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The Effect of Chemical and Physical Regimes on Primary Production off the U.S. East Coast

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Despite higher concentrations of nutrients and chlorophyll *a*, available data indicate that, over an annual cycle, primary production in the Mid-Atlantic Bight is little if any higher than that in shelf waters south of Cape Hatteras. Principal factors regulating productivity in the northern region appear to be the long period of low temperatures and reduced insolation and deep mixing during the winter and dominance of slow growing dinoflagellates during the late summer. Periods of very high production occur during the spring and fall. In contrast, the productivity to the south seems to show little seasonal fluctuation. Warm temperatures and adequate light maintain high growth rates year-round and although the biomass is low, the rapid turnover of cells results in a relatively high total productivity.

INDEX DESCRIPTORS: Primary production, dinoflagellates, biomass

The majority of studies of primary production in the shelf water off the east coast of the United States have been conducted in the Mid Atlantic Bight. Here production reaches 3 gC/m^2/day in the early spring in the mid shelf region off Long Island but drops below 0.4 g/m^2/day during the summer. Winter values are generally between 0.4 and 0.8 gC/m^2/day (Ryther and Yentsch, 1958). Estimates of the rate of carbon fixation generally lie between 100 and 200 gC/m^2/year in the Mid-Atlantic Bight (Smayda, 1973).

One of the few measurements of seasonal primary production in the South Atlantic Bight is that of Haines and Dunstan (1975) who made four cruises between Charleston, South Carolina and Jacksonville, Florida. They found no apparent seasonality of primary production in these waters and estimated the annual production over the shelf to be about 170 gC/m^2/year, a value that falls within the range reported for more northerly waters. This apparent similarity is surprising since it is well established that the waters north of Cape Hatteras contain substantially higher nutrient and chlorophyll concentrations than do those to the south (Ryther and Yentsch, 1958; Ketchum *et al.*, 1958; Vaccaro, 1963; Garside, *et. al.*, 1976; Stefansson and Atkinson, 1967; Haines, 1974; Haines and Dunstan, 1975). However, it must be remembered that at low nutrient concentrations it is the *rate* of nutrient flux that limits phytoplankton growth rates. In addition, chlorophyll levels are related to primary production in a complex way determined partially by nutrients but also by light, temperature, prehistory of the cells and species composition. A small standing crop growing rapidly can produce as much new carbon as a large, slow growing population and can endure the same amount of grazing pressure.

This presentation considers the possibility that the annual primary production of the regions north and south of Cape Hatteras really is approximately equal. I will compare standing stocks and estimated growth rates for both regions and look for factors which may equalize the product, (primary production) over an annual cycle.

The South Atlantic Bight

Very few studies have been carried out on primary production of the South Atlantic Bight, here defined as the region between Cape Hatteras and Cape Canaveral. The work of Haines (1974; and Haines and Dunstan, 1975) has shown a consistent peak in chlorophyll and primary production in the Georgia coastal waters although even here surface chlorophyll levels seldom exceed 2 mg/m^3 less than one-half the maxima found in coastal waters off Long Island (Ryther and Yentsch, 1958; Mandelli, *et al.*, 1970; Walsh *et al.*, 1978).

Surface data from one of Haines' cruises, conducted in September, 1971, is displayed in Figure 1. All stations indicated were over the inner shelf (water depths less than 25 m). The relatively high levels of nutrients and chlorophyll in Georgia waters is apparent, but the maximum nitrate concentration is only 0.1 μg-moles/1 which corresponds to the minimum values encountered off Long Island (Ketchum, *et al.*, 1958). Carbon fixation closely mimicked chlorophyll *a*, despite the large fluctuations in standing stock. The surface productivity index (carbon fixed per mg chlorophyll *a*/day) was almost always high, averaging 215 mgC/mg Chl *a*/day off Georgia and 340 off South and North Carolina. A productivity index of 300 indicates that the population is doubling approximately every 12 hours (2.0 times per day) based on the equation, $K = 3.32 \log(1 + A/F)$ where K is the doubling rate, A is the productivity index, and F is the carbon: chlorophyll ratio of the phytoplankton (taken to be 100 based on determinations made in the area).

