuarine area is available in the correct salinity range in years with a higher average salinity. The correlation of river discharge with fish production may be the creation of habitat of the correct salinity. Research in the Atchafalaya delta shows that many estuarine-marine species also use a freshwater location as nursery ground (Thompson and Deegan in press). It is possible, as mentioned before, that the role of low salinity is secondary. It has a neutral effect on juveniles, but a negative effect on adult predators (Blaber and Blaber 1980).

Many marine organisms seem affected more by temperature than salinity, within tolerance ranges. And again, many adult species are less tolerant than juveniles of wide fluctuations. Therefore temperature may exclude adult predators from shallow creeks or limit their foraging time. The higher temperatures of marsh creeks also may be reflected in growth. Many fish in the Gulf of Mexico showed increased metabolism and growth at higher temperatures (Hoese 1981). Higher growth rates result in larger fish that are less susceptible to predation (Cushing 1975). Some evidence indicates temperatures of 20 C or greater are necessary for optimal efficiency (Eldred et al. 1961; Wohlschag et al. 1968; Moore 1976).

We know little about how fish respond to simultaneous changes in temperature and salinity. Often large changes in salinity are due to the influx of river flood waters that are much colder than estuarine waters. What are the combined effects of rapid changes in temperature and salinity? Also, what are the effects of these extremes on fish productivity. How do exceptionally cold temperatures or river discharges affect fish productivity? Do they change the amount of habitat available because of species tolerance limits? If extreme weather events cause large fish die-offs and change the mortality schedules, does this change the growth rates for the fish that survive? Do they attain a larger size because of reduced competition? We also do not know the lower limits of change in temperature or salinity that most estuarine fish can detect. Do fish recognize a change of 5, 1 or 0.01 parts per thousand as being significant?

SUMMARY

Consistent life-history patterns, statistical correlations, and general observation point to the importance of shallow inshore estuarine areas in fisheries production. An understanding of the relationships between fish and habitat requirements would be useful for evaluation, design and mitigation of activities affecting estuaries. Clearly we cannot avoid all human impacts on nursery grounds. How do we maintain fisheries production in the presence of human modification? Particularly important fish habitat areas seem to be marshes, sea grass beds and nearshore shallow areas. The major questions yet to be answered are the specifics of the relationships between habitat and fish production. How general are the relationships? Are they species-specific, or are there commonalities in the patterns of use? Some specific questions that need to be answered are:

(1) What are the characteristics of a good nursery?

(2) Would these fish service if they were not in estuaries?

(3) How general can we be when we construct broad relationships such as those between commercial catch and wetland area? Do we need species-specific relationships? What is the fishery yield from an acre of salt marsh?

(4) What do the correlative studies between fish catch and river discharge, wetland/water ratios and primary production mean? What are the underlying mechanisms?

(5) What is the role of the different sources of primary production? What is the role of detritus? What is the trophic base of fishery production? Does it vary among estuaries? What is the effect on fisheries production of differing primary production sources?

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HABITAT CHOICES IN ESTUARINE FISH: DO THEY HAVE ANY?

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We continue to hear questions about estuaries that Birge and Juday answered about lakes a hundred years ago. Why are generalities so difficult to extract from such a narrow strip of water? After all, estuaries are small mixing zones, and those in the same zoogeographic province share a similar and relatively depauperate fauna. Perhaps our classification of fish or estuaries is wrong. Is it possible that we have created an illusion of integrity with our choice of a single word to describe this narrow strip of water? Or do we continue to overlook some major organizing, or disorganizing, factor in the ecology of estuaries?

This is not a paper on estuarine taxonomy. Rather, what we want to consider is the question of whether or not it is likely that we can reach any level of generality in estuarine ecology without a critical reexamination of our current paradigms and significant changes in research emphasis. We will restrict our comments to the Atlantic strip and to the subject of fish.

The Atlantic estuarine fish fauna is largely comprised of a few marine species that have invaded low salinity waters. In addition, there are occasionally large numbers of anadromous species (Haedrich 1983; McHugh 1967). Also present, especially in north temperate estuaries, are resident species (Jeffries and Johnson 1974; Nixon 1980; Nixon and Oviatt 1973; Tyler 1971; Werme 1981). And, depending on the distance upstream or downstream, there are freshwater or stenohaline marine fishes. But a few species dominate the biomass (Bozeman and Dean 1980; Miller et al. 1983; Ross and Epperly in press; Weinstein and Walters 1981). And for the most part, these species are in the juvenile stage of their life (northern estuaries again tend toward exception) (Gunter 1961). The dominant species change with season and are generally reduced in numbers in winter (Haedrich 1983; Hoff and Ibara 1977; Tyler 1971).

Three provisions of nursery areas were suggested by Joseph (1973) as important: 1) a food supply, 2) refuge from predation, and 3) a benign abiotic environment. Certainly because these contribute to the production of fish, they also can potentially limit production. We will examine each, emphasizing our experience in North Carolina estuaries. Hopefully we can pinpoint critical research needs. As guideposts, we will consider the principles of natural selection and fish physiology. This approach is chosen over the more traditional one of trying to distill generality out of everything we know.

FOOD SUPPLY

It is not sufficient to know what fish eat; rather we are interested in how food supply relates to food demand. This requires an estimate of production and the requirements of (potential) competitors and the fishes of interest. Is food typically limiting in estuarine habitats? We think not. Occasional invasions of large numbers of pre-spawning anadromous fish may temporarily depress food supplies. But most evidence suggests an adequate food supply for good growth and survival of juvenile fish in estuaries.

1) Estuaries are comparatively productive aquatic environments (Adams 1976; Mann 1982; Odum and Heald 1975).

2) Inter-specific competition is low, and most fish are generalists (Kinne 1967; Miller and Dunn 1980; Sheridan 1979).

3) Growth rates of fish are high, even at elevated abundances in cages (Currin 1984; Currin et al. in press).

4) Specific production (P/B) of fishes is not biomass-dependent; production is (Currin et al. in press).

5) Diet overlap, indicating high food availability, is common (Woodward 1981).

REFUGE FROM PREDATION

Although we know some details of the food web in estuaries, we know far less about the rates of predation on or by estuarine fishes. It seems more likely that predators may limit the production of juvenile fish than food availability, especially in combination with environmental perturbation (Dovel 1968). We suggest that other considerations outweigh this.

1) Adult fish (potential predators) are comparatively rare in estuaries, perhaps due to their reduced tolerance of low salinity.

2) Visual predators are probably hindered by the high turbidity, shallow depths and large amount of structure.

3) Many of the (potential) predators would necessarily be cannibalistic.

4) Predator saturation would seem likely on occasions when predators did invade juvenile habitat.

ABIOTIC ENVIRONMENT

The concept of estuaries as stressful environments is derived largely from observations that a variety of animals seem to respond negatively to rapidly fluctuating conditions, especially outside their apparent preferred ranges (Hettler 1976; Hoar 1966; Hochachka 1965; Kinne 1967; Knudson and Herke 1978). Many researchers noticed the coincidence of distribution patterns with salinity (Carriker 1967; Gunter 1961; Khlebovich 1969; Remane 1934). A few (e.g. Day 1967) have suggested other factors, such as wave action may be more important than salinity. In fact, some data support the concept of estuaries as stressful, even for estuarine species (Burton et al. 1979; Costlow et al. 1960; Haefner 1969). But the data are largely on stenotopic species or stages, or the experimental conditions are outside the likely rates of change that most vagile organisms experience in estuaries. And the stress of an environmental factor cannot be assessed without knowing the organism's resistance to it or its ability to adapt to it. Scant evidence indicates less stress on the dominant fish than the current paradigm suggests. Several species evolved efficient adaptive or compensatory strategies to withstand or avoid the potential stresses in estuaries (Kinne 1967; Segal 1967).

1) Juvenile stages of many species of fish (even stenohaline marine) are more tolerant of environmental variability than adults (Holliday 1971).

2) The high growth rates of fish in estuaries suggest an absence of a chronic high level of stress (Currin 1984; Currin et al. in press; Knedson and Herke 1978).

3) An intermediate salinity is close to isosmotic for fish.

4) Many marine species of fish can be cultured in estuaries when enough calcium is provided (Gunter 1961; Kinne 1967).

5) Our (unpublished) data on juvenile spot and croaker show almost a complete energetic disregard for rapidly fluctuating salinity.

Where does the suggestion that estuaries are good, not particularly stressful, habitats leave us? Before proceeding, let's reconsider the idea of limiting. We are not saying that improvements in the above habitat qualities would not result in increased production of estuaries fish. Nor are we suggesting that all species should thrive in the estuarine habitat. Rather we are saying that for the dominant estuarine fish, the concept of estuaries as stressful is probably overstated. Food, predation and the abiotic environment do not restrict their production---at least not like the stunted Centrarchid populations in lakes. Finally, we do not believe that estuaries are dispensable for even these fishes. The low salinities may be necessary for metamorphosis or production of preferred food (June and Chamberlain 1959). But, whether these species would be competitively inferior in the marine environment or could not survive without estuaries has not been tested.

It is tempting to infer from a distribution pattern that an animal prefers the environment near the center or that it cannot tolerate the edge environment. But these inferences need to be made in the perspective of the alternate choices available. In distribution patterns derived largely from dispersal of relatively passive swimmers, such inferences are dangerous. Estuarine organisms prefer certain environments because they have no other choices. In such situations an understanding of the factors involved in dispersal is essential. For most estuarine organisms, they are related to the hydrological regime. We know little about the currents of estuaries and the responses of the larval or juvenile estuarine organisms to them? We know that currents, as well as other conservative properties of estuaries (such as salinity, temperature, inorganic turbidity, et al.), are highly variable in time and space. In many cases, animals' distribution patterns in estuaries can be predicted by the distribution patterns of these properties. But the leap to inferences about their function as limiting factors seems unwarranted. If currents control the distribution of estuarine fish, and the patterns are (probably) dependent on the particular morphometry, meteorology, etc., we should not expect to find generality among estuaries (on our sampling stations) until we can ordinate them on the appropriate physical axes. And a lack of physical data for most estuaries precludes this.

