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Lagrangian analysis of multi-satellite data in support of open ocean Marine Protected Area design



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A B S T R A C T

Compared to ecosystem conservation in territorial seas, protecting the open ocean has peculiar geopolitical, economic and scientific challenges. One of the major obstacle is defining the boundary of an open ocean Marine Protected Area (MPA). In contrast to coastal ecosystems, which are mostly constrained by topographic structures fixed in time, the life of marine organisms in the open ocean is entrained by fluid dynamical structures like eddies and fronts, whose lifetime occurs on ecologically-relevant timescales. The position of these highly dynamical structures can vary interannually by hundreds of km, and so too will regions identified as ecologically relevant such as the foraging areas of marine predators. Thus, the expected foraging locations suggested from tracking data cannot be directly extrapolated beyond the year in which the data were collected. Here we explore the potential of Lagrangian methods applied to multisatellite data as a support tool for a MPA proposal by focusing on the Crozet archipelago oceanic area (Indian Sector of the Southern Ocean). By combining remote sensing with biologging information from a key marine top predator (*Eudyptes chrysolophus*, or Macaroni penguin) of the Southern Ocean foodweb, we identify a highly dynamic branch of the Subantarctic front as a foraging hotspot. By tracking this feature in historical satellite data (1993–2012) we are able to extrapolate the position of this foraging ground beyond the years in which tracking data are available and study its spatial variability.

1. Introduction

The open ocean environment represents the largest realm on Earth (99% of the biosphere) (Game et al., 2009) and plays a key role in our economy with >50% of the fish consumed by humans coming from open ocean fisheries (<http://www.greenfacts.org/en>). Under pressure by increasing resource exploitation, pollution and maritime traffic, it is one of the least protected ecosystems on Earth. Juridically encompassing both national exclusive economic zones (EEZ) and “high seas”, i.e. not part of any country's EEZ, beyond 200 nautical miles from any nation's territory, open ocean regions present difficulties in their spatial management and enforcement (Hobday and Hartog, 2014). Only 3% of the marine environment is protected,

and of this fraction, high seas protected areas constitute a minority (Game et al., 2009): in 2013, the U.N. Millennium Goal Report states that less than 1% of the high seas are protected.

At the scale of 1000 s of km, Longhurst (2010) described world oceans' biogeographical provinces according to abiotic and biotic pelagic factors. He identified four biogeographical provinces within the polar biome in the Southern Ocean: the South Subtropical Convergence province (SSTC), the Subantarctic water ring Province (SANT), the Antarctic province (ANTA) and the Polar Southern province (APLR). Each of these provinces theoretically delimits the particular types of environmental or hydrological forcing that can be encountered. More recently, De Broyer et al. (2014) used a bioregionalisation multivariate procedure to delineate regions according to sea

Abbreviation: MPA, Marine protected area; EEZ, Exclusive economic zone; FSLE, Finite size Lyapunov exponent; SAM, Southern annular mode; SST, Sea surface temperature; ACC, Antarctic Circumpolar Current; APLR, Polar southern province; ANTA, Antarctic province; SANT, Subantarctic Water province; SSTC, South Subtropical Convergence

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surface temperature, depth and sea ice. The identified provinces are proxies of ecoregions which are “assemblages of flora, fauna and the supporting geophysical environment contained within distinct but dynamic spatial boundaries” (Vierros et al., 2009). Depending on the availability of data, the approach to the bioregionalisation can be based on species lists by regions or mapping of species distributions (either observed data or prediction of species or community presence/abundance based on environmental factors). For example, Koubbi et al. (2011) determined ecoregions based on modelling mesopelagic fish assemblages in the Indian part of the Southern Ocean.

However, how to identify key ecological areas 100 s of km wide (the typical manageable size of a pelagic Marine Protected Areas, MPA) inside these basin-wide biogeographical provinces is not trivial. In particular, the practical and juridical need of defining fixed boundaries for a Marine Protected Area clashes with the intrinsically dynamical nature of ecologically relevant pelagic features, whose position is not fixed in time (Scales et al., 2014; Maxwell et al., 2015). Unlike terrestrial and benthic systems, from which most management approaches are borrowed, the ecosystems of the open ocean upper layer are only weakly constrained by bottom topography, often thousands of meters below. Life of pelagic marine organisms depends on oceanographic features like eddies, the ocean equivalent of atmospheric cyclones and anticyclones, and fronts, highly dynamical boundaries between distinct water masses. Such features belong to the so-called (sub-)mesoscale regime, which spans spatial scales of 1–100 km, and temporal ones ranging from few days to months. Eddies and fronts create a dynamical “seascape” characterised by strong gradients in physical and biogeochemical properties including temperature, salinity and nutrient availability (Mahadevan and Campbell, 2002; Gaube et al., 2013; Klein and Lapeyre, 2009; Pérez-Muñuzuri and Huhn, 2010; Lévy et al., 2012). These features have been observed to structure the distribution of ocean life from phytoplankton (both in terms of primary production (Strass et al., 2002; Abraham, 1998; Martin, 2003; Lehahn et al., 2007; Lévy et al., 2015), community structure (d’Ovidio et al., 2010) and biodiversity (Sunagawa et al., 2015; De Monte et al., 2013) to zooplankton (Labat et al., 2009), bacteria (Baltar et al., 2010), micronekton (Sabarros et al., 2009; Godø et al., 2012) and top predators (Bailleul et al., 2010; Cotté et al., 2011; Waluda et al., 2001; Polovina et al., 2006; Nel et al., 2001; De Monte et al., 2012; Cotté et al., 2007; Scales et al., 2014). Identifying which of these dynamical features are of relevance for marine organisms, finding the boundaries of the ecoregion in which they evolve, and anticipating their drift in response to scenarios of climate change are therefore issues of primary concern in the definition of open ocean MPAs. Due to the chaotic nature of the ocean dynamics and to the temporal dependence of their external forcing, mesoscale features present a high degree of interannual variability. Much like atmospheric weather patterns, oceanic fronts and eddies may show some predictability, but their position and trajectory can vary by hundreds of km from one year to another. This characteristic poses a problem when biologging data have to be extrapolated in time for the establishment of an MPA (Delord et al., 2014). An oceanographic feature that has been targeted by some tagged animals during some years may appear at a different location in the future, possibly falling outside the perimeter of an MPA established with previous information. In order to address this issue, multisatellite data, which nowadays span several decades, offer a potentially powerful tool, because once an ecologically relevant physical feature has been identified, its interannual variability, drift, and statistical relation to modes of climate variability can be identified. This way, the perimeter of an MPA can be designed so to include this spatial range of variability, encompassing possible trends under scenarios of climate change.

