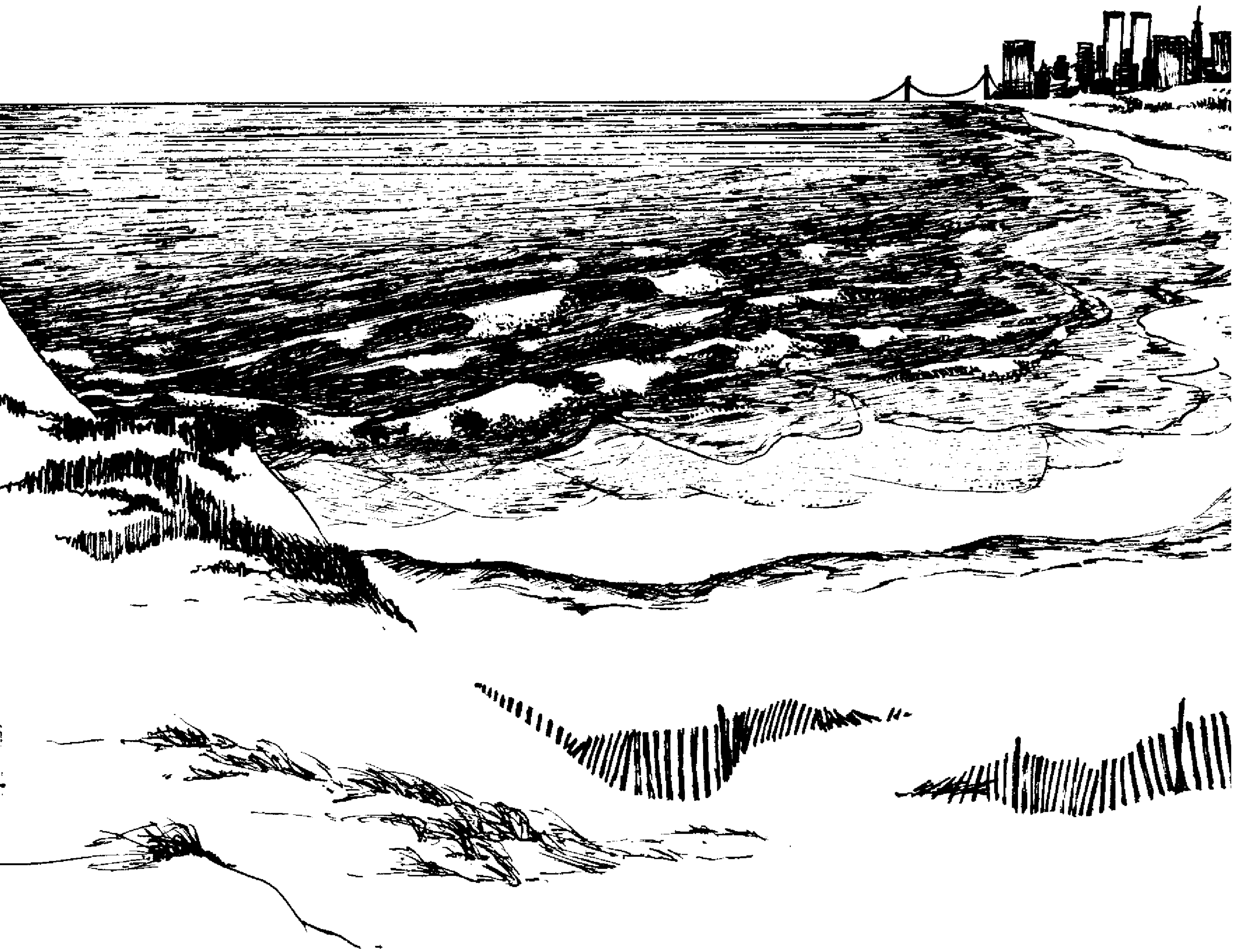
Plankton Production

Charles S. Yentsch



MESA NEW YORK BIGHT ATLAS MONOGRAPH 12

The offshore water in the bend of the Atlantic coastline from Long Island on one side to New Jersey on the other is known as New York Bight. This 15,000 square miles of the Atlantic coastal ocean reaches seaward to the edge of the continental shelf, 80 to 120 miles offshore. It's the front doorstep of New York City, one of the world's most intensively used coastal areas—for recreation, shipping, fishing and shellfishing, and for dumping sewage sludge, construction rubble, and industrial wastes. Its potential is being closely eyed for resources like sand and gravel—and oil and gas.

This is one of a series of technical monographs on the Bight, summarizing what is known and identifying what is unknown. Those making critical management decisions affecting the Bight region are acutely aware that they need more data than are now available on the complex interplay among processes in the Bight, and about the human impact on those processes. The monographs provide a jumping-off place for further research.

The series is a cooperative effort between the National Oceanic and Atmospheric Administration (NOAA) and the New York Sea Grant Institute. NOAA's Marine EcoSystems Analysis (MESA) program is responsible for identifying and measuring the impact of man on the marine environment and its resources. The Sea Grant Institute (of State University of New York and Cornell University, and an affiliate of NOAA's Sea Grant program) conducts a variety of research and educational activities on the sea and Great Lakes. Together, Sea Grant and MESA are preparing an atlas of New York Bight that will supply urgently needed environmental information to policy-makers, industries, educational institutions, and to interested people.

ATLAS MONOGRAPH 12 discusses the major physical and biochemical factors controlling primary production in New York Bight. Since bight waters have extremes in temperature, the water column is well mixed during winter and strongly stratified during summer. This sharp, seasonal distinction is reflected in the seasonal changes in phytoplankton. Yentsch explores the direct interactions between pollutants and phytoplankton and warns that the level of primary production is approaching the maximum yield in many areas. In the coming years it will take the combined efforts of scientists, engineers, and legislators to accurately assess how the Bight will fare under further exploitation.

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Plankton Production

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MESA NEW YORK BIGHT ATLAS MONOGRAPH **12**

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Acknowledgments

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Collection of much of the data was due to the efforts of a group of biological oceanographers at Woods Hole Oceanographic Institution under the direction of B.H. Ketchum. It is to this group and their efforts that I would like to humbly dedicate this monograph.

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Abstract

The principal mechanism for regulating primary production in the waters of New York Bight is vertical mixing. The intensity of this mixing is caused by a unique blend between local meteorological conditions and the physiology of photosynthetic phytoplankton. In winter the distribution of phytoplankton is largely due to the intensity of vertical mixing and water depth: primary productivity in slope waters is limited by vertical mixing, which in effect reduces the amount of sunlight received by the phytoplankton. The spring bloom arises from the reduction in vertical mixing because of heat (via sunlight) being added to surface waters and the relaxation of winds. During summer, primary production is low throughout most of the Bight, apparently because of the limited quantities of nitrogen in the euphotic zone. Intense production occurs in autumn as a result of the breakdown of the summer thermocline with the onset of winter temperatures and strong winds.

Introduction

Plankton are minute plants *(phytoplankton)* and animals *(zooplankton)* that float or swim weakly in a body of water. The plankton ecosystem at the initial stage is run by sunlight and fertilizing nutrients which produce phytoplankton by photosynthesis. This is referred to as *primary production.* The fate of phytoplankton is to be eaten by herbivorous zooplankton.

This monograph discusses the major physical and biochemical factors controlling primary production in New York Bight. The early work of H.B. Bigelow (1933) and Bigelow and Sears (1935) revealed a close coupling between plankton abundance and vertical mixing in the water column. First is a description of a general model to illustrate the abundance/vertical mixing coupling, then a discussion of actual data for the general model, followed by a description of how certain factors control production. The magnitude of primary production and why Bight waters are more productive than the open ocean are discussed; the amount of energy flowing into other levels of the food web is estimated. Finally, the effects pollution may have on primary production and thus on the marine ecosystem are looked at.

A General Descriptive Model

Seasonal Extremes

New York Bight represents a unique blend of open ocean characteristics modified by seasonal climatology. Compared to most other coastal ocean areas, Bight waters rank highest in temperature extremes. Because of these extremes the water column is well mixed during winter and strongly stratified during summer. This sharp, seasonal distinction is reflected in the seasonal changes in phytoplankton abundance.

Related to phytoplankton growth are composites of seasonal climatological trends, which in turn influence specific factors, such as solar radiation, water transparency, temperature, and wind stress. These regulate vertical mixing and set plankton growth limits. Vertical mixing has two biochemical roles: regulation of mean light energy reaching a phytoplankton population in a water column, and vertical transport of deep, nutrient-rich water to surface water. Vertical mixing can be either detrimental or beneficial to phytoplankton, depending upon season and mixing depth. If, for example, mixing is extremely deep, the mean light intensity for the phytoplankton population could be so reduced that there would be little or no growth.

Vertical mixing is also a prime physical means for restoring nutrients to surface waters from deeper water layers. For instance, Figure 1 shows two extremes of climatology, water mass conditions, and phytoplankton abundance. Summer generally produces *oligotrophic conditions* (poor in growth nutrients) in shelf and slope waters. The high solar energy and light winds characteristic of summer promote a thermally stratified water column in which vertical mixing is negligible. During winter, extensive vertical mixing occurs throughout the entire area. Mixing starts in autumn with the cooling of surface waters and an increase in wind velocity. Winter phytoplankton populations in continental shelf waters can be quite large even though the amount of solar radiation has decreased. Conversely, offshore coastal populations are saved, so to speak, by the bottom depth. However, offshore populations do not have this advantage when mixing exceeds 100 m (328 ft); hence, growth can become light-limited.