As an example, we consider the distribution pattern of juvenile fish in Pamlico Sound (Fig. 1) (Ross and Epperly in press). A two-year analysis of monthly trawl collections of juvenile fish in 51 designated (N.C. Division of Marine Fisheries) nursery areas showed the stations could be separated into five groups based on faunal similarity. Habitat characteristics (distance from inlets, depths, sediment particle size, nitrogen, carbon and C/N) were combined in a discriminant function analysis and resulted in a similar definition of the groups. The distributions and abundances of 22 of the 24 most important demersal species of fish and

FIGURE 1

Bathymetry of Pamlico Sound, North Carolina and 51 juvenile nursery areas, divided into five groups (different symbols) based on faunal similarity of 24 species. See Ross and Epperly (in press) for explanation of analyses.

invertebrates were correlated with at least one of the habitat characteristics measured. All of these are intimately related to hydrology. These 24 species were separable into eight categories based on their distributions and abundances. Did these dominant juvenile organisms select their habitats or were their distribution patterns derived from their initial dispersals?

The two station groups north and west of Bluff Shoal are instructive because Pamlico Sound is divided by the shoal into two subbasins with different orientations. The dominant juvenile fish and shrimp, which originate from winter-spawned eggs offshore, are probably transported from inlets to their nursery areas by wind-driven currents (Miller et al. 1984). Juvenile croaker (*Micropogonias undulatus*) colonize Chesapeake Bay and other estuarine nursery areas north of North Carolina in fall and colonize in spring in North Carolina and southward. They were found in fall almost exclusively at stations north of Bluff Shoal. Similarly, juvenile spot (*Leiostomus xanthurus*) appeared at stations north of Bluff Shoal earlier in spring than at any other station. Oregon Inlet, north of Cape Hatteras, is a potential source of juvenile fish from Virginia coastal waters. But the other inlets to Pamlico Sound are contiguous with the southern subbasin and represent sources of juveniles from Carolina coastal waters. Separation of these two water masses and their attendant biota at Cape Hatteras is well-known (Magnuson et al. 1981; Pielou 1979). The two most abundant juvenile fish in Pamlico Sound show colonization patterns suggesting a strong influence of currents and water mass origin. This simpler hypothesis should be explored as an alternative to active habitat selection based on preferred or prohibitive environmental factors. Other species may respond differently. There are stenotopic marine species that are excluded from certain estuarine habitats. And for eurytopic species, we should expect a spectrum of responses. These other species, not the dominants of estuaries, are most likely influenced by the biotic and abiotic variability of estuaries.

If we suggested or implied that we expected to find the same controls (or lack of) in all estuaries, we would be committing the same error that has led to present overgeneralizations. Where does Pamlico Sound fit in to the spectrum of estuaries on the East Coast? We need a reasonable schema of estuaries, emphasizing the factors that have the most significance to the fish. Unfortunately, the necessary physical data are often lacking for an accurate categorization; Pamlico Sound is no exception. Most of the important biotic and abiotic factors can vary greatly along primary and secondary axes of estuaries. Many are also temporally unstable. While this variability is recognized by most researchers, neither our research protocol or many of our reports adequately demonstrate this. Not even our attempts to classify estuaries recognize their dynamic nature. And no research protocol exists to encourage researchers to measure relevant physical variables that could permit comparisons of estuaries. We lag behind limnologists and oceanographers in this area. Considering the greater variability in "standard" variables in time and space, any useful research protocol should include some continuous recording of temporal changes. If scales of weeks and kilometers are relevant in oceans, then minutes and meters are relevant in a typical estuary.

In the nursery areas of western Pamlico Sound (lagoon), we tentatively concluded that the environment for juvenile fish is benign, biotically and abiotically. Indeed, we think the environment could support more juvenile fish production than it currently does. Production seems constrained by the number of juveniles that initially colonize the nurseries. In the tidally dominated lower reaches of the Cape Fear River estuary, Copeland and Hodson (1977) concluded that entrainment of up to 460,000 post-larvae spot per day by a power plant would have no effect on their production. In other words, the numbers of juvenile fish exceeded the carrying capacity. In fact, the apparent differences in controlling factors would be expected if one considers: 1) the lower shoreline development (Hakanson 1981) that characterizes narrow river valley estuaries like the Cape Fear and 2) the decreased probability that wide river mouths restrict the entry of ocean-spawned post-larvae.

Thayer et al. (1974) reached a different conclusion from ours about food limitation for the Newport River estuary, located near one of the inlets to Pamlico Sound. They hypothesized that zooplankton may control the survival of post-larval spot and other species. The mouths of estuaries are less likely to support large populations of deposit-feeding benthos (Peterson and Peterson 1979; Wolff 1983). Fish living in these higher salinity regions may be more dependent on plankton production (Day 1967) especially larvae or species that are more planktivorous. Nearshore marine fish also may be food limited in the north Atlantic (Tyler 1972). And predation is more likely to be a major structuring factor near the mouths of estuaries than elsewhere.

The estuarine literature is replete with divergent conclusions about the importance of major controlling factors. Space does not permit examination of all of these. Estuaries are no less dynamic and have much smaller spatial and temporal scales. But lacking appropriate scalars on which to ordinate different estuaries (or subregions of estuaries) and sufficient physical or chemical data, we have been guilty of excessive generalization. This had led to the attribution of some of the differences within estuaries to differences among estuaries.

Where does this leave us? We believe that little progress toward understanding estuarine ecosystems is likely without more research emphasis in the following areas:

1) We need more complete descriptions of how biologically relevant abiotic factors within estuaries affect biologically relevant scales of time and space. Without this, we cannot hope to untangle the biological processes or to compare results from different estuaries. Biologists need to involve more physical oceanographers and meteorologists in our research.

2) We need to recognize the importance of advective processes in determining the distribution and abundance of estuarine biota, especially where their patterns

arise from dispersal of immature stages.

3) We need to borrow from ecological theory, not past estuarine paradigms, some ideas of what to expect when we embark on our surveys. We do not need more undirected descriptions. Even though our ideas may be wrong, we should approach our surveys and our experiments from an hypothesis-testing perspective (Weinstein 1982).

4) Advective processes, such as river flow and wind-driven currents, can transport biota and conservative properties (e.g. salinity) over long distances quickly. We should expect to find correlations between them if they are measured synoptically. If they are not, we should expect to find chaos. But because many physico-chemical properties of estuaries are linked, we must recognize that such corrections may be spurious. We should distinguish between causal and predictive factors with laboratory or field experiments.

5) Although the variability of an estuarine environment suggests a high level of stress, data to substantiate this hypothesis are lacking. We need additional measures of biota responses before promoting estuaries as stressful. In fact, the dominant species may be preadapted to tolerate wider ranges and changes than previously believed.

Once we appreciate the importance of the different hydrographics of various estuaries, perhaps we can see patterns through the apparent biological chaos. Some day, we might even consider some hydrological management practices (Kapetsky 1981) to supplement our conventional management strategies. Owing to their small size and convenient location, estuaries perhaps offer the greatest potential for management---not just ranching---of living marine resources.

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FISHERY HABITAT REQUIREMENTS: RESEARCH PRIORITY AND MANAGEMENT STRATEGY PERSPECTIVES FROM THE SACRAMENTO-SAN JOAQUIN ESTUARY OF CALIFORNIA

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INTRODUCTION

The symposium's goal is to develop directions for future research in the nation's estuaries. Such knowledge is needed to establish managerial strategies designed to protect valuable estuarine resources. My response to the challenge paper emphasizes the critical link between research and management that must exist if we are to protect these resources. My views are based on experience gained in the Sacramento-San Joaquin Delta and San Francisco Bay system of California. Our research documents potential impacts on fish and wildlife caused by the diversion of water from the delta by state and federal water projects. Results are being used to develop facilities and water quality standards that will prevent adverse effects of the projects. The California State Water Resources Control Board mandates that these standards be met by the projects as a condition for permission to divert water. Participating agencies include the California Fish and Game, and Water Resources departments; U.S. Fish and Wildlife Service; and the U.S. Bureau of Reclamation.

RESPONSES TO THE CHALLENGE PAPER

General

Deegan and Day (1984) provided an extensive list of fish habitat issues plaguing fishery biologists. Although they offer an interesting overview of the subject, they do not identify research priorities in a concise manner. The numerous questions are not all equally important for making critical management decisions designed to protect estuarine fish populations. This highlights the need to continually define the specific management goals applicable to the estuary in question. The challenge paper did not provide any discussion on management application, needs or strategies. This appears to be a major shortcoming.

Research priorities must be set in the context of management goals. This does not eliminate the need for basic research, for good science and for a better understanding of the system's basic structure and function. We must have clear, sound justification for work that directly relates to resource objectives. We need to ask: What do we need to protect? What management opportunities are available? Can we use the information being sought? What are the benefits/and costs of studying an issue? Answers to these questions and others provide the framework to set priorities and to develop protection strategies. Funding problems for research are often related to the failure to address these issues.The Issue

The challenges indicate these issues : Why and to what degree do nekton use estuaries as habitat? These are the priority research issues. Another approach is to ask: What are the habitat requirements of the important stocks?

This focuses on the management goal and raises certain questions such as: Where in the estuary is this occurring? What potential need is lacking? If the stocks are reasonably stable, what potential changes might cause harm? These questions help prioritize and justify our research.

Our interagency research-management program in the Sacramento-San Joaquin system provides an example. We used long-term monitoring to establish the structure of our estuarine biological community. Part of this program, monitoring the abundance of young striped bass, was initiated in 1959 by the California Department of Fish and Game. Although emphasis has been on striped bass (Morone saxatilis) and chinook salmon (Oncorhynchus tshawytscha) populations, other species captured in our nets also were recorded. From this, useful information has been developed.

We also documented variations in stock abundance and survival, assessed if the variation is important to the stock as a whole and attempted to quantify the causal mechanisms for that variation. We asked the classical ecological question: What influences fish distribution and abundance? This approach brought about the need for good interaction between habitat-oriented and population-oriented biologists. We documented certain influences of river flow on fish and their food organisms in the estuary (Chadwick et al. 1977; Stevens and Miller 1983; Herrgesell et al. 1981; Kjelson et al. 1981).

Flow proved to be a broad habitat requirement that correlated to additional classical fish habitat needs (food, protection from predators and toxics, transport processes, chemical suitability and temperature) as discussed by the challengers. Defining flow volume as a major fish habitat requirement simplified management and made it easier for the public to understand. Flow standards for striped bass and salmon were established by the California Water Resources Control Board to restrict diversion operations of the state and federal water projects. Although freshwater flow may not be a limiting factor in all estuaries, it influences the character of all estuarine systems and must be considered. Water is a major resource, and its use has enormous management implications.

Degree of Use

An overview of the variety of estuarine uses by nekton is provided by the challenge paper. Research needs to define the life stage that is dependent upon estuarine habitat and that is critical in setting year class strength. Correlations suggest that recruitment of a striped bass year class in the Sacramento-San Joaquin estuary is affected by abundance in the first summer of life (at 38 mm in length). Numbers of fish at 38 millimeters correlate well with abundance of 7-millimeter to 10-millimeter larvae. Hence, priority was given to assessing factors impacting abundance of young bass (Stevens et al. In press.).