Ammonia and phosphate were more plentiful than nitrate. The very low amount of nitrate and its relatively close correlation to primary production tentatively identifies it as the limiting nutrient. But when the daily nitrogen demand is computed from the carbon fixation rate (based on a C:N uptake ratio of 6:1 by atoms) we find that the amount of available nitrate would have to be replaced approximately every hour to keep pace with uptake. Even when we include the more abundant ammonia, uptake will deplete nitrogen stocks in less than a day. Run-off is low in this region and intrusions of nutrient-rich deep water are sporadic indicating the productivity of the South Atlantic Bight is dependent upon rapid and efficient recycling (Haines and Dunstan, 1975). Since recycling is not 100% efficient, new nitrogen must be brought in periodically. However, recycling permits these introductions to be intermittent maintaining a nearly steady production rate between nutrient injections.

Recycling does not allow any increase in standing stock. To do so requires tying up an increased amount of nitrogen in cellular material, and this must come from a new nutrient source or production rates will have to decline. Thus, although Haines and Dunstan (1975) determined that even the highly productive region of the Georgia coast is based 90% on recycled nitrogen, it must receive more new nitrogen (nitrate) than the adjacent waters to support its high standing stock of phytoplankton. As we have already seen, the data depicted in Figure 1 indicate that this is in fact the case. Nitrate values off the Georgia coast are about three times those found in coastal waters off the Carolinas. The source of this nitrate has not been determined, but since the Georgia system differs from adjacent waters to the north primarily in its large river discharge, it seems likely that this represents the major nutrient source. In addition, the large tidal range off Georgia enhances the mixing of run-off with coastal waters and the recycling of nutrients from bottom sediments.

Moving north from Georgia nearshore surface primary production

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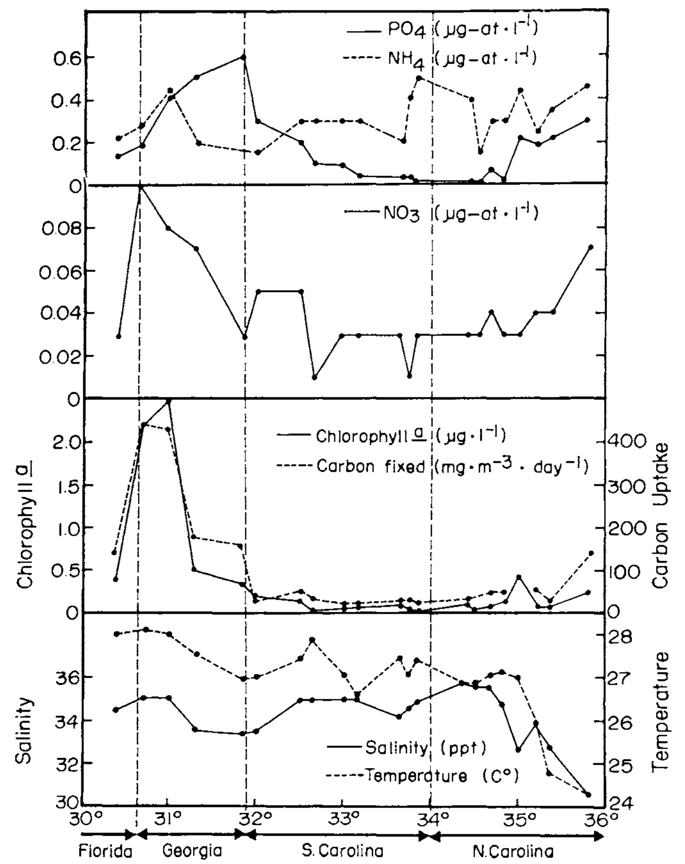

