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CHAPTER 11

Influence of River Flow and Nutrient Loads on Selected Ecosystem Processes

A Synthesis of Chesapeake Bay Data

Walter R Boynton and W. Michael Kemp

Abstract

In this chapter we assembled and analyzed two data sets, one a discontinuous 22-year time series (1972–1977, 1985–1993) of observations from a single mesohaline site in Chesapeake Bay, and the other, a much shorter time series from that site plus similar sites in four bay tributaries. For all locations, the data set includes measurements of river flow, nutrient-loading rate, phytoplankton primary production rates and biomass, water-column nutrient concentrations, and sediment-water exchanges of ammonium. In addition, data on sedimentation rates of chlorophyll a and bottom-water dissolved oxygen concentrations were analyzed at one site.

We examined a series of hypotheses concerning the influence of river flow and nutrient loading on these variables toward the goal of understanding underlying mechanisms. Significant relationships to flow and associated nutrient loads were found for all variables, some being stronger than others. In most cases, the influence of flow was found to extend over relatively short time periods (months to 2 years) and there were temporal lags between flow events and ecosystem responses on time scales of weeks to months. Results of analyses based on the time series from one location and on comparative analyses of data from five different sites were qualitatively similar; in this system it was not necessary to invoke comparative analyses to capture a large enough signal in forcing and response to observe interpretable patterns. Analyses generally indicated that relationships proximal to flow or nutrient loading rate were stronger (for example, nutrient load versus water-column nutrient mass) than those more removed from the direct influence of flow or nutrient load (for example, flow versus sediment nutrient releases).

These analyses indicate the importance of freshwater flow and associated nutrients in shaping chemical and biological responses in this estuary. Analyses are continuing and the next step will be to examine the effects of flow and nutrient loads on submersed vascular plant distributions and zooplankton and benthic communities.

Introduction

During the last decade there has been an increasing number of environmental measurements taken in coastal and estuarine systems, and this trend seems destined to continue for the foreseeable future. In part, this activity has been stimulated by increased awareness of natural resource deterioration in these environments due to human activities in the drainage basin as well as in the receiving water bodies. Common now are reports of declining or collapsed fisheries, toxic algal blooms, development of hypoxia and anoxia in deeper waters, and loss of submersed aquatic vegetation communities (Nixon 1990).

Despite much larger databases for many of these systems, we are still unable to confidently answer many fundamental questions concerning how these systems work and, from a practical viewpoint, what resource managers need to do to reverse declines in water quality and abundance of living resources. One reason for this state of affairs is that analyses and interpretations of these data sets have been limited. This is particularly true for many data sets collected in monitoring programs and ad hoc field surveys. In addition, scientific data collected in research programs are often interpreted within relatively narrow areas of scientific interest having little value at the larger scales of organization relevant for resource management (Malone et al. 1993). To be useful, these data need to be pulled together into some sort of synthesis that focuses on time, space, and organizational scales appropriate to the questions being asked.

In recent years, some very ambitious numerical efforts have been initiated and serve as one type of data synthesis. For example, sophisticated hydrodynamic models have been developed for a number of estuarine systems (for instance, Long Island Sound, Tampa Bay Chesapeake Bay) and act as a framework for synthesis of large data sets as well as forecasting tools. In other cases, these models have been coupled with water-quality models and used as diagnostic tools in water-quality management programs, as is the case in Chesapeake Bay (Cerco and Cole 1992). While these tools have obvious advantages, they are expensive and time consuming to construct, analyze, and maintain.

The purpose of this chapter is to present the results of a direct, empirical type of synthesis whereby variations in key properties of coastal ecosystems are related to changes in riverine nutrient loading (Rigler 1982; Peters 1991). Specifically we describe here the results of regression modeling based on data

collected in Chesapeake Bay. In this work we have primarily focused on examining the influence of freshwater inputs (and associated nutrient loads) on several ecological processes. The importance of freshwater inputs is obvious; it is a central feature in the definition of estuarine systems, it influences physical dynamics (Boicourt 1992), is well correlated with nutrient inputs (Summers 1993), and has been implicated in regulating either directly or indirectly estuarine processes ranging from primary production (Boynton et al. 1982; Cloern et al. 1983) to benthic secondary production (Flint 1985) to fish recruitment (Stevens 1977) and catch (Sutcliffe 1973; Sutcliffe 1977; Ennis 1986). The emphasis here is the exploration of data sets for patterns that conform to expected relationships or suggest new relationships (see Meeuwig et al. 1998) rather than statistical testing for significant differences or temporal trends. We wish to examine environmental data for relationships and to use these as clues to suggest underlying mechanisms.

Approach and Methods

Conceptual Model

The focus of these analyses is to investigate the influence of river flow and associated nutrient inputs on selected ecological processes in Chesapeake Bay. Most, if not all, of these hypothesized direct or indirect effects of river flow on ecological processes have been documented in other systems. For example, phytoplankton biomass and community composition have been shown to be regulated by river discharge in San Francisco Bay (Cloern et al. 1983) and Texas estuaries (Flint 1985), while buoyancy effects of fresh water have been extensively investigated in various estuaries (Boicourt 1992), and responses of benthic respiration and nutrient regeneration to variations in phytoplankton production and deposition have also been examined (Flint 1985; Cowan et al. 1996). Here we consider the extent to which these effects of river flow are manifest in Chesapeake Bay and we have organized this analysis around a simple conceptual model (figure 11-1). In this model, river flow adds directly to the nutrient pools (1) and influences buoyancy of the water-column. River flow also determines the geographic positioning of water-column events (that is, events such as plankton blooms tend to shift seaward in high-flow periods and landward in low-flow periods) and the location of water-column deposition of organic matter to the benthos. Phytoplankton production (2) and biomass (3) are responsive to nutrient pools and phytoplankton biomass is lost to the benthic community via sinking (4). The benthic community recycles nutrients to the water column (6). Finally, deep-water dissolved-oxygen depletion (5) is influenced by stratification of the water column, organic matter derived from

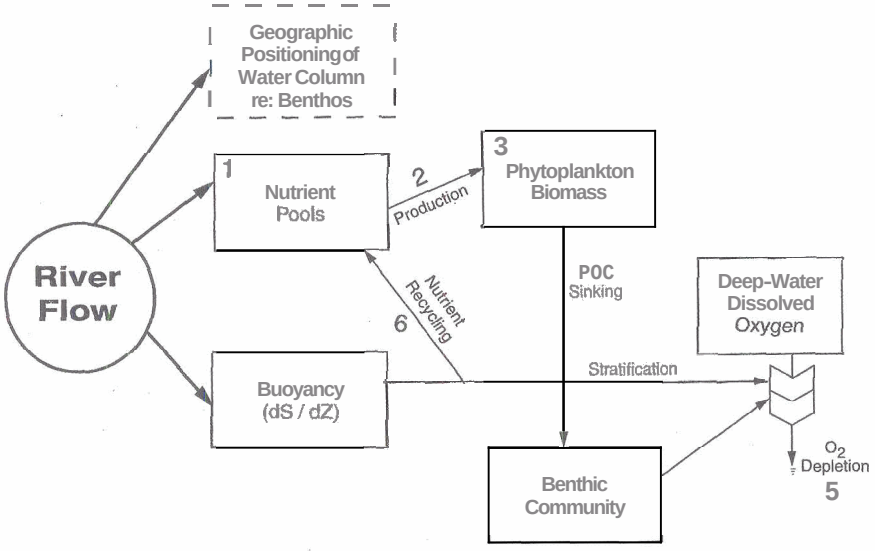

FIGURE 11-1 A simple schematic diagram showing the influences of river flow on ecosystem stocks and processes examined in this study. The mechanistic relationships between river flow and the stocks and processes shown in the diagram are explained in the text.

phytoplankton, and respiration of this organic matter by the benthic community.

Obviously, the perspective in this conceptual model is heavily biased toward bottom-up (as opposed to top-down) control of ecological interactions. We recognize that top-down effects can be important, and dominant, in some estuarine situations. For example, Alpine and Cloern (1992) found dramatic changes in the temporal pattern of phytoplankton production and biomass in San Francisco Bay following the introduction of a suspension-feeding clam. Meeuwig et al. (1998) found that herbivory by mussels was a strong modifier of algal biomass-nutrient relations in some Canadian estuarine systems. There are also more numerous and well-known examples from limnology (Carpenter and Kitchell 1988). In this preliminary analysis, we chose to emphasize the bottom-up perspective for simplicity and elegance.

