Estimation of new primary production in the Benguela upwelling area, using ENVISAT satellite data and a model dependent on the phytoplankton community size structure

Ana Silío-Calzada, Annick Bricaud, Julia Uitz, and Bernard Gentili

Received 11 November 2007; revised 1 April 2008; accepted 19 May 2008; published 29 November 2008.

The spatial and temporal variations of oceanic new primary production have a crucial importance for the study of biogeochemical fluxes in the ocean; however, they have been poorly documented. In this paper, we propose a revision of the “shift-up” new production model developed for upwelling areas by Dugdale et al. (1989), and later adapted by Kudela and Dugdale (1996), using ocean color and sea surface temperature satellite data as inputs. The major improvement of the model is that the estimation of nitrogen uptake rates takes into account the phytoplankton community size structure, estimated for each pixel using the method of Uitz et al. (2006). Appropriate physiological parameters are then used for each size class. This revised model has been applied to Medium-Resolution Imaging Spectrometer and Advanced Along Track Scanning Radiometer data acquired over the year 2003, using the Benguela upwelling area as a test site. The combination of the new production model with a total production model allows the seasonal variations of new and total productions (including the respective contributions of the three size classes) to be estimated and compared. Even though microphytoplankton are generally considered to be responsible for new production, our results show that the contribution of small cells should not be overlooked in the upwelling-affected areas.


1. Introduction

The fact that coastal upwelling systems, which represent less than 1% of the total area of the oceans, are responsible for about 11% of the world oceanic primary production [Chavez and Toggweiler, 1995], emphasizes the interest to study their spatial-temporal biological variability, due to the role they can play in the air/sea carbon exchange processes. While synoptic views of algal biomass and oceanic primary production, generated by combining satellite data and light-photosynthesis models [e.g., Antoine et al., 1996; Behrenfeld et al., 2001], have become available both at the global and regional scales, the spatial-temporal variations of new production are much less documented.

New production has been defined as the fraction of primary production which is supported by nitrogen imported from outside the euphotic zone [Dugdale and Goering, 1967]. This fraction of primary production has a crucial importance for the study of biogeochemical fluxes as, in a steady state system, it is usually considered to correspond to the flux of organic matter exported out of the euphotic zone [Eppley and Peterson, 1979; Sarmiento and Siegenthaler, 1992]. The major part of new production is nitrate-based production, even if other sources (e.g., atmospheric nitrogen fixation) can contribute to this new production [Dugdale and Goering, 1967; Dugdale et al., 1990; Flynn and Fasham, 1997].

The first model for deriving oceanic new production from satellite data was proposed by Dugdale et al. [1989], and applied to CZCS (chlorophyll and sea surface temperature) data for the Mauritanian upwelling area. The basic assumptions of this model were that (1) the nitrate (NO₃⁻) surface concentration can be derived from sea surface temperature (SST), and (2) the phytoplankton nitrate uptake rate is both nutrient-dependent and time-dependent, owing to the inhibitory increasing presence of ammonium during upwelling development. The operation of the Dugdale et al. [1989] model was limited at that time by the insufficient acquisition frequency of CZCS, and by the fact that thermal CZCS data were available only in relative (uncalibrated) values. This model was later adapted by Kudela and Dugdale [1996] and Kudela and Chavez [2000], and applied to SeaWiFS and AVHRR data from the coastal upwelling region off California [Kudela and Chavez, 2002]. Simpler models were also tested in other areas, such as the Georges Bank region off Massachusetts [Sathyendranath et al., 1991] or the North Pacific Ocean.
The Benguela region (14°S–36°S, ~10°E–22°E) off the southwest coast of Africa is one of the four major coastal upwelling regions of the world oceans, and has been found to be the most productive, with a potential production of 0.37 Gt C a⁻¹ [Carr, 2002]. Therefore, this region represents an ideal test site for the analysis of spatial-temporal variations of algal biomass and primary production in highly dynamic upwelling areas.

The objectives of this paper are (1) to propose a revised version of the new production model proposed by Dugdale et al. [1989] and Kudela and Chavez [2000], taking into account the phytoplankton size structure; (2) to apply this model to the Benguela upwelling area as a test site, so as to derive the spatial variations of new production in this area along 1 year (2003), and its repartition among the three phytoplankton size classes; and (3) to compare the estimates of new and total primary production, along the same year.

Because of the data limitation due to cloud cover, monthly satellite images were used in this study. It is acknowledged that this temporal resolution is insufficient to resolve the actual physical and biogeochemical variability of the Benguela system, which typically has a 3- to 6-day period, due to the frequency of upwelling favorable winds (see below). Therefore, the seasonal variability of the system is presented in this study only as a test of the method, as the actual variability is largely undersampled. As an example, satellite-derived chlorophyll a concentrations in the inshore area may present standard deviations between 1 and 55% in summer, and from 5 to 80% in winter.

