NOAA Technical Report NMFS Circular 410

The 1976 *Ceratium tripos* Bloom in the New York Bight: Causes and Consequences

Thomas C. Malone

May 1978

WORKSHOP PARTICIPANTS

Mark Brown, Lewis-Calden Conservation & Ecology Center, 31 Whippoorwill Rd., Armonk, NY 10504

Mira Chervin, Department of Biology, City College of CUNY, New York, NY 10031

Myra Cohn, NOAA Sandy Hook Laboratory, Highlands, NJ 07732

Michael Dagg, Oceanographic Sciences, Brookhaven National Laboratory, Upton, NY 11973

Wayne Esaias, Marine Sciences Research Center, State University of New York, Stony Brook, NY 11784

Paul Falkowski, Oceanographic Sciences, Brookhaven National Laboratory, Upton, NY 11973

Chris Garside, Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, MA 04575

Steven Howe, Oceanographic Sciences, Brookhaven National Laboratory, Upton, NY 11973

John Mahoney, NOAA Sandy Hook Laboratory, Highlands, NJ 07732

Thomas Malone, Marine Biology, Lamont-Doherty Geological Observatory, Palisades, NY 10964

Garry Mayer, MESA New York Bight Project, Old Biology Building, SUNY Stony Brook, NY 11794

Joel O'Connor, MESA New York Bight Project, Old Biology Building, SUNY Stony Brook, NY 11794

Paul Olsen, New Jersey Department of Environmental Protection, Division of Water Resources, Trenton, NJ 08625

Jay O'Reilly, NOAA Sandy Hook Laboratory, Highlands, NJ 07732

Daniel Smith, NOAA MARMAP Field Group, Narragansett Laboratory, Narragansett, RI 02882

Frank Takacs, New Jersey Department of Environmental Protection, Division of Water Resources, Trenton, NJ 08625

James Thomas, NOAA Sandy Hook Laboratory, Highlands, NJ 07732

Sylvia Weaver, Biology Department, New York University, New York, NY 10023

Paul White, New Jersey Department of Environmental Protection, Division of Water Resources, Trenton, NJ 08625

CONTENTS

Figures

Table

iv

The 1976 *Ceratium tripos* Bloom in the New York Bight: Causes and Consequences[1]

THOMAS C. MALONE[2]

ABSTRACT

An extensive bloom of the dinoflagellate *Ceratium tripos* occurred throughout the New York Bight between January and July 1976. Population size peaked during April-June and declined rapidly during July. A floc consisting primarily of decaying *C. tripos* cells was observed to cover the bottom during July between Sandy Hook and Atlantic City between 5 and 50 km offshore. The distribution of the floc roughly coincided both temporally and spatially with the development of a subthermocline oxygen minimum layer and extensive fish kills.

Prior to the onset of thermal stratification (January-March), the *C. tripos* population was uniformly distributed throughout the water column and was growing photosynthetically. As the water column began to stratify in April, the population aggregated in a layer 1-3 m thick near the base of the thermocline between the 0.1 and 10% light depths. If photosynthetic growth was occurring during May-June, it was at a very low rate (about 0.02 g C/m^2 d^{-1} at the 1% light level). The possibility of no growth or heterotrophic growth cannot be dismissed, especially in the apex of the New York Bight and along the New Jersey coast.

The *C. tripos* bloom resulted in a gradual accumulation of a large quantity of particulate organic matter which did not enter pelagic food chains. Respiration of this biomass and its decay below the thermocline were probably major factors in the development of oxygen-poor bottom waters in June and July. Localization of the oxygen minimum layer off the New Jersey coast probably reflects the bottom topography of the New York Bight and the distribution of the *C. tripos* biomass within the Bight.

The occurrence of *C. tripos* blooms per se is not unusual. The bloom was unique only in terms of the size of the population produced, its areal extent, and its duration. Because high densities of *C. tripos* developed throughout the New York Bight during January-March with maximum densities between midshelf and the shelf break, it is unlikely that the bloom occurred in response to local nutrient enrichment (related to the disposal of domestic and industrial wastes) during the period of the bloom. However, causes of the bloom and its collapse cannot be determined, based on existing information.

INTRODUCTION

An extensive bloom of the dinoflagellate *Ceratium tripos* (O. F. Muller) Nitzsch developed throughout the Middle Atlantic Bight (between lat. 36°N and lat. 41°N, and the continental shelf break) from January through July 1976. By late June-early July, an oxygen minimum layer (<2.0 ppm) had developed below the thermocline between the 20- and 40-m isobaths off the New Jersey coast from Atlantic City to Sandy Hook.[3] Local anoxic conditions were most widespread east of Barnegat Inlet (lat. 39°45′N) in early July and east of Great Bay (lat. 39°30′N) by late July. Presence of this subthermocline oxygen minimum layer and associated sulfide production apparently resulted in mass mortalities of demersal fishes and benthic invertebrates.[4]

The occurrence of the *C. tripos* bloom and the subsequent development of the oxygen minimum layer has led to the hypothesis that *C. tripos* was involved in generating the BOD (biochemical oxygen demand) required to produce the oxygen minimum. In an effort to clarify the role of *C. tripos*, this workshop addressed the following questions: 1) What was the areal extent of the bloom and the time course of its development? 2) What are the most likely causes of the bloom and its collapse? 3) What were the effects of the bloom on the distributions of organic matter and dissolved oxygen? The session was concluded with recommendations for future monitoring and research strategies.

For purposes of this discussion, the New York Bight (Fig. 1) was divided into 5 regions: 1) Long Island and 2) New Jersey coastal areas (<20 m deep within 5 km of

[3]National Marine Fisheries Service. 1976. Red Flag Report: Mortalities of fish and shellfish associated with anoxic bottom water in the Middle Atlantic Bight. Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service, NOAA, Sandy Hook, N.J. Unpubl. manuscr.

[4]Interagency Committee Investigating the 1976 New York Bight Oxygen Depletion Phenomenon. 1976. Results of the Benthic Workshop. Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service, NOAA, Sandy Hook, N.J. Unpubl. manuscr.
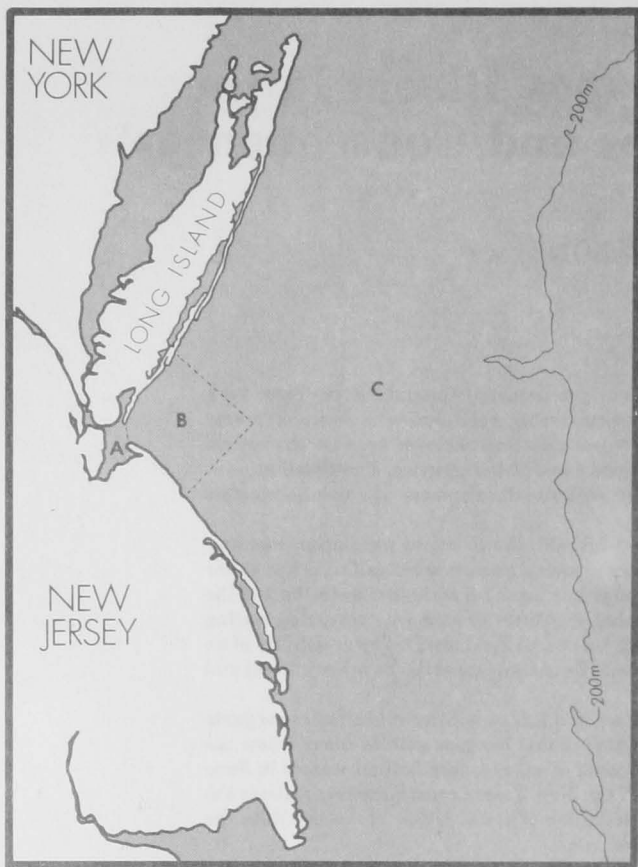
Figure 1.—The New York Bight: A) lower Hudson and Raritan River Estuaries, B) apex of the New York Bight, and C) outer New York Bight. Station locations are shown in Figures 7, 11, and 12.

the coastline), 3) lower Hudson Estuary (including the Upper and Lower Bays of New York Harbor), 4) the apex (bounded by lat. 40°10′N and long. 73°30′W), and 5) the outer New York Bight (south and east of the apex to the shelf break between Cape May and Montauk Point).

BACKGROUND: PHYTOPLANKTON ECOLOGY IN THE NEW YORK BIGHT

Water Column Stratification and Dissolved Oxygen

Seasonal variation in water column stratification and dissolved oxygen in bottom water parallel each other off the New Jersey coast. During winter months, the water column is well mixed and dissolved oxygen concentrations are near saturation (6-8 ml liter^{-1}). As the water column begins to stratify in April, dissolved oxygen concentration in the subpycnocline layer begins to decline so that by July-August concentrations are usually 10 to 40% of saturation (2-4 ml liter^{-1}). Local anoxic conditions occasionally develop during the summer below the thermocline near the sludge dump site in the apex (Fig. 1).[5] Dur-

ing the summer of 1976, the oxygen minimum layer was more widespread, had existed over a longer period of time, and was characterized by lower oxygen concentrations.

Phytoplankton Productivity

Major studies of phytoplankton productivity include those of Ryther and Yentsch (1958) in the outer Bight, Mandelli et al. (1970) along the Long Island coast, and Malone (1976a, b; 1977; in press) in the lower Hudson Estuary and apex of the New York Bight. The following synthesis is based on these studies.

Annual phytoplankton productivity decreases with increasing depth and distance from the mouth of the Hudson-Raritan estuarine complex (Fig. 1). Phytoplankton productivity in the apex is about 430 g C/m^2 yr^{-1}, or 70 to 80% of the annual input of particulate organic carbon (POC) to the apex. The remainder is related to sewage wastes generated in the New York-New Jersey metropolitan region transported into the apex by estuarine runoff and ocean dumping (Garside and Malone in press). Phytoplankton productivity in the outer Bight decreases from 160 to 100 g C/m^2 yr^{-1} as water column depth increases from less than 50 m near the Long Island and New Jersey coasts to 1,000 m over the continental slope.