The ecological potential of combining satellite data and biologging is in large part yet to be explored. Only recently data from remote-sensing (Surface Chlorophyll concentration, Sea Surface Temperature, etc.), their Lagrangian analyses (De Monte et al., 2012; Cotté et al., 2011; Hernández-Carrasco et al., 2011), biologging (Rutz and Hays, 2009), in situ measurement networks, and high resolution models have

converged together to a spatial and temporal resolution capable to resolve mesoscale (and in some cases even submesoscale) dynamical mechanisms. Remotely sensed sea surface temperature has been used to infer location and frequency of thermal fronts as proxies for biodiversity in the planning of marine protected areas (Miller and Christodoulou, 2014; Miller et al., 2015). Because of the lack of data on the prey distribution (macrozooplankton and micronekton), information from biologging (in particular animal tracking data) is regularly used in habitat modelling for large marine animals to predict the spatial distribution of foraging grounds for top predators (Torres et al., 2008; Hazen et al., 2013). All these studies have used the environmental fields measured from satellite (like Sea Surface Temperature or Sea Surface Height). However, in recent years advanced analytical tools have been developed, which allow the extraction of dynamical information of the oceanic environment. Adapted to satellite observations of the ocean a few decades ago (Abraham, 1998; d’Ovidio et al., 2009; Waugh and Abraham, 2008; Hernández-García et al., 2002; Hernández-Carrasco et al., 2011; Beron-Vera et al., 2008; Olascoaga et al., 2006), Lagrangian tools in particular now provide a mature and powerful technique for exploring the (sub)mesoscale regime, yielding useful ecological properties like stirring pathways (i.e. where from and how a water parcel has reached a specific location), retentive regions, and frontal systems (d’Ovidio et al., 2013, 2015). More recently, these tools have been shown to be particularly adapted to complement biologging observations, helping to interpret the environmental context which shapes the habitat and behavior of various marine vertebrates, including seabirds, whales, and seals (Tew Kai et al., 2009; De Monte et al., 2012; Della Penna et al., 2015; Cotté et al., 2015, 2011; Bon et al., 2015; d’Ovidio et al., 2013). Nevertheless, to our knowledge Lagrangian tools have not been considered as a tool for conservation. This work aims to bridge this gap, adapting the Lagrangian approach to a specific conservation context (the definition of an MPA in the Southern Ocean) and exploring its potential.

In this study we combine Lagrangian analysis of remote sensing and biologging to identify which open ocean transport structures are targeted by Macaroni penguins - *Eudyptes chrysolophus* - which are key consumers of the Southern Ocean foodweb and have important colonies on Crozet Island (Indian Sector of the Southern Ocean). The Macaroni penguins are listed by IUCN as a vulnerable species (Crossin et al., 2013). Our study focuses on the incubating phase of their life cycles and identifies a dynamic branch of the Subantarctic front as a foraging ground for these penguins. Once this oceanographic feature targeted by penguins has been identified in terms of remote sensing data, we map its position for years in which biologging data are not available. In particular, we employ the multi-decade temporal availability of altimetry information in constructing an interannual density kernel. Studying the correlation between the location of the estimated foraging ground and a climatic mode, we finally evaluate internal vs. climatic interannual variability, thus inferring possible trends in its position in the face of climate change.

1.1. Regional context

1.1.1. The Crozet ecosystem

The Crozet archipelago is located in the Indian sector of the Southern Ocean (Fig. 1 a) and represents a region of high productivity in the otherwise High Nutrient Low Chlorophyll environment of this basin (see Sanial et al. (2014), Pollard et al. (2007a), Venables et al. (2007), Pollard et al. (2007b) for more details). The re-suspension of iron-enriched sediments from the Crozet Plateau is thought to naturally fertilize the iron depleted waters downstream and trigger a diatom dominated phytoplanktonic bloom during the southern springtime. The chlorophyll-rich plume is initially carried north toward the Antarctic Circumpolar Current (ACC), which then disperses it eastward (Fig. 1 b). Crozet bloom’s spatial distribution is largely constrained by the dynamical landscape of mesoscale fronts and structured by