Fig. 1. *The surface distribution of nutrients, chlorophyll, primary production, salinity and temperature between northern Florida and Virginia. Samples were taken between 2 and 17 km from the coast in water less than 25 m deep. Data from Haines (1972).*

declined sharply in the low run-off areas of South and North Carolina. During *our* studies in Raleigh Bay in 1971-1975, (Barber, R.T. and S.A. Huntsman, unpublished) we found evidence for a very narrow band of enhanced production that extended no more than 5 km from the coast. This zone was not related to the proximity of an inlet and so did not appear to result from run-off from Pamlico Sound. We conducted a study in 1971 tracing phosphate and salinity from the mouth of the Neuse River across Pamlico Sound to Ocracoke Inlet on Raleigh Bay. A plot of phosphate against salinity shows that phosphate loss exceeded that explainable by dilution until the salinity increased to 10 ppt (Figure 2). Beyond this almost no further loss in phosphate occurred despite a nearly two-fold dilution. However, beyond the inlet phosphate levels continued to drop, while salinity remained unchanged. Since there is no major source of pollution at the inlet, we must conclude that these high phosphate values represent reworking of the sediments. Unfortunately no nitrogen data was collected, but assuming that it behaved like phosphate it is apparent that in regions where run-off is low, elevated near-shore production is not a direct result of freshwater discharge but may result from benthic release of nutrients during warmer months when biological activity is high. During the winter the sediments presumably replenish their stocks by removing nutrients (possibly as detritus) from the water column.

Deep water intrusions from the Gulf Stream are frequently mentioned as a major source of new nutrients for the shelf waters of the South Atlantic Bight. The nitrate content of the source water at the shelf break is quite variable (Figure 3). Consequently the nitrate content of the water intruding over the shelf varies from less than 1 to greater than 3 μg-moles/1. Temperature profiles from Haines' September, 1971 cruise are plotted in Figure 4. It is evident that shelf width is of primary importance in determining the influence of an intrusion on the water structure over the shelf. Narrow shelves off Raleigh Bay, N.C. and Cape Canaveral permit deep water to intrude over the bottom to within 10 or 20 km of the coast. Wide shelves such as those off Georgia and Onslow Bay, N.C. restrict its penetration to the outer shelf, emphasizing that this is unlikely to be a reliable source of nutrients for the highly productive inshore waters off Georgia.

Not only the intensity but also the frequency and duration of intrusions are important in determining their effect on the nutrient budget of the shelf. Data in this regard is extremely sparce, although the ongoing cooperative studies at North Carolina State University, the University of Miami, and Skidaway Institute of Oceanography are rapidly overcoming this deficiency. Current measurements from mid-shelf in Raleigh and Onslow Bays are available for several weeks in 1975 (Barber, Huntsman, and Pillsbury, unpublished; Pietrafesa, *et al.*, 1975). Although the two bays were monitored at intervals approximately a month apart, both were sampled during the summer intrusion period. In both cases onshore bottom flow was generally dependent upon southwesterly winds but onshore velocity in Onslow Bay was about one-third that recorded in Raleigh Bay reflecting the greater distance from the Gulf Stream's influence. Nutrients in the waters intruded over Onslow Bay are depleted during their journey over the shelf, (Atkinson, *et al.*, 1976). Although the more sluggish circulation in Onslow Bay should favor efficient recycling and ameliorate the need for fresh nutrients somewhat, low chlorophyll levels in this bay indicate that it is less productive than Raleigh Bay. Current meter data from Long Bay (North and South Carolina) waters are lacking but its wide shelf suggests a circulation pattern similar to Onslow Bay, requiring prolonged periods of favorable winds to bring intruded bottom water across the shelf. Nonetheless, in view of their intensity during the prolonged periods of southwesterly winds intrusions are probably the most important source of new nutrients to the Carolina shelf waters during the spring and summer.

Our studies in Raleigh Bay (Barber and Huntsman, unpublished) indicated that surface production is fairly constant across the shelf and as water deepens to 40-50 m, the total integrated production increases. Thus, unlike the Georgia Bight where Haines and Dunstan (1975) found maximum production in water less than 20 m deep, we found maximum production in the mid to outer shelf waters. Here we encountered values of 0.4 to 1.4 gC/m²/day during both summer (July-August) and fall (November-December) indicating annual primary production rates similar to those reported by Haines and Dunstan (1975) for inner shelf waters further south. However, primary production seems highly variable particularly during the fall, and an intense monitoring program would be required to obtain a meaningful seasonal comparison. For example, production over the shelf was very low averaging 0.21 gC/m²/day, during the cruise in December, 1974, as the region was flooded with low nutrient, low chlorophyll water brought in from the surface of the Gulf Stream by the prevailing southerly winds. In contrast, a cruise at the end of November 1975 found productivity an order of magnitude higher (1-2 gC/m²/day). This productivity was associated with an influx of nutrient enriched high chlorophyll Virginia Water around Cape Hatteras. The temporal and spatial extent of these Virginia Water incursions is not clear. Stefansson, *et al.*, (1971) reported a good correlation to northeasterly winds. Since these winds dominate the entire period from September through February, a mechanism for maintaining production throughout the winter period is ap-