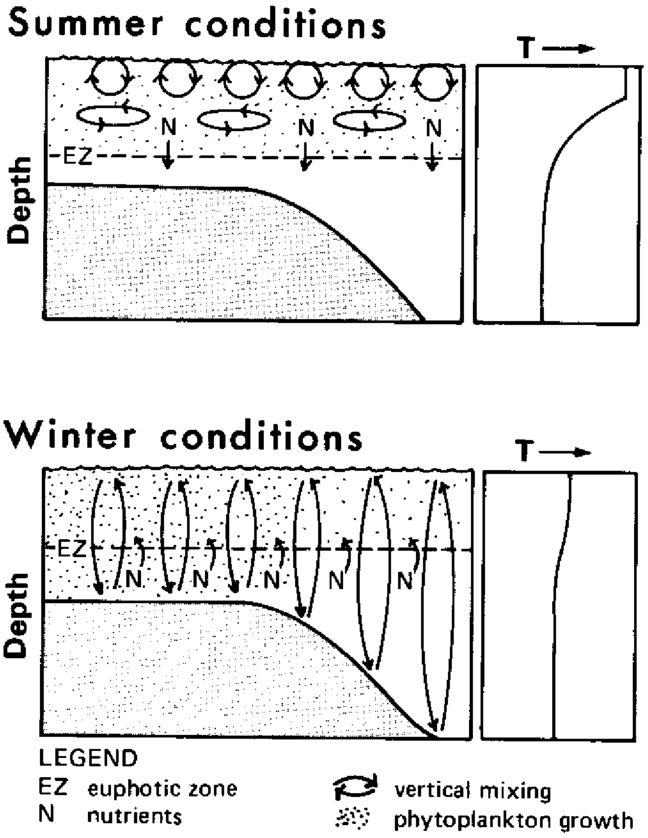
Between winter and summer is a strong pulse of growth referred to as a spring bloom. This results from an increase in solar radiation and water temperature, a reduction of thermal stratification, and a lowered wind velocity. Generally, the spring bloom is more distinctive in slope waters than in shelf waters. A fall bloom occurs during autumn in the transition from a stratified to a mixed water column. In contrast to the spring bloom, the fall bloom is the result of recovery from nutrient impoverishment.

Oceanic Variables

The oceanographic data examined here were collected by Woods Hole Oceanographic Institution from 1957 to 1963. The Woods Hole group seasonally traversed the continental shelf along two sections of stations (Map 1)—Montauk Point to sea (stations A-G) and Bargate, NJ, to sea (stations J-S). These traverses were closed by sections paralleling the shore at the seaward (station H) and nearshore (stations T-Z) extremes.

The Montauk section, analyzed by Ketchum and his associates (1958), is representative of water mass conditions for most of the shelf and slope.

Density. Since vertical mixing has been emphasized, we will examine the seasonal density structure of the water column. The summer conditions of the general model are exemplified by the July and September



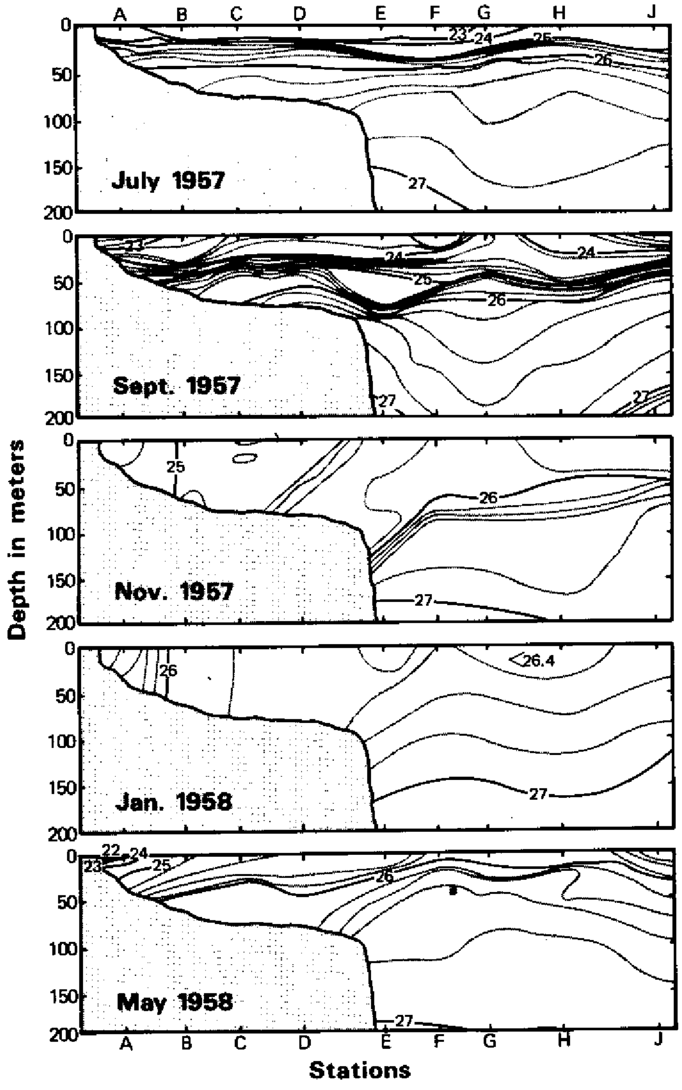
Source: Yentsch 1971

Figure 1. Factors controlling primary plankton production on continental shelf in temperate latitudes

observations in Figure 2. During both months, the water masses covering the continental shelf and slope are characterized by a 25 m (82 ft) surface water layer with a density less than sigma T (σ_T=[density x 10^3]$^{-1}$) 25.0 over a thick water layer with a density exceeding σ_T 26.0. The stability of this water mass is great, that is, the amount of energy necessary to mix it with the rest of the water column. The difference in density between 50 m (164 ft) and the surface equals 3.0 σ_T units. No imperial relationship exists between vertical mixing and stability; however, if we assume that no difference in density over 50 m (164 ft) represents maximum vertical mixing, the limit representing little or no vertical mixing must be near a difference of 3.0 σ_T units.

Lack of stability and intense vertical mixing characterize the November and January observations (Figure 2), examples of winter conditions of the general model. Between November and January a seasonal trend of decreasing stability occurs, apparent from the increase in density of the surface waters covering the shelf and slope areas. For example, in November the density is about σ_T = 25.0; by January this has increased about 1.0 σ_T unit because deep waters of higher density have been mixed into the surface of the water column.

May represents a transitional period—the warming cycle (Figure 2). Vertical mixing is impaired first in shallow waters and then progressively seaward into deep waters. The spring bloom follows the same pattern.

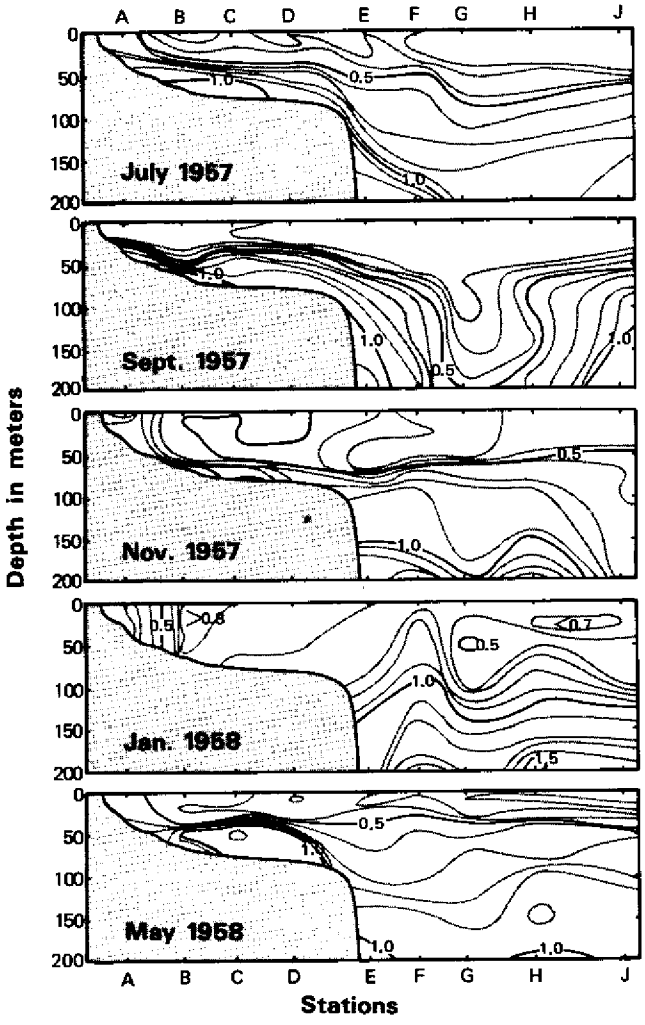


0—20 Statute miles
0—20 Kilometers
0—20 Nautical miles

Stations refer to Map 1
Units are sigma T
Vertical exaggeration 400:1

Source: Ketchum et al 1958

Figure 2. Density distribution



0—20 Statute miles
0—20 Kilometers
0—20 Nautical miles

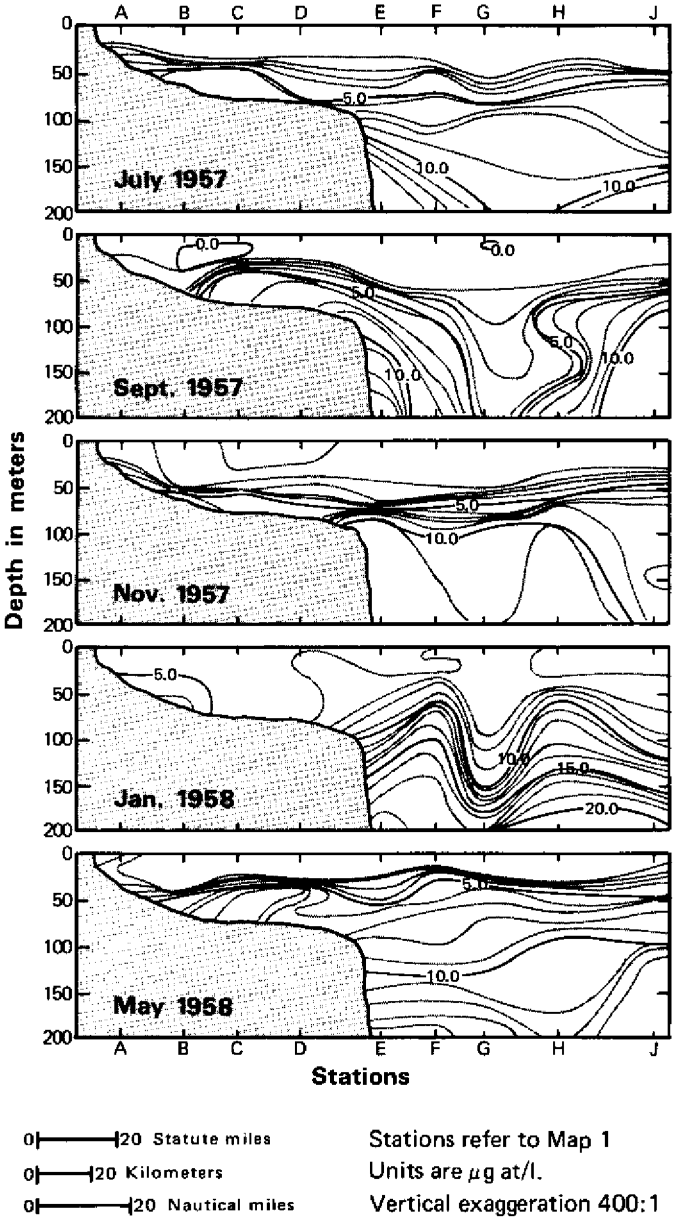
Stations refer to Map 1
Units are μg at/l.
Vertical exaggeration 400:1

