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An analysis of factors affecting oxygen depletion in the New York Bight

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ABSTRACT

Low oxygen water, of varying spatial extent, has been observed during the summer over past years in the New York Bight. In the summer of 1976 a \$60 million loss of shellfish resulted from anoxia along the New Jersey coast. The development of anoxia has been attributed to increased anthropogenic carbon loading from urban areas adjacent to the Bight, an unusual climatological regime that restricted renewal of oxygen to the bottom waters, and an unusual abundance and subsequent respiratory demand of the dinoflagellate, *Ceratium tripos*, beneath the pycnocline. In an attempt to distinguish between man-induced and natural generic causes of oxygen depletion within the New York Bight, we have analyzed historical data extending back to 1910. As a result, we have identified a causal chain of events which led to the observed 1976 anoxia: namely, a warm winter with large runoff, a low frequency of spring storm events, a deep summer thermocline, persistent southerly winds with few reversals, a large autochthonous carbon load (e.g. *Ceratium tripos*), and low grazing pressure by zooplankton. Our calculations suggest that anoxia could have occurred off the New Jersey coast in the summer of 1976 without any carbon loading from New York City, and that anoxia in this open shelf system can result from natural physical forcing and biological response.

1. Introduction

Oxygen depletion within enclosed fjords and ocean basins is a common feature of areas of restricted flow (Richards, 1965) such as off the coast of Norway and in the Cariaco Trench. Anoxic regions of open coastal zones are usually restricted to upwelling systems (Brongersma-Sanders, 1957) as on the Peruvian shelf, where intense carbon production, sinking of organic matter, and subsequent oxygen demands may override the greater flushing rate of these areas (Walsh, 1975). However, low oxygen water of varying spatial extent has also been observed over past years within the open, less productive (Walsh, 1980) coastal area of the New York Bight (Fig. 1). A \$60 million loss of shellfish resulted from the most recent anoxic event along the New Jersey coast during the summer of 1976 (Sindermann and Swanson, 1980).

A number of separate hypotheses have been advanced to explain the 1976 anoxic

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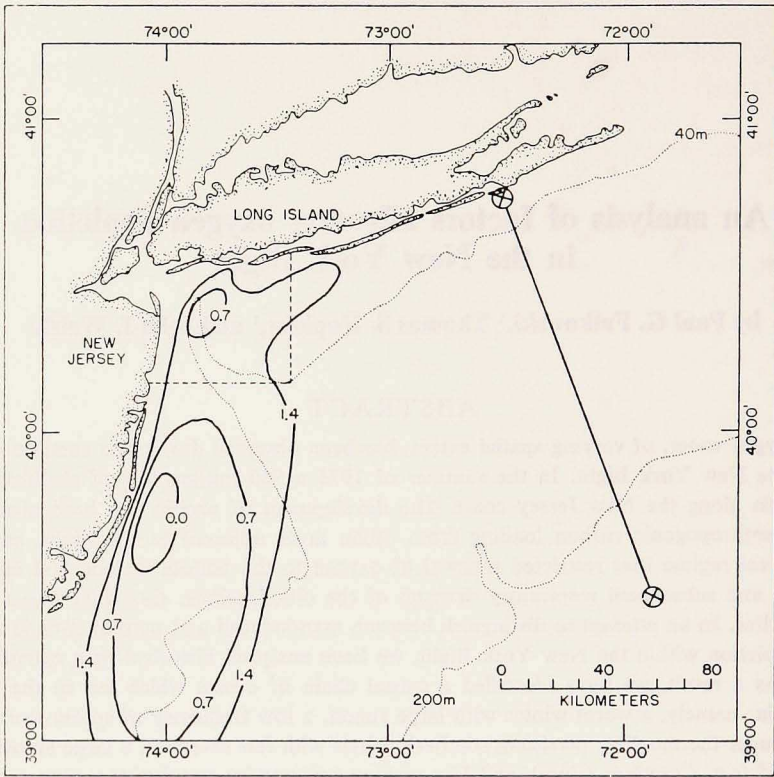


Figure 1. The mean distribution of anoxia during July 1976 in relation to the New York Bight Apex (-----), and the location of the offshore Shinnecock transect as shown between X.

event: 1) an unusual climatological regime of the previous winter; 2) an unusual summer wind and current regime; 3) the respiratory demand of the dinoflagellate, *Ceratium tripos*, which occurred in unusual abundance within the aphotic zone, and 4) an overload of sewage, sludge, and other waste material from New York City and adjacent areas. Any attempt, however, to distinguish between man-induced and natural generic causes of oxygen depletion within the New York Bight (Officer and Ryther, 1977) must place the 1976 anoxic event within the context of the natural variability of the system. We feel that all of the hypotheses may be linked in a causal chain of biological interactions keyed to the duration of seasonal physical events. Based on historical data from 1910 to 1978, a discussion of these relationships comprises the subject of this paper.

2. Physical processes affecting oxygen stocks

As the New York Bight ecosystem progresses into the summer stratified mode, the sub-pycnoclinal waters hold an initial spring stock of heat, salt, and nutrients,

Table 1. Oxygen content of bottom waters in the New York Bight.

Period	Cold pool cross- sectional area ¹ (km ²)	O ₂ solubility (ml/l)		Cold pool ² O ₂ stock ($\times 10^8$ m ³ /m)	Percent of May 75
		Cold pool	mid-shelf Surface		
May 75	2.83	7.09	6.58	20.06	100%
June 75	1.90	7.00	5.63	13.30	66%
May 76	0.98	6.79	6.10	6.65	33%
June 76	0.82	6.84	5.75	5.61	28%

1. Taken as the average of the two cross-sections of stations C2 to F5 and D1 to G4 (c.f. BNL Data Report No. 24770) using the area enclosed by the $\leq 6.5^\circ$ isotherm for 1975 and $\leq 7.75^\circ$ isotherm for 1976. These temperatures were taken as the regional mean plus one standard deviation for the cold pool in the New York Bight.

2. The volume is per meter of alongshore length.

as well as oxygen. The spring stock of oxygen in the bottom layer becomes an important variable in any consideration of summer anoxia. This stock is a function of the bottom water mass volume and its saturation capacity. It is assumed that this water mass is a product of winter water mass production. We make a simple comparison between the May-June 1975 and May-June 1976 cold pool stocks (Table 1) to demonstrate the oxygen disadvantage of the 1976 summer aphotic zone, even before carbon loading and plankton respiration are considered.

The spring stock of O₂ in the bottom water is relatively unaffected by those vertical mixing processes that depend on the vertical gradient, since in the case of oxygen, the saturation content during spring is less in the surface layer, thus acting to reduce the vertical gradient. For example, the oxygen capacity was 10% greater in the bottom waters than the surface waters in May 1976 and 20% greater in June 1976 (Table 1). Vertical diffusion processes do not provide a source of oxygen to the bottom layer until this saturation difference is consumed *in situ* below the pycnocline. The difference in the spring stock between the two years is primarily due to the difference in the bottom water volumes.

The March surface temperature anomaly (Fig. 2) of the New York Bight reflects the vertically homogeneous heat content of the winter shelf water column (Walsh et al., 1978) and is an index of both previous local winter mixing and the amount of heat extracted by winter's end. A negative March anomaly indicates a colder than normal winter and a larger than normal volume of cold shelf water going into the vernal heating cycle. Delays in spring runoff and/or a decrease in occurrence of spring storms act to increase the spring vertical heat transfer on the shelf. In general, cold winters precede shallow summer thermoclines (10-20 m) south of Long Island, whereas deeper summer thermoclines (15-30 m) are observed in the same area after the warm winters (e.g. Ketchum and Corwin, 1964).