Ryther and Dunstan (1971) presented evidence that organically rich water from the apex extends eastward for less than 80 km and south along the New Jersey coast for at least 240 km. Based on the distribution of dissolved inorganic nitrogen and phosphorus during September 1969 and on biomass experiments with *Skeletonema costatum*, they concluded that phytoplankton growth is nitrogen-limited in the Bight.

Phytoplankton productivity in the apex fluctuates between 0.1 and 6.6 g C/m^2 d^{-1} (mean = 1.17) compared with 0.1 to 1.1 (mean 0.35) in the outer Bight. Seasonal variations in the outer Bight are characterized by a single bloom period which appears to decrease in length and increase in amplitude as depth increases. Inshore (<50 m in the outer Bight), productivity ranges between 0.5 and 1.0 g C/m^2 d^{-1} from December through April and is less than 0.5 for the remainder of the year. Offshore (>100 m), productivity exceeds 0.5 g C/m^2 d^{-1} only during March and April. In contrast, seasonal variations in the apex are characterized by two bloom periods which coincide with periods of minimum surface temperature change in February-March (2°-8°C) and June-July (19°-23°C). Chain forming diatoms (net plankton retained on a 20-μm mesh screen) with mean euphotic zone generation times of 1 to 3 days dominate phytoplankton blooms in February-March. During these months, the water column (20-30 m deep) is well mixed, the euphotic zone extends to the bottom, and phytoplankton populations are nearly uniformly distributed in the water column. Phytoplankton productivity is generally higher during the June-July bloom period when small (nanoplankton with mean spherical diameters less than 10 μm) green algae growing at mean euphotic zone generation times of

0.5 to 1.5 days dominate phytoplankton blooms. During this period, the water column is well stratified with the thermocline located between 5 and 15 m (5-20 m from the bottom); the euphotic zone is 5 to 15 m deep; and phytoplankton populations are concentrated near the surface with maximum densities along the New Jersey coast within 20 km of the mouth of the estuary.

These variations in phytoplankton productivity reflect the seasonal cycle of incident radiation and temperature, limits imposed by water column depth on vertical mixing and rates of nutrient recycling, fluxes of "new" nutrients into the euphotic zone from subpycnocline layers and adjacent waters, and grazing. High productivity and the occurrence of two major bloom periods in the apex reflect 1) the continuous input of nutrient-rich estuarine water (Hudson River), 2) effects of thermal stratification on the distribution of estuarine water, and 3) seasonal variations in grazing pressure. Winter diatom blooms develop because grazing pressure is low. It appears that very little of the diatom crops produced is grazed and that most of this biomass sinks to the bottom where it may serve as an organic substrate for seabed oxygen consumption during the spring and summer. Thus, winter diatom blooms in the apex may be a factor in the development of oxygen minimum layers during the summer.

Phytoplankton blooms during the spring and summer do not appear to have a similar fate. These blooms are concentrated in the surface layer (upper 10 m) where they are rapidly grazed and dispersed throughout the Bight because of the low sinking rates characteristic of the bloom species as well as high grazing rates.

In the outer Bight, vertical mixing, upwelling, and the breaking of internal waves are the most important processes involved in euphotic zone nutrient enrichment. Nutrient supplies are not continuous and thermal stratification limits rather than enhances the flux of nutrients into the euphotic zone. Consequently, phytoplankton productivity is low throughout the summer, and phytoplankton blooms are most frequent during March, April, and May.

Based on nutrient distributions and experimental observations, dissolved inorganic nitrogen (DIN) supply and phytoplankton uptake are closely coupled during late spring and summer in both the outer Bight and the apex. Euphotic zone DIN concentrations are typically less than 1.0 μm from May through August. In the apex, high nanoplankton productivity and low DIN concentrations are reflected in DIN turnover times of 0.5 to 2.0 days in the surface mixed layer.

Distribution of Phytoplankton Species

A review of species abundance and distribution of presented by Malone (in press). Phytoplankton cell densities are usually in the range of 10^6 to 10^9 cells liter^{-1} in estuarine and coastal waters compared with 10^4 to 10^7 liter^{-1} in the apex and 10^3 to 10^5 liter^{-1} in the outer Bight. Phytoplankton populations are typically dominated by diatoms (cold months) and chlorophytes (warm months)

in estuarine and apex water and by diatoms in the outer Bight.

The diatoms *Skeletonema costatum*, *Asterionella japonica*, *Leptocylindrus danicus*, *Thalassionema nitzschioides*, and *Chaetoceros debilis* are abundant in both estuarine and Bight waters. *Rhizosolenia atala*, *R. faeroense*, *Chaetoceros socialis*, and *Nitzschia closterium* usually make up a larger proportion of the diatoms present in the outer Bight than in the apex. The chlorophyte, *Nannochloris atomus*, frequently dominates estuarine and apex phytoplankton during the summer. The dinoflagellates *Prorocentrum micans*, *Peridinium* spp., and *Ceratium* spp. are often abundant during the spring, summer, and fall.

More specifically, Mandelli et al. (1970) described the species composition of the net plankton along the southern coast of Long Island. Phytoplankton biomass peaked during fall and late winter. Both of these peaks were produced by blooms of *S. costatum*. Diatoms dominated the September-March 1966 period, while dinoflagellates were most abundant during the April-August 1966 period. Among the diatoms, *S. costatum*, *Thalassiosira* sp., *Chaetoceros* sp., and *R. alata* were successively abundant from September through December. This succession appeared to be repeated during February and March. *Peridinium depressum* and *Ceratium massilence* bloomed in April and May, respectively. *Ceratium tripos* was the dominant net plankton from June to August. During March 1967 a succession of species was observed in which *S. costatum* dominated during the first week; *Thalassionema nitschioides*, *Rhizosolenia* sp., *A. japonica*, and *Nitzschia seriata* the second week; and *Ceratium tripos*, *C. macroceros*, *C. furca*, and *Peridinium depressum* the last 2 wk. This alternating pattern of diatom and dinoflagellate abundance appears characteristic of shallow coastal waters off western Long Island.

More recently, observations along the New Jersey coast (Myra Cohn, pers. commun.) indicated that *C. tripos* was abundant during the summers of 1974 and 1975. Cell densities ranged from 40 ml^{-1} to 740 ml^{-1} (geometric mean = 133 ml^{-1} in June 1975 and 222 ml^{-1} in July 1975). Increases in *C. tripos* cell densities are also typical of Fire Island Inlet on the Long Island coast (Sylvia Weaver, pers. commun.). From 1973 to 1975, peaks in cell density (as high as 5 ml^{-1}) occurred in May and June following slow increases beginning as early as January 1974.

Biology of *Ceratium tripos*

The following summary is based largely on an overview prepared by Theodore J. Smayda (University of Rhode Island) for the IDOE/NSF (International Decade of Ocean Exploration/National Science Foundation) sponsored workshop held in Washington, D.C., on 15 and 16 October 1976.

Ceratium tripos is an armored (cell wall comprised of cellulose plates) dinoflagellate. It is a holoplanktonic species commonly found along the east coast of the

United States north of Cape Hatteras to the Gulf of Maine. It is motile, capable of swimming at speeds of 40 to 100 cm h^{-1}. Because of its large size $(1-10 \times 10^5 \text{ m}^3)$, this swimming behavior is required for *C. tripos* to remain in suspension for extended periods in stratified water; cells which have lost their motility will sink at about 8 m d^{-1} (Laws 1975).

The organism is eurythermal and euryhaline on the basis of both distribution and experimental growth studies. *Ceratium tripos* is photosynthetic with light-dependent growth rates of 0.3 to 0.4 divisions d^{-1} (Nordli 1957). Like most other species of *Ceratium*, cell division usually occurs between midnight and sunrise.

Large, aphotic zone populations of *C. tripos* have been observed, but the extent to which this is a consequence of photosynthetic growth at subeuphotic zone light intensities, long dark survival times, or heterotrophic growth is unknown. Circumstantial evidence suggests that *C. tripos* may have the potential for heterotrophic growth on particulate organic matter (POM). Observations of particle ingestion by *Ceratium* sp. have been reported, and morphologically, *C. tripos* appears to be capable of phagotrophy.

DISTRIBUTION OF *CERATIUM TRIPOS*: JANUARY-SEPTEMBER 1976

Time-Course of the Bloom

Ceratium tripos was abundant in the apex at least as early as 7 February 1976, but showed little increase in population size during February (Fig. 2). Cell densities increased steadily from a geometric mean of 5.8 cells ml^{-1} to 29 cells ml^{-1} by the end of March. The growth rate of 0.06 doublings d^{-1} calculated from these changes hields a mean water column cell density of 240 ml^{-1} by late May, which is within the range of densities reported from the layer of maximum cell density in the apex at this time (Fig. 2).

A similar pattern was observed at Fire Island Inlet (Fig. 2) where cell density increased from less than 0.1 ml^{-1} in January to 22 ml^{-1} by the end of March, a rate of 0.05 d^{-1}. The population remained relatively stable through April and May and declined from a maximum of 50 ml^{-1} in May to less than 0.1 ml by the end of July. This pattern roughly paralleled variations at a station 8 km south of Fire Island Inlet where cell density peaked in May and June and declined rapidly thereafter to near zero in August (Fig. 3).

Mean cell densities along the New Jersey shore peaked near mid-June (Fig. 2). In the New York Harbor region, cell densities were highest in March (29-75 ml^{-1}), declined to 10 ml^{-1} by the end of May, and remained constant at 10 ml^{-1} through mid-July.