The term "classical estuarine dependent species," which refers to many Southeast and Gulf Coast stocks, has been used for many years.

Unfortunately, it may have conveyed the idea that other species are not as dependent on estuarine habitat, therefore estuarine research is not needed. Until recently, this seemed to be the case with Pacific salmon stocks (Healey 1982; Levy and Northcote 1982).

Relatively short-term exposure to estuarine habitat can significantly impact survival. Our work with Sacramento River chinook salmon indicates that the survival of out-migrant juveniles (smolts) as they migrate through the delta from upstream rearing areas is directly related to the amount of freshwater flow entering the delta (Fig. 1 and Kjelson et al. 1982). We are evaluating several mechanisms that explain this relationship including predation, food, diversions and temperature. We will use the findings to recommend mitigation measures to help overcome the impact of planned, additional diversions of water from the estuary.

Relative Contribution to Stock and Relative Survivorship

These are two issues the challengers raised. They highlight possibly the most critical research needs in establishing estuarine habitat requirements for nekton. Defining a life stage's contribution to adult stock and its survival rate under different habitat conditions is a powerful tool for evaluating management strategy. Contribution to the adult stock links the habitat to the resource we are protecting. The survival rate quantified, in a net sense, how well the multiple interacting factors we call "habitat" are doing in meeting the organisms' needs.

We are studying the relative importance of the Sacramento-San Joaquin estuary as rearing habitat for fall run chinook salmon stocks (Kjelson et al. 1982). Chinook fry (the pre-smolt stage) are reared in upstream freshwater sites at and below spawning locations, in the delta (fresh to low salinity water), and in the brackish waters of San Francisco Bay. Preliminary estimates of differential survival based on adult coded wire tag recoveries from the ocean fishery are shown in Table 1. Survival appears to vary by the rearing location and the magnitude of freshwater runoff.

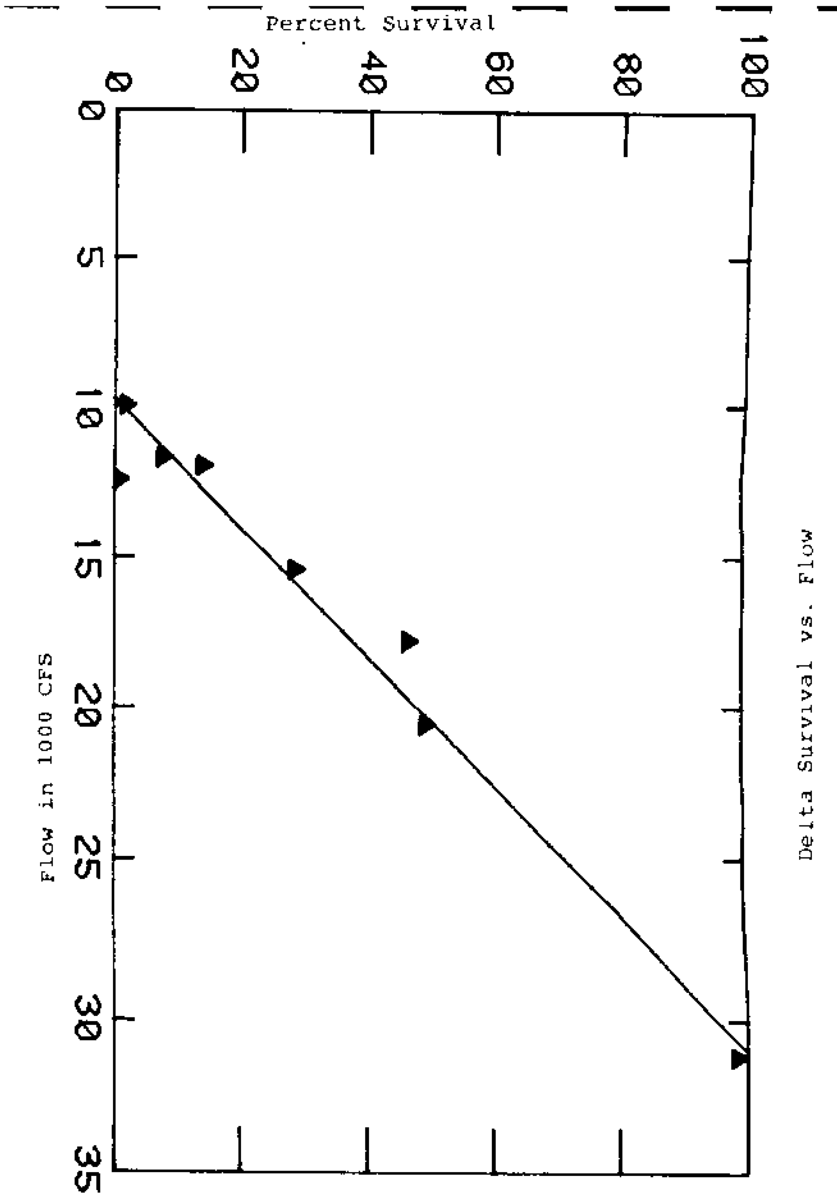

FIGURE 1
Percent survival of coded wire tagged chinook salmon smolts (approximately 70 mm to 90 mm) as they migrate through the Sacramento-San Joaquin River Delta during late May and early June, 1969-1971 and 1978-1981, under varied flow. Flow measured at "I" Street in Sacramento.

TABLE 1

Relative survival of fall-run nose tagged chinook salmon fry released in the Sacramento-San Joaquin Estuary and Sacramento River in March of 1980 and 1981 and recovered in the ocean fishery as adults.

Habitat	1980 (wet)	1981 (dry)
Upper Sacramento River	370	48
North Delta	130	39
Central Delta	NS	27
San Francisco Bay	5	6

Such data, combined with abundance estimates from each rearing habitat, will enable us to define the relative contribution of chinook fry reared in selected habitats.

Our greatest challenge in documenting chinook fry contribution to adult stock is the need to obtain total measures of abundance from the various habitats to which fry survival is linked. Sampling strategies are important if one is to achieve unbiased fish abundance and survival measures (Kjelson 1977). Research assessing the interrelationships between sampling gear, fish behavior and environmental factors must be given more priority if our data are to be unbiased and our interpretations sound. We are attempting to improve estimates of total salmon abundance in each rearing habitat by estimating fry catch efficiencies for several types of gear in various habitats. Catch efficiencies are obtained using mark-recapture techniques and other methods (Kjelson and Colby 1977). Applying the reciprocal of the catch efficiency---the fraction of fish captured that are present in the area sampled---to the raw catch data, yields a measure of total abundance or biomass (Kjelson and Colby 1977). We use haul seines and electrofishing gear to measure abundance. Chinook salmon fry, during rearing, concentrate in shoreline habitats that vary (sand, mud, gravel/riprap, marsh and riparian). As usual, the cost increases as we seek to refine estimates of abundance. We must critically evaluate how accurate an answer must be for our management purposes.

Another example of an attempt to use catch efficiencies and biomass data to develop total biomass values of nekton for selected estuarine habitats is shown in Table 2. These results are based on research in the Newport estuary near Beaufort, N. C. (Kjelson 1977; Kjelson and Colby 1977). It represents the use of six sampling gears for which catch efficiencies for the dominant nekton species were obtained by direct experimentation.

Quantitative Studies of Larvae and Juveniles

The influences of hydrodynamic processes on the distribution and movements of estuarine nekton and

TABLE 2

Mean seasonal and annual total biomass (g/m^2) of fish, shrimp and crabs for nine habitats in the Newport River Estuary of North Carolina. Values represent raw biomass data multiplied by the reciprocals of gear catch efficiencies.

	TOTAL BIOMASS (GRAMS/METER^2)				
Habitat	Spring	Summer	Fall	Winter	Annual X
Freshwater River	3	5	1	T	2
Brackish Water River Channel	3	39	10	T	13
Ditched High Marsh (Juncus)	4	6	1	T	3
Tidal Creek High Marsh (Juncus)	12	11	3	4	8
Estuarine Shoreline	2	4	1	T	2
Shallow Open Water	9	15	6	2	8
Low Marsh Tidal Pond (Spartina)	7	33	28	T	17
Eelgrass Bed	11	24	28	6	17
Deep Open Water	2	4	T	T	2

T = Trace =<0.7 g/m^2

their food sources has been suggested as important. The initial habitat "selection" by fish larvae is usually determined by circulation patterns, although it is recognized that behavior mechanisms often influence utilization to some degree. Hydrodynamics play a major role in defining habitat characteristics of an estuary. The need for interdisciplinary research between fishery biologists and estuarine hydrodynamics is great. Such interaction should, in fact, be a research priority in itself.

Although research on striped bass and salmon and efforts to understand the estuarine food chain have yielded valuable knowledge, one of the most difficult problems has been measuring and interpreting the relationship between hydrodynamic processes and fish abundance. This was particularly true in our modeling of phytoplankton dynamics in the estuary (HydroQual 1981; Arthur and Ball 1979). Most recently, we saw these problems in our efforts to define freshwater outflow needs for fishery resources inhabiting San Francisco Bay (Herrgesell et al. 1983). Preliminary findings indicated that variations in circulation patterns in the bay attributed to changes in freshwater inflow, influenced the numbers and distribution of post-larval flatfish. Higher freshwater flows into the bay results in stronger upstream gravitational circulation. Hence, numbers and distribution are expanded in high flow years (Table 3; Armor and Herrgesell. In press.). Again, in setting research priorities to establish fish hydrodynamic needs, we must ask what type of hydrodynamic information is needed and how refined it must be.

Expenses for hydrodynamic studies are high, however cost sharing is possible between programs with different management goals but similar hydrodynamic data needs. We pooled funds from our water development-related bay program with that of the effluent discharge monitoring program in the bay area to be more cost effective.

Coordinated efforts are another high priority research/management objective that often takes much energy to achieve. Although everyone talks about coordination, it is seldom accomplished in the full sense. Funding agencies should make appropriate coordination a formal requirement in

TABLE 3

Catches of post-larval flatfish for each area of the San Francisco Bay studied from 1980 to 1982. Data are expressed as mean number/10^3 m^3/stations. Numbers in parentheses are the total annual freshwater flow in million acre feet (maf) entering the bay.