2. Data and Models

2.1. Study Area

The area selected for this study covers most of the Benguela system, from 15°S to 35°S, and from 10°E to 20°E (Figure 1). Physical and dynamical features of the Benguela system have been described in detail in several reviews [Nelson and Hutchings, 1983; Shannon, 1985; Shannon and Nelson, 1996; Shillington, 1998; Strub et al., 1998], and therefore only a brief summary is provided here. The Benguela system is physically dominated by a surface current flowing equatorward from its southern border at approximately 35°S (although occasionally it stretches farther south to Cape Agulhas), alongshore Namibia, to a position varying between 14°S and 17°S off Angola [Lutjeharms and Meeuwis, 1987; Shannon et al., 1987; Field and Shillington, 2004]. The cool Benguela Current is bounded by two warm currents, the Angola Current at the

Figure 1. Map of the Benguela Upwelling System [after Hardman-Mountford et al., 2003]. The light blue area marks the continental shelf (500 m).
northern end and the Agulhas Current at the southern end. The combined equatorward Benguela Current and the southeast trade winds result in upwelling of nutrient-rich South Atlantic Central Water along the west coast of southern Africa (14°S–36°S). The extent and intensity of the coastal upwelling is mostly determined by the wind and pressure fields that, together with topographic features and the orientation of the coast, are responsible for the formation of a number of upwelling cells [Lutjeharms and Meeuws, 1987; Shannon and Nelson, 1996; Shannon and O’Toole, 1999]. The dominant physical forcing mechanism of the Benguela upwelling region is the SE Atlantic high-pressure anticyclone. Seasonal shifts in its position are responsible for the temporal variability of the upwelling-favorable winds. This seasonality is most evident in the southern Benguela region, south of 30°S, where very little upwelling takes place during austral winter (June-August), a period when the South Atlantic anticyclone presents its northernmost position. Upwelling in the northern Benguela region, north of 25°S, although mostly perennial, shows a pronounced maximum from April to November, whereas the central (25°S–30°S) and northern bounds of the system are unaffected by upwelling relaxation [Boyd, 1987; Shannon and Nelson, 1996].

As stated in previous studies [Shannon, 1985; Shannon and O’Toole, 1999; Mackas et al., 2005], the Benguela upwelling system presents four major levels of temporal variability affecting the physical and biogeochemical characteristics of the area: diurnal, daily to weekly (typically 3–6 days), seasonal and interannual, all of which are highly influenced by the pulsed nature of the upwelling-favorable winds. In the present study, owing to satellite data constraints, only a rough view of the seasonal variability is obtained.

2.2. Data

2.2.1. In Situ Data

The estimation of surface nitrate concentrations in the upwelling system is based on empirical relationships using both SST and chlorophyll a surface concentrations (section 2.4.1; for more details see Silió-Calzada et al. [2008]). In situ data from the study area were used in the development of such algorithms. The in situ measurements were provided by the “World Ocean Database 2005” (WOD05) of the NOAA-NESDIS-National Oceanographic Data Center [Boyer et al., 2006], which includes vertical profiles of water temperature, salinity, nitrate and chlorophyll a concentrations collected in the Benguela system. The procedures for data quality control and data fusion are described at the address: http://www.nodc.noaa.gov/OC5/WOD05/docwod05.html.

2.2.2. Satellite Data

The new production model requires sea-surface temperatures (SST) and chlorophyll a concentrations (Chl a), derived from satellite data, while the total production model requires SST, Chl a, and photosynthetically available radiation (PAR) values. For these various inputs monthly averages were used, as weekly averages generally suffered from insufficient coverage of the studied area, due to cloud cover. As stated before, this results in an inevitable under-sampling of the short-term variability of the system, and the perception of its dynamics will be biased.

As many as 1278 level 2 AATSR daily images were used for the computation of SST monthly averages for the year 2003. Only images from ascending passes (nighttime) were used in order to avoid daylight heating. During daytime, solar heating may lead to the formation of a very thin warm layer, particularly in regions with low wind speeds. Since SST signals originate from this layer, this diurnal warming effect strongly influences the measurements, and result in notable differences between daytime and nighttime measurements. Nevertheless, night measurements may be also affected by warming, owing to the early time at which the satellite passes at night over the Benguela region (between 1900 and 2300 local time). The error (resulting from the limited time for the water cooling between the sunset and the satellite pass) is likely variable with the season. This possible bias should be kept in mind when considering the seasonal trends in SST. Monthly averages (“maximum likelihood” [Campbell et al., 1995]) of SST were computed with a 4 km spatial resolution, as a compromise between the high spatial variability of the area and the data limitation due to cloud cover.

Chl a concentrations were obtained via the ESA GRID Processing on Demand service, that generated upon request monthly estimates from the standard Level 2 MERIS “alg1” daily images. Such monthly estimates were calculated after discarding the pixels affected by sun induced glint (high and medium glint), white scatterers (whitecaps and coccolithophores), and dust and aerosol anomalies, using the appropriate flags. Case 2 pixels were also identified, and were essentially confined around the outlet of the Orange River. The corresponding pixels were also discarded. As for SST, monthly maximum likelihood averaged composites of Chl a were computed with a 4 km spatial resolution.

Monthly estimates of PAR, derived from 9.3 km SeaWiFS Level 3 data, were provided by the NASA Goddard Space Flight Center Distributed Active Archive Center. These monthly estimates are derived from daily PAR images, obtained by the use of the algorithm proposed by Frouin et al. [2003]. These data were then regrided to be spatially consistent with SST and Chl a 4 km data using a customized program.