Cell densities in the outer Bight increased from 1-60 ml^{-1} (mean = 10 ml^{-1}) near the end of March to 10-400 ml^{-1} by mid-June (mean 240 ml^{-1}). Based on qualitative net phytoplankton samples collected from 10 m with a Hardy Continuous Plankton Recorder (225 × 234 μm mesh), *C. tripos* was present throughout the Bight in
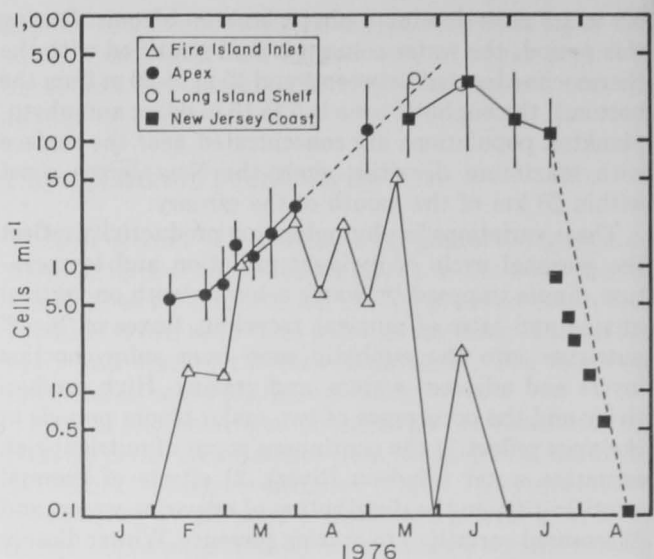
Figure 2.—Temporal variations in *Ceratium tripos* cell density in the New York Bight from January to August 1976. △ - Fire Island Inlet, data provided by Sylvia Weaver; ● - apex of the New York Bight, data provided by Thomas Malone, O - Long Island shelf inshore of the 75-m isobath, data provided by Paul Falkowski and Wayne Esaias; ■ - New Jersey coastal waters, data provided by Myra Cohn, Paul Hamer, Paul Olsen, and Frank Takaca.
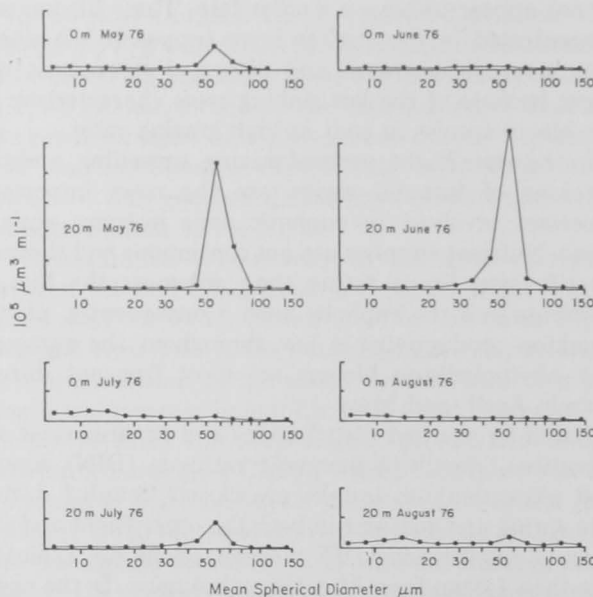
Figure 3.—Particle size frequency distributions (peak due to *Ceratium tripos*) from 8-km offshore of Fire Island (Long Island), data provided by Michael Dagg.

January and increased to a maximum in May (Fig. 4). The decrease from May to June was probably a consequence of an aggregation of cells below the thermocline, as discussed in the next section.

Vertical Distribution

Vertical profiles of temperature, chlorophyll a, and *C. tripos* cell density showed little stratification from

4
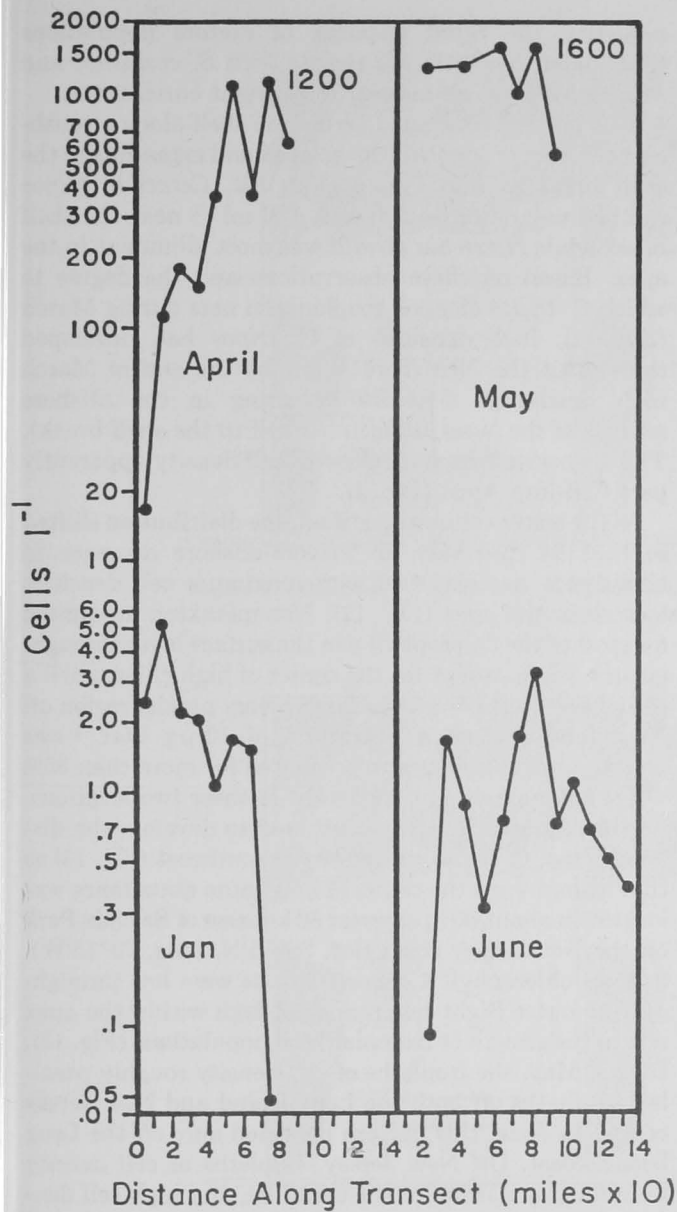
Figure 4.—Relative abundance of *Ceratium tripos* along a transect which bisects the New York Bight from the apex to the continental slope; samples were collected with a Hardy Continous Plankton Recorder towed at 10 m; data provided by Daniel Smith and Robert Marrero.

January through March when net plankton (phytoplankton retained on a 20-μm mesh screen) accounted for more than 80% of chlorophyll a in the water column. As the water column began to stratify in April, vertical distribution of chlorophyll and *C. tripos* began to exhibit patterns of stratification, which varied systematically across the shelf (Fig. 5). Based on continuous vertical profiles between 30 April and 5 May, seaward of the shelf break (stations 93 and 94), maximum chlorophyll a concentrations occurred in the upper 25 m and diatoms dominated the phytoplankton. Across the shelf break (stations 95-97) a broad maximum between 10 and 35 m was observed, which was dominated by diatoms near the
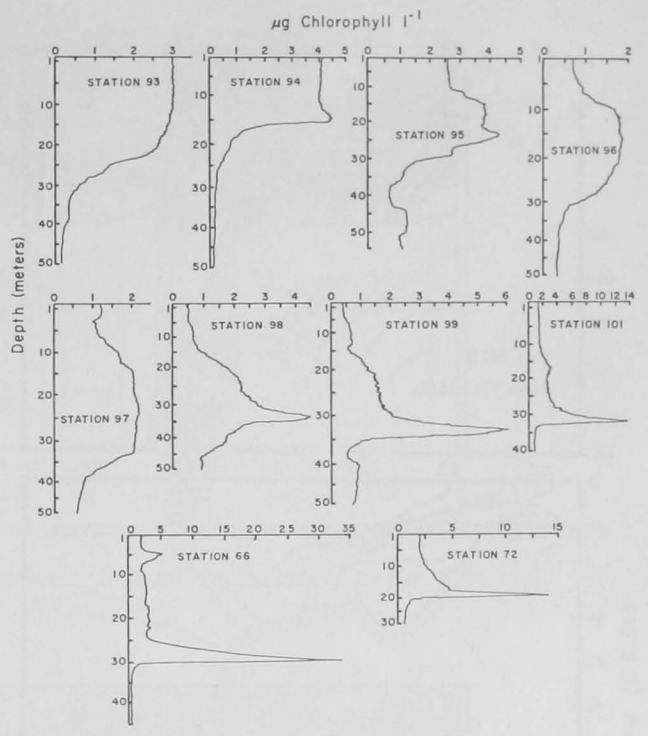
Figure 5.—Vertical profiles of chlorophyll concentration along a transect normal to the Long Island coast to the continental slope (stations 93 and 94 - continental slope; stations 95-97 - offshore of the 75-m isobath; stations 98-101, 66 and 72 - inshore of the 50-m isobath), data provided by Wayne Esaias.

surface and by *C. tripos* at depth. Further inshore (stations 98-101, 66, 72), a strong narrow band maximum developed as the diatom population dropped out. The layer consisted almost entirely of *C. tripos* (>90% of total cells) and was located between 0.3 and 3% light depths in association with the 10° and 13°C isotherms. The depth of the layer, which varied in thickness from 1 to 3 m, decreased gradually from 35 m at station 98 (75 km offshore) to 20 m at station 72 (10 km offshore). This trend apparently persisted as thermal stratification continued to develop so that by May and June (Fig. 6) most of the *C. tripos* population was concentrated in a thin layer immediately below the thermocline, in association with the 10°C isotherm and between the 0.1 and 10% light depths. Because of nanoplankton blooms in the upper 10 m and high concentrations of detritus, the *C. tripos* maximum was below the 1% light depth in the apex and south along the New Jersey coast within 20 km of the shoreline to about Barnegat Inlet (lat. 39°45′N).

