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Seasonal characteristics of phytoplankton bloom phenology in the northern Benguela Upwelling System

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Declaration

I declare that this dissertation has been written by me. I am aware plagiarism is wrong. All contributions to this work have been clearly acknowledged through text reference.

Abstract

Seasonal phytoplankton blooms in the Benguela Upwelling System (BUS) play a crucial role in ecosystem services and driving climate change through air-sea gas exchanges. Upwelling systems are particularly are sensitive to effects of climate change including the transport of nutrients, which influence the composition of phytoplankton communities. This is important because species composition affects a number of key processes that have significant climate feedbacks. This study uses historical long-term in situ data (at 10 and 70 NM stations) as well as OC-CCI satellite ocean colour data to investigate seasonal phytoplankton bloom phenology and community structure of diatoms, dinoflagellates and coccolithophores in the northern BUS. The seasonal cycle of satellite chlorophyll was used to determine the timing of bloom initiation at inshore and offshore boxes that overlapped the in situ stations. An ocean colour algorithm to detect coccolithophore presence and absence was used to determine the inshore-offshore seasonal cycle of coccolithophores. Results indicate a gradual decrease in chlorophyll concentration further offshore as well as high intra-seasonal, inter-annual and spatial variability. Offshore blooms initiate later and last longer than inshore blooms which have a higher magnitude. Diatoms are dominant over dinoflagellates and coccolithophores throughout the northern BUS, with higher concentrations observed at the inshore station (10 NM) for all three phytoplankton groups. However, satellite results show a higher presence of coccolithophores in the offshore region during spring and summer that is associated with periods of strong stratification. This study provides a better understanding of the characteristics of the phytoplankton seasonal cycle in the northern BUS which is useful for detecting trends and possible change associated with climate change forcing in response to global warming.

Acronyms

BUS Benguela Upwelling System

Chl-a Chlorophyll-a

$CaCO_3$ Calcium Carbonate

DMS Dimethyl sulphide

DMSP Dimethylsulfoniopropionate

KI Potassium Iodide

I_2 Iodine

IPCC Intergovernmental Panel on Climate Change

$mg\ m^{-3}$ Milligram per cubic metre

MERIS Medium Resolution Imaging Spectrometer

MFMR Ministry of Fisheries and Marine Resources

MODIS Moderate Resolution Imaging Spectroradiometer

NM Nautical Miles

OC-CCI Ocean Colour Climate Change Initiative

OWT Optical Water Type

PFT Phytoplankton Functional Type

SeaWiFS Sea-Viewing Wide Field-of-View Sensor

SOCCO Southern Ocean Carbon and Climate Observatory

MLD Mixed Layer Depth

SACW South Atlantic Central Water

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1. Introduction

The Benguela Upwelling System (BUS) is located across the south-west coast of Africa and forms part of the world's four major eastern boundary currents (Boyer et al., 2000). The region is highly productive, contributing ~11% of the world's ocean production and supports large amount of fish with nutrient-rich waters transported to the ocean surface following upwelling (Carr and Kearns, 2003). The BUS is subdivided into the northern and southern BUS by an upwelling cell known as the Lüderitz cell (Figure 1), with information from the literature being split into the two subsystems. The northern BUS, located off the coast of Namibia is primarily influenced by the Angola current, south-east trade winds and continental shelves, whereas the southern Benguela, off the coast of South Africa is influenced by the Agulhas current and the subtropical gyres (Lachkar and Gruber, 2012).

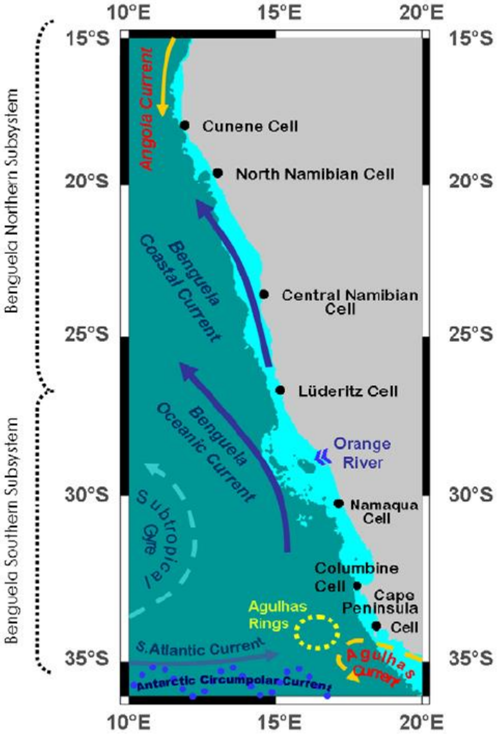

Figure 1: A map of the BUS overlayed on the continental shelf (500 m) from.

The northern BUS is experiences the poleward propagation of warm tropical South Atlantic Central Water (SACW), which supplies nutrients and low oxygen-water to the system during summer, whereas the eastern SACW transports oxygen water with less nutrients during winter (Mohrholz et al., 2008). The seasonal variation in the propagation of tropical water results in a seasonal cycle of the ocean temperature, salinity, oxygen and nutrient concentration (Siegfried et al., 2019). The wind forcing in the northern BUS has a strong seasonal cycle. Strong winds occur during winter (July - September) and during summer (December to March) the winds relax (Mohrholz et al., 2014). During upwelling temperature and salinity decrease from offshore towards the coast from 17 to 13 °C and 35.56 to 35.15 respectively (Mohrholz et al., 2014). The Central Namibian Cell has a unique wide double-shelf structure at different depths, with the first shelf edge located at 150 m depth and the second shelf separates from the open ocean at a depth of 350 m (Siegfried et al., 2019). The Central Namibian Cell allows for two upwelling centres at 23°S at the coast and above the first shelf edge (Huthnance, 1995).

Phytoplankton are the primary producers in the marine food chain and their production plays a crucial role in marine ecosystems, contributing ~50% to the net primary production in the world and supports the growth of living marine resources and food security (Ryther, 1969; Chassot et al., 2010; Perry et al., 2011; Stock et al., 2017). In addition, this production drives marine biogeochemical processes affecting the global carbon cycle and export flux (Doney, 2006; Laufkötter et al., 2016). For example phytoplankton community structure can influence the production of dimethyl sulphide (DMS) produced by dinoflagellates and coccolithophores and subsequently increase cloud albedo. Phytoplankton blooms vary through time and space as a result of changes in physical factors such as winds, sea surface temperature, precipitation and cloud cover, which are all influenced by climate patterns (Friedland et al., 2018). As such, phytoplankton are key indicator species of climatic change in response to global warming and threats such as ocean acidification from anthropogenic forcing (Friedland et al., 2018).

1.1. Significance of phytoplankton communities

The BUS is sensitive to impacts of climate change, particularly to changes in atmospheric forcing, which affects the wind patterns at a regional scale and subsequently impacts upwelling events, phytoplankton blooms and the fisheries industry that their production supports (Louw et al., 2016). One of the key anticipated responses of the BUS to climate variability is a shift in the timing of phytoplankton blooms and their seasonal development (Henson et al., 2010). A shift in the timing of blooms can significantly affect the survival of zooplankton and the larval fish community as the lack of synchrony between the timing of food production and important life stages can be detrimental to the ocean food chain (Henson et al., 2009). Understanding past seasonal variability blooms can assist in predicting and monitoring the ocean response to climate threats. An important part of this research is on understanding seasonal signals in the characteristics of phytoplankton bloom composition and phenology. Such information is valuable for assessing changes to ecosystems that are related to climate change.

There are a couple of explanations as to why phytoplankton bloom composition is important. For example, changes in climate are expected to change the species composition in such a way that alters the cell size, particulate matter and carbon exchange in the ocean food chain and ultimately affect the size of biomass transported to depth with feedbacks on climate (Finkel et al., 2010). Other reasons include the occurrence of harmful algal blooms as well as the role of specific phytoplankton species in mediating global climate through their contribution to the release of aerosol particle precursors such as DMS (Stefels et al., 2007).

1.2. Upwelling succession

As a consequence of upwelling along the coast, phytoplankton blooms in the Benguela region are highly variable with respect to both biomass and species composition. Phases of upwelling experience species succession. According to literature, the active phase of upwelling takes place at inshore with turbulent and nutrient-rich waters where blooms are dominated by small-sized diatoms followed by high biomass of larger diatoms with occasional dinoflagellate blooms towards the end of the upwelling phase (Kruger, 1980). The second phase of upwelling known as the relaxation phase takes place offshore with less nutrients and stratified waters characterized by low biomass of flagellates (Kollmer, 1958), coccolithophores (Mitchell-Innes and Winter, 1987) and *Pseudo-nitzschia* species (Louw et al., 2017). The succession of phytoplankton from diatoms to dinoflagellates in newly to aged upwelled water can be seen in Figure 2 (Hansen et al., 2014). This inshore t offshore change in community composition from diatoms to flagellates has similarly been reported in the Canary upwelling systems (Claustre, 1994; Babin et al., 1996) and the Arabian Sea (Barlow et al., 1999).

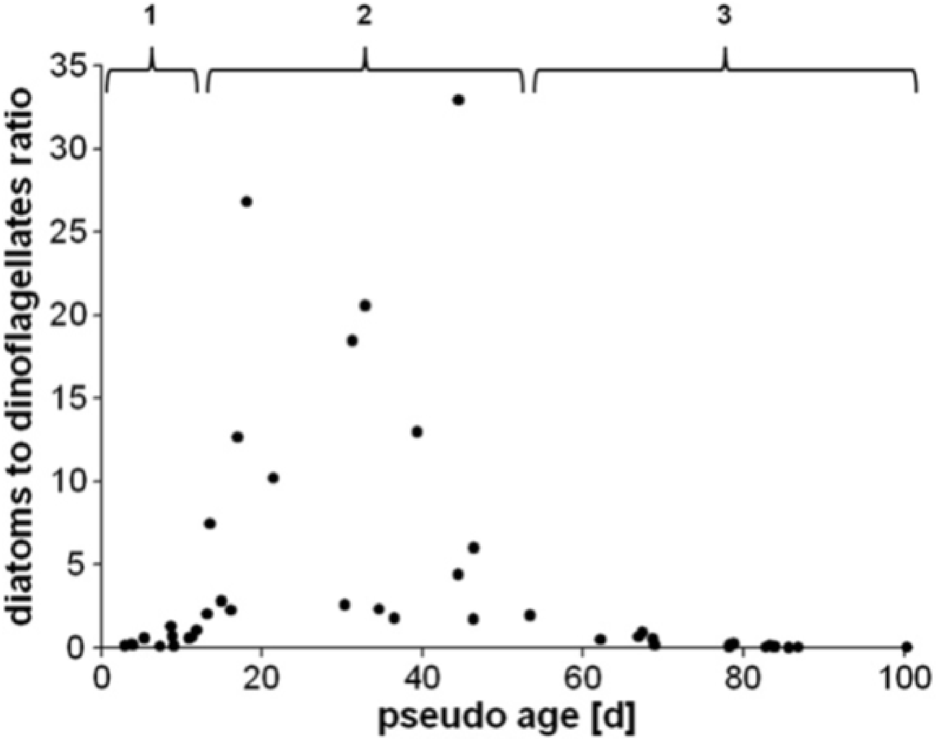

Figure 2: Succession of diatoms to dinoflagellates ratio through the following three stages of upwelling represented in days (1 = newly upwelled water; 2 = matured upwelled water; 3 = aged upwelled water), from Hansen et al. (2014).

This inshore-offshore distinction in phytoplankton community composition was similarly observed by Barlow et al. (2006) who demonstrated that species diversity increased further offshore in the southern Benguela. Other studies have similarly reported an increase in population diversity and a decrease in biomass with increasing distance from the shore in the Benguela. However, Giraudeau et al. (1993) observed the highest number of cells at inshore stations and less species diversity offshore in a study in the northern BUS, highlighting the variable nature of the system. Vertical stratification is said to play an important role in influencing phytoplankton community structure. Studies by Barlow et al. (2006) and Plessis (1967) show that the thermocline inshore ranges between 10 - 20 m while offshore it increases to 20 - 50 m with biomass typically being greater above the thermocline. Temporal variability of the environment also plays a crucial role in determining phytoplankton diversity (Barton et al., 2010). Higher environmental variability is known to enhance phytoplankton diversity and coexistence of multiple phytoplankton species, whereas less environmental variability typically results in competitive exclusion of phytoplankton and less diversity (Barton et al., 2010).

1.3. Harmful algal blooms

Most of the phytoplankton blooms in the BUS are a useful contribution to the marine ecosystem, however some blooms can be harmful and/or toxic. Less than 2% of the approximated 5000 marine phytoplankton species produce toxins (Stephen and Hockey, 2007), and only specific species can form blooms. The intensity and frequency of harmful algal blooms (HABs) are increasing globally and posing a growing threat to human health, aquaculture and fisheries (Parsons and Dortch, 2002; Stephen and Hockey, 2007). Studies have attributed the increase in abundance of HAB’s to coastal eutrophication since the 1980s and an increase in nutrient content due to anthropogenic activities and climate change (Baohong et al., 2010; Brooks et al., 2016). Non-toxic blooms can also be harmful by potentially increasing mortality, either through eutrophication and bloom collapse that may lead to anoxic conditions, or through mechanical damage to fish gills (Stephen and Hockey, 2007; Wells et al., 2015). Such blooms mostly attributed to dinoflagellates where reported in 1962 (Grindley and Taylor, 1962), 1994 (Matthews and Pitcher, 1996), 1997 (Pitcher and Cockcroft, 1998) and in 2007 (Pitcher et al. 2008) in the southern BUS.

