

Primary production calculations in the Mid-Atlantic Bight, including effects of phytoplankton community size structure

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Abstract

We developed an absorption-based primary production model that includes the effects of phytoplankton community size structure for the continental margin and adjoining Gulf Stream waters of the Middle Atlantic Bight (MAB). The model uses seasonal cycles of phytoplankton community size structure from previously published results, representative absorption spectra, remotely sensed chlorophyll concentration, sea surface temperature, photosynthetically active radiation, in situ determination of mixed layer dynamics, and previously determined nitrate concentration. The model allows for both light- and nutrient-limitation during the MAB seasonal cycle. Primary production was calculated every month for 5 yr for study areas representing shelf, shelf break, slope, and Gulf Stream waters. Two main approaches were taken to calculate production: using satellite observations integrating to the depth of the mixed layer and using profile observations integrating to the depth of the euphotic zone. The profile euphotic zone production estimates were greater than the satellite mixed layer estimates. Additionally, the timing of production peaks and troughs was largely related to the depth of integration, with profile euphotic zone peak production occurring generally 2 months after the satellite mixed layer estimates. Relative to cell size and seasonality, primary production was regulated more by biomass than light acquisition capability. Comparison of remotely based production estimates and estimates made with in situ depth-dependent data revealed that approximately 30% of daily water column photosynthesis was missed by satellite-based estimates.

Many primary production models have been derived for use with remotely sensed chlorophyll concentration (Behrenfeld and Falkowski 1997a,b; Campbell et al. 2002; among many others). Estimates of primary productivity relate phytoplankton standing stock biomass (chlorophyll *a*) to the rate of carbon fixation. This relation is not constant but varies with light, nutrients, mixing, species composition, physiological stress, and other factors. Our goal is to combine remotely sensed data with in situ observations of phytoplankton absorption based on cell size to better describe the ecological and physiological processes affecting primary productivity estimates within the Middle Atlantic Bight (MAB). We focus on the incorporation of community size structure to improve estimates of primary production.

Many biogeochemical processes are directly related to the distribution of phytoplankton size classes in a given environment or time (Longhurst 1998), and size distribution is a major biological factor that governs the functioning of pelagic food webs (Legendre and Le Fevre 1991). The size of

the cell determines how the pigments are packaged within the cell affecting the absorption of light. The absorption coefficient is a measure of the fraction of incident light absorbed per unit volume in relation to the light incident on the surface (Kirk 1994). In this study, the chlorophyll-specific mean spectral absorption of phytoplankton (\bar{a}_{ph}^*) is used. \bar{a}_{ph}^* is the absorption per unit volume normalized by the phytoplankton chlorophyll concentration and averaged over the range of photosynthetically available radiation (Falkowski and Raven 1997).

Ciotti et al. (2002) described a strong covariation of the size of the dominant organism and several factors controlling the spectral shape of the absorption coefficient. Despite the physiological and taxonomic variability in phytoplankton community structure, variation in the spectral shape of the absorption coefficient can be described by changes in dominant cell size (Ciotti et al. 2002). Although simple parameterizations have already been proposed regarding changes in the absorption spectra of phytoplankton with chlorophyll *a* (Bricaud et al. 1995; Sathyendranath et al. 2001), the parameterization proposed by Ciotti et al. (2002) has an explicit ecological interpretation and no direct dependence on chlorophyll *a*.

There are inherent limitations to satellite-based productivity estimates. Satellite sensors are only able to measure bio-optical properties in the first optical depth, whereas primary production extends at least three times deeper (Morel and Berthon 1989). The first optical depth corresponds to different physical depths but the same overall diminution of irradiance (Kirk 1994). In addition, the deep chlorophyll maximum, characteristic of oligotrophic oceanic waters, where nutrient depletion occurs in the upper layers, is completely missed (Cullen 1982). Production that is potentially missed by satellite-based estimates can be quantified by comparison with profile production estimates that use depth-dependent

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chlorophyll, temperature, cell size, and nitrate concentration profiles.

The MAB extends along the North American East Coast from Cape Hatteras to Georges Bank. Shelf waters within this region are among the most productive in the world ocean with seasonality characteristic of the temperate zone (O'Reilly and Busch 1984). The MAB is characterized by light-limited, well-mixed, nutrient replete conditions in the winter (Malone et al. 1983; O'Reilly and Zetlin 1998) and stratified, nutrient-limited conditions in the summer (Ketchum et al. 1958; Walsh et al. 1978). The physical and chemical transition that occurs from light-limited to nutrient-limited phytoplankton growth is also marked by a change in phytoplankton assemblage from microplankton ($>20\ \mu\text{m}$) to nanoplankton and smaller size fractions ($<20\ \mu\text{m}$, collectively referred to as nanoplankton) dominance (O'Reilly and Zetlin 1998). In addition, the regional characteristics of the continental shelf, shelf slope front, Slope Sea, and Gulf Stream produce seasonally varying production gradients through different physical mechanisms. The range of physical, chemical, and geologic conditions and their consequences on biology make this region fascinating for studying phytoplankton ecology and physiology. The objectives are to quantify primary production in several regions of ocean margin and adjoining Gulf Stream waters of the MAB, investigate seasonal variability in production based on cell size variability, estimate interannual variability during the period 1997–2002, and quantify production that is potentially missed by satellite-based estimates.

Methodology

Four study areas were selected along the mean track of the merchant vessel *Oleander*, serving in the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) volunteer observing program providing oceanographic measurements on a weekly basis during its crossings within the MAB from New Jersey to Bermuda. The study area selection was based on bathymetry, resolution of the in situ datasets, and chlorophyll concentration gradients. The locations correspond to shelf, shelf break, slope, and Gulf Stream waters. The study areas were each $33.4\ \text{km}^2$ (Fig. 1). The time period was the first 5 yr of the sea-viewing wide field-of-view sensor (*SeaWiFS*) mission (September 1997–August 2002).

Satellite-derived observations—Chlorophyll *a* and photosynthetically active radiation (PAR) were derived from individual *SeaWiFS* satellite passes over the study region using *SeaWiFS* version 4 University of Rhode Island standard processing (Yoder et al. 2002). Individual scenes were mapped at the highest resolution ($1\ \text{km}\ \text{pixel}^{-1}$). Monthly chlorophyll and PAR composites were calculated from digital byte values by determining the geometric mean (median) of all non-missing and nonmasked pixels and then converting to geophysical values (Fig. 1). Chlorophyll and PAR monthly composited data were extracted for the study areas and averaged over the entire area to obtain a single monthly estimate of each parameter for each of the four study areas. The geometric mean was selected rather than the arithmetic mean

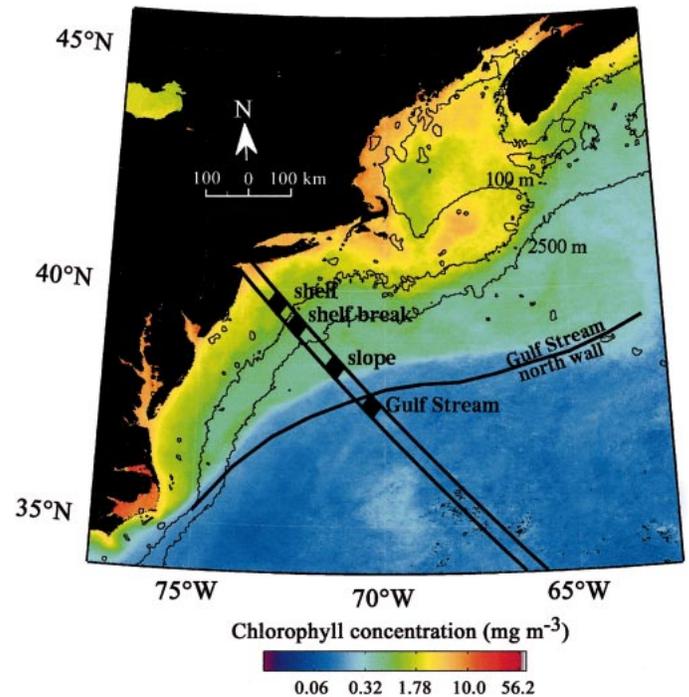


Fig. 1. Location of shelf, shelf break, slope, and Gulf Stream study areas within the MAB and adjoining Gulf Stream waters overlaid on a monthly *SeaWiFS* chlorophyll concentration composite image of October 2000. The mean track of the MV *Oleander* between New Jersey and Bermuda along with the 20-yr mean location of the Gulf Stream north wall is displayed.

because chlorophyll concentrations in continental margin and Gulf Stream waters are approximately log normally distributed (Campbell 1995; Yoder et al. 2001). The geometric mean has the advantage of reducing the effect of a small number of high or low values (outliers) on the mean (Yoder et al. 2002).

