

A comparative study of *Phoebetria* albatrosses' interactions with mesoscale oceanographic features south of the African continent.

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Abstract

Two sympatric *Phoebetria* albatrosses, *P. fusca* and *palpebrata* breeding at Marion Island in the South Indian Ocean were studied. Adult individuals were tracked between 2008 and 2011. The study examined the foraging distribution of the two species in relation to environmental parameters such as sea surface temperature. Interaction with mesoscale features expressed by sea surface temperatures, was tested with statistical models. Tracked *P. fusca* demonstrated positive association with sea surface temperatures in the Southern Indian Ocean, in particular during incubating and chick-provisioning periods, by travelling shorter distances to the interfaces of mesoscale features created as a result of the Agulhas Return Current located << 500 km to the north of breeding islands. During nest construction, tracked *P. fusca* travelled greater distances in search of food possibly because they had no chick to return to at the colonies. Contrastingly, tracked *P. palpebrata* did not demonstrate any positive association with sea surface temperatures. During incubating and chick-provisioning periods, tracked *P. palpebrata* travelled shorter distances to foraging grounds located to the south of breeding islands possibly to maximise returns to chicks while minimising efforts. During nest construction, tracked *P. palpebrata* travelled to distant foraging grounds to the south of the Antarctic Polar Front in areas of low mesoscale variability suggesting that greater distances can be achieved when they have no chick to feed at the colonies. Individuals of both tracked species foraged within close proximity during energy-demanding periods indicating their ability to employ an efficient foraging strategy that ensures minimal effort whilst maximising returns. Generalised Linear Models with the response variable being species and explanatory variables comprised of sea surface temperatures, annual breeding stages, distance traversed and activity, were conducted to examine the effect of environmental factors on seabird foraging distribution. These models were subjected to robust fitness tests and those that represented ecological reality of the two tracked albatrosses were chosen. The study demonstrates that the most important foraging areas for these two tracked seabird species overlap with the Indian Ocean Tuna Commission Convention area making them vulnerable from incidental capture from high longline fisheries. These results have implications to the conservation of these albatrosses suggesting a need for a multi-faceted approach on fisheries management particularly on mitigation of seabird bycatch in the Indian Ocean Tuna Convention area.

Keywords: *Phoebetria*; Agulhas Return Current; Antarctic Polar Front; sea surface temperature; sea surface height; Mesoscale features; IOTC; Fitted Model; Southern Indian Ocean

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Chapter 1. Introduction

1.1 Biological background of albatrosses

Fifteen of the world's 22 species of albatrosses are threatened with extinction due to interactions with global fisheries (BirdLife International 2004). Sooty albatrosses are long-lived, marine top predators that are physiologically suited to thrive in the harsh conditions of the pelagic environment. They belong to the genus *Phoebastria* which comprises two species, the *P. fusca* and *palpebrata*. Unfortunately, the populations of these apex predators are decreasing (Weimerskirch and Jouventin 1987, Croxall et al. 1998, Arnold and Croxall 2006) and they are listed endangered and near-threatened by the International Union for Conservation of Nature (IUCN 2012).

Phoebastria albatrosses are known to travel great distances in search of unpredictable and unevenly distributed marine prey (Weimerskirch et al. 2005). Unfortunately, their high-seas foraging habitats overlap considerably with longline fishing effort. They are vulnerable to being accidentally captured on longlines (Gales et al. 1998).

In South African territorial waters, however, these seabirds are often in conflict with commercial fisheries that target tunas *Thunnus* spp and Hake *Merluccius paradoxus* and *M. capensis* (Ryan and Moloney 1988, Ryan et al. 2002, Petersen et al. 2008, Watkins et al. 2008). Fisheries have been implicated as the main reason behind the unsustainable declines of albatross populations (Weimerskirch and Jouventin 1987, Croxall et al, 1990).

While in search of patchily distributed prey, these albatrosses are able to exploit the dynamic pelagic environments (Hyrenbach et al. 2002) and the associated nutrient-rich oceanographic features. Such features can be referred as foraging habitats of marine apex predators such as albatrosses (Balance et al. 1997, Inchausti et al. 2003, Hyrenbach et al. 2006). Thus, the aggregation of albatrosses in the vicinity of an oceanographic feature is indicative of prey availability (Pocklington 1979, Nel et al. 2001, Hyrenbach et al. 2006).

Studies have shown that oceanographic features characterised by increased environmental variability are associated with high primary productivity (Schneider 1990, Hyrenbach et al. 2006). The inherent dynamic nature of pelagic environments provides suitable conditions for the aggregations of prey and in turn that of upper trophic-level predators such as albatrosses. Albatrosses overlap with trophic and

oligotrophic habitats (Hyrenbach et al. 2002, Thorne 2010) but are capable of exploiting these dynamic environments.

Physical and biological processes (Hunt and Schneider 1987, Schneider 1991, Waluda et al. 1999) regulate the distribution of marine productivity and thus, control the trophic structure in pelagic environments. These processes regulate the at-sea distributions of albatrosses which depend upon marine prey (Abrams 1985, Brown and Gaskin 1988, Hunt et al. 1992, Balance et al. 2006). Thus, these processes are vitally important for the maintenance and sustenance of marine ecosystems (Mann and Lazier 1996).

The ocean south of Africa provides a dynamic environment dominated by mesoscale activities (Pocklington 1979, Abrams 1985, Lutjeharms 1985). Mesoscale features such as eddies and fronts are associated with increased primary productivity which localise the marine prey (Haney 1986b). These features vary in space and time (Schneider and Duffy 1985, Schneider and Piatt 1986) and support aggregations of top predators such as seabirds (Furness and Camphuysen 1997, Nel et al. 2001, Parsons et al. 2008).

1.2 Ecology, population and distribution of the two *Phoebetria* albatrosses

Phoebetria albatrosses are biennial breeders on subantarctic islands and they forage in Antarctic waters (ACAP 2010). They are known for optimising foraging efficiency by concentrating efforts on specific foraging zones in order to maximise returns and minimise effort (Weimerskirch 1986). Their populations are declining at a non-sustainable rate owing to incidental capture on longline fisheries and perhaps on a smaller scale to introduced predators on breeding subantarctic islands (ACAP 2010, BirdLife International 2014). It is a difficult task to estimate breeding pairs of these *Phoebetria* albatrosses because they breed on cliffs that are dangerous and inaccessible (Ryan et al. 2009).

P. fusca

Approximately 48-75% of the total breeding population of *P. fusca* is found on Gough Island, in the South Atlantic Ocean and Prince Edward Islands and Crozet Islands, in the southern Indian Ocean. These three subantarctic islands comprise approximately 12,500 – 19,000 breeding pairs (BirdLife International 2014).