Ecological Inference

Our approach to ecological synthesis consists of several steps, the first of which involves developing empirical models to specify the relationships of interest and to aid in selection of appropriate variables. Rigler (1982) differentiated ecological research into empirical and explanatory categories, the

former with the goal of prediction and the latter with mechanistic explanations of predictions. In regression modeling the mechanistic relationships between variables are not specified while in explanatory approaches (such as simulation modeling) every interaction is exactly specified. In a sense, empirical approaches are more holistic while explanatory schemes are more reductionistic.

As an example of empirical model development, interannual variability in algal biomass may be of interest and appropriate variables might be chlorophyll a concentrations or some other measure of algal stock. The next step is to select a group of probable causative variables and in the above example these might be river flow, nutrient-supply rate, light availability or others. Much of the above obviously requires previous knowledge in establishing relationship between variables so there is a natural interaction between reductionist and holistic approaches. We also recognize the need to establish alternative hypotheses in empirical approaches as suggested by Peters (1991). The idea here is to explore all reasonable explanations, rejecting most because they do not support the hypothesis and leaving us with one (or more) that can be supported and further explored. It is this step that largely differentiates this approach from a simple statistical examination of a data set for statistically significant relationships.

We have also employed comparative approaches in a portion of the analyses presented in this chapter wherein similar data from a variety of systems are used in the analysis. This technique has the advantage of increasing the signal range for both independent and dependent variables and hence increasing the chance of interpretable patterns emerging from what is admittedly a complex set of interactions (Vollenweider 1976; Nixon 1988). However, comparative approaches generally require "scaling" of variables in a fashion that makes them comparable among systems and this in itself can be a complex and interesting problem (Schnieder 1994).

In this chapter we present two groups of empirical analyses; the first is based on a data set collected at one location in Chesapeake Bay for a number of years (~13 years) while the second examines similar issues but uses a comparative approach based on data collected at multiple locations in Chesapeake Bay for shorter periods of time (1 to 4 years). We take advantage of a long data record in the former and inherent differences among systems in the latter; in a sense this can be thought of as a time-space substitution with both approaches being useful in testing ideas about ecosystem behavior (Pickett 1991).

Study Area

Chesapeake Bay is the largest estuary in the United States, having an area of 6,500 km^2, a length > 300 km, a width of 5–30 km, and mean depth of 8.4 m; it is closely embraced by the land (drainage basin surface area: bay surface area = 28:1). The surface area of the bay system is equally divided between the

mainstem bay and the numerous (approximately thirty) tributary rivers and bays; however, about 66% of the volume is contained in the deeper mainstem (figure 11-2).

The hydraulic fill time (volume divided by freshwater inputs) is approximately 1 year and water residence times range from 3 to 6 months. The mainstem bay is stratified from late winter through early fall; stratification in tributaries is generally weaker and less persistent (Boicourt 1992). Water-column stratification is in part responsible for chronic hypoxic and anoxic conditions in deeper regions of the system (Kemp et al. 1992). It appears that the volume of hypoxic water has increased since colonial times (Cooper and Brush 1991), much of it in the last three to four decades (Boicourt 1992).

The bay and its watershed lie in the coastal corridor of dense human population between New York and Virginia; population in the watershed is now 13.6 million and is projected to soon be 16.2 million (Magnien et al. 1995). Current nitrogen- and phosphorus-loading rates averaged for the entire bay are about 13 $gN\ m^{-2}\ yr^{-1}$ and 1 $gP\ m^{-2}\ yr^{-1}$, respectively; however, loading rates to distinct portions of the bay system range from both a factor of 5 higher and lower than these and thus provide a good opportunity for comparative analyses. Since European settlement, bay-wide loading rates of nitrogen and phosphorus have increased about six- and seventeenfold, respectively (Boynton et al. 1995).

One of the important characteristics of estuarine systems such as Chesapeake Bay is temporal variations in inputs such as freshwater flow (figure 11-3). During the past several decades, the magnitude of annual average freshwater input to the head of Chesapeake Bay has varied by a factor of 2.4; average annual flows from the Susquehanna River are about 1,200 $m^3\ sec^{-1}$ and represent about 50% of the freshwater flow to the entire Chesapeake system. However, seasonal patterns of flow are even more variable, especially during the "spring freshet." This important hydrological event has occurred between January and May in recent decades, though typically during March or April, and has varied in magnitude by a factor of 5 (figure 11-3).

Data Sources

Chesapeake Bay and associated tributaries is one of the most studied estuarine systems in the United States and a tremendous amount of data are available, especially from the last decade. Much of this information has been collected as part of the EPA's Chesapeake Bay Program and closely related monitoring programs conducted by the states of Maryland and Virginia.

To provide some indication of the intensity of this program, about 40,000 measurements of such variables as chlorophyll a have been made in the mainstem bay alone during the last decade. During the last decade the challenge

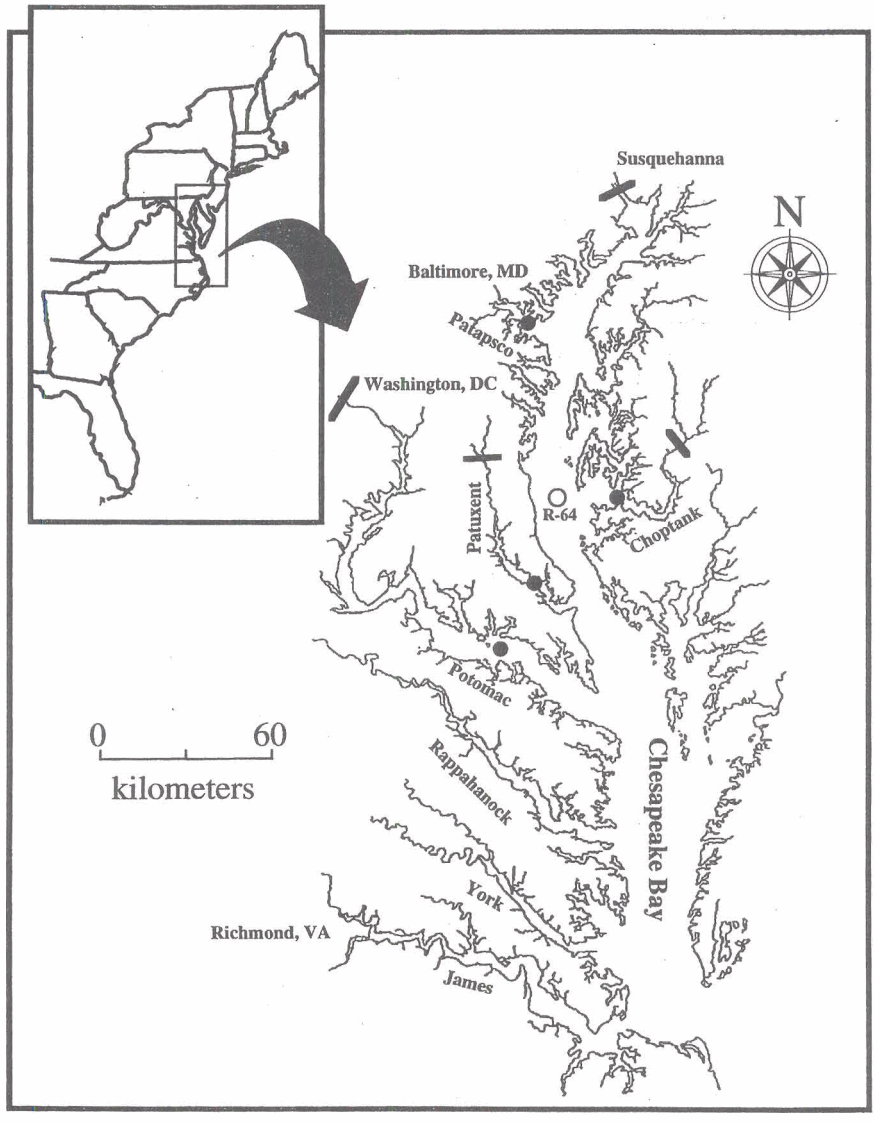

FIGURE 11-2 A map showing Chesapeake Bay and major tributary rivers and location of this estuarine system on the East Coast of the United States. Bold lines indicate locations at the fall line where freshwater inflows and nutrient loads are monitored, Bold dots indicate locations where water-quality, phytoplankton, and sediment-water flux measurements were made; these measurements as well as sedimentation rates were made at the site indicated by the open circle (R-64).