Horizontal Distribution in the Layer of Maximum Chlorophyll

Interpretation of areal distributions of *C. tripos* cell density in terms of population size must be made in the context of temporal variations in the vertical distribution of cells. The population was nearly uniformly distributed with depth in the upper 30 to 40 m during January-March when the water column was well mixed

5

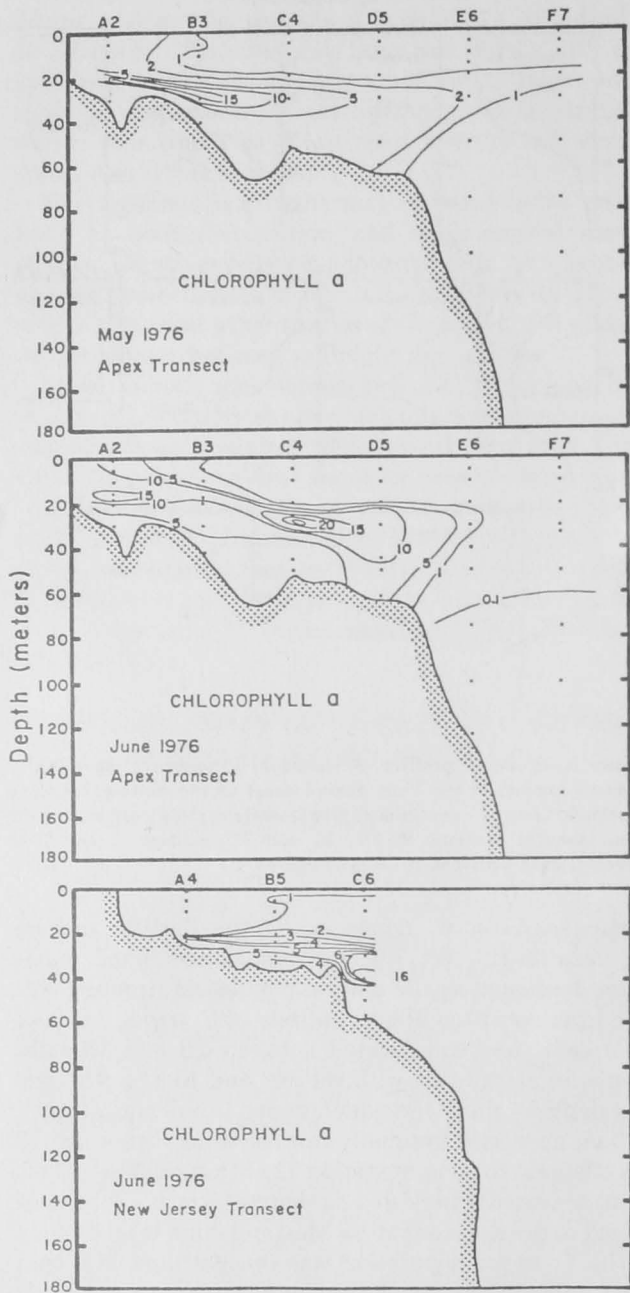Figure 6.—Distribution of chlorophyll a (μg liter^{-1}) across the shelf along transects originating in the apex and off the New Jersey coast (Seaside Park) and extending southeast; data provided by Wayne Esaias.

and was aggregated near the base of the thermocline during April-June when the water column was thermally stratified.

Within the apex in February and March, population size increased with distance from the mouth of the estuary, especially along the New Jersey coast (Fig. 7). This pattern was closely related to the flow of estuarine water (Fig. 8) so that cell densities were lowest when the proportion of estuarine water was greatest. Conversely, maximum chlorophyll a concentrations (Fig. 9) paralleled the distribution of low salinity estuarine water,

reflecting the rapid response of diatom populations (dominated by *Nitzschia seriata* with *S. costatum* and *Rhizosolenia* sp. abundant) to nutrient enrichment.

This pattern continued across the shelf along a southeast transect originating in the apex and extending to the shelf break in late March (Fig. 10). *Ceratium tripos* reached maximum cell density (60 ml^{-1}) near the shelf break while *Nitzschia seriata* was most abundant in the apex. Based on these observations and the degree to which *C. tripos* clogged zooplankton nets during March (Fig. 11), high densities of *C. tripos* had developed throughout the New York Bight by the end of March with maximum densities occurring in the offshore reaches of the outer Bight (midshelf to the shelf break). This inshore-offshore increase in cell density apparently persisted into April (Fig. 4).

As the water column stratified, the distribution shifted so that by mid-May an inshore-offshore decrease in abundance was observed with maximum cell densities located in the apex (Fig. 12). Nanoplankton accounted for most of the chlorophyll a in the surface layer throughout the Bight except for the center of high chlorophyll a (6 μg liter^{-1}) off Long Island and a very patchy region off New Jersey where a maximum of 10 μg liter^{-1} was reported. *Ceratium tripos* accounted for more than 85% of the chlorophyll a at all depths at these two locations. As thermal stratification continued to develop, the distribution of *C. tripos* shifted to the southeast (Fig. 13) so that by mid-June the center of maximum abundance was located in about 60 m of water 80 km east of Seaside Park on the New Jersey coast (lat. 39°55'N, long. 73°15'W). Surface chlorophyll a concentrations were low throughout the outer Bight but remained high within the apex due to the growth of nanoplankton populations (Fig. 13). During May, the isopleths of cell density roughly paralleled isobaths off both the Long Island and New Jersey coasts. In June, this pattern persisted only off the Long Island coast. Off New Jersey, isopleths of cell density were roughly normal to the coastline, and high cell densities intruded closer to the coastline. As a consequence, high cell densities were distributed over a larger area of the New Jersey shelf in relatively shallow water (20-40 m). Comparable cell densities over the Long Island shelf were in waters 40 to 60 m deep.

Conclusions

While the data were not collected synoptically in time or space, coastal observations correlated well with those in the apex and outer Bight (Figs. 2, 4, 12, 13). Temporal variations in *C. tripos* cell density at Fire Island Inlet reflected the early stages of the bloom prior to stratification, and mean cell densities along the New Jersey shore appeared to reflect at least the latter stages of the bloom during the period of thermal stratification.

The *C. tripos* bloom apparently began throughout the New York Bight in January with maximum cell densities developing in the midshelf to shelf break region in late March prior to the onset of thermal stratification. During this period (January-March), vertical distribu-
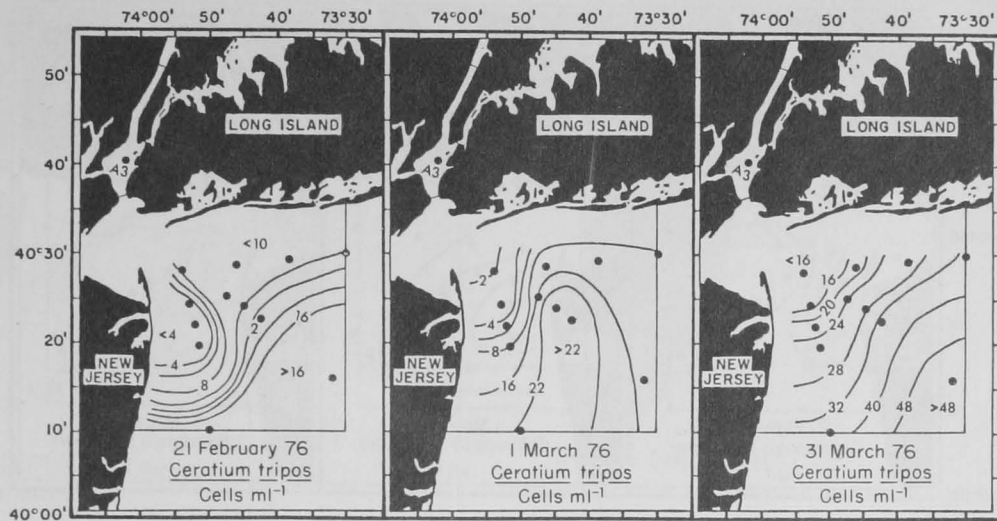
Figure 7.—Distribution of maximum *Ceratium tripos* cell density (cells ml^{-1}) in the apex of the New York Bight; data provided by Thomas Malone.
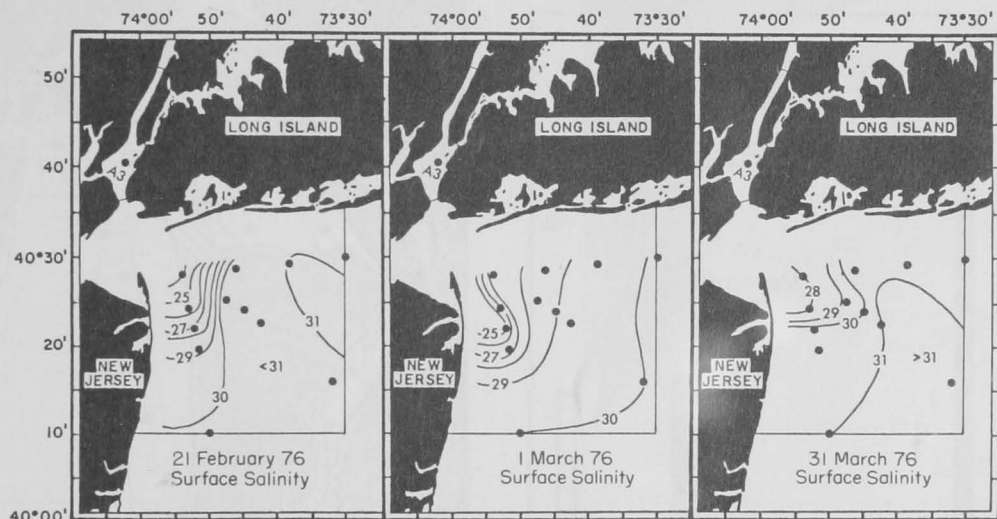

Figure 8.—Distribution of surface salinity (ppt) in the apex of the New York Bight, data provided by Thomas Malone.

tions of cells were relatively uniform, the bulk of the population was in the euphotic zone, and population size was increasing at a relatively constant rate of 0.05 to 0.06 doublings day^{-1}. The temporal and spatial distributions of cells indicate that the population was increasing most rapidly in the outer Bight during March or that the outer Bight received a larger initial inoculum of cells than the inner Bight. The large area over which the bloom occurred indicates that it did not develop in response to local nutrient enrichment of the coastal zone during the actual period of the bloom. This is supported by the observation that *C. tripos* cell densities were lowest in the apex where local nutrient enrichment is greatest. *The causes of the bloom, whether they were related to increased growth or decreased mortality rates, must have involved processes operative on spatial scales on the order of the continental shelf and time scales on the order of months to years.*