Table 1: Counts of albatross and giant petrel populations (number of breeding pairs) at Prince Edward Island in 2001 (from Ryan et al, 2003) and 2008. Because wandering albatrosses start breeding in mid-summer, the December counts on Prince Edward estimate the following year's breeding effort (2002 and 2009, not 2001 and 2008). The best estimates are for current population, compensating for breeding failures prior to the census period. (Ryan et al, 2009).

Species	Count		Change (%)	Best estimate
	2001	2008		
Wandering albatross	1 687	1 640	-3	1 800
Grey-headed albatross	1 897	1 506	-20	2 000
Indian yellow-nosed albatross	4 870	5 234	7	7 000
Dark mantled sooty albatross (<i>P. fusca</i>)	637	1 210	90	1 500
Light mantled sooty albatross (<i>P. palpebrata</i>)	92	129	40	200
Northern giant petrel	133	191	44	350
Southern giant petrel	567	723	28	1 350

P. fusca confines its foraging patterns to the south of 30°S latitude (BirdLife International 2004). Immature and non-breeding individuals disperse widely in pelagic waters between 30°S and 60°S in the southern Indian and Atlantic Oceans (BirdLife International 2004). *P. fusca* spends most of austral summer in the south of 35°S in both the subtropical and subantarctic waters (BirdLife International 2004). It is mostly abundant near the STC in summer (Tickell and Woods 1972; Weimerskirch et al. 1986). In autumn and winter, however, it forages in the subtropical zone (Tickell and Woods 1972). Immature and non-breeding individuals spend the entire year within the subtropical zone (BirdLife International 2004).

P. fusca has three annual breeding stages which include incubating, chick-provisioning and nest construction periods (ACAP 2010). Incubating period runs from 16 September through

31 December at the breeding colony. Chick-provisioning period is conducted from 1 January through 31 May. Nest construction is done during the 1 June – 15 September period (ACAP 2010).

P. palpebrata

The total breeding population of *P. palpebrata* was estimated between 19,000 – 24,000 breeding pairs each year (BirdLife International 2014). South Georgia Island comprised its largest population with approximately 5,000 – 7,000 breeding pairs (Gales 1993). Marion Island comprised approximately 600 breeding pairs (Ryan et al. 2009). *P. palpebrata* has a circumpolar distribution in the Southern Ocean and it is highly dispersive over pelagic waters (Weimerskirch and Robertson 1994). It is considered to have the most southerly distribution than any other albatross, extending as far south as the border of the Antarctic continent in austral summer (ACAP 2010). Incubating individuals forage south of the Antarctic Polar Front (ACAP 2010). Immature individuals return to their natal breeding grounds (Weimerskirch 1987). It breeds on cliff-ledges on subantarctic islands (Cooper and Klages 1995) in the southern Indian and Atlantic Oceans, New Zealand and Australia. (BirdLife International 2004).

P. palpebrata has three annual breeding stages which include incubating, chick-provisioning and nest construction periods (ACAP 2010). Incubating period runs from 16 October through 31 December at the breeding colony. Chick-provisioning period is conducted from 1 January through 15 June. Nest construction is done during the 16 June – 15 October period (ACAP 2010).

1.3 Conservation status of the two *Phoebetria* albatrosses

Hundreds of Thousands of seabirds (predominantly albatrosses and petrels) are accidentally killed in longline fisheries annually (Brothers et al. 2010; Anderson et al. 2011). Incidental mortality of *Phoebetria* albatrosses in longline fisheries remains a key threat driving declines of breeding populations around the world (Brothers et al. 1995, 1999; Belda et al.2000, Anderson et al. 2011 and Croxall et al. 2012).

Phoebetria albatrosses are vulnerable because they are long-lived species with low fecundity and are therefore highly susceptible to any change in their survival rates (Ryan et al.1999). Incidental deaths of breeding adults often lead to subsequent deaths of dependent chicks left back on breeding islands. Even low levels of anthropogenic adult mortality can result in population declines (Croxall and Gales 1997; Gales 1998).

Previous studies have shown a devastating 60% decline of *P. fusca* (Cuthbert and Sommer 2004). *P. fusca* are known to occasionally follow fishing vessels and scavenge on the discarded offal and bait (ACAP 2010). They are accidentally killed on longlines as they seize baited hooks, and also when they feed on discarded offal and fish during fishing operations. Once hooked, they are dragged underwater and drown (Melvin 2001; Reid et al, 2004). *P. fusca* and *P. palpebrata* are listed as endangered and near-threatened, respectively, on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (ACAP 2010).

1.4 Physical environment south of the African continent

Dominating Currents

The physical ocean environment south of the African continent provides a laboratory to study the extent and role of mesoscale activities in supporting the marine ecosystem. The area is dominated by one of the strong western boundary current, Agulhas Current (AC) and the fast-flowing jet, Antarctic Circumpolar Current (ACC). The Agulhas Current (AC) follows the wide continental shelf break of the south-eastern Africa closely until the southern tip of Africa (Grundlingh, 1983). The AC assumes a zonal flow which is accompanied by meridional excursions (Lutjeharms and van Ballegooyen, 1984, 1988). The AC retroflects almost completely south of the African continent, and forms a retroflection current termed the Agulhas Return Current that is zonally continuous and terminate at up to 70° East of Longitude (Lutjeharms and van Ballegooyen 1984, Lutjeharms and Ansorge, 2001).

The Agulhas Return Current lies between the 15° and 20° East of Longitude, south of the African continent (Lutjeharms and Valentine, 1988). Lutjeharms (1988) postulated that the westward extent of the Agulhas Retroflection loop is up to 5°E. Due to lack of any physical obstacle, the ARC flows downward south of Africa, uninhibited. The widest continental shelf off the southern Africa, enhances increased environmental variability that propagates downward. This wide continental shelf off the southern Africa is crucial for sustaining the ichthyo-ecology of both the west and coasts of South Africa.

The ARC constitutes an intense flow along the Subtropical Convergence (STC) and plays a major role in the exchange of water between South Atlantic and South Indian. Evidence of eddy formation near the ARC was affirmed using expendable bathythermographs (Lutjeharms and Emery 1984). Furthermore, anticyclonic eddies were observed to shed from Agulhas Current at its retroflection (Penven et al. 2001). These anticyclonic eddies were observed to ultimately drift into the South Atlantic. Although, smaller in size, cyclonic eddies were also observed near the ARC in the south-east Atlantic (Duncombe Rae et al. 1996, Grundlingh 1995).