Sea surface temperature (SST) data derived from the satellite-borne advanced very high-resolution radiometer (AVHRR) were mapped to the same resolution as the chlorophyll and PAR data. After declouding each individual scene (an automated process by which clouds and their artifacts are identified and marked to eliminate these pixels from further computation) (Cayula and Cornillon 1992) monthly composites were calculated, and data were extracted and averaged, identical to the chlorophyll and PAR procedure.

In situ observations—In situ hydrographic data were collected aboard the MV *Oleander*. Monthly expendable bathythermograph (XBT) temperature profiles available from NMFS were used to determine the depth of the seasonal mixed layer of the water column. The mixed layer depth was defined as the physical depth at which the ambient temperature within a profile is within 0.5°C of the sea surface temperature (Monterey and Levitus 1997). The XBT profile data were binned into 1-m increments. Profiles that did not extend deeper than 25 m or that had a more than 200-m measurement gap within the profile were excluded. When more than

a single profile fell within a study area in a given month, the profiles were averaged. When monthly profiles were missing, the depth of the mixed layer was determined by linearly interpolating between the months before and after the gap.

Phytoplankton community size structure information was acquired from previously published results. Generalized trends of seasonal mean water column percentage of microplankton ($>20 \mu\text{m}$) based on size fractionated chlorophyll, for the shelf, shelf break, and slope study areas were acquired from a 12-yr (1977–1988) NOAA NMFS Marine Resource Monitoring and Prediction (MARMAP) survey of the Northeast U.S. continental shelf (O'Reilly and Zetlin 1998). The mean water column percentage of microplankton was determined from the closest subarea of the survey to the study area. Based on previous results, the Gulf Stream mean water column microplankton percentage was assumed to be zero, i.e., all phytoplankton were assumed to be smaller than $20 \mu\text{m}$ through all seasons (Olson et al. 1985, 1990; Cavender-Bares et al. 2001) (Fig. 3).

Vertical profile information was also available for chlorophyll concentration and percentage of microplankton. For the shelf, shelf break, and slope study areas, the profile information was taken from the MARMAP dataset and determined from generalized hydrographic subsections of the survey in the closest proximity to the study areas. The shelf break and slope study areas share the same generalized profiles for these parameters. A percentage microplankton profile for the Gulf Stream study area was unnecessary due to the assumption that no phytoplankton cells in this region are greater than $20 \mu\text{m}$ (Olson et al. 1985, 1990; Cavender-Bares et al. 2001). The Gulf Stream vertical chlorophyll profile was determined from a single generalized profile within the Gulf Stream biogeographic province as described by Longhurst (1998).

Nitrate concentration, used in the calculation of the quantum yield of photosynthesis, was obtained from the World Ocean Atlas 2001 of the NOAA National Oceanographic Data Center (NODC) (<http://www.nodc.noaa.gov/OC5>) (Conkright et al. 2002). Mean nitrate concentration profiles were extracted for the 1° box closest to the center of each study area. Owing to their close proximity, the shelf and shelf break study area share the same 1° nitrate data.

Production model development—The general form of the production model was based on the Jassby and Platt (1976) hyperbolic tangent model of the photosynthesis versus irradiance relationship. Theoretical and empirical relationships of the physiological parameters have been substituted into the basic model to formulate an absorption-based approach, which is dependent on the dominant size of the phytoplankton community. Chlorophyll concentration and depth have been included in the basic manipulation of the Jassby and Platt (1976) model to incorporate the remote nature of the data collection and information known about the physical structure of the water column. Primary production was integrated to the depth of the mixed layer for satellite observations or to the depth of the euphotic zone for the profile observations and calculated as

Notation

Environmental variables

Chl	chlorophyll concentration (mg m^{-3})
K_{PAR}	diffuse attenuation coefficient for photosynthetically active radiation (m^{-1})
E_0	sea surface irradiance ($\text{mol quanta m}^{-2} \text{d}^{-1}$)
E_z	irradiance at depth ($\text{mol quanta m}^{-2} \text{d}^{-1}$)
Z_{MLD}	physical depth of the mixed layer (m)
Z_{EU}	physical depth of the euphotic zone (m)
Z_0	sea surface (m)
T	temperature ($^\circ\text{C}$)

Physiological variables

PP	primary production ($\text{mol C m}^{-2} \text{d}^{-1}$)
Φ	quantum yield of photosynthesis ($\text{mol C mol quanta}^{-1}$)
Φ_{max}	theoretical maximum quantum yield of photosynthesis ($\text{mol C mol quanta}^{-1}$)
\bar{a}_{ph}^*	mean absorption coefficient of phytoplankton per unit of chlorophyll ($\text{m}^{-1} [\text{mg m}^{-3}]^{-1}$)
\bar{a}_{pico}^*	mean absorption coefficient of picoplankton per unit of chlorophyll ($\text{m}^{-1} [\text{mg m}^{-3}]^{-1}$)
\bar{a}_{micro}^*	mean absorption coefficient of microplankton per unit of chlorophyll ($\text{m}^{-1} [\text{mg m}^{-3}]^{-1}$)
P_{max}^b	maximum photosynthetic rate ($\text{mg C} [\text{mg Chl}]^{-1} \text{h}^{-1}$)
α	maximum light utilization coefficient ($\text{mol C m}^2 [\text{mg Chl}]^{-1} \text{mol quanta}^{-1}$)
E_k	photosynthesis saturation irradiance ($\text{mol quanta m}^{-2} \text{d}^{-1}$)
S_f	size parameter, percentage of microplankton in a population (%)
f_a	Φ_{max} reduction factor due to nonphotosynthetic pigment absorption (dimensionless)
f_{Δ}	Φ_{max} reduction factor due to inefficiency in energy transfer and charge recombination (dimensionless)
$f_{c(N)}$	Φ_{max} reduction factor due to nutrient effects (dimensionless)
$f_{c(\tau)}$	Φ_{max} reduction factor due to large depths (dimensionless)
$f_{c(\text{PAR,inh})}$	Φ_{max} reduction factor due to photoinhibition (dimensionless)
$f_{E, t}$	Φ_{max} reduction factor due to dependence of photosynthesis on light and temperature (dimensionless)

$$\text{PP} = \int_{Z_{\text{EU,MLD}}}^{Z_0} (\bar{a}_{\text{ph}}^* \Phi) E_k \tanh(E_z/E_k) \text{Chl} dZ_{\text{EU,MLD}} \quad (1)$$

where PP is daily water column primary production ($\text{g C m}^{-2} \text{d}^{-1}$), \bar{a}_{ph}^* is the mean absorption coefficient of phytoplankton per unit of chlorophyll ($\text{m}^2 \text{mg}^{-1}$), Φ is the quantum yield of photosynthesis ($\text{mol C mol quanta}^{-1}$), E_k is the photosynthesis saturation irradiance ($\text{mol quanta m}^{-2} \text{d}^{-1}$), E_z is the irradiance at depth ($\text{mol quanta m}^{-2} \text{d}^{-1}$), Chl is the chlorophyll concentration (mg m^{-3}), Z_0 is sea surface (m), $Z_{\text{EU,MLD}}$ is the depth of either the mixed layer or the euphotic zone (m) (refer to Table 1 for full notation).