As the water column began to stratify, the *C. tripos* population aggregated in a narrow band at the base of the thermocline, and by mid-June the center of maximum abundance had moved from offshore near the shelf break to within 100 km of the New Jersey coast east of Seaside Park. The temporal and spatial developments of the bloom suggest an onshore transport of cells, once the population began to aggregate below the thermocline. By mid-June a large population of cells was situated below the thermocline in a relatively flat region of the New Jersey shelf between the 20 and 40 m isobaths. Much of this population was below the euphotic zone in a subthermocline layer about 15 m thick[6]. This is in marked contrast

[6]Armstrong, R. S. 1976. Climate conditions related to the occurrence of anoxia in water off New Jersey during summer, 1976. Atlantic Environmental Group, National Marine Fisheries Service, NOAA, Narragansett, R.I. Unpubl. manuscr.
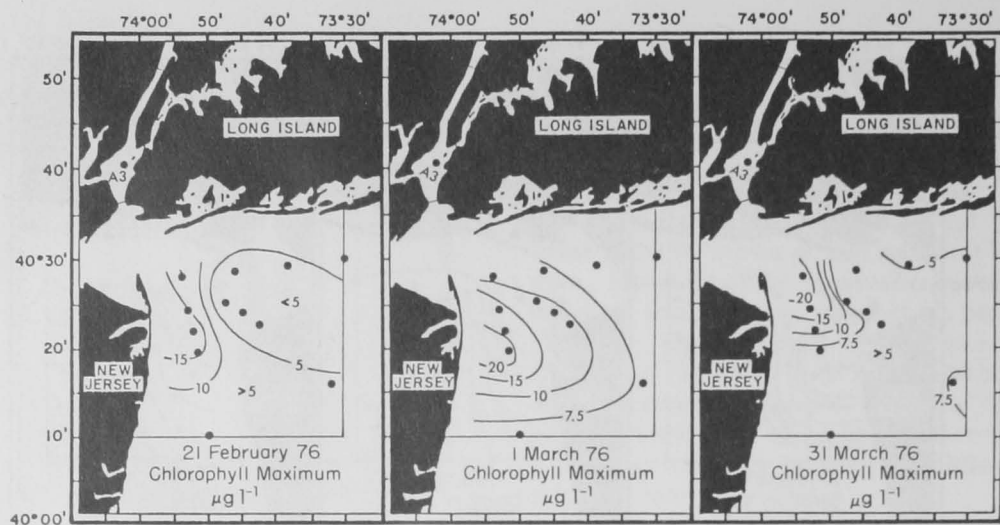
Figure 9.—Distribution of maximum chlorophyll a concentration (μg liter^{-1}) in the apex of the New York Bight; data provided by Thomas Malone.
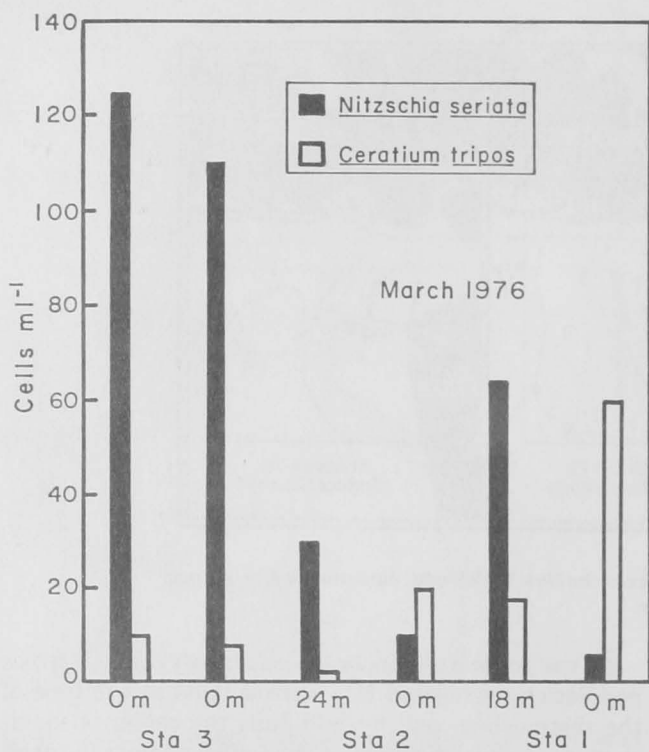
Figure 10.—Histogram of cell density across the shelf originating off Long Island (station 3) and extending south to the shelf break (station 1); stations 1, 2, and 3 were located in water 100, 50, and 30 m deep, respectively; data provided by Wayne Esaias.

to the population off the Long Island coast where the slope of the shelf is initially greater and the maximum layer was well off the bottom in a subthermocline layer about 30 m thick (see footnote 6) over most of its extent, i.e., the layer of maximum cell density tended to intersect the shelf along an isobath rather than to distribute over a surface. Maximum population size was probably achieved after March and before July, and population size declined rapidly during July.
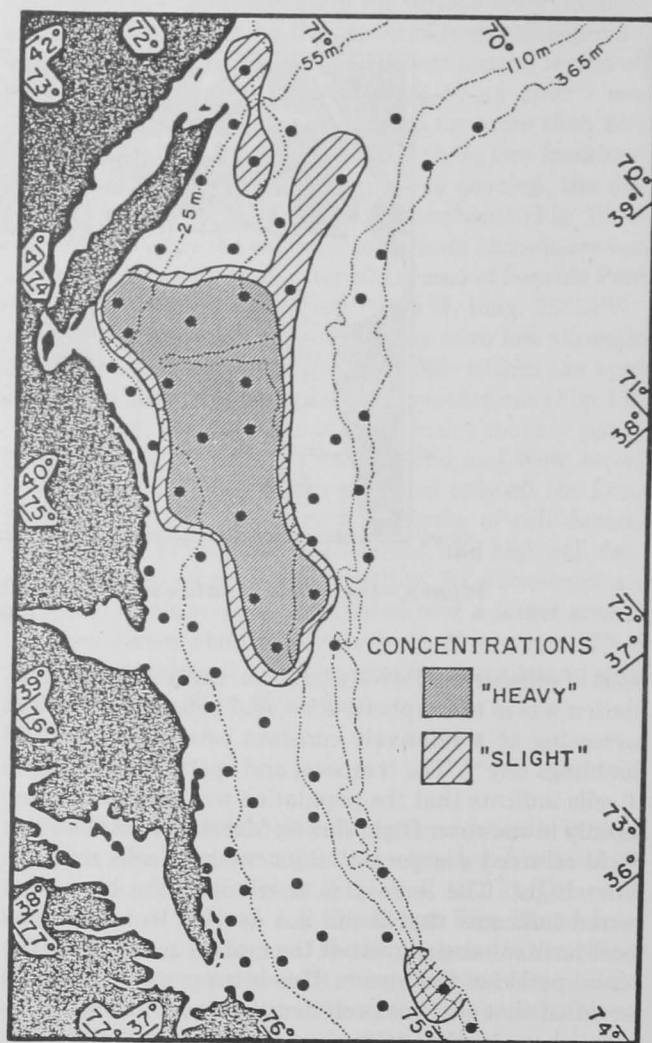
Figure 11.—Distribution of Ceratium tripos as indicated by the degree to which 0.333-μm mesh nets were clogged by Ceratium tripos during March 1976; data provided by Sandy Hook Laboratory, National Marine Fisheries Service, NOAA.

