Insights into the spatio-temporal productivity distribution in the Indian Sector of the Southern Ocean provided by satellite observations

by

Anne-Cécile DRAGON* (1, 2), Stéphane MARCHAND (3), Matthieu AUTHIER (1), Cédric COTTÉ (4), Stéphane BLAIN (5) & Christophe GUINET (1).

ABSTRACT. - In the Indian sector of the Southern Ocean, satellite data were used to investigate the spatio-temporal dynamics of phytoplankton bloom in relation to physical oceanographic variations. Three geographical sectors were considered: the interfrontal zone, the Kerguelen Plateau and the Antarctic sector. The Kerguelen Plateau produces a very large phytoplankton bloom due to its relatively shallow depths and strong vertical mixing, that contrast with the surrounding high-nutrient low-chlorophyll (HNLC) waters of the interfrontal zone of the Southern Ocean. Understanding the spatio-temporal dynamics of phytoplankton biomass, as a proxy of primary production, is of fundamental importance since primary production sets a first-order constraint on the energy available to sustain the entire ecosystem. Analyses of high quality ocean color datasets revealed details of the inter-annual, seasonal and spatial dynamics of phytoplankton over the plateau, in the interfrontal zone and in the Antarctic sector. The parts of the plateau north and south of the polar front were found to exhibit different patterns. The plateau surface chlorophyll-a concentration and the productivity conditions available in the western and eastern interfrontal zones were also compared. This approach highlights the spatio-temporal variability of primary production in the Indian sector of the Southern Ocean and introduces a new prospect of investigation regarding the hydrography and biological richness of the Kerguelen Plateau.

RÉSUMÉ. - Distribution spatio-temporelle de la productivité à partir de données satellitaires dans le secteur Indien de l'océan Austral.

Des données satellitaires ont permis l'étude du bloom phytoplanctonique du secteur indien de l'océan Austral. La dynamique spatio-temporelle de ce bloom a ainsi pu être mise en relation avec les variations de différentes variables d'océanographie physique. Nous nous sommes particulièrement intéressés à trois aires géographiques : la zone interfrontale, le plateau de Kerguelen et le secteur Antarctique. Contrairement à la zone interfrontale australe caractérisée par des eaux riches en nutriments mais avec de faibles concentrations en chlorophylle (HNLC), le plateau de Kerguelen est à l'origine d'un important bloom phytoplanctonique en raison de ses eaux peu profondes et de l'important mélange vertical qui s'y effectue. La production primaire est connue comme étant le facteur limitant majeur à l'origine de l'énergie disponible pour approvisionner le reste de l'écosystème. Dès lors, la compréhension de la dynamique spatio-temporelle de la biomasse phytoplanctonique, utilisée comme un indicateur de la production primaire, est d'importance fondamentale. Dans nos trois aires géographiques d'intérêt, l'analyse de données de couleur de l'océan de très bonne qualité a permis de révéler les détails des dynamiques inter-annuelle, saisonnière et spatiale du phytoplancton. Les parties du plateau situées au nord et au sud du front polaire n'ont ainsi pas présenté la même dynamique. Une inter-comparaison des zones interfrontales à l'ouest et à l'est de Kerguelen avec le plateau de Kerguelen a également été réalisée. Notre approche a ainsi permis de comparer la variabilité spatiale et temporelle de la production primaire dans le secteur indien de l'océan Austral. Cette approche introduit de nouvelles perspectives de recherche en ce qui concerne l'hydrographie et la richesse biologique sur le plateau de Kerguelen.

Key words. - Chlorophyll-a - Biological richness - Interfrontal zone - Remote sensing - SeaWIFS - Phytoplankton biomass.

High latitude marine ecosystems contribute for more than 75% of the global ocean primary production, with the Southern Ocean as a major contributor (Sarmiento *et al.*, 2004). Photosynthesis by oceanic phytoplankton, inducing about half of the biosphere's primary production, is a vital link between living and inorganic stocks of carbons (Field *et al.*, 1998; Behrenfeld *et al.*, 2001). Since primary production sets a first-order constraint on the energy available to sustain the entire ecosystem, understanding its spatio-temporal dynamics is of fundamental importance. Primary production

(1) CEBC-CNRS, 79360 Villiers-en-Bois, France. [matthieu.authier@cebc.cnrs.fr] [christophe.guinet@cebc.cnrs.fr]
(2) MAP5, UMR CNRS 8145, Paris, France. [acdragon@cebc.cnrs.fr]
(3) Muséum national d'Histoire naturelle, Département milieux et peuplements aquatiques, UMR 7159, CP 26, 43 rue Cuvier, 75231 Paris CEDEX 05, France. [marchand@mnhn.fr]
(4) LOCEAN, UPMC, UMR 7159, 4 place Jussieu, 75252 Paris CEDEX 5, France. [cecotte@cebc.cnrs.fr]
(5) Laboratoire d'Océanographie biologique, UMR CNRS 7621, 66650 Banyuls-sur-Mer, France. [stephane.blain@obs-banyuls.fr]
* Corresponding author [acdragon@cebc.cnrs.fr]

and a close proxy, phytoplankton biomass, are regulated by a complex interaction of physiological, oceanographic and ecological factors (Irwin and Finkel, 2009). Their distributions, in space and time, are partly constrained by the availability of light and nutrients (Behrenfeld *et al.,* 2006). These growth-limiting factors are tightly linked to physical processes like the mixed-layer dynamics, magnitude and occurrence of upwelling, among others (Behrenfeld *et al.,* 2006). In the Southern Ocean, still the least exploited of the world's oceans, cloud-cover make year-round observations difficult with satellite instruments. However, long term high-quality datasets have been provided by various satellite devices, measuring biological and physical oceanographic variables in the remote and otherwise poorly sampled areas of the Southern Ocean. Among them the Sea-viewing Wide Field-of-view Sensor (SeaWiFS, Hooker and McClain, 2000) was launched in September 1997. Since then, SeaWiFS provided the global monthly measurements of oceanic phytoplankton chlorophyll-a biomass. This continuous high-quality dataset allows the determination of phytoplankton dynamics on a wide range of spatial and temporal scales.

In contrast with the productive waters of the Kerguelen Plateau, the interfrontal zone of the Southern Ocean is characterized by high-nutrient-low chlorophyll (HNLC) environment with locally rich productive mesoscale structures (Martin *et al.*, 1990; Minas and Minas, 1992). Highly dynamic, the interfrontal zone of the Southern Ocean is shaped by several strong fronts within the Antarctic Circumpolar Current (ACC, Deacon, 1933). Those circumpolar fronts structure the transition between warm Subantarctic surface waters and colder Antarctic ones, and are important boundaries in terms of air-sea fluxes and heat budget of the Southern Ocean (Deacon, 1982). Several studies have shown the variability of locations exhibited by the circumpolar fronts, especially by the Polar Front (PF) whose dynamics is strongly influenced by bottom topography (Moore *et al.*, 1999). The PF current flows drive relatively high phytoplankton bloom concentrations (Moore and Abbott, 2002) in contrast to the HNLC surface waters of the Southern Ocean (Moore and Abbott, 2000). Under laboratory and field conditions, numerous studies on phytoplankton dynamics have demonstrated growth rate dependence upon various oceanographic factors: light intensity, temperature, water mixing, sea-ice concentration and nutrient supply (Behrenfeld *et al.,* 2006; Irwin and Finkel, 2009; Montes-Hugo *et al.*, 2009). Comiso *et al.* (1993) noted that phytoplankton blooms occur primarily in several regions including areas associated with sea ice retreat, shallow waters, areas of strong upwelling, and regions of high eddy kinetic energy (mainly associated with Southern Ocean fronts). The strongest correlation was a negative correlation between ocean depth and pigment concentrations, possibly the result of higher available iron concentrations in shallow water regions (Blain *et al.*, 2007; Hiscock *et al.*, 2009). Considering nutrient availability, artificial iron-fertilization experiments in HNLC waters have shown that iron, among other nutrients, especially promotes phytoplankton growth (De Baar *et al.*, 2005; Blain *et al.*, 2007). Few studies however have described the interaction of the five physical environmental parameters with chlorophyll-a concentration. These same environmental parameters vary greatly with season in the polar seas and presumably affect the interannual variability of phytoplankton concentration in the Indian sector of the Southern Ocean.