2.3. Total Primary Production Model: A Size-Class Approach

To quantify the spatial-temporal variations in total primary production of the Benguela system, a light-photosynthesis model [Morel, 1991], adapted to satellite data [Antoine and Morel, 1996], was used. This model accounts for the absorption of radiant energy and its subsequent transformation into photosynthetic assimilate, expressed as mass of organic carbon fixed per unit of time and volume, P, based on chlorophyll content, Chl, chlorophyll-specific absorption, a, photosynthetically available radiation, PAR, and quantum yield for carbon fixation, φc:

\[ P(z, t, \lambda) = 12 \text{Chl}(z, t) \times a^* (z, t, \lambda) \times \text{PAR}(z, t, \lambda) \times \phi_c (z, t, \lambda). \]

In the original model, estimates of total primary production are based on the chlorophyll a content for the
whole water column (actually the layer comprised between
the surface and 1.5 times the bottom limit of the euphotic
zone), derived from surface chlorophyll measurements.
Satellite-derived estimates of surface chlorophyll concen-
tration are used for determining the vertical pigment profile,
based on the estimation of the euphotic-to-mixed-layer-depth
ratio [Morel and Berthon, 1989]. In the present study,
the estimation of primary production was limited to the
surface layer, in accordance with the new primary production
estimations which are based on surface-oriented, and
not column-integrated, algorithms (see section 2.4).

Reason for this limitation resides in the difficulty of recon-
structing nitrate concentration profiles in the water column
within highly dynamic areas, characterized by a succession
of upwelling cells and quiescent zones. The model was then
adapted to run on a pixel-by-pixel basis (instead of using
look-up tables, as in work by
adapted to run on a pixel-by-pixel basis (instead of using
upwelling cells and quiescent zones. The model was then
adapted to run on a pixel-by-pixel basis (instead of using
look-up tables, as in work by Antoine and Morel [1996]),
and for the surface layer only.

[18] In the standard version of the model, mean photo-
physiological parameters are applied regardless of the
trophic state of the system (note however that the assimila-
tion number is made temperature-dependent [Morel,
1991]). This constitutes a major source of uncertainty, as
these photophysiological parameters (chlorophyll-specific
absorption coefficients \(a^*\), maximum quantum yield for
carbon fixation \(\phi_{\mu,max}\), assimilation number \(P_{B,max}\)) may
vary significantly according to the trophic state and the
algal populations present [e.g., Babin et al., 1996]. In
the current study, the relative contributions of three phytoplank-
tonic size classes, microphytoplankton (20–200 \(\mu\)m),
nanophytoplankton (2–20 \(\mu\)m), and picophytoplankton
(0.2–2 \(\mu\)m), to total biomass were derived for each pixel
from the surface chlorophyll \(a\) concentration, using the
method developed by Uitz et al. [2006]. This method
requires the identification of the trophic state of the water
column corresponding to each pixel. This identification is
performed using the euphotic-to-mixed-layer-depth ratio,
derived from estimates of the euphotic depth [Morel and
Berthon, 1989] and the mixed layer depth (monthly clima-
tologies from de Boyer-Montégut et al. [2004]). Indepen-
dent estimates of primary production were then calculated
for each size class, with appropriate photophysiological
parameters, as described by Uitz [2006] and Uitz et al.
[2008] (Table 1). Essentially, these phytoplankton class-
specific parameters were obtained from the statistical anal-
ysis of a large database comprising HPLC-determined
pigment concentrations, algal specific absorption coeffi-
cients, and photosynthesis-irradiance curve parameters,
collected in various tropical and temperate open ocean regions.

The range of variation in these parameters may reach a
factor of 1.5 for \(P_{B,max}\), or 18 for \(\phi_{\mu,max}\), for example, from
microphytoplankton to picophytoplankton. Total primary
production was then estimated as the sum of the contribu-
tions of each phytoplanktonic size class. A similar approach
was used for the new primary production estimates (see
section 2.4).

### 2.4. New Production Model: A Revised Version Taking
Into Account the Phytoplankton Community Structure

[19] New primary production is generally estimated as the
result of nitrate uptake by phytoplankton, with a smaller
contribution from atmospheric nitrogen fixation. In our
study, only nitrate uptake is considered in the estimation
of new primary production. The model that we have used
as a basis was first developed by Dugdale et al. [1989],
and later adapted by Kudela and Dugdale [1996] and
Kudela and Chavez [2000]. This model was previously referred to
in literature as the “shift-up” model. The “shift-up”
hypothesis [Dugdale and Wilkerson, 1989; Dugdale et al.,
1990; Kudela and Dugdale, 1996; Kudela and Chavez,
2000] states that phytoplankton at depth are initially in a
low-light, high-nutrient environment. The vertical upwell-
ing flux of water to the surface imposes a physiological
adaptation due to the high-light exposure; while environ-
mental changes associated with upwelling processes initially
stimulate carbon fixation, phytoplankton are not yet adapted
to fully consume the available nitrogen. In terms of nitrate
uptake, the adaptation process starts with low uptake values
that will progressively increase (“shift up”) until the
increasing presence of ammonium causes a preferential
selection against nitrate uptake, leading to a “shift down,”
or deceleration in the nitrate depletion. Wilkerson and
Dugdale [1987] and Zimmerman et al. [1987] showed that
the acceleration at which nitrate is consumed is not constant,
but dependent on the initial nitrate concentration in the
upwelling center. The time and nutrient dependency of
new primary production may then be explained by
these assumptions.