Source: Ketchum et al 1958

Figure 3. Inorganic phosphorous distribution

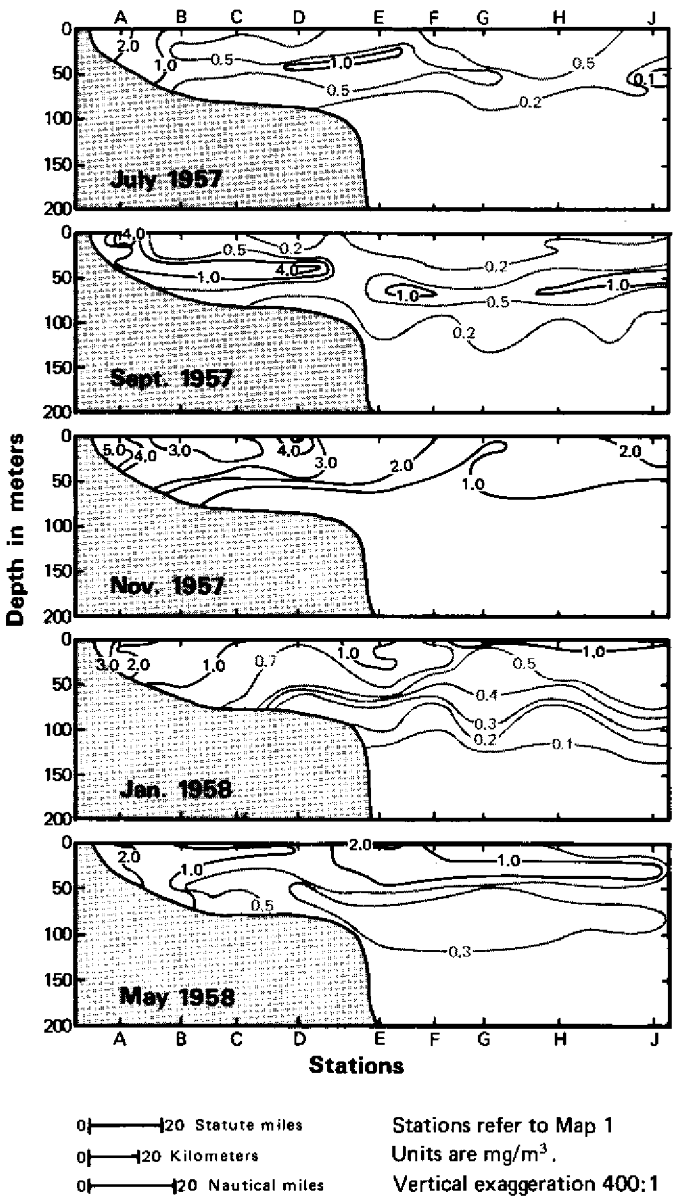
Phosphate and Nitrate. The marked changes in the density structure are apparent in the distribution of nutrients (Figures 3 and 4). During summer (July and September), surface waters of the thermally stratified water column have low phosphate concentrations and in some cases undetectable nitrate concentrations. In autumn and winter the increase in vertical mixing can be seen by the departure of nutrient chemical *isopleths* (lines of equal concentration) from the horizontal. Since mixing begins in shallow shelf waters and moves into slope waters, the pattern of phosphate and nitrate renewal to the surface layers follows this progression. By May the isopleths regain the horizontal characteristics typical of summer; however, at this time the concentrations of both substances are considerably greater than in summer.

Chlorophyll *a* is the primary photosynthetic pigment of all plants. To demonstrate the change in phytoplankton biomass, Figure 5 shows the seasonal change in phytoplankton chlorophyll, an index of abundance. Throughout most of summer, the ocean surface layers have low chlorophyll concentrations, except in the first 16 km (10 mi) of the section. Higher concentrations here are associated with upward sloping nutrient isopleths and density surfaces, suggesting the existence of local upwelling specific for this area and due to prevailing winds. Also during summer, chlorophyll is concentrated at depths considerably below the surface. This becomes more apparent as the season progresses and is most distinct in slope waters. The chlorophyll concentration resides at depths where water density is increasing most



Source: Ketchum et al 1958

Figure 4. Nitrate nitrogen distribution



Source: Yentsch, unpublished data

Figure 5. Chlorophyll distribution

rapidly. Steele and Yentsch (1960) explain these chlorophyll concentrations as due to phytoplankton losing buoyancy and sinking until their density equals that of the surrounding water. This midwater accumulation of chlorophyll disappears with the destruction of stratification of the water column in autumn.

During autumn and winter, concentrations of chlorophyll decrease, moving from near shore to the open sea. As winter conditions intensify, open ocean chlorophyll concentrations become much lower than shelf water concentrations. By spring, with the start of the warming cycle (May), some stratification returns. Chlorophyll concentrations in surface layers respond by becoming twice as great as observed in winter.

An "aerial view" of the seasonal pattern of surface water chlorophyll is shown in Figure 6. The greatest change in concentration occurs from shelf waters seaward. Shelf waters nearly always exhibit higher concentrations than slope waters, except during spring when shelf and slope waters are about equal. The fall bloom, which occurs during the cooling cycle, may be the most extensive and intense feature of the seasonal cycle in shelf waters. In slope waters the seasonal cycle is characterized by two pulses of chlorophyll—one during the cooling cycle and the other during the warming cycle. These pulses appear to be equally intense.

To summarize, seasonal abundance of phytoplankton is regulated by vertical mixing, which in turn is driven by the energy available to move the water minus the attenuation of this energy by the bottom. We will now look at factors specifically limiting the growth of phytoplankton, emphasizing how they interact in Bight waters.

Factors Regulating Phytoplankton Production

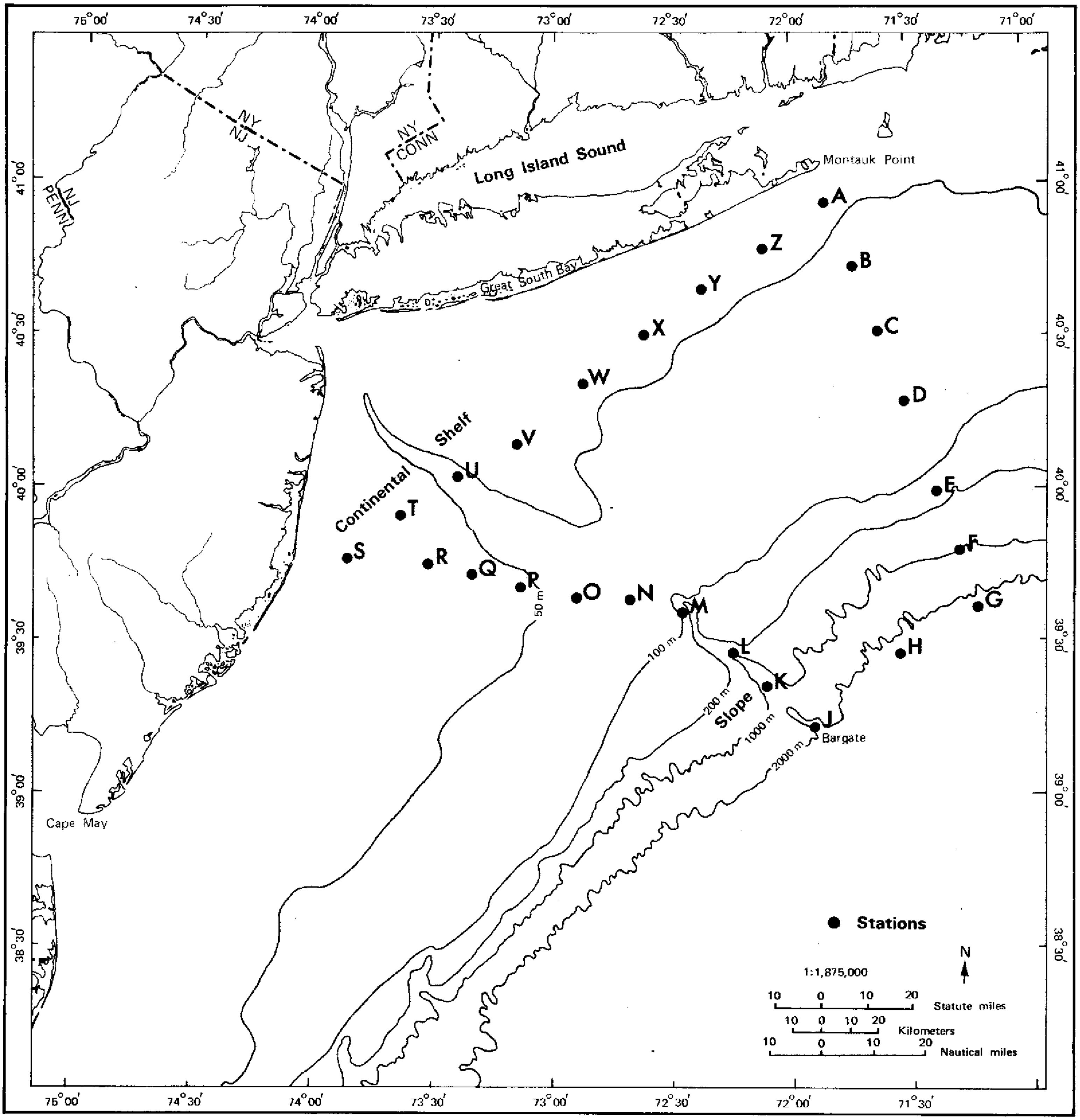
Vertical Mixing

The rate of vertical mixing cannot be easily measured at this time; however, the extent to which the water column can be mixed vertically can be estimated by the change of temperature with depth. The depth at which the surface water layers cease to be *isothermal* (constant temperature for each layer) is called the mixed layer. Generally, deep wind-mixed layers mean intense vertical mixing, and shallow wind-mixed layers mean minimal vertical mixing.

