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Seasonal variation in remotely-sensed phytoplankton size structure around southern Africa

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ABSTRACT

The three-component model of Brewin et al. (2010) computes fractional contributions of three phytoplankton size classes (micro- (> 20 μm), nano- (2–20 μm), picophytoplankton (< 2 μm)) to the overall chlorophyll *a* concentration (Chl_a). Using *in situ* pigment data, model coefficients were adjusted for application to the southern African marine region. The refined model was applied to seasonal and monthly climatologies of MODIS Aqua Chl_a around Southern Africa. Chl_a > 1 mg m⁻³ was limited to shelf regions along the coasts of Southern Africa and Madagascar, while values < 0.1 mg m⁻³ were found over most of the open ocean between the equator and 38°S during austral summer and autumn. In winter and spring, low values (< 0.1 mg m⁻³) were restricted to smaller regions within subtropical gyres, while values up to 0.7 mg m⁻³ extended over a much greater area of the open ocean. Shelf regions in the northern (NB) and southern Benguela (SB), Agulhas Bank (AB), Agulhas region (AR), and Mozambique Channel (MC) all showed similar seasonal cycles of size structure. On average, microphytoplankton comprised > 50% of the total Chl_a in these regions with little change throughout the year. The AR shelf differed, with picophytoplankton dominating in summer, and micro- and nanophytoplankton the rest of the year. In the open ocean domains of the NB, SB, and AB regions, nanophytoplankton dominated for most of the year, with picophytoplankton being more prevalent during summer and autumn. In contrast, in the AR open ocean, nanophytoplankton were dominant only during winter and early spring, whereas picophytoplankton dominated throughout the year in the MC open ocean. The refined model characterised previously unknown spatial and temporal changes in size structure in various ecosystems around Southern Africa.

1. Introduction

Phytoplankton play a critical role in a number of key marine processes, including the modulation of food webs, CO₂ exchanges, and the cycling of carbon and other nutrients such as nitrate, phosphate, and silicate. The size distribution of phytoplankton has a strong influence on community structure, physiology, metabolism, and the trophic organisation of the pelagic ecosystem (Chisholm, 1992). Partitioning phytoplankton communities according to size provides a more detailed and integrative means of investigating phytoplankton structure and function in relation to key physical processes and biogeochemical cycles (IOCCG, 2014). Communities dominated by large-sized phytoplankton have the potential to export organic matter, through a short food chain, to the seabed or transfer it to upper trophic levels and to neighbouring regions, while communities predominated by small-sized

phytoplankton are mainly characterised by complex microbial food webs that favour recycling of organic matter within the euphotic zone (Cermeño et al., 2006). Although large-sized phytoplankton can sustain higher rates of photosynthesis (Cermeño et al., 2006), small-sized phytoplankton are an important fraction (35–60%) of the total biomass and may account for over 50% of daily primary production in oligotrophic regions and 25–30% in more productive coastal regions (Platt et al., 1983; Tremblay and Legendre, 1994; Marañón et al., 2001).

The marine region around Southern Africa hosts a complex interplay between a number of major oceanic systems including the Benguela upwelling system, the greater Agulhas Current system, and the Southern Ocean, and plays a key role in the global ocean circulation and biogeochemical cycling (Hutchings et al., 2009; Lutjeharms, 2006). On the west and south coasts of Southern Africa, the Benguela upwelling system and the Agulhas Bank have ecological and economic

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significance for driving a very productive ecosystem which supports a complex trophic structure and a multitude of commercially harvested resources (Hutchings et al., 2009; Verheye et al., 2016). Most of the primary production in this ecosystem can be attributed to microphytoplankton dominated communities, but nanophytoplankton dominated communities are also known to be important due to their larger spatial extent (Hirata et al., 2009).

Located on the east and south coasts of Southern Africa, the Agulhas Current system feeds the upper limb of the Atlantic meridional overturning circulation through the flow of warm, saline surface waters from the Indian Ocean to the Atlantic Ocean (Lutjeharms, 2006). The Agulhas ecosystem and Mozambique Channel are characterised as oligotrophic, where mainly nano- and picophytoplankton dominate in the surface layers further offshore, with microphytoplankton being more important in the shelf regions (Barlow et al., 2010; Sá et al., 2013). Located south of the African continent, the Southern Ocean plays a critical role in regulating the global organic carbon flux and modulates nutrient supply to thermocline waters, which in turn drives productivity in the lower latitudes (Sarmiento et al., 2004; Schlitzer, 2002). The Southern Ocean is unique in that it has high nutrient concentrations and low phytoplankton biomass, with high spatial and temporal variability (Thomalla et al., 2011a). These extremely different environments provide a good opportunity to investigate seasonal variations in phytoplankton biomass and size structure under varying environmental conditions.