Species	West Delta	San Pablo Bay	Central S.F. Bay	South S.F. Bay
1980 (22.9 maf)				
English sole *Parophrys vetulus*		13	24	19
Starry Flounder *Platichthys stellatus*		36	139	31
Sand Sole *Psettichthys melanosticutus*			9	5
1981 (11.5 maf)				
English Sole			3	
Starry Flounder			3	6
Sand Sole				
1982 (32.9 maf)				
English Sole	15	459	400	31
Starry Flounder		15	24	14
Sand Sole		15	9	6

contracts to assure it is accomplished. Thorough coordination between the public, educational institutions and regulatory/research and development agencies can yield huge rewards for the resources we are attempting to protect. This is at the heart of many of our problems.

A need exists for the coordination of data stored in common computer files. This would enable researchers to have access to the data for their individual use. The system could help encourage interdisciplinary approaches that would benefit all. We initiated use of the EPA STORET system, normally used to store water quality data, to store fishery data. These modifications are presently being tested, and we are hopeful they succeed. The risks of others using "your" data erroneously exist but the potential benefits outweigh them.

Are Fish in Estuaries Food Limited?

The question of food limitation is one of the most researched problems in fishery biology. Deegan and Day (1984) described this problem by saying there was "a lot of research, but no real answer."

This does not mean that trophic studies have been useless. However, questions arise. How often do food shortages impact stock abundance? And is the problem truly less in estuaries than other systems as is inferred by the "fact" estuaries are productive systems. Again, if it is a research priority, it must be justified in terms of what we are trying to preserve and the likelihood that it is a problem or a potential one.

Evaluation of the recent striped bass decline in the Sacramento-San Joaquin estuary suggests that a potential cause is a reduced availability of zooplankton during initial larval feeding. Another probable cause is a decline in egg production caused by reduced abundance of adults (Stevens et al. In press.). Stevens et al. found a significant relationship between young bass abundance and (1) zooplankton densities when the larvae began feeding, and (2) mean May to July river flow. We have evidence that there also is an overall decline in the productivity (primary and secondary as measured by phytoplankton and zooplankton densities) in the bass nursery area, which may be limiting the survival of larvae.

A major research need has arisen in Pacific northwest estuaries related to potential food limitations. The problem concerns the carrying capacity of estuarine systems exposed to huge releases of salmon from hatchery facilities. This has been one of the driving forces in initiating salmon research in estuaries. Again, the most direct approach to this problem is to measure survival under varied salmon rearing and food densities. Intensive sampling programs and marking experiments required to achieve such information are expensive. An alternative research strategy is to measure growth, via scale and otolith analysis and residence time, with the assumption that better growth yields greater size and better survival later.

Protection From Predators

If there are few predators in nursery areas, great. But is it necessary to know more for management decisions? The relationship of turbidity to predation is significant and may partly explain our salmon smolt survival to flow relationship (Fig. 1). High flows are usually accompanied by high turbidity and may decrease the efficiency of sight-feeding predators. We are evaluating the variation in predator abundance during the smolt migration period (April to June) from our gill net, fyke trap and electrofishing survey data.

Our program gained some knowledge in predator-prey interactions from our Interagency Fish Screen Research Study. Fish screens are becoming more common as a mitigation measure in estuarine waters, yet predation can be a significant negative impact associated with such facilities. Experiments with marked juvenile salmon that were released in the state water project pump/storage forebay in the South Delta indicated that mortalities were over 90 percent (Hall 1980). The mortalities were apparently from observed high predator populations (striped bass and catfish) in the forebay and adjacent to louver fish screens near the pumps. Research of predator-prey

interactions is needed to develop management strategy to solve such problems.

Chemical Suitability

Although the challenge paper does not include a discussion of man-made pollution on estuarine fish habitat, this is a research area needing high priority since it influences habitat quality in many estuarine systems. Toxic substances are a potential cause of the declines of striped bass, phytoplankton and zooplankton in the Sacramento-San Joaquin estuary. However, the lack of sufficient data prevents us from testing the theory. Evidence suggests that adult bass have accumulated some toxins in their flesh at levels exceeding those recommended (Whipple et al. In press.). It also shows that herbicides drained from rice fields in the spring could affect eggs, larvae or adult bass in the Sacramento River. Although these effects are defined, we don't know the overall population consequences. Further study is needed.

There is evidence that ambient river temperature alone may be a major source of mortality for smolt salmon as they pass through the delta. Such data is taken from June during years when the amount of flow entering the delta is relatively low (Kjelson et al. 1982). It complicates the smolt survival/flow relationship noted earlier during low flow periods because it is difficult to separate the individual impacts of flow and temperature. We seldom see low temperatures and low flows, thus temperature is correlated inversely with flow and is influenced by ambient air temperature. More data will be necessary to refine this relationship.

Summary

The challengers provided a broad theoretical view of the issues involved in estuarine fish habitat requirements. Research priorities were not well defined, and the critical link between research and management goals in terms of important stocks was not discussed. They raised some important questions that are justified research priorities.

However, many of the questions do not have a high benefit/cost ratio to support further study.

My discussion has recommended research priorities and management strategies that we found to be justified from our experience in the Sacramento-San Joaquin Estuary of California. These priorities and strategies appear to be useful for most estuarine systems. The following list summarizes these recommendations (not necessarily in order of importance):

Research Priorities

1. Develop long term data bases.
2. Identify critical habitat/stock relationships.
3. Identify relative contribution to total stock of different habitats.
4. Identify flow requirements for critical life stages.
5. Identify sampling gear-fish behavior, habitat interrelationships.
6. Identify hydrodynamic influences on organism distribution, abundance and survival.
7. Identify contaminant impacts on estuarine fishes
8. Emphasize interdisciplinary approaches.
9. Document if food is limiting to estuarine fishes

Management Principles/Strategies

1. Prioritize management goals.
2. Require coordination between researchers and managers
3. Define information needs for management decisions.
4. Develop fish habitat requirements to prevent adverse impacts to fish stocks.
5. Encourage open communication between researchers, managers and the public.
6. Make data available to all research/management disciplines.
7. Initiate cost sharing to support research.

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FISHERY HABITAT REQUIREMENTS: UTILIZATION OF NURSERY HABITATS BY JUVENILE PENAEID SHRIMP IN A GULF OF MEXICO SALT MARSH

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INTRODUCTION

This paper responds to the challenge issued by Deegan and Day (1984) regarding characteristics of a good estuarine nursery. The discussion is primarily based on data from juvenile shrimp in a Texas *Spartina alterniflora* marsh, but the principles outlined may extend to other species and have implications elsewhere. The principles as summarized are:

1) Direct exploitation of the salt marsh intertidal by natant estuarine species may be extensive and highly useful for feeding and protection.

2) Since direct exploitation of the marsh by estuarine species depends upon intertidal flooding, the dynamics of water level changes and marsh geomorphology will control accessibility to the marsh. For instance, tides of relatively low diurnal and high seasonal amplitude may improve accessibility through seasonal stands of high water in intertidal areas. Likewise, increased intertidal edge in marshes may facilitate access for exploiting estuarine species.

3) The degree of marsh exploitation by natant estuarine species differs among species and may differ within species depending upon availability of alternative habitats.

In the northwestern Gulf of Mexico, tides are dominated by seasonally high and low water stands, and estuarine marshes tend to be highly reticulated, having a large amount of edge. We propose that for brown shrimp (*Penaeus aztecus*), these characteristics may partially explain the high nursery value of Gulf salt marshes.

THE PROBLEM

In the past, information on estuarine-dependent juveniles of fishery species in the salt marsh (vegetated intertidal areas) has been limited due to the inherent difficulty of sampling in marsh vegetation. Most measurements of natant macrofauna abundance were restricted to subtidal channels, bayous and creeks that weave through and bound the marsh (Weinstein 1979). Increased abundances of some species were associated with the marsh edge (Mock 1966; Faller 1979), but comparisons of animal densities in marsh and nearby open water were not made. To compare these and other habitats, sampling techniques that measure relative abundances are inadequate, and accurate density measurements of estuarine macrofauna are needed. Once distributional comparisons are based upon actual densities, the degree of habitat specificity can be established for each species. Hypotheses regarding space, feeding and protective utility to species between habitats can be formulated and tested.
We examined the significance of density differences for estuarine species between Spartina marsh and adjacent subtidal open water when both habitats were equally accessible (i.e., flood tide). For penaeid shrimp, we also designed manipulative field and laboratory experiments to test the utility of Spartina habitat in providing nutrition and protection.

HABITAT SPECIFICITY

We assumed that animal densities reflected the degree of usage and perhaps habitat selection by an estuarine species. To compare densities between adjacent vegetated and nonvegetated habitats, we employed large (2.8 square meters) corer-type samplers in pairs (Zimmerman et al. 1984). Through replicate pairwise comparisons of vegetated intertidal and nonvegetated subtidal, we analyzed density differences in monthly sample sets between March 1982 and March 1983.

Our results demonstrated that juveniles of fishery species, including white shrimp (P. setiferus), brown shrimp (P. aztecus) and blue crabs (C. sapidus), were abundantly found in marsh vegetation at flood tide (Fig. 1; Zimmerman and Minello 1984). Brown shrimp were significantly more abundant in vegetation in all but winter months, and blue crabs were always more numerous in vegetation ($P < 0.01$; paired t-tests). White shrimp were frequently numerous in vegetation but overall were not more abundant in either habitat. Major influxes of postlarval brown shrimp into the marsh correlated positively with seasonal stands of high water during spring and fall. Blue crab peak abundances coincided with the fall high-water stand, the highest seasonal tides (Hicks et al. 1983). White shrimp abundances appeared unrelated to water level as were abundances of the resident grass shrimp Palaemonetes pugio. Grass shrimp were numerous throughout the year and were essentially restricted to vegetation during flood tide (Fig. 1). By species, fishes were variable in their attraction to marsh habitat. Among 29 species collected, 14 species each had 75 percent of their mean monthly abundance in vegetated habitat and 10 species had 75 percent of monthly abundances in adjacent nonvegetated habitat. Using the 75 percent abundance criteria, only five species did not select either habitat. Of the 11 most abundant fishes (93 percent of all fish numbers), Gobiosoma bosci, Lagodon rhomboides, Fundulus spp., Cyprinodon variegatus, and Cynoscion nebulosus selected vegetation. Leiostomus xanthurus, Anchoa mitchilli, and Brevoortia patronus selected nonvegetated habitat, and Micropogonias undulatus, Paralicthys lethostigma and Mugil cephalus were indifferent to either habitat.