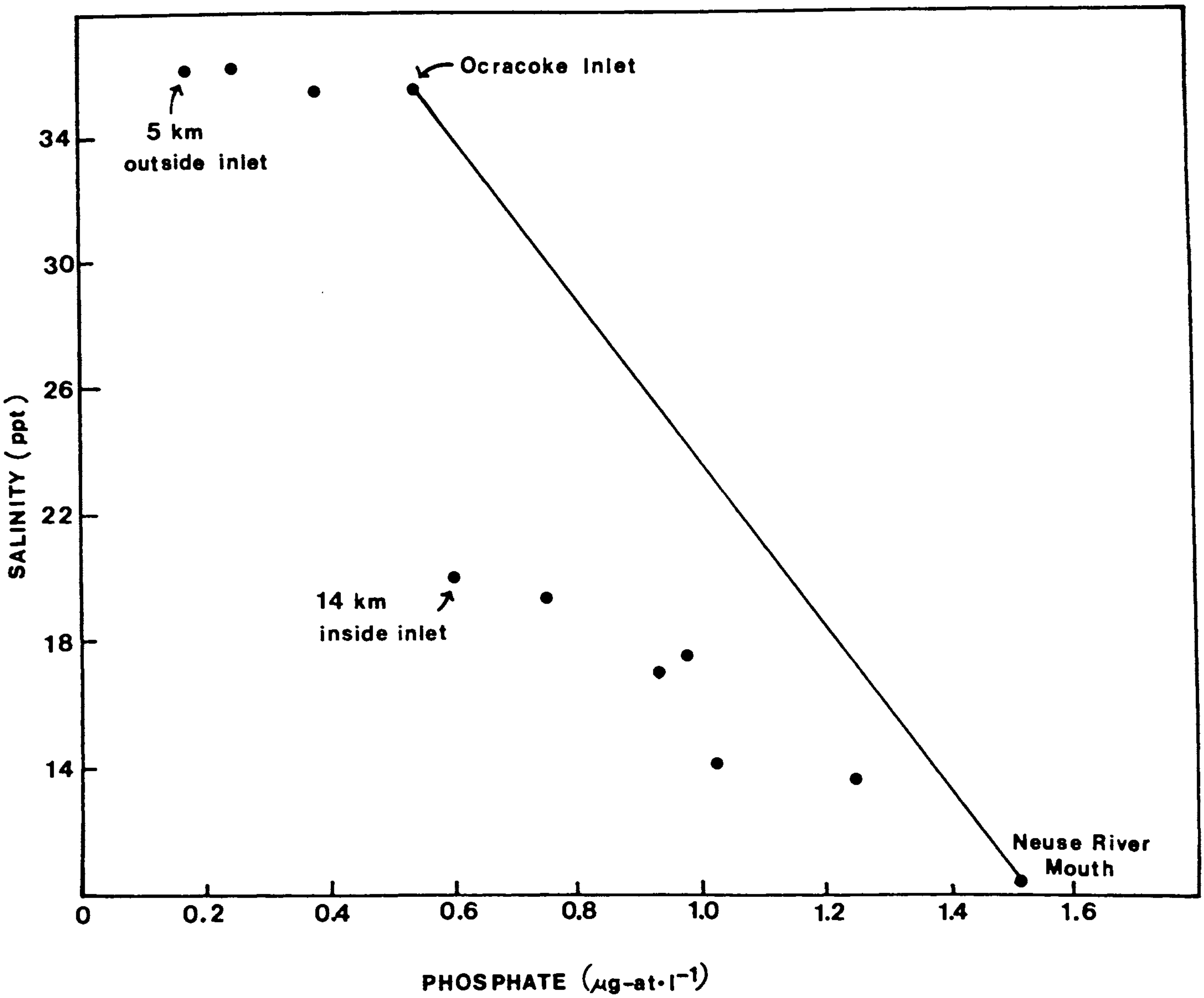

Fig. 2. *The change in the phosphate:salinity ratio between the mouth of the Neuse River in Pamlico Sound and Ocracoke Inlet. The straight line indicates changes that would be expected from dilution with sea water alone. Instead, phosphate values are lower than expected, indicating that the sound is a sink for the nutrient. Beyond the inlet phosphate levels continue to drop but no sea water dilution occurs suggesting that release from the sediments in the shallow water of the sound and inlet maintains phosphate concentrations above those found in sea water further offshore.*

parent. However, these waters seldom if ever extend south of Onslow Bay, and productivity off South Carolina may be depressed in winter months.

Light and temperature limitation are not major problems in the South Atlantic Bight. Temperatures above 15°C do not exert an effect on the growth rates when they are restricted to two doublings/day or less by nutrients (Eppley, 1972). In the South Atlantic Bight minimum temperatures in coastal waters drop below this value only in February and to a lesser extent in January and March (Schroeder, 1966). Light also remains high enough in the winter so that net photosynthesis occurs in the upper two-thirds of the shelf water column. In the summer, the entire water column over the shelf is in the euphotic zone.