HABs in the eastern boundary upwelling systems have become prolific due to the variety of phytoplankton species that produce toxins and bloom forming species responsible for red tides (Stephen and Hockey, 2007; Trainer et al., 2010). The frequency of HABs and the impact of bloom species such as the poisoning syndromes, toxins and high biomass blooms may vary based on the species composition, variable toxicity of the species between the systems and the food web structure through which toxins can be transmitted (Trainer et al., 2010). Although the physical, chemical and biological characteristics of the four eastern boundary upwelling systems may be similar, certain qualities within each system may favour one species over the other. For example a dinoflagellate species; *K. cristata* responsible for widespread mortalities was reported to be unique to the BUS, particularly restricted to the western Agulhas Bank (Trainer et al., 2010).

Some genus species of diatoms (e.g. *Pseudo-nitzschia*) are known to form HABs as they are capable of producing the neurotoxin domoic acid (DA). Although the BUS has not reported any *Pseudo-nitzschia* related HABs, other regions such as the southern California (Trainer et al., 2012; Seegers et al., 2015) and U.S. west coast (Anderson et al., 2008) have reported massive damage caused by *Pseudo-nitzschia* species. Recently studies have reported a prevalence of *Pseudo-nitzschia species* in the BUS (Hubbart et al., 2012; Louw et al., 2017; Barlow et al., 2018). *Pseudo-nitzschia* species are favoured by conditions with moderate nutrients, a temperature around 13-16°C and blooms tend to occur after a major peak in wind (Louw et al., 2017). Studies have linked the increase in the abundance of *Pseudo-nitzschia* to high availability of nutrients as a result of upwelling (Trainer et al., 2000; Ryan et al., 2014).

Most of the harmful algal blooms that occur in the Benguela are however attributed to dinoflagellates (Pitcher and Calder, 2000), which are responsible for most of the red tides in the southern Benguela (Pitcher and Calder, 2000). An increase in seasonal stratification increases the abundance of dinoflagellates relative to diatoms (Wells et al., 2015). Large dinoflagellate blooms may change the colour of the water and are commonly referred to as red tides. Dinoflagellates tend to bloom during periods of high irradiance and occur on the ocean surface near the upwelling front (usually offshore) during the active phase of upwelling, but can occur inshore following the relaxation phase of upwelling (Pitcher and Calder, 2000). These blooms tend to mostly occur between January and May in the southern Benguela (Pitcher and Calder 2000). If a large dinoflagellate bloom collapses and decays, anoxic conditions may occur due to increased bacterial activity with high respiratory demand of oxygen and result in an increase in the rate of marine mortality (Stephen and Hockey, 2007). Phytoplankton monitoring programmes with a focus on understanding species composition has become essential in many regions to protect aquaculture industry and to provide knowledge on the dynamics of toxic phytoplankton (Karlson et al., 2010; Kudela et al., 2017).

1.4. Aerosol particle precursors

Dinoflagellates and coccolithophores are the primary source of dimethyl sulfoniopropionate (DMSP) and convert it to DMS using an enzyme known as DMSP-lyase (Quere et al., 2005). DMS affects cloud albedo and the climate by producing sulphate aerosols that backscatter solar radiation and form cloud condensation nuclei (Keller, 1989; Stefels et al., 2007). An increase in the production of DMS from the ocean thus promotes the formation of clouds and subsequently increase cloud albedo, which ultimately decreases the quantity of solar radiation to the earth's surface (Brévière et al., 2015). The link between DMS production and the dynamics of the community phytoplankton is complex, however it is typically considered to be influenced by phytoplankton groups such as coccolithophores and dinoflagellates that produce DMSP (Keller et al., 1989; Stefels et al., 2007). Upwelling regions have characteristically high biomass with diverse community structure and strong offshore gradients which results in district seasonal and spatial patterns in the production of DMS (Siegel et al., 2007).

Coccolithophores are productive calcifying organisms responsible for ~50% of the $CaCO_3$ precipitation in the ocean and they have contribute significantly to the marine carbon cycle (Milliman, 1993; De Vargas et al., 2007) and in producing DMS (Quere et al., 2005). The increasing CO_2 emissions eventually dissolve in the ocean resulting in ocean acidification, which threatens marine organisms, especially those with shells made up of $CaCO_3$ such as coccolithophores corals and molluscs (Lohbeck et al., 2012; Schlüter et al., 2014). Studies have reported a decline in the growth and calcifying rate of coccolithophores as well as an increase in coccoliths malformation during high CO_2 concentrations in the ocean (Zondervan, 2007; Riebesell and Gattuso, 2014). Coccolithophore blooms tend to occur during conditions with high solar radiation, stable ocean stratification and available nitrate and low silicate concentration (Iglesias-Rodríguez et al., 2002; De Vargas et al., 2007). Small-celled phytoplankton species such as coccolithophores (due to their efficient surface area to volume ratio) require minimum concentrations of nutrients to grow (Friebele et al., 1978; Zondervan, 2007; Wells et al., 2015). Hence they are mostly dominant in nutrient limited oligotrophic conditions, although they tend to thrive in eutrophic waters in the presence of stratified water columns (Giraudeau and Bailey, 1995), more characteristic of mature waters (Dupouy and Demarcq, 1987; Kleijne, 1990). About 12 species of coccolithophores are found in the northern Benguela upwelling region, mostly dominated by *Emiliania huxleyi* at the surface and close to the thermocline (Giraudeau et al., 1993). The abundance of this species in the BUS was attributed to its rapid response to mesoscale variability and its ability to colonize surface water in a short period of time during the relaxation phase (Giraudeau et al., 1993).

1.5. Phytoplankton bio-optical properties and functional type

The spectral nature of light that emerges from the ocean is naturally associated with the biogeochemical components of the surface waters such that the satellite ocean colour output (specifically remote sensing reflectance [*Rrs*]) can indicate the concentration and constitution of phytoplankton communities in surface waters of the world's oceans (Evers-King, 2014). Ocean colour remote sensing observations have the added advantage of being routine, synoptic and available over decadal time scales. Various ocean colour satellite algorithms have been developed that determine phytoplankton bloom composition and chlorophyll-a (Chl-a) concentrations based on spectral reflectance algorithms (Siegel et al., 2007), reflectance band-ratio algorithms (Dierssen, 2010), spectral band difference algorithms (Hu et al., 2005; Xing et al., 2007) and bio-optical models (Claustre et al., 2005; Brewin et al., 2011).

Different phytoplankton groups have distinct optical properties (Robertson Lain et al., 2014), as they absorb and scatter light according to their characteristic pigments, size and shape (Alvain et al., 2012). An increase in cell size or intracellular pigment concentration reduces the efficiency of pigment absorption (Hoepffner and Sathyendranath, 1991; Platt and Jassby, 1976; Sathyendranath et al., 1987; Sosik and Mitchell, 1994). Collier (2000) observed specific scattering signals for cells with distinct properties such as diatom cells with long thin pennate shape, coccolithophore calcium carbonate cell walls and cyanobacteria's gas vacuoles. The radiance of Chl-a and algal pigments such as fucoxanthin for diatoms and peridinin for dinoflagellates also affects the colour of the water as a result of their characteristic backscattering during bloom formation (Blondeau-Patissier et al., 2014). Therefore, spectral absorption characteristics of phytoplankton change as the pigment composition changes (Hoepffner and Sathyendranath, 1991; Nair et al., 2008). This can in turn be utilized to determine phytoplankton functional type (PFT) products such as the distinct light scattering properties of coccolithophores on the ocean surface. Siegel et al. (2007) demonstrated that the high concentration of calcium carbonate shells of coccolithophores off the Namibian coast appear as plumes of milky water as a result of the scattering near 440 nm and 670 nm on the visible light spectrum.

1.6. Phytoplankton phenology

Phenology refers to a natural temporal cycle of events of plants and animals. This process has been described in the IPCC report as the most efficient method of tracking trends of ecosystems' response to climate change (Rosenzweig et al., 2007). For example, the subpolar regions are experiencing earlier blooms due to climate warming that results in a reduction of the ice covered period (Leu et al., 2011; Henson et al., 2013). The timing of a phytoplankton bloom is particularly important for the survival of consumers such as zooplankton, fish larvae (Cushing, 1990; Edwards and Richardson, 2004) and shrimps (Koeller et al., 2009). For example, early blooms in the northwest Atlantic were found to improve the survival of haddock larvae (Platt et al., 2003). Seasonal variability in primary productivity also affects the timing for ocean carbon exchange and storage (Lutz et al., 2007). One of the benefits of high resolution long term data sets derived from satellite ocean colour is that they provide the possibility to distinguish the drivers of trends as natural variability or climate change (Henson et al., 2010).

The timing of phytoplankton blooms also affects how long the bloom lasts, with early blooms typically lasting longer relative to late starting blooms in the Atlantic ocean (Racault et al., 2012; Friedland et al., 2018). Results have demonstrated that blooms have been starting earlier and lasting longer during the past 20 years, on a global scale (Friedland et al., 2018). This shift to earlier bloom timing correlates with ocean warming conditions observed in the past decades. Increase in the occurrence and duration of blooms can potentially be detrimental to the northern BUS (Louw et al., 2016), as demonstrated in the southern BUS, resulting in the formation of anoxic or hypoxic conditions following decomposition of phytoplankton (Pitcher and Calder, 2000). Three blooms usually occur in the northern Benguela each year and wind forcing has a significant influence on the formation and duration of the blooms (Louw et al. 2016). An increase in wind stress increases the mixed layer depth (MLD), which consequently affects the intensity of the bloom (Friedland et al. 2018).

Temporal resolution of the data is however important when predicting phytoplankton bloom initiation and the characterization of bloom phenology. A high temporal resolution data set is suitable for predicting a precise start date of the spring bloom, while a lower temporal resolution data is more suitable for detecting long-term trends in bloom timing (Ferreira et al., 2014; Friedland et al., 2018). The initiation dates for phytoplankton blooms tend to be delayed for monthly resolution relative to 5 day resolution, however, spatial patterns of bloom timing is similar for both high and low resolution data sets (Henson et al., 2018). Demarcq et al. (2012) have found that monthly averaged data provide sufficient resolution to capture phytoplankton phenology at a global scale.

Cloud cover introduces data gaps in satellite time series, especially at regional scales. Cloud cover has been of particular concern when using ocean colour products for the northern BUS, with cloud cover levels generally below 30% (Cole and Villacastin, 2000), coupled with fog at the coastline (Shannon et al., 1984; Lamont et al., 2019). A merged product such as the CCI dataset can provide better temporal coverage over a cloudy area like the northern BUS. The lack of long term in situ data over the previous decades has limited the comprehension of phytoplankton seasonality (Parmesan and Matthews, 2006; Richardson and Poloczanska, 2008; Nair et al., 2008). A better understanding of phytoplankton phenology requires a merging of high temporal resolution satellite data, in situ time series and models (Ji et al., 2010). Comparing results from satellite ocean colour with in situ data can in addition result in a better understanding of the ocean colour algorithm performance and influence future research in an area.

1.7. Research aims

The aim of this study was to investigate the seasonal and spatial characteristics of phytoplankton bloom phenology and community structure in the northern BUS using both historical in situ data and satellite ocean colour data. Such an understanding will provide valuable information towards ecosystem assessment, which can aid in predicting and monitoring ecosystem change in response to global warming and associated climate change. This is of particular importance for the region given the principal role of phytoplankton in supporting the fisheries industry (seasonal blooms), HAB's (typically dinoflagellates), and climate feedbacks via the biological carbon pump (e.g. efficient export via diatoms) and albedo from DMS producers (e.g. coccolithophores).

Key objectives:

1. To use historical in situ data collected from 2001-2012 to quantify the seasonal phytoplankton biomass and community structure characteristics (including coccolithophores, diatoms and dinoflagellates) at both inshore and offshore stations of the BUS.

2. To use satellite ocean colour data from the Ocean Colour Climate Change Initiative (OC-CCI) from 1997-2017 to quantify the seasonal cycle characteristics of Chl-a as well as remote sensing reflectance for coccolithophore presence to produce descriptive characteristics of bloom phenology inshore and offshore of the northern BUS.

2. Methods

2.1. Cruise description

The 23°S cross-shelf transect extends seaward from the coast of Namibia down side of the Lüderitz upwelling cell. Two stations were sampled monthly for phytoplankton groups and chlorophyll a (Chl-a) concentration at inshore and offshore from 2001 to 2012, however phytoplankton group sampling were not always taken. The inshore station was located ten nautical miles (10 NM) from the coastline with sampling commencing in January 2001 and ending in November 2012. Phytoplankton group sampling inshore however excluded years 2002, 2003 and 2007 thus resulting in 9 years of data in total. The offshore station is located at seventy nautical miles (70 NM) offshore and was sampled between May 2006 and November 2012. Year 2007 was however excluded from phytoplankton group sampling resulting in 6 years of data in total. Sampling was executed on the RV Welwitschia by the Namibian Ministry of Fisheries and Marine Resources (MFMR) Environment subdivision team (http://www.mfmr.gov.na/marine), providing a valuable long-term in-situ time series.