Lutjeharms and Valentine (1988) postulated that the increased mesoscale variability near the ARC is due mainly to recurrent eddy generation and shifts and time-varying meanders in the path of the ARC along the STC. Ring shedding at the retroflection plays an important role in the exchange of water south of Africa (Lutjeharms and van Van Balloogyen, 1988). The object of this study is to investigate seabird movements in relation to mesoscale features created as a result of the Agulhas Return Current south of the continent.

The Antarctic Circumpolar Current is the fast eastward-flowing jet current in the Southern Hemisphere. It inhibits warm surface subtropical water originating north of the ACC from intruding south across the northern limit of the ACC (Karsten et al. 2002). It provides insulation properties to the formation of the Antarctic ice. The ACC carries nutrient-rich upper Circumpolar Deep Water (CDW) eastwards (Tynam 1998).

The study area, Prince Edward Islands (PEI), lies in the Antarctic Polar Frontal Zone (APFZ) and downstream of these Islands, the flow pattern of the ACC is distributed. The flow intensity of the ACC in the vicinity of the PEI is affected by a weak front, the Sub-Antarctic Front (SAF) (Lutjeharms 1993, Pakhomov et al. 2000).

The Antarctic Circumpolar Current supports the ecological functioning of the Southern Ocean ecosystem. Its southern boundary provides highly productive foraging habitats for seabirds and other upper trophic predators in summer (Tynam 1998). The interaction of the ACC and the Prince Edward Islands plateau results in the modification of physical and biological processes downstream of the Island group (Pakhomov et al. 2000).

Dominating Fronts

The STC or STF is the most northerly and most prominent surface thermal front in the Southern Ocean (Lutjeharms and Valentine 1984). It exhibits strongest horizontal thermal and saline both at the sea surface and at depths below sea surface (Lutjeharms 1985). The front on average, lies at 41°S (Lutjeharms 1985) but it also experiences great latitudinal variability in its position directly south of the African continent (Lutjeharms and Valentine 1984). The south of Africa represents a zone of high dynamic variability characterised by shedding of eddies and rings (Lutjeharms 1985).

The Subantarctic Front (SAF) on average lies at about 45°S and has a latitudinal spread of about 2.5°C either side (Lutjeharms 1985). SAF lies at about 400 km north of the Antarctic Polar Front (APF) with a subsurface temperature gradient lying between 3°C and 5°C. Lutjeharms (1985) found that the SAF's latitudinal variability has no relation to its longitudinal position. It is postulated that the unstable meanders of the SAF and the interaction of meanders with bathymetry, influence the formation and propagation of cold core eddies (Morrow et al. 2004). Instability of meanders and bathymetry influence eddy spawning.

The Antarctic Polar Front is defined as the strong jet flowing within the eastward flowing Antarctic Circumpolar Current (ACC) (Moore et al. 1997). Its subsurface expression coincides with the northern limit of 2°C isotherm which forms part of the subsurface minimum (Lutjeharms and Emery 1984, Moore et al. 1997). The area between the SAF and APF is called the Antarctic Polar Front Zone (APFZ). APFZ is the zone located north of the APF and south of the SAF. Lutjeharms and Valentine (1984) found that the APF's surface expression is less distinct than its subsurface expression.

The mean latitudinal position of the APF was found to be 50°S (Lutjeharms and Valentine 1984). Its mean path and location are strongly influenced by bottom topography (Lutjeharms and Valentine 1984, Dong et al. 2006) but attains high temperature gradients in summer especially in the Atlantic and Indian Ocean. Due to other factors including but not limited to light limitation, the APF exhibits high nitrates values and low chlorophyll concentration at the

sea surface (Moore and Abbott 2002). High chlorophyll values could only be attained in December when it is a peak surface solar radiation period.

1.5 Study Area: Marion Island of the Prince Edward Island group

The Prince Edward Islands are located in the southern Indian Ocean and comprise two volcanic islands; Marion and Prince Edward Islands. Marion Island is the largest ($\sim 270 \text{ km}^2$) whereas the Prince Edward Island is only about 45 km^2 in extent (Lutjeharms 1985). These Islands lie directly in the path of the eastward-flowing Antarctic Circumpolar Current (ACC) within the Antarctic Polar Frontal Zone and are bordered in the north by the SAF and APF in the south (Lutjeharms 1985, Ansorge and Lutjeharms 2002). They lie east of the Southwest Indian Ridge (SWIR) which bisects the ocean between Africa and Antarctica.

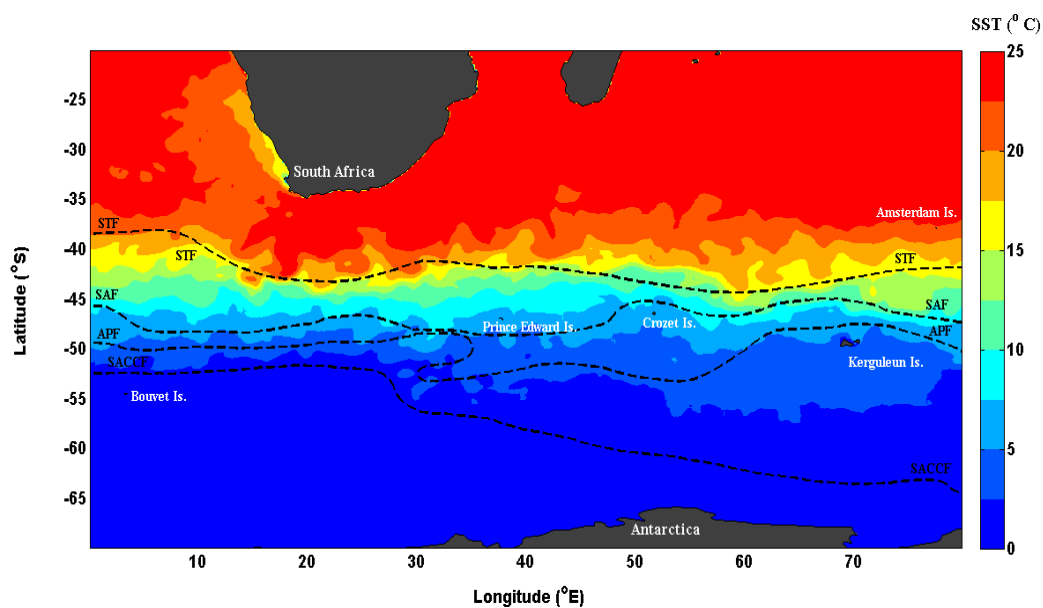


Figure 1. A geographical representation of the study area as indicated by SST overlaid by approximate positions of main frontal systems (Belkin and Gordon, 1996). Frontal systems are indicated by the white dashed line. STF = Subtropical front, SAF = Sub Antarctic front, APF = Antarctic Polar front and SACCF = Southern Antarctic Circumpolar Current Front.