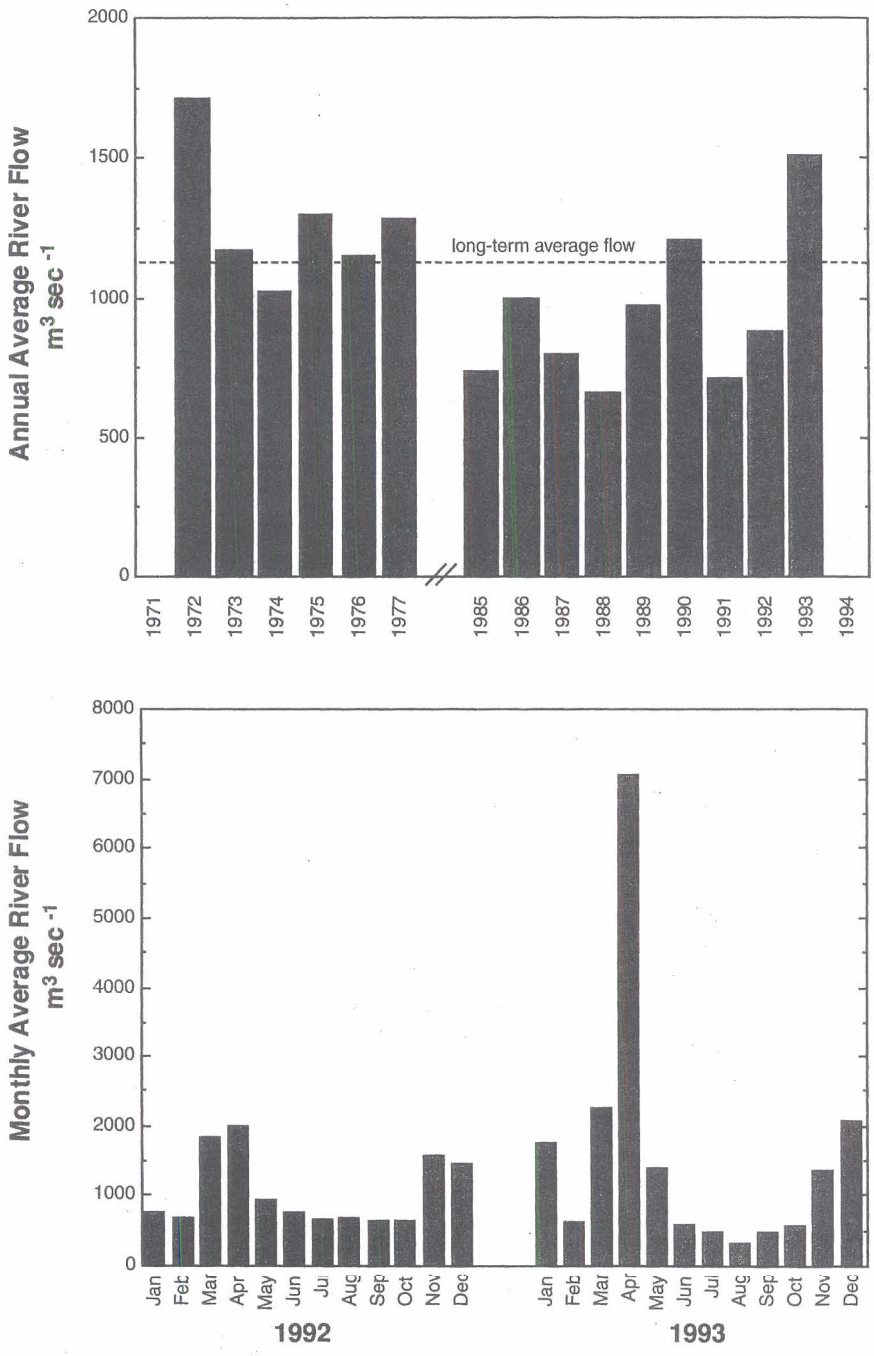

FIGURE **11-3** Estimates of annual average river flow (1972–1977 and 1985–1993) from the Susquehanna River entering the head of Chesapeake Bay. Flows are for the years used in regression analyses. Also shown are monthly average flows for the years 1992 and 1993 from the same location to indicate the variation in magnitude and seasonal patterns of freshwater inputs (USGS 1993).

of simply finding enough data to see if interpretable seasonal patterns exist has changed to one of managing large databases in such a way that any patterns present can be found. A brief description of the data collection program is provided in table 11-1 for the variables used in the analyses presented here; details concerning collection and analytical methodologies have been described in detail elsewhere (see sources listed in table 11-1).

Statistical Methods

Regression techniques have been applied to ecological problems for quite some time, often yielding useful results. In part, the attraction of this approach lies in its simplicity. As opposed to water quality, fisheries, and ecosystem models, data requirements can be relatively small, the time required to explore many possible relationships short, and there are few, if any, assumptions to be made concerning the form of mechanistic relationships. The relative ease of using the technique makes it, therefore, very attractive as a tool for scanning data in search of suspected relationships and as a tool that often suggests new interpretations.

While regression can be straightforward there are, of course, limitations that are both practical and conceptual. As with any statistical technique, strong correlation between variables does not, however tempting, indicate causal relationships. In addition, covariance among variables can lead to spurious conclusions. Assumptions concerning the distribution of data and other criteria for strict application of parametric techniques are often difficult or impossible to check.

In spite of these problems, and the apparent simplicity of the approach, there have been many useful applications of regression techniques to ecological problems. During the 1960s and early 1970s, Vollenweider and his colleagues developed a series of "mixed reactor regression models" relating algal standing stock (used as an indicator of trophic condition) to nutrient loading (primarily phosphorus loading to lakes). They found significant relationships that were useful in classifying lakes according to trophic status and in suggesting the amount of nutrient loading needed to change the trophic status of a lake (Vollenweider 1976). Similar, but less inclusive, efforts have been made relative to estuarine systems (Boynton et al. 1982; Meeuwig et al. 1998). It has long been taken as a fundamental tenet of ecology that there is some relationship, probably complex, between rates of primary production and fishery yields. Such a relationship was documented by Oglesby (1977) for lakes and later by Nixon (1988) for estuarine, coastal, and marine systems. More complex relationships between standing stock size, growth rates, and production in marine food webs have also been determined using regression modeling approaches (Sheldon et al. 1977; Ennis 1986).

TABLE 11-1

Brief description of dam sources used in development of regression models presented in thii chapter. Each program component is a part of the Chesapeake Bay Water Monitoring Program, which was initiated in 1984 and continues through the present time (Magnien et al. 1995). Phytoplanktonic production and chlorophyll *a* data from the 1972–1977 period are from Mihurshi et al. (1977).

Program Component	Variables Measured	Number of Stations	Field Technique	Sampling Frequency and Duration	Reference
Water-quality variables	T, S, DO, pH, chl *a*, dissolved and particulate N, P and Si concentration (vertical profiles)	50	One to five water column samples depending on total depth. Standard oceanographic analytical techniques.	16–20/yr 1984–present	Magnien et al. 1994
Freshwater and nutrient-loading rates	T, DO, conductivity, pH, chl *a*, E. *coli*, BOD, COD, TSS, total and dissolved N,	Fall line of all major rivets	Standard river gauges estimating daily flow. Regular parameter sampling and statistical modeling of Aow-concentration relationships.	1–4/month (daily flow) 1972–present'	Summers 1993
Sedimentation rates	Sedimentation rates of C, N, P, Si, chl a, and seston	One site in middle Chesapeake	One fixed vertical array. Collecting cups positioned in upper mixed layer, just beneath the pycnocline, and 1 m above the bottom.	Spr, sum, fall (-1/week) 19861993	Boynton et al. 1994
Sediment-water exchange rates	Net sediment exchanges of 02, N02, N03, DIP, Si, C02	8	Estimated from shipboard incubation of intact sediment cores. Incubations were under ambient conditions.	Spr, sum, fall I/month 1984–1996	Boynton et al. 1994
Phytoplankton component	Primary production rates, chl a concentration, and species composition	34	Short-term (3-hr), constant light ^{14}C incubations. Fluorometric chl a determinations.	16–20/year 1984–present	Sellner 1993

Results and Discussion

Time-series Observations at a Single Site

In this section, we examine the influence of river flow on phytoplanktonic production and biomass, deposition rate of spring-bloom phytoplankton, deep-water dissolved-oxygen declines, and recycling of ammonium from estuarine sediments. General pathways of the influence of river flow on these processes are summarized in figure 11-1. All of these analyses are based on time-series data collected at one location in the central portion of Chesapeake Bay (R-64, figure 11-2). We used seasonally or annually averaged data (6–8 or 16–20 observations, respectively) in these analyses rather than single, instantaneous values because these were the time scales of interest and because we wanted to avoid short-term variablity related to organism response times, changes in water residence times, and the like. These results were selected to serve as examples of the utility of synthesis as a framework to think about interrelationships of estuarine processes; there is a great deal of additional analysis that could be conducted on these and other data sets.

