Phytoplankton primary production on the northwestern Atlantic shelf

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Phytoplankton production of particulate and dissolved organic carbon was measured using the \(^{14}\text{C}\) simulated \textit{in situ} sunlight incubation method during 23 surveys of the Mid-Atlantic Bight, Georges Bank, and the Gulf of Maine. Annual phytoplankton production (particulate plus dissolved) ranged between 260 and 470 g C m\(^{-2}\) yr\(^{-1}\) in various regions, which places this continental shelf system among the most productive in the world. The highest rates of daily phytoplankton production were consistently found off the coast of New Jersey in the sewage-polluted apex of the New York Bight, followed by the shallow, well-mixed waters on Georges Bank. In general, high daily rates of primary production (1 g C m\(^{-2}\) d\(^{-1}\)) were observed during most of the months sampled and were not limited to the 'spring bloom' period.

Available data indicate that microheterotrophs above the thermocline (not the seabed) supply most of the mineralized nutrients required by the productive summer phytoplankton communities. Size-fractionation of the \(^{14}\text{C}\)-labeled particulate organic carbon revealed that netplankton (> 20 \(\mu\)m) are major primary producers during the spring and fall blooms in the Mid-Atlantic Bight, on Georges Bank, and in the Gulf of Maine; however, the nanoplankton (< 20 \(\mu\)m) are responsible for most of the annual photosynthesis of organic carbon. On an annual basis, the percentage of particulate carbon productivity by nanoplankton increased from the shallow to the deep water. Euphotic per cent extracellular release (PER) of dissolved organic carbon by phytoplankton ranged between 0 and 55 %, averaging 15 %, and increased from the shallow to the deep waters of the continental shelf. No well-defined seasonal cycle in euphotic PER was evident from our data.

Introduction

Published information on annual phytoplankton production on the Northwest Atlantic continental shelf is limited to studies of Georges Bank (Riley, 1941), the New York Bight (Ryther and Yentsch, 1958), the coastal water off Long Island (Mandelli \textit{et al}., 1970) and a study of the apex of the New York Bight (Malone, 1976a, b). In this paper we present the first comprehensive shelf-wide baseline estimates of annual phytoplankton carbon production for northwestern Atlantic continental shelf water between Cape Hatteras and Nova Scotia.

Methods

Our estimates of annual phytoplankton carbon production are derived from measurements of \(^{14}\text{C}\) uptake made throughout the euphotic layer at 628 stations during 23 Northeast Fisheries Center interdisciplinary MARMAP (Marine Resources Monitoring, Assessment and Prediction) and Ocean Pulse surveys. Twenty-one surveys took place between August 1978 and June 1980 and two surveys were made in spring and midsummer 1977. The locations of the study area and sampling stations for MARMAP surveys are depicted in Figure 1. Measurements of primary productivity were usually
made at two stations each day. Incubations lasted 5 h, with morning stations ending and afternoon stations commencing at approximately local solar noon. The details of our procedure for measuring primary productivity are described in 'A manual for the measurement of total daily primary productivity using \(^{14}\text{C}\) simulated \emph{in situ} sunlight incubation' (O’Reilly and Thomas, 1983). Estimates of daily productivity were made by integrating data over depth and extrapolating the \(^{14}\text{C}\) uptake measured during the 5 h incubation to a ‘light-day’.

**Results**

Recurrent gradients in concentrations of phytoplankton are often found in the Mid-Atlantic Bight and over Georges Bank (O’Reilly \textit{et al.}, 1981). In these two regions, average water column concentrations of chlorophyll \(a\) decrease as the depth of the water column increases. Chlorophyll \(a\) is often 5–10 times more concentrated in inshore water (< 20 m) in the Mid-Atlantic Bight than in water adjacent to the shelf break. Likewise, chlorophyll \(a\) concentrations often decrease
Figure 2. Regions of the continental shelf defined by recurrent patterns of phytoplankton biomass concentration. GM = Gulf of Maine; GB = Georges Bank; LI = Long Island; NJ = New Jersey; DE = Delaware; CH = Chesapeake; and slope = 200–2000 meters.

progressively 5–10 fold from the central, shoal area (< 60 m) on Georges Bank to the perimeter of the Bank. Patterns of phytoplankton abundance were not as obvious in the Gulf of Maine, partly because sampling there was not as extensive as sampling in southern areas of the shelf. However, during most surveys, the lowest average water column concentrations of chlorophyll \( a \) are found in the Gulf of Maine. When relatively high levels of chlorophyll \( a \) (\( > 3 \text{ mg m}^{-3} \)) are observed in the Gulf of Maine, they are usually found at stations less then 70 m deep near the coast (Penobscot Bay, Casco Bay, Cape Anne, Massachusetts Bay, and Cape Cod Bay).