2.2. Chlorophyll concentration

Chl-a samples were collected and analysed by the MFMR Environment team on the 23°S line at various surface depths between 1 - 5.6 m, at 10 NM and 70 NM between January 2001 and December 2012. Contrary to phytoplankton sampling, Chl-a samples were collected and analyzed every year of the survey period. Surveys typically took place every month with cruises being approximately 30 days apart. On rare occasions two surveys took place in one month to compensate for the previous month not being sampled. Chl-a samples were vacuum filtered through glass fibre filters (Whatman GF/F) from 100 mL bottles and filters were immediately stored in a -20°C freezer on the ship. To extract the Chl-a from the sample, filters were grinded in a few milliliters of 90% acetone in a glass homogenizer with a motor-driven Teflon petle for 1 minute in an ice bath (10-12 °C). The sample extract was transferred into a stoppered and graduated centrifuge tube. The glass homogenizer and pestle were rinsed properly with 90% acetone and the rinsing volume was added to the centrifuge tube. The extract volume was made up to exactly 10 mL of 90% acetone. Calibrations were done using a standard Chl-a concentration (mg m^{-3}) with a Turner Model 10 fluorometer (Welschmeyer, 1994). The sample extracts were transferred from centrifuge tubes to the fluorometer cuvette by pipetting. The fluorescence measurement of the sample extract was measured against the 90% acetone blank. Approximately 0.2 mL of 1% HCL was added to the cuvette, mixed and left for 2-5 minutes to measure the fluorescence again. Chlorophyll-a concentration was calculated according to the equation of Holm-Hansen et al. (1965):

$$Chlorophyll\ a = K\left(\frac{F_m}{F_m - 1}\right) x\ V_e\ x\ \frac{(F_o - F_a)}{V_f}$$

Where

K = calibration coefficient = µg Chl-*a* per ml 90 % acetone per instrument fluorescence

F_m = unit maximum acid ratio (FJ/Fa) of pure chlorophyll *a* standard

F_a = sample fluorescence before acidification

F_o = sample fluorescence after acidification

V_e = extraction volume in millilitres

V_f = filtered volume in litres

Non-parametric box plots were used to analyse the data set at two locations, 10NM and 70 NM from the coast.

2.3. Phytoplankton counts

The following phytoplankton counts were executed by the MFMR Environment team. Water samples were collected inshore at 10 NM and offshore at 70 NM for quantitative analysis of phytoplankton. Samples were preserved in ~250 ml amber bottles by adding 1 ml of Lugols solution immediately after sampling. The bottles were sealed, shaken gently and stored in a dark space. The Lugols solution was prepared by adding 20 g of Potassium iodide (KI) and 10g Iodine (I_2) to 200 ml of distilled water (Willén, 1962). The Lugols preserved solutions were settled in a 25 ml chamber 24 hours prior to counting. Cells were typically classified into three phytoplankton groups (coccolithophores, diatoms and dinoflagellates), although coccolithophores were not always specifically counted due to difficulty identifying them on a light microscope (see Table 1 & 2 for details on which phytoplankton groups were sampled when). Groups were identified to species or genus level and counted with a Zeiss Axiovert 200 inverted light microscope, although a polarized microscope would easily/accurately identify coccolithophores. The concentrations of cells were calculated using the equation by Utermöhl (1958); ~400 cells with a precision of ±10% and 50-200 cells with a precision of 15-30% (Andersen and Throndsen, 2003).

2.4. In situ phytoplankton data analysis

The total abundance of cells for each phytoplankton group per station, per survey was considered to be representative of the month of sampling. On the few occasions when a month was sampled twice (9 times inshore and 3 times offshore), the counts were averaged. In order to determine the seasonal and regional (inshore versus offshore) distribution of the three phytoplankton groups, the data set had to be reduced to only include months when all three phytoplankton groups were sampled (see Table 1 in the results section 3.1.). Not doing so would make it impossible to distinguish the difference between the absences of coccolithophores in a sample versus the sample not being counted for the presence of coccolithophores.

Since this reduced the number of months significantly, the decision was made to group the months into seasons so that each season was typically sampled at least once each year (summer = December to February, autumn = March to May, winter = June to August and spring = September to November). However, some seasons in a year were sampled more than once. To overcome inconsistencies in the sampling, cell counts for each season were summed and divided by the number of months that data were available for that particular season of that year. To estimate the seasonal climatology, all seasons were in turn summed and divided by the number of years that each season was represented. However, it is important to have an understanding of how well certain seasons were represented with available in situ data versus others, as such, the percentage number of months in each season was calculated at both inshore and offshore stations as follows: the number of months with available data were summed and divided by the total number of months in each season for the number of years that the sampling took place (for example the inshore station had 9 years of phytoplankton group data such that each season could have a maximum number of 27 months).

To facilitate the comparison of relative proportions of different cell counts, the data were normalised using minimum and maximum cell counts; this resulted in a rescaling of the cell counts of diatoms, coccolithophores and dinoflagellates to range between 0 and 1 according to the following equation:

$$X_{normalized} = \frac{(x - x_{minimum})}{(x_{maximum} - x_{minimum})}$$

This enabled all three phytoplankton groups to be compared to allow visualisation of seasonal variation in relative dominance at inshore and offshore stations.

Since more surveys had more available data for diatoms and dinoflagellates than for coccolithophores (see Table 2 in the results section 3.1.), the value of this data was retained by performing a separate comparison of the relative dominance between only these two phytoplankton groups. In this analysis, monthly average cell counts were calculated. Months were similarly grouped into seasons for diatoms and dinoflagellates inshore and offshore.

2.5. Satellite ocean colour data and analysis

Satellite ocean colour data from the Ocean Colour Climate Change Initiative (OC-CCI) Version 3.1 (Sathyendranath et al., 2018) were obtained for the study region from the THREDDS NetCDF Subset Service (https://rsg.pml.ac.uk/thredds/ncss/grid/CCI_ALL-v3.1-8DAY/dataset.html) for September 1997 to November 2017, with 929 time steps; these data were obtained as 8-day temporal composites at a spatial resolution of 4 km. Selected datasets included the satellite Chl-a concentration product (a combination of

OC3, OCI and OC5 algorithms), as well as the Remote Sensing Reflectance (*Rrs*) for coccolithophores at 490, 510 and 555 nm. The OC-CCI dataset is created by using band-shifting and bias-correcting in order to merge reflectances from SeaWiFS, MERIS, Aqua-MODIS and VIIRS (Grant et al. 2017). To create inshore and offshore stations at the northern BUS, 2 equal rectangular boxes were subset making sure to overlap the in situ stations (see Figure 3). The inshore and offshore boxes were subsetted with the following coordinates respectively: Inshore latitude = 24°S - 22.5°S and longitude = 13.7°E - 14.4°E and offshore latitude = 24°S - 22.5°S and longitude = 12.5°E - 13.2°E.

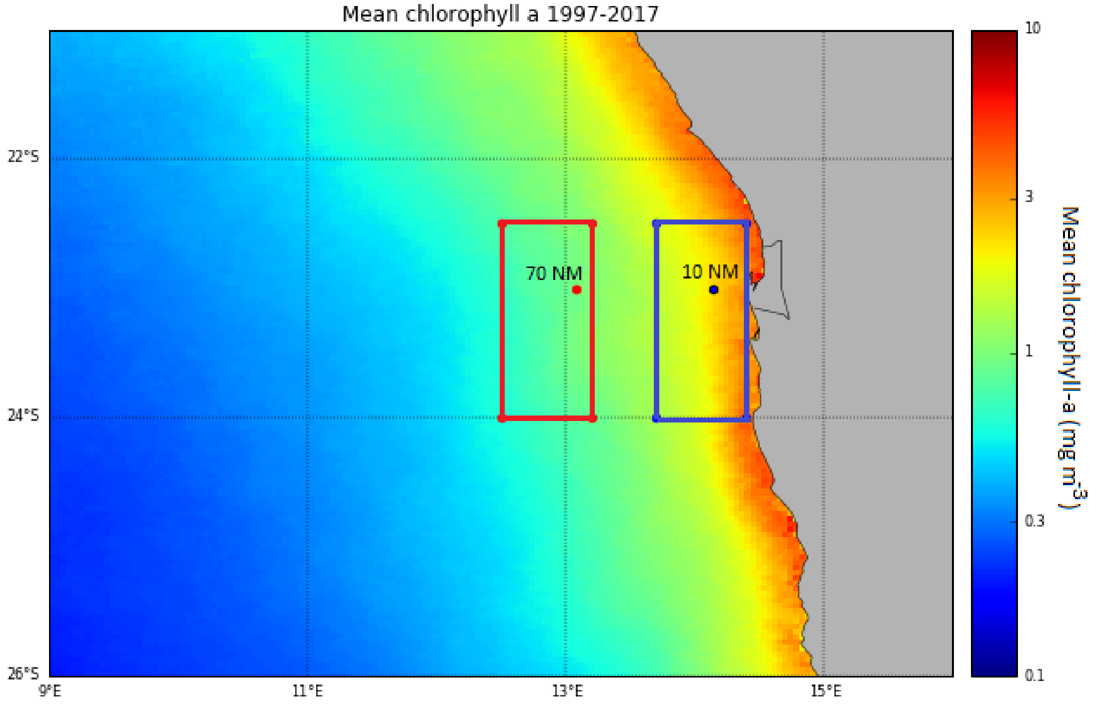

Figure 3: Map of the study area off the coast of Namibia overlayed on the mean Chl-a concentration of the OC-CCI dataset between 1997 and 2017. In situ stations are on the 23°S transect, where the blue dot represents the 10 NM station and the red dot represents the 70 NM station. The two boxes represent the regions for extracting satellite data over the inshore (blue) and offshore (red) stations.

All calculations such as averages and standard deviations for the time series and climatologies of Chl-a concentration (mg m^{-3}) at the inshore and offshore boxes were computed using Python. The phytoplankton bloom initiation dates were calculated using the threshold method (Siegel et al., 2002), which relies on the median of the annual cycle of Chl-a concentration and threshold of 5% above the annual median. Bloom initiation dates for each year (2001-2017) were estimated using 8-day resolution time series of satellite Chl-a concentration, where the first week to exceed the threshold line (median + 5% of the median) is the date of the bloom initiation. Chl-a climatology was computed using OC-CCI data from September 1997 to November 2017.

In order to assess coccolithophore bloom presence, an algorithm based on Moore et al. (2012)was used that detected the magnitude of the water-leaving reflectance in the blue-green spectral bands. Due to a lack of in situ reflectance data for the study region, the spectral characteristics and optical water types (OWTs) associated with coccolithophore blooms were obtained from the generalised spectral detection approach of Moore et al. (2012) who showed that coccolithophore-dominated pixels are characterised by a reflectance peak around 490 nm, as opposed to sediment-laden waters that traditionally have a reflectance peak at around 560 nm (e.g. Moore et al. (2009). However, while the classification of coccolithophore blooms in Moore et al. (2012) was based upon the degree of similarity of reflectance observations to predefined classes at six spectral bands, the current study used a threshold approach based on the integral of reflectance between 490 and 510 nm. The integral threshold was calculated from the reflectance of the class mean with the lowest magnitude in the blue-green (i.e. cluster 1 in Moore et al., 2012), which consisted of $Rrs(0-)$ values of 0.0155 and 0.0145, or $Rrs(0+)$ of 0.0083 and 0.0077 sr^{-1}, for 490 and 510 nm respectively (Figure 4). The algorithm is designed to be able to detect the presence or absence of a bloom. In order to avoid incorrectly classifying waters with a high sediment content as a coccolithophore bloom, only pixels with an integral > 0.14 and $Rrs(510) > Rrs(555)$ were classified as coccolithophore blooms.

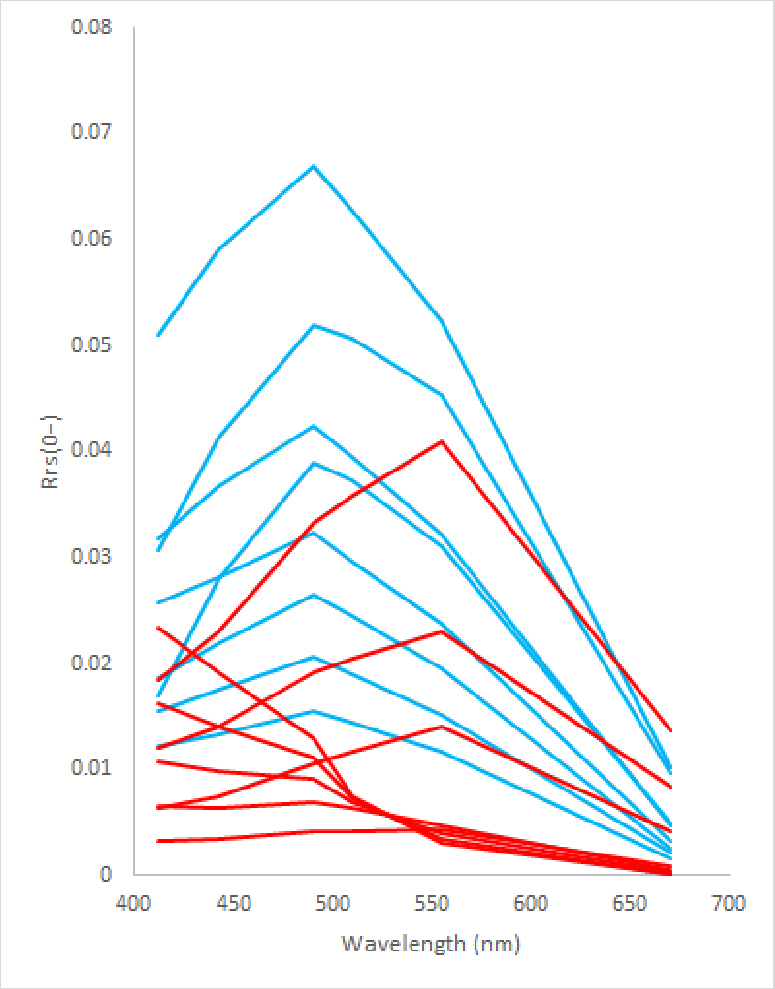

Figure 4: A combination of coccolithophore cluster means (blue) from Moore et al. (2012) derived from SeaWiFs spectra, together with the eight original optical water type (OWT) means (red) from Moore et al. (2009) derived from the NOMAD dataset.