Mesoscale variability around these islands is due to the obstruction of the eastward-flowing ACC. The oceanic environment around these islands is dominated by mesoscale activities (Ansorge and Lutjeharms 2005). The immediate vicinity of these islands experiences a climate controlled by oceans. One can divide their oceanic environment into 3 sub-regions; the distinct upstream (in the east), inter-island and the downstream region (in the west).

Increased environmental variability in the vicinity of the Prince Edward Islands can be ascribed to the latitudinal position of the SAF (Duncombe Rae 1989b). SAF is the main physical ocean feature that affect the Prince Edward Islands (Perissinotto et al. 2000) whilst the APF crosses at a distance south of the islands. The latitudinal shift of the SAF and APF creates cross frontal mixing and exchange of waters which enhance high mesoscale variability. This enhanced mesoscale variability results in the formation of mesoscale eddies and meanders in the downstream region of the Islands.

The enhanced mesoscale variability in the immediate environment of the Prince Edward Islands provides foraging habitats for marine top predators such as seabirds (Ryan and Bester 2008). Creation of mesoscale eddies in the upstream of the Islands play a crucial role in sustenance of upper trophic predators. Anson and Lutjeharms (2002) postulated that these eddies have their origin in the SWIR. The ecosystem of the Prince Edward Islands (Grindley 1978) provides foraging and breeding habitats to vast populations of marine organisms and a great diversity of seabirds (Ryan and Bester 2008).

Dietary studies (Cooper and Klages 1995, Phillips et al. 2005) conducted on the two *Phoebetria* albatrosses, have shown that the *P. palpebrata* concentrates its foraging effort to the south of the APF whereas the *P. fusca* forages north of the Prince Edward Islands. In this study, however, we aim to investigate foraging patterns of the two *Phoebetria* albatrosses in relation to mesoscale features.

1.6 Study Outline

Dynamic mesoscale features south of the African continent (Abrams 1985, Nel et al. 2001) provide suitable conditions for prey aggregations and thus sustain top predators that depend upon these prey. These features are known to localise primary productivity (Abram 1985). Top predators such as grey-headed albatross (*Thalassarche chrysostoma*) have demonstrated the ability to exploit such mesoscale features (Nel et al. 2001).

This study recognises that an understanding of spatial and temporal aspects of these mesoscale features is equally important in assessing their role in creating foraging habitats for upper trophic predators such as albatrosses. It is thus the objective of this study to investigate the interactions of the tracked *Phoebetria* albatrosses with these features.

This study builds from the work done by Nel et al, (2001) but with the focus on the foraging movements of tracked *Phoebetria* albatrosses in relation to mesoscale features. This study recognises the need to investigate smaller scale hydrographic such as frontal systems (Duncombe Rae 1989a, Hyrenbach et al, 2006) when assessing and quantifying seabird interactions with oceanographic features. Frontal systems are equally important for the enhancement of local primary productivity and thus, providing foraging habitats (Pocklington 1979, Abrams 1985) for seabirds.

The study uses tracking data of tracked *Phoebetria fusca and palpebrata* from Marion Island of the Prince Edward Island group to investigate their movements in relation to mesoscale features south of the African continent. It is the object of this study to explain the association of these seabirds in terms of space and time. The study will make use of tracking data coupled with remotely sensed data to characterise areas targeted by tracked *Phoebetria* albatrosses. Tracking data provide valuable information of the at-sea distribution of these birds which would otherwise not be possible due to the remote nature of the targeted areas of the oceans.

Chapter 2. Data and methods

2.1 Satellite tracked seabird data

Position-determining units

Platform terminal transmitters (PTTs) from Sirtrack Limited (New Zealand) were attached to 20 adult seabirds (Table 1). The birds were tagged and satellite-tracked between April 2008 and 2011 in different breeding areas on Marion Island, of the Prince Edward Islands. All the devices were attached to birds' feathers using waterproof, cloth-backed Tesa tape. The devices weighed approximately 20 g which is less than $\gg 10\%$ of their mean weight (BirdLife International 2014). Eleven of the twenty tracked seabirds were *P. fusca* which were all tagged during the chick-provisioning stage which runs from 1 January – 31 May (ACAP 2010). Seven of the nine *P. palpebrata* were tracked during the chick-provisioning which runs from 1 January – 15 June whereas two were tracked during the incubating period running from 16 October – 31 December (ACAP 2010).

The devices recorded a number of parameters but for the purpose of this study, we only extracted the following variables; absolute location (latitude and longitudes), flight speed (km/hr) and total distance travelled (calculated using the equidistant azimuthal (South Pole)). Seabirds flying at ≤ 10 km/hr were assumed to be foraging in this study (Sagar and Weimerskirch 1996). We have grouped and analysed both foraging and travelling locations separately in accordance to the three annual breeding stages which include incubating, chick-provisioning and nest-construction periods.

2.2 Longline fisheries data

We used longline fishing effort data from the Indian Ocean Tuna Commission (IOTC) data (<http://www.iotc.org/data/datasets>). The fishing effort was reported by a 5°x 5° grid cell. We used estimated positions of where longline fishing activities were conducted within the Indian Ocean Tuna Commission (IOTC) Convention area for both South African and Japanese fleet.

2.3 Remotely-sensed parameters

Sea Surface Temperature (SST)

The study used daily sea surface temperatures from Advanced Very High Resolution Radiometers (AVHRR) and Advanced Microwave Scanning Radiometer (AMSR) prepared and analysed by NOAA- NCDC National Climatic Data Center. AVHRR + AMSR uses AVHRR and additional data from Advanced Microwave Scanning Radiometer - on the Earth Observing System (AMSR-E), which is available from 2002 to 2011. AVHRR has the longest record (from 1981 to the present) of sea surface temperature measurements from a single sensor design. Advanced Very High Resolution Radiometers can make observations at relatively high resolution but cannot see through clouds.