[20] New primary production (i.e., the nitrogen assim-
ilation rate per unit volume of seawater, \(\rho_{NO3}\), in mg-N
\(m^{-3}\ h^{-1}\)) can be analytically expressed as the product
of the specific rate of nitrate uptake \(V_n\), in h \(^{-1}\)) and
the biomass present in the area, expressed in the form of
particulate organic nitrogen (PON, in mg-N \(m^{-3}\))
this expression by including the length of daylight (D, in h),
as a limitation factor,

\[
\rho_{NO3}(t) = V_n(t) \times PON \times (D/24).
\]

[21] Daylight limitation was included according to the
analysis performed by Gilbert and Garside [1992] and
Kudela et al. [1997], among others. These studies showed
that nitrate uptake in the dark is less efficient, as it requires
more energy during the absence of light. This is not the case

### Table 1. Photophysiological Parameters Extracted From
Uitz et al. [2008] and Used for the Estimation
of Total Primary Production at the Water Surface

<table>
<thead>
<tr>
<th>Phytoplankton Class</th>
<th>Microphytoplankton</th>
<th>Nanophytoplankton</th>
<th>Picophytoplankton</th>
</tr>
</thead>
<tbody>
<tr>
<td>(P_{B,max}) [mg C (mg Chl a(^{-1}) h(^{-1})]</td>
<td>4.264</td>
<td>2.938</td>
<td>3.751</td>
</tr>
<tr>
<td>(\phi_{\mu,max}) [mol C (mol quanta(^{-1})]</td>
<td>0.071</td>
<td>0.021</td>
<td>0.004</td>
</tr>
<tr>
<td>(a^*_{\max}) [m(^2) (mg Chla(^{-1})]</td>
<td>0.018</td>
<td>0.093</td>
<td>0.149</td>
</tr>
</tbody>
</table>

*aParameters: \(P_{B,max}\), assimilation number; \(\phi_{\mu,max}\), maximum quantum yield for carbon fixation; and \(a^*_{\max}\), maximum chlorophyll-specific absorption.
for ammonium, which can be assimilated similarly in both dark and light [Kudela et al., 1997; Mulholland et al., 1999]. The day length D is derived from the year day and latitude [see, e.g., Kirk, 1994].

[22] Despite the known variability in the organic carbon-to-organic nitrogen ratio, we have adopted the Dugdale et al. [1989] approach, according to which particulate organic nitrogen (PON) is obtained from the conversion of satellite-derived chlorophyll surface concentration. Unlike Dugdale et al. [1989] who used a general relationship (derived from in situ data in the Mauritanian upwelling), and Kudela and Chavez [2000] who used a constant PON:Chl ratio (1 mg-at N (mg Chl)−1 [Eppley et al., 1992]) in the Equatorial Pacific, we derived PON versus Chl relationships specific to phytoplankton size classes. The in situ data collected in the Benguela southern subsystem by Probyn et al. [1990] were used for establishing the following empirical relationships (Figure 2):

\[
PON_{\text{micro}} = 0.9488 \times \text{Chl}_{\text{micro}} + 0.1133 \quad r^2 = 0.7736, \quad (3a)
\]

\[
PON_{\text{nano}} = 0.461 \times \ln(\text{Chl}_{\text{nano}}) + 1.366 \quad r^2 = 0.5633, \quad (3b)
\]

\[
PON_{\text{pico}} = 0.6794 \times \text{Chl}_{\text{pico}} + 0.7287 \quad r^2 = 0.594, \quad (3c)
\]

where PON is in mg-at N m−3 and Chl is in mg m−3. Figure 2 shows that the PON versus Chl a relationships differ notably between phytoplankton size classes, especially at low (<0.5 mg m−3) and high (>2 mg m−3) Chl a concentrations. Note that the relationship observed for microphytoplankton is close to that used by Kudela and Chavez [2000].

[23] In the shift-up model, the specific rate of nitrate uptake, \( V_m \), is assumed to be dependent on both nutrient concentration and time. It is estimated according to the Michaelis-Menten equation,

\[
V_m = \frac{V_{\text{max}}(t) \times NO_3}{K_s + NO_3},
\]

where the half-saturation constant, \( K_s \), represents the nutrient concentration at which \( V_m = V_{\text{max}}/2 \), and \( V_{\text{max}} \), the maximal (i.e., not nutrient-limited) specific nitrate uptake rate, varies with time (see section 2.4.2). Operating the model pixel by pixel using equations (2)–(4) therefore needs, in addition to the computation of PON and D, the estimate of (1) the surface NO3 concentration, (2) the time dependence of \( V_{\text{max}} \), and (3) the half-saturation constant \( K_s \).