To summarize conditions in this region:

1) The nitrogen supply for primary production comes largely from recycled nutrients. Due to the high temperature and light conditions the productivity index is high year round with growth rates of one to two doublings per day.

2) Intrusions are the primary source of new nutrients for North and South Carolina. Their impact is greatly affected by shelf width. Typically, nitrate values of 2-3 μg moles/l are associated with this near

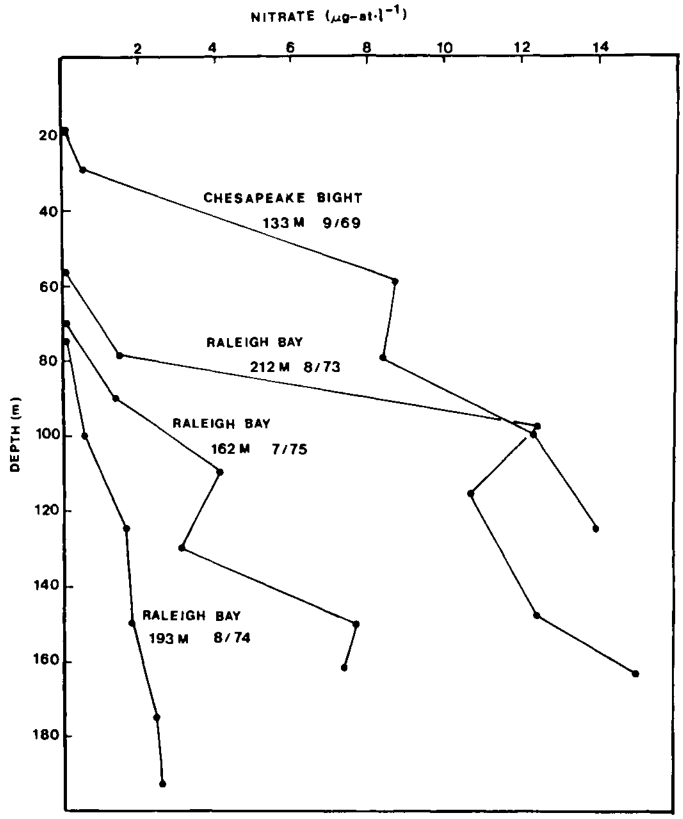

Fig. 3. *The variable nitrate profile of water impinging on the shelf in Raleigh Bay during cruises made in three consecutive summers. Depths indicated represent total water depths at each station. Data from ATLANTIS II cruise 52 off Virginia is included to demonstrate the much shallower extent of high nutrients in slope water north of Cape Hatteras (Data partly from Smith and Barber (1974) and Corwin (1970)).*

bottom layer and the amount of nitrate brought in is sufficient to supply the total nitrogen requirement of the shelf for 2-3 days. However since it is generally restricted to the bottom 10-15 m it may not be efficiently utilized except during unusually strong intrusions or those followed by intense mixing. Where the shelf is narrow intrusions may regularly enter the well-lit inshore zone and contribute to the elevated productivity of this zone.