Due to its great meridional extent and relatively shallow depths, the Kerguelen Plateau constitutes a major barrier to the eastward flowing ACC in the Indian sector of the Southern Ocean. It extends for more than 2200 km southeast from the Kerguelen Islands (49.20°S, 69.20°E) and reaches as far south as the Princess Elizabeth Trough near 63°S. The Polar Front has been documented to be divided into two major currents, one skirting around the northern boundary of the Kerguelen Plateau and the other flowing across it (Roquet *et al.*, 2009). High-energy internal tidal waves that interact with the bathymetry enhance the vertical eddy diffusivity above the plateau, and hence the supply of nutrients (Park *et al.*, 2008a). This supply from below appears to be the main source to fuel the large phytoplankton bloom (Mongin *et al.,* 2008). Because of its shallower waters, PF interconnection and more intense bloom, our interest is focused on the portion of the plateau north of the Fawn Trough, between and to the east of the Kerguelen and Heard Islands (Fig. 1). In this paper, the region will be referred to as "the plateau". Con-

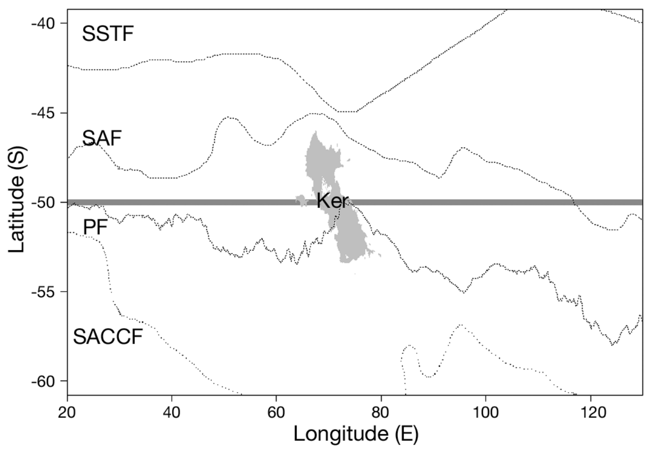

Figure 1. - Interfrontal zone surrounding the Kerguelen Plateau with light grey shading that represents the surface of the Kerguelen Plateau (depths less than 1,000 m). Kerguelen archipelago (Ker) and Heard Island are depicted in white over the plateau. The dark grey shaded line indicates the study surface of productivity in the interfrontal zone whose area is precisely equal to the light grey area of the Kerguelen Plateau. Dotted lines symbolised fronts (Orsi *et al.*, 1995): Southern Sub Tropical Front (SSTF), Sub-Antartic Front (SAF), Polar Front (PF) crossing the Kerguelen Plateau and Southern Antarctic Circum-Polar Front (SACCF).

sidering the regional eastward-current dynamics, the plateau is expected to present a phytoplankton dynamic which should either be connected to the dynamics observed West of Kerguelen or influence the one located East of Kerguelen through the panache of the eastward flowing ACC.

In this study, we combined the time series of satellite-based chlorophyll-a values available from 1997 to 2009 in the Indian sector of the Southern Ocean with the time series of satellite-based sea-surface temperature, sea-ice concentration, wind pressure, sea level anomalies and photosynthetically active radiation values. All these environmental factors have been chosen as previous studies have shown that they act on phytoplankton development through surface nutrient enrichment by vertical mixing such as wind and mesoscale activity, but also light availability and temperature influencing phytoplankton growth (Comiso *et al.*, 1993; Martinez *et al.*, 2005). Several studies have stressed the importance of winter Antarctic sea-ice extent (SIE) on the level of phytoplankton biomass for the Southern Ocean (Arrigo *et al.*, 1997; Brierley and Thomas, 2008). We examined the variations of the phytoplankton dynamics, inferred from chlorophyll-a concentrations, over the plateau, in the surrounding interfrontale zone, along the western and eastern flows and in the Antarctic sector of the Southern Indian Ocean. These data were used to (1) evaluate the spatial variability of phytoplankton over the plateau especially during the summer bloom and in particular if differences could be found for parts of the plateau laying north and south of the Polar front (i.e., north or south of 50°S), (2) determine the temporal similarity of chlorophyll-a time series between the Kerguelen Plateau, the western and eastern interfrontal zones on both sides of the plateau and the Antarctic zone, and finally, (3) assess for the four geographical areas considered, the possible influence of physical factors on the temporal dynamics of phytoplankton biomass. We present here a description of the spatial, seasonal and inter-annual variations in the distribution of phytoplankton biomass, a close proxy of primary production, in relation to ocean-climate factors.

MATERIAL AND METHODS

Bathymetry and satellite data

The bathymetry used to define the offshore boundaries of the plateau was extracted from the ETOPO version 2, a 2' (approximately 3.6 km) worldwide global relief model of Earth's surface and bathymetry (available at https://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html). We delimited the Kerguelen Plateau at 100 m (to avoid coastal processes, see details in Cloern and Jassby, 2001) and 1000 m-isobaths. This represents a total of 34,315 pixels and a surface of 3.8×10^5 km² (Fig. 1).

Satellites enable global coverage of the polar oceans, providing a unique monitoring capability of various oceanographic variables. For instance, SeaWIFS and AquaMODIS sea color views of the Southern Ocean allow the estimation of the seasonal and inter-annual variability of sea surface chlorophyll-a concentrations. In order to avoid calibration uncertainties inherent in the use of multiple instruments, we used the most recent and single origin datasets. Accordingly, we exclusively used the 12 years of the SeaWIFS data set from September 1997 to August 2009, the longest continuous single ocean color measurement available today. Ocean color data, e.g., chlorophyll-a, is provided by the SeaWIFS NASA project (http://oceancolor.gsfc.nasa.gov/) from the level 3 data set.

One of the objectives of this study was to evaluate links between chlorophyll-a dynamics and physical oceanographic factors within the Indian sector of the Southern Ocean. Considering that we did not know *a priori* what was affecting the dynamics of chlorophyll-a in this area, we decided to explore links with four oceanographic variables thought to influence the level of primary production. Monthly satellite maps of five ocean-climate factors were downloaded from free-access databases. Sea-surface temperature (SST) maps indicating the water masses types, while wind pressure (WP) and sea-level anomalies (SLA) were used as a proxy for the intensity of water mixing (Messié and Radenac, 2006). Sea-ice extent had previously been described to impact significantly the level of primary production in Antarctic waters (Cotté *et al.*, 2007). Finally, photosynthetically active radiation (PAR) and cloud cover were used as a proxy for light intensity.