Algal Production and Biomass

The starting point for these investigations was suggested by previous analyses from lakes (for example, Vollenweider 1976) and coastal and estuarine systems (for example, Boynton et al. 1982; Nixon 1988) where statistically significant relationships were found between nutrient-loading rates and algal production and algal biomass. In our case, we used river flow as the independent variable because in Chesapeake Bay it is strongly correlated with nutrient-loading rates (Summers 1993) and provides most of the buoyancy that results in seasonal water-column stratification and hence definition of the upper mixed layer (Boicourt 1992).

We were initially doubtful about the possibility of finding strong relationships between flow and algal parameters. Previous investigators had adopted comparative approaches to obtain a sufficiently large range in loads and phytoplanktonic responses to observe significant relationships (Nixon 1988). Our initial concept was that there were so many factors controlling algal parameters that any one variable, even one like river flow that has multiple influences on the system, would explain only a small portion of the observed variability

It appears that this is not the case. Results indicate strong relationships of river flow to biomass and, to a lesser extent, production (figure 11-4). In both, a large percentage (59% and 78%) of interannual variability was explained by river flow alone. This result reinforces the general conclusion that river flow is a dominant factor regulating some basic ecosystem processes in systems like Chesapeake Bay.

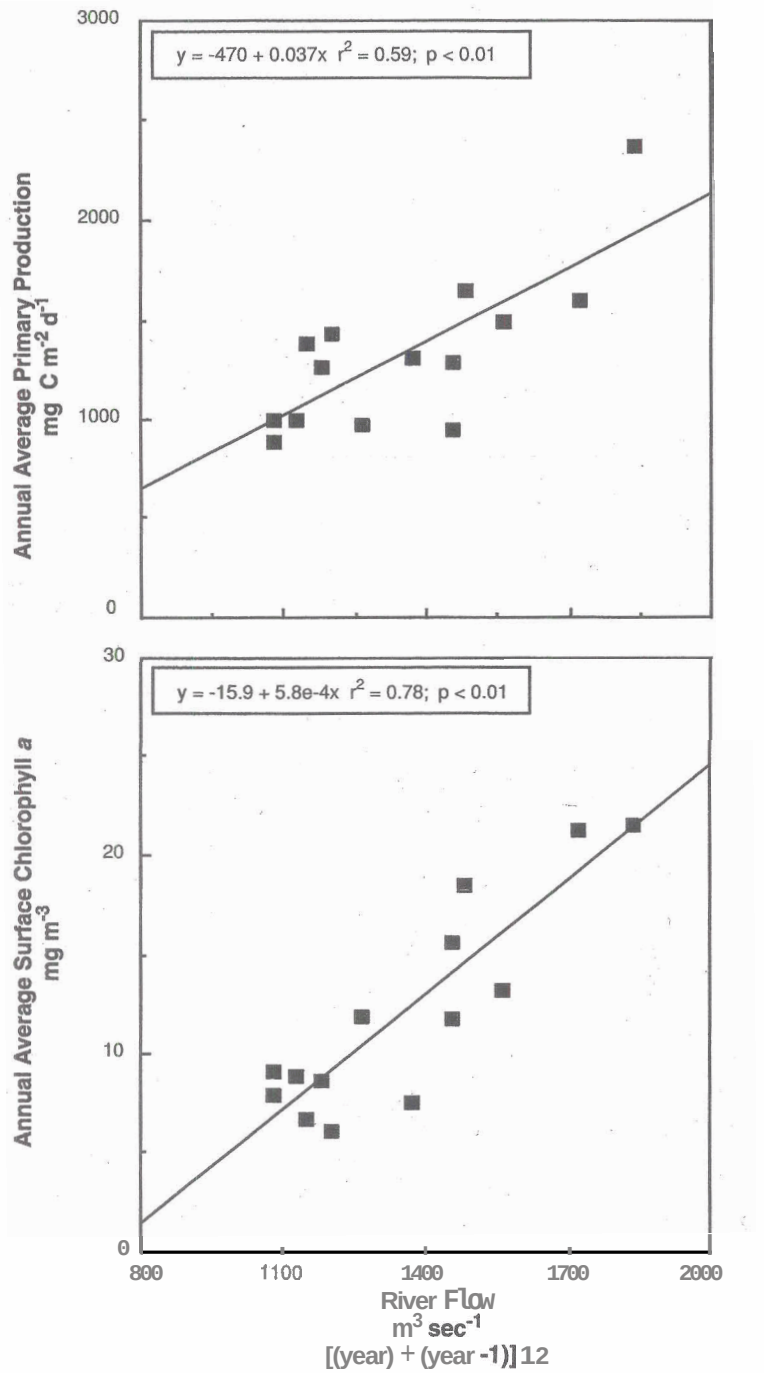

FIGURE 11-4 Results of linear regression models showing relationships between annual average phtoplankton primary production and surface chlorophyll a concentrations and freshwater flows from the Susquehanna River. River flow was calculated as the average of flow in the present and preceding year. Production and chlorophyll *a* data are from the R-64 site during the periods 1972–1977 and 1985–1993.

In this analysis several variations of independent (river flow) and dependent (phytoplankton production and biomass) variables were also tested, each being a variation representing a modified hypothesis concerning river influence on algal parameters (table 11-2). For example, in some trials just the spring freshet was used as the flow variable to explore the idea that this short but high period of flow was a key event in the annual or summer portion of the phytoplankton cycle. Many were statistically significant indicating the general importance of river flow. However, the flow variable that explained the most variability was an average of annual flow from the current year and from the previous year. This combination was suggested by examination of field data where it was noticed that production and biomass in years of average flow were higher than expected if they were preceded by a year of exceptionally high flow. This, in turn, suggests some nutrient retention or "nutrient memory" over time scales of a year rather than seasonal periods as suggested by bay water residence times (Boynton et al. 1990). Given the shallow depths of the bay, interannual retention of nutrients in the water column is not likely. The only likely multiyear nutrient storage site is sediments (Boynton et al. 1995). We suggest that in years of especially high flow, above-normal algal biomass is generated during the spring bloom. Recycling of this material supports high production through summer, which serves to conserve nutrients in the bay and make possible a large fall bloom. The deposition of the fall bloom to sediments, coupled with falling water temperatures, preserves nutrients through winter and they become available the next spring to support production and algal biomass at higher than expected levels. Kemp and Boynton (1984) proposed a similar sequence of

TABLE 11-2

A summary of results from linear regression analyses examining data sets for relationships between river flow and phytoplankton production and biomass. Entries in the table are r^2 values. Single and double asterisks indicate significance at the 0.05 and 0.01 probability levels, respectively. The number of observations in each analysis was fourteen. Data are from Mihurski et al. (1977), USGS (1993), and Magnien et al. (1994).

	River Flow Averages					
Phytoplankton Variables	Jan.–Mar.	Jan.–May	Jan.–Jun.	Jan.–Jul.	Avg. Annual	Two-Year Avg.
Annual average chlorophyll a	0.22	0.50**	0.67**	0.47**	0.64**	0.78**
Annual average production	0.14	0.20	0.15	0.13	0.22	0.58**
Summer average chlorophyll a	0.17	0.47**	0.74**	0.74**	0.62**	0.56**
Summer average production	0.18	0.31*	0.25	0.23	0.26	0.51**

events based on observations made in the Patuxent River estuary, but in that case the sequence did not include more than one annual cycle.

Spring-&hornDeposition

In most years, the annual cycle of phytoplankton biomass accumulation exhibits a distinct maxima associated with the spring bloom in the mesohaline regions of the Chesapeake Bay and there is considerable interannual variability in the magnitude of this spring peak as a consequence of interannual differences in nutrient input from the watershed (Malone et al. 1988). Studies by Sellner (1993) and White and Roman (1992) indicated that the spring bloom was not extensively grazed by zooplankton, If it was deposited to deep waters, as seems likely, it would become available to support a host of processes including macrofaunal growth, microbial respiration, and associated oxygen consumption and sediment nutrient releases.