Three dataset files of *Rrs* at 490, 510 and 550 nm were used to detect the presence of coccolithophores. The coccolithophore presence was calculated by dividing the total number of valid pixels in the subset box by the number of coccolithophore pixels in the subset box. A loop through the three *Rrs* was used to create a matrix of size longitude step by time step (169 x 929) for the entire time series. A time series of coccolithophore presence (%) was computed for the inshore and offshore boxes using monthly averages from September 1997 to November 2017. Climatologies of coccolithophore presence for inshore and offshore boxes were computed by averaging months from 1997 to 2017 into 12 months in a year. To analyse the presence of coccolithophores on a larger spatial scale, a climatology of the entire northern BUS was computed using longitude and 8-day intervals represented in a Hovmöller diagram. The northern BUS region was defined using longitude from 9°E to 15°E and latitude from 22°S to 24°S. The climatology was created by averaging the 8-day results (which indicated better seasonal cycle compared to monthly averages) from September 1997 to November 2017 into 53 weeks in a year.

3. Results

3.1. In situ chlorophyll sampling

Chl-a concentrations were sampled every month at inshore (10 NM) and offshore (70 NM) stations for a period of 12 years from 2001 to 2012 (Table 1). The least sampled months are January and February with only 3 years (2001, 2004 & 2010) and 4 years (2002, 2003, 2005 & 2009) of data, respectively. The most sampled months are May and December, both with 11 months of data out of the 12 years of sampling.

Table 1: Survey dates for Chl-a on the 23°S transect during the 12-year sampling period (2001–2012) for the inshore station (10 NM) and offshore station (70 NM). The colours are representative of when both inshore and offshore stations were sampled (black), when only the inshore station was sampled (blue) and only the offshore station (red).

	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Jan	🟦			⬛						⬛		
Feb		⬛	⬛		⬛				⬛			
Mar	⬛	🟥	⬛	🟦	⬛	⬛		⬛		⬛	⬛	⬛
Apr	⬛	⬛	⬛	🟦		⬛		⬛	⬛	⬛	⬛	
May	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	
Jun	⬛	⬛	⬛	⬛	⬛							
Jul	⬛	⬛	⬛	⬛		⬛	⬛	⬛		⬛	⬛	
Aug	⬛	⬛	⬛	⬛		⬛		⬛	⬛			
Sep	⬛	⬛	⬛	⬛	⬛		⬛	🟦	⬛		🟥	⬛
Oct	⬛	⬛	⬛	⬛				⬛	⬛	⬛		⬛
Nov	⬛	⬛	⬛	🟥	⬛	⬛	⬛					⬛
Dec	⬛	🟥	⬛	⬛	⬛		⬛	🟦	⬛	⬛	🟦	⬛

3.1.1. In situ Chl-a concentration and seasonal cycle

Chl-a concentrations at the 10 NM station are ~3 times higher than concentrations at the 70 NM station with an overall median of 4.24 mg m^{-3} and 1.27 mg m^{-3} respectively (Figure 5). Seasonal peaks in concentration occur during spring (September), summer (December-February) and autumn (April-May) at the inshore (10 NM) station with a seasonal minima in July and November. Offshore (70 NM), the seasonal peaks occur in autumn (April), winter (July, August) and spring (September) with minima in December and May.

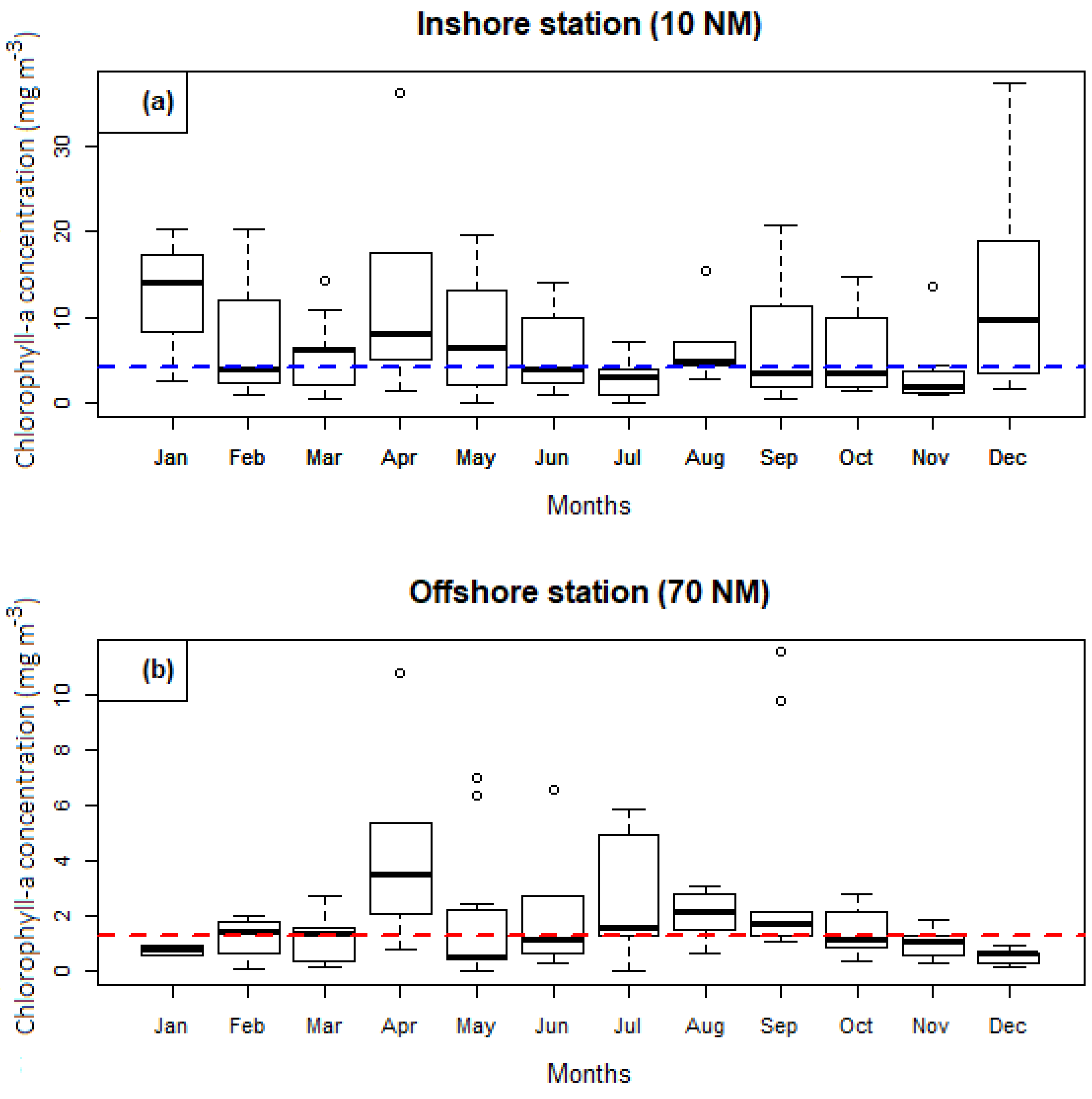

Figure 5: Monthly in situ Chl-a concentration (mg m^{-3}) at (a) 10 NM and (b) 70 NM stations on the 23°S monitoring line of the northern Benguela from 2001-2012. The dashed line marks the overall median value. Solid black lines for each month represent the monthly median with box depicting the lower and upper quartile and the whiskers depicting minimum and maximum range and the circles are the outliers.

3.2. In situ phytoplankton community structure and seasonal cycle

3.2.1. In situ phytoplankton sampling

During the 12 years of the sampling period, coccolithophores were not always counted or analysed in the laboratory, resulting in gaps in the data set. Three years were not sampled (2002, 2003 and 2007), whereas in some years only one month was sampled (2001, 2004 and 2005), while the most sampled years (2008 and 2010) were sampled for a total of five months (Table 2). Although the results have been merged into seasons and averaged to avoid sampling bias, it is important to apply caution when interpreting results from seasons that were not well represented. For example, the results in summer are only represented by one month (inshore) and two months (offshore) throughout the sampling period and the percentage number of months is 4% and 11% respectively (Figure 6). In comparison, the most sampled season was autumn offshore with 9 sampled months (50%), while winter had a 22% representation both inshore and offshore (Figure 6).

Table 2: Survey dates for coccolithophores on the 23°S transect during the 12-year sampling period (2001–2012). The colours depict months when both inshore and offshore stations were sampled (black), when only the inshore station was sampled (blue) and only the offshore station (red).

Months	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Jan	🟦									🟥		
Feb												
Mar						⬛		🟦		🟥	🟥	🟦
Apr									⬛			🟥
May						⬛		🟥		🟥	🟥	
Jun				🟦					🟥			
Jul						⬛		⬛		⬛	🟦	
Aug						🟦						
Sep								🟦				
Oct												
Nov					🟦			🟦			🟥	🟥
Dec										🟥		

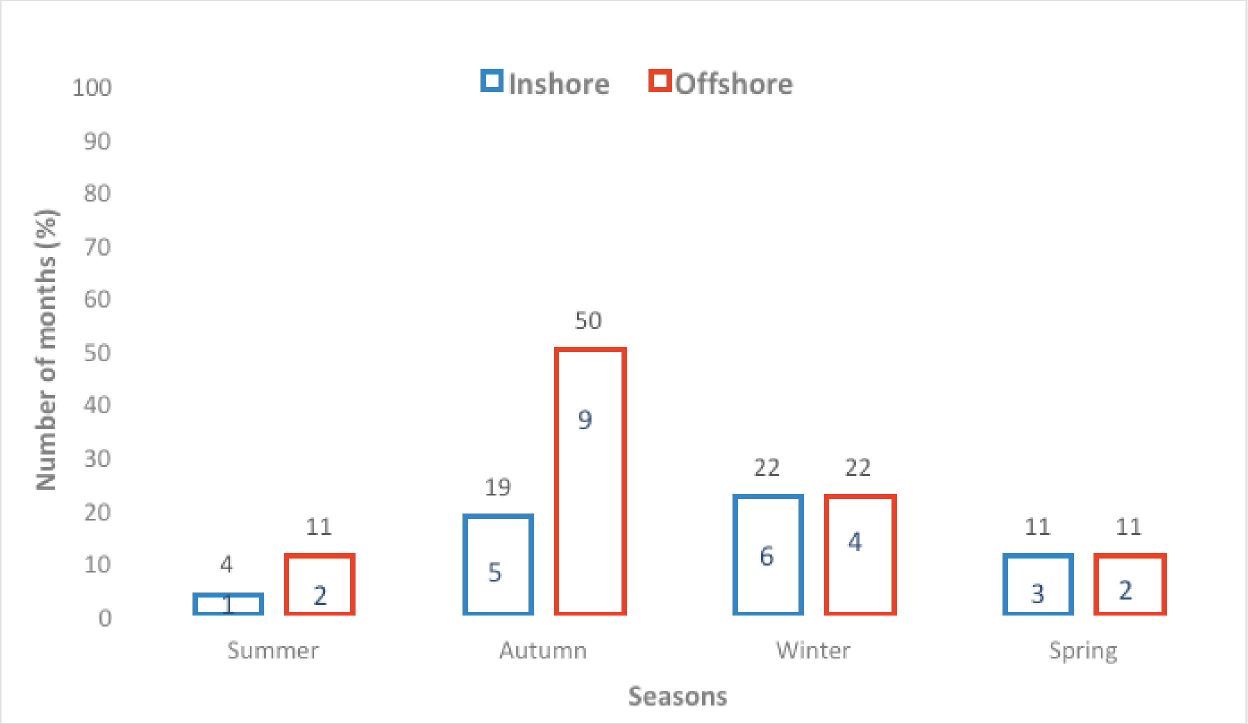

Figure 6: Percentage number of months represented in the seasons for all three phytoplankton groups (coccolithophores, diatoms and dinoflagellates) at inshore (10 NM) and offshore (70 NM) stations. The inshore and offshore stations were sampled for 9 and 6 years respectively during the 12 year sampling period such that a 100% representation would imply a possible total of 27 months inshore and 18 months offshore. For ease of reference the actual number of months sampled are specified inside each bar.

More data was available for diatoms and dinoflagellates which were sampled more frequently than coccolithophores. As such, the value of this information was retained through a more detailed seasonal cycle assessment of these two groups alone (excluding coccolithophores).

Table 3: Survey dates for diatoms and dinoflagellates on the 23°S transect during the 12-year sampling period (2001–2012) for the inshore station (10 NM) and offshore station (70 NM): The colours depict months when both inshore and offshore stations were sampled (black), when only the inshore station was sampled (blue) and only the offshore station (red).