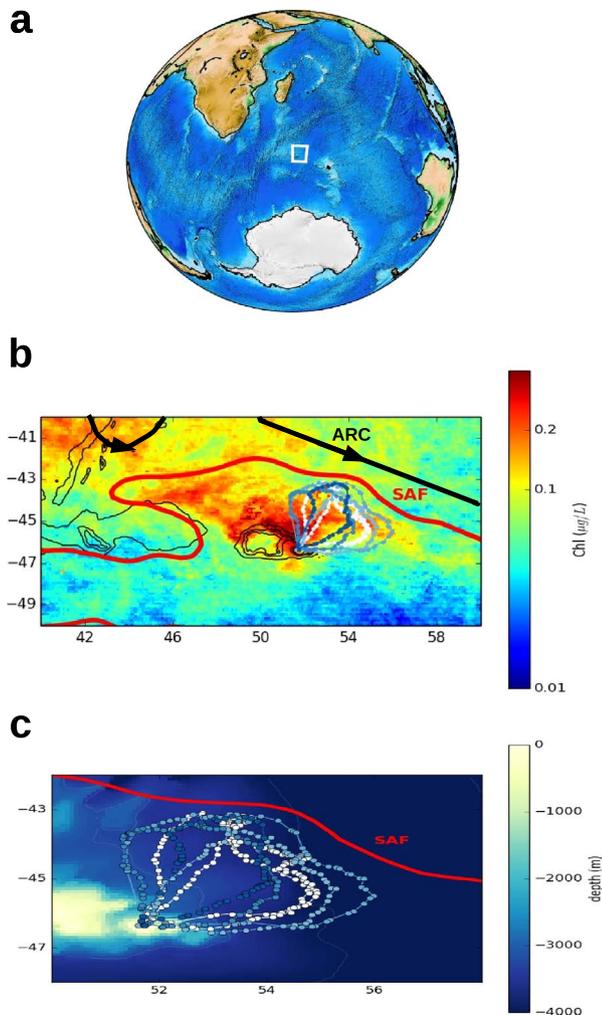


Fig. 1. a) Location of the study region, the Crozet Archipelago, Indian Sector of the Southern Ocean. b) Chlorophyll climatology between the 15 November to 15 December (years 1997–2012, colorscale) overlapped by the main large scale dynamical structures, the Subantarctic Front (SAF, red line) and the Agulhas Retroflexion Current (ARC, black line) and the Macaroni penguin trajectories (shades of blue). c) Zoom on the penguins trajectories and the local bathymetry (colorscale). Dots along the trajectories show the penguins' positions every 6 h. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mesoscale eddies and submesoscale filaments induced by the interaction of two of the Antarctic Circumpolar large-scale fronts, the Subantarctic and Polar fronts (north and south of Crozet islands respectively), with the shallow bathymetry of the Crozet Plateau and the Del Caño Rise located upstream in respect to the plateau. Pollard et al. (2007a), Pollard et al. (2007b) indicate that a major branch of the Antarctic Circumpolar Current, corresponding to the Subantarctic Front (SAF), flows anticyclonically round the Del Caño Rise west of the Crozet Plateau. The region's circulation is also affected by the Agulhas Return Current (ARC) which flows east along 40 °S with major meanders and gradually turns to the southeast to cross 60 °E at about 44 °S. The ARC and the SAF north of Crozet show that they remain separate, usually about 200 km apart, coming closest north of Crozet, where the ARC turns sharply south and meets the SAF at its northernmost excursion. This S-bend in the SAF seems to be a permanent feature, controlled by the bathymetry (Pollard and Read, 2001). It is the area of weakest circulation where entering water resides for about 2 months. Mesoscale structures such as meanders in the S-bend are responsible for the spatial patchiness of plankton bloom (Read et al., 2007 (Read et al., 2007)). Such patchy and productive environment and the presence of islands where mammals and seabird can breed

create an ecological hotspot both in terms of biomass and diversity. The area around Crozet includes the foraging and breeding areas of several endangered and threatened species such as wandering albatross and giant petrels (Woehler and Croxall, 1997). As a consequence, this region has been identified as a candidate to be part of a system of MPAs that will capture the set of specific conservation features within the Southern Ocean including benthic and pelagic ecosystems (Koubbi et al., 2012).

1.1.2. The national marine and terrestrial nature reserve of Crozet

The national marine and terrestrial nature reserve of the French southern territories was created in October 2006. This MPA is managed by “Terres Australes et Antarctiques Françaises (TAAF)” having established a management plan in 2011. Covering 22,700 km² of land and sea, it is France's largest national reserve which encompasses 6651 km² of the territorial sea (12 nautical miles from the coast) of the Crozet Archipelago. Islands are rare in the southern Indian Ocean, but those that are present are essential for land-breeding marine species. Four islands of the Crozet Archipelago (Apostles Island, Hogs island, Penguins island and East Island) are comprehensively protected; their territorial seas are “no take areas” for fisheries, and access to these islands is strictly controlled. A fifth island, Possession Island, is also within the terrestrial reserve and human activity is authorized for scientific purposes. The territorial sea of Possession Island is not included within the marine reserve but TAAF regulations forbid fisheries activities in adjacent waters. It is the aim of the TAAF administration to seek scientific advice to geographically extend the marine reserve into the open ocean by adopting an ecoregionalisation approach and spatial planning including sustainable use of marine resources such as toothfish (*Dissostichus eleginoides*).

1.1.3. Study species

In this study we used 6 trajectories of Macaroni penguins (Fig. 1 c), a pelagic diving predator that forages within the mixed layer to mean depths of 50 m (Bon et al., 2015; Green et al., 1998). The birds were tracked during the incubation season (end of the austral spring) of 2012. This study focused on male Macaroni penguins during the incubation phase that is particularly critical in the penguins' breeding cycle. First, when foraging at sea, penguins during the incubating phase have a strong time constraint to go back to the colony in order to allow their partner to forage and restore her body condition. Second, the foraging time at sea occurs between two fasting periods while they are incubating at the colony (Bon et al., 2015). The combination of these two constraints is likely to have shaped the adaptation of Macaroni penguins to their environment: they have been observed to slow down their swimming velocities in presence of strong currents (probably to optimize their energetics) and to limit the upstream swimming (Bon et al., 2015). The diet of Macaroni penguins mainly consists of crustaceans (krill and amphipods) and micronekton (mainly myctophids) (Green et al., 1998; Deagle et al., 2007). Considering that Macaroni penguins can swim hundreds of kms in search of food, tracking their foraging grounds is a way of identifying open ocean hotspots with large biomasses of their prey.

Previous studies suggest that Macaroni penguins tend to exploit frontal regions and shelf areas to forage (Bon et al., 2015; Thiebot et al., 2011; Barlow and Croxall, 2002). In particular, the trajectories discussed in this study refer to individuals who went foraging in the dynamical area of the SAF, presenting a foraging behaviour that is similar to the one of Crozet's King penguins targeting the Polar Front (Bost et al., 2015). King penguins have been observed to increase their foraging success when they reach the front and to be affected strongly and immediately by its displacement due to large scale climatic anomalies of the subtropical Indian Ocean.