With decreasing opportunities and continually rising costs associated with the collection of *in situ* data, research efforts globally have become more focussed on the use of satellite data and models to elucidate oceanographic processes and variability (IOCCG, 2014). In recent years, the use of satellite ocean-colour data has been extended to the derivation of phytoplankton functional types and size classes, with the aim of improving our understanding of oceanic biogeochemical cycles. A number of different abundance-based, spectral-based, and ecological approaches to determine phytoplankton size classes (PSC) have been developed and implemented (Brewin et al., 2010; Hirata et al., 2009; Uitz et al., 2006, among others). Although Brewin et al. (2011) highlighted the need for continued and improved *in situ* data availability to further improve the estimation of satellite-derived PSCs, their initial comparison indicated that the various models performed with similar accuracy. While these models have been applied globally, there have been relatively few models tuned for regional applications, and none for around Southern Africa. One approach that has been successfully tuned to different regions is the three-component model of Brewin et al. (2010), including: the Atlantic Ocean (Brewin et al., 2010; Brewin et al., 2014); the eastern Atlantic Ocean (Brotas et al., 2013); the Indian Ocean (Brewin et al., 2012); the South China Sea (Lin et al., 2014); the Western Iberian coastline (Brito et al., 2015); the Mediterranean Sea (Sammartino et al., 2015); the Red Sea (Brewin et al., 2015a); as well as the global ocean (Brewin et al., 2015b; Ward, 2015). The primary goals of this study are to: (1) refine the parameterization of the Brewin et al. (2010) model for regional application to the marine environment around Southern Africa; (2) to use the model to identify the dominant size class; and (3) describe previously unknown seasonal and spatial variations in Chla and phytoplankton size structure in this region.

2. Data and methods

2.1. Re-tuning of the Brewin et al. (2010) model

Brewin et al. (2010) developed an abundance-based PSC model to estimate the Chla concentrations of three phytoplankton size classes (micro- (> 20 μm), nano- (2–20 μm), and picophytoplankton (< 2 μm)), as a function of the total Chla concentration (C). The model is based on two exponential functions (Sathyendranath et al., 2001), where the chlorophyll concentration of picophytoplankton (denoted C_p)

and combined nano-picophytoplankton (denoted $C_{p,n}$) are computed as:

$$C_p = C_p^m [1 - \exp(-S_p C)], \quad (1)$$

and

$$C_{p,n} = C_{p,n}^m [1 - \exp(-S_{p,n} C)], \quad (2)$$

where the parameters $S_{p,n}$ and S_p determine the initial slope between size-fractionated chlorophyll and total chlorophyll (denoted C in the Eqs. (1) and (2)), and C_p^m and $C_{p,n}^m$ determine the asymptotic maximum values for the two size-classes. Once $C_{p,n}$ and C_p are obtained, nanophytoplankton chlorophyll (denoted C_n) and microphytoplankton chlorophyll (denoted C_m) can be computed as $C_n = C_{p,n} - C_p$ and $C_m = C - C_{p,n}$. The fractions of each size class (F_p , F_n and F_m) can then be computed by dividing the size-fractionated chlorophyll (C_p , C_n and C_m) by total chlorophyll (C).

The original global model was parameterized using coefficients determined from refined relationships between HPLC (High Performance Liquid Chromatography)-derived biomarker pigments and the total Chla (Uitz et al., 2006), and linking specific biomarker pigments to each size class following Uitz et al. (2006), with further refinements as proposed by Brewin et al. (2010) and Devred et al. (2011). Details of the development, parameterisation and application of the model are described in Brewin et al. (2015b). Application of the model to satellite data has been extensively validated with independent *in situ* data in a variety of marine environments (Brewin et al., 2010; Brewin et al., 2012; Brewin et al., 2015b; Lin et al., 2014).

Here, we regionally-tuned the global model using HPLC data collected in the Southern African marine region (Fig. 1). This included data from: the BEAGLE cruise (November–December 2003; Barlow et al., 2007); the Atlantic Meridional Transect (AMT) cruises 6, 15, 16, and 17 (May 1998, October 2004, May 2005, November 2005; Brewin et al., 2010); the Agulhas ecosystem and Tanzania (November 2006, August–October 2007; Barlow et al., 2008; Barlow et al., 2011); the Mozambique Channel (November–December 2008, October–November 2009, April–May 2010; Barlow et al., 2014); Version 2.0 ALPHA of the NASA bio-Optical Algorithm Dataset (October 2002; Werdell and Bailey, 2005), following the removal of any AMT data so as to avoid duplication; and a cruise in the Atlantic sector of the Southern Ocean (February–March 2009; Gibberd et al., 2013). Only samples in the top 20 m of the water column were used (within the surface mixed-layer, rarely < 20 m, de Boyer Montégut et al., 2004), and where the difference between Chla and the total accessory pigments was < 30% of the total pigment concentration (Aiken et al., 2009; Brewin et al., 2015b). In total, 407 samples were available and Fig. 2a shows the spatial distribution and number of samples for each dataset.

Following the methods described in Brewin et al. (2015b), size-fractionated chlorophyll (C_p , C_n and C_m) was estimated from the HPLC pigment data. The total chlorophyll concentration was estimated from the weight of seven diagnostic pigments (Uitz et al., 2006), and then the fractions of chlorophyll in each size class were estimated. The fraction of picophytoplankton chlorophyll (C_p) was computed using zeaxanthin, total chlorophyll *b*, and by allocating part of the 19'-hexanoyloxyfucoxanthin pigment to the picophytoplankton pool at total chlorophyll concentrations $\leq 0.08 \text{ mg m}^{-3}$. The nanophytoplankton chlorophyll fraction (C_n) was estimated using 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin, alloxanthin, and by apportioning some of the fucoxanthin pigment to the nanophytoplankton pool, using the method of Devred et al. (2011). The microphytoplankton chlorophyll fraction (C_m) was estimated using the remaining fucoxanthin (that was attributed to the micro size class) and peridinin as diagnostic pigments (Devred et al., 2011; Brewin et al., 2015b).

Samples were matched to daily, level 3 (4 km binned) satellite chlorophyll data, from MODIS-Aqua v2014.0 (downloaded from the Ocean Biology Processing Group (OBGP) at NASA's Goddard Space Flight Center (GSFC)). Each *in situ* sample was matched in time (daily

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