	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Jan	🟦			🟦						⬛		
Feb		🟦	🟦		🟦				⬛	🟥		
Mar	🟦		🟦	🟦	⬛	⬛		⬛		⬛	⬛	⬛
Apr		🟦	🟦				🟥	⬛	⬛	⬛	⬛	⬛
May			🟦	⬛	⬛	⬛	⬛	⬛		⬛	⬛	🟥
Jun		🟦	🟦	⬛	⬛				⬛			
Jul		🟦	🟦			⬛	⬛	⬛		⬛	⬛	
Aug		🟦	🟦	🟦	🟦	⬛			⬛			
Sep		🟦		🟦	⬛			🟦	⬛		⬛	⬛
Oct		🟦	🟦							⬛		⬛
Nov			🟦	🟦	⬛	⬛		⬛			⬛	⬛
Dec		🟦			🟥		⬛	🟦	⬛	⬛		

3.2.2. Phytoplankton community structure (3 groups)

To investigate the relative seasonal dominance among the three phytoplankton groups at inshore and offshore stations, concentrations were normalized for each phytoplankton group, as described in section 2.4. (Figure 7). Worth noting is that the maximum cell count of diatoms was two orders of magnitude higher than either dinoflagellates or coccolithophores. Results highlight differences in community structure and phenology at the inshore versus offshore stations. Maximum cell counts for all three groups (diatoms, dinoflagellates and coccolithophores) occurred at the inshore station whereas offshore maxima only reached ~50% of inshore maxima in the case of dinoflagellates and 20% and 10% for diatoms and coccolithophores respectively. Normalized cell counts of coccolithophores were generally low (below 10% of their measured maxima), except during spring at the inshore station when a coccolithophore bloom took place. Worth noting however is that during spring inshore station was only sampled for 3 months out of a possible total of 27 months over the full time series (i.e. only 11% representation; Figure 6). Maximum cell counts of dinoflagellates were found inshore in autumn and winter decreasing in spring and reaching a minimum in summer. The offshore station saw a similar summer minimum in dinoflagellates with a maximum in autumn and low cell counts in winter. Diatoms had a summer minima both inshore and offshore with an inshore maxima in spring and an offshore maxima in winter. The two parameters, season and location (inshore and offshore) showed no significant effect on the cell counts of coccolithophores (GLM test, $F = 0.4903$, $p = 0.7428$), diatoms (GLM test, $F = 0.7625$, $p = 0.5589$) and dinoflagellates = (GLM test, $F = 01.89$, $p = 0.1423$). This is likely a result of small sampling size and large variability which lowers the chances of detecting a statistical significant difference even though an effect may be present.

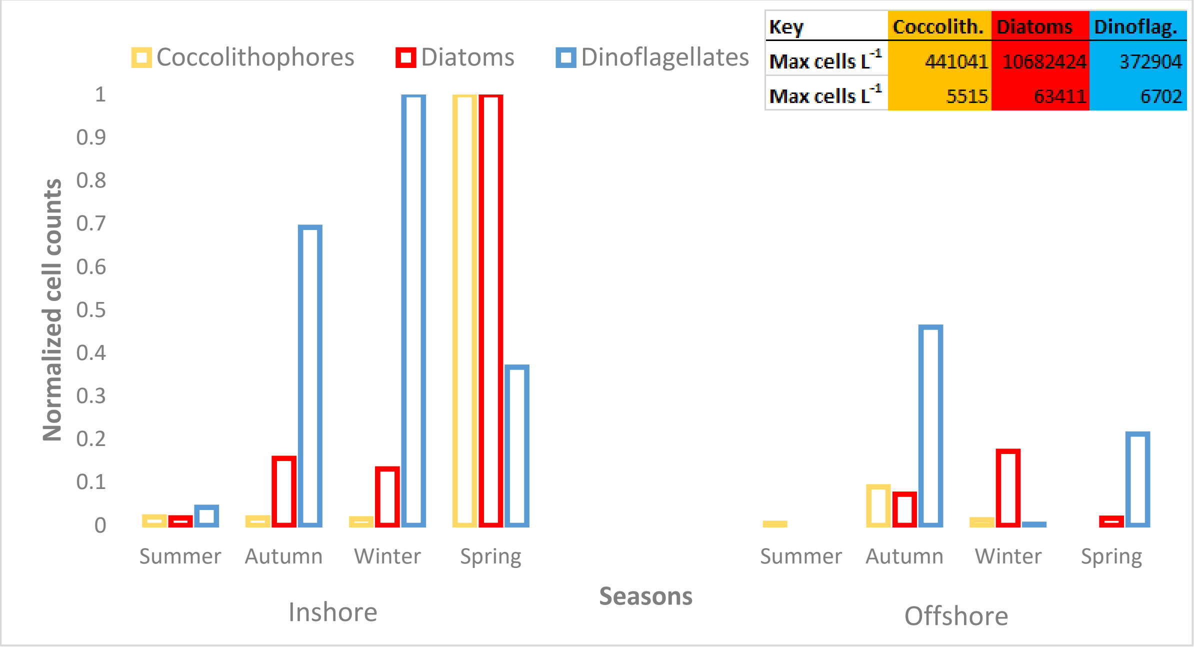

Figure 7: Normalized cell counts of coccolithophores, diatoms and dinoflagellates at inshore (left) and offshore (right) stations. Normalized cell counts range from 0 – 1, where 0 represents the lowest cell count and 1 represents the highest concentration measured in each phytoplankton group.

3.2.3. Diatoms and Dinoflagellates community structure

It is again apparent that cell counts are higher at the inshore station compared to the offshore station (Figure 8a & b) and that diatoms are an order of magnitude higher (~14 times) than dinoflagellates. Diatoms showed an inshore seasonal maxima in spring - summer with peak cell counts in October, December and February, while low cell counts were evident through March to September (Figure 8a). Although the spring peak is similar to that observed in Figure 7, the summer peak found in diatoms inshore is contrary to the minimum observed with data collated in Figure 7. Offshore diatoms were somewhat reversed with peaks in April, July and September and low cell counts from October through to February (Figure 8b). The highest cell count for dinoflagellates were inshore in June (similar to that observed in Figure 7), with a secondary bloom taking place in November (Figure 8a) that was not apparent in Figure 7. At the offshore station, diatoms show a more gradual increase in cell count up to September (compared to a winter peak in Figure 7), while dinoflagellates peaked in March and April (Figure 8b) consistent with the autumn peak in Figure 7. Worth noting is that the timing of peaks at inshore and offshore stations do not coincide, i.e. months with cell count peaks at inshore stations typically show lowest cell counts at the corresponding offshore station and vice versa. Another point worth noting is the sporadic nature of the peaks and the absence of a gradual increase and decrease more typical of a seasonal cycle.

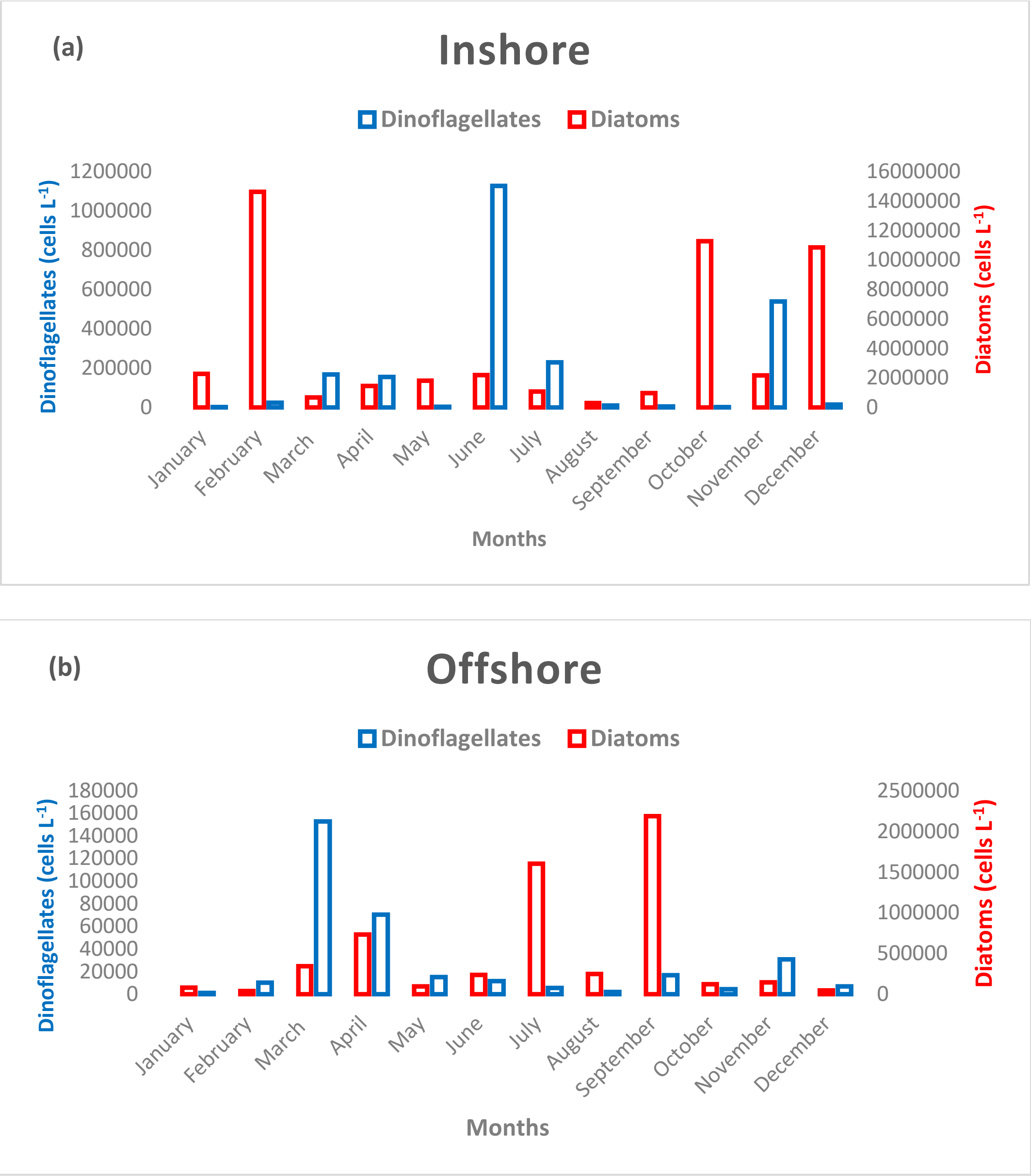

Figure 8: Averaged monthly time series of diatom and dinoflagellate cell counts (cells L^{-1}) at (a) inshore station (10 NM) and (b) offshore station (70 NM) from 2001 to 2012. Note the difference in cell counts ranges between diatoms and dinoflagellates and between inshore and offshore stations.

3.3. Satellite chlorophyll seasonal cycle

Using two subset boxes selected to represent inshore and offshore stations for the satellite data, described in section 2.5. (Figure 3). Monthly averages of the data in each box were used to plot a time series for inshore (blue) and offshore satellite Chl-a concentration (red) from 1997 – 2017 (Figure 9). Concentrations inshore are double the magnitude of the offshore box. Both time series show high intra-seasonal and inter-annual variability. The highest concentration peaks occur in 2002 and 2012 inshore, while the highest offshore peak occurs in 2007. At certain times inshore and offshore experience concentration increase/decrease synchronously (e.g. 2005, 2007, 2006 & 2016), while other times an increase inshore is associated with a decrease in offshore concentrations and vice versa (e.g. 2000, 2002, 2010, 2012) and a coefficient correlation (r) of 0.22.

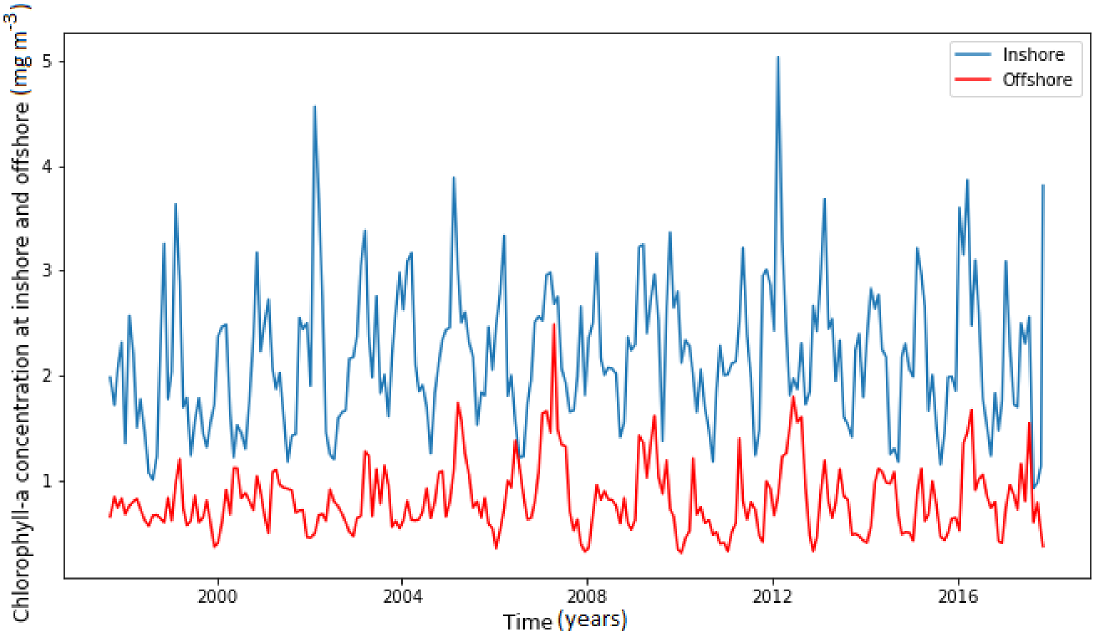

Figure 9: Time series of Chl-a concentrations (mg m^{-3}) at inshore and offshore stations at the northern BUS from 1997 to 2017.