Deposition rates of total chlorophyll *a* were measured using fixed sediment traps (weekly or biweekly measurement periods) from 1985 to 1992 (Kemp and Boynton 1992; Boynton et al. 1994; Roden et al. 1995). Deposition-from spring blooms (integrated from day 50 through day 150 in-all years) ranged from 541 mg m^{-2} in 1989 to 1,190 mg m^{-2} in 1990. Estimates of spring-bloom deposition rates followed qualitative trends in algal biomass for some years but not others (Magnien et al. 1994).

Inspection of spring-bloom deposition rate and river flow data suggested that there might be a more consistent relationship between deposition and flow than to algal biomass during the spring bloom and deposition. A series of analyses was performed (Boynton at al. 1993) wherein the period of time during which flow was averaged was different (figure 11-5).

These analyses indicated that river flow that occurred just prior to the spring bloom had the most influence on the magnitude of subsequent deposition rates. Low river flow from December through February was always associated with small spring deposition rates as were freshets that occurred late in the spring after the time of normal spring-bloom development (for example, May 1989); the largest deposition events (1987, 1988, and 1990) were all associated with river flow patterns that featured a distinct above-normal pulse in flow from December through February. In this case, analyses suggested a close temporal coupling between flow and an ecosystem response. Spring-bloom deposition appears to be responsive to relatively recent river flow events, with integrated effects of flows from previous seasons not being evident.

A strong departure from the expected pattern was observed in 1991 wherein a relatively small deposition event was associated with very high and sustained river flows that began in fall and continued throughout the winter. This

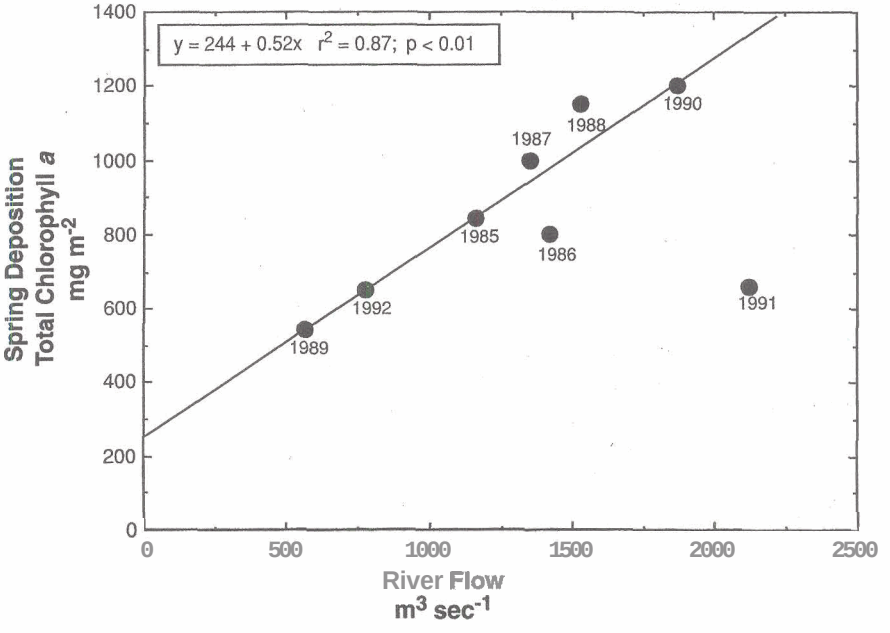

FIGURE 11-5 Results of linear regression model showing relationships between the magnitude of spring phytoplankton bloom deposition and freshwater inflows from the Susquehanna River. Spring-bloom deposition of total chlorophyll a was estimated from moored sediment trap arrays (duplicate weekly or biweekly measurements from collecting cups positioned beneath the pycnocline). Spring-bloom deposition was calculated as the total chlorophyll a mass collected from the initiation to termination of bloom deposition during each year. River flow was averaged for the months of December through March for each year preceding the spring bloom. All data ate from the R-64 site. The 1991 data were not included in the regression model.

suggested that either the bloom did not develop or that deposition did not occur as usual. Water-column chlorophyll data suggested a strong bloom in 1991 (Magnien et al. 1994), which weakens the former hypothesis. It appears probable that the 1991 bloom deposited farther downstream than usual and thus was not measured at our fixed station. Maps of chlorophyll concentration in surficial sediments made immediately after bloom deposition in 1993 (another year with a strong freshet) indicated that most of the bloom deposited 20–30 km downstream of the sediment trap location. This analysis suggests that these systems are responsive to forcing events of relatively short duration and that the spatial location of the spring-bloom epicenter can be shifted seaward in years of high sustained river flow. These observations generally, but not always, conformed to the simple "bottom-up" control model presented earlier. The outlier in this data set was useful, as is often the case, leading us to consider

additional explanations that eventually resulted in a better understanding of these systems.

Seasonal Declines in Deep-water Oxygen

In many coastal areas, including Chesapeake Bay, there is strong interest in the scientific and management communities to better understand processes regulating dissolved-oxygen declines. In Chesapeake Bay low dissolved-oxygen conditions occur primarily in those areas where the water column is stratified and where there is substantial deposition of organic matter from the upper water column to deep waters and sediments. Establishing relationships between myriad environmental variables and oxygen conditions has not been a simple task in the bay. For example, Seliger and Boggs (1988) pointed out that low dissolved-oxygen conditions in the bay could be explained by river flow and water-column stratification and concluded that nutrient inputs (and the organic matter produced) may have little to do with anoxia. Kemp et al. (1992) argued that physical and biological processes are coupled, with freshwater flow providing buoyancy for stratification as well as nutrients for organic matter production. Boicourt (1992) has suggested the possibility of a phase shift in freshwater flow versus anoxia relationships.

Our data are not adequate to entirely resolve this problem but it is possible to test for relationships between deep-water oxygen characteristics and organic matter deposition rates for one region of the mainstem bay where seasonal oxygen problems are chronic. Several anecdotal observations indicated that such relationships might exist. First, hypoxic or anoxic conditions developed in deep waters for some period of time during each year since intensive monitoring began in 1984. Low oxygen concentrations in deep waters were associated with even the lowest flow conditions observed. Second, in 1989, the spring freshet (and associated nutrient load) did not enter the bay until mid-May. The spring phytoplankton bloom did not develop to any significant extent and deep-water oxygen depletion was delayed for about a month.

Finally, in 1992, the spring freshet was very small. Spring chlorophyll a concentration in the water column and chlorophyll a deposition rates were among the lowest on record and dissolved-oxygen concentrations declined slowly, not reaching mg l^{-1} until early July. These results suggest that deep-water oxygen conditions are regulated, at least in part, by the amount of organic matter deposited during spring.

Bottom-water oxygen concentrations were routinely measured (weekly or biweekly) at the R-64 station from 1985 to 1992 (figure 11-2). Water depth at this site is about 17 m and vertical water-column stratification is generally strong in this region of the bay. The daily rate of change of oxygen concentration (d DO/dt) was calculated using spring measurements from 1985

through 1992. The time period over which rates of change were calculated varied slightly among years but in most cases included the period from the beginning of March through the middle of May. The criterion used to determine the starting point was that the first observation should not be followed by any oxygen measurements of higher concentrations. Typically, during late winter and early spring, deep-water oxygen concentrations exhibit both small increases and decreases over time but are usually close to saturation. The final oxygen measurement used was the last measurement made before oxygen concentration declined below 1 mg l^{-1}. The rates of oxygen decline for the years 1985 through 1992 calculated from these data were linear, statistically significant ($p < 0.01$; $r^2 > 0.90$), and differed appreciably among years (by more than twofold).

The fact that dissolved-oxygen concentrations began declining during early spring suggested that these declines were caused by respiration of spring deposition events rather than later summer events. Accordingly, average spring deposition rates of total chlorophyll a were calculated for each year using deposition data collected between early February and the beginning of May. Chlorophyll a deposition rates were regressed against the rate of dissolved-oxygen decline derived from regressions of time versus dissolved-oxygen concentration (figure 11-6). These results suggest a strong influence of organic matter availability on the rate of oxygen decline. However, at least two alternative explanations exist. First, it can be hypothesized that different spring rates of oxygen decline are caused by interannual differences in temperature regimes. Oxygen decline would be more rapid in warm years than in cold years because of the influence of temperature on respiration rates (Sampou and Kemp 1994). This explanation seems unlikely to be the prime cause because interannual temperature differences have been small over the period of record. Additionally, warm and cool springs were nor correlated with high and low rates of oxygen decline. The second hypothesis is that the cause is related to interannual differences in the strength of water-column stratification. In years when the water column is highly stratified, less mixing of oxygen from surface to deep-water occurs and rates of oxygen decline would be greater. Stratification certainly plays a major role in determining deep-water oxygen characteristics. However, the case for stratification being the dominant cause of interannual differences in oxygen decline rates is weak because years of high and low stratification do not correspond well to years of high and low rates of oxygen decline.