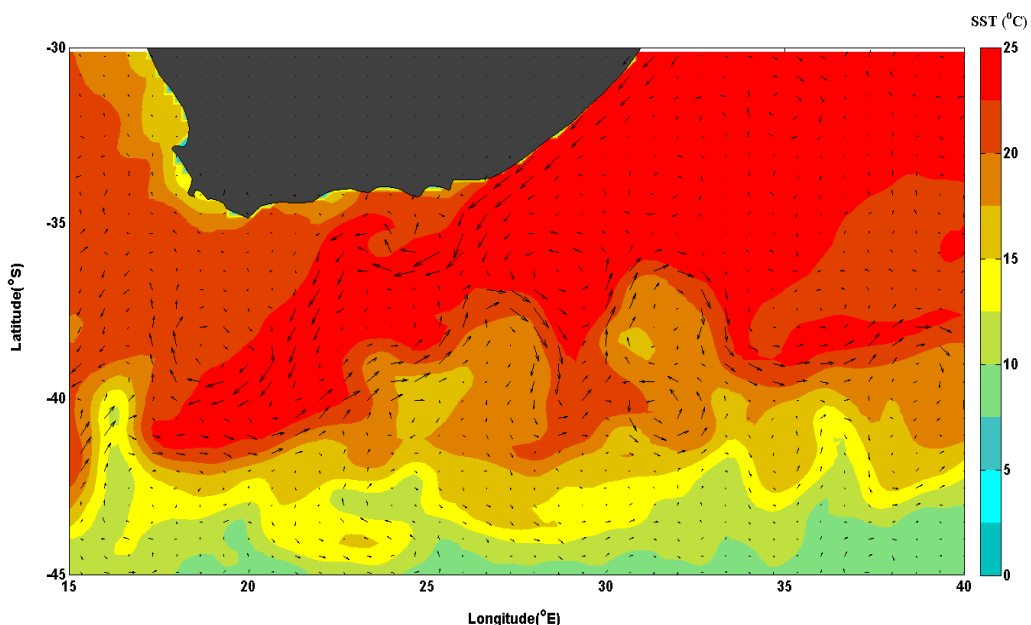


Figure 2. An example of AVHRR + AMSR sea surface temperature ($^{\circ}\text{C}$) overlaid by geostrophic velocity vectors (cm/s) to represent the flow of an Agulhas Current during April 2009.

Microwave instruments like AMSR-E can measure sea surface temperatures in most weather conditions (except heavy rain) but not adjacent to land. Thus, in AVHRR+AMSR, observations near land come from AVHRR, while AMSR-E has superior spatial coverage over the open ocean. The combined use of infrared and microwave in cloud-free regions reduces systematic biases due to the independent error characteristics of the two sensors. After AMSR-E lost its full functionality in Oct 2011, AVHRR+AMSR production ended. Sea surface temperature

products have a spatial grid of degree and temporal resolution of 1 day. The AVHRR + AMSR data were extracted from (<http://www.ncdc.noaa.gov/oa/climate/research/sst/griddata.php>)

Sea Surface Height (SSH)

The study used data analysed in relation to delayed-weekly satellite-derived AVISO Sea Surface Height data produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>). Ssalto/Duacs system processes data from all altimeter missions (Saral, Cryosat-2, Jason- 1 & 2, T/P, Envisat, GFO, ERS-1 & 2 and Geosat) to provide a consistent and homogeneous catalogue of products for varied applications, both near real time as well as offline studies.

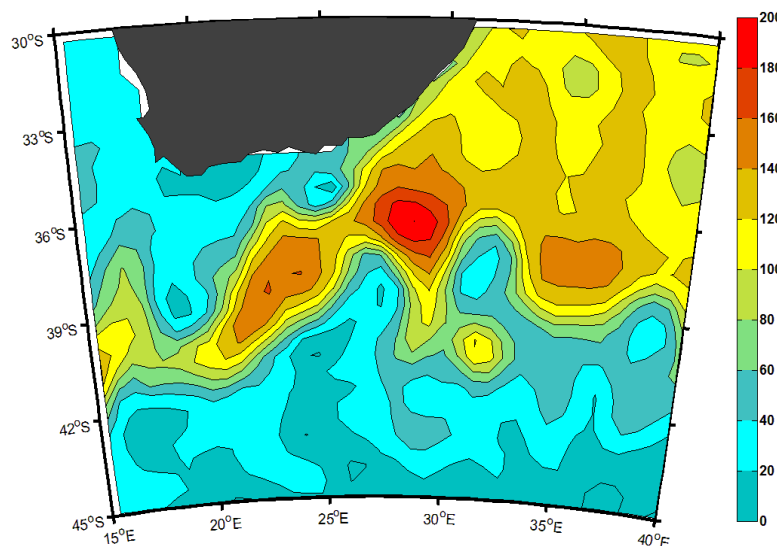


Figure 3. An example of delayed –weekly Sea Surface Height in cm computed from along-track Absolute Dynamic Topography (ADT) during April 2009.

Along-track Absolute Dynamic Topography (ADT) products generated by SSALTO/DUACS are obtained as follows: $ADT = \text{Sea Level Anomaly (SLA)} + \text{Mean Dynamic Topography (MDT)}$. The Mean Dynamic Topography is the part of Mean Sea Surface Height due to permanent currents, thus Mean Dynamic Topography corresponds to the Mean Sea Surface Height minus Geoid. Absolute Dynamic Topography products have been computed with consistent Sea Level Anomaly and Mean Dynamic Topography fields.

Absolute Geostrophic velocities

The study used delayed-weekly absolute geostrophic velocities data products produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>). These gridded products have a spatial resolution of $1/4^\circ \times 1/4^\circ$. Absolute geostrophic velocities were computed from absolute dynamic topography.

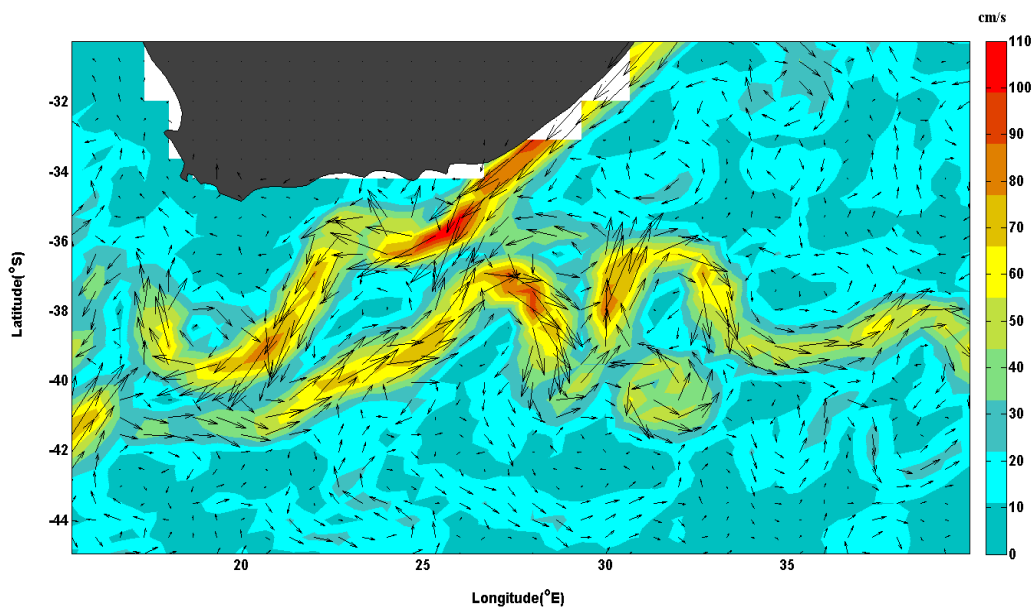


Figure 4. An example of absolute geostrophic velocity vectors in cm/s computed to trace the Agulhas Current off the east and south-eastern coast of South Africa during April 2009.