8
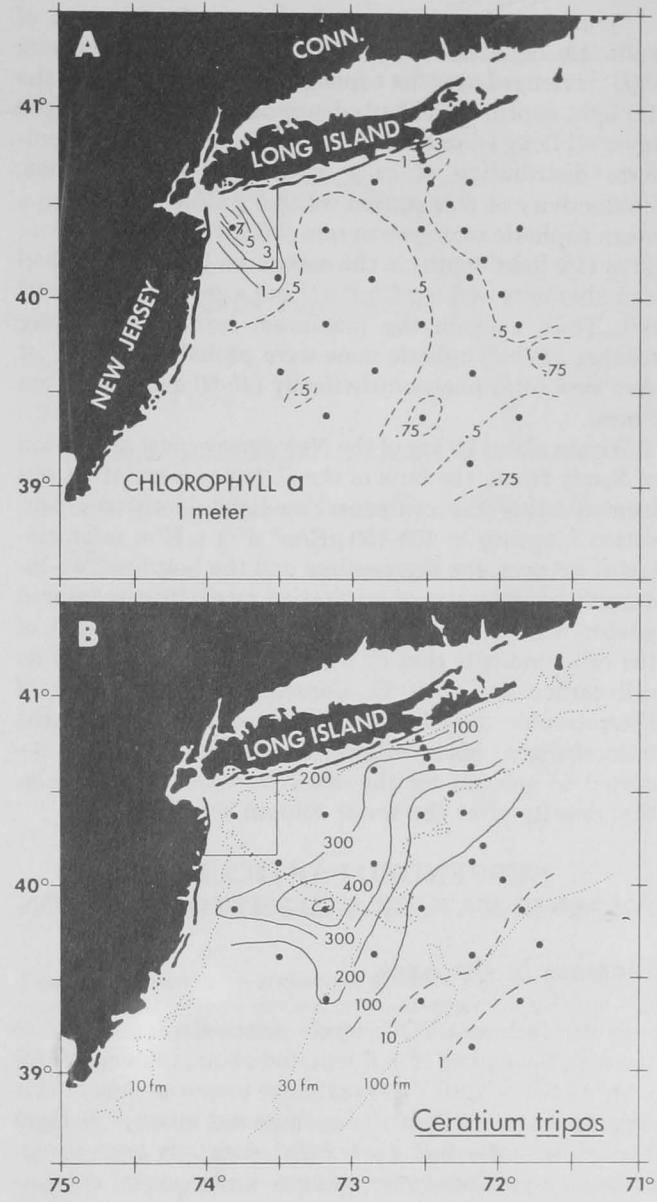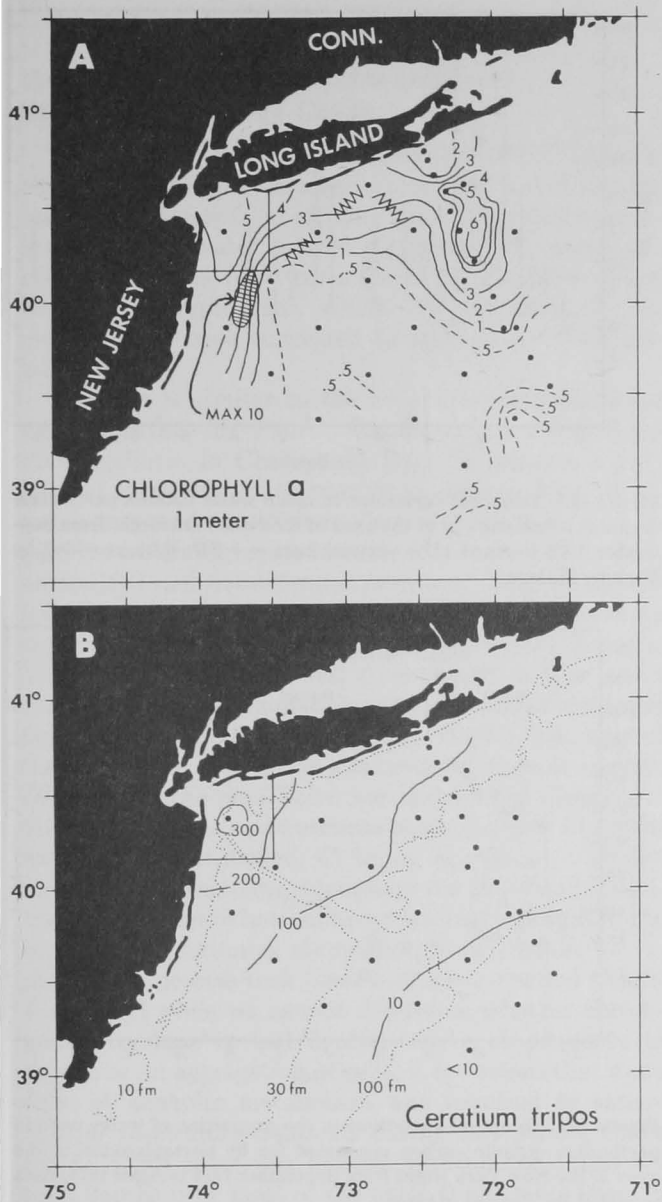
Figure 12.—Distribution of surface chlorophyll a (μg liter^{-1}) from underway fluorescence (A) *Ceratium tripos* cell density (cells ml^{-1}) in the chlorophyll a maximum layer (B) during 17-24 May 1976; data provided by Wayne Esaias.

There is no evidence that the *C. tripos* bloom influenced the growth of net plankton diatoms or nanoplankton populations. The distribution and abundance of these groups were similar to previous years' observations.

GROWTH AND RESPIRATION OF
CERATIUM TRIPOS

Measurements of photosynthesis in the apex during February and March and off Long Island in late April to early May indicate that *C. tripos* was growing at a mean euphotic zone growth rate of 0.04 doublings d^{-1} (carbon specific growth; C:Cl = 275). Light saturated rates were

Figure 13.—Distribution of surface chlorophyll a (μg liter^{-1}) from under fluorescence (A) and *Ceratium tripos* cell density (cells ml^{-1}) in the chlorophyll a maximum layer (B) during 9-13 June 1976; data provided by Wayne Esaias.

0.3 to 0.4 d^{-1} in agreement with the rates of cell division reported by Nordli (1958). Photosynthetic growth could account for the increase in population size observed prior to thermal stratification (January-March).

Once the water column stratified, the problem becomes more complex as euphotic zone nutrients were depleted and the *C. tripos* population aggregated near the base of the thermocline. While maximum cell densities were observed in June, it is possible that population size did not increase. Mathematically, the population was large enough by the end of March to account for observed cell densities in the maximum layer during June. Changes in cell density reflected changes in the distribution of cells as well as the balance between growth and mortality.

9

Ceratium tripos photosynthesizes in the presence of sufficient light. In late April, *C. tripos* growth rates were $0.06\,d^{-1}$ averaged over the euphotic zone and $0.02\,d^{-1}$ at the 1% light depth. Local turbulence disrupted the *C. tripos* layer off Long Island in May (Fig. 12), resulsting in a uniform distribution of cells across the euphotic zone. Productivity at this station was $3.5\,g\,C/m^2\,d^{-1}$, giving a mean euphotic zone growth rate of $0.2\,d^{-1}$. A sample from 30 m (1% light depth) in the maximum layer in May had a productivity of $8\,mg\,C/m^3\,d^{-1}$ and a growth rate of $0.02\,d^{-1}$. Thus, cells in the maximum layer in the lower reaches of the euphotic zone were probably growing at very slow rates photosynthetically (45-60 day generation times).

Within about 20 km of the New Jersey coast and 80 km of Sandy Hook, the bulk of the *C. tripos* population was located below the compensation light depth (compensation intensity = 100-$150\,\mu E/m^2\,d^{-1}$) (μE = microeinstein) between the thermocline and the bottom. Two independent estimates of respiration rates (from measured photosynthesis-light curves and the carbon content of the cells) indicate that *C. tripos* respires about 3% of its cell carbon d^{-1} at $10°C$. Consequently, some form of heterotrophic metabolism or continuous recruitment from offshore photosynthetic populations must have occurred to account for the observed increase in population density after the water column stratified.

SUSPENDED PARTICULATE ORGANIC MATTER AND PHYTOPLANKTON

Biomass in the Apex

Water column POC levels from September 1973 through November 1975 fluctuated about a mean of 9.8 g C/m^2 (1 SD = 2.9). The maximum turnover time of this organic matter is 2 to 15 days (annual mean = 8 days) and reflects the fact that POM does not tend to accumulate in the water column under most circumstances.

This rapid turnover of POM was not observed in February and March 1976 (Fig. 14). During this period, POC accumulated in the water column to levels which were 2 to 3 times higher than previously observed. This increase coincided with the initial phases of the *C. tripos* bloom (Fig. 2). *Ceratium tripos* accounted for 25 to 45% of suspended POC until the end of March when it accounted for 64%. Elimination of the carbon accounted for by *C. tripos* from the suspended POC pool gave water column POC concentrations which reflected the diatom bloom in early March and were in the range of values previously reported (Fig. 14).

The influence of *C. tripos* on the pool of phytoplankton-C was enormous (Fig. 15). Prior to 1976, phytoplankton-C accounted for 15 to 45% of suspended POC with proportions of 35 to 45% typical of phytoplankton blooms regardless of time of year and dominant species. However, during February and March 1976, phytoplankton-C increased from 56 to 84% of the suspended POC pool. Removal of *C. tripos* brings the proportion of
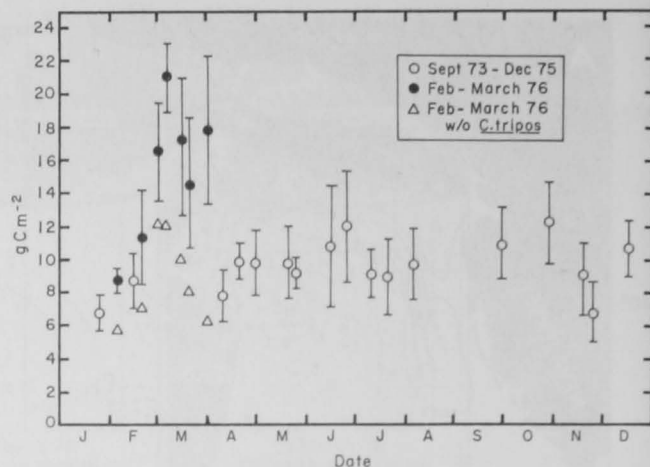

Figure 14.—Temporal variations in mean water column particulate organic carbon content of the apex of the New York Bight from September 1973 to April 1976; vertical bars = 1 SD; data provided by Thomas Malone.
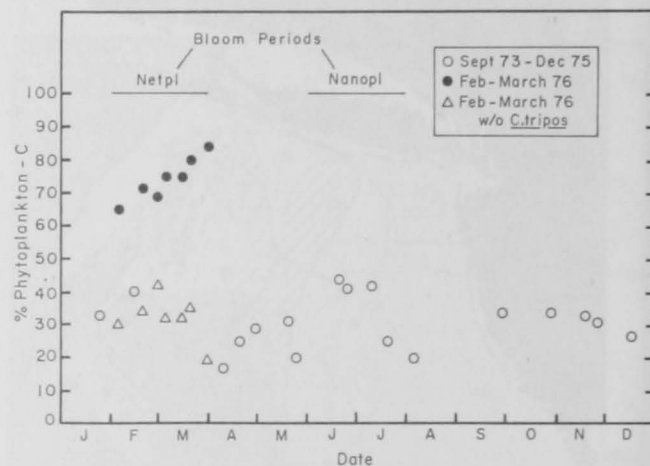
Figure 15.—Temporal variations in the proportion of water column particulate organic carbon accounted for by phytoplankton in the apex of the New York Bight from September 1973 to April 1976; data provided by Thomas Malone.

phytoplankton-C back into the range usually observed in the apex and shows the diatom bloom peaking in early March (Fig. 15). The gradual increase in the biomass of *C. tripos* and the accumulation of POC in the water column which occurred as a consequence did not appear to influence the typical development of the winter-spring diatom bloom.