Sediment Ammonium Fluxes

The final example in this sequence concerns possible relationships between river flow and sediment nutrient recycling. It is hypothesized that variations in river flow and associated nutrient inputs regulate spring-bloom size and

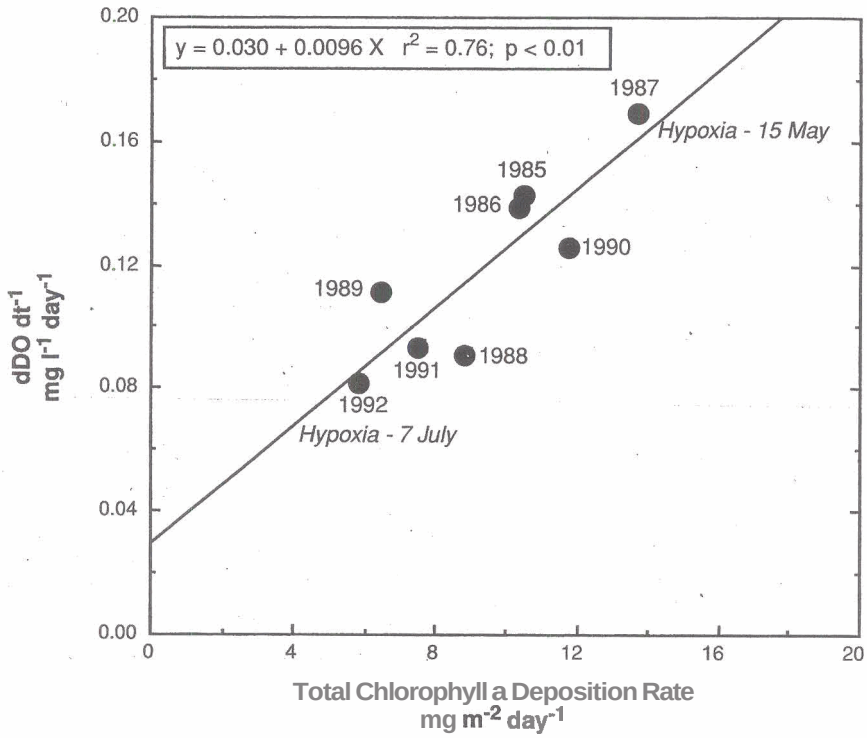

FIGURE 11-6 A scatter diagram showing the relationship between the rate of decline in dissolved-oxygen concentrations in deep water ($dDO\ dt^{-1}$) and average deposition rates of total chlorophyll a during the spring-bloom period. Data are from the 1985–1992 period and were collected at the R-64 site. The date on which hypoxia (DO concentration <1 mg l^{-1}) was first encountered during highest (1987) and lowest (1992) deposition years is also indicated.

organic matter deposition rates. Deposited organic matter, in turn, serves as a substrate for decomposers, which eventually regulates nutrient releases from sediments. We attempted again a series of regressions using different time averaging of flow and benthic nutrient recycling rates. Again, most combinations indicated a positive relationship; the strongest relationship between river flow and sediment ammonium flux was found using winter (December to February) flow rates, as in the deposition-versus-flow relationship, and summer (June to September) average benthic ammonium fluxes (figure 11-7). This implies a time delay between nutrient input and benthic nutrient recycling. In this estuary, springtime respiration rates remain relatively low at temperatures below 10°C for both benthic (Boynton et al. 1990) and water-column communities (Smith and Kemp 1995); rates increase exponentially with vernal warming beyond these thresholds. Deposition of organic matter to sediments derived from the spring bloom starts in late February and ends by

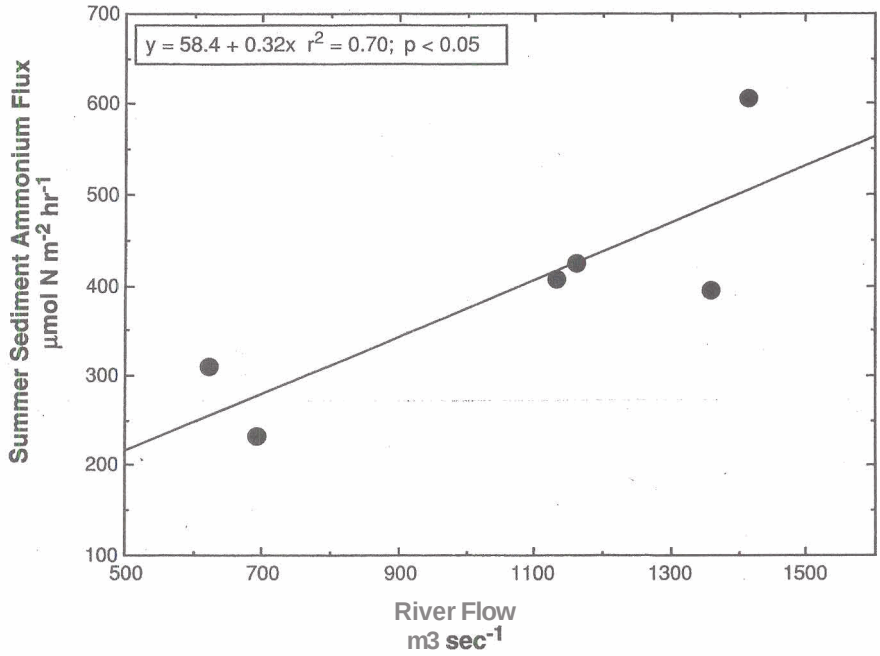

FIGURE 11-7 A scatter diagram indicating the relationship between summer sediment ammonium flux (June–September) and winter flow from the Susquehanna River. Sediment-water flux data are from the R-64 site and were collected during the 1988–1993 period.

mid-May. However, large sediment fluxes of ammonium are not evident until June when bottom waters are above 15°C and coupled rates of nitrification and denitrification begin to decline with oxygen depletion (Kemp et al. 1390). Relative to the other relationships presented here, the river flaw-nutrient cycling relationship was the weakest. In part, this may be due to a more limited data set. It may also be because this process is the farthest removed from the influence of flow, at least as conceptualized here. In this view, other factors have more of a chance to come into play (for instance, infaunal community activities, sediment redox conditions, nitrification-denitrification, focusing of organic matter from shoal areas to deeper waters) modifying or fundamentally changing the nature of the flow-recycling relationship.

Intersite Comparative Analyses

In this section, we present additional examinations of estuarine features as they relate to variations in river flow and attendant nutrient-loading rates. The approach here is comparative wherein data from fivesites with different nutrient-loading rates were used rather than a time series from a single site.

Here we use space (different sites) to examine the possible causes of temporal variability just as we used a time series of observations in the previous analyses (Pickett 1991). There are several distinct advantages to a comparative approach to synthesis. The range in both independent and dependent variables can be expanded if sites are chosen with this in mind, thereby increasing the possibility of observing patterns, if they exist. Additionally, the inclusion of multiple sites or different systems inherently increases the generality of conclusions; the possibility that observed relationships are only unique to a single site is diminished. However, difficulties present themselves with comparative analyses as well, the most prominent being the differences in the characteristic scales (such as volume, depth, residence time) among sites. Hence, there is a need to analyze data in a way that accounts for scaling differences so that ecological variables of interest are comparable among different systems. In fact, the use of nutrient-loading rate was adopted here because nutrient loads were known to be different among the systems we studied and could be scaled to the respective estuarine areas. The scaling of variables (such as nutrient-loading rate to estuarine area) is, in itself, an issue that could benefit from some serious consideration.

Nutrient Stocks

Perhaps the most direct relationship to consider is that between nutrient loads and water-column stocks (figure 11-8). Our analyses indicated a very strong relationship between annual average total nitrogen (TN) load and average annual TN mass in the water column; to a lesser extent the same was found for total phosphorus (TP). The weaker TP relationships may have resulted from the fact that a large percentage of the TP load is in the form of inorganic particulate phosphorus and hence not as prone to remain in the water column (Boynton et al. 1995). However, all results were poor when specific chemical species (such as nitrate) rather than totals were used. Apparently, specific nutrient species are transformed rapidly enough so that simple relationships to load are not apparent at that level of detail.