1.1.4. Climate change scenarios

The effects of climate change of the Crozet region are difficult to

assess, since only recently observational time series allow the study of the interannual variability of physical and biological ocean landscape. Yet, studies in Crozet (Weimerskirch et al., 2003; Inchausti et al., 2003) and in other sub-Antarctic islands (e.g. Marion Island, at approximately the same latitude of the Crozet archipelago (Smith, 2002)) show that since the 1950 s (and in particular after the 1970 s) simultaneous increases in air and sea temperatures have been documented. Such changes are consistent with the observed and predicted changes for the entire Southern Ocean: Argo floats and hydrographic surveys registered a warming and freshening over the entire basin (Böning et al., 2008; Gille, 2008).

The observed Southern Ocean warming and freshening is associated with a shift in the fronts of the ACC. The ACC is strongly wind-forced and in turn it has been observed to respond readily to variations in the Southern Annular Mode (SAM), the dominant mode of extratropical variability of the Southern Hemisphere (Sallée et al., 2008; Lovenduski and Gruber, 2005).

Climate projections suggest a further (although slower) positive change of the SAM (Cai et al., 2005; Mayewski et al., 2009; Miller et al., 2006) with a possible consequent enhancement of westerly winds (Sallée et al., 2008). Whether increased wind stress will intensify the ACC and increase its transport is still an open question (Yang et al., 2007). However, an estimated major consequence would be a poleward movement of the ACC fronts in the Indian sector of the Southern Ocean, including the branches of the SAF, one of the dominant structures of the ocean circulation around Crozet.

2. Methods

In our analysis we integrated different datasets to locate putative foraging regions for Macaroni penguins and study their interannual variability. First, we combined the animal tracking with multi-satellite observations (chlorophyll, SST) and altimetry analysis (Finite Size Lyapunov Exponent, water age and water origin) to identify the properties of the front targeted by the tracked Macaroni penguins in November–December 2012. In analogy with what was recently discovered for southern elephant seals, which can swim even faster, we assumed that, when reaching a profitable area, Macaroni penguins would focus their movements into diving and chasing preys and not into searching for new foraging grounds and therefore tend to be transported by the horizontal ocean dynamics (Della Penna et al., 2015). Consistent with this hypothesis, we used the altimetry-derived horizontal velocity field to advect a patch of simulated passive tracer and we compared the temporal evolution of its location with the penguins trajectories. Then, we gathered the same, when possible, information from previous years and we estimated the location of the “entry point” of penguins on the front and the evolution of the patch. The interannual variability of the location of the patch and its distance from the colony was then related to the Southern Annular Mode, the main atmospheric mode influencing the interannual climate variability of the region.

2.1. Tracking data

The trajectories used in this study refer to male Macaroni penguins during the incubation seasons and they are the same ones studied by Bon et al., 2015. The dataset underwent the process of filtering mentioned in Bon et al. (2015) consisting in deleting location implying speeds larger than 10 km/h, the maximum travel speed recorded for Macaroni penguins (Brown, 1987), and interpolating the GPS observations with a six hours temporal resolution.

2.2. Multi-satellite data

Altimetry-derived geostrophic velocities were provided by AVISO, SSALTO/Duacs products, version April 2014. The product is gridded

with a spatial resolution of $1/4^\circ$, it is provided with daily interpolation (Handbook, 2014) and is available for all the years considered in this study (1993–2012). To quantify the chlorophyll spatial distribution we used the GlobColour (GlobColour, 2015) gridded chlorophyll (Chl) product for case 1 waters (adapted for open ocean waters). The resolution of this product is 4 km and daily, however, it is available only for the years after 1997. For the Sea Surface Temperature (SST) we used the GHRSSST web portal (GHRSSST, 2011) to identify the product with the highest spatial resolution available for the different years of the study. We used AVHRR (resolution: 25 km) for the years 1993–2001, AVHRR-AMSR-01 (25 km) for the years 2002–2004, mw-ir-O1 (9 km) for years 2005–2009 and the L4 product G1SST (1 km, integrating also in-situ observations and model output) for the years 2010–2012. More details about the products can be found in (GHRSSST, 2011).

2.3. Lagrangian approaches

We used Lagrangian approaches to locate Lagrangian fronts (defined by Prants et al. (2014) as boundaries between surface waters with strongly different Lagrangian properties, e.g. their origin) in the regions explored by the tracked penguins and to identify favourable foraging areas. In fluid dynamics, Lagrangian approaches are based on following individual fluid parcels (in this case water parcels) through time as they move in a velocity field. In this study the velocity field consists of horizontal geostrophic velocities measured from altimetry. To calculate the trajectories of water parcels we integrated the geostrophic velocity field using a 4th order Runge-Kutta algorithm.

We mainly use three Lagrangian diagnostics: the Finite Size Lyapunov Exponents and water ages and origin from bathymetric features.

We used ridges of Finite Size Lyapunov Exponents (FSLE) to locate fine-scale Lagrangian fronts (d'Ovidio et al., 2009). The FSLE measures the rate of separation between particles initialised nearby. Maxima (ridges) of Lyapunov exponents computed backward in time are used to identify fronts defined as regions of water parcels' confluence, that is, where water parcels originating far away are advected in close proximity. Technically they are computed as:

$$FSLE(lon, lat, t, \delta_0, \delta) = \frac{1}{\tau} \log \left(\frac{\delta}{\delta_0} \right) \quad (1)$$

where δ_0 represents the initial separation of water parcels, and τ the time taken for the water parcels to reach a separation δ . For this study the values of δ and δ_0 were of 0.01° and 0.6° respectively. (t,lon,lat) refer to the location in time and space of the region where the FSLE is computed.