Eddy Kinetic Energy

Eddy Kinetic Energy (EKE) was computed from absolute geostrophic currents produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>). Mesoscale studies using altimetry allows us a global observation of eddy variability. Absolute geostrophic currents come as both zonal (U) and meridian (V) geostrophic current components. The following formula was employed to compute Eddy Kinetic Energy:

$$\text{EKE} = 0.5 \times (\text{U}^2 + \text{V}^2) \quad \text{measured cm}^2/\text{s}^2.$$

An example of a computed Eddy Kinetic Energy is shown below:

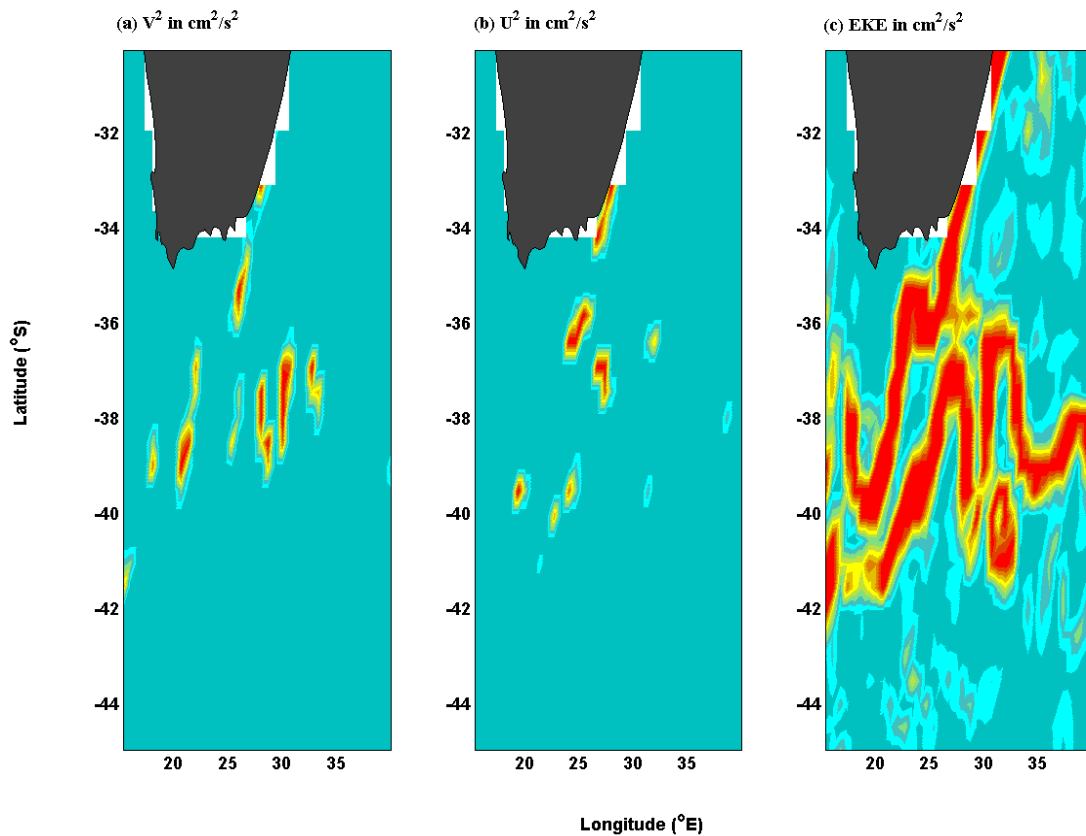


Figure 5. Left – Meridian geostrophic velocity - V , middle – Zonal geostrophic velocity - U , right – EKE.

Ocean bathymetry

This study uses a 2-minute Gridded Global Relief Data (ETOPO2v2) derived from 1978 satellite radar altimetry of the sea surface, to estimate ocean bathymetry. The ETOPO2v2 is produced and processed by David T. Sandwell (Scripps Institution of Oceanography) and Walter H.F Smith (Geosciences Laboratory, NOAA). ETOPO2v2 eliminates a 1-cell westward bias that was present in ETOPO2 which was produced in 2001. ETOPO2v2 data is available on the Smith & Sandwell data and can be downloaded from the following website (<http://www.ngdc.noaa.gov/mgg/global/etopo2.html>).

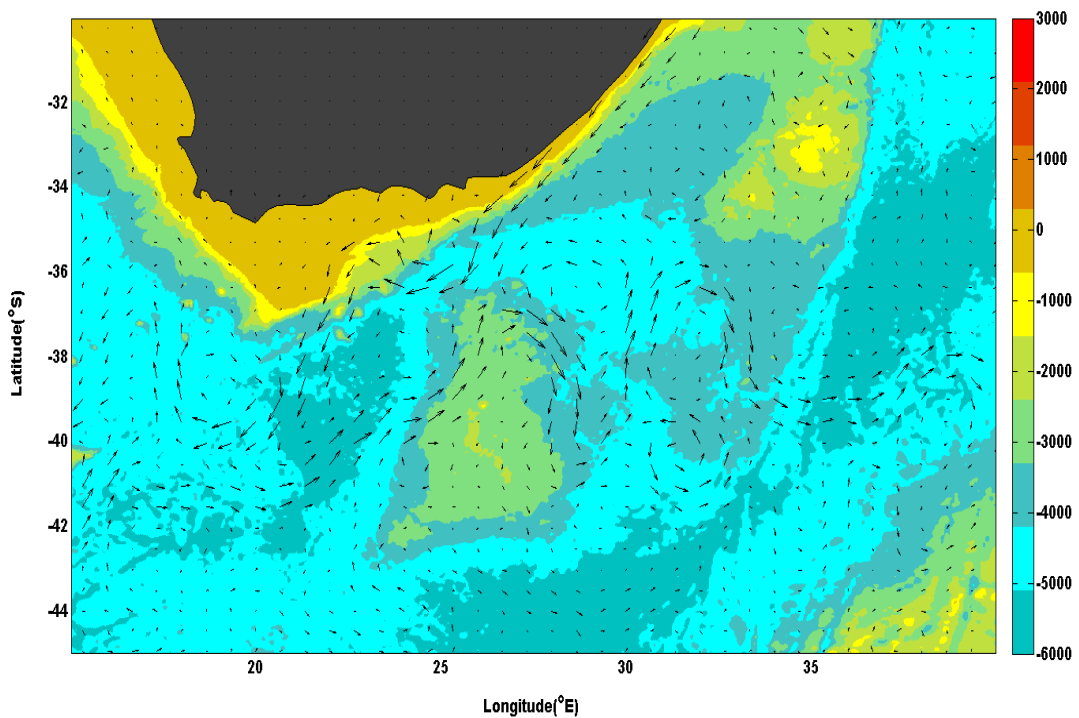


Figure 6. An example of a bathymetric product in metres (m) overlaid by absolute geostrophic velocities (cm/s) off the South African coastline during April 2009.