Another feature of these relationships is the attenuated response of concentrations to loads. For example, TN loads varied by a factor of about 10 while water-column mass varied by only a factor of 3. Similar attenuated responses were found for a variety of variables examined in a series of estuarine nutrient budgets (Boynton et al. 1995) and in a set of marine mesocosms exposed to a range of nutrient-enrichment rates (Nixon et al. 1986). This suggests that either internal sinks (such as sediment burial and denitrification) are quite active or that these nutrients are efficiently transported out of the system. In the case of Chesapeake Bay, both seem to be involved (Boynton et al. 1995). Finally in some regression models the intercept values contain information of

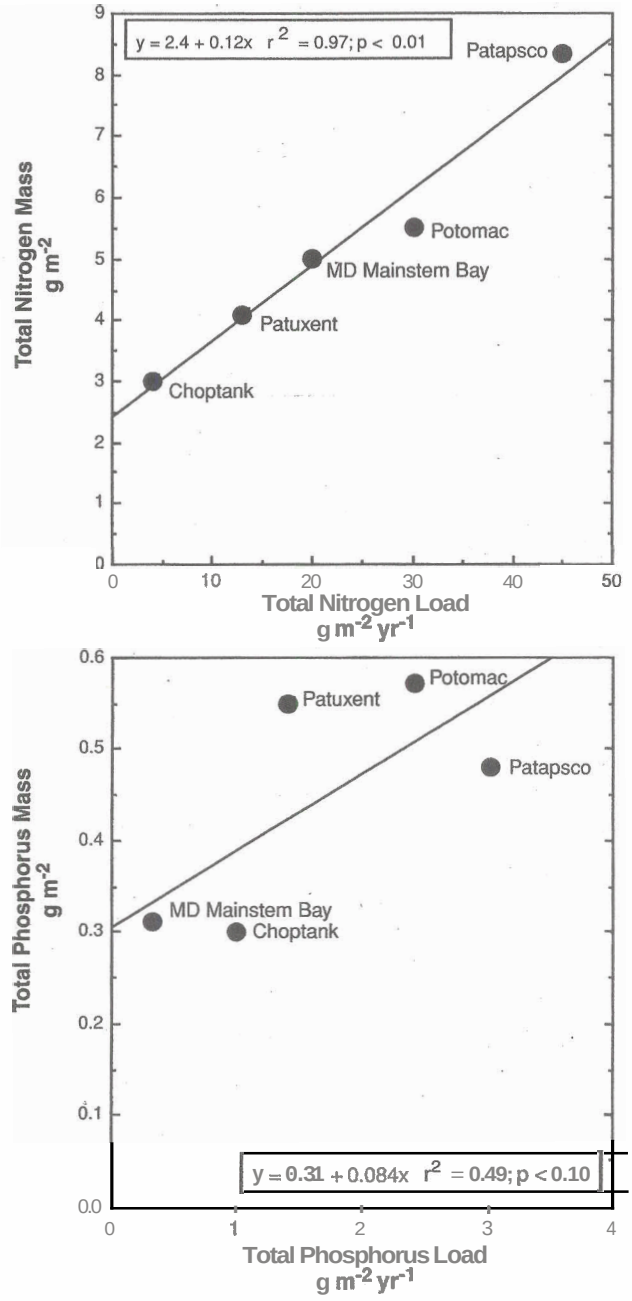

FIGURE 11-8 Scatter diagrams indicating relationships between annual average total nitrogen (TN) and total phosphorus (TP) mass in the water-column and average annual TN and TP loads to five locations in the Chesapeake Bay system. Loads and water-column masses were measured at the fall-lime sites and estuarine stations, respectively, indicated in figure 11-2. Data were averaged for the 1985–1996 periods.

ecological interest. In this case, TN and TP values at zero loading rates are still substantial (~17 μM N and 1 μM P for a 10 m water column) and suggest potentially high productivity even under pristine conditions.

Phytoplankton Chlorophyll Stocks

In the mid-1970s limnologists developed a series of useful statistical models relating nutrient-loading rates and algal biomass for a large sampling of lakes (Vollenweider 1976). These relationships were used to estimate the degree to which nutrient-loading rates would need to be decreased to move a particular lake from one trophic state (as defined by chlorophyll a concentration) to another. Surprisingly, few comparable relationships have been developed for coastal and marine ecosystems (Nixon et al. 1986; Nixon 1988). We initially attempted a direct duplication of the Vollenweider (1976) model using average annual (or ice-free periods) surface-water chlorophyll *a* concentration ($\mu g\ l^{-1}$) as the dependent variable and annual average phosphorus loading rate (adjusted for the freshwater fill time and mean depth of the receiving water body) as the independent variable. This selection of variables did not produce either predictive or significant statistical results ($r^2 < 0.10$; $p > 0.10$) We then reasoned that, because algal blooms often develop in deep waters, particularly in spring in Chesapeake Bay, vertically integrated water-column chlorophyll a ($mg\ m^{-2}$) would be a better estimate of algal biomass; however, results were only marginally better. We then substituted nitrogen for phosphorus and results improved to the degree shown in figure 11-9. We have also obtained sufficient data to add results of the MERL eutrophication experiment (Nixon et al. 1986) and portions of Hillsborough Bay, Florida, data (Johannson 1991) to this analysis.

The results support the concept that, for some estuarine systems, phytoplankton biomass levels respond in positive linear relation to nutrient-loading rates. Further, there is some indication that different systems respond in a similar fashion when loading rates are scaled for local conditions of depth and flushing rates. This sort of analysis could be expanded to include other systems to explore the robustness of the relationship; a successful test would increase confidence in the conceptual model on which it is based. However, the conceptual model used here explicitly favors bottom-up control. It is almost certain that such a model would not work in instances where top-down controls become dominant, as in cases where intensive benthic grazing by introduced species (Alpine and Cloern 1992) or aquacultural activities are important (Meeuwig et al. 1998). Finally, the scaling of the nutrient load for estuarine flushing characteristics used in this example is primitive and would not be appropriate for estuarine systems with larger tides or limited freshwater inflows (Monbet 1992). More realistic formulations are needed. However, this is an example of where a synthesis

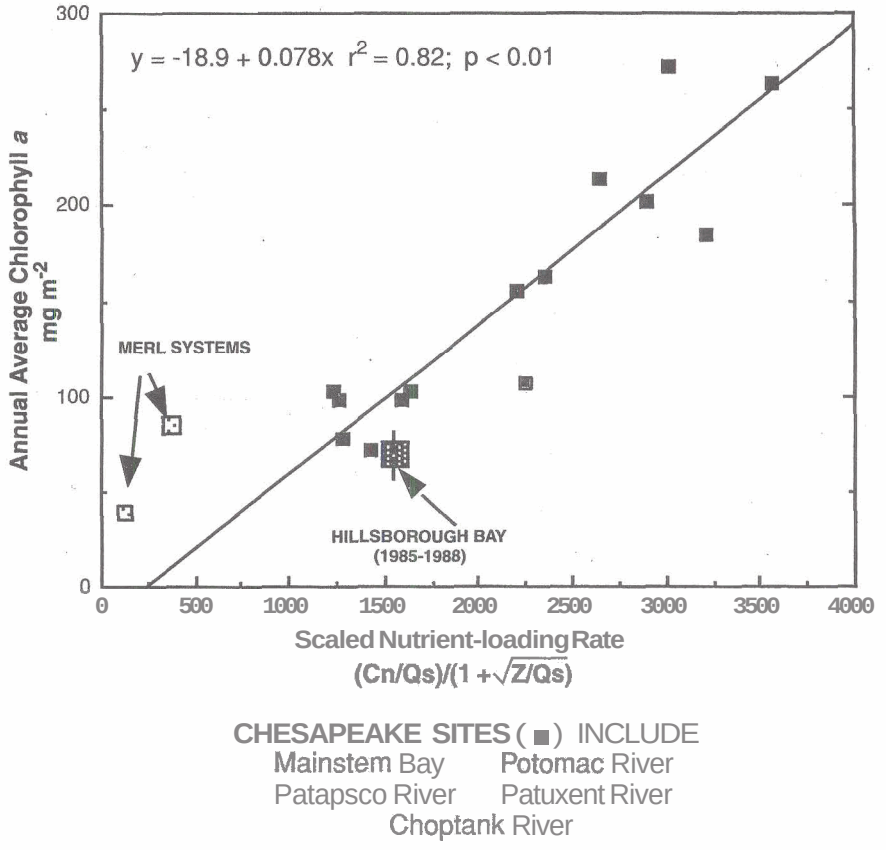

FIGURE 11-9 A scatter diagram relating annual average total chlorophyll a mass to nitrogen-loading rate; Data are from the five estuarine sites indicated in figure 11-3 and were collected during the 1985–1987 period. Nitrogen-loading rates were scaled following the method used by Vollenweider (1376) where: C_n = nitrogen-loading rate (mg N m^{-2} yr^{-1}); Q_s hydraulic fill time (years); Z = mean depth (m). Hillsborough Bay, Florida, data are from Johnson (1991) and the MERL data are from Oviatt et al. (1986).

activity clearly suggests some additional lines of inquiry; in this case, the scaling of important characteristics of ecosystems.