In March 1976 anomalously warm sea surface temperatures (Fig. 2) were associ-

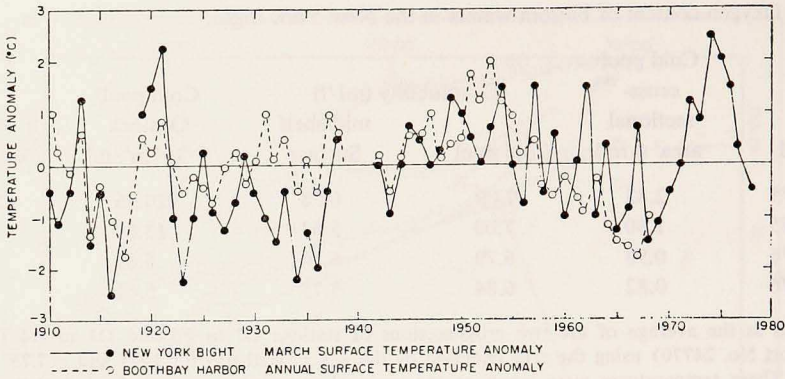


Figure 2. The annual surface temperature anomaly off Boothbay Harbor, Maine and the March anomaly within the New York Bight from 1910 to 1978 (after Colton, 1972; Diaz, 1980; Taylor *et al.*, 1957).

ated with anomalously warm air temperatures and above normal insolation (Diaz, 1980). The 1976 February and March mean air temperatures in New York were the second warmest in the last 100 years. Anomalous atmospheric patterns for February-June 1976 consisted of winds much more westerly and southerly in origin, with very few major cyclones during this period (Diaz, 1980). An unusually large fresh water runoff was coupled with the warm winter of 1976 and the high frequency of southwesterly winds (Armstrong, 1980).

River discharges of the Hudson Valley were early and high during the winter-spring of 1976. The spring maximum occurred in February, two months before the normal April maximum at the Battery, and constituted a record for the last 30 years. The rainfall in May 1976 was higher than average, 33 mm above normal in Central Park (Swanson *et al.*, 1978), and the 1976 discharge from the Hudson River at Troy, New York, was then much higher than the mean 30 year fresh water input (Fig. 3). The 1976 May discharge was exceeded only 4 times in the last 30 years.

Ketchum and Keen (1955) and Ketchum *et al.* (1951) have reported on fresh water accumulation in the New York Bight. They found only 6-10 days accumulation of fresh water in the Apex at any one time, whereas in May 1976, we found nearly 2 months accumulation. The fresh water fraction is given as $F = \frac{S - S_0}{S}$ where S_0 is the observed salinity and S the reference salinity. To compare the years of 1975 and 1976 we used (Table 2) the salinity of Georges Bank (Hopkins and Garfield, 1979) as a reference because it has very low variance and is insensitive to coastal runoff fluctuations.

The fresh water values in Table 2 demonstrate the difference between the two years of the salinity contribution to spring stratification of the water column. The amount of fresh water in the Bight Apex was ~ 12 times greater in May and ~ 5

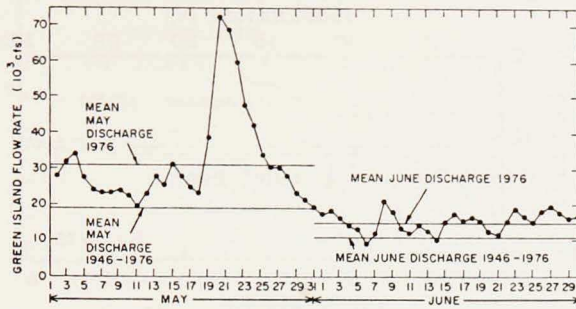


Figure 3. The Hudson River runoff at Green Island for May-June 1976 in comparison with the mean discharge over the last 30 years (after Malone, 1978).

times in June of 1976 than in the same months in 1975. A storage of fresh water in the New York Bight system is enhanced by a seasonal switch to southwesterly winds and thus the seasonal accumulation between each May and June is not unexpected. However, the unusual accumulation of fresh water by May 1976 strongly suggests a combination of both southwesterly weather and high runoff.

During the stratified season, the New York Bight waters are typically characterized by a sharp pycnocline reaching σ_t gradients of 0.2 m^{-1} (Walsh *et al.*, 1978). This vertical density structure is usually controlled by a temperature gradient which can change by 17°C over 15 m (Bowman and Wunderlick, 1976). The sea surface temperatures begin to rise in April and peak in early August. This seasonal temperature structure has been summarized by Bigelow (1933), Beardsley *et al.* (1976), Bowman and Wunderlick (1976), and Hopkins and Garfield (1979).

The June 1976 thermocline was thicker than normal with a constant slope. The thermocline (Fig. 4) has a fairly low decrease of $\sim 0.3^\circ\text{C m}^{-1}$ within the 10-30 m depth band off Long Island (40 m isobath) in June 1976, compared to a 0.7°C m^{-1} decrease over the 10-20 m band in June 1975. A critical factor leading to this broad thermocline was the small number of cyclones which occurred (Diaz, 1980)

Table 2. Relative amounts of fresh water in New York Bight Apex.*

Period	Freshened volume (km ³)	Fresh water volume (km ³)	Percent fresh water
May 75	85	0.8	0.9
June 75	246	3.2	1.3
May 76	536	9.9	1.8
June 76	574	14.5	2.5

* Based on an area defined by the station grid of 4 transects, D1 to G4, C2 to F3, A2 to E6, and A4 to C6 defined the axis of an offshore volume segment (c.f. BNL Data Report No. 24770).

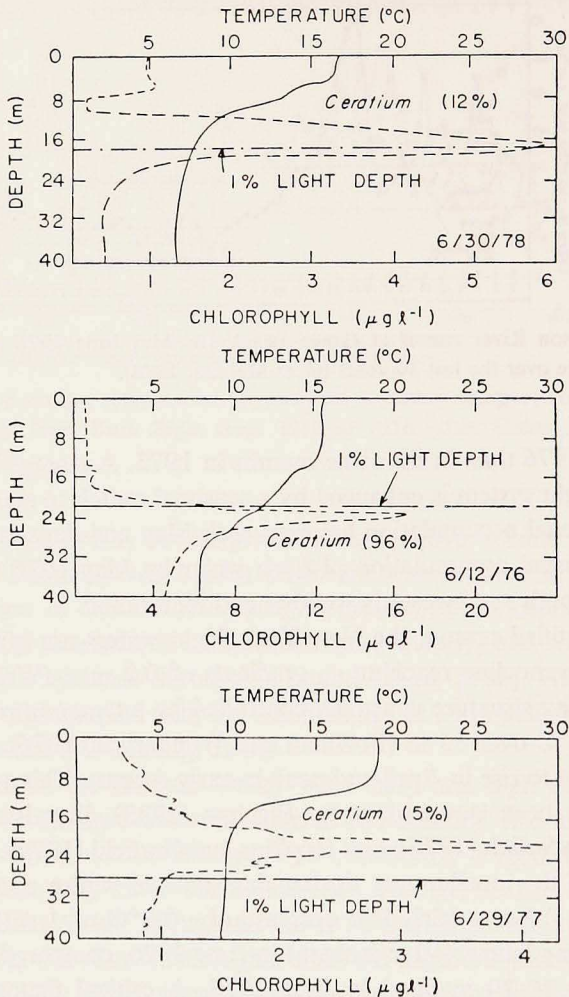


Figure 4. The nearshore phytoplankton distribution in relation to the depths of the seasonal thermocline and euphotic zone during June 1976, 1977, and 1978 off Long Island.

during spring 1976. Consequently the high runoff and small amount of wind mixing allowed the shelf waters to stratify approximately a month earlier than normal. The warm winter and high runoff (in February) resulted in March shelf bottom waters which were warmer and fresher than normal. The summer "cold pool" (Bigelow, 1933; Ketchum and Corwin, 1964) in 1976 was manifest deeper in the water column, it was warmer, and it extended across most of the shelf. This contrasts to the thicker, less extended, and colder distribution of the cold pool in 1975 (Mayer *et al.*, 1980). The interannual temperature of the cold pool varies from 5° to 10°C during August-September at a bottom depth of 60 m, south of Long Island. When the cold

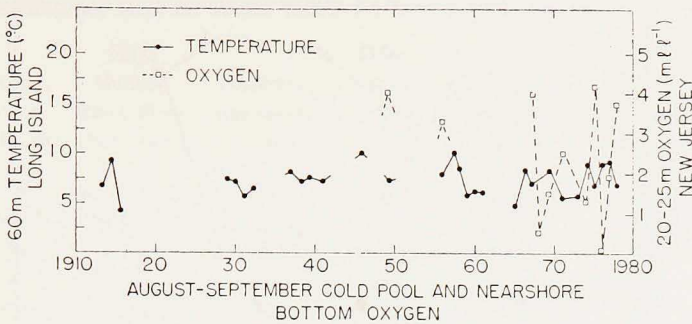


Figure 5. The bottom temperature at 60 m south of Long Island and the near bottom oxygen content at 20-25 m east of New Jersey during August-September 1910-1978 (after Alexander and Alexander, 1976; Bigelow, 1915, 1927, 1933; Bowman and Wunderlick, 1976; Colton *et al.*, 1968; Cresswell, 1967; Ketchum *et al.*, 1951; Ketchum and Corwin, 1964; Ogren and Chess, 1969; Whitcomb, 1970; Clarke, 1940).

pool in this area is warm, low bottom O_2 values are found off New Jersey and vice versa (Fig. 5).