The basic form of the primary production model employs several assumptions. These include (1) phytoplankton biomass (chlorophyll *a*) is uniformly distributed throughout the

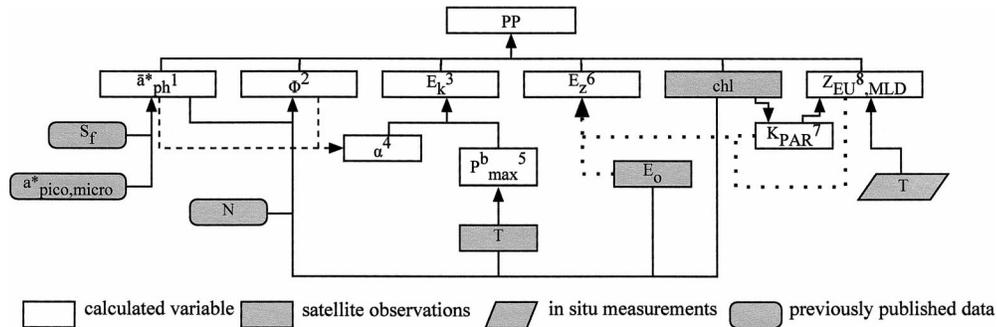


Fig. 2. Flow schematic of the primary production model. The arrows point from the independent variables to the dependent variable for each equation. The dashed lines are used for clarity and do not signify a different type of relationship. The previously published equations that are integrated into the model are (1) $\bar{a}_{ph}^* = [(1 - S_f) \bar{a}_{pico}^*] + [(S_f) \bar{a}_{micro}^*]$ (Ciotti et al. 2002); (2) $\Phi = \Phi_{max} \times f_a \times f_{\Delta} \times f_{c(N)} \times f_{c(\tau)} \times f_{c(PAR,inh)} \times f_{E,T}$ (Wozniak et al. 2002); (3) $E_k = P_{max}^b / \alpha$ (Sakshaug et al. 1997); (4) $\alpha = \bar{a}_{ph}^* \times \Phi$, (5) $P_{max}^b = f(T)$ (Behrenfeld and Falkowski 1997b); (6) $E_z = E_0 e^{-(K_{PAR} \times Z)}$, (7) $K_{PAR} = 0.121 (Chl)^{0.428}$ (Morel 1988); (8) $Z_{EU} = 4.6 / K_{PAR}$ (Morel and Berthon 1989). The flow chart was designed for the satellite mixed layer approach of the model.

mixed layer and euphotic zone, (2) the available irradiance decreases exponentially with increasing depth according to the attenuation coefficient, (3) absorption per unit chlorophyll varies depending on cell size, (4) the maximum potential of primary production is a function of temperature only, and (5) nutrient availability is a function of nitrate concentration only and it affects the quantum yield of photosynthesis.

Size dependence: The cell size dependence of the model was captured in the characterization of \bar{a}_{ph}^* . \bar{a}_{ph}^* was determined by weighting the size dependent absorption by the dominant cell size of the community (after Ciotti et al. 2002)

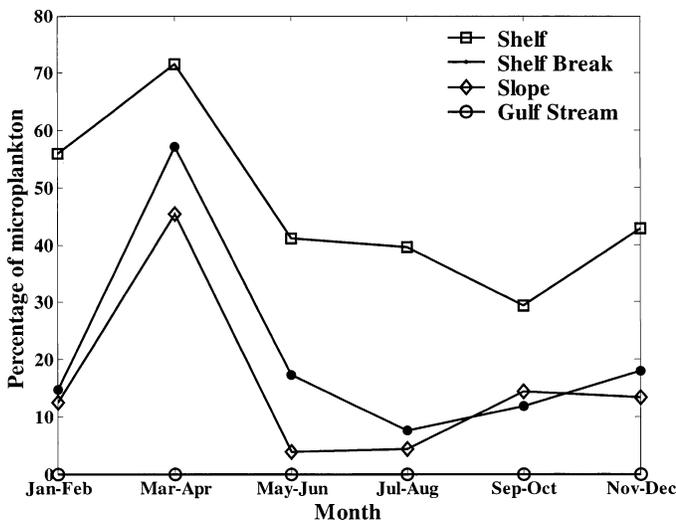


Fig. 3. Percentage of microplankton (>20 μm) by season for the shelf, shelf break, slope, and Gulf Stream study areas. The shelf, shelf break, and slope study area seasonality was derived from the MARMAP dataset (O'Reilly and Zetlin 1998) while the cells in the Gulf Stream study area were assumed all smaller than the microplankton size class as described in published literature (Olsen et al. 1985, 1990; Cavender-Bares et al. 2001).

(Figs. 2, 3, 4). The Ciotti et al. (2002) equation was modified so the size parameter (S_f) represents the percentage of the phytoplankton community within the microplankton size class (>20 μm). The mean chlorophyll-specific absorption coefficients for both picoplankton (\bar{a}_{pico}^*) (Ciotti unpubl. data) and microplankton (\bar{a}_{micro}^*) (Ciotti et al. 2002) were calculated from normalized absorption spectra (Fig. 4) and are 0.037 and 0.007 $m^2 mg^{-1}$, respectively.

Quantum yield of photosynthesis: Quantum yield of photosynthesis is an expression of the efficiency of the conversion of light energy into chemical energy and is defined as the number of CO_2 molecules fixed in biomass per quantum of light absorbed (Kirk 1994). The theoretical limit for the quantum yield of oxygen evolution predicted by the Z scheme of photosynthesis is one molecule O_2 evolved per

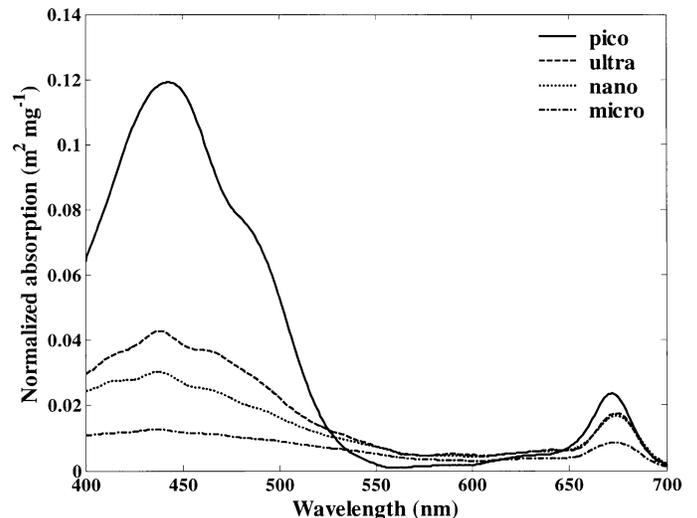


Fig. 4. Size fractionated chlorophyll-normalized absorption spectra for picoplankton, ultraplankton, nanoplankton, and microplankton (Ciotti et al. 2002).

eight quanta absorbed ($1/8 = 0.125 \text{ mol C mol quanta}^{-1}$) (Myers 1980). The theoretical maximum quantum yield is reduced by six physiological, dimensionless factors related to environmental parameters (Wozniak et al. 2002). The dimensionless factors are dependent upon nitrate concentration, chlorophyll concentration, temperature, irradiance, and the mean absorption coefficient of phytoplankton per unit chlorophyll. Quantum yield was determined from the model described by Wozniak et al. (2002) (Fig. 2).