2.4 Data analysis

Tracking data, fisheries data and remotely-sensed data

MATLAB R2011a was employed to analyse and visualise the seabird tracking data in relation to remotely-sensed data. Fisheries was also analysed using MATLAB. 2D plots were produced using MATLAB to demonstrate spatial-temporal distribution of seabird species in response to environmental variables such as Sea Surface Temperature, Sea Surface Height, Eddy Kinetic Energy (EKE), Net primary productivity and ocean bathymetry. MATLAB R2011a was employed to produce 2D overlays of seabird movement over each environmental variable, to demonstrate how these seabird distributions vary in space and time, in relation to environmental parameters listed above. I used MATLAB R2011a to derive and compute seasonal variation in the movements of seabird in relation to sea surface environmental variables.

Statistical Modelling.

Differences in the foraging and at-sea distribution patterns of the two *Phoebetria* albatrosses were analysed using the R Language (R Core (2014)). To understand the complex oceanographic surface, General Linear Models (GLMs) were employed using GLM function in R (ver. 3.1.1) to fit a series of linear models to the data.

The objective of this exercise was to model the response of both foraging and travelling locations of the two tracked *Phoebetria* albatrosses to environmental and ecological variables. The response variable for these models was bird species whereas explanatory variables included Sea Surface Temperature, flight speed, distance traversed, activity and annual breeding stage. Seabird data were prepared and filtered for unreliable values before they were used to fit this model.

In order to evaluate the effect of SST and other ecological and environmental variables which included flight speed, distance traversed, annual breeding stages and activity (i.e. whether the bird was foraging or travelling) on the species distribution, a Generalised Linear Model with a negative binomial regression was employed. In this analysis, distance travelled is defined as departure from the island to the next return to the breeding island. In this analysis, we have grouped and analysed foraging ($<< 10$ km/hr) and travelling ($>> 10$ km/hr) locations separately. A negative binomial regression was selected over the other due to the way these data were collected. Negative binomial models assume the conditional means aren't equal to the conditional variances. Such inequality is captured by estimating a dispersion parameter that is held constant in a Poisson model. The negative binomial regression employed was able to cater for the heterogeneous nature of the open ocean environment.

A model which incorporated both the sympatric *Phoebetria* albatrosses was employed to test the significance of each explanatory variables on these species distribution. A best-fit model based on the lowest Akaike Information Criterion (AIC) and other statistical test such as Hosmer and Lemeshow Goodness of Fit test (Hosmer and Lemeshow, 2000) was chosen amongst the rest. AIC estimates the quality of each model. Further models which treated each species individually but tested under the same explanatory variables were conducted and had undergone similar goodness of Fit tests and were examined for ecological realism of the fitted

response variable – species. Inferences on these models were based on the theory of maximum likelihood estimation, and likelihood ratio tests and analysis of deviance (ANOVA) of the standard regression model (McCullagh and Nelder 1989).

Chapter 3. Results

Tracking data

The devices provided invaluable data for determination of the movements of far-ranging seabirds such as *Phoebetria albatrosses*. For the purpose of this study, the following parameters were extracted from tracking devices; Absolute location (latitude & longitudes), flight speed (km/hr) and total distance travelled. Data were subjected to rigorous filtering to remove unreliable data points. Tracked individuals flying at speeds equal or less than 10 km/hr were assumed to be foraging (Weimerskirch et al 2002).

The 11 devices attached on tracked *P. fusca* transmitted for 392 days whilst 9 devices attached to *P. palpebrata* transmitted for 940 days. Eleven of these tracked *P. fusca* were adults and were tagged at the breeding colony during chick-provisioning period which runs from 1 January – 31 May (ACAP 2010). Seven of the nine tracked *P. palpebrata* were tagged at the breeding colony during chick-provisioning period which runs from 1 January – 15 June whereas the other 2 were tagged during incubating period running from 16 October – 31 December (Table 2).

Table 2. Total number of transmission days of tracking devices attached to each individual bird during each annual stage.

Year	Period	Species	Annual stage	Numbers	Sex confirmed	Transmission
2008	1 Jan – 15 June	<i>P. fusca</i>	Chick-provisioning	2	Yes	67
	1 Jan – 31 May	<i>P. palpebrata</i>	Chick-provisioning	2	No	380
	16 Sep – 31 Dec	<i>P. fusca</i>	Incubating	0	0	0
	16 Oct – 31 Dec	<i>P. palpebrata</i>	Incubating	2	Yes	380
2009	1 Jan – 15 June	<i>P. fusca</i>	Chick-provisioning	7	No	175
	1 Jan – 31 May	<i>P. palpebrata</i>	Chick-provisioning	3	No	78
2011	1 Jan – 15 June	<i>P. fusca</i>	Chick-provisioning	2	No	150
	1 Jan – 31 May	<i>P. palpebrata</i>	Chick-provisioning	2	No	112

The results demonstrate that tracked individuals of *P. fusca* flew relatively faster than those of tracked *P. palpebrata* (Table. 3). Tracked *P. fusca* attained an average flight speed of 27.53

± 21.61 km/hr whereas tracked *P. palpebrata* attained flight speed of 14.41 ± 8.52 km/hr (Table. 3).

Table 3. Descriptive statistics of parameters recorded from tracking devices.

Species	Parameter	Mean + Std Deviation	Std Error	Max
<i>P. fusca</i>	Flight Speed (km/hr)	27.53 \pm 21.61	0.33	90.13
	Distance (km)	124,983.12 \pm 20,690.41	3200	1,854935.03
	Flight Angle (°)	73.92 \pm 65.71	0.99	180
<i>P. palpebrata</i>	Flight Speed (km/hr)	14.41 \pm 8.52	0.31	90.22
	Distance (km)	60,413.21 \pm 19,120.41	2700	5,961693.01
	Flight Angle (°)	51.82 \pm 44.8	0.94	180

No austral summer (December – February) records for tracked *P. fusca* were received for this analysis, due to limited battery life of the devices. Devices on tracked *P. fusca* transmitted for the following number of days: 213 (austral autumn: March - May), 157 (austral winter: June – August) and 22 (austral spring: September – November). Data for the tracked *P. palpebrata* were received for the following days of each season; 180 (austral summer), 370 (austral autumn), 220 (austral winter) and 180 days (austral spring). These results demonstrate that tracked *P. palpebrata* transmitted 40 % more days than tracked *P. fusca* (Table 2). Tracked individuals of *P. palpebrata* traversed more distance than tracked *P. fusca* (Table 3).