3. Physical factors affecting the distribution of Ceratium

The sub-pycnoclinal shelf waters of the mid-Atlantic Bight are comprised of two water masses during the stratified season (Fig. 6): the cold pool (CP) and the shelf bottom (SB) water (Hopkins and Garfield, 1979). Under conditions of southwest alongshore bottom flow, these bottom waters are advectively renewed, with their T - S drift controlled by the upstream source water type (Hopkins and Garfield, 1979). The thermohaline properties of the bottom water are also modified by vertical mixing processes (Ketchum and Corwin, 1964). In the case of sluggish alongshore flow, the T - S characteristics may be dominated by mixing instead of advection, as was apparently the case in 1976. From bottom current meter observations over the New Jersey shelf, Mayer *et al.* (1980) estimated the spring-summer travel time of bottom water through the New York Bight to be on the order of 100 days in 1975 and 500 days in 1976. Similarly, Mayer, Hansen, and Ortman (1979) show the bottom water displacements in May-June 1976 to be less than half that of 1975 at the 47 m isobath, 30 km northwest of the Hudson shelf valley.

The temporal T - S drifts of the New York Bight water masses are compared for the years 1957-1958 and 1975-1976 in Figure 6. The water masses are represented by a mean water type calculated from six or more of the recent observations, and from data at 60 m on the 70-80 m isobath during 1957-1958 (Ketchum and Corwin, 1964). Variance envelopes are not shown for reasons of clarity. In 1975 and 1957 the shelf bottom waters show little effect of shelf surface (AS) water mixture compared to 1976 and 1958, i.e. a decline in the latter salinity content. By June 1976,

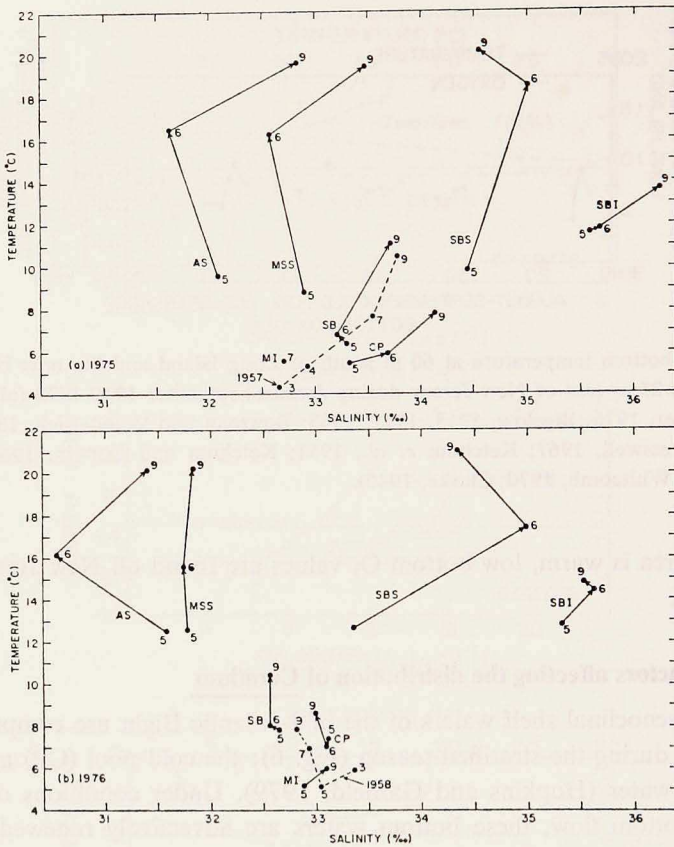


Figure 6. Water mass characteristics for the New York Bight in A) March-September 1957 and 1975, and B) March-September 1958 and 1976. The 1957-58 data are single observations from a depth of 60 m at the 70-80 m isobath, south of Long Island, while the more recent data are means from grid stations occupied by BNL (BNL Data Rep. 24770).

the New York cold pool was still New England shelf water rather than Maine Intermediate Water. In this qualitative way, the shelf bottom waters clearly experienced less alongshore renewal in 1976 than 1975, as indicated by the salinity increase in the latter year. Furthermore, even though the mean flow was only half, the total current energy density in 1976 was up to 100% greater than in 1975 (Mayer *et al.*, 1980), suggesting that more energy was available for mixing in 1976. Also it is clear from the volume estimates in Table 1 that the 1976 cold pool was losing volume, while in 1975 its volume was being sustained.

With establishment of a deep pycnocline, the vertical exchange between surface and bottom regions of the water column becomes more "diffusive", i.e. slower. The most significant difference between 1975 and 1976, in terms of mixing, was that the energy available for mixing in 1976 was stored as potential energy in a broad pycno-

Table 3. A contingency table for anoxia within the New York Bight.

	Warm winter (March)	High Hudson River Flow (Feb.-Apr.)	Onshore transport (April)	Deep thermo- cline (June)	Large Ceratum population (June)	Steady SW wind (summer)	Extent of anoxia
1966	no	yes	no	no	no	no	no
1967	mild	no	no	?	?	yes	no
1968	no	no	no	?	yes	no	mild
1969	no	yes	yes	?	?	no	no
1970	mild	no	no	?	?	no	no
1971	mild	no	yes	?	?	yes	mild
1972	mild	no	no	no	no	yes	no
1973	mild	yes	no	?	no	no	no
1974	yes	no	yes	yes	yes	no	mild
1975	yes	no	no	no	no	yes	no
1976	yes	yes	yes	yes	yes	yes	large

cline, creating a third layer. The volume of this layer was generated at the expense of the bottom water rather than the surface layer. A two layered flow regime (Beardsley and Butman, 1974) then became three-layered with inclusion of a flow (onshore) within the thermocline (16-30 m) that responds to (offshore) wind forcing (Hopkins, 1974). As the spring water column stratifies in this mode, a persistent onshore convergence develops in the pycnocline with upwelling circulation dynamics, at both midshelf (Han *et al.*, 1980) and near the coast (Walsh *et al.*, 1978) that both erodes the bottom water volume and advects plankton onshore (Table 3).

Within several cross-shelf transects during April-May 1976, the subsurface chlorophyll maximum (Fig. 7) increased from 4-5 μg Chl l^{-1} offshore to 15-30 μg Chl l^{-1} inshore within an onshore salinity tongue of 32-32.5‰ water (the 25.0-25.5 σ_t band). The vertical location of these chlorophyll maxima were carefully determined

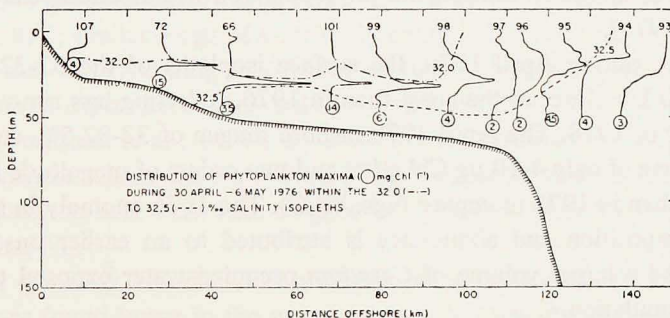


Figure 7. The cross-shelf distribution of phytoplankton (after W. Esaias, personal communication) in relation to the 32.0-32.5‰ salinity band during April-May 1976.