Irradiance: The photosynthesis saturation irradiance (E_k) is theoretically the quotient of the maximum photosynthetic rate (P_{max}^b) and the maximum light utilization coefficient (α) (i.e., the initial slope of the photosynthesis vs. irradiance relationship) (Sakshaug et al. 1997) (Fig. 2). P_{max}^b and α were calculated separately for the above relationship to determine E_k . P_{max}^b , the rate of photosynthesis at light saturation, characterizes the photosynthetic capacity. Dark reactions of photosynthesis are enzymatically controlled and thus are dependent on ambient temperature. P_{max}^b is calculated from temperature according to an empirical relationship derived by Behrenfeld and Falkowski (1997b) (Fig. 2). The maximum light utilization coefficient (α) is an index of the efficiency of photosynthesis and is the product of the mean chlorophyll-specific absorption coefficient (\bar{a}_{ph}^*) and quantum yield (Φ) (Fig. 2).

The photosynthetically active irradiance (PAR) at depth is assumed to decrease exponentially with increasing depth according to the attenuation coefficient (K_{PAR}), defined by Beer's Law. The attenuation coefficient is determined as a function of water itself and chlorophyll concentration through an empirical relationship derived by Morel (1988) (Fig. 2). Accordingly, irradiance was calculated at 1-m increments within the mixed layer of the water column. Primary production was determined at each of these depths and integrated through the mixed layer. The calculations made with this approach are termed "satellite mixed layer."

In situ application of the model—To estimate production potentially missed by satellite-based estimates, the model was also applied to available in situ data. Chlorophyll profiles (Longhurst 1998; O'Reilly and Zetlin 1998), XBT temperature profiles, percentage microplankton profiles (O'Reilly and Zetlin 1998), and nitrate profiles (Conkright et al. 2002) were used instead of *SeaWiFS* chlorophyll concentration, AVHRR SST, mean water column percentage microplankton, and surface nitrate concentration. The same procedure was repeated as above for this in situ application of the model but integrated through the euphotic zone instead of the mixed layer. The calculations made with this approach are termed "profile euphotic zone." The euphotic depth (m) is defined as the physical depth where light penetration is equal to 1% of ambient surface radiation and is equal to an optical depth of 4.6 (negative natural log of 1%) (Morel and Berthon 1989) (Fig. 2). Depth-dependent K_{PAR} (as a function of chlorophyll concentration) was calculated. The instantaneous value for all parameters at depth was used in all calculations except the depth of the euphotic zone. The depth of the euphotic zone was determined by taking the average K_{PAR} through the water column.

The profile euphotic zone and the satellite mixed layer approaches used to estimate daily water column production reflect the advantages and limitations of the method of observation. For the profile euphotic zone approach, we calculated photosynthesis to a depth where light levels were approximately 1% of the surface irradiance, and thus production is integrated through the euphotic zone. The satellite mixed layer approach was based on the concept that phytoplankton are confined by physical mixing processes within the mixed layer of the water column, and thus production is integrated only through the mixed layer. With the assumption that the mixed layer is homogeneous, the satellite estimates of chlorophyll can be extended from the first photic depth to the depth of the mixed layer. To best represent each method of observation, satellite estimates were integrated to the depth of the mixed layer while in situ estimates were integrated to the depth of the euphotic zone.

Considering both the satellite mixed layer and profile euphotic zone application of the model together, production potentially missed by the satellite can be estimated. To avoid the problem of differing time series and specifically address the importance of cell size, the chlorophyll concentration observations had to be from the same time period. A third calculation of production termed "hybrid mixed layer" was completed by taking the satellite mixed layer approach and replacing the *SeaWiFS* chlorophyll concentration with depth-dependent chlorophyll profiles from the MARMAP survey, synonymous with the profiles used in the profile euphotic zone approach. All other parameters of the hybrid mixed layer approach were treated identically to those of the satellite mixed layer approach. Thus, the missed production reflects the influence of cell size and physiology rather than biomass along with the difference in integration depth. The profile euphotic zone production was considered the total production for the water column. Missed production was calculated by taking the difference between the total production and the hybrid mixed layer estimated production for each study area and month of the time series. The percentage of missed production was quantified by taking the quotient of the missed production to the total production.

Results

Estimates of primary production—The satellite mixed layer production estimates are highly regulated by the seasonal extent of the mixed layer depth. The mixed layer depth changed with the season for all study areas, with deep mixing beginning in the fall and strengthening through the winter while shoaling occurred in the spring and summer (Fig. 5). The seasonal cycle of mixing depth was rather constant during the 5 yr of our study within the shelf study area, reaching approximately the same extent (~ 70 m) and shoaling (~ 8 m) to similar depths every year. The mixed layer at the shelf break study area was less cyclic than the shelf study area but did display two sustained deep mixing events in the late winter to early spring of 1999 and the fall and winter of 2000. The other winter seasons in the time series at this location also displayed periods of deep mixing, but they were smaller in magnitude and did not persist for several

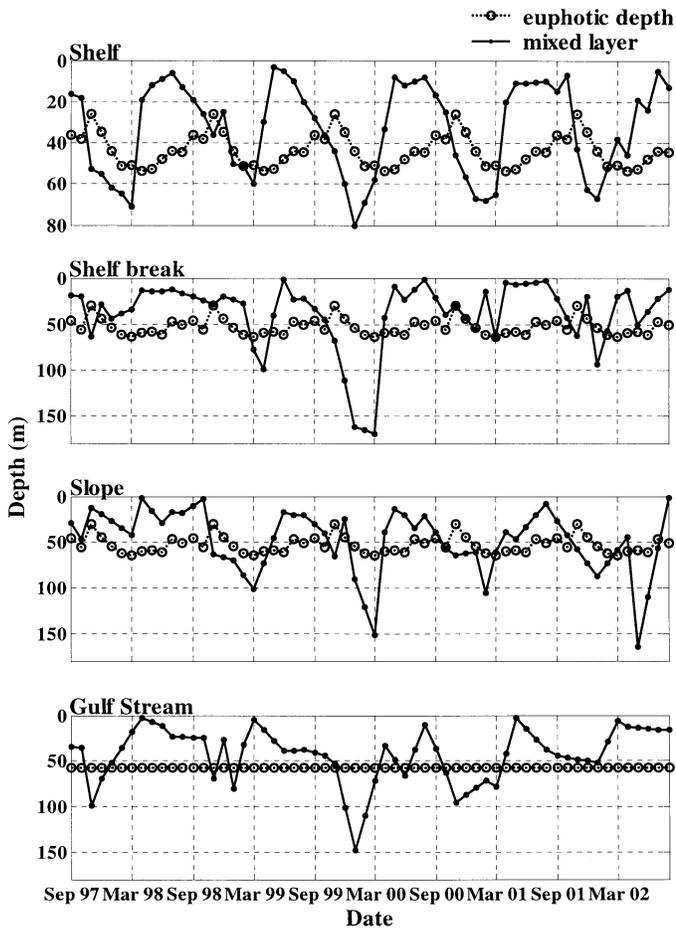


Fig. 5. Monthly in situ profile euphotic depth and mixed layer depth for the shelf, shelf break, slope, and Gulf Stream study areas over the 5-yr time series. The euphotic depth was determined from K_{PAR} and defined as 1% irradiance from ambient light. The single depth of the profile euphotic zone for the Gulf Stream study area was a result of the single annual generalized chlorophyll profile used. The mixed layer was determined from XBT profiles collected aboard the MV *Oleander*.

months. The mixed layer for slope waters displayed rather consistent deep winter mixing, except for the winter of 1998 when no extensive mixing occurred. The mixed layer of the Gulf Stream study area was also rather cyclic, with very short periods of shoaling. The depth of the mixed layer at this study area was the consequence not only of wind events but also of the lateral movement of the Gulf Stream front. For all study areas, the deepest mixing occurred during the winter of 1999–2000 (Fig. 5).

The euphotic zone depth was out of phase with the mixed layer depth. Owing to the dependence of the euphotic depth on K_{PAR} , which is related to chlorophyll concentration, the shallowest extent of the euphotic zone occurred in fall (October–November) with a slight shoal also occurring in the late winter to early spring. The uniform euphotic depth of the Gulf Stream study area results from the single generalized chlorophyll profile used for the entire annual cycle (Fig. 5).