To characterize the annual cycle of phytoplankton primary production, the measurements of daily integral phytoplankton production were grouped, irrespective of year, according to the regions of the continental shelf depicted in Figure 2, based on recurrent patterns of average water column concentration of phytoplankton and on shelf hydrography and bathymetry. Annual car-
Figure 3. Daily integral phytoplankton production (particulate and dissolved organic carbon) plotted against time for 14 regions. Line in figures = arithmetic mean of data clusters. Data points indicated by 'a' (apex of New York Bight) and 'd' (near Delaware estuary) not included in the arithmetic mean.
Figure 4. Estimates of annual phytoplankton production (particulate and dissolved organic carbon) by region, g C m⁻² yr⁻¹. Data collected in hatched areas not included in the regional estimates of annual production.

Carbon production curves for the shelf regions are shown in Figure 3. Measurements of phytoplankton in Regions CH1, 2, and 3 were pooled since too few measurements were made in each of these three regions to permit characterization of the production cycle.

Apparent from many of the annual production curves is that high daily rates of phytoplankton production (1 g C m⁻² d⁻¹) were observed during most of the months sampled and were not limited to the 'spring bloom' period. In fact, in many of the regions some of the highest values during the year were measured in May through August, when the water column was vertically stratified. Throughout the shelf, production was sustained at levels of 1 g C m⁻² d⁻¹ throughout the summer period. A vigorous October 'fall bloom' also appears to be a main event in the annual production cycle in several regions (GM, GB1, LI1, LI2, NJ2, DE1, DE2). Generally, sampling was not adequate in December and January to characterize average production for these months in many of the regions. However, in several
regions where sampling was adequate (GM, GB2, LI2, NJ1, NJ2, DE1, DE2) daily production was lowest during the months of December, January, and February.

The area under each curve in Figure 3 was integrated over a year to generate estimates of annual phytoplankton production for each of the regions. The values, ranging from 260 to 470 g C m\(^{-2}\) yr\(^{-1}\) are shown by region in Figure 4. During this study the rate of phytoplankton production exceeded 2 g C m\(^{-2}\) d\(^{-1}\) at 47 of 628 stations. Thirteen were in the apex of the New York Bight, nine in the shoal area (< 60 m) on Georges Bank (GB1 region).

The highest rates of daily phytoplankton production of particulate and dissolved organic carbon were consistently in the apex of the New York Bight adjacent to the coast of New Jersey. Values exceeded 2·5 g C m\(^{-2}\) d\(^{-1}\) during spring, summer, and fall. Omitting the high daily productivity values in the apex of the New York Bight near the New Jersey coast lowers the estimates of annual production for the NJ1 region from 460 to 370 g C m\(^{-2}\) yr\(^{-1}\). Since the apex represents less than 10 % of the area of the NJ1 region, the estimate of 370 g C m\(^{-2}\) yr\(^{-1}\) is taken as representative of the NJ1 region. Similarly, the estimate for the DE1 region is 360 g C m\(^{-2}\) yr\(^{-1}\), after deleting values near the mouth of the Delaware estuary. The second most productive (470 g C m\(^{-2}\) yr\(^{-1}\)) region of the shelf is the area of Georges Bank less than 60 m deep. The area on Georges Bank deeper than 60 m is less productive (300 g C m\(^{-2}\) yr\(^{-1}\)). The Gulf of Maine, the mid-shelf region off Long Island, the mid-shelf region off the Delaware—Maryland—Virginia coasts, and the slope region between Georges Bank and Cape Hatteras are among the least productive with 290, 280, 260, and 280 g C m\(^{-2}\) yr\(^{-1}\), respectively. Among the most productive are the three regions off New Jersey and the region adjacent to the Delaware—Maryland—Virginia coast with annual production of 370, 370, 390, and 360 g C m\(^{-2}\) yr\(^{-1}\).