Besides identifying frontal areas, we also discriminated water parcels coming from different regions. In order to do that, we used two Lagrangian diagnostics defined in Sanial et al. (2014), d'Ovidio et al. (2015): the water age and the water origin from a bathymetric feature. The water age quantifies the time period before a specific water parcel has been in contact with a specific bathymetric isoline and the water origin the location (in terms of longitude and latitude) where the water parcel has left such bathymetric line (for this study, following Sanial et al. (2014) we used the -2000 m isobath). In Sanial et al. (2014) such diagnostics have been used to validate the hypothesis that iron (the limiting factor for phytoplankton growth in this region) advection from shallow bathymetries is largely responsible for chlorophyll plumes in the proximity of islands. In particular, these diagnostics were used to predict the extent and the structure of the Crozet (Sanial et al., 2014) and Kerguelen (d'Ovidio et al., 2015) plumes during the KEOPS2 (Kerguelen Ocean and Plateau compared Study 2) voyage and to interpret the observations of high chlorophyll concentrations sampled with bio-argo autonomous profilers (Grenier et al., 2015). The altimetry-derived water age computed from the -2000 m

isobath that we use in this study has been shown to be in quantitative agreement with the same quantity estimated from the tracking of non-biogenic isotopes and from the trajectory of a drifter (Sanial et al., 2014).

To predict areas of interest for the studied penguins, we started from the observation detailed in Bon et al. (2015) and Bost et al. (2015). Bon and co-authors studied trajectories of Macaroni penguins that went foraging in the dynamical region located near the Subantarctic Front (SAF). A comparison with geostrophic ocean currents showed that the studied trajectories presented a recurring pattern of active swimming from the colony to a frontal area, followed by few days when the difference between the penguin velocities and the currents ones were very low and concluded by active swimming from the frontal area to the colony. As a consequence, to identify putative foraging regions, we tracked the spatial distribution of a simulated passive tracer, whose dynamics is only determined by the horizontal geostrophic currents, that is initialised where we observe (and for the interannual variability study, where we estimate) penguins enter the SAF.

2.5. Interannual variability data

The spatial evolution of the patch was computed for years 1993–2012 by initialising a circular patch around the closer location to Possession Island having the properties detailed in the results. An isotropic Gaussian kernel was computed (with a grid space of 10 km) to quantify the density of the passive tracers through the years.

To compare the location of the estimated region of interested for Macaroni penguins with climate interannual variability we used the “Southern Annular Mode/Antarctic Oscillations” dataset from NOAA/CPC (CF-1.0). SAM is measured as pressure gradient between the polar and subpolar regions of the Southern Hemisphere. The dataset contains monthly estimates of the SAM values from 1979 to 2015. The value of the SAM was compared with three diagnostics (the initial latitude of the center of the patch, the mean latitude of the patch after one week and the mean distance from the colony after one week) by using a correlation matrix.

3. Results

3.1. Putative foraging regions for Macaroni penguins

The comparison between the trajectories of Macaroni penguins from the colony in Possession Island and multi-satellite observations suggests that, as detailed in Bon et al. (2015), once the penguins reach a strong Lagrangian front (within the envelope of the SAF) characterised by strong gradients, their movements tend to be horizontally advected by the currents, in analogy to what has been observed on Southern Elephant Seals (Della Penna et al., 2015). The front where the penguins change direction (and swimming behaviour) presents a strong gradient in Chl concentration and SST and separates waters having a strong difference in origin and age as shown in Fig. 2. The change in penguins' swimming behaviour occurs in a location of strong transport ($FSLE > 0.2 d^{-1}$), between water parcels closer to the colony and likely to be enriched on the Crozet plateau having very high Chl content and less productive ones originating from a much more northerly latitude.

A patch of simulated passive tracer initialised at the latitude where these conditions are satisfied (that is also where the “entry-point” of penguins in the SAF is) and at the longitude of Possession Island is transported east by the strong transport of the front, with a considerable overlap with the penguins' trajectories (see Fig. 3). The tracer is initialised as a circular patch, whose radius is lower bounded by the spatial resolution of altimetry (~ 30 km) and upper bounded by the typical size of mesoscale structures (~ 100 km). In this example, and in the analyses presented next, we used a radius of 50 km that is also

representative of the typical latitudinal spread between different individuals' entry points on the front. As the tracer is advected horizontally along the front, its shape changes, eventually separating into two branches of the front. One of these branches corresponds with the one followed by the tracked penguins. Out of 233 GPS locations of the central phase of foraging trips (identified by Bon et al. (2015)), 199 (85% of the total) overlap with the advected patch. This co-localisation is calculated over all the locations of the patch advected for 15 days (the color scale in Fig. 3 shows the temporal evolution of the location of the patch) in order to take into account (i) the fact that not all the tracked penguins reach the entry point on the front at the same time and (ii) the general underestimation of altimetry-derived velocities that could introduce a delay in the simulated trajectories.

3.2. Interannual variability of the key structures

To study the interannual variability of the dynamical structure identified in the previous section, each year a 50 km radius circular patch of simulated passive tracer was initialised in locations satisfying the following criteria:

1. a **longitude** within 50 km east from the one of Possession Island. The tracked penguins tended to swim heading north or northeast and the current in the crossed regions to reach the SAF tend to advect them eastward.
2. a **Lagrangian front** is present. The SAF branches are strong Lagrangian fronts that we can identify using the FSLE. We use a threshold of $FSLE > 0.1 d^{-1}$, after Lehahn et al. (2007), that is considered to be appropriate to identify fronts in dynamic regions such as the ACC.
3. a **water origin** (latitude) contrast is between origin $\sim -44^\circ$ and $\sim -41^\circ$. Besides imposing condition 2, we also require a candidate entry point to be at the confluence of water parcels having a specific difference in water origin. We make the hypothesis that the targeted confluence region is approximately always at the interface between waters having recurring origin through the years (see Fig. 2). We do not consider gradients in the longitude of water origin given the strongly zonal structure of the ACC.
4. **SST** in the range $7 - 8^\circ\text{C}$. The 7 and 8°C isotherms are commonly used as indicators for the southern branches of the SAF that is a well assessed foraging area for several species of the region and has been observed to be a strong biogeographical boundary for mesozooplankton communities (Fielding et al., 2007; Bost et al., 2009; Park et al., 1993). Fig. 2 suggests that some of the tracked penguins tended to start the central phase of their foraging trip when crossing these surface isotherms.
5. **Chl gradient**, when available. The presence of a Chl gradient was considered as a further criterion to indicate that the converging water masses hosted different biogeochemical characteristics that may be related to why penguins target a specific ocean feature.