The study is focused on the Kerguelen Plateau, defined from bathymetry, the interfrontal zone located between 20° and 130°E with latitudes ranging from 40° to 60°S, and the Antarctic sector with latitudes under 60°S and longitudes between 20° and 130°E. The interfrontal zone is centered on the Kerguelen Plateau and presents numerous oceanographic features, such as the Sub-Antarctic Front (SAF) and the Polar Front (PF) structures (Fig. 1). To remove all surface-related signals in the comparison between the interfrontal and plateau productivity dynamics, we focused on a band, illustrated on Figure 1, that has the same surface as the Kerguelen Plateau (34,315 pixels). This band extends from 48.9°S -50.2°S and from 20°E-130°E with shelf values (bathymetry < 1000 m) excluded for the west and east of Kerguelen. Maps of chlorophyll-a, and the oceanographic variables, over the interfrontal zone and the Antarctic sector were therefore computed with a ground resolution of 9 km × 9 km. Due to cloud cover causing a large percentage of missing pixels, especially during winter, monthly data and computed monthly average series for the Antarctic sector and the interfrontal zone west and east of the Kerguelen Plateau was used. For the Antarctic sector, monthly mean values only when satellite data covered at least 30% of the considered surface was considered (Preunkert *et al.*, 2007).

Data analyses

Satellite data

For each month between September 1997 and August 2009, pixel values of the maps of chlorophyll-a, SST, SLA, WP and PAR were extracted. Monthly average maps were then computed from the time series data per pixel.

Similarity of spatio-temporal productivity dynamics between Kerguelen Plateau and the interfrontal zone

The study searched for seasonal patterns in the computed time series, for instance, synchrony of the time series and amplitudes of monthly variability. Because of the strong seasonal signal in the productivity cycle of the Southern Ocean, this study focused on the time series of monthly residuals (e.g., trend and seasonal components removed) by using calculated anomalies about the monthly mean for each pixel. To evaluate the similarity between eastern, western parts of the interfrontal zone and northern, southern parts of the plateau, a linear relationship was assumed and calculated the pairwise Pearson correlation coefficient between time series of residuals calculated for the different geographical sectors. Care must be taken when computing numerous correlation coefficicents from the same data set since chance alone may result in spuriously significant correlations. In order to minimize this risk and assess the significance of the correlations, a parametric bootstrap was performed (Efron and Tibshirani, 1993; for details see Dragon *et al.*, 2010). The significance of each correlation was determined at probability $\alpha = 0.05$.

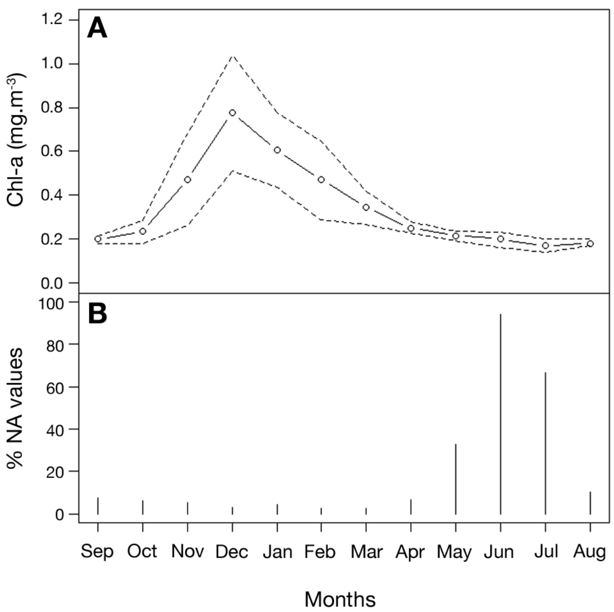

Figure 2. - **A**: Chlorophyll-a annual cycle from averaged SeaWIFS data over the Kerguelen Plateau from 1997 to 2009. Austral spring and summer present increasing values of chlorophyll-a indicating the occurrence of the bloom of productivity. **B**: Percentages of NA (data not available) values on satellite images, as a proxy of the cloud cover density.

Relationship between regional primary productivity and physical oceanographic dynamics

For each of the geographical sectors considered, the pairwise Pearson correlation between chlorophyll-a residuals time series and the SST, WP and PAR ones was calculated. Various temporal lags were computed from 0 to 6 months in order to evaluate the temporal variations in the relationships between chlorophyll-a and the physical oceanographic variables. Indeed, several studies have shown that environmental conditions occurring during winter and spring, such as the intensity of winter water mixing, were found to influence the level of primary production reached during the following spring and summer (Park *et al.*, 2008b). In the Antarctic sector, the influence of SIE on chlorophyll-a regional dynamics was also considered with various temporal lags, since winter SIE was suggested to influence the level of primary production of consecutive spring and summer (Arrigo *et al.,* 1997; Loeb *et al.*, 1997).

RESULTS

Climatology of summer satellite chlorophyll-a concentration over the Kerguelen Plateau

Ocean-color satellite images revealed that Kerguelen Plateau was a very productive area especially during the austral summer. Mean satellite chlorophyll-a values over the plateau reached up to 0.7 mg.m^{-3} in December whereas, during the winter months, values stayed close to 0.2 mg.m^{-3} (Fig. 2A). Besides winter season, average cloud cover, approximated by the percentage of NA values in the dataset, stayed globally weak in the area and rarely raised above 10% (Fig. 2B).

The 1997-2009 climatology of the chlorophyll-a over the plateau indicated the spatial dynamics variability within areas of the plateau (Fig. 3). Chlorophyll-a concentration peak occurred in December both for the northern and southern sectors of the plateau (Fig. 4). January presents a decrease of the bloom intensity in both northern and southern sectors. Finally in February, the bloom disappears in the southern sector but extends until March-April in the north. Due to the longer bloom period, the overall chlorophyll-a concentration was slightly higher for the northern sector of the plateau compared to the southern one. Globally high values of chlorophyll-a were segregated in the eastern parts of the plateau while western parts supported low chlorophyll-a concentration.