Vertical mixing has two roles: regulation by light, and nutrient transport from deep to surface layers of the water column. A population of phytoplankton spread equally over a very deep mixed depth can become light-limited because the mean light intensity reaching the population is not great enough to promote growth. This concept of a *critical mixing depth* was first observed in the Bay of Fundy by Gran and Braarud (1935) and first considered quantitatively by Sverdrup (1953). Critical depth conditions arise when vertical mixing is very deep, deeper than the *compensation depth* (depth where respiration is equal to photosynthesis). Parameters necessary for estimating critical depth are light penetration, transparency of the water column, and rate of photosynthesis and respiration of the phytoplankton. The combination of reduced sunlight and deep mixing during winter sets the stage for critical depth. Gran and Braarud estimated that the critical depth in the Bay of Fundy was five times the compensation depth. The compensation depth for Bight waters is not precisely known—I estimate it would not exceed 40 m (131 ft) and would average about 25 m (82 ft), placing the critical depth somewhere around 150 m (492 ft). If this estimate is at all accurate, it means that critical depths are not encountered on the shelf since the maximum water depth there is about 50 m (164 ft). Slope waters, however, are deep enough for critical depth conditions to occur during winter. Low and photosynthetic carbon fixation in these waters during winter support the idea that critical depth accounts for the sparsity of phytoplankton at this time of year (Yentsch, unpublished data).

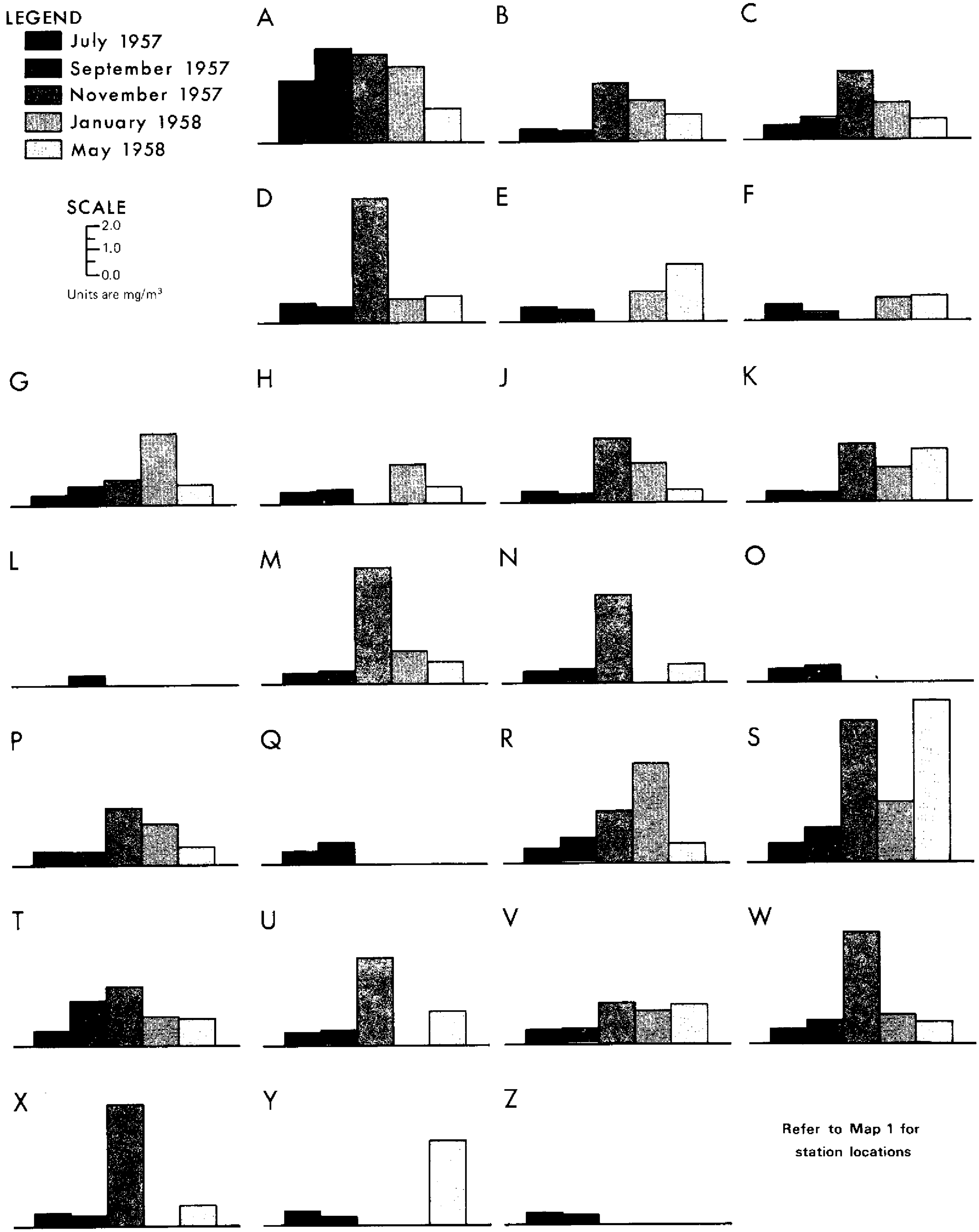
The other role of vertical mixing is the transport of nutrients from depth to the surface. Generally, as mixing depth increases, the nutrient concentration at 10 m (33 ft) increases (Figure 7). Highest concentrations of nitrate occur during winter in surface water when mixed layers are greater than 100 m (328 ft). The relationship between phosphate concentrations and nitrate concentrations and vertical mixing differs in that the highest values for phosphate concentrations occur when mixing is about 50 m (164 ft).

Map 1. Station locations, WHOI



Lambert Conformal Projection

Source: Ketchum et al 1958

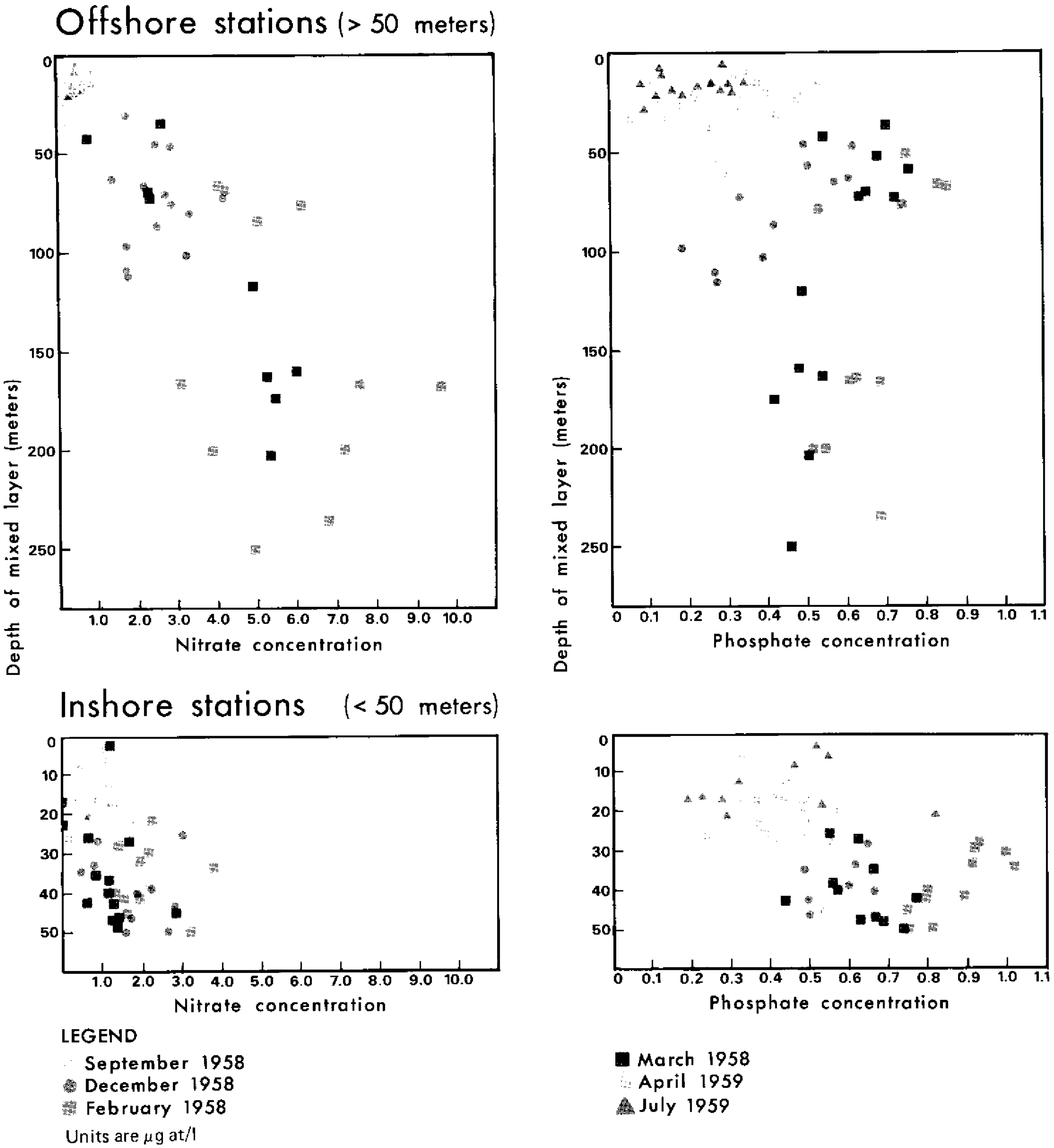


Source: Yentsch, unpublished data

Figure 6. Surface chlorophyll concentrations

This is not the case for nitrate, which has been implicated as the limiting nutrient in many ocean areas. To restore nitrate nitrogen to the surface waters offshore, at quantities greater than 1.0 microgram atoms per liter (µg at/l), mixing must be over 50 m (164 ft); this does not happen until autumn (Figure 7). Throughout summer, phytoplankton populations must rely on the nitrate available in the shallow surface layer. However, some evidence indicates that ammonium nitrogen is of sufficient quantity to sustain the populations during summer, though not sufficient for net growth (Vaccaro 1963).

Nitrate values greater than 5.0 µg at/l do not appear in the shallow surface layers. This is presumably because of high utilization by the large nearshore phytoplankton populations and because vertical mixing cannot draw on the high nitrate concentrations of the deep waters.