The location of the patch shows strong spatial variability between the years 1993–2012. Fig. 4 shows the location of the patch after 7 days of advection calculated for years 1993–2012. The patch's shape is generally stretched by the strong velocities on the front and the latitudes ranges from -45° to -42° . However, there is a moderate interannual variability in both latitudinal and longitudinal stretches. Furthermore, in some cases recirculation features (such as eddies and small meanders) strongly affect the distribution of the patch by entraining the tracer to the same location for days or weeks. The Gaussian kernel of the spatial distribution of the passive tracer, that takes into account of the location of the patch during 15 days of advection, shows very high concentration of the tracer between $52-54^\circ\text{E}$ and 43°S (see Fig. 5). Other recurring patches occur around 52°E , 44°S and 54°E , 44°S . However, the interannual spatial variability is particularly evident when looking at the spread of the

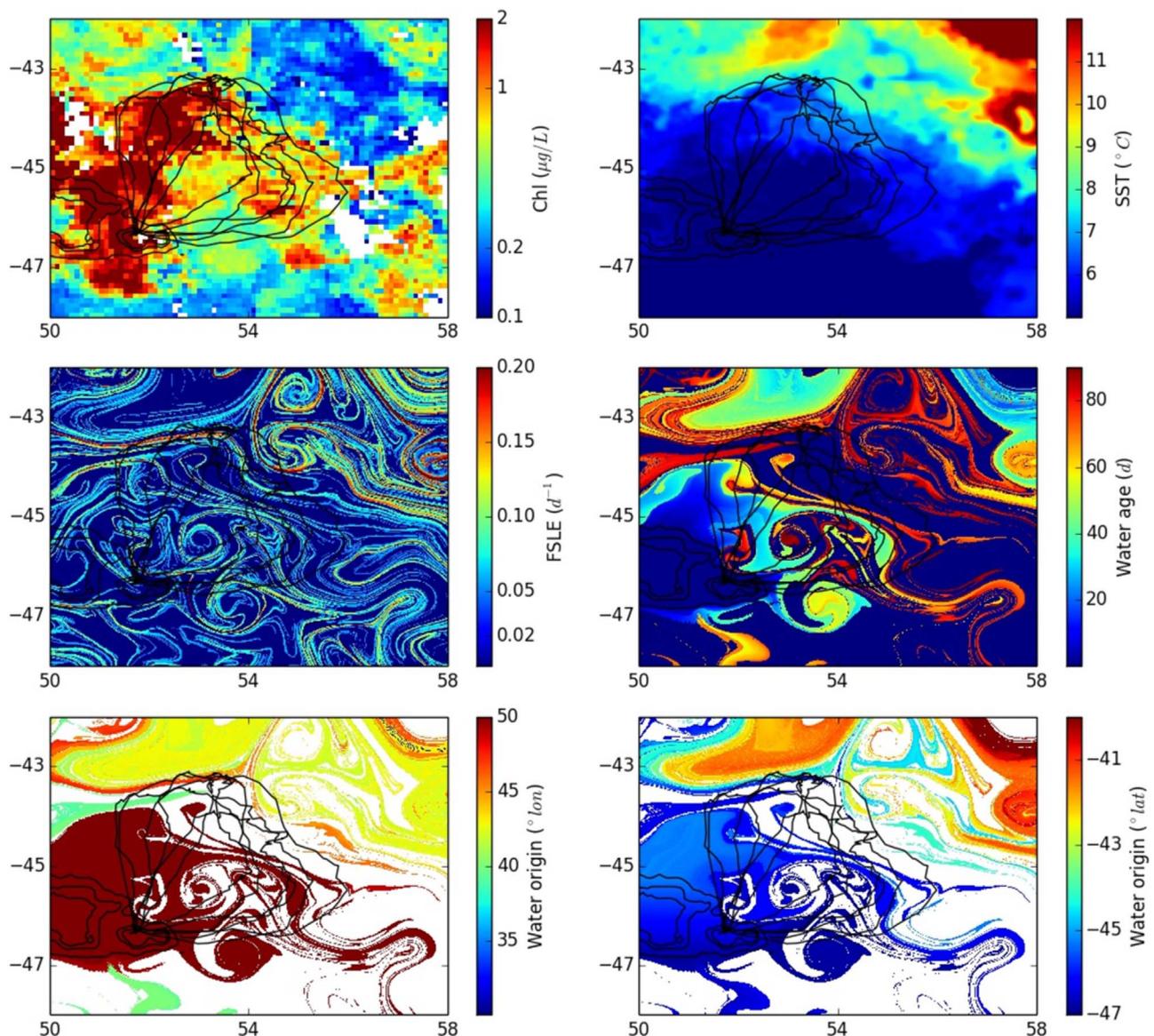


Fig. 2. Multi-satellite observations and analysis for November 2012 (period referring to the Macaroni penguins foraging trajectories, black lines). a) Chlorophyll climatology (15 Nov–15 Dec), b) Sea Surface Temperature (daily image, referring to the 27/11/2012), c) Finite Size Lyapunov Exponent, d) water age, water origin: e) longitude, f) latitude, referring to 27/11/2012.

patch east of 55 °E.

The initial latitude of the patch (i.e. the entry point of the penguins on the front), the mean latitude after one week and its distance from the colony calculated for several years did not show any significant relationship with the SAM ($p > 0.05$ for all the three variables).