The time series of chlorophyll-a residuals were weakly correlated between the northern and southern sectors of the

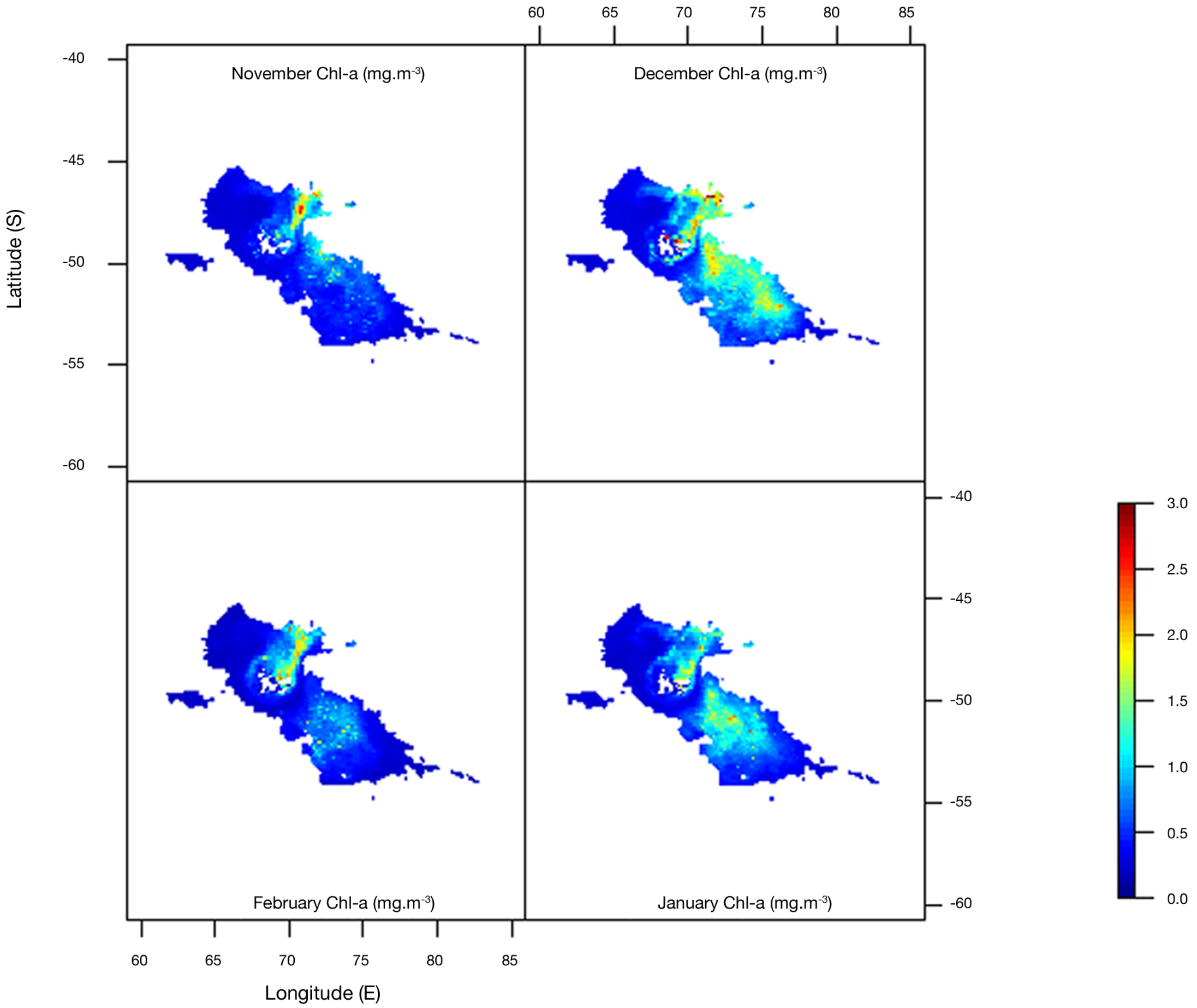

Figure 3. - Average chl-a concentration mapped over the Kerguelen Plateau from SeaWIFS dataset during the austral summer. Appearances of the bloom in the northern and southern sectors of the Plateau are not simultaneous. The northern bloom is more localised than the southern one which spreads over the whole shelf.

plateau. When comparing the monthly climatology of the chlorophyll-a concentration calculated for the sectors of the plateau north and south of the polar front, it was found that northern and southern sectors of the plateau present differences in bloom intensity and duration (Fig. 4).

All these results suggest that the northern and southern sectors of the plateau may function as two independent subsystems.

Similarity of productivity temporal dynamics between sectors of the interfrontal zone and the Kerguelen Plateau

Time series of the various geographical zones are presented in figure 5. High seasonality can be detected for all time series and all regions are characterized by a very large inter-annual variability. Compared to the interfrontal zone, both the northern and southern sectors of the plateau were found to exhibit higher mean chlorophyll-a concentrations. The mean yearly cumulative concentration of chlorophyll-a for the northern sector of the plateau represented 1.05, 1.37 and 1.83 times the cumulative chlorophyll-a concentrations found for the southern sector of the plateau, the eastern and the western interfrontal zone respectively.

Western and eastern parts of the interfrontal zone also presented high differences in chlorophyll-a: mean December bloom values for the eastern part were almost twice higher than the western ones (0.61 *vs*. 0.31 $mg.m^{-3}$) and the mean chlorophyll-a values of the eastern interfrontal zone were 1.33 times larger than in the western interfrontal zone. The most productive years in the eastern and western parts of the

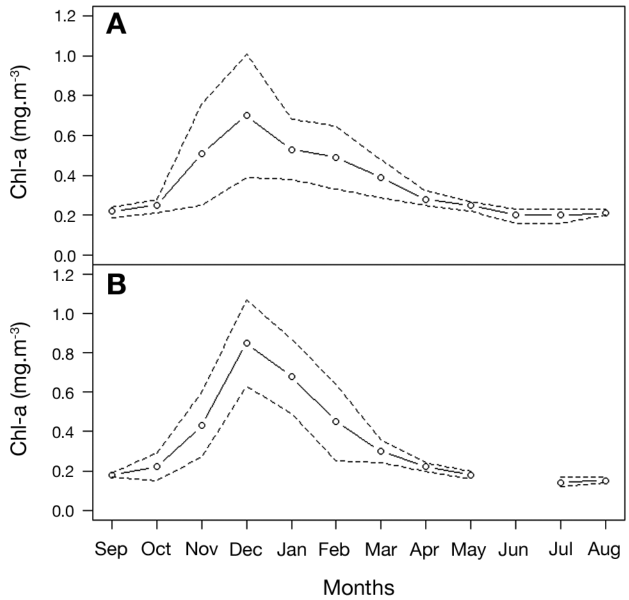

Figure 4. - Chlorophyll-a annual cycle from averaged SeaWIFS data over the Kerguelen Plateau from 1997 to 2009. **A**: Northern sector and **B**: Southern sector of the Kerguelen Plateau. Dotted lines represent the standard deviations. Increasing values of chlorophyll-a in Austral spring and summer indicate the occurrence of the bloom of productivity. Winter values are missing because of dense cloud cover.

Table I. - Correlation coefficients between the Interfrontal zone productivity time series (western (Z.Int.W) and eastern (Z.Int.E) sectors), the Kerguelen Plateau time series (northern (KP.N) and southern (KP.S) sectors) and the Antarctic sector (Z.Ant). Non-significant correlation coefficients ($\alpha > 0.05$) are indicated by "ns".

	Z.Int.W	Z.Int.E	KP.N	KP.S	Z.Ant
Z.Int.W	1				
Z.Int.E	ns	1			
KP.N	0.20	0.30	1		
KP.S	ns	ns	0.19	1	
Z.Ant	ns	ns	0.23	0.28	1

interfrontal zone do not occur in same years. However, winter values of both parts tend to be in the same range.

Besides the seasonal driving of the bloom, northern and southern sectors of the plateau were weakly correlated; very productive years were not the same in the two sectors (Tab. I, Fig. 5). The highest significant correlation identified among the residual time series was between the northern sector of the Kerguelen Plateau and the eastern part of the interfrontal zone (Tab. I). The western part of the interfrontal zone presented a weak correlation with the northern sector of the plateau ($\varrho = 0.20$). Finally, significant correlations were found between the Antarctic sector and the northern ($\varrho = 0.23$) and the southern sectors ($\varrho = 0.28$) of the Kerguelen Plateau.