Source: Yentsch, unpublished data

Figure 7. Relationship between depth of mixed layer and nitrate/phosphate concentrations

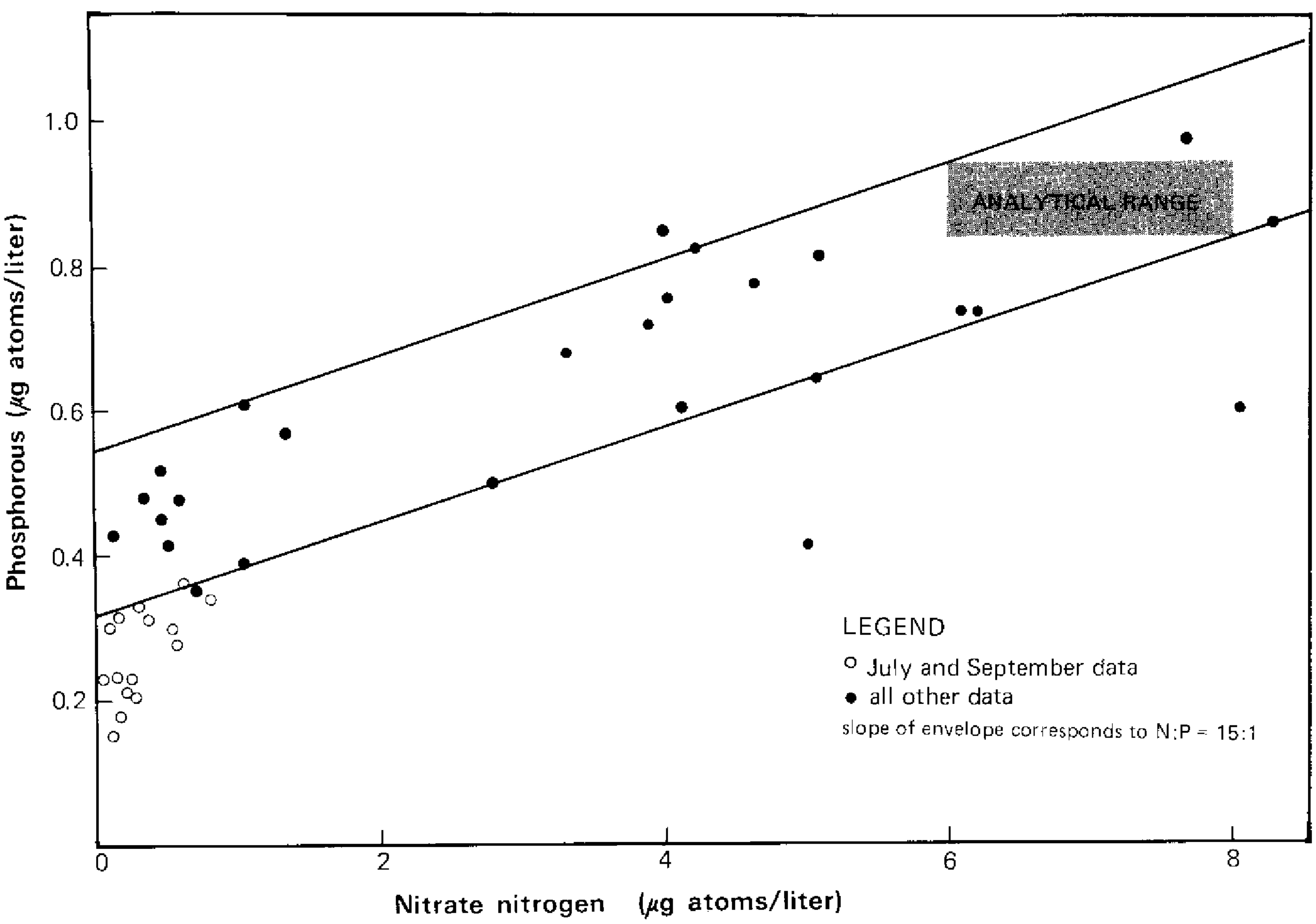
Nutrients isolated by thermal stratification produce growth stagnation. The strongest argument for nitrate limitation in these waters is demonstrated by plotting the ratio of nitrate to phosphate for concentrations of each element measured at 10 m (33 ft) in the water column (Figure 8). The envelope enclosing data points for months other than July and September represents a ratio of change in concentration of 15:1, that is, $\Delta N:\Delta P = 15:1$. This is basically the proportion in which the two substances are found in living organisms, and normally the uptake and decomposition rates are expected to follow this ratio. The data points for July and September are less than 15:1, and where nitrate is undetectable, zero. Extrapolation of the data to the ordinates indicates that when nitrate is undetectable phosphate exists at 0.32 to 0.55 μg at/l, whereas nitrate nitrogen has been exhausted. The departure of the ratio from 15:1 is partially due to limited vertical mixing during summer, enriching surface waters in a proportion favoring phosphate addition. For example, vertical mixing increases the concentration of phosphate in surface waters by as much as 0.5 μg at/l, with little or no change in nitrate concentration.

Seasonally, nitrate limitation, based on N:P data, begins with the onset of stabilization of the water column in spring (Figure 9). From here through summer no N:P ratio exceeds 5:1 in surface layers. In early summer the ratios average about 3:1, and by September near zero values are observed in the surface layers throughout the entire area.

To summarize the sequence of nitrogen limitation: in the transition from spring to late summer the photosynthetic demand of phytoplankton rapidly removes nutrients from the surface waters. Nitrate disappears faster than biochemical regeneration or vertical mixing can resupply the surface layers. Thus, during summer, plankton population growth is limited by lack of nitrogen.

Temperature

As mentioned earlier the cold temperature of winter waters in the Bight can limit productivity by slowing down physiological processes like photosynthesis. However, in natural populations of phytoplankton the role of temperature is difficult to evaluate



Source: Ketchum et al 1958

Figure 8. Ratio of change for 10 m samples at stations B,C,D in Map 1

because other limiting factors, such as light and nutrients, obscure temperature's role (Yentsch and Lee 1966; Eppley 1972). The effect of temperature on phytoplankton photosynthesis has been derived empirically for natural populations in the Gulf of Maine (Yentsch, Strube, and Morris 1974). For about every 10°C (50°F) change in water temperature between 0°C and 20°C (32°F and 68°F), photosynthetic efficiency* is altered by about 50%. The range in temperature in the gulf is comparable to that in the Bight. However, Bight waters warm up earlier in the season; by late summer they are about 5°C (41°F) warmer than Gulf of Maine waters.

Examining the seasonal temperatures of Bight surface waters, I estimate that temperature has a major influence only during three winter months (January, February, and March), which is what was observed (Mandelli et al 1970). The greatest effect appears in the shallow nearshore areas. Offshore, slope water populations are not affected by low water temperatures to the same extent as those inshore. Ryther and Yentsch (1958) anticipated that the effects of water temperature would show up in primary production. The relative efficiency of photosynthetic production was measured partially with this in mind. The efficiency varied for reasons that were not clear. It was concluded that many factors affect this efficiency and it is very difficult to sort out the single effects of temperature, but during February (the coldest month) efficiency was observed to be lower than the annual average.

Floristic Characteristics of Phytoplankton Populations

Using chlorophyll concentration as an index of biomass facilitates the discussion of seasonal change and limiting factors. But another school of thought reasons that species diversity reflects environmental stress: high productivity is aligned with low diversity and vice versa. New York Bight has been in the limelight of diversity research largely because of the highly *euthrophic* (rich in growth nutrients) bays and sounds of Long Island (Smayda 1973). E.M. Hulburt studied the species of phytoplankton populations in the open coastal waters, comparing species and numbers offshore and inshore seasonally (Hulburt and Rodman 1963; Hulburt 1963; Hulburt 1970).

As measurements of chlorophyll concentration show, largest populations (by cell number) are near shore; however, this is masked by large fluctuations in species number. Hulburt observed some general trends concerning cell size and shape. During spring, elongate and cylindrical species of diatoms tend to dominate inshore populations though growth peaks do occur in *isodiametric* cells (cells with equal diameters) or very small cells. In summer the nearshore waters are dominated by long, thin cells and isodiametric cells.

Major changes in species composition occur inshore to offshore. Diatoms do not dominate offshore populations, which belong mainly to coccolithophore, dinoflagellates, and flagellates; in general, these have a high percentage of motile cells.

Hulburt computed the diversity index** for phytoplankton populations, providing a comparison of the ratio of species to numbers, independent of sample size. The index ranges from 1 to 10, with no distinguishable trend between coastal and oceanic populations. Seasonal change is apparent. During poorest growth conditions (summer) no species is successful—diversity is high. Other times of the year, when growth conditions are more favorable, a very successful form appears and the diversity index is lowered.

The significance of diversity as it reflects oligotrophic and euthrophic conditions really becomes apparent when populations of coastal ponds and estuaries are compared with open coastal and oceanic populations (Figure 10). Clearly, euthrophic areas have low diversity; open ocean oligotrophic populations are diverse.

There is a tendency to interpret these differences in diversity as interspecific competition. Yet selective feeding by herbivores cannot be ruled out. Hulburt argued that much of the "noise" in the diversity of coastal populations is due to their intermediate oceanographic position between the euthrophic coastal ponds and bays and oligotrophic open ocean.

*Photosynthetic carbon fixed per unit of chlorophyll, frequently referred to as the assimilation coefficient or assimilation number.

**$S = \ln\left(\frac{N+1}{\alpha}\right)$

N = number of cells
S = species number
α = diversity index

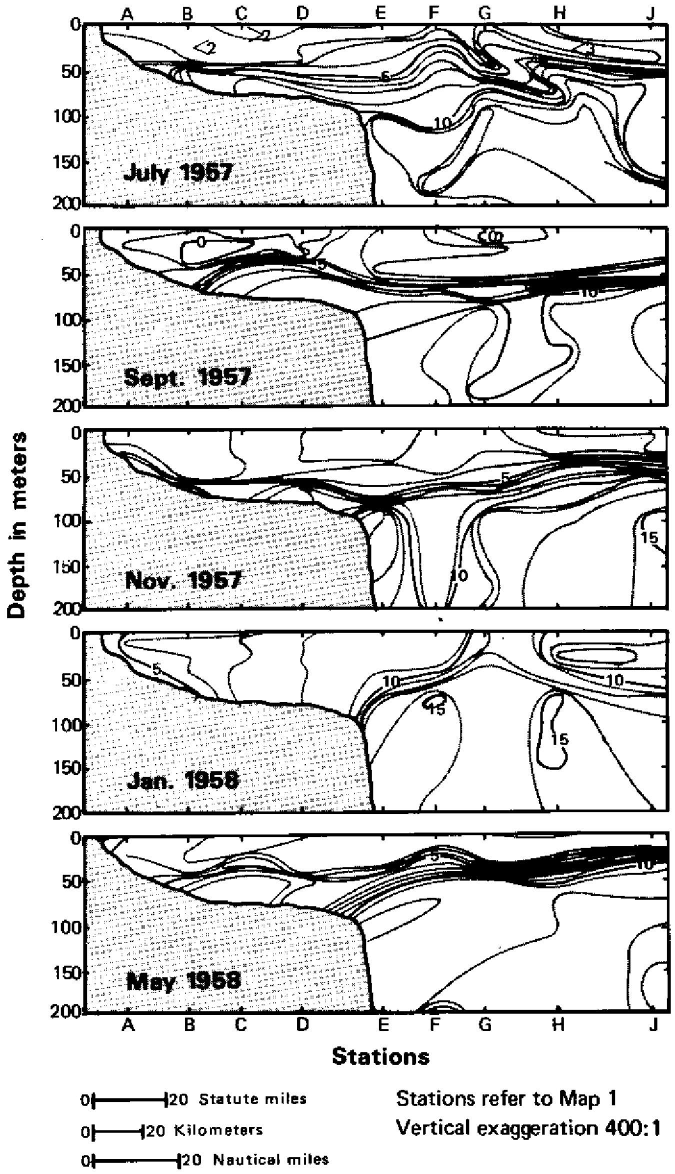
Hydrographic Influences

Variation Across the Shelf. Figure 11 summarizes primary production as a function of water depth. The values indicate the amount of photosynthetic carbon fixed under a square meter of sea surface. Two field methods were used to gather these data: radioactive carbon 14 was used to trace photosynthetic rate, and the rate of carbon fixation was estimated from the measurement of chlorophyll and light (Ryther and Yentsch 1957). For future discussion it is worthwhile to summarize important points concerning seasonal and spatial variation in primary production.