3) Run-off is low throughout most of the South Atlantic Bight and, with the exception of the Georgia coastal waters, has little direct impact on productivity. The elevated summer-time production encountered in some inshore waters (regardless of proximity to an inlet) probably results from mineralization and dissolution of nutrients from the sediments and in some locations from surfacing of the intrusion layer as discussed above.

4) During winter months production is not seriously limited by light or low temperatures. However, intrusions are infrequent and run-off is low so that productivity throughout much of the South Atlantic Bight is limited by the efficiency of recycling. Advection of water from north of Cape Hatteras is probably the major source of new nutrients to North Carolina waters. More important perhaps are the large phytoplankton populations associated with this water. As they move south and mix with the warmer water surrounding them, their productivity is enhanced and may equal that found in summer. The temporal extent of these incursions have not been defined, but in view of their correlation with north-easterly winds, they may occur throughout much of the fall and winter (September through February). Since, unlike deep water intrusions, Virginia Water enters at the surface and brings its own phytoplankton, its impact on primary production may be greater.

With an observed production of 0.2-2 gC/m²/day up to it seems likely that primary production over the shelf of the South Atlantic Bight averages 100-200 gC/M²/year.

The Mid Atlantic Bight

This region, running from Cape Hatteras to the Nantucket Shoals has received more intensive investigation than the shelf waters to the south. Seasonal studies of nutrients and primary production while not intense, are sufficient to give confidence in their conclusions.

Two physical factors change sharply as we move north of Cape Hatteras: 1) run-off increases dramatically reducing the salinity in coastal waters to below 31 ppt in the spring. The high nutrients associated with run-off disappear more rapidly. Garside *et al.* (1976) found the nutrient effects of the New York estuary diminished sharply 20 km from the mouth but the phytoplankton that result from these enhanced nutrients may become dispersed over a large area, contributing to the productivity and providing a potential source for recycled nutrients. 2) The influence of the Gulf Stream declines. Its place over the continental slope is relinquished to slope water, a mixture of southward flowing water from several sources containing an abundance of nutrients extending close to the surface (Figure 3). This water readily moves over the shelf in response to favorable winds, and in so doing high nutrient, low temperature water is brought virtually to the coast (Figure 4). Although penetration of this water into the euphotic zone is inhibited by the generally deeper water column in Mid Atlantic Bight shelf waters and by stratification during the summer, it keeps the shelf supplied with nutrients during the period of deep mixing from November through April (Walsh *et al.*, 1978). Stratification reduces surface nitrate values to near-zero by September (Ketchum, *et al.*, 1958) but ammonia remains close to 1 μg-mole/1 (Vaccaro, 1963). Chlorophyll *a* values decline during the summer but seldom go below 1 μg/1 (Ryther and Yentsch, 1958), in contrast with values less than 0.1 μg/1 frequently encountered in Carolina shelf waters.

Throughout the year chlorophyll *a* ranges from about 1 to 5 mg/m³ and nitrogen from 1 to 10 μg-at/1. Yet primary production exceeds 1 gC/m²/day only in March and April, (Ryther and Yentsch, 1958). The reason for low growth rates in winter is obvious. Temperatures drop below 5°C in coastal waters. At this temperature the maximum potential growth rate is about one-half that at 15°C (Eppley, 1972). Day length and light intensity are also greatly reduced. Incident light averages less than 100 langleys per day from November through January. Photosynthesis at the surface under these light conditions is only about one-fourth of the light saturated level and almost no net photosynthesis occurs below the upper 1-2 meters. Since intense wind mixing keeps the phytoplankton distributed down to 80 m or more, the overall productivity index becomes extremely low.