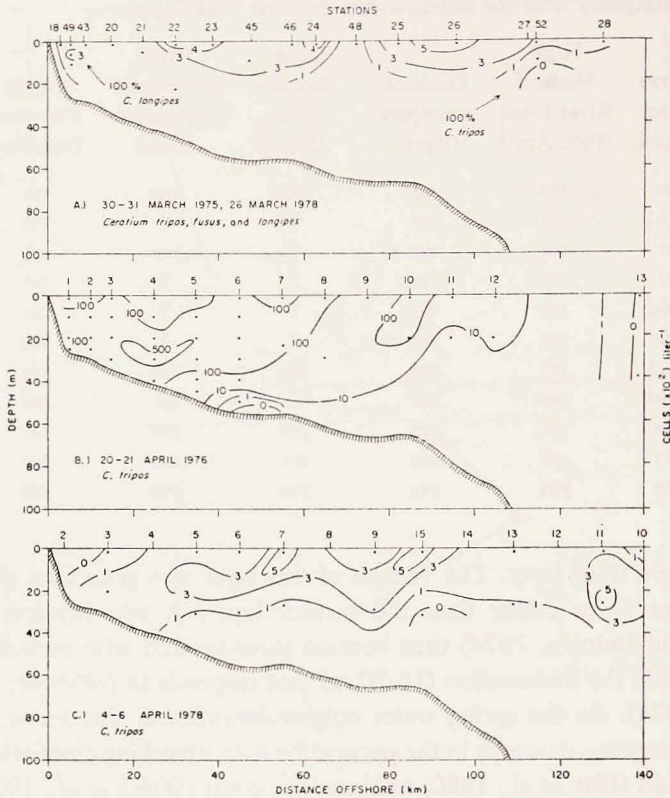
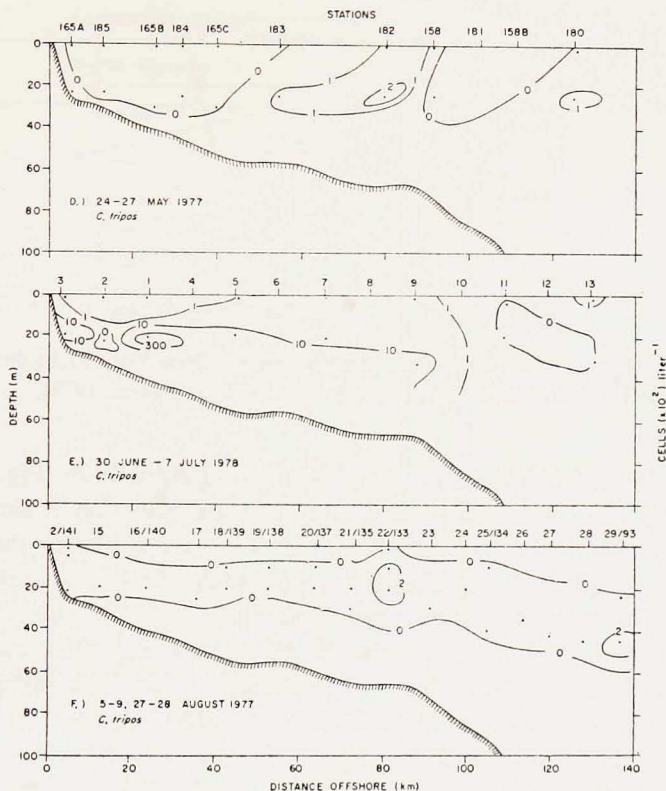


Figure 8. Cross-shelf distributions of *C. tripos* ($\times 10^3$ cells l^{-1}) in "normal" years of 1975, 1977, and 1978 and during the *Ceratium* bloom of 1976 off Long Island.

at each station with a continuous chlorophyll pump and an *in situ* fluorometer, equipped with a depth sensor. These data strongly suggest an onshore subsurface accumulation of the phytoplankton populations in the New York Bight during the spring of 1976, similar to transport of phytoplankton within Chesapeake Bay (Tyler and Seliger, 1978).

In contrast, during April 1978, the surface isopleths of the 32-32.5‰ salinity band were 60 km closer to the coast than in 1976, reflecting less run-off during the colder winter of 1978. The April 1978 inshore tongue of 32-32.5‰ contained subsurface maxima of only 4-10 μg Chl l^{-1} and two orders of magnitude less *C. tripos* populations than in 1976 (compare Figs. 8B,C). The 1976 anomaly in spring phytoplankton composition and abundance is attributed to an earlier onset of species succession and a larger volume of *Ceratium*-occupied water exposed to subsurface onshore accumulation.

A comparison of *C. tripos* distributions in "normal" shallow pycnocline years with that during deep or broad pycnocline years (Fig. 4) provides a description of



the differences in timing of seasonal succession within the phytoplankton niche as regulated by changes in the circulation field. The "normal" seasonal, onshore progression of *C. tripos* across the New York shelf can be seen in a composite of March to August sections (Fig. 8), taken south of Long Island (Fig. 1) in 1975, 1977, and 1978, i.e. during years of no anoxia. At the end of a "normal" winter, $\sim 1-5 \times 10^2$ cells l^{-1} of *C. tripos* are usually found offshore within the upper 20 m of the water column (Fig. 8A); similar levels of *C. tripos* were found in this area in March 1975, 1977, 1978 and 1979. During mid-winter of the "abnormal" year 1976, surface populations of *C. tripos* were again only predominant at the outer part of the New York Bight (Fornshell et al., 1977). By early March, however, $1-5 \times 10^3$ cells l^{-1} were found inshore within the New York Bight Apex and off Fire Island (Malone, 1978). Zooplankton nets were then clogged by *Ceratium* from Cape May, N.J. to Montauk Point, N.Y.

With onset of spring stratification and depletion of the surface nutrients, maxima of *C. tripos* are found lower in the water column, but usually at the same level of winter abundance. There is an onshore gradient of *C. tripos*, however, suggesting an onshore accumulation of the populations at mid-depth by April-May (Fig. 8C,D).

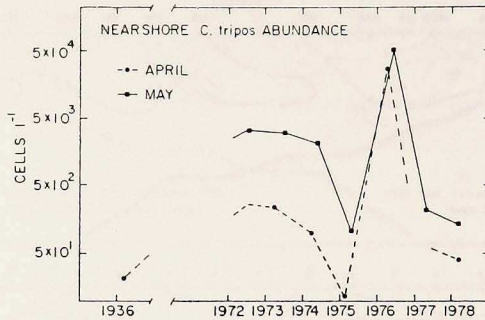


Figure 9. The surface standing crop of *Ceratium* within the New York Bight during April (●) and May (■) 1933-1978 (after Lillick, 1937; Baylor, 1973; S. Weaver, 1979).

Although, more cells were found in the anoxia year of April 1976 (Fig. 8B) than in 1978 (Fig. 8C), the cross-shelf pattern of *C. tripos* distribution is similar in both years. The inshore May populations of *C. tripos* are always larger than the April stocks (Fig. 9), suggesting seasonal increase of these dinoflagellates in this area.

By June 1976, the nearshore phytoplankton of the subsurface chlorophyll maximum (Fig. 4) was 99% *C. tripos* with an abundance up to 5×10^5 cells l^{-1} . Similarly, *C. tripos* constituted 65% of the phytoplankton population during June 1964 (Grumman *et al.*, 1975), but only 12% in June 1978 (Fig. 8E). In both August 1976 (Thomas *et al.*, 1980) and August 1977, however, very few *C. tripos* were found across the shelf (Fig. 8F). *Ceratium* was also less than 1% of the phytoplankton in September 1971 (Nuzzi, 1973). The disappearance of this dinoflagellate from the New York Bight by late summer is part of the normal species succession pattern (Lillick, 1940); the phenomenon of most importance is thus the length of their residence time during early summer.