Frequency (%) histograms of integral daily rates of total phytoplankton production by region (Figure 5) show that the shallow water on Georges Bank is more productive annually than the deeper water of Georges Bank or the Gulf of Maine. The mode for the daily production for the shallow water is 1·375 g C m\(^{-2}\) d\(^{-1}\) whereas the modes for the Gulf of Maine and the deeper water on Georges Bank are 0·875 and 0·625 g C m\(^{-2}\) d\(^{-1}\), respectively. These histograms also show that primary production of the inner-, mid-, and outer-shelf areas of the Mid-Atlantic Bight are similar.

In nearly all of the areas, the nanoplankton contribution to particulate carbon production is lowest during February/March and October/November, periods which coincide with spring and fall ‘blooms’ when net-phytoplankton (particularly diatoms) are relatively more abundant. In several regions (GB2, NJ1, NJ2, DE1, DE2, DE3, CH1, CH2, CH3) netplankton dominated particulate production at a few stations during the season when the water column was stratified. In the shallow area on Georges Bank and the shallow inshore regions NJ1 and DE1 netplankton played a greater role in total production.

In addition to the seasonal trends in nanoplankton production, there are differences in the contribution of nanoplankton to annual particulate carbon production among regions of the shelf. Figure 6 gives frequency (%) histograms of the percentage of daily integral particulate organic carbon production by nanoplankton (< 20 µm) by region. The percentage of particulate production due to nanoplankton increases from inshore to offshore in the Mid-Atlantic Bight (Fig. 6). Nanoplankton dominated (accounted for greater than 50 % of the particulate synthesis) particulate production in 50 % of the observations made in the shallow mid-shelf region, 89 % of the observations in the deeper outer shelf region and 90 % of the observations from the slope water. A similar bathymetric relationship exists for Georges Bank, where nanoplankton dominated particulate production in 38 % of observations in the shallow area compared with 87 % in the deeper waters of the Bank. The pattern of relative production by nanoplankton and netplankton in the deep waters of the Gulf of Maine was similar to the pattern observed on the deep outer shelf of the Mid-Atlantic Bight and the deeper water over Georges Bank. Nanoplankton dominated particulate production in 81 % of the observations in the Gulf of Maine. Strong dominance of particulate production by the netplankton (< 10 % nanoplankton) occurred infrequently in the Gulf of Maine, Georges Bank, Mid-Atlantic Bight, and the slope, whereas strong dominance of particulate production by nanoplankton (> 90 % nanoplankton) was frequently observed in all of these areas except in the shallow waters of Georges Bank and the Mid-Atlantic Bight.

Euphotic per cent extracellular release (euphotic PER) of dissolved organic carbon by phytoplankton greater than 15 % was observed often in most regions, with a range of 0 to 55 %. A clear seasonal cycle of euphotic PER is not evident from our data. However, PER increased with depth on the continental shelf (Fig. 7). In the shoal area of Georges Bank, only 25 % of the measurements of euphotic PER exceeded 15 %, whereas in the deeper areas on Georges Bank, 41 % of the observations of euphotic PER exceeded 15 %. The arithmetic mean euphotic PER for the shallow and deep water of Georges Bank was 10 % and 17 %, respectively. Euphotic PER for the Gulf of Maine is similar to that observed for the deep water on Georges Bank. Euphotic PER exceeded 15 % in approximately 32 % of the observations with a mean of 13 %. In the Mid-Atlantic Bight, euphotic PER exceeded 15 % in 32 % of the observations inshore, in 50 % of the observations from mid-shelf, in 51 % of the observations on the outer shelf, and in 55 % of the observations from the slope. The arithmetic mean euphotic PER for the
Figure 5. Frequency (%) histograms of daily integral phytoplankton production (particulate and dissolved organic carbon) by region. Number in upper right corner, under region = number of observations. Ordinate = % of observations. Data collected in apex and near Delaware estuary excluded from Mid-Atlantic Bight inshore.
Figure 6. Frequency (%) histograms of the percentage of daily integral particulate organic carbon production by nanoplankton (<20 μm) by region. Number in upper left corner, under region = number of observations. Data collected in apex and near Delaware estuary excluded from Mid-Atlantic Bight inshore.
Figure 7. Frequency (%) histograms of the euphotic per cent extracellular release of dissolved organic carbon by phytoplankton. Number in upper right corner = number of observations. Data collected in apex and near Delaware estuary excluded from Mid-Atlantic Bight inshore.
inner-, mid-, and outer-Mid-Atlantic Bight shelf and slope is 14 %, 17 %, 18 %, and 19 %, respectively.