4. Discussion

Many marine predators are known to congregate over specific regions of oceanic fronts (Bost et al., 2009; Scales et al., 2014). In contrast to terrestrial landscapes, the pelagic physical context is dynamic and its changes occur on a scale that is comparable with the one in which marine predators forage. The position of fronts in the open ocean may move substantially from one year to another, creating a challenge for the definition of the boundaries for a Marine Protected Area, especially given observed and projected climate change. This problem is typically addressed by pooling together observations of animal location from different years. Although MPAs are often spatially defined with the core of ecoregions where environmental factors are more stable, this concept cannot be used for highly dynamic areas or

borders of ecoregions (Maxwell et al., 2015). Fronts and transitions between ecoregions can be important for conservation as they can be highly productive, constitute typical foraging grounds (Cotté et al., 2015; Della Penna et al., 2015) or mark sharp biogeographic transitions as observed by De Broyer et al. (2014) and Koubbi et al. (2011). It is obvious that in such dynamic systems, potential MPAs have to integrate spatial variations of dynamic features such as meanders of frontal zones.

Taking into account the dynamical nature of oceanic features is especially relevant for planning and managing MPAs in the face of climate change. Ocean warming and changes in the current patterns have been observed to have important biological consequences from the species to the community level (Hughes, 2000; Walther et al., 2002; Hazen et al., 2013; Forcada and Trathan, 2009; Bost et al., 2015).

Here we propose a supporting tool, based on the multi-annual tracking of the fine-scale congregation region over the physical front itself. The congregation region is firstly identified by comparing satellite data to animals' positions within a Lagrangian scheme; then its position is tracked in historical satellite data. This approach is obviously not intended as an alternative to habitat modelling with

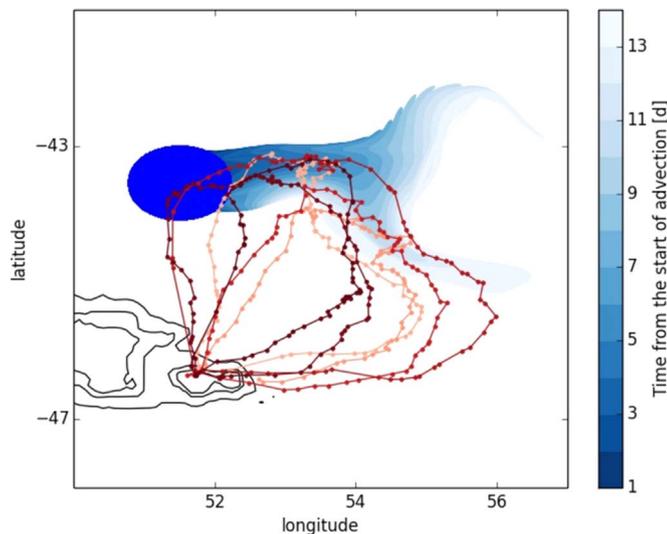


Fig. 3. Example of patch advection for year 2012. The simulated passive tracer is initialised north of the Possession Island colony (bright blue patch) and advected for 15 days by altimetry-derived geostrophic currents (black patch). The temporal evolution of the patch is represented by different blues (as number of days since the beginning of advection). The trajectories of the penguins are represented in shades of red and the black contours represent the bathymetry. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

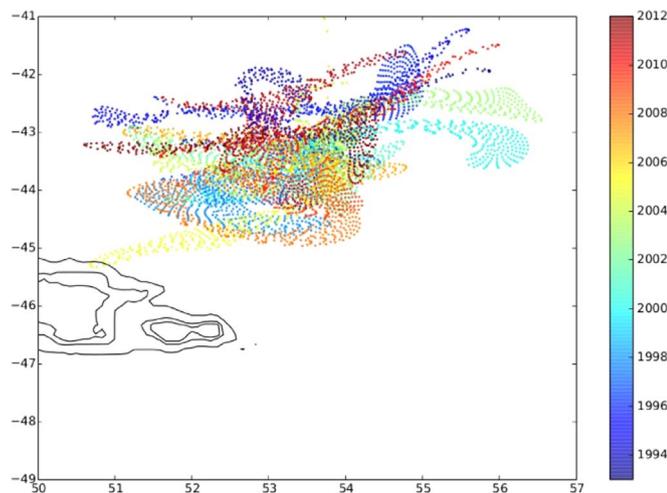


Fig. 4. Interannual variability of the patch spatial distribution after 7 days of advection.

animal telemetry, but as a complementary one. Indeed, in this study instead of calculating probability of spatial distributions using the animal trajectories themselves, we consider the variability of the physical structure on which animals appear to congregate.

Furthermore the Lagrangian diagnostics used in this study could be relevant in the context of dynamical ocean management strategies (Hobday and Hartmann, 2006; Hobday and Hartog, 2014; Lewison et al., 2015; Maxwell et al., 2015) that aims at changing protection (and generally management) measures according to the changes in ocean conditions complementing the use of near-real time Sea Surface Temperature and animal tracking data with Lagrangian diagnostics as indicators of Lagrangian fronts and converging waters. A dynamic ocean management strategy would be particularly efficient for the protection of the dynamical feature targeted characterised in this study. For the design of a MPA whose boundaries are “fixed” in space it is fundamental to consider the interannual variability of the penguins’ estimated foraging region and therefore the area of the total protected area has to be relatively large. Instead, if the location of the foraging region (where activities that could affect penguin foraging may be

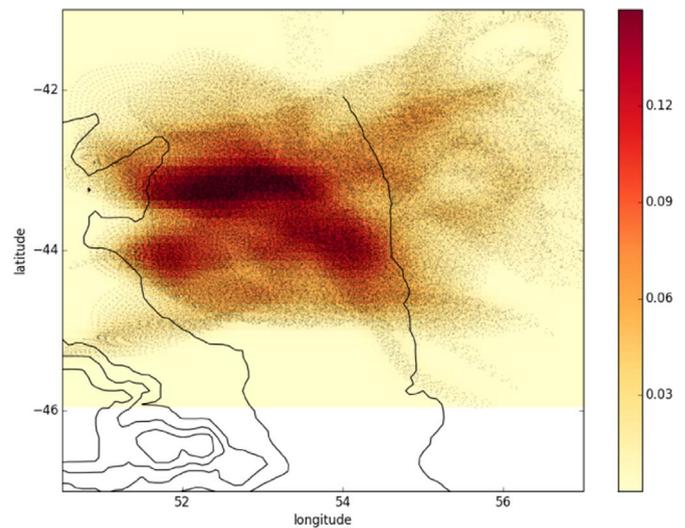


Fig. 5. Density plot of the spatial distribution of the simulated passive tracer. The grey dots represent the locations of the simulated passive tracer (from day=1 to day=15 of advection). In color, the Gaussian kernel of their spatial distribution.

restricted or banned) is determined on a yearly basis, the MPA’s surface may be restricted to 10–60% (according to different years).