The normal wind pattern within the New York Bight during early summer is an air flow from the southwest with frequent reversals from the northeast. Over the last 15 years, however, there were several cases (June 1967, July 1971, July 1972, July 1975, and June 1976—see Table 3) with more than 12 days of steady wind stress from the southwest direction (Tingle *et al.*, 1979). After a month of such anomalously strong and steady June winds from the southwest in 1976, the Hudson River plume was shifted towards the east as indicated by salinity patterns and a reversal to the northeast of the normal southwest surface (3 m) current occurred by 10 June 1976 (Swanson *et al.*, 1978). This wind event was of sufficient duration to allow a longshore flow reversal within the thermocline in addition to the onshore-offshore Ekman response of the upper layer. The current velocities, found in the thermocline, are usually about 0.5-1.0 cm sec^{-1} of residual drift to the southwest off Long Island and New Jersey (Bumpus, 1973). During June 1976, the flow at 16-30 m off New Jersey was instead 1.0-2.0 cm sec^{-1} toward New York and Long

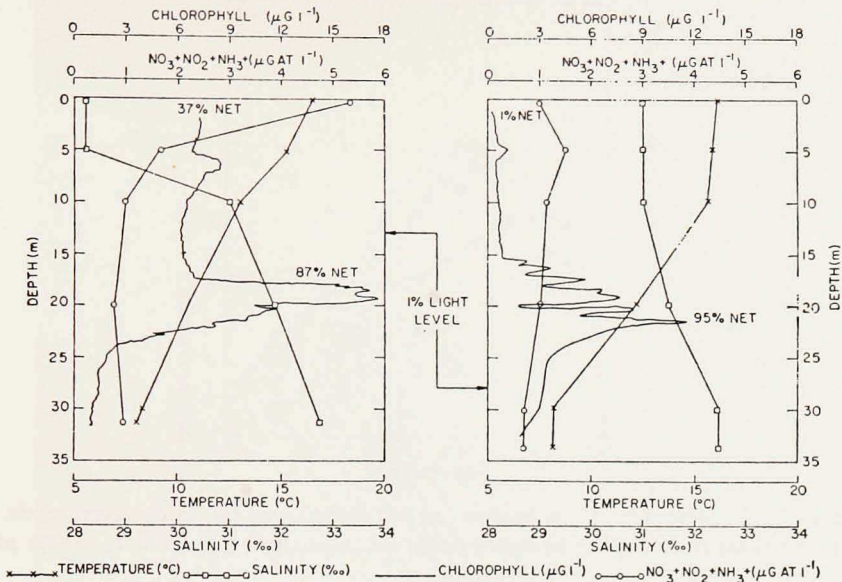


Figure 10. The vertical distribution of phytoplankton (after W. Esaias, personal communication) in relation to light, temperature, salinity, and nutrients during June 1976 A) within the Hudson River Plume and B) outside the Bight Apex.

Island, while the bottom flow was still sluggish to the southwest (Mayer *et al.*, 1980).

The biological impact of such a flow reversal was to retain and apparently concentrate *C. tripos* populations within the northwest sector of the New York Bight (Malone, 1978). An additional spatial pattern was a change in the depth of the chlorophyll maximum of *C. tripos* in relation to the pycnocline (Fig. 10). The populations outside the New York Bight Apex (Fig. 10B) were still found within the pycnocline and above the 1% light level. However, *C. tripos* populations at the same depth, but beneath the Hudson River plume, were located below both the 1% light level and the pycnocline within the Apex (Fig. 10A), i.e. the area where the 1976 anoxia event was first observed. The chlorophyll content of the *C. tripos* maximum within the pycnocline was also greater beneath the Hudson River plume than outside the Apex and may thus reflect onshore accumulation within this area in response to the June 1976 wind and current reversal events.

A change in seasonal circulation modes thus sets the stage for both the introduction and retention of *C. tripos* populations in the New York Bight. As a result of heavy runoff in February and weak March winds, earlier onset of stratification was associated with a deep pycnocline and less nutrients in April 1976 (Walsh *et al.*, 1978). These conditions would favor those species of phytoplankton adapted to low light and nutrient regimes. The early onset of spring abundance and the unusual persistence of *Ceratium tripos* throughout the summers of 1968 (Gold, 1970), 1974

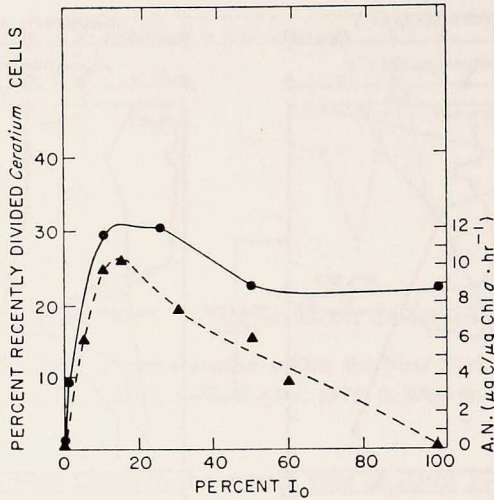


Figure 11. Light curves for carbon fixation (▲) and cell division (●) in *Ceratium tripos*. These data were taken from samples incubated under natural sunlight (i.e. 100% $I_0 \approx 2000 \mu\text{E m}^{-2} \text{sec}^{-1}$).

(Weaver, 1979), and 1976 suggests that initiation of the normal seasonal phytoplankton species succession was simply advanced in time during the spring of these years. Occurrence of extensive anoxia only in 1976, however (Table 3), suggests that physical events later in the season are of equal importance in leading to anoxic conditions.

4. Biological factors influencing the distribution of Ceratium

The effect of light intensity on the photosynthetic response and growth rate of *Ceratium tripos* has been studied in both unialgal laboratory cultures (Nordli, 1957) and in natural field populations (Stemann Nielsen, 1934; Mandelli *et al.*, 1970). The results of these studies suggest that *C. tripos* is a "shade" species, preferring low light intensities as would be found deep in the euphotic zone. A comparison of photosynthesis vs. irradiance (P vs. I) curves for the common neritic diatom *Skeletonema costatum* and *Ceratium* spp. (mostly *tripos*) was made under similar temperature and light regimes off Long Island in March 1966 (Mandelli *et al.*, 1970). The results suggest that *Ceratium* has a two-fold higher assimilation number and becomes light saturated at lower light intensities than the diatom. Similar P vs. I curves obtained in the New York Bight in 1976 and 1977 (Fig. 11) indicate that light saturation occurs at *ca.* 15% of surface intensity and that photosynthesis can be completely inhibited at full sunlight. The compensation intensity for photosynthesis in *C. tripos*, estimated from P vs. I curves obtained in 1976 and 1977 ($n=12$), is estimated to be between 0.7 and 1% of the surface irradiance (i.e. $\sim 16 \mu\text{E m}^{-2} \text{sec}^{-1}$).

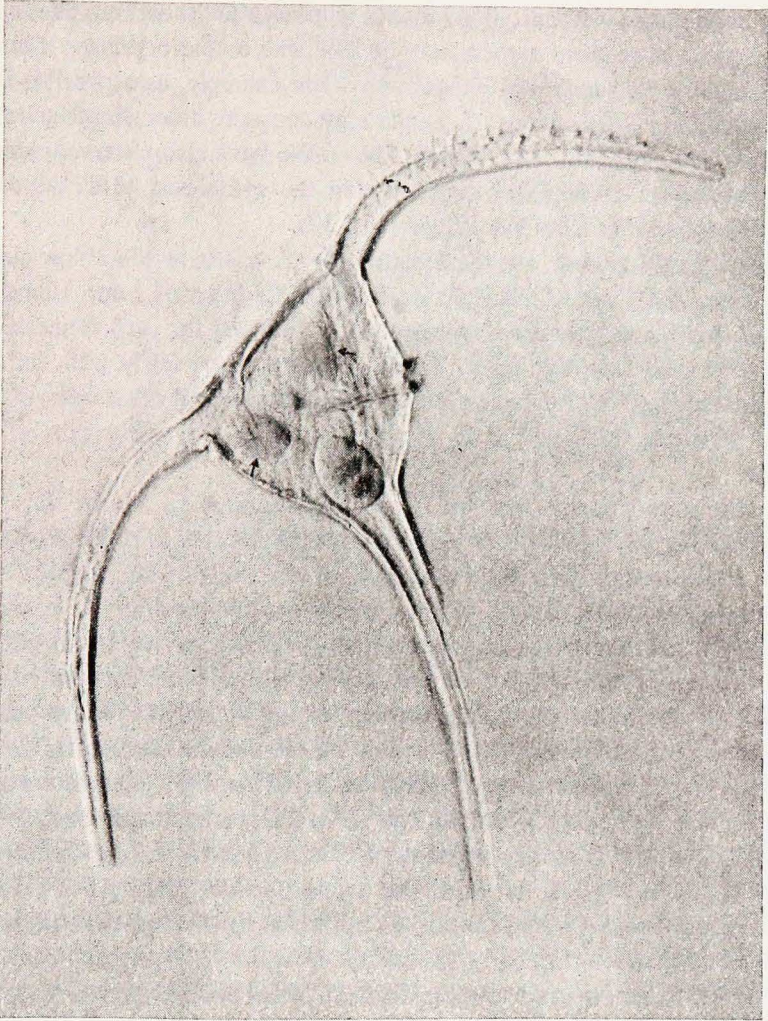


Figure 12. Nomarski differential interference photomicrograph of *Ceratium* sp. stained with acetocarmine. Nuclear inclusions of extracellular origin are indicated by the arrows.