In March and April stratification becomes apparent and as the phytoplankton are held in the well-lit zone their production climbs sharply. By July production is down again as chlorophyll and nutrients decline. The surface productivity index doesn't exceed 85 mgC/mc Chl *a*/day during the summer (Mandelli, *et al.*, 1970). The four-fold difference between these values and those reported for the South Atlantic Bight may reflect differences in the composition of the phytoplankton communities. Whereas diatoms dominate the phytoplankton year-round in southern waters (Marshall, 1971), dinoflagellates, which typically have slow growth rates, become important in northern waters during the summer (Mandelli *et al.*, 1970). The growth rate of *Ceratium tripos* one of the dominate dinoflagellates was estimated to be

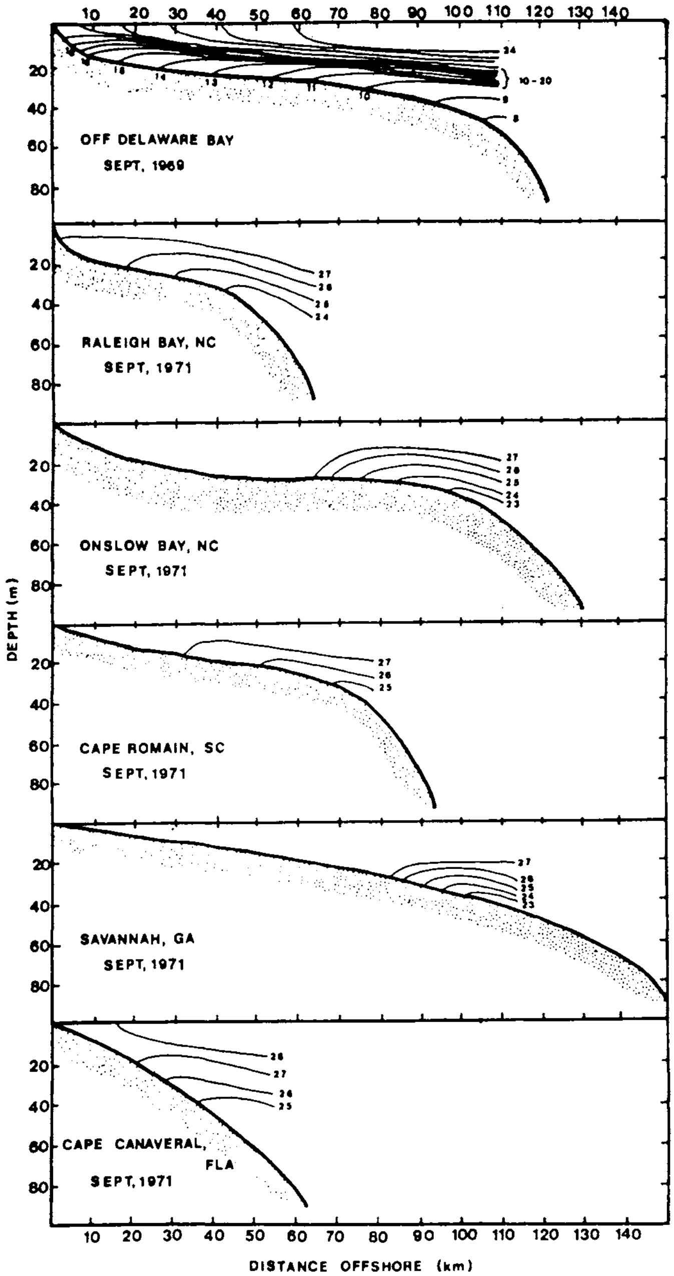

Fig. 4. *Temperature profiles made during EASTWARD cruise E-22C-71, between Cape Canaveral and Raleigh Bay, N.C. The transect off Delaware Bay was made on ATLANTIS II cruise 52. Data from Haines (1972) and Corwin (1970).*

only 0.2 doubling per day (Walsh *et al.*, 1978).

SUMMARY

Primary production in the South Atlantic Bight fluctuates primarily in response to short-term wind-driven events which affect the circulation over the shelf. No seasonal pattern is apparent since light and temperature are adequate year-round.

In contrast, the Mid Atlantic Bight is characterized by periods of very low production in the summer and winter separated by highly productive spring and fall blooms. The result is that both systems appear to sustain primary production rates of 100-200 g carbon per year.

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