NUTRITION OF SHRIMP IN MARSH HABITAT

Since brown shrimp were strongly attracted to flooded Spartina habitat, we designed an experiment to examine potential nutritional benefits for shrimp exploiting the vegetated intertidal areas versus nonvegetated subtidal areas. Six replicate cages (2 x 4 m) split lengthwise to provide experimental and control portions were set in each vegetated and

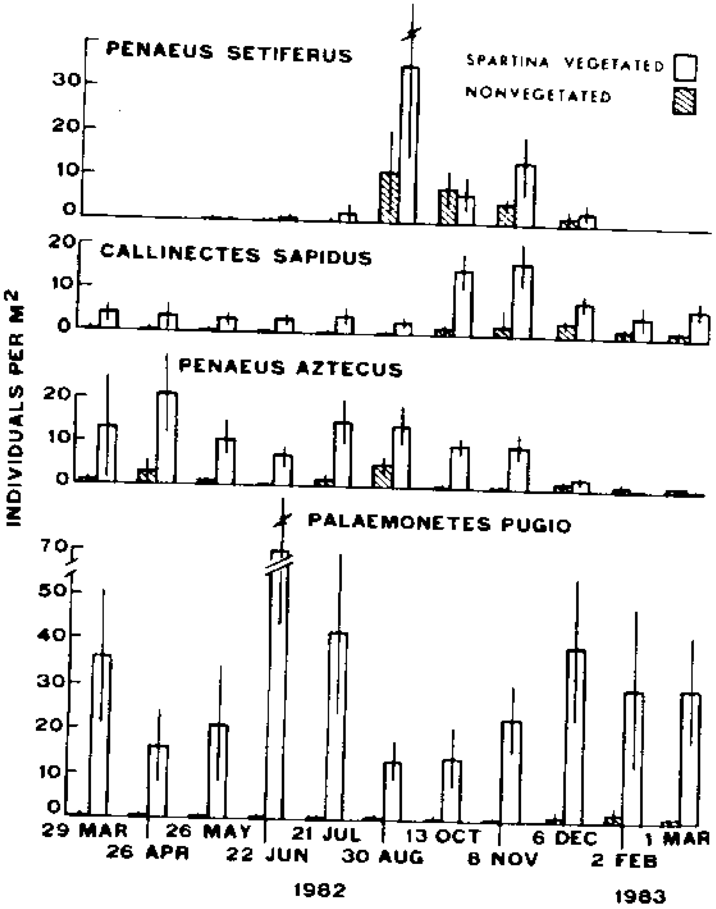

FIGURE 1

Comparative densities (mean and 95% C.I., untransformed data) of macrocrustaceans from *Spartina alterniflora* habitat and adjacent nonvegetated habitat in a Galveston Bay salt marsh (taken from Zimmerman and Minello, 1984).

nonvegetated habitat. Vegetated cages included one half nonvegetated subtidal to allow a refuge during low tide. After placing the cages, a coarse mesh seine was passed once through the cage during low tide to remove fish, crabs and shrimp larger than 30 millimeters total length. Postlarval white and brown shrimp easily passed through this seine. Small brown shrimp (50/cage) of uniform size (approximately 30 mm TL) were added to the experimental part of each cage. After 27 days, all shrimp were removed and measured for total length.

Sizes of brown shrimp in vegetated cages at the end of the experiment were significantly larger ($P < 0.01$, Kolmogrov-Smirnov test; Fig. 2) than those in nonvegetated cages. These data demonstrated that even under limitations imposed by a natural tidal regime, significant additional nourishment was derived from direct exploitation of intertidal marsh by brown shrimp. Sizes of white shrimp (initial sizes were less than 30 mm) did not differ between cage treatments. Furthermore, stable carbon isotope ratio values did not overlap between white shrimp (-13.4 o/oo ± 0.2 SE) and brown shrimp (-16.4 o/oo ± 0.2 SE) in the cages. These data strongly imply resource partitioning and separate habitat needs exist for white and brown shrimp.

PROTECTIVE FUNCTION OF MARSH VEGETATION

The structure of sea grasses offers amphipods and caridean shrimp protection from fish predation (Nelson 1979; Stoner 1979; Coen et al. 1981; Heck and Thoman 1981). *Spartina* apparently functions similarly for amphipods and small gastropods (Vince et al. 1976; Van Dolah 1978). In laboratory experiments (Table 1), we demonstrated that simulated *Spartina* structure reduces predation on juvenile brown shrimp (50-69 mm) by pin fish (*Lagodon rhomboides*) and Atlantic croaker (*Micropogonias undulatus*) (Minello and Zimmerman 1983). No effect on predation rates was detected, however, for spotted sea trout (*Cynoscion nebulosus*) or red drum (*Sciaenops ocellatus*) ranging from 119 millimeters to 245 millimeters in length. This variability in the protective nature of marsh vegetation for brown shrimp may also depend upon size or developmental

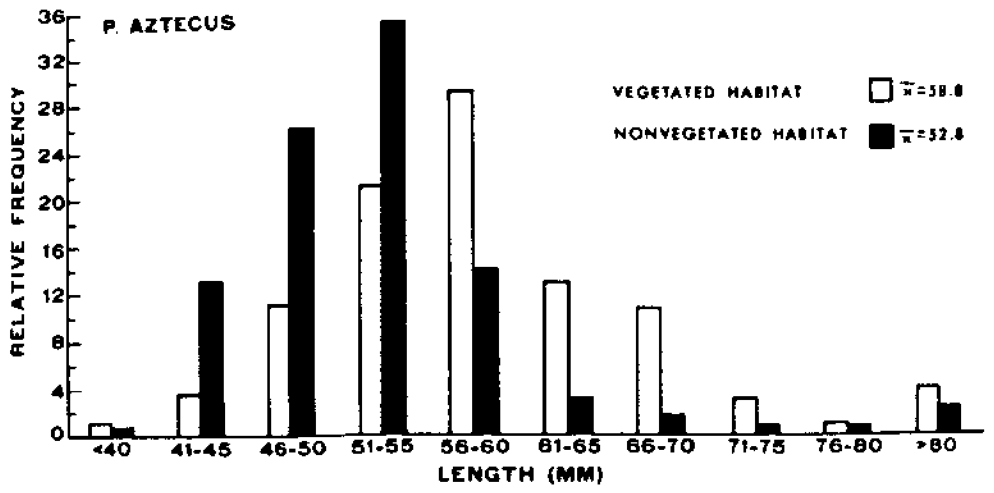

FIGURE 2

Comparative size-frequencies of brown shrimp (*Penaeus aztecus* after 27 days (June 1983) in *Spartina alterniflora* habitat (222 shrimp, x size = 58.6 mm TL) versus adjacent nonvegetated habitat (375 shrimp, x size = 52.8 mm TL) in a Galveston Bay salt marsh (unpublished, Zimmerman and Minello).

Table 1. Mean number of *P. aztecus* eaten/fish/day at different vegetation densities for predators examined (taken from Minello and Zimmerman 1983).

Predator	Pred. Size (mm TL)	#Obs/ Mean	Mean number of shrimp eaten/fish/day				ANOVA P
			No Veg.	220 Stems/m^2	440 Stems/m^2	880 Stems/m^2	
Pinfish	61-77	9	2.2	1.4	1.4		0.03+
Atlantic Croaker	115-133	3	3.4		2.6	2.0	0.04
Red Drum I	154-182	3	6.7			6.3	0.86
Red Drum II	190-245	3	10.3			9.3	0.67
Red Drum III	160-195	3*	9.7			8.5	0.52
Speckled Trout	119-170	3	3.8			3.8	1.0

* n=2 for vegetated treatment
\+ Taken from Table II

stage. In experiments using live Spartina in small aquaria, we found that the presence of Spartina reduces predation on postlarval brown shrimp (7-19 mm) by juvenile pinfish and red drum between 37 millimeters and 59 millimeters in length (unpublished data). Although these results are preliminary, no effect of vegetation was detected on predation rates of Fundulus grandis or juvenile Atlantic croaker.

The protective nature of Spartina also appears to differ between species of shrimp. Selective predation experiments in the laboratory indicate that juvenile white shrimp are more susceptible to predation by Atlantic croaker than brown shrimp in the presence of simulated Spartina structure (manuscript in preparation). Atlantic croaker did not select for either prey species in nonvegetated treatments. In partially and completely vegetated treatments, however, there was a significant selection for white shrimp over brown shrimp. This difference in the protective nature of vegetation between brown and white shrimp coincides with a difference in selection for vegetation between the two prey species.

In combination, our predation studies indicate that a generalization across all species cannot be made regarding the protective nature of salt marsh vegetation. As cover, the vegetation apparently functions differently dependent upon size and/or species of prey and predators.

DISCUSSION AND SUMMARY

The nursery function of salt marsh estuaries is generally known (Herke 1971; Thayer et al. 1978; Weinstein 1979; Montague et al. 1981), and correlations of increased marsh area and edge with high fishery yields have been reported (Turner 1977; Faller 1979). The evidence for utilization of marsh habitats or marsh materials by fishery species has been indirect and not well established. For the most part, theories coupling the nursery function with marsh habitats have relied upon transport of detritus or nutrients from the marsh into estuarine open-water habitats (Odum 1980). In contrast, Bell and Coull (1978) and Bell (1980) suggested that direct predation by natant estuarine macrofauna may account for

numerical reductions in populations of marsh macrofauna. Our studies demonstrate that certain estuarine species may invade the marsh at flood tide in significant numbers and derive important nutritional and protective benefits from its exploitation.

If we accept direct utilization of marsh habitats by large numbers of some estuarine-dependent juveniles, then tidal dynamics in the estuary become an important controlling mechanism. When daily tide ranges are relatively high and are equivalent to or greater than seasonal variability, the time available for marsh exploitation, especially seasonally, may be diminished. This case is increasingly more apparent from lower to higher latitudes in the western North Atlantic and is evident along the eastern coast of the U.S. (Provost 1976). Conversely, in the Gulf of Mexico where seasonal tides dominate, marshes may be periodically more available for direct exploitation. This may be particularly valuable in expanding feeding grounds to a structurally diverse habitat where food is more abundant and concentrated. Included in exploitation is utilization of marsh cover as protection from predation. In regions where tidal ranges are low and marsh is more accessible, mortality due to predation may be reduced. Low ranges tend to contract and expand estuaries less radically, and that may facilitate use of protective cover for prey. In regions where diurnal tidal ranges are high, predation may be more extensive due to longer periods of prey exposure in unprotected open water. In addition, larger tides may force prey into a smaller estuarine area and volume at lowest ebb, which may increase prey densities away from protective cover and extend the advantage to predators.