Temporal variations in copepod abundance and grazing rates indicate that very little of the diatom bloom is grazed at temperatures below $10°C$ (M. Chervin, pers. commun.). Above $10°C$ selective grazing could become important since estuarine copepods (the major particle grazers in the apex) do not eat *C. tripos*, and increased copepod grazing pressure during the spring is probably a factor in transition from net plankton to nanoplankton dominated phytoplankton blooms. *Ceratium tripos* appears to be a slow growing species which is subject to low predation pressure.

10

CONCLUSIONS

Accumulation of *Ceratium tripos* off the New Jersey Coast

The temporal and spatial distributions of *C. tripos* in the New York Bight show an increase and a shift in maximum abundance from offshore prior to stratification to inshore as the water column stratified. The increase in cell density was most pronounced off the New Jersey coast. Two hypotheses, which are not mutually exclusive, have been suggested to account for these distributions.

The first is similar to the accumulation mechanism demonstrated for *Prorocentrum micans* and other dinoflagellates in Chesapeake Bay.[7] It requires a two-layered circulation pattern with an onshore flow of bottom water and an offshore flow of surface water; organisms which aggregate in the bottom layer; and, often, an ability to survive extended periods of darkness. A two-layered, thermohaline circulation has been described for the New York Bight (Ketchum and Keen 1955; Bumpus 1965), and it has been well documented in this report that the *C. tripos* population aggregated near the upper boundary of the bottom layer. It is possible that most of the increase in population size occurred prior to stratification when the population was distributed throughout the euphotic zone and nutrients were plentiful. Once the water column stratified, *C. tripos* aggregated near the base of the thermocline throughout the Bight and the onshore movement of bottom water resulted in a shift in the location of maximum abundance from offshore to inshore. This process took place over a 3 mo period (April-June), and while we cannot determine whether the observed increase in cell density was a consequence of growth or an aggregation of cells, it is obvious that some form of anabolic metabolism was required to satisfy cellular respiratory demands during this period. Since the *C. tripos* layer was located between the 1 and 3% light depths over most of the outer Bight more than 20 km off the New Jersey coast, it is likely that the population in this region was synthesizing organic matter by photosynthesis. Within 20 km of the coast and especially in the apex, the *C. tripos* layer was usually below the 1% light depth. This has led to the hypothesis that the subeuphotic zone coastal population was maintained and possibly increased by recruitment from actively growing, photosynthetic populations further offshore.

While some form of shoreward entrainment must have taken place, several objections exist which question the importance of this mechanism. 1) A shoreward flow of bottom water would not only transport *C. tripos* into the region where the oxygen minimum layer was most pronounced, but also oxygenated water. 2) Estimates of photosynthetic growth rates at the 1% light depth were
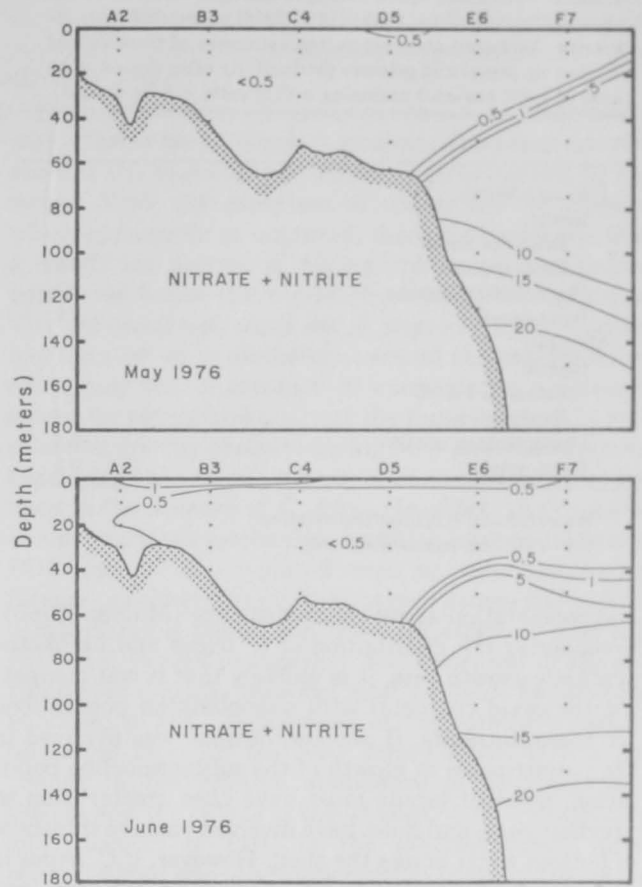

Figure 16.—Distribution of dissolved nitrate + nitrite (μg-at. N/liter) across the shelf along a transect originating in the apex of the New York Bight and extending southeast; data provided by Wayne Esaias.

0.02 d^{-1} in both late April and in May. However, the rate of increase of population density from May to June off the New Jersey coast and along the New Jersey coast was 0.04 d^{-1}. If the coastal population was being maintained by recruitment from offshore populations, the increase in cell density must have reflected an increase in concentration rather than an increase in population size. 3) Nitrate + nitrite concentrations were low throughout the water column across the shelf except in the apex (Fig. 16). The nitrogen budget for the apex during May-July 1975 (Table 1) indicates that the nitrogen supply to the euphotic zone and phytoplankton uptake rates are high and closely coupled and that regenerated ammonia is the main source of nitrogen. Phytoplankton blooms during May and June are usually dominated by small-celled phytoplankters growing at mean euphotic zone rates of 0.5 to 2.0 d^{-1}. These blooms are localized in the surface mixed layer (upper 10 m of the water column) and are most pronounced off the New Jersey coast. There is no evidence that *C. tripos* influenced the development of these blooms during June 1976, and nanoplankton chlorophyll concentrations in the surface layer were similar to previous years. The nutrients required for nanoplankton growth are derived from estuarine runoff

Tyler, M. A., and H. H. Seliger. 1976. Long-range, subsurface transport of the mahogany tide-forming dinoflagellate in the Chesapeake Bay. Abstract, 39th Annual Meeting, Am. Soc. Limnol. Oceanogr. Unpubl. manuscr.

Months	10^5 kg N d^{-1}
February-March	
Inputs:	
Estuarine runoff	1.6
Regeneration[1]	2.2
Phytoplankton uptake	2.7
Input-uptake	2.3
May-July	
Inputs:	
Estuarine runoff	1.4
Regeneration[2]	3.2
Phytoplankton uptake	3.8
Input-uptake	0.8

[1]Water column + benthic regeneration.
[2]Water column regeneration only.

and regeneration above the thermocline (Malone 1976b). Considering the distribution of *C. tripos* and its photosynthetic growth rate, it is unlikely that it was competing (or could compete) with nanoplankton populations for these nutrients. If photoautotrophy was involved in the maintenance or growth of the subthermocline population, nutrient inputs must have been greater than in previous years and must have involved onshore transport of bottom water across the shelf. However, if *C. tripos* is capable of "luxury" nutrient uptake and can store nutrients for periods of weeks to months, the nutrient distributions of May and June might not be a factor (although luxury consumption of this magnitude has never been reported).

Presumably, the collapse of the bloom in June and July was a consequence of the exhaustion of nutrient supplies (internal or external). Grazing is unlikely since copepods have been shown not to eat *C. tripos*.

The second hypothesis involves heterotrophic growth (or maintainance) by the *C. tripos* population situated below the Hudson River plume off the New Jersey coast. This hypothesis is also based on circumstantial evidence. Growth of *C. tripos* had no obvious effect on growth of diatom populations during May and June in the apex. Yet, growth of *C. tripos* during February and March increased the POC content of the water column by a factor of two or three over previous years. Also, *C. tripos* did not respond (as reflected in distribution of biomass) to estuarine runoff as other photoautotrophic populations did. The observed downstream increase in biomass (in contrast with the distribution of diatoms in February and March and nanoplankton in May and June) would develop if *C. tripos* was feeding phagotrophically on POM of estuarine origin or phytodetritus. Since *C. tripos* may have the ability to ingest POM, it is possible that the observed accumulation of *C. tripos* in the water column was a consequence of phagotrophic uptake of POM which settled to the bottom or washed out of the system in previous years. Aggregation near the bottom of the thermocline would be advantageous in that the pop-

ulation is in a region where POM tends to accumulate as it settles through the water column. By metabolizing POM in the water column which was previously lost from the system, a substantial increase in water column BOD would be generated without necessarily increasing the input of nutrients or POM. Based on the proportion of *C. tripos*-C in the POC pool of the water column at the end of March (64%), it is possible that as the discharge of the Hudson River began to decline in May and June (Fig. 17), the population off the New Jersey coast suffered mass mortalities due to limited food supplies.

Ceratium tripos and the Oxygen Minimum Layer

The role of *C. tripos* in the development of the oxygen minimum layer off New Jersey is difficult to evaluate in the absence of data on the time and space distribution of dissolved oxygen in the bottom layer and more complete information of the time and space distributions of POC, chlorophyll a, and *C. tripos*. The apex of the New York Bight has been subject to considerable organic loading over the past two decades, and the development of oxygen minimum layers and local anoxia are not unusual during the summer in the apex.

However, based on the effect of *C. tripos* on the content of POC in the water column and on the development of large, subthermocline populations, it is likely that *C. tripos* was involved in producing the oxygen demand required to account for the oxygen minimum layer. In the latter context, a flocculent suspension of organic matter at least 1 cm thick coated the bottom during July between Sandy Hook and Atlantic City from 5 to 50 km offshore (Frank Steimle, pers. commun.). The floc consisted primarily of phytoplankton cells dominated by *C. tripos*. Microscopic examination indicated a steady increase in decomposition of *C. tripos* cells during July. The few diatoms present appeared to decay more slowly, and decomposition was more complete off northern than southern New Jersey by the end of July.