Discussion
Comparison with other estimates of annual primary production

Estimates of annual phytoplankton production of organic carbon (particulate and dissolved) for 14 regions of the northwest Atlantic continental shelf range between 260 and 470 g C m⁻² yr⁻¹. These estimates place this continental shelf system among the most productive shelf ecosystems in the world (Table 1). Using comparable methods based on phytoplankton assimilation of inorganic ^14C, annual phytoplankton particulate production has been estimated to be 90–100 g C m⁻² yr⁻¹ for the North Sea (Steele, 1974); 102–128 g C m⁻² yr⁻¹ for the eastern Scotian Shelf (Mills and Fournier, 1979); 127 g C m⁻² yr⁻¹ for the northern Baltic (Wulff, 1979); 154–194 g C m⁻² yr⁻¹ for the Baltic Proper (Ackefors and Lindahl, 1979); 370–480 g C m⁻² yr⁻¹ for the sewage-polluted apex of the New York Bight (Malone and Chervin, 1979); 370–480 g C m⁻² yr⁻¹ for water along the coast of Georgia off the Altamaha River (Thomas, 1966). The majority of these studies measured particulate organic carbon production, whereas we measured both particulate and dissolved organic production by phytoplankton. About 15 % of the measured carbon photoassimilated by phytoplankton is released as dissolved organic carbon (< 0.45 μm), and 85 % is retained in a particulate form (> 0.45 μm), based on the arithmetic mean of all our measurements (628) of daily euphotic PER. In the most productive regions such as the shallow area on Georges Bank, euphotic PER averaged 10 %, whereas in the least productive regions such as the area over the slope between 200 and 2000 m, euphotic PER averaged 19 %. Consequently, estimates of annual phytoplankton production of particulate organic carbon for the 14 areas ranged between 216 and 423 g C m⁻² yr⁻¹.

Our estimate of total annual phytoplankton production for the inner shelf region off the coast of Long Island, New York (290 g C m⁻² yr⁻¹), is slightly lower than estimates of annual particulate production made by Mandelli et al. (1970) for water 20 m deep off Long Island (343 g C m⁻² yr⁻¹). Malone and Chervin (1979) estimated particulate annual production in the apex of the New York Bight to be between 370 and 480 g C m⁻² yr⁻¹. Our measurements support the finding of Malone (1976a, b) and Malone and Chervin (1979) that the apex of the New York Bight is an exceptionally productive, highly eutrophic area. Our estimate of average (arithmetic mean) integral daily primary production in the portion of the apex adjacent to the New Jersey coast is 2.34 g C m⁻³ d⁻¹. Four values measured in the apex

Table 1. Comparison of our estimates of annual primary production for Mid-Atlantic Bight, Georges Bank, and Gulf of Maine shelf water with annual estimates for other systems.

<table>
<thead>
<tr>
<th>Area</th>
<th>g C m⁻² yr⁻¹</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oceanic</td>
<td>55–70 P</td>
<td>Steemann Nielsen and Jensen (1957)</td>
</tr>
<tr>
<td>North Sea</td>
<td>90–100 P</td>
<td>Steele (1974)</td>
</tr>
<tr>
<td>Coastal water, Japan</td>
<td>90 P</td>
<td>Hogetsu (1979)</td>
</tr>
<tr>
<td>Northern Baltic</td>
<td>127 P</td>
<td>Wulff (1979)</td>
</tr>
<tr>
<td>Eastern Scotian Shelf</td>
<td>102–128 P</td>
<td>Mills and Fournier (1979)</td>
</tr>
<tr>
<td>Washington and Oregon coast, USA</td>
<td>60–152 P</td>
<td>Anderson (1964)</td>
</tr>
<tr>
<td>New York Bight</td>
<td>100–160 P</td>
<td>Ryther and Yentsch (1958)</td>
</tr>
<tr>
<td>Hanu Bight (Baltic Proper)</td>
<td>154–194 P</td>
<td>Ackefors and Lindahl (1979)</td>
</tr>
<tr>
<td>North Sea (Central, Southern Bight)</td>
<td>200–250 P</td>
<td>Fransz and Gieskes (1984)</td>
</tr>
<tr>
<td>Georgia Bight, USA</td>
<td>132–285 P</td>
<td>Haines and Dunstan (1975)</td>
</tr>
<tr>
<td>Off Long Island coast, 20 m</td>
<td>343 P</td>
<td>Mandelli et al. (1970)</td>
</tr>
<tr>
<td>Coastal water off India</td>
<td>434 P</td>
<td>Quasim (1979)</td>
</tr>
<tr>
<td>Gulf of Maine</td>
<td>252 P</td>
<td>290 T</td>
</tr>
<tr>
<td>Georges Bank</td>
<td>249–423 P</td>
<td>300–470 T</td>
</tr>
<tr>
<td>Mid-Atlantic Bight</td>
<td>216–320 P</td>
<td>260–390 T</td>
</tr>
<tr>
<td>Georgia coast off Altamaha River</td>
<td>547 P</td>
<td>Thomas (1966)</td>
</tr>
</tbody>
</table>