### 2.4.1. Estimating the Surface Nitrate Concentration

[24] This estimate is based on the inverse correlation between SST and NO3 concentrations existing in upwelling areas [e.g., Dugdale et al., 1989; Sathyendranath et al., 1991; Morin et al., 1993], owing to the fact that when water is upwelled to the surface, progressive heating occurs simultaneously to nitrate consumption. The regional biogeochemical characteristics and hydrodynamic conditions, however, strongly influence the NO3-SST relationships, which reveal high spatial-temporal variability. In order to reduce the scatter in the NO3 versus SST relationships, Silio-Calzada et al. [2008] have proposed replacing SST with the difference between SST and Tup (hereafter called \( \delta T \)), where Tup is the temperature of upwelled source water. The rationale for this modification is that nitrate consumption is expected to be related to the surface heating of upwelled water rather than to SST. The temperature of upwelled water was estimated using the simultaneous in situ profiles of temperature and salinity collected in the Benguela upwelling area, and available in the WOD05 data set (see details in work by Silio-Calzada et al. [2008]). This temperature was found to vary notably with latitude and season. The use of \( \delta T \) instead of SST reduced the scatter associated with latitudinal and seasonal variability, and \( \delta T \) was found to be more tightly correlated with nitrate concentration than SST. The scatter in nitrate-temperature relationships was further reduced by taking into account the variations in chl a concentration in regression analyses, as demonstrated by Goes et al. [1999, 2000]. Finally, the algorithms obtained by multiple regression analysis are for the spring-summer period (October-March), equation (5a), and autumn-winter period (April-September), equation (5b), respectively,

\[
NO_3 = 21.747 - 4.840\delta T + 0.273(\delta T)^2 - 0.342\text{Chl} a \\
\cdot (n = 214, \ r^2 = 0.823) \quad (5a)
\]

\[
NO_3 = 24.992 - 9.463\delta T + 0.947(\delta T)^2 - 0.4345\text{Chl} a \\
\cdot (n = 145, \ r^2 = 0.782). \quad (5b)
\]

One advantage of the approach proposed by Silio-Calzada et al. [2008] is that it allows the development of a single algorithm representative of the whole Benguela system...
(15°S–35°S), and avoids the strong discontinuities provoked by the regionalization of the area into several subsystems.

2.4.2. Estimating the Maximum Specific Uptake Rate \( V_{\text{max}} \)

In the original model of Dugdale et al. [1989], the shift-up hypothesis was represented by a linear dependence of \( V_{\text{max}} \) with time (their equation (5)). Kudela and Chavez [2000] proposed a still more dynamic approach for the \( V_{\text{max}} \) estimation,

\[
V_{\text{max}} = V'_{\text{max}} \times A_t,
\]

where \( V'_{\text{max}} \) is the phytoplanktonic cell volume (\( \mu m^3 \)). \( V'_{\text{max}} \) was estimated considering an average size for each of the phytoplankton size classes: 1 \( \mu m \) for picophytoplankton, 5 \( \mu m \) for nanophytoplankton and 20 \( \mu m \) for microphytoplankton, which leads to \( V_{\text{max}} = 0.026, 0.074 \) and 0.180 h \(^{-1} \) for pico-, nano- and micro-phytoplankton, respectively. The average value of 0.0943 h \(^{-1} \) used by Kudela and Chavez [2000] is included in this range, however it appears more representative of nanophytoplankton than of microphytoplankton which is expected to dominate algal populations in the upwelling areas.

2.4.3. Estimating the Half-Saturation Constant \( K_s \)

The half-saturation parameter, \( K_s \), represents a good indicator of the affinity of phytoplankton for nutrients, and has been observed to vary according to the phytoplanktonic group [e.g., Chisholm, 1992]. It has also been reported that small species have lower \( K_s \) values for nitrate, ammonia and phosphorus than larger species [Eppley and Thomas, 1969; Collos et al., 2005]. Finally, Collos et al. [2005] have shown that local environmental factors (water temperature, upwelling frequency, nutrient concentration, etc.) may affect the acclimation of cells, leading to significant differences in \( K_s \) for the same species in different locations. \( K_s \) is proportional to the number of carrier sites per unit area of membrane [Neame and Richards, 1972; Caperon and Meyer, 1972], therefore any increase in \( K_s \) could be due to an increase in the number of such sites [Collos et al., 2005].

Former versions of the new production model were based on the assumption of constant values, regardless the phytoplankton community composition (\( K_s = 3 \) mg-at N m \(^{-3} \) [Dugdale et al., 1989]), or the use of thresholds based on nitrate concentration in the surface layer (\( K_s = 1.0 \) mg-at N m \(^{-3} \) for \([NO_3] > 1 \) mg-at m \(^{-3} \), \( K_s = 0.1 \) mg-at m \(^{-3} \) for \([NO_3] < 1 \) mg-at N m \(^{-3} \) [Kudela and Chavez, 2000, 2002]). This latter formulation was proposed to account for the dominance of microphytoplankton and picophytoplankton in high-nutrient and low-nutrient waters, respectively. Collos et al. [2005] went a step further, evidencing a continuous variation of \( K_s \) as the nitrate concentration increases, and proposed the following parameterization:

\[
\log K_s = 0.62 \times \log([NO_3]) - 0.09.
\]