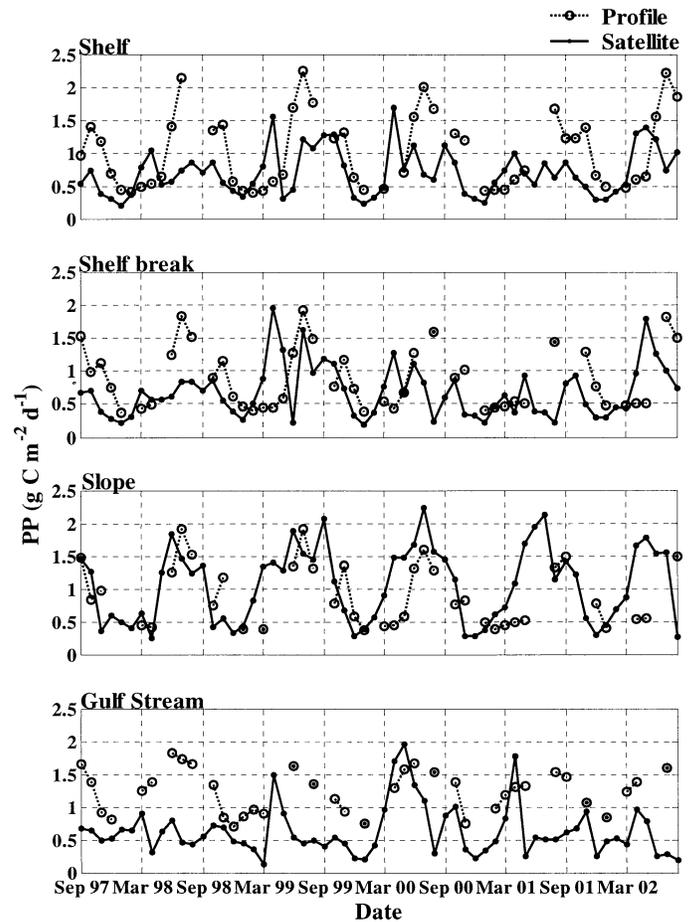


Fig. 6. Monthly primary production estimates ($\text{g C m}^{-2} \text{d}^{-1}$) for both the satellite-based mixed layer and profile euphotic zone approaches for the shelf, shelf break, slope, and Gulf Stream study areas over the 5-yr time series. The missing estimates in the profile euphotic zone approach are due to missing XBT profiles during those months.

Satellite mixed layer estimates of primary production in the shelf study area were characterized by high rates in the spring and summer and lower rates in the late fall, with the winter yielding the lowest rate. Seasonality was similar year after year (Fig. 6). The annual average daily production rates for the time series ranged from 0.76 to 0.94 $\text{g C m}^{-2} \text{d}^{-1}$, with a mean daily rate of 0.87 $\text{g C m}^{-2} \text{d}^{-1}$ yielding annual production of approximately 320 $\text{g C m}^{-2} \text{yr}^{-1}$ (Table 2). The seasonal cycle of production for the shelf break study area was similar to the shelf study area, but the magnitude of the peak production rates varies interannually (Fig. 6). The annual average daily production rates over a year for the shelf break study area ranged from 0.68 to 0.97 $\text{g C m}^{-2} \text{d}^{-1}$, with a mean daily rate of 0.83 $\text{g C m}^{-2} \text{d}^{-1}$ yielding annual production of approximately 304 $\text{g C m}^{-2} \text{yr}^{-1}$ (Table 2). The slope study area was marked by the highest production rates of all the study areas. The peak in production at this study area was delayed a few months from that observed in the shelf and shelf break study areas (Fig. 6). The annual average daily production rates over a year for the slope study area ranged from 1.05 to 1.21 $\text{g C m}^{-2} \text{d}^{-1}$, with a mean

Table 2. Mean daily ($\text{g C m}^{-2} \text{d}^{-1}$) primary production rate for shelf, shelf break, slope, and Gulf Stream study areas over the 5-yr time series for satellite mixed layer depth, profile euphotic zone, hybrid mixed layer approaches, and mean daily missed production. The missed production is the difference between the hybrid mixed layer approach and the profile euphotic zone approach that use the same chlorophyll data set. The values in the table do not calculate directly because of the averaging scheme used. Percentage of missed production is the quotient of missed production divided by the profile euphotic zone approach estimated production.

Year	Daily production ($\text{g C m}^{-2} \text{d}^{-1}$)				Percentage missed production
	Satellite	Profile	Hybrid	Missed	
Shelf					
1	0.76	0.94	0.58	0.39	41.65
2	0.93	1.05	0.63	0.47	45.01
3	0.94	1.11	0.64	0.46	41.35
4	0.81	0.85	0.62	0.38	44.56
5	0.92	1.12	0.63	0.45	40.46
Shelf break					
1	0.68	1.03	0.53	0.31	29.95
2	0.97	0.88	0.57	0.24	27.02
3	0.88	0.84	0.52	0.27	31.91
4	0.78	0.71	0.37	0.25	34.43
5	0.85	0.92	0.62	0.27	29.03
Slope					
1	1.05	1.11	0.54	0.31	27.76
2	1.16	1.04	0.54	0.29	27.93
3	1.21	0.87	0.58	0.26	29.86
4	1.11	0.66	0.55	0.24	36.32
5	1.10	0.88	0.57	0.29	33.51
Gulf Stream					
1	0.90	1.40	0.76	0.34	24.56
2	0.73	1.07	0.87	0.27	24.67
3	0.85	1.27	0.91	0.28	22.27
4	0.81	1.21	0.83	0.29	23.68
5	0.75	1.26	0.77	0.27	21.32

daily rate of $1.13 \text{ g C m}^{-2} \text{d}^{-1}$ yielding annual production of approximately $411 \text{ g C m}^{-2} \text{yr}^{-1}$ (Table 2). The Gulf Stream production rates were similar in magnitude to the shelf and shelf break study areas and were characterized by very abrupt increases beginning around March and usually subsiding by June to relatively low consistent levels (Fig. 6). The annual average daily production rates over a year for the Gulf Stream study area ranged from 0.73 to $0.90 \text{ g C m}^{-2} \text{d}^{-1}$, with a mean daily rate of $0.81 \text{ g C m}^{-2} \text{d}^{-1}$ yielding annual production of approximately $294 \text{ g C m}^{-2} \text{yr}^{-1}$. For each month, the general pattern was a decrease in production from the shelf to the shelf break study area, increase at the slope study area, and then decrease again in the Gulf Stream study area (Table 2).

The profile euphotic zone approach yielded higher production estimates than the satellite mixed layer approach for all study areas except the slope study area (Fig. 6). The high satellite production estimates at the slope are related to the anomalously high remotely sensed chlorophyll concentration in this area. In our calculations using the profile euphotic

zone approach, photosynthesis only occurs when irradiance levels are 1% of the surface irradiance or greater. When the mixed layer extends below the euphotic zone, production only occurs to the depth of the euphotic zone, resulting in identical estimates for both the profile euphotic zone and satellite mixed layer approaches. Conversely, when the euphotic zone extends below the mixed layer, the in situ profile euphotic zone estimates will be higher than those of the satellite mixed layer approach due to the difference in the depth of integration. Generally, production peaked in the summer and remained elevated until the late fall or early winter. The annual cycle of profile euphotic zone production lagged behind satellite mixed layer production by approximately 2 or 3 months (Fig. 6). Daily mean production estimated by the profile euphotic zone approach tended to decrease slightly across the shelf and onto the slope and then increased to a maximum in the Gulf Stream. The annual average daily production rates were 1.03, 0.94, 0.90, and $1.26 \text{ g C m}^{-2} \text{d}^{-1}$ for the shelf, shelf break, slope, and Gulf Stream study areas, respectively. The range of daily production estimates was greatest for the shelf and smallest for the Gulf Stream (Fig. 6; Table 2). There were several months when primary production estimates could not be made because of missing XBT temperature profiles.