P = particulate production.
T = particulate and dissolved organic carbon production.

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exceeded 4 g C m\(^{-2}\) d\(^{-1}\) (Fig. 3). These values are quite high, particularly when compared with the theoretical maximum sustainable daily production for nearshore eutrophic waters of 9 g C m\(^{-2}\) d\(^{-1}\) (Takahashi and Parsons, 1972).

Ryther and Yentsch (1958) reported a value of 160 g C m\(^{-2}\) yr\(^{-1}\), 135 g C m\(^{-2}\) yr\(^{-1}\), and 100 g C m\(^{-2}\) yr\(^{-1}\) for annual phytoplankton production in New York Bight water between 25 and 50 m deep, between 50 and 1000 m deep, and between 1000 and 2000 m deep, respectively. These estimates were derived from calculations of daily primary production based on chlorophyll, incident radiation, and vertical extinction of light in the euphotic layer (Ryther and Yentsch, 1957). Data from five stations, in each of the three depth ranges, from six surveys (September, December, February, March, April, and July, 1956/1957) were used to estimate annual production. Our estimates of annual production in six regions of the New York Bight, less than 200 m deep, range between 280 and 390 g C m\(^{-2}\) yr\(^{-1}\). These estimates are double the production estimates made by Ryther and Yentsch (1958) who stated that ‘No accurate calculation of annual production may be made from six scattered points’ (p. 334). The estimates of annual production made by Ryther and Yentsch overlap with our estimates when low sampling frequency is taken into consideration. P. Falkowski (Brookhaven National Laboratory, pers. comm.) estimated annual particulate production in the New York Bight at 280 g C m\(^{-2}\) yr\(^{-1}\), based on measurements made primarily on a transect off the coast of Long Island between 1975 and 1979. This estimate is in good agreement with our estimates of particulate annual production (230–270 g C m\(^{-2}\) yr\(^{-1}\)) for the three regions off Long Island.

Differences in annual primary production between inner-, mid-, and outer-shelf areas of the Mid-Atlantic Bight are minor when compared on a square meter basis. However, it should be kept in mind that both standing stocks of chlorophyll (O'Reilly et al., 1981) and primary production, expressed per cubic meter, are several times higher inshore than offshore. The mean euphotic depth is 10, 19, 28, 38, and 44 m for the apex of the New York Bight, the inner-, mid-, and outer-shelf of the Mid-Atlantic Bight, and over the slope, respectively; therefore primary production per cubic meter, and the concentration of food for herbivores, in nearshore water is roughly 2–5 times greater than in offshore water.

On 6 cruises, Riley (1941) measured the production and consumption of dissolved oxygen by plankton collected in surface water and incubated in light and dark bottles on shipboard for 24 h. He estimated gross production on Georges Bank at 0.84 g C m\(^{-2}\) d\(^{-1}\) (January), 1.27 g C m\(^{-2}\) d\(^{-1}\) (March), 3.95 g C m\(^{-2}\) d\(^{-1}\) (April), 1.70 g C m\(^{-2}\) d\(^{-1}\) (May), and 1.26 g C m\(^{-2}\) d\(^{-1}\) (June). He estimated net production at 0.11 g C m\(^{-2}\) d\(^{-1}\) (January), 0.14 g C m\(^{-2}\) d\(^{-1}\) (September), 0.02 g C m\(^{-2}\) d\(^{-1}\) (February), 0.05 g C m\(^{-2}\) d\(^{-1}\) (March), 0.95 g C m\(^{-2}\) d\(^{-1}\) (April), 0.54 g C m\(^{-2}\) d\(^{-1}\) (May), and 0.63 g C m\(^{-2}\) d\(^{-1}\) (June). Riley’s estimates of gross production fall within the range of our average values except in April when his estimate is four times our estimate (Fig. 3). However, his net production estimates are lower than the range of most of our measurements, except in April when the estimates are similar (≈ 0.9 g C m\(^{-2}\) d\(^{-1}\)). Differences are probably due to methodology or sampling frequency, or both.