A computer simulation model was built to explore the combined effects of benthic respiration and *C. tripos* respiration on the rate of oxygen depletion below the thermocline, *Ceratium tripos* respiration rates were calculated
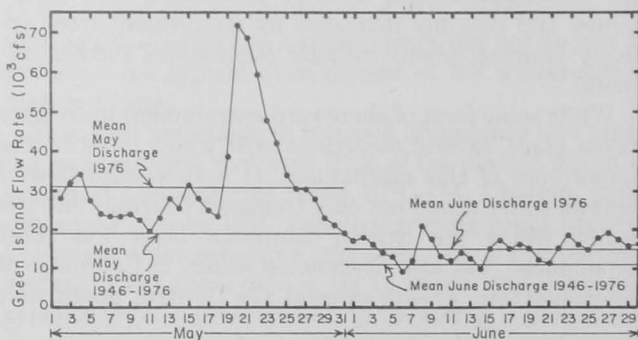

Figure 17.—Freshwater flow (10^3 f/s^3 = 28 m^3/s) of the Hudson River at Green Island during May and June 1976; data provided by the New York Department of Water Resources.

from the expression $R = aW^b$ (Banse 1976) where a and b are temperature-dependent constants and W and R are the weight of the cell in picograms of carbon and the respiration rate in picograms of carbon/cell per hour, respectively. Carbon content of *C. tripos* was calculated from both carbon hyrogen oxygen (CHN) analysis and regression of net plankton chlorophyll a on net plankton carbon. The values range from 20,000 to 30,000 pg/cell (pg = picogram), and a mean value of 25,000 was chosen for calculation of respiration rates. Using a $Q_{10} = 2.3$ the specific respiration rate of a single cell was calculated as 0.003 h^{-1} at 10°C.

The following additional information was input: 1) A mean benthic respiration rate of 11 ml O_2/m^2 hr^{-1} (1.0 mg at. O_2/m^2 hr^{-1}) was calculated from Thomas et al. (1976) for an "average" community in the New York Bight. 2) Eddy diffusion coefficients of 1.0 cm^2 s^{-1} across the thermocline and 10 cm^2 s^{-1} below the thermocline were used. 3) The thermocline was placed 25 m above the bottom. 4) The overlying water was nearly saturated with oxygen, starting with 0.6 mg at. O_2/liter (= 6.72 ml/liter). 5) Using data collected on six cruises, the following numbers of cells were placed in the bottom 20 m: a) 0-5 m (above the bottom) 2×10^7 cells/m^3; b) 5-10 m, 4×10^7 cells/m^3; c) 10-15 m, 6×10^7 cells/m^3. (Exclusion of cells from the upper 5 m is due to the consideration that these cells may be at or above the compensation depth and do not contribute substantially to oxygen depletion).

The model output indicates that within 2 mo the oxygen concentration in the bottom 5-m layer reaches a steady state concentration which is 45% of the initial oxygen concentration. The simulated rate of oxygen depletion below the thermocline is extremely sensitive to changes in eddy diffusivity, and small decreases in diffusivity are sufficient to cause simulated anoxia.

These calculations show the potential metabolic influence of *C. tripos*. The water column integrated *C. tripos* respiration rate exceeds the benthic oxygen consumption rate by a factor of 19.5. *C. tripos* biomass is also a large potential source of BOD. Oxidation of the *C. tripos* biomass (3,255 mg at. C/m^2) within 20 m of the bottom would require 8,463 mg at. O_2/m^2 or 71% of the initial oxygen content. Thus, the combined effects of respiration and subsequent death and decay of the biomass are more than sufficient to produce anoxia.

The occurrence of an oxygen minimum layer and local anoxic waters off the New Jersey coast in contrast to the Long Island coast may reflect differences in bottom topography, residence time of water in the bottom layer, and turbulent mixing. The shelf within 50 km of the coast is much flatter and shallower off New Jersey than off Long Island. As a consequence, the *C. tripos* layer between the 20 and 40 m isobaths off New Jersey was distributed over the bottom surface in a subthermocline water column 5 to 15 m thick while the *C. tripos* maximum off Long Island intersected the bottom along an isobath and was well off the bottom (>30 m) over most of its extent. In addition, high cell densities occurred over larger areas off New Jersey. These observations and the possibility that the residence time of bottom water is longer off New Jersey than off Long Island could explain the development of a more intense and widespread oxygen minimum layer off New Jersey.

Phytoplankton productivity per se was probably not a major factor even though it quantitatively accounts for most of the input of particulate organic matter to the region. With the exception of winter diatom blooms, which apparently go ungrazed, there is no evidence that a significant portion of phytoplankton production accumulates below the thermocline during the summer. The dominance of small celled phytoplankton (usually less than 1μ m in diameter), vertical chlorophyll a distributions, the importance of ammonia as a nitrogen source for phytoplankton, and the rapid increase in zooplankton grazing pressure during May and June are consistent with the rapid turnover of POC calculated for the apex in the absence of *C. tripos*. In effect, the *C. tripos* bloom provides a mechanism by which large quantities of POC can be accumulated over an extended period (several months). Respiratory oxygen consumption by a subthermocline population below the euphotic zone and the rapid (weeks to months) decomposition of the accumulated biomass were the most probable factors contributing to the development of the extensive oxygen minimum layer off the New Jersey coast. It was the change in the relative abundance of phytoplankton species and the effects of this change on the distribution and quantity of POC in the subthermocline water column which was most important in terms of the role of phytoplankton. Unfortunately, it is this type of species succession problem which we understand least. The basic question of why the *C. tripos* bloom occurred in the first place remains unanswered.

FUTURE RESEARCH AND MONITORING

Our inability to deal with the question of why *C. tripos* became so abundant over such a large area is indicative of two major problems, one related to basic research and the other to communications between the various government agencies and private research groups working in the New York Bight and adjacent waters. Scientifically, we do not know enough about the processes which influence the succession of species in planktonic communities. Of prime importance is increased funding for field and laboratory research designed to study the biology of planktonic species and the environmental regulation of their growth and distribution in the field.

In terms of the organization of field and laboratory studies and monitoring programs, emphasis should be placed on 1) coordinated sampling programs which involve measurement of a minimum number of easily determined variables and 2) rapid collation and dissemination of data between agencies and research groups. The "minimum number of easily determined variables" includes concentrations of particulate organic carbon, particulate nitrogen and chlorophyll a, phytoplankton and zooplankton species abundance, and zooplankton dry weight. Other variables which should be measured in

conjunction with these include dissolved oxygen, ammonia, nitrite, nitrate, phosphate, and silicate concentrations; incident solar radiation; and the rate of attenuation of downwelling radiation in the water column. Samples should be collected weekly at selected stations along the coast (e.g., Barnegat Inlet, Ambrose Light Tower, and Fire Island Inlet) from at least surface and near-bottom depths. Each month, three transects should be run across the continental shelf to 1,000 m, one originating from and normal to the Long Island coast, a second originating from and normal to the New Jersey coast, and a third originating from the Ambrose Light Tower and bisecting the Bight. Stations should be located at 5 to 20 km intervals and samples collected from standard depths. Wherever and whenever possible, continuous vertical and horizontal profiles of temperature, salinity, dissolved oxygen, and chlorophyll a should be obtained.

Such a monitoring program should be designed with three major goals in mind: 1) to provide information which can be used to evaluate the causes of anomolous phenomena after the fact, 2) to provide information which can be used to make management decisions (e.g., "The dump site will have to be moved to this location for the next two months."); and 3) to provide information which can be used to develop research programs in advance of anticipated events. Success of this program will be determined by the quality of the information produced and by how rapidly it can be made available to groups involved. The speed with which information is disseminated is critical. All samples must be processed within 1 wk of collection. Unusual observations, events, or trends should be verbally communicated, and hard copy data reports (with comments on anomalies) should be made available to all involved parties each month within 1 mo of sample collection.

ACKNOWLEDGMENTS

LITERATURE CITED

BANSE, K.
  1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size—A review. J. Phycol. 12:135-140.
BUMPUS, D. F.
  1965. Residual drift along the bottom on thecontinental shelf in the Middle Atlantic Bight area. Limnol. Oceanogr. 10 (Suppl):R50-R53.
GARSIDE, C., and T. C. MALONE.
  In press. Monthly oxygen and carbon budgets of the New York Bight Apex. Estuarine Coastal Mar. Sci.
KETCHUM, B. H., and D. J. KEEN.
  1955. The accumulation of river water over the continental shelf between Cape Cod and Chesapeake Bay. Deep-Sea Res. 3(Suppl.):346-357.
LAWS, E. A.
  1975. The importance of respiration losses in controlling the size distribution of marine phytoplankton. Ecology 56:419-426.
MALONE, T. C.
  1976a. Phytoplankton productivity in the apex of the New York Bight: September 1973-August 1974. NOAA Tech. Memo. ERL MESA-5, 46.
  1976b. Phytoplankton productivity in the apex of the New York Bight: Environmental regulation of productivity/chlorophyll a. In M. Grant Gross, editor, The Middle Atlantic Shelf and New York Bight, p. 260-272. Limnol. Oceanogr. Spec. Symp. 2.
  1977. Environmental regulation of phytoplankton productivity in the Lower Hudson Estuary. Estuarine Coastal Mar. Sci. 5:157-171.
  In press. Plankton systematics and distribution. MESA New York Bight Atlas Monogr. 13, N.Y. Sea Grant Inst., Albany.
MANDELLI, E. F., P. R. BURKHOLDER, T. E. DOHENY, and R. BRODY.
  1970. Studies of primary productivity in coastal waters of southern Long Island, New York. 6. Mar. Biol. (Berl.) 7:153-160.
NORDLI, E.
  1957. Experimental studies on the ecology of eratie. Oikos 8:200-265.
RYTHER, J. H., and W. M. DUNSTAN.
  1971. Nitrogen phosphorus, and eutrophication in the coastal marine environment. Science (Wash., D.C.) 171:1008-13.
RYTHER, J. H., and C. S. YENTSCH.
  1958. Primary production of continental shelf waters off New York. Limnol. Oceanogr. 3:327-335.
THOMAS, J. P., W. C. PHOEL, F. W. STEIMLE, J. E. O'REILLY, and C. A. EVANS.
  1976. Seabed oxygen consumption in the New York Bight Apex. U.S. A. In M. Grant Gross (editor), The Middle Atlantic Shelf and New York Bight, p. 354-369. Limnol. Oceanogr. Spec. Symp. 2.