First, during summer, productivity is uniformly low over the entire Bight; values rarely exceed 0.5 $g/m^2/day$. Second, throughout winter, productivity offshore is low–most values approach 0.5 $g/m^2/day$; inshore productivity is close to 1.0 $g/m^2/day$. Third, highest productivity occurs in spring when values exceed 2.0 $g/m^2/day$; these productive blooms spread from coastal waters seaward and are more pronounced in slope water than in shelf water populations.

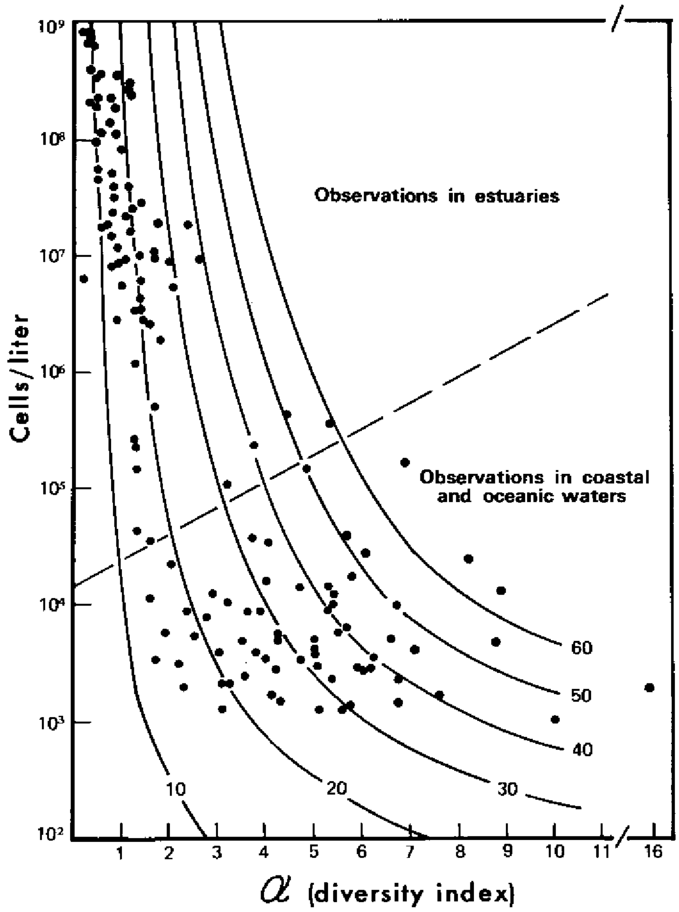
Production in shallow waters is about twofold greater than that offshore. The same magnitude of difference occurs between open ocean and coastal waters. Extremes in productivity are summarized in Table 1 for open coastal waters, closed sounds, and bays throughout the New York area. In richness, the open coastal waters off New York are intermediate between the euthrophic sounds and bays and the oligotrophic Sargasso Sea.

Proximity to Land and Freshwater Entry. Basically two sources can account for the transition in nutrient richness: nutrient introduction by land drainage (via fresh water), and oceanic waters, mainly those at depth. Although the decrease in the amount of primary production with increasing distance from shore and with water depth is generally explained on the basis of the proximity of coastal waters to land and drainage systems, such a decrease–spatial change



Source: Ketchum et al 1958

Figure 9. Seasonal distribution of N:P ratios



Source: Hulburt 1963

Figure 10. Relation of diversity to population size

—can actually be explained by vertical mixing alone. This is especially true during winter. However, bottom sediments cannot be entirely ruled out as a factor in the rapid biochemical cycling of organic material and release of nutrients to the water column. Measurements of phosphate, nitrate, nitrite, and ammonia show concentrations 10 to 100 times higher in the interstitial waters of sediments than in the overlying waters (Yentsch, unpublished data). The flux of these to the water column is poorly understood; hence their quantitative importance cannot yet be ascertained. But it seems likely that during winter when vertical mixing is actively scouring the shelf, concentrations of nutrients that accumulated during summer are released and swept into the water column.

Table 1. Summary of annual gross carbon production

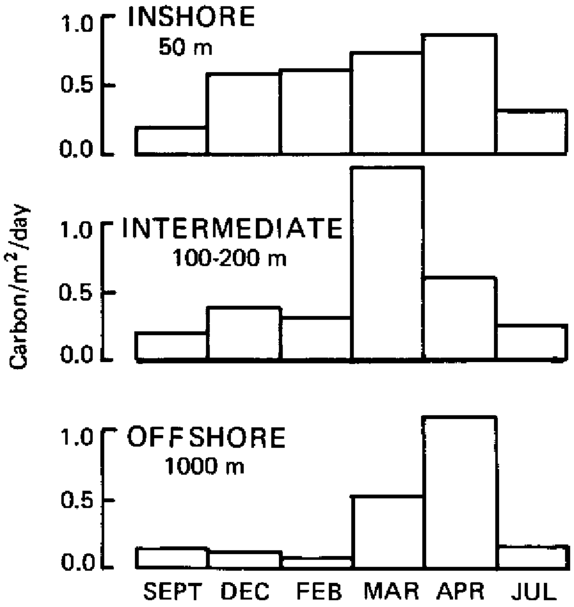
	g/m^2
Long Island Sound[a]	470
Block Island Sound[b]	365
Continental shelf[c]	
50 m	160
100-200 m	135
1,000 m	100
Sargasso Sea[c]	78-80

Sources: [a]Riley 1956
[b]Riley 1952
[c]Ryther and Yentsch 1958

The most straightforward assessment of the potential influence of freshwater drainage in coastal waters comes from measuring the seasonal pattern of salinity, an approach used in estuaries and applied to studies of shelf water (Ketchum and Keen 1956). The concentration of fresh water in a water column is estimated in sections across the continental shelf. First, however, we must assume that salinity is a conservative property (biology has no effect), that is, the only changes are brought about by mixing and that rainfall or evaporation are of little importance to the distribution. Second, we must assume that the Bight is basically ocean water diluted by fresh water. For example, if C represents the water mass and A the ocean source and B the freshwater source, then $C = A + B$, where A and B are fractions of the mixture C. Then if a reference salinity of 35 parts per thousand (°/oo) is assigned to A, the percentage of fresh water in the source (B) can be estimated. In this case the percentage of fresh water ($F\%$) equals A-S/A (100) where S is the observed salinity. Ketchum and Keen (1956) computed the percentage of fresh water in water masses on the shelf and slope for three seasons (Figure 12). These estimates show that freshwater concentration never exceeds 10% in coastal waters. Mixing of the two sources (A and B) appears to follow an exponential trend where fresh water decreases with increasing depth. Seasonally, there is not a great change in this trend; largest amounts of fresh water in summer are about 1% greater than smallest amounts in winter. Values for spring are intermediate between the two seasonal extremes.

The important point is that in the freshwater source any substance having a potential to regulate productivity is heavily diluted by ocean water by the time it arrives in coastal waters. Furthermore, if chemical substances (for example, phosphate) are subjected to biological utilization, then levels will be reduced even more before entering coastal waters. This does not mean that freshwater input into coastal waters cannot be significant. The unknowns necessary to assign significance are the initial concentration of biologically important elements and their utilization prior to their introduction into coastal waters. One point is certain: the water mass characteristics of most of the Bight are strongly dominated by the open ocean.

Influence of Oceanic Water. The outermost oceanic boundary of continental waters is a ribbon of warm,



Source: Ryther and Yentsch 1958

Note: Five stations per depth for each of six cruises

Figure 11. Mean daily primary production beneath 1 m^2 of sea surface

high-velocity water called the Gulf Stream. Although seemingly independent and isolated from immediate continental waters, this ocean current accounts for most of the influx of ocean waters into the continental region. To describe this interaction a little theory behind Gulf Stream flow is appropriate. Rossby (1936) likened the Gulf Stream to a jet driving into a rotating, statified water medium. His theory predicted that the water from the surrounding medium was drawn in from the right of the jet. Some water is transported laterally and discharged to the left of the jet, forming a weak countercurrent representing coastal waters (Redfield 1936). The model suggests that in the ocean water is transferred to the continental shelf from the deep ocean along lines of equal density.

Verification of the model and theory is demonstrated by the water mass structure of the Gulf Stream and adjacent waters. Figure 13 shows that at depth the water mass characteristics are altered in crossing the Gulf Stream. Figure 14 shows that biochemical properties such as nitrate exhibit similar depth transitions. The influx of high-density, nutrient-rich water into surface waters is associated with increased concentration of phytoplankton chlorophyll (Figure 15). This feature of steady-state, high productivity (Yentsch et al 1974) is brought about by a regular influx of high-density, nutrient-rich water entering continental waters in the pattern indicated by density distribution (Figure 13).

This nutrient enrichment process is similar to upwelling but is not strictly dependent upon wind direction. In either case, productivity is augmented when deep, nutrient-rich waters enter *euphotic surface waters* (penetrable by light for plant growth). The transfer of ocean and coastal waters is also influenced by wind-driven surface currents and Gulf Stream eddies. No clear means of assessing the relative importance of these mechanisms exists.