Production potentially missed by satellite estimates— Missed production was quantified by calculating the difference between hybrid mixed layer production estimates and profile euphotic zone production estimates. The hybrid estimates underestimated the amount of primary production that occurred. Over the entire 5-yr time series, approximately 42%, 30%, 30%, and 23% of the in situ primary production was missed from the shelf, shelf break, slope, and Gulf Stream study areas, respectively. Of these estimates, the least amount of confidence is placed in the Gulf Stream estimate since the profile euphotic zone production estimates were based on a single generalized annual chlorophyll profile. Thus, approximately 30% of water column production was missed in the MAB (Table 2).

The percentage of missed production was pooled into four seasons; fall (September–November), winter (December–February), spring (March–May), and summer (June–August) (Fig. 7). The shelf study area was noisy across seasons over the 5 yr time series. The greatest amount of missed production occurred over the entire year in 1999 and the least in the spring of 2000. The shelf break, slope, and Gulf Stream study areas display a similar trend in missed production. The percentage of missed production was intermediate at the beginning of the time series, climbed to a maximum in 1999, and sharply decreased after the winter of 1999. From the fall of 2000, the percentage of missed production has been relatively constant and minimal for these study areas (Fig. 7). The interannual variability is more easily discerned than the seasonal variability. The summer of 1999 yielded the greatest amount (near greatest for the slope study area) of missed production across all study areas, while the summer of 2000 yielded the least amount of missed production for the shelf break, slope, and Gulf Stream study areas (Fig. 7).

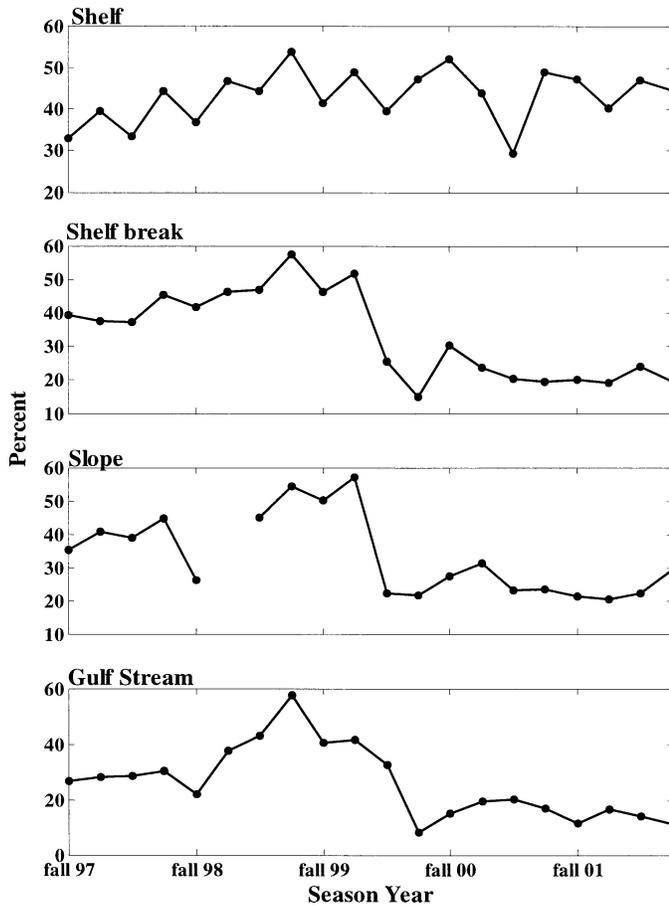


Fig. 7. Seasonal percentage missed production for all 5 yr of the time series for the shelf, shelf break, slope, and Gulf Stream study areas. The missing estimates during the winter in the slope study area are due to missing XBT profiles for all winter months.

Model behavior and performance—In an effort to validate the model, published in situ production estimates were compared with the model estimated values of primary production. Our annual production estimates for the shelf, shelf break, and slope study areas for both the satellite mixed layer and profile euphotic zone approaches ranged from approximately 250 to 500 $\text{g C m}^{-2} \text{ yr}^{-1}$. The range of daily primary production for both approaches over these study areas was 0.2 to 2.2 $\text{g C m}^{-2} \text{ d}^{-1}$, with an average of daily production of approximately 1 $\text{g C m}^{-2} \text{ d}^{-1}$.

In a study conducted between 1973 and 1981, Malone et al. (1983) found that the annual shelf production was approximately 290 $\text{g C m}^{-2} \text{ yr}^{-1}$ with an annual maximum daily rate in excess of 1.0 $\text{g C m}^{-2} \text{ d}^{-1}$. They estimated the average daily production for the shelf during the unstratified period (November–April) to be 0.68 $\text{g C m}^{-2} \text{ d}^{-1}$ and the stratified period (May–October) to be 0.85 $\text{g C m}^{-2} \text{ d}^{-1}$. The satellite mixed layer model estimates for the unstratified and stratified periods were 0.59 and 1.16 $\text{g C m}^{-2} \text{ d}^{-1}$, while the profile euphotic zone model estimates were 0.64 and 1.42 $\text{g C m}^{-2} \text{ d}^{-1}$, respectively. Our annual model production estimates for the shelf study area over the 5-yr time series for the satellite mixed layer and profile euphotic zone approach-

es were 320 and 370 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively. The lower bounds of our daily production estimates for both approaches are similar to the in situ estimates made by Malone et al. (1983). However, the upper bounds of the daily production and also the overall annual mean production estimated by our model is greater than those estimated by Malone et al. (1983). This discrepancy is likely related to the mismatch in time of the observations.

An additional study conducted by O'Reilly and Busch (1984), during 1977 to 1988, estimated annual primary production for the area corresponding to the shelf, shelf break and slope study areas to be 280, 300, and 280 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively. The average annual production estimates for the shelf, shelf break, and slope are 320, 304, and 411 $\text{g C m}^{-2} \text{ yr}^{-1}$ for the satellite mixed layer approach and 370, 319, and 333 $\text{g C m}^{-2} \text{ yr}^{-1}$ for the profile euphotic zone approach. The shelf break model estimates for both the satellite mixed layer and profile euphotic zone approaches are similar to estimates of O'Reilly and Busch (1984). However, the average annual production for the shelf and slope study areas is significantly higher than the estimates of O'Reilly and Busch (1984). The greatest anomaly between the in situ estimates of O'Reilly and Busch (1984) and our model estimates is for the slope satellite mixed layer approach. The remotely sensed chlorophyll concentration for this particular study area was an anomaly in relation to previous in situ observations in the area and lead to rather high production estimates. Although our model annual estimates for the shelf and slope are higher than those of O'Reilly and Busch (1984), they reported daily rates of phytoplankton production of 1 $\text{g C m}^{-2} \text{ d}^{-1}$ during most of the months sampled, which match well with our estimates.

The performance of our satellite mixed layer model was evaluated through comparison with the global vertically generalized production model (VGPM) in situ production estimates of Behrenfeld and Falkowski (1997b). This model was chosen because of its extensive use. The Behrenfeld and Falkowski (1997b) VGPM is different from ours in that it does not incorporate cell size or nutrient availability information and estimates are integrated through the euphotic zone. The models are similar in the fact that they both use chlorophyll concentration, photosynthetically available radiation, and the same parameterization of the maximum rate of photosynthesis. The annual trend of production of our model and that of Behrenfeld and Falkowski (1997b) were similar, but our estimates were slightly lower. The greatest discrepancy was found at the slope study area, and the best agreement was found in the Gulf Stream study area (Fig. 8).