Still more recently, Irwin et al. [2006] proposed a new parameterization of \( K_s \) based on the phytoplankton community size class composition,

\[
K_s = 1.00 V_{\text{cell}}^{0.33},
\]

where \( V_{\text{cell}} \) is the phytoplanktonic cell volume (\( \mu m^3 \)); the size-scaling exponent is based on theoretical considerations concerning cell membrane diffusion and size-dependent nutrient requirements as stated by Aksnes and Egge [1991], and the factor 1.0 is derived from nitrogen uptake measurements by Eppley and Thomas [1969], as interpreted by Stolte et al. [1994]. The average sizes for phytoplankton size classes considered for the \( K_s \) estimations are identical to those used for \( V_{\text{max}} \). This provides \( K_s \) values equal to 0.8, 4.0 and 15.7 mg-at N m \(^{-3} \) for pico-, nano-, and micro-phytoplankton, respectively.

The main modifications of the new production model, with respect to the previous versions [Dugdale et
can be summarized as follows: (1) the particulate organic nitrogen concentration, PON, is estimated by taking into account the local phytoplankton community composition, as derived for each pixel; (2) the surface nitrate fields are estimated from seasonal empirical relationships linking the NO₃ concentration to the SST increase with respect to the temperature of upwelled source water (variable with latitude and season) and chl_a concentration; and (3) both the maximum specific uptake rate V_max and the half-saturation constant K_s are made variable with the phytoplankton community composition for each pixel. The general computational scheme is summarized in Figure 3.

### 3. Application to the Benguela Upwelling Area

#### 3.1. Seasonal Cycles of Chlorophyll Concentration, SST, and Surface Nitrate Concentrations

As previously mentioned, a complete set of monthly estimates of averaged chlorophyll a concentration was produced for 2003 using MERIS data (Figure 4), as an input to the productivity models but also as an observational tool for discerning biomass seasonal trends. During summer (January-March), strong chlorophyll gradients are visible from the coast toward offshore. High chlorophyll values (4–16 mg m⁻³) are confined along a narrow fringe between the coastline and the continental shelf, generating a strong front between eutrophic and oligotrophic waters. Approaching autumn and winter, chlorophyll gradients decrease in intensity, accompanied by marked differences between northern and southern subsistems. While biomass increases offshore in the northern area, in the southern region the high biomass area remains confined close to the coast. The histograms of Chl_a concentrations for each month (not shown) confirm that, as reported by Barlow et al. [2004], biomass is "generally lower along the Namibian coast than in South African water, because the phytoplankton are more uniformly distributed, with less well-defined chlorophyll fronts at the oceanic boundary." In the southernmost Benguela region, maximum concentrations tend to occur inshore, although exceptions may appear when strong upwelling processes occur.

The above mentioned biomass front is also reflected in the monthly AATSR SST products (Figure 5), although much less intense. Thermal infrared imagery also shows this discrepancy between the northern and the southern Benguela regions, in terms of seaward extension of the upwelling domain. Because of major differences in wind regimes, in shelf morphology and in direction of the coastline between the two regions [Shannon, 1985; Holmes et al., 1997; Shannon and O’Toole, 1999; Giraudeau et al., 2000; Blanke et al., 2005], the upwelling tends to cover a narrower area with a sharper front in the south, and a broader area with a weaker front in the north, exceeding 150–250 km from the coast [Bakun and Nelson, 1991]. Between May and October there is a wide-scale cooling of the system, with coastal upwelling phenomena and the intrusion of waters from the Agulhas Current breaking the

---

**Figure 3.** Scheme of the new production model dependent on phytoplankton community structure.
uniformity. Permanent upwelling cells (Walvis Bay, Lüderitz and Orange River) are discernable in the SST monthly images.

[33] The monthly maps of surface nitrate concentrations, derived from Chl \( a \) and SST maps using equations (5a) and (5b), are displayed in Figure 6. As expected, the spatial-temporal variations of nitrate concentrations mimic those of SST, with some nuances induced by variations in chlorophyll concentration.

3.2. Seasonal Cycles of New and Total Primary Production

[34] Figures 7 and 8 show the seasonal variability of new and total primary production, respectively, in the Benguela upwelling area for the year 2003. Not surprisingly, the estimates of new primary production reproduce the seasonal and latitudinal variability encountered in surface temperature, with the highest production values from June to September when SST is lowest. The chlorophyll distribu-
tion, which determines the PON values, also directly governs new production patterns. Overall, there is a strongly marked seasonal cycle, with a general trend toward high and low values in winter and summertime, respectively. For most of the year, the new production patterns seem consistent with the South Atlantic anticyclone seasonal displacement that reaches its northernmost position through winter, progressively descending toward summertime. Between January and March, however, new production might be underestimated, because the lowest SST values are disregarded in SST monthly estimates. Note also that SST images (and consequently, new production images) suffer large gaps, particularly in summer and in the northern subsystem.