The configuration and slope of marsh and open water areas in estuaries may also have bearing on the nursery function. More reticulation between habitats increases the amount of edge, and more edge may facilitate access to marsh for exploiting species. On the other hand, if the banks along channels or bayous are slightly elevated above the interior marsh or the marsh is relatively unbroken by small entry channels and streams, access may be impeded for estuarine species.

In conclusion, we agree that marshes differ, especially regionally, in their utility as nursery habitat for juveniles of many fishery species. The primary mechanisms controlling the nursery function may be tidal dynamics and geomorphology of the marsh, either through facilitation or limitation of access for exploiting juveniles. Finally, the utility of marsh may differ among estuarine species dependent upon their particular strategy of habitat utilization in the estuary.

We propose that manipulative experiments in the field and laboratory can lead to separating habitat effects and understanding controlling mechanisms for estuarine species. The data and information derived from such studies are an essential prerequisite to the evaluation, conservation and management of our coastal fishery resources.

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WHAT FACTORS DETERMINE HABITAT USE IN FISH?

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INTRODUCTION

Ecologists and fishery managers are interested in what sorts of habitats fish occupy. We want to understand the habitat requirements of fish to protect necessary habitats from destruction, pollution or damage. But the term "habitat requirements" suggests that we are attempting to elucidate the essential, and perhaps minimum, requisites for life by these fish. We need to examine habitat use by fish in terms of the possibilities for growth or reproduction in various habitats rather than to define the boundary conditions for life.

I will begin this paper with a clarification of terms. The habitats fish occupy (i.e., where we find them) may or may not have anything to do with the habitat selection or preferences of fish. For example, larval estuarine fish initially may occupy a bay because the water they were being transported in slowed down there. Their abundance in the bay may have nothing to do with habitat selection. Thus, when we examine the distribution of larval fish, we must be cautious about invoking habitat choice behavior without first eliminating the simple alternate hypothesis.

Once we have documented that active habitat selection is occurring, we will be interested in how fish make their choices. What are the fish trying to maximize or optimize? If fish respond predictably to habitat characteristics or available resources, then it may be possible to establish reasonable generalizations about what fish will do with a set of habitats. Again, knowing where the fish are abundant does not necessarily allow us to describe their optimal habitat. Multiple factors control the value of habitat to fish, but compromises and use of suboptimal habitats may be common. The distribution of fish is influenced by environmental factors including temperature, salinity, light, dissolved oxygen and other physical/chemical habitat characteristics. Fish distributions also are influenced by the presence of predators or competitors for resources such as food or spawning sites.

What criteria might fish use to make habitat selection decisions? Organisms maximize fitness during natural selection so one might expect fishes to choose available habitat to maximize fitness. Because these choices are complex and involve trade-offs in costs and benefits, we expect habitat selection patterns in fish to be complex and difficult to predict. Recent research on optimal foraging theory (Pyke et al. 1977) and other behavioral optimization hypotheses (Ware 1982; Crowder and Magnuson 1983; Dill 1983), as well as experimental tests of these ideas relative to habitat selection in lakes and ponds, (Mittelbach 1981; Werner et al. 1983a) have demonstrated that fish behave in ways that are consistent with maximizing fitness.

Habitat characteristics influence absolute abundance of fish and their distribution. Fish recruitment highly variable and poorly under-stood. Causes of recruitment variability in fish are unknown. But hypotheses concerning starvation of larvae (Hjort 1914; Lasker 1975, 1978) and predation or cannibalism on eggs and larvae (Crowder 1980; Hunter and Kimbrell 1980; MacCall 1981) are often used to explain critical periods in the ontogeny of pelagic fish. Larvae of estuarine-dependent fish are pelagic and migrate or are transported long distances to enter estuaries. The pattern and stability of larval transport may be critical to these species (Miller et al. 1984). As Sharp (1981) pointed out, larval fish may face a series of critical periods that serve as mortality bottlenecks, reducing recruitment. Recruitment of estuarine-dependent fish that spend a portion of their lives in the estuary may be determined in the larval stage in the open sea. But the ecology of these larvae is unknown relative to what we know about juveniles in the estuary or the larvae of marine pelagic species.

ESTUARINE HABITATS

Though estuaries defy generalization, the conventional wisdom is that physical factors dominate the distributional ecology of juvenile estuarine fish (Joseph 1973). Competition for food appears to be relatively unimportant. Broad overlaps in diets, the abundance of available foods relative to the juveniles' density, and the rapid growth achieved by these fish suggest that food is not often in short supply. Competition may only be important during seasonal bottlenecks when critical resources are temporarily in short supply. Predation may be an important factor in the mortality of juvenile estuarine fishes. But it is frequently argued that predation is reduced in nursery areas due to reduced predator densities in these typically shallow, turbid or vegetated habitats. We know little about the distribution of predators relative to juvenile fishes in estuaries, and we know even less about the importance of predators to juvenile fishes.

Perhaps the density of juvenile fish in estuaries is limited by recruitment of larvae into estuaries from the sea. Environmental variability in available food, intensity of larval predation or larval transport may reduce the density of potential colonists to such a degree that resources within the estuary rarely become limited. The second possibility is that juvenile fish densities are reduced below the carrying capacity of the available food by predation. Little is known about either of these potentially important factors.

GREAT LAKES COMPARISONS

Lake Michigan is dominated by fish of recent marine origin. The major piscivores include Pacific salmon and the major forage species are alewife and rainbow smelt (Smith 1968, 1970; Christie 1974). Of all the native and exotic fishes in Lake Michigan, we have no true estuarine-dependent species, which spawn offshore and whose larvae depend on nursery areas in nearshore bays or rivers. Numerous species (salmon, alewife, smelt, yellow perch, shiners) are anadromous and move to nearshore areas, rivers and bays to spawn. Their larvae are abundant in these habitats. Other species (bloater, sculpins) spawn offshore and move to a nearshore environment later in their lives. Lake whitefish spawn offshore, and the larvae drift into bays where they go through a brief nursery period. But they also pass through this period in the open lake successfully (Frederick 1981).

Physical factors are important to the distribution of fishes in Lake Michigan. Larval and adult fish distributions nearshore are influenced by movements of water masses such as upwellings (Brandt et al. 1980; Heufelder et al. 1982). Frequent upwellings may reduce larval survival or drive larvae offshore, away from productive nearshore habitats. Shifts in predominant wind direction determine whether larval lake whitefish reach nursery bays. Intense storms that occur after spawning and before the eggs hatch may determine year class strength (Frederick 1981). Temperature may determine the distribution of adult fishes that occupy the thermal gradient where the thermocline intersects the bottom of the lake (Brandt et al. 1980).

We tested the hypotheses that starvation or predation on larvae may determine year class strength in bloater or alewife in Lake Michigan. Laboratory experiments suggested that bloater larvae are relatively insensitive to starvation. They do not experience a critical period associated with first feeding or a point beyond which death is inevitable even if food becomes available. When 20 fish that had been starved 30 days since hatching were exposed to food, 70 percent fed within one hour. But starvation does lead to reduced growth rates and swimming speeds, which may prolong the period of predation risk and increase the probability of capture by predators (Rice unpublished data). We are testing the idea that predation by adult and juvenile fish might be an important mortality source for juvenile bloaters. We are also examining mechanisms of larval survival in alewife. Because alewife larvae are smaller at hatching, we expect food availability to be more critical than for bloaters.

Unlike estuaries, competition appears important in the recent history of Lake Michigan. Because sea lamprey killed all the top piscivores in the lake, alewife increased exponentially in the absence of predation during the early 1960s. Mean zooplankton size also was reduced significantly (Wells 1970), suggesting food limitation, and a number of native fishes were lost. Alewives are extremely efficient pelagic planktivores. They have a foraging advantage over the native fishes because they can filter feed even on small zooplankters (Janssen 1976; Crowder and Binkowski 1983). Because of the historical evidence for competition, we examined the evidence for resource partitioning. Current habitat and diet partitioning is consistent with the hypothesis that competition is important in this community (Brandt et al. 1980; Crowder et al. 1981). But we had no direct evidence for competition. Only one native deep-water cisco, the bloater, remained abundant following the alewife invasion. I recently compared the resource use patterns and trophic morphology of bloaters caught before alewife abundance with those caught 19 years later. I found that bloaters now have fewer and shorter gill rakers (Crowder 1984). In addition, bloaters shift to bottom habitats and benthic prey as much as two years earlier in their life history than before alewife became abundant. These shifts are likely due to selection for benthic foraging efficiency in response to alewife competition.

Predation is probably an important factor in the distribution and abundance of Lake Michigan fish. In fact, predation by alewife and smelt on the eggs and larvae of native fishes may have contributed to their decline (Crowder 1980). Of the 21 species common prior to the invasion of alewife and smelt, 10 have eggs or larvae that tend to be pelagic. Following the invasion, only one species remained abundant---bloater. The other 11 species that have demersal eggs and larvae may have fluctuated during the alewife increase, but they did not disappear. Salmon and lake trout stocking that began in 1965 after sea lamprey were reduced by lampricides has increased predation on alewife, which is the primary forage of these predators. But how do we evaluate the importance of predators to a forage base?

We wanted to answer one major question about salmonid stocking: How many predators are too many? When we began our study, salmon stocking was increasing due to growing pressure from fishermen and managers to expand this increasingly valuable fishery. We were concerned because alewife, like other clupeids, undergo dramatic fluctuations in abundance from year to year. Because the numerical response of the predators is limited by hatchery capacity, it is not linked directly to the numerical dynamics of the forage base. Bioenergetic models of the stocked salmonids (lake trout and Pacific salmon) revealed that these predators could consume from 20 percent to 33 percent of the annual alewife production (Stewart et al. 1981). We suggested that salmonid predators may cause mortality in alewife, and weak alewife year classes could be reduced further by predatory mortality. We predicted that: (1) salmonid predation might reduce alewife dominance, allowing an increase in rare planktivores; (2)growth rates and condition factors should increase for alewives and their competitors and decrease for the salmonids; (3) changes in competitive interactions should result in habitat and diet shifts among the forage fishes; and (4) reduced total planktivory should increase zooplankton size and perhaps shift species composition to larger zooplankton.

Unpublished data suggest that alewives are declining. The alewife biomass estimate for 1982 is lower than the estimated alewife biomass after the 1967 population crash. The 1983 estimate is only 14,000 metric tons (Edward Brown Jr., Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, personal communication). This constitutes the lowest biomass since the early increase of alewife in Lake Michigan (1962). If the predators continue to feed primarily on the reduced alewife population, they may be consuming 80 percent to 100 percent of the annual alewife production. Several native fishes that are planktivorous in early life stages, such as bloater, yellow perch and shiners, seem to be increasing. And some evidence suggests that growth rates of some salmonids are declining (R. Rybicki, Michigan Department of Natural Resources, G. Eck, U.S. Fish and Wildlife Service). I am unaware of any published data on shift in growth or condition of alewife or any of the other forage fishes.