The sensitivity of the model to chlorophyll concentration and cell size was further explored by comparison of model results derived using full ecological variability to model results derived by constraining the variability of chlorophyll concentration and cell size to a constant mean value, one parameter at a time. When plotting the full model variability against the constrained estimates, the divergence from the 1:1 line reflects the extent to which the calculations are sensitive to the observed parameter variability (Sosik 1996). The satellite mixed layer approach production estimates were used as the full ecological variability model ($n = 60$). The mean square errors relative to the 1:1 relationship for

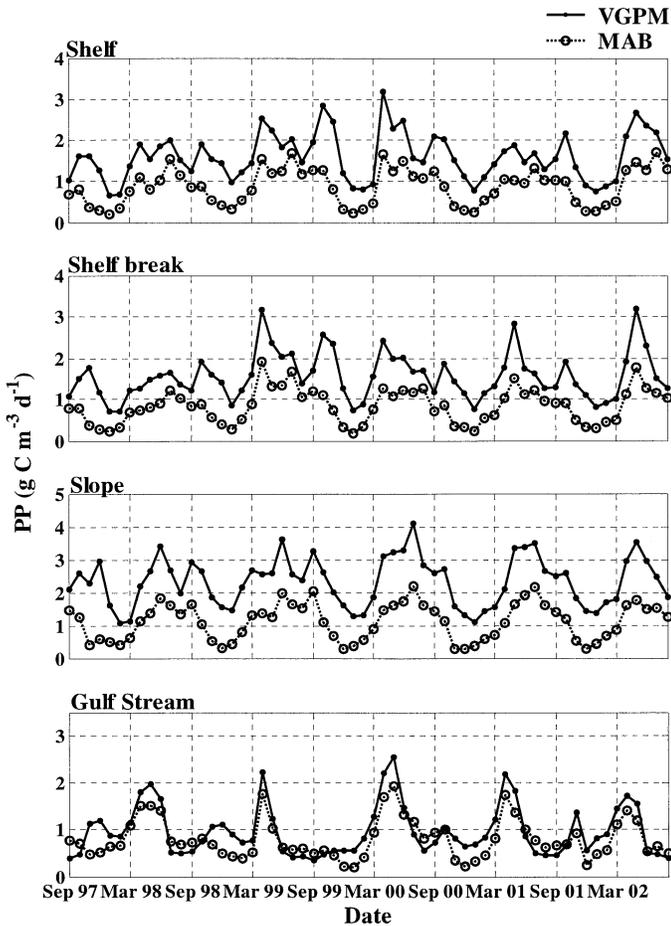


Fig. 8. Comparison of the regional MAB cell size model with the global vertically generalized production model (VGPM) (Behrenfeld and Falkowski 1997b) for the shelf, shelf break, slope, and Gulf Stream study areas over the 5-yr time series.

the variability of chlorophyll held constant are 0.14, 0.19, 0.28, and 3.08 and for the cell size variability held constant are 0.06, 0.16, 0.02, and 0.01 for the shelf, shelf break, slope, and Gulf Stream, respectively. The results indicate the model is more sensitive to chlorophyll concentration than cell size. To isolate the magnitude of the significance of cell size, model results were calculated for the full variability, and constraining the cell size to all picoplankton and all microplankton (Fig. 9). The mean square errors relative to the 1 : 1 line for the picoplankton are 0.11, 0.03, 0.03, and 0 and for the microplankton are 0.24, 0.31, 0.82, and 0.30 for the shelf, shelf break, slope, and Gulf Stream study areas, respectively. The lower mean square error for picoplankton for all study areas is indicative of the larger percentage of picoplankton in the phytoplankton assemblage. Over the entire time series and across all study areas, the estimated primary production for the all picoplankton scenario was approximately 16% greater and for the all microplankton scenario was approximately 70% less than the full model variability estimates. These differences attest to the importance of considering cell size in production calculations.

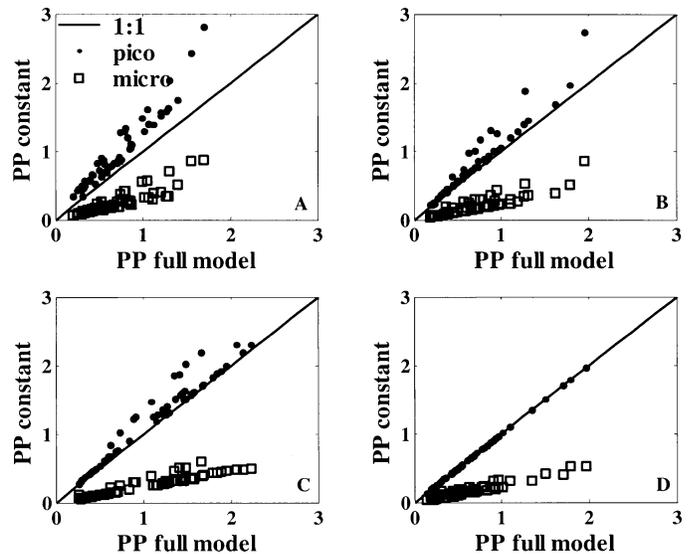


Fig. 9. Scatter plots of modeled primary production comparing estimates when cell size is held constant at minimum and maximum values for all observations, with estimates using the full measured variability in all parameters; (A) shelf study area, (B) shelf break study area, (C) slope study area, and (D) Gulf Stream study area. The 1 : 1 line is plotted for comparison.

Discussion

General production trends in relation to MAB dynamics—

The continental margin of the northwest Atlantic Ocean is one of the most productive systems in the world (Ryther and Yentsch 1958; O'Reilly and Busch 1984; Csanady 1990). Phytoplankton growth within the shelf study area is light limited during the fall and winter and nutrient limited in summer (Malone et al. 1983; O'Reilly and Zetlin 1998). This study area is controlled by coastal processes and shallow bathymetric features. The shift in peak production from the spring for the satellite mixed layer approach to the summer for the profile euphotic zone approach is likely attributed to the presence of a deep chlorophyll maximum. The change in depth of integration also plays a large role. In relation to our calculations, the mixed layer is shallow during the summer while the euphotic zone is deep.

A characteristic feature of the shelf break study area is the shelf break front that occurs generally near the 100-m isobath persisting year round (Houghton et al. 1988; Marra et al. 1990). The front forms biomass and cell size gradients with respect to adjacent water (Malone et al. 1983; Marra et al. 1990; Ryan et al. 1999) as a combined consequence of growth in situ and aggregation of biomass at the frontal convergence (Malone et al. 1983; Longhurst 1995). The shelf break production estimates are similar to the shelf and are not any greater than any of the other study areas. The location of the shelf break front changes seasonally (Linder 1998), and our stationary study area likely did not capture the full extent of the enhanced biomass at the front.

The Slope Sea lies between the shelf break and the Gulf Stream in the MAB (Csanady 1990). Phytoplankton distribution in the Slope Sea is greatly influenced by Gulf Stream

dynamics (Garcia-Moliner and Yoder 1994; Ryan et al. 2001; Schollaert et al. 2004) and receives more or less a constant supply of nutrients of subsurface Gulf Stream origin (Csanady 1990; Schollaert et al. 2004). The production in the slope study area was highest across all study areas for the satellite mixed layer approach, while production remains relatively constant across the shelf to the slope for the profile euphotic zone approach. The high production in this area by the satellite estimates can be attributed to the anomalously high chlorophyll concentration observed remotely. Of all the study areas, the timing of the peak production between the two approaches in this area is most synchronized, peaking in the summer.

Phytoplankton biomass has been documented to decrease rapidly from the shelf break front to low concentrations in the slope (Malone et al. 1983; Yoder et al. 2001, 2002). However, our data suggests the opposite. The mean *SeaWiFS* chlorophyll concentration over the entire 5-yr time series was 1.21, 1.16, 2.13, and 0.49 mg m⁻³ for the shelf, shelf break, slope, and Gulf Stream study areas, respectively. The apparent anomaly was likely due to the specific location of the slope study area. The dynamics of the Gulf Stream north wall could have played a role in enhancing biomass in this area.