The Chl-a monthly distribution from 1997 to 2017 for inshore and offshore boxes (Figure 10a & b) shows an inshore bloom that peaks in February with an August minimum whereas the offshore bloom peaks two months later in April, with a seasonal minima in December. The dashed line marks the overall median value. Solid black lines for each month represent the monthly median with the box depicting the lower and upper quartile and the whiskers depicting minimum and maximum range and circles are the outliers. The offshore plot has the biggest outlier, indicative of a wider range of variability, particularly during the peak bloom period in April.

The Chl-a climatology from 1997 to 2017 using weekly averages (bold lines) and standard deviations (shading) for inshore and offshore boxes (Figure 10c) shows an earlier bloom initiation date inshore (3rd week of January) whereas the offshore bloom initiation date occurs much later (1st week of March). The error bars illustrate the minimum and maximum range of bloom initiation dates encountered over the time series, with inshore showing a broad range compared to offshore. The duration of the bloom inshore, although greater in amplitude is typically shorter in duration (~8 weeks) when compared to the offshore bloom which typically lasts (~14 weeks). The bloom initiation offshore also appears to be later with in situ data when compared to satellite estimates.

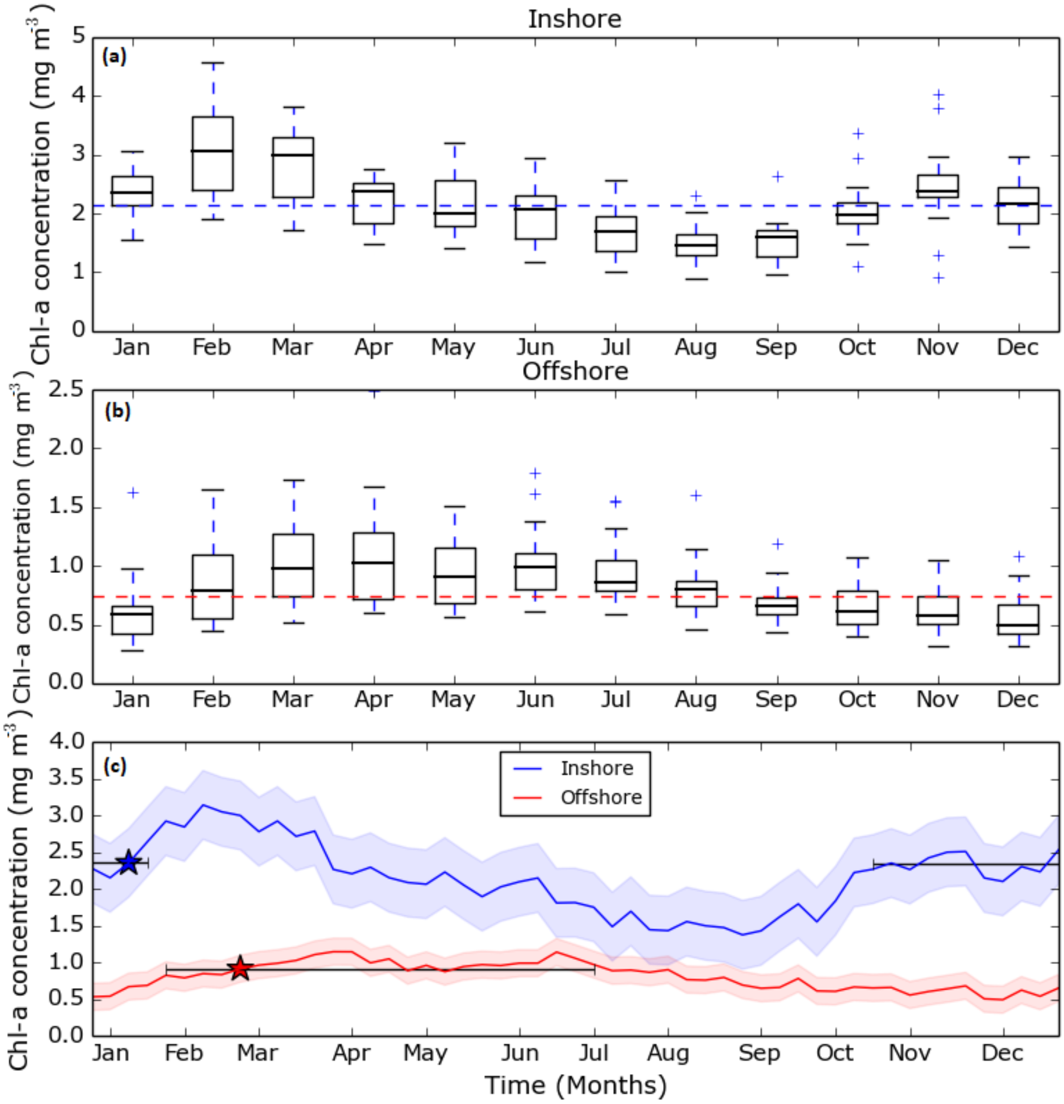

Figure 10: Monthly satellite concentrations of Chl-a (mg m^{-3}) at the (a) inshore box and (b) offshore box at the northern BUS from 1997-2017. The dashed line marks the overall median value. Solid black lines for each month represent the monthly median with box depicting the lower and upper quartile and the whiskers depicting minimum and maximum range and plus signs are the outliers. The mean Chl-a climatology is depicted in (c) for inshore (blue) and offshore (red) boxes with the shaded area representing the standard deviation. The mean bloom initiation date for each time series is depicted as a star with error bars representing the minimum and maximum range and the circles are the outliers.

3.4. Satellite versus in situ chlorophyll comparison

In order to highlight the seasonality (and not differences in amplitude, which are to be expected), different scales were used to plot in situ versus satellite Chl-a. For the inshore in situ station versus satellite box comparison (Figure 11a) it is clear that satellite concentrations are typically 60% lower (max = ~3 mg m^{-3}) than in situ concentrations (max = ~12 mg m^{-3}). The offshore in situ versus satellite box shows a smaller discrepancy in amplitude with an in situ maximum of ~6 mg m^{-3} and a satellite maximum of ~1.2 mg m^{-3}. Most notable discrepancies are the dips in Chl-a concentration observed with in situ data but not in the satellite data inshore in February, March and offshore in March, May, June and July.

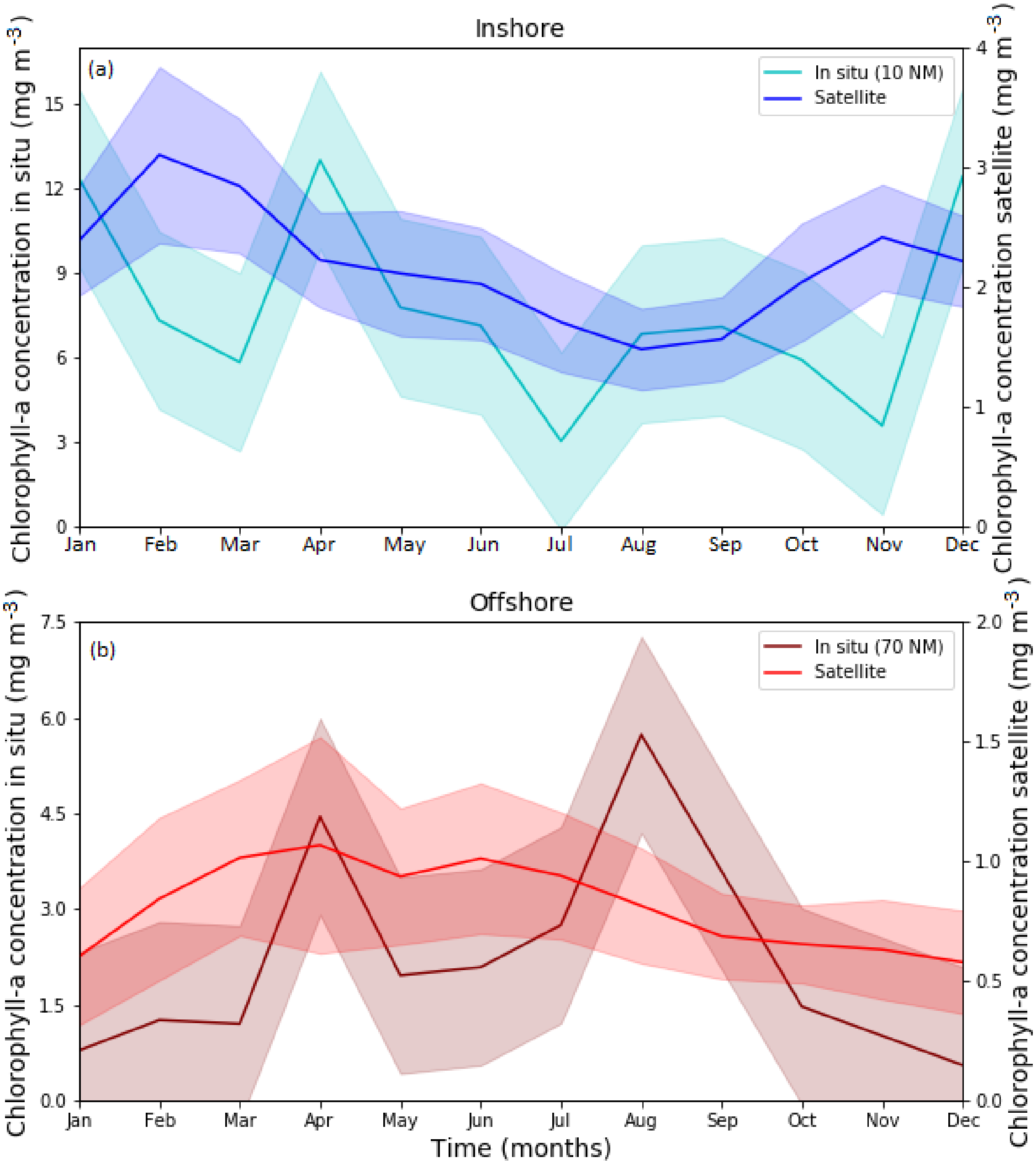

Figure 11: Monthly Chl-a concentration of in situ (mg m^{-3}) from 2001-2012 and satellite (mg m^{-3}) from 1997-2017 at the (a) inshore station and (b) offshore station of the northern BUS.

3.5. Coccolithophore bloom presence

The coccolithophore algorithm detected the percentage presence of coccolithophores as the total number of pixels classified as coccolithophores versus the total number of valid pixels within each subset box. A time series of coccolithophore presence at inshore and offshore boxes shows a higher presence offshore relative to inshore with both boxes showing high intra-seasonal and inter-annual variability (Figure 12). The overall increase and decrease in coccolithophore presence is synchronous for inshore and offshore boxes (r = 0.62), with the exception of some months during 1999 and 2017. The monthly distribution of coccolithophore presence (Figure 13) confirms the offshore presence as being almost twice as high as inshore. The more frequent occurrence of coccolithophores offshore versus inshore contradicts the in situ data (Figure 7), which shows higher concentrations of coccolithophores at the inshore station (10 NM). From a seasonal perspective, a higher presence is evident both offshore and inshore in spring - summer with a very low presence of coccolithophores detected in mid-winter (June). The inshore station experiences a wide range of variability in Feb-March, while the highest variability offshore is detected in December (Figure 13). An apparent peak in presence inshore in September is similar to in situ data, which showed the highest concentration of coccolithophores inshore in spring (Figure 7).

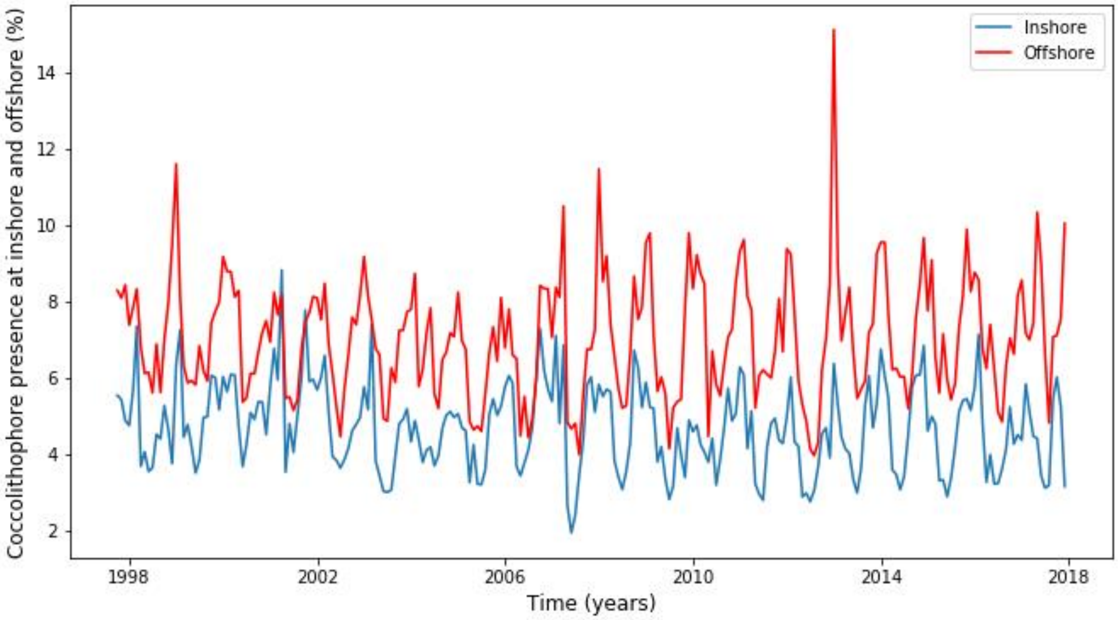

Figure 12: Time series of coccolithophore presence (%) at the inshore and offshore box at the northern BUS from 1997 to 2017.