Some evidence of recent habitat shifts in alewife and smelt is available (Crowder and Magnuson 1982), but the data are limited to short-term observations in late summer. The available salmonid diet data contains little evidence of diet shifts away from alewife, although alternative forage species, such as bloater and yellow perch, appeared in salmonid diets in late summer 1983 (J. Hagar and J. Kitchell, Center for Limnology, University of Wisconsin-Madison). Although the alewife population and salmonid growth rates may be declining, the predators are not readily switching to abundant alternate forage (e.g. bloaters). Zooplankton size, a sensitive indicator of the intensity of planktivory, has increased in recent years (Gitter 1982), and larger <u>Daphnia pulicaria</u> are found in zooplankton samples (Glenn Warren, Center for Great Lakes Studies, UW-Milwaukee, personal communication). Water clarity has increased in southeastern Lake Michigan (Claire Schelske, University of Michigan), perhaps due to increased filtering by zooplankton.

FUTURE RESEARCH

Three priorities for research on estuarine fishery habitat requirements emerge from my experience in estuaries and in the Great Lakes:

(1) Critical aspects of the life histories of estuarine-dependent species occur offshore on the continental shelf. One might argue that juvenile estuarine fish populations are ocean dependent because the number of successful spawners and the subsequent number of larvae that reach the estuaries are dependent upon poorly-known oceanic processes. The effects of environmental variation on larval survival, food limitation and predation on larvae need to be understood to forecast the number of larvae available for transport into the estuaries. Further, the larval transport process needs to be related to weather and wind conditions during the period when larvae enter the estuaries. Then we can project whether a particular year is "good" or "bad" in respect to the success of larval transport to estuarine nurseries. In short, we need to examine potential critical periods of estuarine fish throughout their life history, not just during the period when they

accumulate in coastal estuaries. While management cannot control the weather, they could monitor it and forecast year class strength of fish.

(2) If predation is a major mortality source in juvenile estuarine fish, we need to document where and when the predation occurs and who the major predators are. But we cannot stop there. To say that flounders or blue crabs eat larval or juvenile spot does not estimate the importance of predators to spot production. To estimate the importance of a predator to a forage base, scientists make seasonal and spatial estimates of direct predator consumption using gut evacuation rates and compare the results to estimates of juvenile fish production. But this approach is tedious and costly. An alternative is to employ a bioenergetic model such as we used on the Lake Michigan salmonid predator-prey interaction. The models require a prodigious amount of data, but one may be able to estimate the importance of predators with a simplified form of the model. If predators are an important factor limiting juvenile fish production, various management strategies could reduce predator effectiveness or the number of predators.

(3) Our approach to estuarine fish communities has been primarily empirical and descriptive. The literature is replete with open-ended questions, but few testable hypotheses are seen. Because different estuaries vary in physical-chemical parameters and hydrology, it has even been difficult to exploit the comparative approach successful in lakes. Any science must begin by describing the system, but it usually progresses beyond description toward comparative and experimental approaches. Carefully designed and performed laboratory and field experiments, would provide insights on fish habitat requirements that would be difficult to infer from years of trawling survey data. Management manipulations also should be viewed as experiments. When large-scale management manipulations are performed, the hypothesis or expectations should be clearly stated and the results evaluated to see if the manipulation worked as desired. Only in this way can we see if we understand the system well enough to manage it.

We also are immersed in a period of hypothesis elaboration by various proponents. We have not begun seriously the difficult task of eliminating the competing hypotheses. We also could benefit from an injection of current ecological theory and the application of a evolutionary perspective to estuarine fish. Current ideas on habitat choice, which are based on energetic optimization (Ware 1982; Crowder and Magnuson 1983; Dill 1983) and on trade-offs between foraging and predation risk (Mittelbach 1981; Werner et al. 1983b), have obvious implications for habitat use in estuarine fishes. Further, the theory of life history strategies may help to evaluate the trade-offs fish might take in allocating energy to growth versus reproduction (Ware 1982).

Our estuaries are critically important habitats in need of careful management and conservation. But to manage these ecosystems, we need to understand how they work. If estuarine ecosystems were perfectly predictable and similar from place to place, we could generalize from regressions, ignore mechanisms and make reasonable management decisions. But estuaries are more complex. We do need to search for generalizations and ways of classifying estuaries into groups from which we can generalize. But we also need to understand how these systems respond when the environmental inputs change. To do this, we will require a mechanistic understanding of the relevant ecological processes.

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DISCUSSION

K. THOEMKE: We've heard a lot about the importance of marshes to fisheries habitats. I'm not trained as a fisheries biologist, so maybe my question is too simple. But I would like to know how you feel about the role of mangrove estuaries. How do some of the things said about marshes pertain to mangroves?

R. ZIMMERMAN: Mangrove-dominated estuaries are considered some of the most difficult in which to work. We know that some of the relationships we found for marshes may hold for mangroves. I am thinking specifically about production of pink shrimp in the south Florida mangrove complex.

Working in these habitats is extremely difficult. One cannot do the nice, neat caging experiments within the complex of mangroves. I don't know how to answer your question other than simply to say that they are as important as nurseries. Maybe we can apply the things we're learning in some systems that are more easily manipulated to mangroves.

J. MILLER: Certain habitats are important because of a measurement of abundance of organisms there. The other side of the coin is that managers often ask how critical or how important certain habitats are to the ultimate maintenance of stock. That is a totally different question.

K. THOEMKE: As a follow up to my question, let me mention our Naples Rookery Bay National Estuarine Sanctuary. If anyone is interested in examining the role of mangrove ecosystems in relation to fisheries habitat and management, you are welcome to come to Rookery Bay and work with me.

Rookery Bay is one of about 15 estuarine sanctuary sites in the country. We have a lot of things I think would benefit people. A laboratory is available for visiting scientists, and there are also dormitory facilities, boats and a fairly extensive data base for the area (including water quality and some benthic work).

J. DAY: John Miller talked about the importance of circulation and dispersion. That, coupled with Zimmerman's ideas on how fish use the estuary, may explain some of the differences between East Coast and Gulf Coast fisheries. For instance, in the North Carolina systems you have very restricted inlets. Perhaps lack of circulation restricts how young fish get to the nurseries. On the other hand, in places like Florida Bay or the Deltaic Plain, you have wide inlets or open fronts to the sea.

D. PETERS: I would like to hear a definition of what food limitation is. My experience has been that if you feed fish more, they grow faster up to a point. That would seem to be one kind of food limitation. Miller showed data on spot indicating maximum growth of about 20 percent of their body weight per day. Are those growing at a lesser rate food limited? I saw data showing spot larvae grew at about 20 percent per day when they entered the estuary. However, as soon as they get to the estuary, my measurements show that they grow at about 4 percent per day. That would seem to indicate food limitation in the estuary. From what I have seen, unless we have a lot of definitions of what food limited is, evidence indicates food limitation in the estuaries.

J. MILLER: I think we're looking for the relative importance of which factors are potentially limiting. My purpose in stating this was to suggest that we should be looking at some potentially greater influences on the survival and well-being of juvenile fish than food limitation.

I was also making the point that we may expect to find changes in the relative importance of things like food, depending on where we look in estuaries. Any general concept of either food limitation or other limitation will be strongly tempered by what species we're looking at and by the relative importance of other potentially limiting factors.

I don't think, on the other hand, that I mean limiting in a sense that there is no point in changing any of the other potentially limiting factors. Nor do I mean limiting in the sense of a chemical reaction where the action will proceed no faster than the most limiting or rate limiting step. Biological systems are much more complex than that.

R. ZIMMERMAN: That's an extremely important point. In fact, it may simply be that the abundance of food in different habitats is limited and absolute limitation is not present. For instance, in our cages in vegetated versus nonvegetated habitats, the growth rate was within the range of growth rates found in nature. What we might be seeing is an indication that whatever they're eating is more abundant and available in the vegetated habitats than the nonvegetated ones.

D. BOESCH: We need to avoid defending one issue as being more important than another and to try to work toward integrating models. Various factors need to be discussed in quantitative terms. If we approached this on a regional basis and developed some commonality, we could have certain criteria for management.

How do we begin to do that? Our conceptual models are not sharp enough yet. We don't have the quantitative terms. We don't know how to factor in the issues we can address by experimentation and hypothesis formulation. We have to be content to approach those factors by some sort of existential or circular reasoning.

L. CROWDER: One thing we've talked about here is the notion of limiting factors. We're talking about one factor at a time limiting what animals do. In fact, a whole myriad of factors influence what animals do.

Food limitation, for example, does not occur as a step function; it occurs as a smooth change. So food is always limited to the degree of its availability.

We must approach the problem in much the same way animals integrate the environment. And one way to do this, I propose, is to consider the bioenergetic integration of habitat.

Dan Ware, in *The Canadian Journal of Fisheries and Aquatic Sciences* (1982) talks about the ways that animals integrate the temperature, salinity, available food, and the energy they spend on avoiding predators. All of these are taken away as costs; what is left, Dan calls "surplus power." With that leftover energy, fish can grow, reproduce or do other things.

Behavioral energetics ensues that if natural selection acts on fish so that they maximize this surplus power, they can grow quicker, swim faster to avoid predators, or have more energy for reproduction. You would, therefore, expect fish to behave in ways that maximize the amount of surplus energy per time to do other things.

If you accept that notion, you can state some testable hypotheses about how you expect fish to behave given their environment. Whatever the temperature, salinity, habitat structure and predator risk, you can begin formulating hypotheses that are testable as discreet things. If that sort of idea works, you can ask why fish do something different in another estuary. The impingements on the physiological and behavioral energetics of that individual fish, by which it may be making "rational" decisions about what to do, may be different. This is not easy, but it is an approach to reach rational conclusions.

M. WEINSTEIN: It's very difficult to state hypotheses and alternative hypotheses. It's equally difficult to test them from the standpoint of constructing proper controls and controlling variables in the proper way.

Only then, perhaps 20 or 25 years later, will you find that the single factors are interactive. Then you come back to the drawing board.

R. WISSMAR: We developed a model for one of the estuaries of Puget Sound. Fortunately, about 10 years of good data were available, and we put everything in terms of energetics just as Crowder suggested. We found that carrying capacity was important and that eelgrass beds were essential for the well-being of the fish. They were in the eelgrass bed because of the epibenthic plankton; they can't catch neritic plankton.