The results of this study rely on a number of assumptions. First of all, we assume that Macaroni penguins target each year an equivalent dynamical structure during their foraging trips. While a sample size of six trajectories is fairly limited, the major factor affecting the robustness of the presented approach is the fact that all refer to the same year. Further animal tracking observations are necessary in order to evaluate this assumption and improve the method. In particular, a major priority should be the tracking of Macaroni penguins through different years. Secondly, we assume that, once the penguins encountered a profitable foraging ground, they are horizontally transported by the currents. This assumption relies on the findings from previous studies on foraging penguins (Bon et al., 2015; Bost et al., 2009; Cotté et al., 2007) that in the middle of their trajectories, when they are expected to forage more intensively, they tend to decrease their horizontal swimming velocity. This change in the swimming behaviour results in an overall transport caused by the surrounding flowing medium. A similar result has been found for other diving predators, such as southern elephant seals moving in highly dynamic oceanic regimes (Della Penna et al., 2015) and sea turtles (Gaspar et al., 2006). Finally, our results are based on the reliability and the appropriateness of the altimetry-derived velocity field. Macaroni penguins are diving predators, diving on average to 50 m (ranging 10–154 m) depth (Bon et al., 2015; Green et al., 1998). Altimetry velocities are considered to be representative of the horizontal currents in the mixed layer, that in the region of Crozet ranges between 40 m and 100 m for the season considered in this study (November–December) as detailed in Sallée et al., 2010 and Venables et al., 2007. Although altimetry-derived currents neglect ageostrophic and fine scale (<70 km) features, altimetry-derived stirring patterns in the Crozet region benefit from an excellent validation study, which showed agreement with drifters’ trajectory, chlorophyll patterns and isotope measurements (Sanial et al., 2014).

The criteria used to choose the initial location of the patch for years where animal tracking data are not available are mainly based on observations from the literature and from the comparison between the tracked animals and oceanic features presented in Fig. 2. All these criteria aim at identifying a frontal area characterised by both strong transport and gradients in physical and biogeochemical properties. Many of the mentioned parameters are not independent. For example, transport does not only directly affect the penguins but it also structures the distribution of tracers such as SST and Chl whose gradients are therefore expected to correlate with the location of FSLE

ridges. Yet, we choose to use a set of several variables in order to include the typical increased gradients in both physical and biogeochemical tracers.

It would be an interesting perspective to make the process of selection of the entry-point on the front completely automatic. Potential approaches in this respect include identifying the entry-point using a more selective version of the presented list of criteria or taking advantage of the fact that fronts can also be identified as isolines of Sea Surface Height (SSH). More details about a possible SSH based approach are described in the [Supplementary Information](#). However, the main limitation of these two approaches lies in the possible presence of mesoscale recirculation features for the elected entry-point. If a simulated tracer is initialised within an eddy, for example, it is likely to be confined within the same structure for all the time of advection. Since we have no knowledge of what behaviour the penguins may present in such a condition, we tend not to consider these cases that an automated algorithm may find more difficult to detect. Furthermore, even if the detection of a front based on SSH alone is computationally less involved than the multi-satellite method, it is less reliable also, as it does not allow validation of the identification of a front with hallmarks expected in a frontal region. Typical frontal features include increased gradients in biogeochemical tracers and the presence of a frontogenetic mechanisms like horizontal stretching. These features are instead addressed explicitly by the multi-satellite method, which is based on detection of SST/Chl gradients and stretching (the latter through Lyapunov exponent calculation and synthetic particle advection). Indeed, our results show the SSH method appears in this region to be quite reliable as a first guess, but that several cases exist in which the SSH-based detection is off by 50–100 km.

The interannual variability analysis presented in this study (Fig. 4) suggests that the region's mesoscale turbulence strongly influences the dispersion of the patch. In particular for years where mesoscale eddies are present, it is difficult to infer how the penguins will respond to such a change in the structuring of their prey field. Observations of Macaroni penguins interacting with such features will provide valuable information in this respect. Also, the distribution of Chl (not shown) presents a high spatial variability that makes it harder to predict how it will affect the penguins' movements. Such high variability may be responsible for the non-significant relationship between the patch location and the SAM. Another possible reason behind it, could be that, even if generally the SAF is expected to shift southward, the SAF location in the Crozet area is strongly constrained by the bathymetry, so the expected southward trend may be more difficult to detect, if it occurs.

5. Conclusions

This study presents a proof of concept for the use of Lagrangian approaches as a support tool for the design of MPAs. Lagrangian diagnostics have been successfully used to identify regions of ecological interest like foraging grounds (Cotté et al., 2015; Bon et al., 2015; Della Penna et al., 2015), yet our preliminary results suggest that they can also be a valuable tool for tracking in time and space dynamical ecological key regions, for mapping their interannual variability, and for exploring possible trends associated to mode of climate variability. Future field studies are necessary in order to improve the presented method and evaluate its feasibility as a tool to constantly monitor and protect marine predators such as Macaroni penguins. In particular, a time series of trajectories from several years will be essential to validate and refine the algorithm. It would be also especially relevant to gather data about this species' prey – myctophids, euphausiids and amphipods – concentration and availability in respect to the tracked region of interest.

Competing financial interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.12.014>.

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