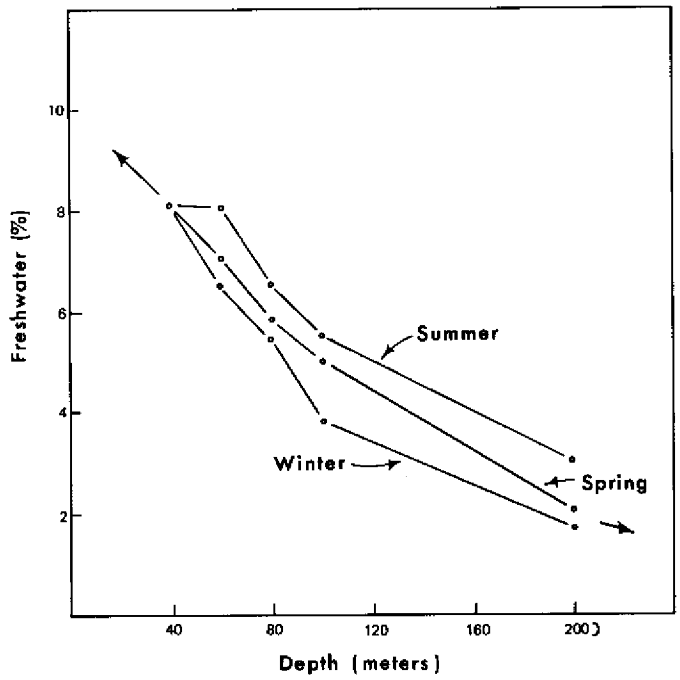
Secondary Production

Phytoplankton is consumed by zooplankton. This represents the first step (*trophic level*) in the transfer of energy through the main food web. Some studies have shown a high correlation between amounts of primary production and animal stocks, such as pelagic fishes. In general, ocean areas with high levels of primary production are expected to be abundant in zooplankton and plankton-feeding animals. However, this is difficult to prove. The interaction between a variety of feeding types in the food web is complex and poorly understood. Much of the complexity is attributed to problems in stock assessment, as is the case with zooplankton. To estimate the level of herbivore production I have to rely on the measurement of the quantity of animals taken by a plankton net tow. This type of audit attempts to answer the following questions.

1. Where in Bight continental waters are zooplankton most abundant?
2. Is there a seasonal cycle of abundance?
3. Are changes in zooplankton abundance in time and space related to phytoplankton distribution?
4. What is the level of zooplankton production?

Regardless of season, the largest numbers of zooplankton are taken on the continental shelf rather than from slope and offshore waters. The biomass of populations on the shelf averages three to four times larger than those in slope waters (Grice and Hart 1962). Zooplankton distribution across the shelf is by no means even; great variability exists over short distances. Largest concentrations of zooplankton occur near shore and at the shelf edge. Seasonally, the greatest abundance is in summer. Zooplankton stocks are poor during winter when water temperatures are coldest. Seasonal variation, that is, magnitude between extremes, is more pronounced in shelf waters than in slope or offshore waters.

Not all animals taken in plankton tows are herbivores, which is one problem with net sampling. The size of carnivores, omnivores, as well as herbivores, overlaps. There is no simple means for separ-



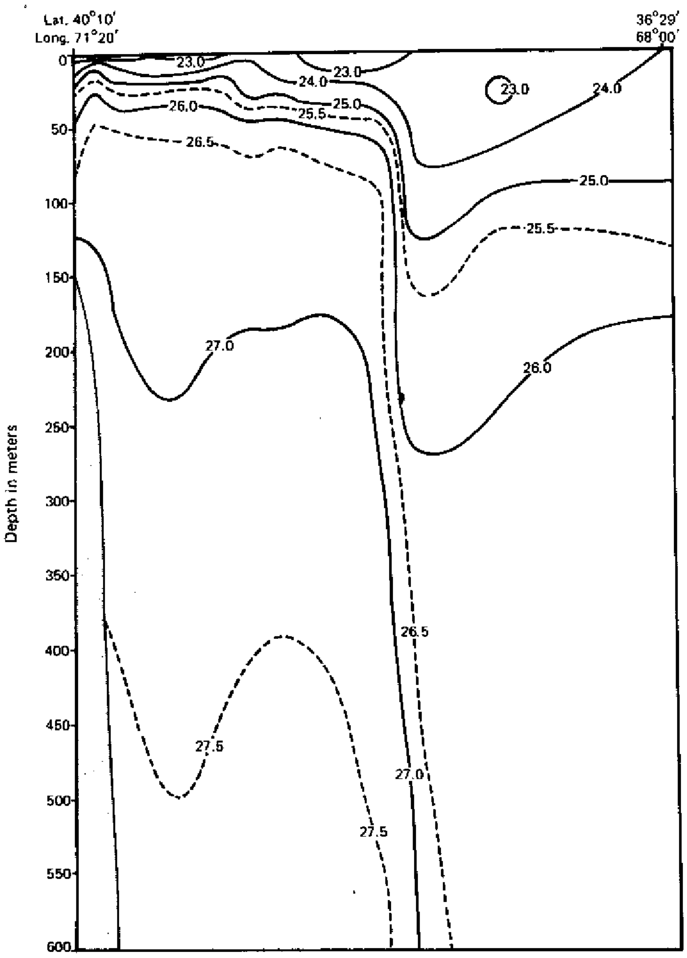
Source: From Ketchum and Keen 1956

Figure 12. Percent fresh water across continental shelf

ating these groups with nets. If, however, we are willing to assign a herbivorous role to copepods, then the problem is not as bad. Copepods are the single largest contributor to the plankton biomass and hence dominate a zooplankton population (Malone, in press). A comparison of the seasonal cycle of grazers with primary production shows a distinctly different seasonal trend. The animals are abundant when conditions for phytoplankton growth are poor.

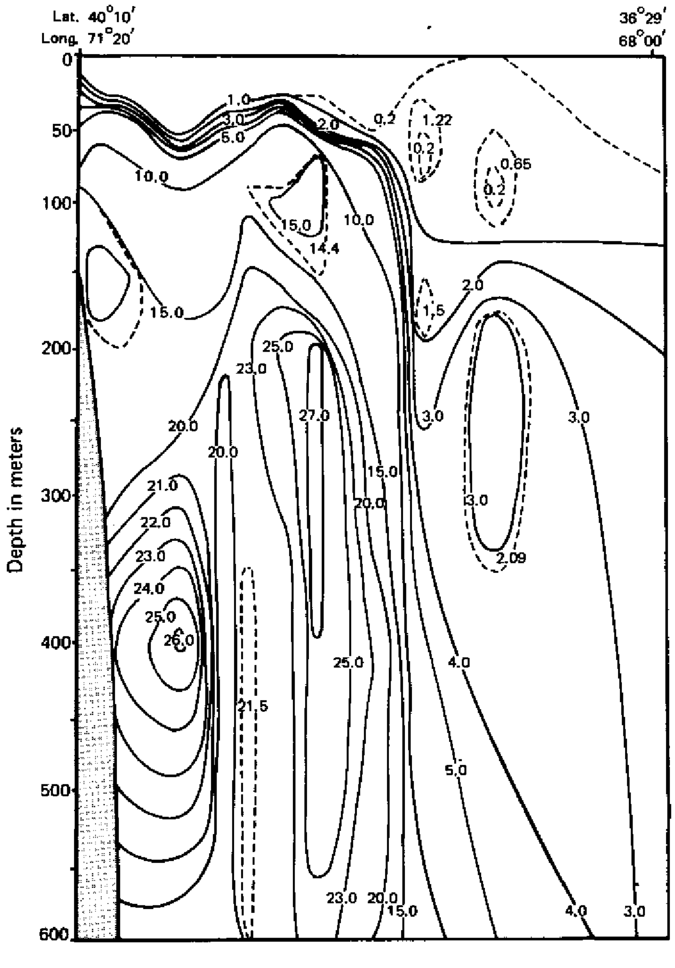
The obvious suggestion is that during summer the large stock of grazers is cropping the phytoplankton. The degree of cropping is determined not only by the numbers of herbivores present but also by their feeding rate. Assuming a high feeding rate and a low phytoplankton growth rate, during summer the size of the phytoplankton population may at times be largely controlled by zooplankton grazing.

According to our present knowledge of the transfer of food energy through the marine web, only a small amount of energy at each trophic level is passed on to the next level. Of the total food energy consumed at any trophic level, most is used to satisfy the needs (for example, respiration) of the animals. Most scientists in this field of research argue that the energy passed on amounts to about 10%; others argue that it is higher. Most calculations using field data are so full of generalizations that the range in percent of transfer is of little significance (Curl 1962). For example, the average annual production in waters of New York is about 175 g/m^2 (5 oz/yd^2) or about 350 g (12 oz) of dry algae*. Of this production, 10% will yield 35 g (1 oz) of dry zooplankton. We can test the validity of this number by estimating the amount of zooplankton carbon from plankton tows. The annual production of zooplankton is about 0.5 g/m^3 (0.02 oz/yd^3). If we assume that this population is evenly distributed over 50 m (64 ft) of the water column, the total yield is 25 g/m^2 (0.7 oz/yd^2). The difference between the predicted value (using 10%) and that estimated from plankton net hauls (35 vs. 25) is not significant.