[35] The total primary production values are mostly governed by the chlorophyll \( a \) distribution and to less extent by PAR values. Seasonally, the northern and southern subsystems present a relatively stable pattern, with a permanent fringe of primary production along the coast, associated with the upwelling activity. Maximum produc-

Figure 5. Seasonal variability of the sea surface temperature (°C) in the Benguela upwelling area along 2003, as represented by 4-km monthly images obtained by averaging AATSR Level 2 images (see text). The 3 months for each season are displayed from top to bottom. These images represent the water temperature at nighttime, in order to avoid the biases provoked by diurnal heating.
The differences observed in the spatial distribution of the new and total primary productions along the Benguela upwelling system may be related to the phytoplankton cell size distribution. Several studies conducted in the past [Malone, 1980; Raimbault et al., 1988; Wafar et al., 2004; Kameda and Ischizaka, 2005] showed that the composition and size structure of the phytoplankton communities are major determinants of the quality (new or regenerated) and quantity of primary production in a given ecosystem [Wilkerson et al., 2000]. It has been observed that in most natural populations, the small-sized phytoplankton fraction have higher preference for ammonium over nitrate, compared to the larger-sized fraction [Dortch, 1990]. As briefly explained in section 2.4.2, cell size can influence rates of nutrient uptake and assimilation, photosynthesis, respiration and growth. The commonly accepted trend, regarding nitrogenous nutrients, is that larger cells become dominant in high-nitrate waters whereas smaller cells tend to dominate in low-nitrate waters [Chisholm, 1992].

Figure 6. Seasonal variability of surface nitrate concentrations (μmol L⁻¹) in the Benguela upwelling area along 2003, as derived from equations (5a) and (5b). The 3 months for each season are displayed from top to bottom.
The spatial and seasonal variations of the $f$-ratio, defined as the new-to-total primary production ratio [Eppley and Peterson, 1979], could in principle be derived at this stage. As new production is expressed in terms of nitrogen whereas total production is expressed in terms of carbon, however, such computation requires a knowledge of the actual C:N ratio. While the C:N ratio was assumed to be equal to the Redfield ratio (6.6) in the model we used as a basis [Dugdale et al., 1989], more recent studies [Kudela et al., 1997; Geider and La Roche, 2002] have evidenced large deviations in this ratio. In particular, Kudela et al. [1997], in their study performed in the upwelling area of Monterey Bay (California), observed a large variability in this ratio associated to the upwelling stage, with values lower than 2.

Figure 7. Seasonal variability of the new primary production (mg-at N m$^{-3}$ d$^{-1}$) in the surface layer, estimated for the Benguela system along 2003. The white areas are due to cloud cover or invalid measurements, and the gray areas are those where new production is virtually 0. The 3 months for each season are displayed from top to bottom. Note that the new production values in the offshore area around 35°S in winter are likely artifactual, as this area is mostly affected by the cold Antarctic Circumpolar Current and nitrate-SST relationships may be not applicable.
in the early stage of the upwelling and at low incident light. Therefore, any estimate of the $f$-ratio using the above new and total primary production values would be very speculative.

3.3. Contributions of Phytoplankton Size Classes to New and Total Primary Production

[38] Taking in account the phytoplankton community structure, in terms of its size class distribution, represents one of the main modifications introduced in the scheme of the new primary production model. So far it has been commonly accepted that the new primary production is mostly due to microphytoplankton activity. This is based on the fact that following an upwelling event, high nitrate concentrations favor the increase in the abundance of large cells (with high $K_s$ and $V_{max}$ values), and consequently the increase in new primary production [Chisholm, 1992; Agawin et al., 2000]. Progressively, as nitrates become depleted, smaller organisms (nanoflagellates and picophytoplankton) with lower $K_s$ values, and with a preference for ammonium rather than nitrate uptake [Dortch, 1990], would be favored. Despite the undersampling of the short-term

Figure 8. Seasonal variability of the total primary production (mg C m$^{-3}$ d$^{-1}$) in the surface layer, estimated for the Benguela system along 2003. The white areas are due to cloud cover or invalid measurements. The 3 months for each season are displayed from top to bottom.
temporal variability due to the necessary use of monthly data, this differentiation of the phytoplankton size classes allows a better understanding of the role played by each class in primary production in these highly dynamic areas. Figures 9 and 10 illustrate respectively the phytoplankton class-specific new primary production, and the relative contributions of the three phytoplankton size classes to the new primary production over the year 2003 (for sake of simplicity, only 1 month is shown for each season).

Even if microphytoplankton generally constitutes the main contributor to new primary production, with production values ranging from 0.1 to 15 mg-at N m⁻³ d⁻¹ (Figure 9), the estimations obtained for nanophytoplankton evidenced a non negligible contribution, with new primary production ranging from 0.01 up to 0.8 mg-at N m⁻³ d⁻¹.

In terms of the spatial distribution of the size class contributions, the division between the two Benguela sub-systems (north and south) is clearest in winter. The northern
subsystem shows an evident dominance of microphytoplankton, whereas the southern region does not display such a net dominance of one class. For other seasons, in spite of the lack of data, it seems that the two subsystems present similar distributions, with a major microphytoplankton bloom, located between 23°S and 30°S, representing 60–97% of the new production.