Nitrogen assimilation in *C. tripos* does not appear to be markedly influenced by light. Nitrate reductase activity, normalized to chlorophyll biomass, is relatively uniform throughout the water column in regions dominated by *C. tripos*, while the activity of this enzyme is normally reduced by low light in diatom dominated areas (Falkowski and Howe, 1976). ^{15}N tracer studies suggest that *C. tripos* is capable of sustaining high dark uptake of NH_4^+ , in contrast to diatom-dominated communities found in the New York Bight (Conway and Whittedge, 1979). Only marginal light limitation of nitrogen assimilation was observed in these dinoflagellates at 0.2% of the surface light intensity. As it is difficult to conceive of a situation where nitrogen

would be assimilated without simultaneous photosynthetic carbon fixation, an alternative source of reduced carbon may be available to the organism. *Ceratia* have been suggested to be capable of phagotrophy. For example, as a possible food supplement within low light regions, *C. lunula* may consume other dinoflagellates (Norris, 1969; Hofeneder, 1930; von Stosch, 1964). We have also observed what appear to be inclusions of extracellular origin within the cytoplasm of *C. tripos* and *C. longipes* taken from the New York Bight (Fig. 12).

Nitrogen specific growth rates, calculated for *C. tripos* in the chlorophyll maximum (between the 1 and 0.4% light depths) off the coast of Long Island, are between 0.03 and 0.1 d⁻¹. Similar estimates were obtained for carbon specific growth (0.02 to 0.09 day⁻¹) in this layer. These estimates agree fairly well with division rates calculated from the frequency distribution of recently divided cells (cf. Apstein, 1911) of between 0.02 and 0.05 divisions d⁻¹ in the subsurface chlorophyll maximum.

Before the water column stratifies, there is sometimes an abrupt shift in spring dominance of net phytoplankton from fast growing diatoms to these slower growing *Ceratum tripos* as in March 1966 (Mandelli *et al.*, 1970). This suggests that some mechanism, other than just differential growth of phytoplankton, is a primary influence on seasonal phytoplankton species succession. Malone (1978) came to the same conclusion in consideration of the spring decline in diatoms and the relative increase of *Ceratum* on the continental shelf during March 1976. The usual spring transition of phytoplankton species from diatom-dominated netplankton to the chlorophyte-dominated nanoplankton community of the Bight Apex is not associated with changes in the rates of biomass specific photosynthesis (Malone, 1977). The disappearance of the winter-spring diatom bloom is attributed to sinking on both the continental shelf (Walsh *et al.*, 1978) and within the Bight Apex (Malone and Chervin, 1979). Species which do not sink out (i.e. motile forms), will accumulate in the region of maximum stability, i.e. the pycnocline.

In a stratified water column, phytoplankton species composition in the subsurface chlorophyll maximum is greatly influenced by the light regime relative to the position of the pycnocline. The June 1976 chlorophyll maximum at the 40 m isobath was between the 0.3 and 1% light depths, the ratio of nanoplankton to netplankton chlorophyll biomass was 0.01-0.10, and ceratian abundance was as high as 5×10^5 cells liter⁻¹ at depth (Fig. 4). In contrast, the June 1977 chlorophyll maximum was found within the 1-5% light depths, the ratio of nanoplankton to netplankton biomass was 10, and the ceratian populations were only a maximum of 1×10^4 cells l⁻¹. Similarly during June 1978, the chlorophyll maximum was above the 1% light level, beneath a shallow thermocline at the same 40 m isobath as the previous observations. Only 3×10^4 cells l⁻¹ of *C. tripos* were then found at 20 m and this species constituted 12% of the total phytoplankton. The nanoplankton (<20 μ) were 27% of the algae in 1978, with *Chaetoceros* spp. composing more than 50%

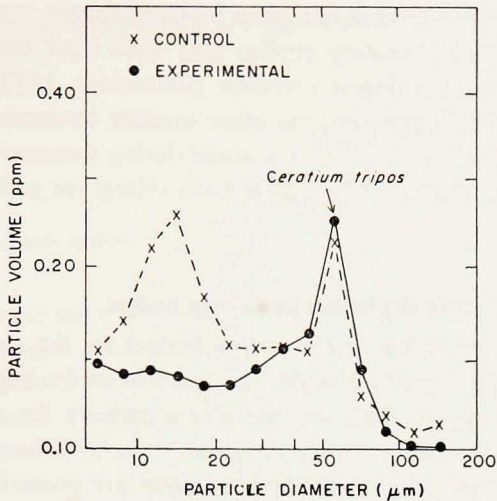


Figure 13. The grazing of *Centropages typicus* on a natural assemblage of phytoplankton during the summer of 1976 (after M. Dagg, personal communication).

of the netplankton (Falkowski and von Bock, 1979). Moreover, only 4-6 $\mu\text{g Chl } a \text{ } l^{-1}$ were found in June 1977 and 1978 in contrast to 15 $\mu\text{g Chl } a \text{ } l^{-1}$ in June 1976. These data suggest that large increases of the summer populations of *Ceratiium tripos* within the New York Bight occur in years of deep thermoclines.

At optimal light intensities, the maximum growth rates of *Ceratiium* (0.3 doublings day^{-1}) in the field (Fig. 11) and in the laboratory (Nordli, 1957) are much lower than nanoplankton (1-2 doublings day^{-1}). At suboptimal light intensities, field populations of *Ceratiium* grow as slow as 0.03 doublings day^{-1} (Elbrachter, 1973). Estimates of carbon and nitrogen specific growth rates, as well as those obtained by direct cell counting all suggest that the doubling time of *C. tripos* within the subsurface chlorophyll maximum of the New York Bight is 20-30 days. The selective removal mechanism of the summer nanoplankton community is considered to be grazing, however, rather than sinking of the spring diatom bloom.

Coastal copepods, some of the major herbivores of this ecosystem, do not appear to eat *C. tripos*, but will ingest the smaller phytoplankton. The water column contained a high percentage of nanoplankton (97%) in August 1977, and shipboard gut fluorescence measurements indicated that the summer copepod community was ingesting these small algal cells of nearshore waters (Walsh et al., 1978). In contrast, grazing experiments of the previous year (1976) suggested that *Centropages typicus*, a co-dominant of the summer zooplankton community in the inner New York Bight, does not ingest many *Ceratiium tripos*.

Particle spectra, obtained with a Coulter counter before and after incubation of zooplankton with the ambient 1976 phytoplankton assemblage (Fig. 13), indicate

that the large *C. tripos* cells were not eaten by *Centropages typicus* (M. Dagg, personal communication). Laboratory studies also show that both *Centropages* and *Pseudocalanus* spp. will not ingest ceratians (Elbrachter, 1973). While, in similar grazing experiments, *T. longicornis*, the other summer co-dominant copepod of the New York Bight, will also not ingest *Ceratium* during summer blooms within Bedford Basin (Conover, 1978) and Bras d'Or Lake (Hargrave and Geen, 1970), Nova Scotia.

5. Factors affecting oxygen depletion: an oxygen budget

In this section we present a simple oxygen budget for the summer water column in the New York Bight Apex to provide a perspective on the importance of *C. tripos* respiration below the pycnocline. We consider separately the oxygen supplies and demands above the pycnocline, below the pycnocline, and the physical mechanisms affecting oxygen resupply. The individual estimates are numerically summarized in Table 4.