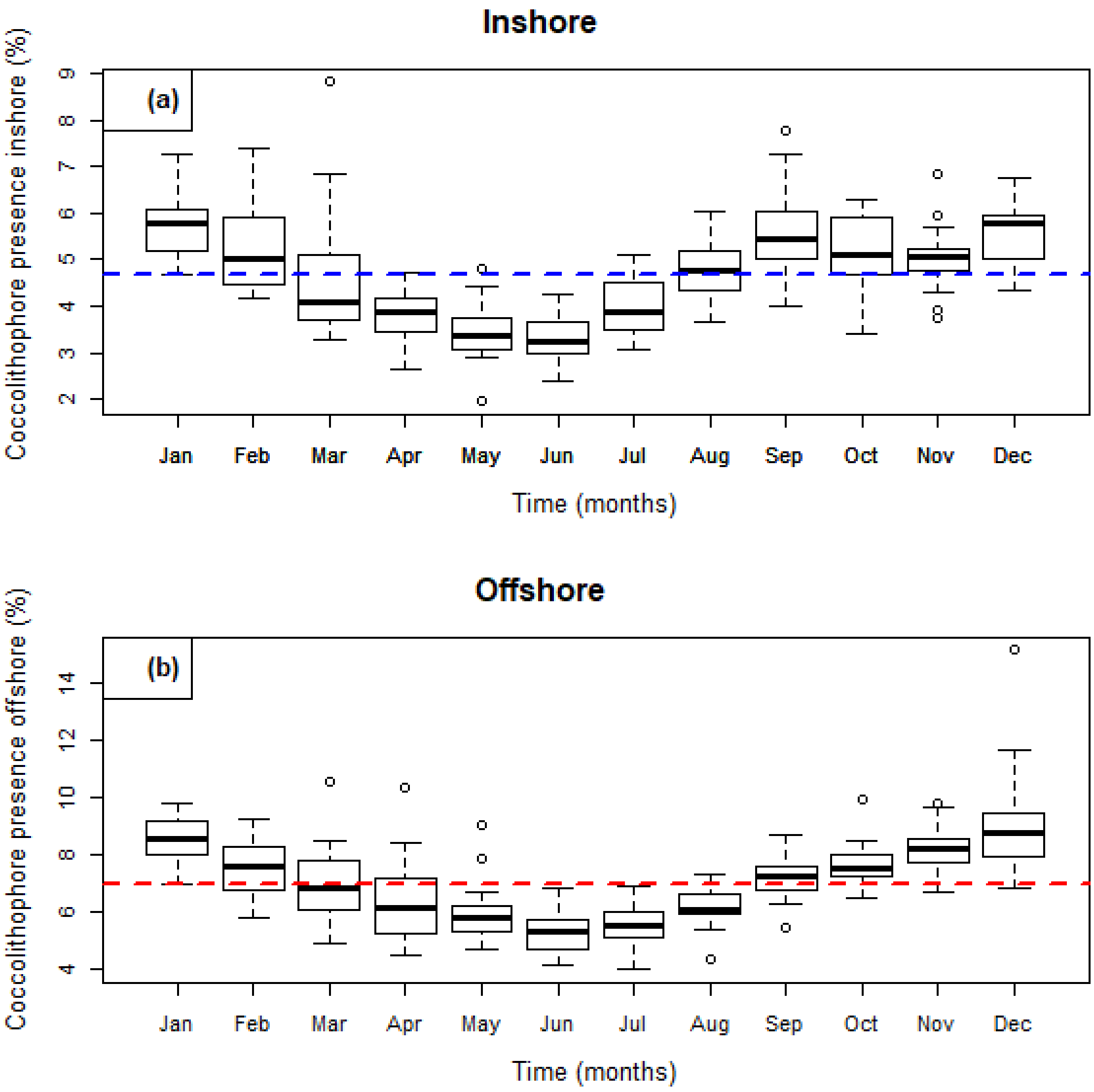

Figure 13: Monthly coccolithophore presence at the (a) inshore box and (b) offshore box at the northern BUS from 1997-2017. The dash line marks the overall median value. Solid black lines for each month represent the monthly median with box depicting the lower and upper quartile and the whiskers depicting minimum and maximum range and the circles are the outliers.

To assess the distribution of coccolithophores on a larger spatial scale, a hovmöller plot of the weekly climatology of coccolithophore presence (from 1997 to 2017) was created for the greater northern BUS area (Figure 14). Similar to Figure 13, Figure 14 shows a low presence of coccolithophores both inshore and offshore in winter with their presence dominating offshore in the late spring and summer months. From the broader region of the hovmöller plot it is clear that the “offshore” subset box selected to coincide with the 70 NM in situ station is indeed located relatively inshore when compared to the greater BUS blooms of coccolithophores.

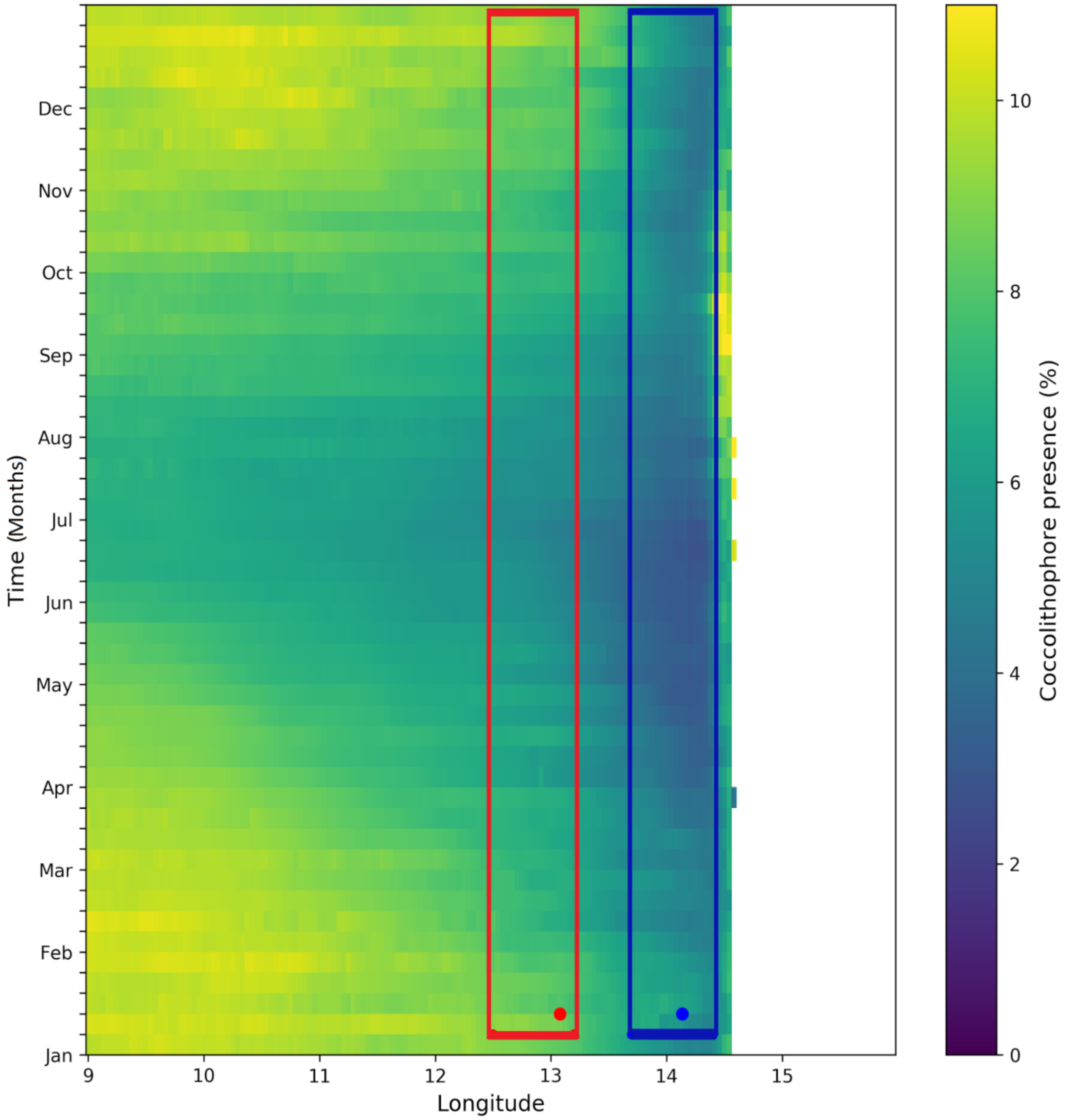

Figure 14: A longitudinal-time hövmoller diagram of the weekly climatology (January to December-y-axis) of coccolithophore presence (%) (colour scale) between 22 and 24 degrees South averaged from 1997-2017. The red and blue subset boxes represent offshore and inshore boxes, respectively. The red and blue dots represent in situ stations at 70 NM and 10 NM, respectively.

4. Discussion

4. 1. Characterising the seasonal cycle of chlorophyll in the BUS

Phytoplankton are the primary producers in the marine food chain and their production plays a crucial role in determining ecosystem health, supporting marine resources and food security and driving biogeochemical processes that affect export flux, air-sea gas exchange and ultimately the global carbon cycle (Chassot et al., 2010; Perry et al., 2011; Stock et al., 2017). Phytoplankton are also sensitive to environmental change, which makes them a key indicator species of climatic change in response to global warming (Friedland et al., 2018). One of the observed responses in the northern BUS is a change in species composition with an increase in the frequency of warm events and a decrease in the occurrence of cold upwelling events (Shannon et al. 2007). Other anticipated responses are shifts in the timing of phytoplankton blooms (Henson et al., 2009), which can have serious impacts on the survival of larval fish community (Henson et al., 2009). An understanding of the characteristics of the seasonal cycle in the BUS will thus prove useful when diagnosing and assessing potential change.

In situ Chl-a concentrations at the inshore station were on average double that found at the offshore station. This decline in concentration further offshore has been reported previously in the northern Benguela and is thought to be associated with nutrient limitation with increasing distance from the shore (Hansen et al., 2014). Although the magnitude of the inshore bloom is higher than the offshore bloom, the duration is typically 8 weeks shorter (Figure 10c). The short duration of inshore bloom could be a result of nutrient limitation. In the northern BUS, wind forcing and nutrient availability have been observed to significantly influence both the magnitude and duration of blooms (Louw et al., 2016), with nitrate typically limiting the bloom during late summer (Wasmund et al., 2014). The time series of surface Chl-a concentration from satellite ocean colour (Figure 9) shows a seasonal cycle with high intra-seasonal and inter-annual variability both inshore and offshore. The inshore region experiences high concentration peaks (Figure 9) and in addition, the selected inshore box covers a large concentration gradient which will impact the observed range of variability. High variability is also evident in the in situ data from the large distribution relative to the median of the whiskers in the box plots in Figure 5. High temporal and spatial variability off the coast of Namibia, has been ascribed to factors such as wind, solar radiation and nutrient availability that influence primary productivity and ultimately phytoplankton biomass (Louw et al., 2016). Shelton et al. (1985) found that the primary driver of the high variability observed here is wind events that typically last for 3-6 days and drive upwelling which transports bottom nutrient rich waters to the surface in support of phytoplankton production.

In addition to high temporal variability, the northern BUS is characterised by high spatial variability, that is evident in the differences between inshore and offshore stations and a very low correlation coefficient (0.22), as most times an inshore increase in Chl-a is associated with an offshore decrease (or vice versa). Shannon (1985) and Louw et al. (2016) also reported high variability in Chl-a concentrations in the inshore region of the northern BUS and attributed this to stronger mesoscale variability of upwelling filaments. During upwelling the inshore region is mostly influenced by physical processes which become less dominant during the relaxation phase towards the offshore where biological and chemical processes become more important as the thermocline develops (Pitcher et al., 1992). The timing of the blooms inshore and offshore is also different, with inshore blooms that peak in spring (November) and summer (February), while offshore blooms peak a few months later in autumn (April) (Figure 10a & b). The delayed bloom timing offshore is a likely result of a bloom that typically initiates inshore and propagates offshore during the relaxation phase of upwelling (Monteiro and Largier, 1999).

The highest concentrations of phytoplankton both inshore and offshore occurs during summer and autumn respectively, while a steep decline in concentration occurs during winter both at inshore and offshore stations (Figure 10a & b). Louw et al. (2016) observed similar elevated concentrations during summer and autumn, which they attributed to high surface temperatures resulting in strong upper water column stratification that improves the light environment, while the lowest concentrations during winter were attributed to high cloud cover, low solar radiation and strong winds that result in deep mixing, the combination of which results in light limitation of phytoplankton production (Henson and Thomas, 2007). Other investigations at the 21°S and 24°S transect lines of the northern Benguela show that the thermocline develops in late spring, persists until summer and gets eroded by upwelling that occurs in autumn and winter (Plessis, 1967; Weeks et al., 2002). Phytoplankton blooms were similarly absent during periods of strong winds in winter (July) at the southern Benguela (Pitcher et al. 1992) and the Oregon shelf, off northern California (Evans et al., 2015). As such, the seasonal cycle characteristics of Chl-a observed here (Figure 10) can be attributed to periodic winds coupled with light availability from solar radiation and associated stratification (Louw et al., 2016).