The Gulf Stream migrates north to south on interannual time scales driven by the variation in outflow of Labrador shelf water (Rossby and Benway 2000). The surface waters of the Gulf Stream are depleted of nutrients and low in biomass, whereas water at depth is characterized by an intense nutrient stream centered at the depth of approximately 500 m (Csanady 1990; Pelegri and Csanady 1991). Lower production estimates by the satellite mixed layer approach in the Gulf Stream are the result of surface oligotrophic conditions low in biomass. Although the very small cells that dominate the Gulf Stream are capable of very efficient production, the low biomass limits the overall estimate of production. Some of the highest production estimates by the profile euphotic zone approach occur in the Gulf Stream study area. The variability of the production estimates by this approach can be attributed solely to changes in temperature, nitrate availability, and irradiance because the same generalized chlorophyll concentration profile was used throughout the time series resulting in a stationary euphotic depth and also constant cell size (picoplankton). The production estimates closely track the seasonal cycles of irradiance: high in the summer and low in the winter. The very high production estimates are likely an artifact of using a constant chlorophyll profile through time.

Importance of cell size—All aspects of life of a phytoplankton cell are influenced, more or less, by its size (Chisholm 1992). In general, smaller size classes dominate and are the constant background upon which larger cells can be found in varying amounts depending upon available light, nutrients, and physical conditions (Yentsch and Phinney 1989; Chisholm 1992). Turbulent, nutrient-rich, and variable light conditions, which occur during winter mixing and the transition into summer stratification, are conducive to the growth of larger cells, usually microplankton diatoms. Nanoplankton prefer stable high light conditions, which occur

during stratified periods (Margalef 1978) and are better adapted for low nutrient conditions because of their high surface area to volume ratio (Chisholm 1992).

The seasonal physical and chemical conditions of the MAB create an environment of varying phytoplankton size class in both time and space. Phytoplankton cells generally decrease in size from inshore to offshore, and larger cells (diatoms) dominate in the spring during the transition from well-mixed winter conditions to stratified summer conditions (Falkowski et al. 1983; Malone et al. 1983; O'Reilly and Zetlin 1998). The offshore decrease in cell size reflects an increase in light absorption efficiency; the more efficient a cell is at absorbing light, the greater its production potential per unit of biomass. Although the contribution of cell size to the overall model variability is small, a change in community structure can greatly influence the overall primary production. This is evident from the simulated changes in the phytoplankton size composition. Changing the cell size spatial and temporal composition from full ecological variability to all picoplankton cells increased the overall production by approximately 16%, while changing the composition to all microplankton cells reduced the overall production by approximately 70%.

The nutrient transition in the MAB is also marked by a change in phytoplankton assemblage from microplankton dominance (>20 μm) in the winter–spring to dominance by nanoplankton and smaller size classes (<20 μm) in the summer (Malone et al. 1983; O'Reilly and Zetlin 1998). The high productivity observed during the spring bloom is the result of a dramatic increase in biomass rather than an increase in photosynthetic efficiency. The remainder of the year is characterized by nanoplankton and smaller size class dominance, and production rates are related more to photosynthetic efficiency than to biomass. The increase in production during the spring bloom for the shelf, shelf break, and slope study areas, where cell size seasonality is documented, is only observed in the satellite mixed layer approach. This is likely due to the mismatch of the depth of integration between the two approaches, which overshadows the contribution of cell size to the model.

Over all study areas, the profile euphotic zone peak production generally occurred a month or two later than peak production estimated remotely. This may be due to the manifestation of spring blooms in surface waters before continued increase with depth over time below satellite detection limits (O'Reilly and Zetlin 1998). In addition, the percentage of production by nanoplankton and smaller size classes increases from near surface to deep waters (O'Reilly and Busch 1984). These small cells have the potential to be more efficient producers than larger surface cells, adding to the production beyond satellite detection.

Missed production—One of the most serious limitations of remote sensing is the inability of satellite radiometers to detect chlorophyll below the first optical depth, whereas production extends at least three times deeper (Morel and Berthon 1989). A satellite radiometer completely misses subsurface chlorophyll maximum layers, which commonly occur in oligotrophic waters, as well as in more eutrophic environments in the summer, when the euphotic zone is

deeper than the mixed layer (Cullen 1982; Longhurst 1995). To capture production below the first optical depth, in situ profiles are needed and production is integrated through the euphotic zone. As explained previously, missed production is best quantified as the difference between estimates based on in situ profiles integrated through the euphotic zone and satellite-based estimates integrated to the base of the mixed layer, with care taken to use observations from the same time frame.

The effect of including information of the vertical distribution of chlorophyll has been considered and included in other production models (Morel and Berthon 1989; Sathyendranath et al. 1995; Ondrusek et al. 2001). Sathyendranath et al. (1995) investigated the effects of assuming a uniform chlorophyll concentration with depth as opposed to depth varying profiles and found that the vertical distribution of chlorophyll leads to small but systematic differences in calculated primary production. Other investigators concluded that production is underestimated if the chlorophyll concentration detected in the first optical depth is extended to the base of the euphotic zone (Morel and Berthon 1989; Ondrusek et al. 2001). The missed production estimated by our approach is not due to changes in biomass. The profile depth-dependent chlorophyll concentration was used in both the hybrid mixed layer and the profile euphotic zone calculations. The missed production is indicative of the effects of considering cell size and also physiological responses due to changes in light, temperature, and nitrate concentration.

The profile euphotic zone approach model considers not only chlorophyll profiles but also temperature, cell size, and nitrate concentration depth dependence. Incorporating the additional in situ information, our calculations show that approximately 30% of daily water column production is missed with satellite-based estimates. In agreement with our estimate, Malone et al. (1983) estimated from in situ measurements that on average 37% of the phytoplankton productivity in the MAB occurred below the pycnocline (i.e., mixed layer) and thus below the depth of satellite detection. The percentage of missed production varied between study areas, with the greatest percentage (42%) missed in the shelf study area and the lowest percentage (23%) missed in the Gulf Stream study area. The percentage missed in the Gulf Stream study area is likely a background level that cannot be attributed to either cell size or biomass, since these parameters were characterized identically in both approaches. The percentage missed production is related to mismatch in integration depth and physiological characteristics being better quantified with the depth-dependent nitrate and temperature information. The great percentage of production missed in the shelf study area is harder to differentiate; both the mismatch in integration depth and the microplankton contribution were greatest at this study area.

The amount of production potentially missed by satellite estimates varies most strongly with year rather than season. The high percentage of production missed in the summer of 1999 across all study areas is likely most strongly related to the very shallow depth of the mixed layer at that time. In accordance with this observation, the small percentage of production that was missed in the summer of 2000 in the shelf break, slope, and Gulf Stream study areas is likely

related to the very deep mixing event that occurred a few months prior, bringing nutrients to the surface waters and improving the physiological condition of the cells. The time of year when production is most underestimated varies spatially. In the shelf study area, although noisy, most production is missed in the summer when a deep chlorophyll maximum develops (Falkowski et al. 1983; Malone et al. 1983; O'Reilly and Busch 1984). The interannual trends are much more discernable than the seasonal trends for the shelf break, slope, and Gulf Stream study areas.

Ecological and physiological characteristics of phytoplankton are dependent upon adjustments to many environmental factors determining the growth conditions experienced in situ at a given moment (Behrenfeld and Falkowski 1997*b*). Behrenfeld and Falkowski (1997*b*) point out that improvement of productivity models is not dependent on improved mathematical formulation or finer detail in the physics of light attenuation and absorption but on improvement of our understanding of phytoplankton ecology and physiology. The model moves beyond biomass and includes additional parameters of ecological significance. The addition of an ecological term (seasonally varying cell size) to a theoretical physiologically based model and estimation of missed production begins to signify the importance of understanding the composition of the phytoplankton in question.

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