Aside the existence of the two subsystems, there is also an important division between the inshore and offshore areas. In the fringe between the coastline and the edge of the continental shelf (located approximately at 500 m depth; see Figure 1), new production is dominated by microphytoplankton, with a relative contribution varying between 50% and 97% of new production. These figures seem realistic considering the high values of nitrate concentrations and new production, due to the existence of several upwelling cells. While the contribution of picophytoplankton is virtually negligible near the coast, the contribution of nano-

Figure 10. Contributions (%) of the phytoplankton size classes to the annual cycle of new primary production. Each season is characterized by the same month as in Figure 9. Note that picophytoplankton contributions (>80%) in the offshore area around 33°S in winter are likely artifactual, as in that area new and total primary production are virtually negligible.
phytoplankton is significant (10–50%). These results are in accordance with those obtained by Barlow et al. [2005] and Irwin et al. [2006], which have shown that small cells may contribute significantly to new production.

In the offshore area (more than 1500 m depth), contributions to new production are more evenly divided between microphytoplankton (20–55%), and the contributions of nanophytoplankton and picophytoplankton, which may reach 30–50% and 15–40%, respectively, of new production. Nevertheless, these contributions should be considered carefully, as new production due to nano- and pico-phytoplankton varies between 0.01 and 0.8 mg-at N m$^{-3}$ d$^{-1}$ (Figure 9).

The same type of analysis was done for total primary production, following the approach proposed by Uitz et al. [2008]. The results obtained (Figures 11 and 12) show that the relative contributions of size classes to total production are slightly different from those observed for new production. In the inshore regions, for instance, the contribution of microphytoplankton is approximately 95% of the total primary production (instead of around 80% for the new production), with values ranging from 150 to 600 mg C m$^{-3}$ d$^{-1}$.

Figure 11. Annual cycle of total primary production (mg C m$^{-3}$ d$^{-1}$) in the surface layer estimated for each of the phytoplankton size classes. Each season is characterized by the same month as in Figure 9.
Note also that in these areas, the contribution of nanophytoplankton (around 15–30%) is higher than that of picophytoplankton (<10%). In the offshore areas, the contribution of nanophytoplankton (2–20 mg C m$^{-3}$ d$^{-1}$, Figure 11) becomes the most significant (around 30–55% similar to the 20–50% contribution for new production).

4. Conclusions

The major improvement in the new production modeling proposed in this study is the estimation of individual contributions of the three main phytoplankton size classes, instead of considering phytoplankton as a whole. This estimation was possible by the inclusion of their respective nitrate uptake rates, their specific contributions to biomass, and size-specific Chl a-to-PON transformations. This approach allowed us to perform a spatial-temporal analysis of the role played by each class in the new primary production along the Benguela upwelling system. The results obtained show that, even though microphytoplankton is responsible for most of the new primary production in the inshore area (reaching a contribution up to 98% in some restricted areas), the role played by nanophytoplankton should not be neglected, with a

Figure 12. Contributions (%) of the phytoplankton size classes to the annual cycle of total primary production. Each season is characterized by the same month as in Figure 9.
relative contribution of 10–30%. This is an important aspect to consider for a better understanding of the variability in export production, and therefore of the role of the upwelling system as a carbon sink. Even though traditionally the contribution of nano- and pico-plankton has been considered negligible, these results suggest otherwise, similarly to those obtained in the equatorial Pacific Ocean and the Arabian Sea by Richardson and Jackson [2007], who observed that “all primary producers, and not just the large cells, can contribute to export from the surface layer of the ocean at rates proportional to their production rates.” Note, however, that in the absence of in situ validation (for lack of in situ measurements of new production simultaneous to satellite data), the values of new production cannot be ascertained and must be considered with caution.

[45] In terms of seasonal variability, the Northern ecosystem (14°S–26°S) presents higher fluctuations throughout the sampled year, as well as wider areas with a predominance of new production. On the basis of the analyzed satellite data, the Southern ecosystem (26°S–35°S), on the contrary, seems to be mostly ruled by regenerated production, which might be linked to the upwelling frequency and wind field variability. Nevertheless, both the spatial and temporal analysis was challenged by the presence of clouds in MERIS and AATSR images. Monthly estimates with a 4 km spatial resolution were used as a compromise, however such spatial and temporal resolutions provide only rough information in highly dynamic areas like the Benguela system. Note, however, that in the absence of in situ validation (for lack of in situ measurements of new production simultaneous to satellite data), the values of new production cannot be ascertained and must be considered with caution.

Acknowledgments. The authors thank ESA for providing MERIS and AATSR data, and NASA and the SeaWiFS Project for SeaWiFS PAR data. They acknowledge the financial support of Centre National d’Études Spatiales and ACRI-ST, through a grant to A.-S.C. We express our particular gratitude to S. Bernard for very useful suggestions on a previous draft. We thank R.C. Kudela, G. Pitcher, T. Probyn, Y. Collos, Y. Huo, M. Chami, and A. Mangin for fruitful discussions, and the Associate Editor and two anonymous reviewers for very constructive comments. This work is a contribution to the ENVISAT Project 886.

References


A. Bricaud, B. Gentili, A. Silió-Calzada, and J. Uitz, Laboratoire d’Océanographie de Villefranche, Université Pierre et Marie Curie-Paris 6, CNRS, BP 08, F-06238 Villefranche-sur-Mer, France. (annick.bricaud@obs-vlfr.fr)