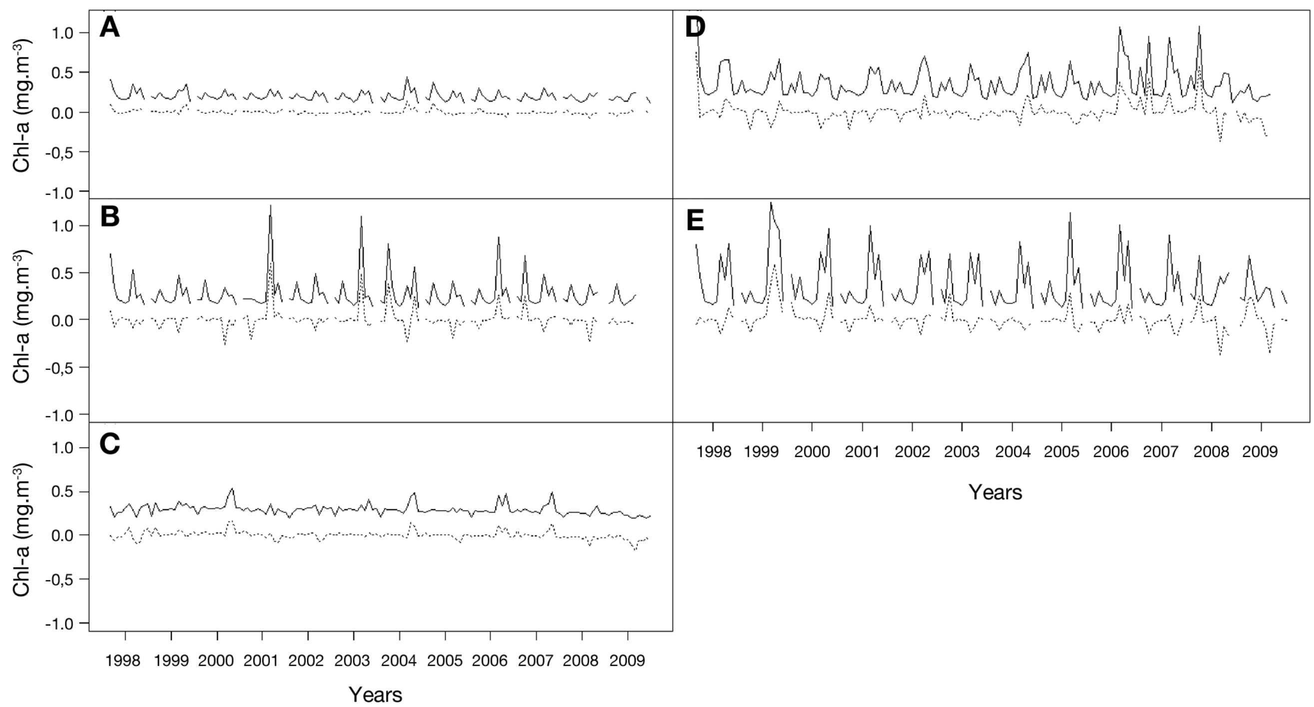

Figure 5. - Chlorophyll-a monthly time series derived from SeaWIFS datasets (black lines), and their residuals after removal of inter-annual and seasonal trends, (dotted lines), by year for the geographical regions considered. **A**: Western interfrontal zone dynamics: **B**: Eastern interfrontal zone and **C**: Antarctic sector; **D**: Northern sector of the Kerguelen Plateau and **E**: Southern sector of the plateau. The strong within-year seasonal signal appears combined with strong inter-annual variability in amplitude. Northern and southern sectors of the Kerguelen Plateau are not correlated in their respective dynamics. The Kerguelen Plateau as a whole is characterised by higher values all along the years in primary productivity than the interfrontal zone.

Table II. - Correlation coefficients between the residuals of Chlorophyll-a time series and sea-surface temperatures (SST), wind pressure (WP), photosynthetically active radiation (PAR) and sea-ice extent (SIE) in the geographical zones considered: western (Z.Int.W) and eastern (Z.Int.E) parts of the interfrontal zone, the Antarctic sector (Z.Ant) and the Kerguelen Plateau time series (northern (KP.N) and southern (KP.S) sectors). Non-significant correlation coefficients ($\alpha < 0.05$) are indicated by "ns". Temporal lags, in months, were used during the bootstrap analyses, maximum significant coefficient correlation are given with the corresponding lags. Calculations with sea-ice concentrations were only computed for the Antarctic sector.

	SLA	SST	WP	PAR	SIE
KP.N	ns	ns	-0.20; lag = 2	0.20; lag = 0	-
KP.S	-0.42; lag = 0	-0.26; lag = 0	ns	-0.24; lag = 1	-
Z.Int.W	ns	0.26; lag = 2	ns	ns	-
Z.Int.E	ns	0.30; lag = 0	-0.23; lag = 6	ns	-
Z.Ant	ns	-0.45; lag = 0	ns	ns	0.61; lag = 0

Relationships between regional primary productivity and physical oceanographic dynamics

Table II presents the significant correlation coefficients obtained between residuals of chlorophyll-a residuals time series and the five environmental variables considered. For the southern sector of the plateau, sea level anomalies and sea-surface temperatures presented a negative correlation with chlorophyll-a (ϱ = -0.42 and ϱ = -0.26 respectively) occurring with no temporal lag. No significant correlation was obtained between sea-surface temperature and chlorophyll-a in the northern sector of the plateau. Sea-surface temperatures in the western and eastern interfrontal zones were positively correlated to chlorophyll-a with either a 2-month or no temporal lag. With respect to the Antarctic sector, sea-surface temperatures were also negatively correlated with Antarctic chlorophyll-a, with no temporal lag. Almost no geographical zone presented significant correlations between chlorophyll-a and wind pressure; only the northern sector of Kerguelen Plateau (with a 2-month temporal lag) and the eastern part of the interfrontal zone (with a 6-month temporal lag) presented a negative correlation between chlorophyll-a and wind pressure. Regarding the PAR variable, northern and southern sectors of the plateau showed opposite signs in correlations with the chlorophyll-a. The PAR in the interfrontal zone and its eastern part were negatively correlated, with a 1-month temporal lag, with chlorophyll-a. Finally a highly positive correlation was obtained in the Antarctic sector between sea-ice extent and Antarctic chlorophyll-a (ϱ = 0.61).

DISCUSSION

In this study, we characterized the spatio-temporal dynamics of phytoplankton biomass over the Kerguelen Plateau with regards to the one in the interfrontal zone. We found evidence of significant correlations between phytoplankton biomass dynamics and various physical oceanographic variables. Previous studies have shown that the Southern Ocean is a major contributor to the global ocean primary production (Sullivan *et al.*, 1993). While the Southern Ocean is characterized by HNLC waters, some areas contribute to the important biosphere's primary production (Lefevre *et al.,* 2008). As found in previous studies, both the Kerguelen Plateau and the eastern interfrontal zone are two of those areas. Our study also highlights the links between the eastern interfrontal zone and the northern sector of the Kerguelen Plateau. Finally, the relationships between chlorophyll-a, proxy for the base of the trophic chain, and sea-surface temperature, as well as light intensity, sea-level anomalies, wind pressure and sea-ice extent were evaluated.