Sediment Nutrient Releases

In an earlier example, we related river flow to sediment nitrogen releases (figure 11-7) using time-series data. We considered the same processes again but used a comparative approach with data from several sites that encompassed a large range in total nitrogen-loading and sediment ammonium-recycling rates. As in the previous case, the conceptual model liking

nutrient loading to the ecosystem from external sources and sediment nutrient recycling involved load-related algal biomass, which was deposited to sediments and eventually served as substrate supporting sediment nutrient releases. Results from one set of analyses are shown in figure 11-10.

The load-recycling relationship suggests several interesting insights. First, the slope of the regression indicates that for every unit reduction in TN load there would be about an equivalent reduction in sediment ammonium recycling. However, flux data are from summer when values are high; typical values from the remaining months are only 10–30% of these values. Overall, there still appears to be a strong linkage between load and flux. The intercept value of 120 μmol N m^{-2} hr^{-1} is sufficient to support relatively low rates of phytoplanktonic primary production (~0.3 g C m^{-2} day^{-1}, assuming Redfield C:N proportions). The intercept value would be lower if data from the Choptank River were excluded, as possibly they should be, because of problems with estimating the TN loads. At low nutrient-loading

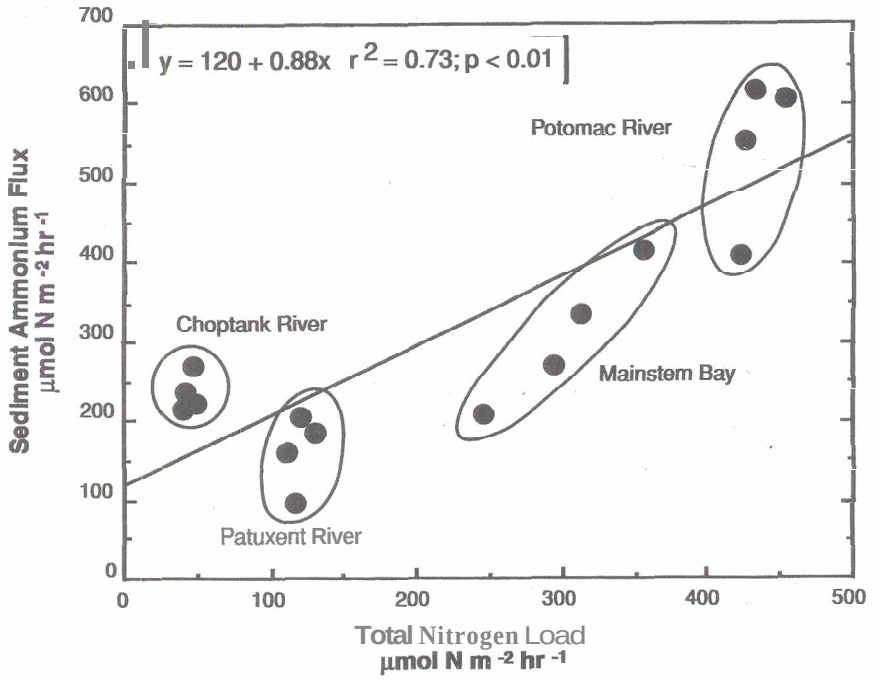

FIGURE 11-10 A scatter diagram relating summer (June through September) sediment ammonium flux to average annual total nitrogen load in four locations in Chesapeake Bay. Loads and sediment fluxes were measured at the fall line and estuarine sites, respectively, indicated in figure 11-2. Data were from the 1985–1988 period.

rates the amount of nitrogen recycled from sediments is small, but this could still be important in more oligotrophic environments.

Choptank River fluxes are higher than expected for a given level of nutrient loading. This discrepancy may be more apparent than real. Results based on nutrient budget calculations indicate that the lower Choptank River receives substantial nutrient additions from the mainstem bay (Boynton et al. 1995). Groundwater discharges directly to tidal waters are also important. If this is the case, nutrient loading to the Choptank River is higher than shown in figure 11-10 and would have the effect of displacing Choptank River fluxes to the right, more in line with those of other systems. The fact that Choptank fluxes diverged so strongly prompted us, and others, to reexamine loads to this system, not an uncommon benefit of synthetic analyses such as these.

While only TN versus ammonium flux is shown in figure 11-10, other load-recycling relationships were examined. In general, sediment-water fluxes (for instance, sediment oxygen consumption, silica) were consistently better correlated with TN loading than with TP Ioading (Boynton et al. 1994). Even sediment recycling of PO_4^{3-} exhibited a stronger relationship with TN loads than with TP loads. In part, this may result from the fact that there is a considerably broader range in TN loads than TP loads (Boynton et al. 1995). It may not be possible to resolve TP influences on sediment nutrient recycling over this relatively narrow loading range. Alternatively, the poor correspondence with TP loads may indicate that most of the phytoplankton debris that reaches sediments, and eventually supports sediment-water nutrient recyling, was produced more in response to N than P availability in the water column. (D'Elia et al. 1986; Fisher et al. 1992).

There may be additional inferences to be drawn from this comparative analysis of TN loading versus sediment ammonium recycling (figure 11-10). Specifically, even in this limited (4 year) data set, there appear to be qualitative relationships of recycling to loading to each system; the pattern is most obvious for the mainstem bay site, but there is a hint apparent for most sites. The provocative observation here is that the slope of each cluster of points for 4 years tends to increase as ecosystem system size decreases. Thus, the fraction of TN loading that appears in summer benthic ammonium recycling is larger with small systems. This implies that smaller systems retain and recycle nutrients more efficiently, or that a larger fraction of primary production is deposited to and recycled in smaller (shallower) systems (Kemp and Boynton 1992; Boynton et al. 1995). Are there some rules for estuarine scaling to be gleaned from these types of observations? We intend to add more observations to this analysis in the future; it may well be that continued empiricism may provide answers to these questions.

Concluding Remarks

Examination of time-series and comparative data at sites in Chesapeake Bay have revealed surprisingly strong and linear relationships of primary production, benthic-pelagic coupling, and nutrient recycling to both freshwater flow and nutrient-loading rates. It appears that in well-sampled systems comparative analyses are not necessary to obtain sufficient range in variables for a pattern to emerge; in the case of Chesapeake Bay, clear signals were seen when river flow varied by about a factor of 2. However, comparative analyses increase the generality of results.

There are extensive data on water quality, physical forces, and ecological processes for Chesapeake Bay; we have only scratched the surface for inferences that could be drawn from these data. Data are available to explore the relations between freshwater flow (and nutrient loading) and distributions of seagrass, zooplankton, and benthic invertebrate communities. In addition, spatial sampling in many regions of the Chesapeake system is sufficient to develop volume-weighted estimates of processes, biomasses, and pool sizes; these variables would presumably be more representative of estuarine conditions than estimates based on samples from a single station.

The approach used here started with a conceptual model of how freshwater flow or nutrient loads influenced key processes and properties of an estuarine ecosystem. We have found these conceptualizations to be far more profitable than approaches that start with a "blind" search for correlations. However, most of our work has utilized simple linear regression techniques. More sophisticated techniques such as multiple linear and nonlinear regression, multivariate analyses, classification, and regression-tree and time-series approaches appear attractive because of the complexity of estuarine processes.

Based on our initial effort comparing ecological responses to variations in physical forces among Chesapeake Bay subsystems, we are optimistic about the utility of applying comparative analysis methods with time-series data for multiple ecosystems. We suggest that contrasting similar time-series analysis among different systems may help identify key scaling relationships needed to generate fundamental scientific understanding that is not site-specific.

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