Primary production by netphytoplankton vs nanophytoplankton

In the Gulf of Maine, Georges Bank, and Middle Atlantic Bight during the early spring period ‘spring bloom’ and during the autumn ‘fall bloom’, the larger netphytoplankton (probably diatoms) are major contributors to the measured primary production. However, Figure 6 demonstrates that the smaller nanophytoplankton are responsible for most of the annual synthesis of organic carbon on the northwestern Atlantic continental shelf. Our measurements of chlorophyll a in netphytoplankton and nanophytoplankton made concurrently with 14C uptake measurements also indicate that the nanophytoplankton predominate. In general, nanophytoplankon strongly dominated primary production during the summer-stratified season throughout the Mid-Atlantic Bight, Gulf of Maine, and deep water on Georges Bank. The shallow water on Georges Bank was an exception, since during the summer netplankton played a larger role in photosynthesis than in any of the other regions studied. Neither net- nor nanoplankton strongly dominated the particulate production during the year in this shoal area, particularly when compared with the patterns observed in the deeper waters of Georges Bank, the Gulf of Maine, and outer shelf areas in the Mid-Atlantic Bight.

Pomeroy (1974) indicated that nanoplankton are the dominant photosynthesizers of carbon in many estuarine, coastal, and oceanic ecosystems. Malone (1971) found that nanoplanketers (< 20 μm) dominated both phytoplankton standing stocks and production in neritic and oceanic waters in the eastern tropical Pacific and Caribbean, although netplankton played a greater role in production in the neritic areas than in the oceanic areas. In a study of the apex of the New York Bight, he found that nanoplankton were responsible for 59% of the annual primary production (Malone, 1976a, b). Thronsden (1978) reported that nanoplanckton < 20 μm dominated carbon uptake in photosynthetic capacity measurements made between May and September at two stations in Oslofjorden, whereas netplankton > 20 μm were responsible for most of the carbon uptake during March.

The pattern of increased nanoplankton contribution to particulate carbon production from inshore to offshore waters of the Mid-Atlantic Bight is similar to the pattern found by Bishop et al. (1980) for the Geor-
Gorgia Bight, south of our study area. Our findings of a progressive increase in the contribution of nanoplankton to particulate production from the inner shelf to the outer shelf and slope of the Mid-Atlantic Bight are supported by studies by Marshall (1976, 1978), who found a shift from a predominantly diatom flora to a phytoflagellate flora, progressing seawards.

Several researchers have investigated the relative roles played by various environmental and biological factors (light, temperature, salinity, nutrients, physical stability of water column, vertical water movement, morphology, and flotation capacity of algal cells and grazing) in controlling the cell-size composition and species composition of the phytoplankton community (Braarud, 1962; Dugdale, 1967; Semina, 1968; Huburt, 1970; Smayda, 1970; Malone, 1971; Parsons and Takahashi, 1973; Durbin et al., 1975; Pingree et al., 1976; Taguchi, 1976; Malone, 1977). It appears to us that the following factors may be important in promoting relatively high netplankton production over Georges Bank. The shallow region on Georges Bank < 60 m is vertically well mixed by tide and wind forces throughout the year. Consequently, vertical density stratification does not occur in this area during the summer (Colton et al., 1968; Bumpus, 1976). Chlorophyll a concentrations are also homogeneously distributed throughout the shallows during the summer (O'Reilly et al., 1981). The euphotic layer over the shallow area on Georges Bank averaged 24.5 m and the ratio of euphotic depth/water column depth averaged about 0.5 over the study. Consequently, phytoplankton may spend a large fraction of the time in the euphotic layer. The relatively high rate of vertical mixing in the shallows may constitute a major factor which offsets the inherent advantages which small phytoplankters have over larger phytoplankters in obtaining nutrients and maintaining themselves in the euphotic layer (Munk and Riley, 1952; Smayda, 1970; Eppliey et al., 1978).