Source: From Yentsch 1974

Figure 13. Density distribution across Gulf Stream off New England



Source: From Yentsch 1974

Figure 14. Nitrate distribution across Gulf Stream off New England

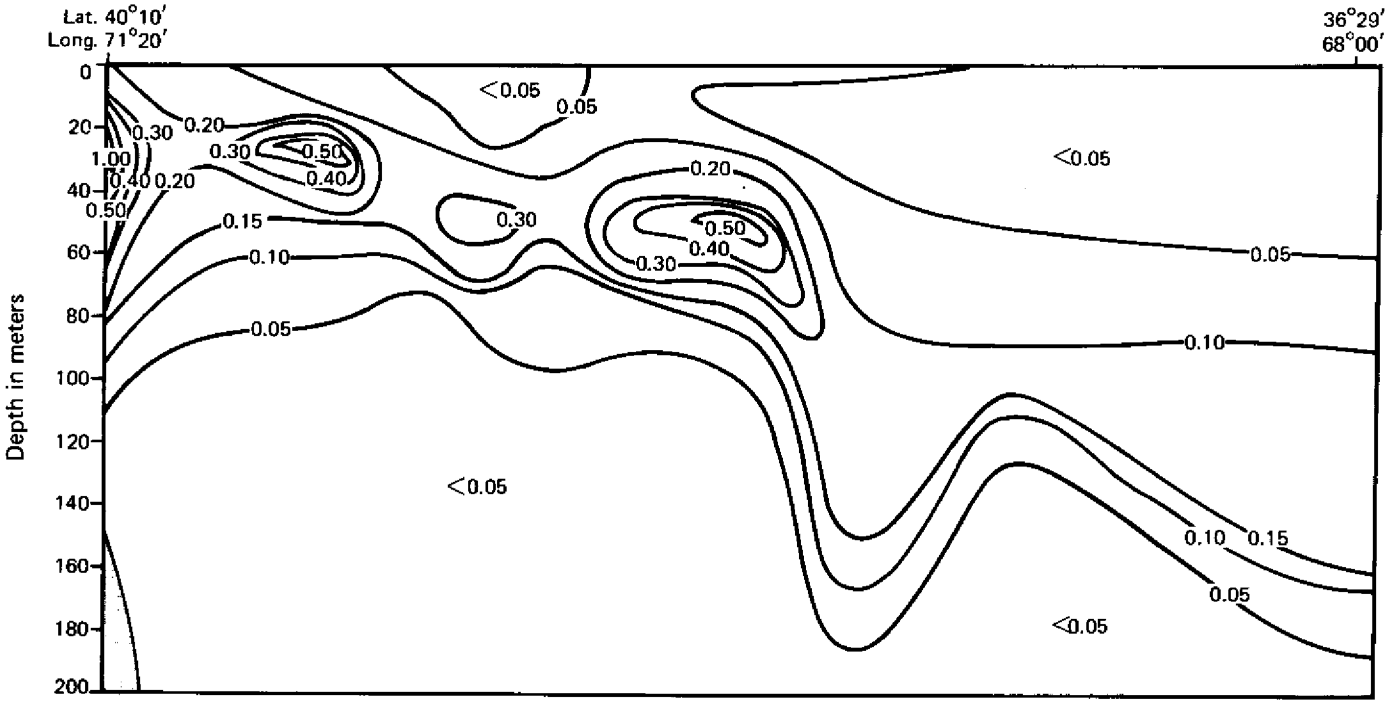
*Carbon content is one-half the dry weight.

Many commercially valuable fish feed directly on the secondary producers—this roughly is the amount of food available to them. In New York Bight, primary production annually amounts to about 175,000 metric tons (386 million lb) of phytoplankton, which yields about 15,000 to 17,000 metric tons (33 to 37.5 million lb) of zooplankton. This means plankton-feeding fishes consume about 2,000 metric tons (4.4 million lb) of plankton per year. The calculation assumes that all phytoplankton are consumed by plankton feeders in the water column; yet we know that some primary as well as secondary production must get to bottom-dwelling animal communities (benthos). Thus the 2,000 metric tons are more applicable to plankton filter-feeders as a whole and not just to fishes.

Environmental Impacts on Primary Production

Hopefully the above discussion has provided a general understanding of "how things work," but no workable scheme is developed for making thoughtful environmental policies. We know New York Bight will be used for man's benefit. We know from other experiences that the ecosystem will be changed. Is the trade-off worth it? This is a difficult question. Any answer must consider 1) how sensitive the system is to the impact, and 2) the consequences.

Primary production can be thought of as a sequence in the transformation of sunlight energy into particulate matter (phytoplankton). The events that design the chemical characteristics of the particulate matter result from mineral elements and pollutants in seawater becoming packed (concentrated) into the small volume of the phytoplankton cell. The cell becomes more dense than the surrounding seawater and the phytoplankton sink slowly through the water column. While sinking, some phytoplankton are cropped by zooplankton for transfer into the pelagic ecosystem; others come to rest on the ocean bottom, providing food for benthos. Any change in the levels or type of primary production will almost immediately affect the entire marine ecosystem of a shallow area such as the Bight. Much of man's polluting activities can directly and quickly "charge" the marine ecosystem through primary production, thus 1) producing more or less phytoplankton algae, 2) changing the type of algae produced, or 3) transferring the pollutant to secondary levels.



Source: From Yentsch 1974

Figure 15. Chlorophyll distribution across Gulf Stream off New England

Would it be beneficial for primary production to be increased? Is primary production in the Bight satisfactory? Could not the yield of fishes be increased with higher production? The answers to these questions depend on the reliability of our estimates of primary production and our knowledge of the environmental physiology of phytoplankton. Without delving into the broad implications for the food web, let's explore the direct interactions between pollutants and phytoplankton.

The most common spoilers of phytoplankton are excessive sewage and industrial waste, which begin by actually enriching rivers, estuaries, and coastal waters but in excess create *eutrophication* (literally "healthy nourishment" but in fact overnourishment). The nutrient phosphates and nitrates cause an algal bloom at first; this restricts light to deeper layers of the water column. As the bloom grows, the euphotic zone becomes very shallow. Below it are large quantities of either dead and decaying or respiring, but not photosynthesizing, algae. More and more oxygen is consumed, more and more carbon dioxide is produced. Eventually, less oxygen is produced in the euphotic zone than is used below. The lower parts of the water column become *anaerobic* (totally stripped of oxygen), and in searching for oxygen bacteria start to break down sulphate and release hydrogen sulphide gas. This ultimately destroys all remaining algae and other organisms.

But the sequence does not always go that far. Prior to the terminal condition, the species composition of the phytoplankton population may change as eutrophication progresses. Initial enrichment may favor a few species, and this may be considered temporarily beneficial, since an increase in total primary production means more food for herbivores (Cronin 1967). In heavy eutrophication one or more species of nonbeneficial, or even harmful, plant may become dominant. This is well illustrated by what happened in Long Island Sound about 20 years ago, the result of conflict of interest between duck raisers and the oyster and clam industry (Ryther 1954). As increasing quantities of excreta from domestic ducks (heavily fed for fattening) in the creeks and shallow waters of Great South Bay washed into the Sound, eutrophication brought on a rich bloom of the algae *Nannochloris*. Unfortunately, oysters and clams can not eat this species. As the bloom continued, the bottom water was depleted of oxygen, and the lack of food and oxygen almost entirely destroyed the mollusk population. Although the problem was arrested by improving the flushing of the area, the only long-term solution is strict control of the levels of nitrogen-rich sewage dumped into the sea (Baalsrud 1967).

Even more potentially dangerous is the widespread dispersal of chemical fertilizers and insecticides (Luce 1974). How farm spraying has spread DDT all over the world, through the atmosphere and through rain, into the oceans and even Antarctic ice, is now well known. The solubility of DDT in water is very low—only 1.2 parts per thousand million—and so we might expect that phytoplankton could hardly absorb enough to harm their metabolic processes. Yet the DDT is much more soluble in fatty tissues than in water, and so there is some possibility that it could become concentrated in algal cells. One approach has been to expose phytoplankton to fairly high DDT concentrations under laboratory conditions. Phytoplankton grown in seawater containing 10 parts per billion of DDT exhibit a drop over 20% in the rate of photosynthesis. However, other experiments indicate that perhaps species type and physiological condition play a role in controlling the sensitivity of phytoplankton (Menzel, Anderson, and Randtke 1970). We hope that the quantity of DDT in coastal waters will never reach high levels, but we cannot be too complacent about prolonged exposure even to low concentrations of various chemical insecticides.

Oil spills, a third type of pollution, affect shellfish, birds, seaweed, and even tourism (Smith 1968). Specifically, oil seems to do greater harm to herbivorous animals than to phytoplankton; one side effect of a spill can actually be to the advantage of the plants—they may flourish in an oil-damaged sea where there are suddenly fewer animals to eat them. Scientific reports on oil effects are confused, partly due to the type of oil (Smith 1968). Tankers carry many kinds of refined and unrefined oils, and oil itself contains a number of aromatic carbon compounds of varying solubility, volatility, and toxicity. The chemicals that would most damage phytoplankton are those that dissolve most readily in water but are relatively nonvolatile. Laboratory experiments indicate that saltwater concentrations of 2 to 100 parts per million of such substances would significantly reduce the growth rate of phytoplankton. Though concentrations of such magnitude can occur only in relatively small patches as a result of oil spillage, they can occur. Toxins absorbed by phytoplankton at levels that do not significantly inhibit algal growth are likely to be ingested by herbivorous zooplankton and shellfish—and some soluble aromatic carbon compounds are *carcinogenic* (cancer-producing). Thus, even very low concentrations in the phytoplankton can result in an accumulation of carcinogenic substances in herbivores and on up the food chain (Luce 1974).

As previously mentioned, pollutants may affect the selection of the type of algae produced by primary production. Sometimes this is disastrous, as, for example, when toxic species such as "red tide" dinoflagellates are favored. These organisms carry an intercellular toxin that can paralyze humans who have eaten shellfish that have grazed on such dinoflagellates. I do not wish to imply that some forms of pollutants *per se* cause red tide. At the moment we know little of the causes. We do know, however, that sewage dumping and dredging can aggrevate the problem (Hanson and Gilfillan 1975).

Occasionally the pollutant entering the ecosystem via primary production may merely be transferred to secondary levels, concentrating it with succeeding moves through the food chain. Mercury, for instance, is concentrated in many terminal elements of the marine food web, namely swordfish and tuna.

With these potential threats to the primary producers, what of prevention? In the environmental movement the single most important and compelling piece of legislation is the impact statement, which documents the extent and duration of activities posing a threat. As important as this statement is, environmentalists are concerned because the intended goals are seldom met and the information necessary for sensible judgment is not at hand. Equally disturbing is the fact that the intended user of the environment, whether government agency or private interest, is eager to satisfy the environmental concerns and get on with proposed developments. Environmental scientists have not yet clearly established methods for testing specific situations, or not enough information is available on particular organisms' processes and interactions. Long lists of existing animals and plants in a specific area alone are not useful to people concerned with environmental design or regulation.

What appears to be emerging is an emphasis on the rate of energy change within the ecosystem, referred to as an analysis of biochemical pathways. This approach modifies conventional baseline studies by changing procedure from observational to experimental.

The primary producer is a prime site for such tests. Independent of environmental problems, biochemical tests (radioactive tracers and enzyme concentrations) to assess certain process rates, namely photosynthesis and respiration, can be applied as a seasonal study under natural conditions so that annual variability can be established. The test results can be used as bioassays for a particular pollutant or as monitors or early indicators of environmental stress.

Much of New York Bight is heavily impacted by man's activities; the level of primary production is approaching the maximum yield in numerous areas. In the coming years it will take the combined efforts of scientists, engineers, and legislators, armed with the best baseline data to accurately assess how the Bight will fare under further exploitation.

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