The Kerguelen Plateau was found to be very productive with variations in the spatio-temporal dynamics of its northern and southern sectors. The two sub-systems had a dominant-12 month (annual) period of variability, commonly expressed as the canonical summer-bloom pattern in high latitudes waters (Boyd *et al*., 2000). Both sub-systems were also not correlated over a decadal time series, therefore highlighting their differences of dynamics. These differences in dynamics can be explained by the geographical separation between the northern and southern sectors of the plateau, a relatively deep trough, called the Polar Front trough, running east-west across the plateau just south of the Kerguelen Island physically segregates the water masses of the two sectors (Mongin *et al*., 2008). Acting as a barrier, the shallow bathymetry of the Kerguelen Plateau forces the large-scale flow of the ACC to divide into two main fluxes, with the majority of the transport going to the northern sector of the plateau exhibiting intense mesoscale activity (Moore and Abbott, 2000; Park *et al*., 2008b; Roquet *et al.,* 2009). The bloom in the northern sector of the plateau reflects to some extent the interaction between the important eastward advection and the shallow bathymetry.

Both the western and eastern interfrontal zones were found to be less productive than the Kerguelen Plateau. A difference in bloom intensity was also observed between the eastern, more productive, and western, less productive, parts. The northern sector of the plateau and the eastern part of the interfrontal zone presented significant positive correlations in terms of chlorophyll-a concentration. This correlation reflects the bloom extension off the plateau, the Kerguelen plume, which follows the significant eastward transport of the ACC flowing across the northern sector of the plateau. We also found a weak correlation with the western interfrontal zone and the northern plateau. Strong westerly winds, combined to the eastward circulation of the ACC and especially the polar front crossing the Kerguelen Plateau, drive the nutrients that are collected over the Kerguelen shelf towards the north-eastern part of the interfrontal zone (Blain *et al.,* 2008; Van Beek *et al.*, 2008). This suggests that the northern plateau may act as an amplifier of the primary production of the water advected from the west and extending eastward through the Kerguelen plume.

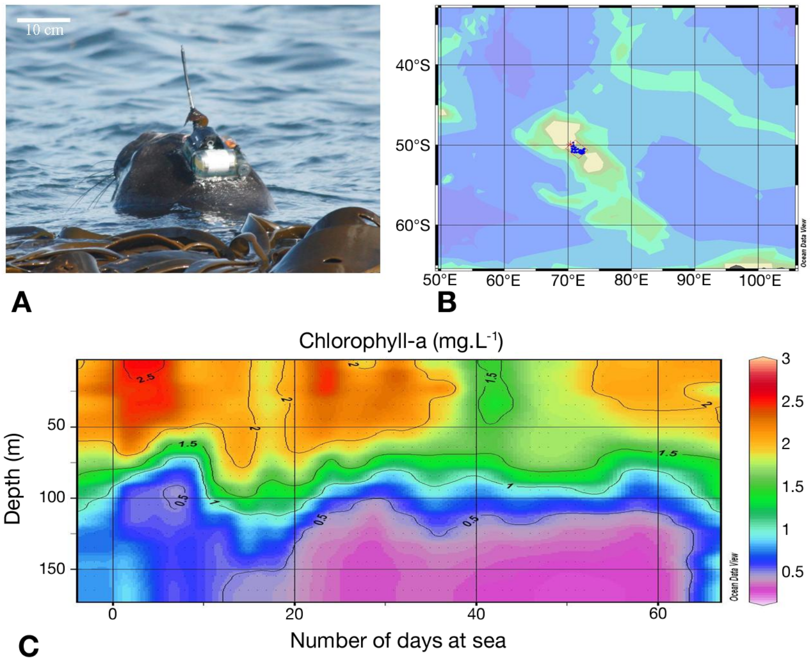

Figure 6. - **A**: Picture of a Southern elephant seal equipped by an Argos tag combined to a temperature, salinity and fluorescence data logger. **B**: Map of the Kerguelen Plateau and bathymetric surroundings. The Argos seal track is represented in blue lines: the seal spent over 60 days on the Kerguelen shelf recording in situ profiles of fluorescence, a close proxy from chlorophyll-a. **C**: Illustration of the vertical variability of chlorophyll-a distribution from the profiles recorded along the water column.

Finally, differences in the importance of climate-related oceanographic factors were found between the various geographical zones. Combined with a strong positive correlation between SIE and chlorophyll-a in the Antarctic sector, sea-surface temperatures were negatively correlated with phytoplankton biomass in this sector. This highlights the importance of sea-ice and Antarctic cold water masses for phytoplankton growth and thus primary production in Antarctic waters. In Antarctica, the most prominent physical process is the annual growth and decay of sea-ice (Brierley and Thomas, 2008). All physical components of the sea-ice system are associated with biological activity, having a profound impact on all levels of the Antarctic trophic chain. Typically, the decay of sea-ice in summer plays a major role in seeding the phytoplankton bloom by releasing dissolved organic matter to the water column (Brierley and Thomas, 2008). Sea-surface temperatures were also found to be positively correlated to chlorophyll-a in the interfrontal zone, underlying the importance of seasonal changes in water temperatures and of frontal features structuring the waters of the area (Park *et al*., 2008a). This relationship could also suggest that a greater input of warmer waters, transported by anticyclonic eddies from a northerly origin could enhance the frontogenesis and stimulate the primary production within the interfrontal zones. These results suggest that we may expect a contrasted effect, with productivity of the Kerguelen and Antarctic shelf decreasing with ocean warming while the productivity of the waters of the interfrontal zone are enhanced. However as shelf waters are the most productive, we may expect an overall decrease of the productivity of the southern sector of the Indian Ocean with global warming. These relationships should now be investigated through dedicated process studies.

In the eastern interfrontal zone, the negative correlation between wind pressure and chlorophyll-a, with a 6-month temporal lag is likely to highlight the importance of the winter water dynamics for the summer bloom especially regarding vertical mixing. Stratification of high-latitude water masses and upper-ocean temperatures strongly influence the availability of nutrients for phytoplankton growth. Therefore reduced wind pressure during winter allows a vertical stratification in the upper-ocean seasonal mixed-layer, inducing important phytoplankton blooms the next summer (Behrenfeld *et al.,* 2006). The same relationship is observed in the northern sector of the plateau where wind pressure is negatively correlated to chlorophyll-a with a 2-month temporal lag. Although some were not significant, all the relationships between the wind pressure and chlorophyll-a concentration were characterised by a negative sign. Finally cloud cover, estimated by the PAR, presented opposite signs of correlation in the northern and southern sectors of the plateau. We are currently unable to explain this relationship unless these two habitats are dominated by different phytoplankton communities exhibiting different levels of sensitivity to light level, which could highlight the regionalisation of the dynamics of phytoplankton between the northern and southern part of the Kerguelen Plateau.

Our analyses further reveal the strong variability in space and season of the phytoplankton biomass. These fluctuations are regulated by physiological, oceanographic and ecological factors that are spatially dependent and organised in a complex interaction which need to be investigated by processes oriented studies.