5a. Normal respiration demands

Photosynthetic oxygen production and atmospheric reaeration are the two sources of oxygen above the pycnocline. More specifically, gas exchange at the air-sea interface (Z_o) acts to maintain saturation values of oxygen in the surface mechanically mixed layer (Z_m), which in the New York Bight is ~ 15 m. This means effectively that the upper boundary condition for a vertical distribution is that of full saturation at $Z = Z_m$ rather than Z_o . With a surface exchange coefficient of 2×10^{-5} cm² sec⁻¹ in a stagnant film model (Garside *et al.*, 1979), present respiration demands of the surface mixed layer (Table 4) would have to be increased more than 10 fold before exceeding the oxygen resupply rate of reaeration. Photosynthetic production, moreover, may contribute down as far as $Z = Z_e$ (Z_e euphotic zone depth), depending on the distribution of phytoplankton. Mean gross photosynthesis, calculated from carbon fixation rates, within the Apex (Malone, 1976; Thomas *et al.*, 1980) is estimated as 4640 ml O₂ m⁻² day⁻¹. Phytoplankton respiration is assumed to be 10% of the daily gross primary production (Falkowski and Owens, 1978), or approximately 460 ml O₂ m⁻² day⁻¹ within the euphotic zone.

The respiration rate of the zooplankton herbivore community (500 ml O₂ m⁻² day⁻¹) is estimated from shipboard measurements (0.07 μ l O₂ animal⁻¹ hr⁻¹ at 10-20°C) of adult *Centropages typicus* during June 1978 (S. Howe, personal communication) and assuming that this individual rate is applicable to the nearshore copepods (3×10^5 animals m⁻²) during June 1975-1976 (Judkins *et al.*, 1980). Similarly, the oxygen demand of the carnivorous zooplankton (48 ml O₂ m⁻² day⁻¹) is estimated from the oxygen uptake rate (0.5 μ l O₂ animal⁻¹ hr⁻¹ at 26°C) of medium size (100 μ g dw) *Sagitta hispida* (Reeve *et al.*, 1970) and the nearshore

Table 4. A summer oxygen budget ($\text{ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$) for the New York Bight Apex during 1976.*Above the pycnocline*

Computed respiration:

Phytoplankton	460
Metazoan	550
Sludge	1000
Dissolved organic carbon	2000
	<hr/> 4010

Observed respiration:

Water column

4050

Gross photosynthetic input: 4640

Time scale for anoxia:

~ infinity

Below the pycnocline:

Computed respiration:

Fecal pellets 300

Observed respiration:

Benthic	360
Water column	1350
<i>C. tripos</i>	5400
	<hr/> 7110

Vertical diffusive input:

with K_z of $1.0 \text{ cm}^2 \text{ sec}^{-1}$ 7000with K_z of $0.1 \text{ cm}^2 \text{ sec}^{-1}$ 700

Horizontal advective

input:

with K_z of $0.01 \text{ cm}^2 \text{ sec}^{-1}$ 700

Time scale for anoxia:

at K_z of $1.0 \text{ cm}^2 \text{ sec}^{-1}$ ~600 daysat K_z of $0.1 \text{ cm}^2 \text{ sec}^{-1}$ ~30 days

Time scale for anoxia:

~30 days

abundance (4×10^8 animals m^{-2}) of *Sagitta* spp. at the same time (Judkins *et al.*, 1980). Finally, when the respiration rate at 8°C ($0.5 \mu\text{l O}_2$ animal $^{-1}$ hr $^{-1}$) of recently hatched ($100 \mu\text{g dw}$) flounder larvae (Laurence, 1977) is applied to the mean ($N = 16$) biomass of yellow-tail flounder larvae within a patch (130 animals m^{-2}) in June 1972 (Smith *et al.*, 1978), an upper bound for oxygen demand of larval fish is $1.6 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$. Therefore we estimate the cumulative metazoan contribution to oxygen demands of the water column of this budget to be $\sim 550 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$.

The annual input of sewage sludge and dredge spoils to the Apex of the New York Bight is equivalent to an oxygen demand added to the euphotic zone of $\sim 1000 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Segar and Berberian, 1976). This input does not fluctuate annually by more than 15% (Mueller *et al.*, 1976). Most of this part of the urban oxygen demand is probably consumed within the water column (Segar and Berberian, 1976), because during the years of both high (1975, 1977) and low (1974, 1976) bottom oxygen concentrations in the Bight Apex the benthic respiration demands remain the same, $\sim 360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Thomas *et al.*, 1976, 1980).

The additional urban carbon loading of this system is in the form of dissolved organic carbon (DOC), which constitutes 90% of the daily carbon flux from the

Hudson River (Segar and Berberian, 1976). Additional DOC is produced by extracellular release from phytoplankton at a rate of $\sim 20\%$ of the net daily primary production, $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$, or $0.02 \text{ mg DOC l}^{-1} \text{ day}^{-1}$ (Thomas *et al.*, 1980). Values of DOC range from 8-10 mg C l^{-1} at the mouth of the Hudson River (Muel-ler *et al.*, 1976; Thomas *et al.*, 1980) and 15 mg C l^{-1} at the sewage sludge dump (G. Harvey, personal communication) to $\sim 1 \text{ mg C l}^{-1}$ at the edge of the shelf (J. Sharp, personal communication). The oxygen demand of DOC is estimated to be $\sim 2000 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Segar and Berberian, 1976) within the Bight Apex, where about 50% of the DOC standing crop appears to be consumed.

Independent estimates of the separate respiratory demands of the budget (Table 4) agree fairly well with the observed total utilization rates in the absence of *Ceratium* from the New York Bight. The Apex surface layer in our budget contains a cumulative oxygen demand of sewage and sludge wastes, dissolved organic carbon, non-ceratian phytoplankton respiration, and metazoan respiration ($1000 + 2000 + 460 + 550$, or $4010 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$). This total computed oxygen demand is close to the observations of the surface water column respiration ($\sim 4050 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$) without *Ceratium*. Such an oxygen demand is just balanced by a gross photosynthetic production (net + DOC production + respiration) of $\sim 4640 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ within the euphotic zone.

Below the pycnocline the two major oxygen sinks are that of benthic respiration and detrital oxidation. In the absence of *C. tripos*, the sub-pycnocline respiration rate (Thomas *et al.*, 1980) of the water column is estimated to be $\sim 1350 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$. This reflects the oxygen demands of particulate material that is sinking out of the lower water column and the DOC suspended within this layer. The benthic oxygen demand of $360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Thomas *et al.*, 1976, 1980) is comprised of both particulate matter which already has sunk to the bottom and that of the benthic infauna. The sum of these respiration demands is $\sim 1700 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$.

The detrital component consists of fecal pellets, phytoplankton particulates, and urban detrital wastes. If we assume an assimilation efficiency of 60% for the zooplankton and that 50% of the phytoplankton standing stock is removed daily from the summer euphotic zone (Walsh *et al.*, 1978; Thomas *et al.*, 1980), the fecal pellets of the herbivores would have an oxygen demand of $\sim 600 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$. Chervin (1978) estimated that, during the summer, the zooplankton ingest as much as 90% of the total particulate carbon (including fecal pellets) within the Bight Apex each day, suggesting a fecal pellet demand of $\sim 300 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ on the bottom. This compares to the measured bottom respiration rate of $\sim 360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$. The herbivores may thus ameliorate bottom oxygen consumption in the New York Bight rather than contribute to anoxia as is the case in Tokyo Bay (Seki *et al.*, 1974).

When *Ceratium* is not abundant below the surface layer, 75% of the oxygen demand of the water column ($N=21$) is located above the pycnocline (Thomas *et al.*,

1980). In August 1976, net ^{14}C production:respiration was $\cong 1.5:1$ above the pycnocline. This suggests that after respiratory demands are subtracted from the gross primary production, more oxygen is evolved from phytoplankton photosynthesis than is consumed by heterotrophic processes. During such times the dissolved oxygen in the water column is sustained near saturation levels above the pycnocline, while oxygen is slowly depleted near the bottom.