I highly recommend the bioenergetic modeling. It has become a powerful tool for us. You can test more than one hypothesis at a time and get at alternative hypotheses.

FUTURE RESEARCH STRATEGIES: A SUMMARY

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The objective of this symposium was to develop research strategies for managing the nation's estuaries. To achieve this, we assembled a cadre of the nation's best estuarine researchers and challenged them to think about future research directions. These experts represented various sections of the U.S. coastal area. The audience, representing a broad spectrum of interests, provided outstanding responses to the challenges. This combination of challenger and responder presentations provided a successful forum to develop themes for future directions of estuarine research. We must continue to develop mechanisms to get objective evaluations to managers in a form they can use and in an appropriate time frame.

The purpose of this final chapter is to summarize the essential points made during the symposium. Although we realize that multidisciplinary approaches are necessary for progress, we organized the symposium into five critical areas so that we could focus on the issues. They were:

(1) Water management and its relationship to estuarine productivity;

(2) Sediment management and estuarine productivity;

(3) Nutrient and other contaminants, and control of primary productivity;

(4) Coupling of primary and secondary production; and

(5) Habitat requirements for fisheries production.

In order to improve management perception of scientific findings, we must develop a means of objective evaluation of ecological risks. After all, the scheme of management is to reduce the number of risks that something bad will happen as a result of management imprecision. Therefore, one research priority involves interactions of mathematics with other scientific disciplines to improve our analysis of risk based on the best scientific information about how an ecosystem functions. We must translate our doubts and uncertainties into the language of risk, and we must educate the public and policymakers about using risk in making decisions.

WATER MANAGEMENT AND ESTUARINE PRODUCTIVITY

One of the important problems facing our nation today is the allocation of freshwater resources. As the demands for water increase from municipal, commercial, industrial, agricultural and recreational sources, the downstream availability of water decreases. Estuaries lie downstream of freshwater resources. And, as land-use activities change around the estuary and near the upstream tributaries, the quantity, quality and timing of freshwater inflows to the estuaries also change. By definition, estuaries are intimately related to the inflow and mixture of fresh water with salt water. Therefore, these changes may significantly alter estuarine productivity.

The prime research question is the coupling between freshwater inflows and primary and/or secondary production in estuaries. We need to know the quantitative relationship between freshwater inflows and fisheries landings from individual estuaries and from regional groups of estuaries.

Our problems range from not enough fresh water in some parts of the country to too much in others. Based on current scientific knowledge, our crude estimates are not good enough to equate the demands of estuaries to the demands of other water users. We have found that merely providing an allocation of water to estuaries based upon a mean, historical schedule has not provided for the maintenance of historical levels of fisheries productivity. The common denominator for maintaining estuarine productivity lies in the management of watershed activities.

SEDIMENT MANAGEMENT AND ESTUARINE PRODUCTIVITY

The sediments deposited during the recent geologic periods are fundamental to the characteristics of

today's estuaries. The two basic effects on estuarine productivity are the amount of sediments entering the estuary and the quality of those sediments. These processes are immensely affected by the activities of man in the watersheds of the estuaries. Compounding the problem are the long time periods (sometimes decades to centuries) required for the movement of sediments from their sources up in the drainage basins of major rivers down into the estuaries. The sediments may originate from external, internal and marginal sources, but those most influenced by man are external sediments along rivers that carry them to the estuaries.

A great difficulty in research stems from the fact that critical experiments on the relationships between ecosystems and major changes in their environment simply cannot be performed. It is not feasible to manipulate tidal flushing, flooding and large scale additions or removals of substrates, and maintain a control system for comparison. Therefore, much of our research has consisted of before-and-after studies of major events.

Major needs in sediment management are dredge and dredge-material management plans and the characterization of the transport of sediments from external sources. One of the primary research needs is a characterization of the processes that control the movement, absorption and desorption of contaminants; rates of accumulation; and transformations of sediment composition between points of entry and sites of accumulation. We must develop an experimental procedure to relate these parameters to the response of estuarine ecosystems. We need to predict the agglomeration of fine-grain particles in the water column and on the estuary floor, and how changes in the degree of the agglomeration affects settling velocity, critical erosion velocity and the availability of particle-associated contaminants. This research, in combination with ecological studies of the relationship between sediments and habitat type, will provide the scientific basis for controlling or mitigating sedimentation and management of the quality and quantity of stream flows.

NUTRIENTS AND OTHER CONTAMINANTS AND ESTUARINE PRODUCTIVITY

For a long time, we believed the higher productivity of coastal waters was supported by nutrient inputs from the land. But recent research has emphasized the importance of nutrient cycling within the system. Yet many relationships between nutrient inputs, recycling and production are still undefined. Analytical techniques to measure nutrients have been available for several decades; but only recently have spatial and temporal variations and seasonal cycles of nutrients in a reasonable number of estuaries been measured. Therefore, we must emphasize that we do not yet understand the fundamental processes underlying the relationship of nutrient flows and coastal productivity. Several fundamental observations indicate that nutrient loadings to estuaries are increasing. Most of the human population in the United States is concentrated around the estuaries and Great Lakes. By 1990, 75 percent of the population of this country is expected to live within 50 miles of the ocean or Great Lakes. In addition, the use of inorganic fertilizers has been increasing exponentially for almost a century. Large-scale conversions of wetlands to urban and agricultural developments eliminate them as potential nutrient and sediment sinks. As a result, we might expect that the amounts of nutrients in our estuaries have increased markedly. The lack of adequate long-term data makes it difficult to determine if this is true.

Our knowledge of the effects of nutrient enrichment on estuarine ecosystems is primarily based on short-term laboratory studies of algal cultures and short-term synthesis experiments involving nutrient additions to plankton communities. These experiments lead to the conclusion that recycling is a dominant factor in the primary production of coastal ecosystems. However, the massive, debilitating algal blooms in the upper regions of many of our nation's estuaries indicate that increased nutrient inputs are major contributing factors.

Therefore, we need fundamental ecosystem-level experiments to test how estuarine ecosystems respond to a combination of nutrient inputs and recycling. Experiments involving large mesocosms and field manipulations, such as those used in limnology and terrestrial ecology, have the potential to yield integrated results useful for management. These efforts will require long-term, multidisciplinary studies of ecosystem responses to nutrient additions and recycling.

Though nutrient loading impacts estuaries, the host of synthetic chemicals and metals also poses a serious scientific question about the impact on downstream estuaries. These facts challenge the scientific community to develop a research protocol to understand long-term, integrated responses of estuarine ecosystems to exotic materials.

COUPLING OF PRIMARY AND SECONDARY PRODUCTIVITY

Estuarine ecosystems are characterized by intrinsically high levels of primary production. Accompanying these well-documented estimates of estuarine primary productivity are high levels of secondary production. Although estimates of secondary production are generally qualitative, the high yields of fish and other organisms offer compelling evidence. Therefore, the fundamental question concerns the specific connections between high primary production on one hand and high secondary production on the other.

Although there is clearly a theoretical relationship between primary and secondary productivity, documentation of the importance and ecological efficiencies of individual pathways remains unresolved. A fundamental management question revolves around the issue of whether one can protect or improve secondary production by managing for a certain level of primary production. For example, what is an acre of salt marsh primary productivity worth in the fisheries production of the receiving estuary?

The most important research need in this area is the development of a quantitative relationship between primary production and secondary production in estuaries. This will require multidisciplinary approaches to unravel the myriad of food chains and relationships that exist in these coastal ecosystems. We need to know: 1) the comparative trophic importance of vascular plant versus plankton organic matter; 2) the degree to which coastal fisheries organisms utilize detritus as an energy source; and 3) the impact of removing large tracts of detritus-producing salt marshes and sea grass beds.

In estuarine ecosystems, food chains are quantitatively and qualitatively interconnected. While it is obvious that the quantity of biomass at one producer level helps determine the quantity of biomass at the next level, the quality may be the more significant factor. For example, the production of a large biomass of blue-green algae might result in very short food-chain circuits because none of the secondary consumers can utilize the blue-green algae. Before estuarine management can improve, we must establish the qualitative relationships and the quantitative dependency. This will require a rather sophisticated research effort. We must also improve traditional feeding experiments to the extent that we can also measure chemical utilization.

HABITAT REQUIREMENTS FOR FISHERIES PRODUCTION

One of the traditional values of estuaries throughout the world is their role as a nursery area for many of the commercially and recreationally important species of fish. Over 90 percent of the fish tonnage taken along the coastal fringes of the United States is dependent upon estuaries during some portion of the life cycle. This dependence has long been viewed the most important societal value of an estuary. However, it has been well documented that more fish are produced in some estuaries than in others. Perhaps the key to more effective fisheries management is the understanding of the role that estuarine habitat plays in the production of the fisheries.

Traditionally, three major reasons have explained why fish use estuaries. The tremendous primary production attributed to estuaries leads to an increased food availability. The shallow, brackish to sometimes fresh water offers young organisms protection from predators. And, certain fundamentally important chemicals such as vitamins

and growth stimulators, as well as suitable physical substrates, are available in the estuaries.

The distinctive attributes of nursery areas are difficult to define. Important research questions are: 1) How specific is the selection for a nursery habitat? 2) What basic criteria are needed to protect those characteristics to provide suitable fisheries production? The distribution of fisheries species in estuaries is life-stage dependent, and many species use different habitats in a predictable sequence. Except for a very few species (salmon, for example), we do not know the cueing mechanisms that initiate and guide these movements; nor do we know the relative importance of each segment in the sequence. We still need answers to basic questions about species migration, times of residence in each segment of the estuary, and the effects of environmental variations on survival, growth and movement.

In terms of effective management programs, the most important questions revolve around the relationship between fish production in the estuary and the quality and quantity of nursery areas in terms of the availability of food and subsequent growth and mortality. In other words, if we improve and enlarge nursery habitat in the nation's estuaries, will we also improve and enlarge the fisheries production along our coastal fringe?

While there is considerable evidence that ecosystem configuration is important to fisheries production, we are far from understanding the complex mix of physiographic features that make estuaries so productive for fish. Important integrators of estuarine habitat and coastal fisheries production are the hydrographic regimes characteristic of estuaries. In order to understand estuarine nursery utilization, it is critical that we also understand the physical characteristics of the estuaries and how these relate to the use of the nurseries by fisheries species.

The solution to all these important questions will require large, multidisciplinary studies based on good, testable hypotheses.

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