The distribution of chlorophyll-a throughout the water column is one of the most important biological parameters in the ocean because it is an indicator of the spatial and temporal variability of primary productivity (Behrenfeld and Falkowski, 1997). However, our understanding of the variability of primary production is restricted to the surface and clearly hampered by the lack of *in situ* optic measurements because of remoteness and poor data sampling cost-efficiency. In the Southern Ocean, cloud-cover makes year-round observations even more difficult with satellite instruments. Furthermore, satellites scan the sea-surface while vertical distribution of phytoplankton pigments is generally non-uniform (Sathyendranath and Platt, 2006) and thus deep fluorescence maximums could be found between 40 and 75 m within the interfrontal zone of the Antarctic Circumpolar Current (Quéguiner and Brzezinsky, 2002). It has been shown that the estimation of total phytoplankton biomass in the photic zone from satellite data can lead to significant errors (Sathyendranath and Platt, 2006; Dierssen, 2010). The recent launching of Argo floats has considerably increased the information available in the world's oceans (Gould *et al.*, 2004), but still, new sources of *in situ* data are most valuable, particularly in the southern part of the Southern Ocean where seasonal sea-ice, remoteness and zonally-oriented strong current diminish the sampling efficiency of Argo floats (Klatt *et al.*, 2007).

The recent development of miniaturized oceanographic instruments to equip diving predators has allowed the recording of 3D foraging movements while continuously sampling their habitats.

Southern elephant seals, *Mirounga leonina* (Linnaeus, 1758), are one of the most important apex predators of the Southern Ocean ecosystem (Boyd and Arnbom, 1991). These animals travel large distances (McConnell *et al.*, 1992) and also display extraordinary diving abilities, achieving up to 2000-m depths (Stewart and Delong, 1990; Hindell *et al.*, 1991). Taken together these factors make the animals exemplary broad-ranging samplers of the Southern Ocean (Biuw *et al.*, 2007; Charrassin *et al.*, 2008). Since 2003, a new approach using elephant seals from Kerguelen Islands as autonomous oceanographic profilers has provided new information on the hydrography and biological richness in the Indian sector of the Southern Ocean (Biuw *et al.*, 2007; Charrassin *et al.*, 2008). Recently, the development of a new technology, e.g., the incorporation of fluorescence sensors to satellite data relayed loggers deployed on deep diving and broad ranging elephant seals, has made possible a spatio-temporal description of primary production dynamics, inferred from fluorescence concentration. Over a 4-year period, from October 2007 to December 2010, southern elephant seals, have been surveying the Indian sector of the Southern Ocean and have provided a large number of temperature, salinity and fluorescence profiles over their home-range and especially over the Kerguelen Plateau (Fig. 6). The vertical profiles of fluorescence gathered by the seals have yet to be processed to provide finely resolved vertical profiles of chlorophyll-a. It is our intention to examine in future works the inter-annual and spatial variability of *in-situ* primary production dynamics. This approach introduces a new prospect of investigation regarding the recording of 3D *in-situ* environmental parameters. Such an approach is valuable because data are cost-efficiently obtained in remote areas and because it also allows the acquisition of valuable hydrographic data for physical oceanography at local and regional scales. Further investigations and process oriented studies are now needed to assess the validity and the underlying mechanisms of the relationships presented in this study for the Indian sector of the Southern Ocean.

Acknowledgements. - This work was carried out in the framework of IPSOS-SEAL (ANR VMC 2008-2011) Program. We are indebted to IPEV (Institut Polaire Français Paul Emile Victor) and TAAF (Terres Australes et Antarctiques Françaises) for financial and logistic support. This work was conducted as part of IPEV research program n°109 (Ecologie des Oiseaux et Mammifères Marins, resp. H. Weimerskirch). This study was also supported by the CNES-TOSCA (Centre National d'Etudes Spatiales-Terre Océan Surface Continentales et Atmosphère) and the Groupe de Mission CORIOLIS-MERCATOR. We are grateful to Gilles Reverdin for his continuous support and to all the colleagues and volunteers involved in the research on southern elephant seals in Kerguelen.

REFERENCES

ARRIGO K.R., WORTHEN D.L., LIZOTTE M.P., DIXON P. & DIECKMAN G., 1997. - Primary production in Antarctic sea-ice. *Science*, 276: 394-397.

BEHRENFELD M.J. & FALKOWSKI P.G., 1997. - Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.*, 42: 1-20.

BEHRENFELD M.J., RANDERSON J.T., MCCLAIN C.R. *et al.* (12 authors), 2001. - Biospheric primary production during an ENSO transition. *Science*, 291: 2594-2597.

BEHRENFELD M.J., O'MALLEY R.T., SIEGEL D.A., MCCLAIN C.R., SARMIENTO J.L., FELDMAN G.C., MILLIGAN A.J., FALKOWSKI P.G., LETELIER R.M. & BOSS E.S., 2006. - Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120): 695-696.

BIUW M., BOEHME L., GUINET C. *et al.* (21 authors), 2007. - Variations in behaviour and condition of a Southern Ocean top predator in relation to *in situ* oceanographic conditions. *Proc. Natl. Acad. Sci. USA*, 104: 13705-13710.

BLAIN S., QUÉGUINER B., ARMAND L. *et al.* (47 authors), 2007. - Effect of natural iron fertilisation on carbon sequestration in the Southern Ocean. *Nature*, 446: 1070-1074.

BLAIN S., SARTHOU G. & LAAN P., 2008. - Distribution of dissolved iron during the natural iron fertilization experiment KEOPS (Kerguelen Plateau, Southern Ocean). *Deep-Sea Res. II*, 55: 559-565.

BOYD I.L. & ARNBOM T., 1991. - Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biol.*, 11: 259-266.

BOYD P.W., WATSON A.J., LAW C.S. *et al.* (35 authors), 2000. - A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature*, 407: 695-702.

BRIERLEY A.S. & THOMAS D.N., 2008. - Ecology of southern ocean pack ice. *Proc. Natl. Acad. Sci. USA*, 105(12): 4775-4780.

CHARRASSIN J.B., HINDELL M., RINTOUL S.R. *et al.* (22 authors), 2008. - Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proc. Natl. Acad. Sci. USA*, 105: 11634-11639.

CLOERN J.E. & JASSBY A.D., 2001. - Complex seasonal patterns of primary producers at the land-sea interface. *Nature*, 410(6826): 360-363.

COMISO J.C., MCCLAIN C.R., SULLIVAN C.W., RYAN J.P. & LEONARD C.L., 1993. - Coastal zone colour and colour pigment concentrations in the Southern Ocean and relationship to geophysical surface features. *J. Geophys. Res.*, 98: 2419-2451.

COTTÉ C., GUINET C., PARK Y.H. & BOST C.A., 2007. - King penguins foraging in dynamic environment. *Proc. R. Soc. Lond. B Biol.*, 274: 2385-2391.

DEACON G.E.R., 1933. - A general account of the hydrology of the South Atlantic Ocean. *Discovery Rep.* 7: 177-238.

DEACON G.E.R., 1982. - Physical and biological zonation in the Southern Ocean. *Deep-Sea Res. I*, 29: 1-15.