Relationship between extracellular release and total primary production

Euphotic PER increases from inshore to offshore water, from eutrophic to oligotrophic water, and as the concentration of phytoplankton m⁻³ decreases (Anderson and Zeutschel, 1970; Thomas, 1971; Ignatiades and Fogg, 1973; Raymont, 1980; Mague et al., 1980). Our findings concur. Mean euphotic PER was 10% in the highly productive water < 60 m on Georges Bank, whereas mean euphotic PER was 17% in the deeper, less productive water on Georges Bank. Similarly, mean euphotic PER increased from 14% to 19% from the inner shelf to the outer shelf and slope in the Mid-Atlantic Bight.

Although the magnitude of annual primary production is similar for inner shelf and outer shelf, mean water column concentrations of chlorophyll a (phytoplankton) are usually five or more times greater in nearshore than in offshore waters in the Mid-Atlantic Bight. However, the percentage of particulate ¹⁴C uptake by nanoplankton, on an annual basis, also increased from the shallow to the deep areas studied. The onshore-offshore gradient in euphotic PER might possibly be due to onshore-offshore shifts in the size composition and species composition of the photo-synthetic community. Hellebust (1967) showed that PER could vary among species of phytoplankton grown under similar conditions. It is also possible that the bathymetric-related shifts in euphotic PER are related to changes in the quantity, activity, and kinds of heterotrophic bacteria or onshore-offshore shifts in the kinds of labile-refractory dissolved organic compounds released by phytoplankton.

Summer phytoplankton production in vertically stratified water

Throughout the shelf, production is sustained at about 1 g C m⁻² d⁻¹ throughout the summer period. This pattern is contrary to the description of annual cycles of production on continental shelves at temperate latitudes given by Ryther and Yentsch (1958), who suggested that reduced primary production in the summer resulted from the presence of a thermocline which restricted the upward transport of nutrients regenerated from below the thermocline to the euphotic layer.

The sustained high phytoplankton production observed throughout the season when the water column is stratified contributes significantly to the annual production of the Northwest Atlantic shelf water. At present, the ecological mechanisms responsible for supplying nutrients to the actively assimilating phytoplankton during the stratified summer period are poorly understood. Harrison (1980) suggested that mineralization in the sediment as a nutrient source for plankton productivity in continental shelf water ranged from over 30% of their requirements inshore, to less than 20% at the shelf break. Thomas et al. (1979) reported that the seabed accounted for an average of 6% of the total (water column and seabed) aerobic oxygen consumption per square meter during summer in the New York Bight. Similar studies of the apex of the New York Bight and Georges Bank (Thomas et al., 1976, 1978) revealed that oxygen consumption by the seabed during the summer was less than 10% of the total oxygen consumption. If the ratio of the nutrients released to oxygen consumed is similar at the seabed and in the water column, then the seabed is not an important source of nutrients required by the actively assimilating summer stocks of phytoplankton in the New York Bight. Thomas et al. (1978, 1979) have pointed out that organic mineralization in the water column represents a major source of recycled nutrients on Georges Bank.
and in the New York Bight. Malone (1976b) indicated that regeneration of ammonium in the upper water column in the apex during the summer months represents an important source of nitrogen for phytoplankton.

Harrison (1980) suggested that most of the regeneration of plant nutrients in shelf water is performed by microheterotrophs (bacteria and microzooplankton) in the euphotic layer. Walsh (1981) estimated that approximately 46% of the annual nitrogen demand of phytoplankton in the New York Bight is supplied by recycling mineralization processes and 37% by slope water. However, more shelf-wide descriptive baseline studies of *in situ* heterotrophic mineralization of organic matter and concomitant release of nutrients are needed before an accurate assessment can be made concerning the relative roles played by recycling and by estuarine and slope-water sources of nutrients in supplying the nitrogen and other nutrients required by the very productive phytoplankton communities throughout the Cape Hatteras–Nova Scotia shelf system.

From our studies, we conclude that the northwest Atlantic continental shelf is one of the most productive in the world, with high rates of production persistent from spring through autumn, and not limited to spring and fall blooms only. These high values are important in sustaining the zooplankton and benthic communities that support fish populations from Cape Hatteras to Nova Scotia. On Georges Bank, this results in a total fish production of from 40 to 70 kcal m$^{-2}$ yr$^{-1}$ (Sissenwine et al., 1984).

References