4.2. Satellite versus in situ chlorophyll comparison

Chl-a concentrations vary with space and extension(Campillo-Campbell and Gordoa, 2004), and differences between in situ stations and satellite box averages are to be expected due in particular to the vast difference in temporal and spatial scales over which the data are collected (Evers-King 2014). For example, the satellite boxes extend much further offshore than the in situ stations and given the characteristic offshore gradient of decreasing Chl-a with distance offshore, it is thus expected that satellite Chl-a concentrations in the box averages would be lower than those at the in situ stations. In addition, SeaWiFs ocean colour has been known to underestimates Chl-a concentrations that are >2 mg m^{-3}, with a correlation of 0.56 with HPLC estimates in the Benguela region (Barlow et al., 2001), while MODIS products have been known to overestimate concentrations below 0.2 mg m^{-3} in some regions (Blondeau-Patissier et al., 2014). Differences between in situ and satellite results are typically attributed to averaging of merged products that generate errors associated with data gaps (due primarily to clouds) and atmospheric corrections which interferes with the accuracy of ocean colour concentration estimates (Barlow et al., 2001; Cole et al., 2012). The purpose of this comparison however was not to identify differences in magnitude, but rather to investigate differences in the characteristics of the seasonal cycle. On the whole, the seasonal cycle of in-situ versus satellite Chl-a was similar with respect to the duration of blooms which appear to be short-lived, further emphasizing the high temporal variability in the northern BUS. A consequence of high spatial and temporal variability was however evident in the differences observed between the climatologies (Figures 9a and b). Here, discrepancies in the seasonal cycle from in situ data (e.g. the notable dip from inshore in situ data in Feb/March relative to satellite data) are most likely a result of patchy blooms in both time and space that are captured by satellite data (averaged over 4 km in space and 8 days) but missed by instantaneous spot measurements taken on a cruise.

4.3. Phytoplankton bloom initiation

The characterisation of the bloom initiation dates is done with the weekly (8-day resolution) satellite ocean colour estimates (Figure 10c), as it is not possible to do so accurately with the poor temporal resolution of the in situ data set (Ferreira et al., 2014; Henson et al., 2018).

Results show that offshore blooms generally initiate during autumn with an average bloom initiation on the 1st week of March and a range of initiation that extends 16 weeks from 1st week of March to 3rd week of July. In contrast, inshore blooms have an average earlier bloom initiation on the 3rd week of January with a much higher range of variability that extends 8 weeks from 3rd week of January to 3rd week of March. The difference in timing inshore versus offshore is a reflection of the bloom characteristics which initiate with the onset of upwelling inshore and then propagate offshore. The increased range of variability in bloom timing inshore is likely a result of averaging across a region with a steeper Chl-a gradient (than the offshore box) and anticipated high variability attributed mesoscale variability of upwelling filaments (Shannon et al., 1984; Louw et al., 2016). An understanding of characteristic bloom phenology can aid climate variability studies as phytoplankton production is dependent on physical processes influenced by climate change (Henson et al., 2009). An increase in global temperatures for example has been observed to influence bloom timing as it affects the development of the thermocline and MLD dynamics (Friedland et al., 2018).

4.4. Seasonal characteristics of phytoplankton community structure

In situ results of the relative proportions of phytoplankton groups (coccolithophores, diatoms and dinoflagellates) show differences between inshore and offshore stations with higher cell counts at the inshore station (10 NM) for all three phytoplankton groups (Figure 7), consistent with enhanced nutrient supply closer to the coast as described in the literature (Hansen et al., 2014). Diatoms and coccolithophores reach their respective maxima inshore in spring while dinoflagellates reach their maximum inshore in winter and autumn (Figure 7). The spring peak in diatoms in the three species comparison (Figure 7) is similar to that observed when only two species were considered (Figure 8a). However, the summer peak found inshore in diatoms in Figure 8a (two species comparison) is contrary to the minimum observed in Figure 7. This discrepancy highlights erroneous results that can occur as a consequence of poor sampling frequency as summer inshore was the least represented (4%) having only been sampled once for all three species for the entire time series (Figure 6). The offshore station shows a different seasonal cycle in community structure to inshore with the most diatoms occurring in winter, coccolithophores and dinoflagellates in autumn (Figure 7). The diatom winter peak is also observed in Figure 8b. Discrepancies however again occur in that the spring peak observed in the better resolved data set (Figure 8b) is absent from Figure 7, and as with summer inshore, spring offshore is the second least sampled season (sampled twice representing 11% coverage) (Figure 6). It is clear that a lack of consistent sampling makes it challenging to understand the seasonal characteristics of phytoplankton community structure. Higher sampling frequency would improve any study of bloom phenology in particular given the high degree of variability observed both temporally and spatially. To this end, many long-term ecological monitoring stations are beginning to invest in optical devices (e.g. on moorings) to quantify community structure characteristics such as imaging flow cytometry that allows for high-resolution mapping of organisms.

According to the literature, temperature is considered a primary driver of the observed regional and seasonal variability in community structure, as seasonal warming increases SST which influences the formation of the thermocline, which affects the nutrient and light supply favoring the production of one species over another (Smayda and Reynolds, 2003; Wells et al., 2015). Additional factors such as nutrient availability and wind variability affect habitat conditions that ultimately influence phytoplankton composition (Hansen et al., 2014).

Seasonal stratification during upwelling favours the production of dinoflagellates relative to diatoms (Horstman, 1981; Pitcher et al., 1993), with widespread populations of dinoflagellates known to dominate stratified waters during the relaxation phase of upwelling in the southern Benguela (Pitcher et al., 1998). This may explain the offshore peak observed in dinoflagellates in autumn and spring and why dinoflagellates were observed to reach maximum cell count inshore in autumn (Figure 7). Their adaptation to stratified water conditions has been attributed to their ability to regulate their depth to deeper nutrient rich waters (Pitcher et al., 1993). A large number of dinoflagellates were however observed inshore during winter (Figure 7), which is associated with less solar radiation and deep mixing resulting in high nutrients. Pitcher et al. (1993) also reported occasional dinoflagellate blooms that persist from autumn to winter (June) in the southern Benguela. Dinoflagellates found inshore seem to be adapted to a set of conditions different from those offshore. Pitcher et al. (1998) found two groups of dinoflagellates in the southern Benguela, one inshore that performed diel vertical migration to manage nutrient uptake and another group offshore that aggregates to a defined stratum that suits their nutrient requirements. Similarly two groups were observed in the northern Benguela, one in the newly upwelled waters inshore characterized by high nutrients and low temperatures and another in the aged upwelled waters offshore with low nutrients and high temperature (Hansen et al., 2014).

Usually diatoms dominate cold nutrient-rich upwelled waters (Olivien 1983; Shannon and Pillar 1986), however, occasional increases in temperature have been found to favour coccolithophores over diatoms in the Benguela region (Mitchell-Innes and Winter, 1987). This may explain why diatoms and coccolithophores were found to reach their respective maxima inshore in spring (Figure 7). Generally, diatoms were dominant at both inshore and offshore stations, with maximum cell counts that were two orders of magnitude higher than dinoflagellates or coccolithophores (Figure 7). This is in agreement with a number of studies, which showed diatoms as the most dominant phytoplankton group in the northern Benguela (Kollmer, 1963; Kruger, 1980; Barlow et al., 2006; Louw et al., 2017; Barlow et al., 2018). In these studies, their dominance was linked to sufficient nutrient availability and their ability to optimize productivity as they can maximize light absorption through photosynthetic chlorophylls and carotenoids (Barlow et al., 2001).

With respect to coccolithophores, in situ results demonstrate highest cell count during spring inshore and autumn offshore, while counts remained low throughout the other seasons (Figure 7). On the contrary, satellite results show a higher presence of coccolithophores offshore, with the least presence during winter (Figure 14). High temporal variability is apparent on the time series, with a good positive correlation coefficient between inshore and offshore satellite averaged boxes (r = 0.62). The correlation coefficient as well as an overall similar seasonal cycle of coccolithophore presence inshore and offshore (Figure 13) implies less spatial variability and highlights the possibility that the offshore in situ station is not far enough offshore to capture the true nature of coccolithophore phenology. As indicated in Figure 14, which shows the presence of coccolithophore blooms and stronger seasonality much further offshore in the greater northern BUS.

Several studies have similarly reported high concentrations of coccolithophores and smaller phytoplankton groups offshore in mature upwelled waters (Mitchell-Innes and Winter, 1987; Barlow et al. 2010), during late winter and spring (Shannon, 1985). Other studies reported high coccolithophore concentrations during high solar radiation and stable ocean stratification conditions (Houghton, 1988; Giraudeau et al., 1993; De Vargas et al., 2007), with a well-defined thermocline (Giraudeau et al., 1993). Coccolithophores' adaptation to the offshore region could also be linked the pH value of the water. During upwelling the pH of the water can lower to a minimum of 6.6 in the inshore region (Pitcher and Probyn 2012). A low pH (high acidity) is unfavorable for the growth and calcifying rates of coccolithophores (Lohbeck et al., 2012; Schlüter et al., 2014). However, a more heavily calcified type of *Emiliania huxleyi* with a distinct morphotype was reported in mature upwelled waters and lower irradiance conditions at the inshore region succeeding a decline of diatoms (Henderiks et al., 2012).Therefore ocean acidification affects the seasonality and species composition coccolithophores.

As a result of their small size, coccolithophores require less nutrients, as low as 0.1 µM nitrates/L, when compared to larger dinoflagellates who require at least 5 µM nitrates/L (Eppley et al., 1969). Hence they are able to outcompete dinoflagellates in low nutrient stratified conditions. Similarly, in a study by Giraudeau et al., (1993), coccolithophores were observed to produce normally when both nitrate and phosphate were depleted (Giraudeau et al., 1993). In another study by Probyn, (1992) an observed increase in coccolithophore occurrence was linked to ammonium production following the collapse of a of diatom bloom with increased stratification and decreased nitrate. Coccolithophores have also been shown to grow faster in conditions of higher radiation associated with stratification whereas diatoms grow faster in cool upwelled inshore waters (Riley, 1974). Our satellite results thus appear to be robust in their indication of a high presence of coccolithophores offshore during spring and summer coincident with depleting nutrients and high radiation whereas a low presence during winter is associated with low solar radiation and less stratification (Figure 13 and 14).

Understanding the regional and seasonal distribution of dinoflagellates and coccolithophores is particularly important given their role in DMS production. For example, the phenology of coccolithophores can be used as a proxy for the seasonal cycle of DMS productions in model simulations such that high production of DMS can be expected during warmer temperatures and periods of intense ocean stratification when coccolithophores and dinoflagellates dominate.

It is important to understand phytoplankton community characteristics in conjunction with their physical drivers because it is the physics that will likely be influenced by climate change. The observed ocean warming over the past decades (Levitus et al., 2009; Friedland et al., 2018) not only has implications on phytoplankton community structure (Lamont et al., 2018) and the production of DMS but also on carbon flux exchange and zooplankton (e.g. copepods) survival, which directly impacts the success of the fisheries industry. It is thus important to continue monitoring vital marine ecosystems such as the BUS so that we can identify changes in key indicator species in response to global warming and threats such as ocean acidification from anthropogenic forcing (Friedland et al., 2018).

5. Conclusion

This study shows seasonal cycles of chlorophyll concentration as well as seasonal characteristics of coccolithophores, diatoms and dinoflagellates and uses remote sensing reflectance to identify the distribution of coccolithophores across the northern BUS. High spatial and temporal variability is apparent for both in situ and satellite results, with inshore and offshore regions showing different seasonal cycles and a gradual decrease in Chl-a concentration offshore. Discrepancies in magnitude between in situ stations and satellite averaged boxes is attributed to the vast difference in temporal and spatial scales over which the data are collected. Although in situ data is patchy and more likely to miss blooms at instantaneous spot measurements taken on a cruise, it is useful to validate satellite algorithms and provide proof of what is observed by satellites. In addition it is able to measure much more than satellites (e.g. species composition down to genus level, particle size and volume etc). Satellite imagery on the other hand has the added advantage of being able to map the seasonal cycle on a much larger spatial and temporal scale especially in regions as high variable as the northern BUS. An 8-day resolution satellite data was able to indicate that blooms offshore initiate later and last longer than inshore blooms which are higher in magnitude. Diatoms are found to be dominant over dinoflagellates and coccolithophores across the region, and in situ results show higher concentrations of coccolithophores inshore during spring, whereas the satellite ocean colour results concurs with several studies showing a higher presence of coccolithophores offshore during warmer temperatures in spring and summer. Temperature has previously been found to influence phytoplankton community structure, however a better understanding of how environmental factors such as wind forcing, solar radiation and nutrient availability affect various phytoplankton groups can further improve our understanding of climate responses to global warming since their combined effects influence phytoplankton composition by changing ocean habitat conditions. Therefore, a good understanding of the characteristics of the phytoplankton seasonal cycle, bloom timing and community composition is useful for detecting change associated with climate forcing.

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