5b. Respiration of *Ceratium* populations

If deep populations of *Ceratium tripos* are not consumed, continue to respire, and are concentrated by currents in a local area of the New York Bight, these dinoflagellates could create an oxygen deficit beneath the pycnocline. Using a measured mean carbon content of $25 \text{ ng C cell}^{-1}$ for *C. tripos*, a Q_{10} of 2.3, and a power law of weight dependent respiration (Banse, 1976), Falkowski and Howe (1976) computed a respiration rate of $1.4 \times 10^{-4} \mu\text{l O}_2 \text{ cell}^{-1} \text{ hr}^{-1}$ at 10°C . In June 1977, the respiration of *C. tripos* was directly measured in the New York Bight using both an oxygen polarographic electrode (Falkowski and Owens, 1978) and electron transport activity assays (Packard, 1971). The mean of the measured respiration rates was also ca. $1.4 \times 10^{-4} \mu\text{l O}_2 \text{ cell}^{-1} \text{ hr}^{-1}$ (C.V. $\pm 18\%$, $n=6$) at 10°C . Using this specific respiration rate, Falkowski and Howe (1976) estimated that the integrated water column respiration beneath the pycnocline was $5400 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ as a result of *Ceratium* respiration during the summer of 1976. This value is ~ 15 times that of the mean benthic respiration rate of $360 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$.

The effect of a deep thermocline and prolonged abundance of *C. tripos* populations thus would appear to shift the normal water column oxygen demand from above to below the pycnocline. Just mineralization, rather than continued respiration, of the ceratian biomass ($3255 \text{ mg at C m}^{-2}$) within 20 m of the bottom during June 1976 would have consumed ca. 70% of the initial mean saturation oxygen levels (Falkowski and Howe, 1976). The benthic respiration was 13-14% of the total respiration (water column and benthos) in August 1976, compared to 6-7% in August 1975, implying that there had been an increased carbon input to the benthos during 1976 (Thomas *et al.*, 1980).

5c. Resupply of oxygen

To prevent anoxia the respiration demands in the bottom layer must be met by resupply of oxygen from either vertical diffusion across the pycnocline or by horizontal advection. Vertical diffusive fluxes of oxygen can be estimated from the equation:

$$\frac{\partial \text{O}_2}{\partial t} = \partial \left(\frac{K_z \frac{\text{O}_2}{\partial z}}{\partial z} \right)$$

where K_z is the vertical eddy coefficient across the pycnocline.

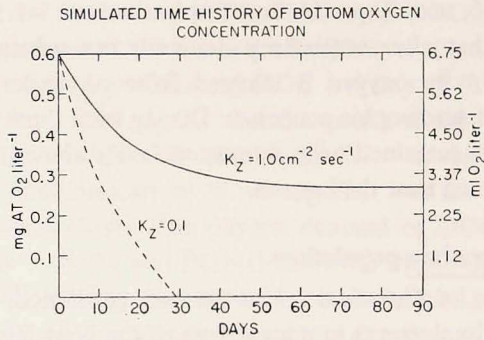


Figure 14. Computed depletion of bottom oxygen by *C. tripos* respiration with apparent vertical eddy coefficients of 0.1 and 1.0 $\text{cm}^2 \text{sec}^{-1}$ across the pycnocline in the Apex of the New York Bight.

Falkowski and Howe (1976) used this formulation with apparent eddy diffusion coefficients of 0.1 $\text{cm}^2 \text{sec}^{-1}$ assumed across the pycnocline and 10 $\text{cm}^2 \text{sec}^{-1}$ above and below the pycnocline. A *C. tripos* respiration rate of $1.4 \times 10^{-4} \mu\text{l O}_2 \text{cell}^{-1} \text{hr}^{-1}$ and the observed distribution of *C. tripos* (Fig. 10) were used to estimate the rate of change in bottom water O_2 . The initial condition of the bottom oxygen was assumed to be 6.75 $\text{ml O}_2 \text{l}^{-1}$. The results of these calculations (Fig. 14) suggest that the layer beneath the pycnocline would become anoxic within ~ 30 days, or a depletion rate of $\sim 0.2 \text{ ml O}_2 \text{l}^{-1} \text{day}^{-1}$. In contrast, if an eddy diffusion coefficient of 1.0 $\text{cm}^2 \text{sec}^{-1}$ was used across the pycnocline, anoxia would not occur (Fig. 14), even in the presence of *C. tripos*. These results suggest that (1) *C. tripos* respiration could have a major influence on bottom water O_2 , (2) small changes in eddy diffusivity could make large differences in bottom water O_2 fluxes, (3) normal benthic respiration does not result in anoxia, and (4) anoxia could result in 3-5 weeks if *C. tripos* is abundant below the pycnocline and the eddy diffusivity is low. Previous estimates of the time scale for anoxia were on the order to 2-3 weeks (Segar and Berberian, 1976).

Using an apparent K_z of 0.1 $\text{cm}^2 \text{sec}^{-1}$ (P. Biscaye, personal communication) the rate of oxygen supplied is sufficient to meet the benthic oxygen demand and part of the oxygen demand of the sub-pycnocline water column in normal years (Table 3). In abnormal years, if a *C. tripos* demand of 5400 $\text{ml O}_2 \text{m}^{-2} \text{day}^{-1}$ is added to the background respiration of the aphotic waters of the Bight Apex, the total oxygen demand of the bottom layer could be as high as 7110 $\text{ml O}_2 \text{m}^{-2} \text{day}^{-1}$. Under these circumstances anoxia is likely to occur within about 30 days provided that *C. tripos* is not flushed from the New York Bight.

Longshore advective processes could both transport *C. tripos* out of the Bight Apex and laterally renew the bottom oxygen stocks (Han *et al.*, 1980). Our calculations suggest, however, that with an apparent K_z of 0.01 $\text{cm}^2 \text{sec}^{-1}$, inclusion of a

southwest flow rate of 1.0 km day^{-1} upstream of the anoxic region, and a long-shore gradient of $0.03 \text{ ml O}_2 \text{ l}^{-1} \text{ km}^{-1}$ within the lower 20 m of bottom water in 1976, only $\sim 700 \text{ ml O}_2 \text{ m}^{-2} \text{ day}^{-1}$ would be renewed (Table 4) by this alternative resupply process. Some dead *C. tripos* cells were observed on the bottom in July and not August 1976 (Mahoney, 1979). These organisms are subject to both parasitism (Arndt, 1967) and ingestion by ciliates and isopods (Elbrachter, 1973), and it is possible that their bloom was terminated within the Apex or along the New Jersey coast rather than flushed seaward. The apparent spread south of anoxia along the New Jersey coast from the Apex during July and the continuation of anoxia in the New York Bight until September 1976 suggests that the near bottom flow was weak. The low oxygen water was not flushed until the fall overturn of this system.

6. Conclusions

In the absence of *Ceratium tripos*, the water column respiration is an order of magnitude greater inside the Apex of the New York Bight than off Long Island. Most of this increased oxygen demand results from the urban carbon wastes, sewage sludge and DOC, with an associated nitrogen loading (Fig. 10) of the Bight Apex. Stimulated by the increased availability of nitrogen (Ryther and Dunstan, 1971), growth of phytoplankton in the summer simultaneously reduces both the nitrogen load and the oxygen demand of the large carbon input of the Apex. Because eutrophication occurs as a result of the present low level sewage treatment processes, the urban carbon loading in the Apex is effectively transformed into phytoplankton, which are normally grazed during stratified conditions of the water column (Malone and Chervin, 1979). While $\sim 1.0\%$ organic carbon is found in some of the Apex sediments, little of this oxygen demand is usually due to remineralization of summer phytoplankton (Officer and Ryther, 1977). Most of their carbon is instead stored in longer-lived components of the metazoan part of the food web.

In abnormal years, when physical conditions allow early onset of phytoplankton species succession, the slow seasonal buildup of *C. tripos* populations represents a large summer carbon pool which is not removed by herbivores. Under these conditions, if a steady summer wind regime allows *C. tripos* populations to accumulate beneath the Apex pycnocline, just the oxygen demand of these organisms exceeds the rate of resupply within the aphotic zone.

We have presented evidence that a causal chain of events (Table 3) leads to aperiodic anoxic events of varying spatial extent within the New York Bight. For example, we believe that most of these events did not occur in 1966 and all in 1976. Our calculations suggest that anoxia could have occurred off the New Jersey coast in July 1976 without any anthropogenic carbon loading from New York City. Prediction of these events has both immediate and future societal value, i.e. removal of shellfish before loss to anoxia and the best mode of sewage treatment. As one moves from prediction of meteorological to biological processes of the coastal

food web, however, increasing sources of error emerge in such prognostications (Tingle *et al.*, 1979). Nevertheless, sufficient information on the appropriate time and space scales of continental shelf processes is beginning to emerge that suggests delineation of cause and effect within a perturbation response of the coastal zone is feasible goal over the next decade.

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