DE BAAR H.J.W., BOYD P., COALE K. & TSUDA A., 2005. - Synthesis of eight *in situ* iron fertilizations in high nutrient low chlorophyll waters confirms the control by wind mixed layer depth of phytoplankton blooms. *J. Geophys. Res.*, 110: 700-724.

DIERSSEN H.M., 2010. - Perspectives on empirical approaches for ocean color remote sensing of chlorophyll in a changing climate. *Proc. Natl. Acad. Sci. USA*, 107(40): 17073-17078.

DRAGON A-C., MONESTIEZ P., BAR-HEN A. & GUINET C., 2010. - Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog. Oceanogr.*, 87: 61-71.

EFRON B. & TIBSHIRANI R., 1993. - An Introduction to the Bootstrap. Monographs on Statistics and Applied Probability. New York: Chapman and Hall.

FIELD C.B., BEHRENFELD M.J., RANDERSON J.T. & FALKOWSKI P.G., 1998. - Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281: 237-240.

GOULD J., ROEMMICH D., WIJFFELS S. *et al.* (17 authors), 2004. - Argo profiling floats bring new era of *in situ* ocean observations. *Eos*, 85(19): 179-191.

HINDELL M., SLIP D. & BURTON H., 1991. - The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.*, 39: 595-619.

HISCOCK M.R., LANCE V.P., APPRILL A.M., BIDIGARE R.R., JOHNSON Z.I., MITCHELL B.G., SMITH W.O. Jr & BARBER R.T., 2009. - Photosynthetic maximum quantum yield increases are an essential component of the Southern Ocean phytoplankton response to iron. *Proc. Natl. Acad. Sci. USA*, 105(12): 4775-4780.

HOOKER S.B. & MCCLAIN C.R., 2000. - The calibration and validation of SeaWiFS data. *Prog. Oceanogr.*, 45(3-4): 427-465.

IRWIN A.J. & FINKEL Z.V., 2009. - Mining a sea of data: deducing the environmental controls of ocean chlorophyll. *Science*, 323(5920):1470-1473.

KLATT O., BOEBEL O. & FAHRBACH E., 2007. - A profiling float's sense of ice. *J. Atmos. Ocean Tech.*, 24: 1301-1308.

LEFEVRE D., GUIGUE C. & OBERNOSTERER I., 2008. - The metabolic balance at two contrasting sites in the Southern Ocean: the iron fertilized Kerguelen area and HNLC waters. *Deep-Sea Res. II*, 55(5-7): 766-776.

LOEB V., SIEGEL V., HOLM-HANSEN O., HEWITT R., FRASER W., TRIVELPIECE W. & TRIVELPIECE S., 1997. - Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387: 897-900.

MARTIN J.H., FITZWATER S.E. & GORDON R.M., 1990. - Iron deficiency limits phytoplankton growth in Antarctic waters. *Global Biogeochem. Cycles*, 4: 5-12.

MARTINEZ E., ANTOINE D., D'ORTENZIO F. & GENTILI B., 2005. - Climate-driven basin-scale decadal oscillations of oceanic phytoplankton. *Appl. Optics*, 44(14): 2857-62.

MCCONNELL B.J., CHAMBERS C. & FEDAK M.A., 1992. - Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct. Sci.*, 4: 393-398.

MESSIÉ M. & RADENAC M.-H., 2006. - Seasonal variability of the surface chlorophyll in the western tropical Pacific from SeaWiFS data. *Deep-Sea Res. I*, 53(10): 1581-1600.

MINAS H.J. & MINAS M., 1992. - Net community production in High nutrient-low chlorophyll waters of the tropical and Antartic oceans: grazing vs iron hypothesis. *Oceanol. Acta*, 15(2): 145-162.

MONGIN M., MOLINA E. & TRULL T.W., 2008. - Seasonality and scale of the Kerguelen Plateau phytoplankton bloom: A remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep-Sea Res. II*, 55(5-7): 880-892.

MONTES-HUGO M., DONEY S.C., DUCKLOW H.W., FRASER W., MARTINSON D., STAMMERJOHN S.E. & SCHOFIELD O., 2009. - Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science*, 326(5957): 1253-1256.

MOORE J.K., ABBOTT M.R., RICHMAN J.G., SMITH W.O., COWLES T.J., COALE K.H., GARDNER W.D. & BARBER R.T., 1999. - SeaWiFS satellite ocean color data from the Southern Ocean. *Geophys. Res. Lett.*, 26(10): 1465-1468.

MOORE J.K. & ABBOTT M.R., 2000. - Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *J. Geophys. Res.*, 105 (C12): 28709-28722.

MOORE J.K. & ABBOTT, M.R., 2002. - Surface chlorophyll concentration in relation to the Antarctic Polar Front: seasonal and spatial patterns from satellite observation. *J. Mar. Syst.*, 37: 69-86.

ORSI A., WHITWORTH III T.& NOWLIN J.W., 1995. - On the meridional extent and fronts of the Antarctic circumpolar current. *Deep-Sea Res. I*, 42(5): 641-673.

PARK Y.H., FUDA J.L., DURAND I. & NAVEIRA GARABATO A.C., 2008a. - Internal tides and vertical mixing over the Kerguelen Plateau. *Deep-Sea Res. II*, 55(5-7): 582-593.

PARK Y.H., ROQUET F., DURAND I. & FUDA J.L., 2008b. - Large scale circulation over and around the Northern Kerguelen Plateau. *Deep-Sea Res. II*, 55(5-7): 566-581.

PREUNKERT S., LEGRAND M., JOURDAIN B., MOULIN C., BELVISO S., KASAMATSU N., FUKUCHI M. & HIRAWAKE T., 2007. - Interannual variability of dimethylsulfide in air and seawater and its atmospheric oxidation by-products (methanesulfonate and sulfate). *J. Geophys. Res.*, 112(D6): D063061-D0630613.

QUÉGUINER B. & BRZEZINSKY M., 2002. - Biogenic silica production rates and particulate organic matterh distribution in the Atlantic sector of the Southern Ocean, during Austral spring 1992. *Deep-Sea Res. II*, 49: 1765-1786.

ROQUET F., PARK Y.-H., CHARRASSIN J.-B., BAILLEUL F. & GUINET C., 2009. - Observations of the Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals. *J. Mar. Syst.*, 78: 377-393.

SARMIENTO J.L., GRUBER N., BRZEZINSKI M.A. & DUNNE J.P., 2004. - High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature*, 427: 56-60 .

SATHYENDRANATH S. & PLATT T., 2006. - Remote sensing of ocean chlorophyll: consequence of nonuniform pigment profile. *Science*, 314(5804):1419-1423.

STEWART B.S. & DELONG R.L., 1990. - Sexual differences in migration and foraging behaviour of northern elephant seals. *Am. Zool.*, 30: **44A**. Verify

SULLIVAN C.W., ARRIGO K.R., MCCLAIN C.R., COMISO J.C. & FIRESTONE J., 1993. - Distributions of Phytoplankton Blooms in the Southern Ocean. *Science*, 262(5141): 1832-1837.

VAN BEEK P., BOURQUIN M., REYSS J.L., SOUHAULT M., CHARETTE M.A. & JEANDEL C., 2008. - Radium isotopes to investigate the water mass pathways on the Kerguelen Plateau (Southern Ocean). *Deep-Sea Res. II*, 55(5-7): 622-637.