Tracked *P. palpebrata* traversed a maximum distance of approximately 6×10^6 km which is approximately 30 % more than the distance traversed by tracked *P. fusca*. These results are consistent with those found by Phillip et al. 2005, that *P. palpebrata* extends its foraging activities to shelf and shelf-slope areas along the Scotia Sea in oceanic waters.

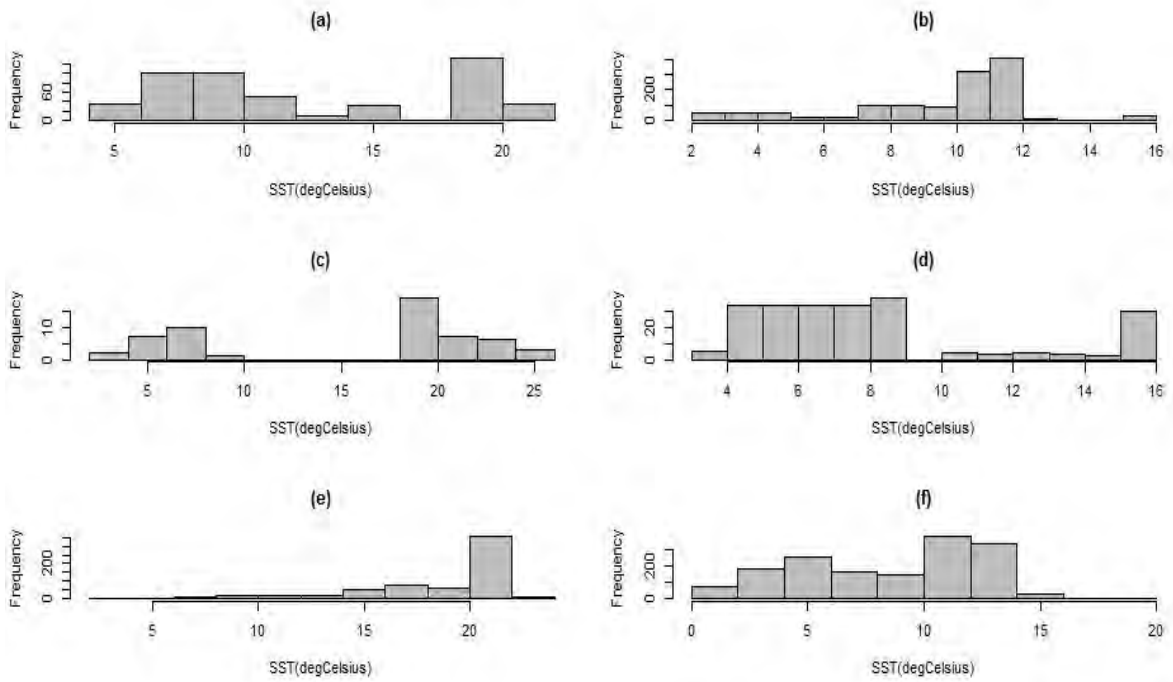


Figure 7a. Number of birds at different foraging (< 10 km/hr) locations expressed by sea surface temperature (SST) during each annual breeding stage. Left panel – *P. fusca* (a) Nest construction, (c) Incubating, and (e) Chick-provisioning period. Right panel – *P. palpebrata* (b) Nest construction, (d) Incubating, (f) Chick-provisioning period.

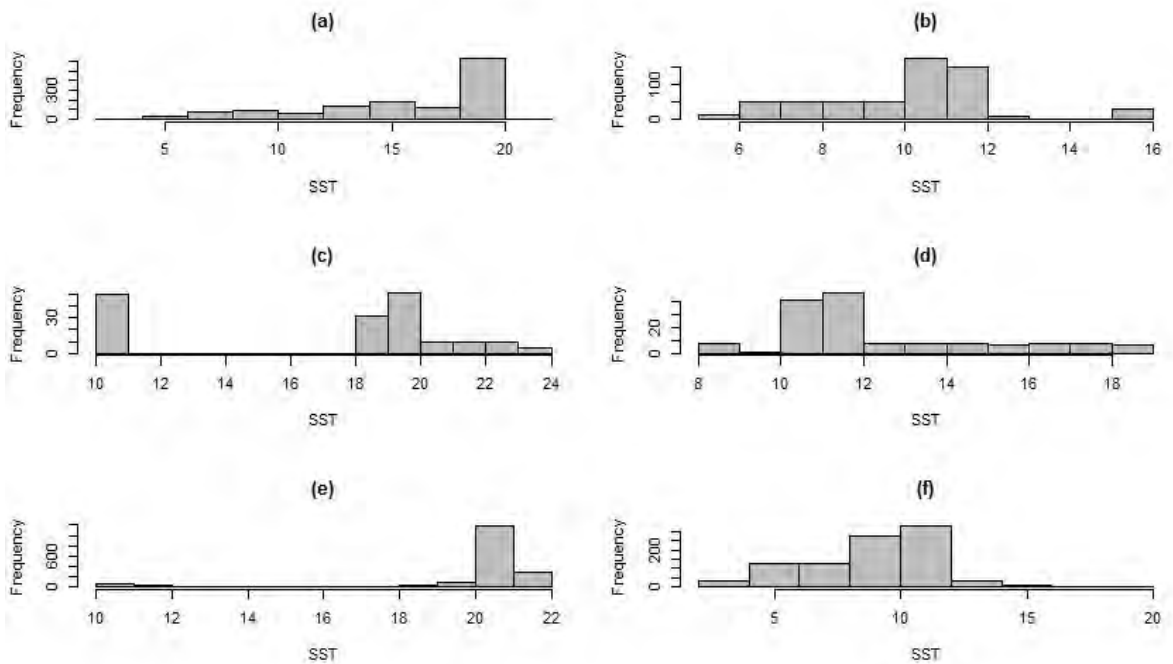


Figure 7b. Number of birds at different travelling (>> 10 km/hr) locations expressed by sea surface temperature (SST) during each annual breeding stage. Left panel – *P. fusca* (a) Nest construction, (c) Incubating, and (e) Chick-provisioning period. Right panel – *P. palpebrata* (b) Nest construction, (d) Incubating, (f) Chick-provisioning period

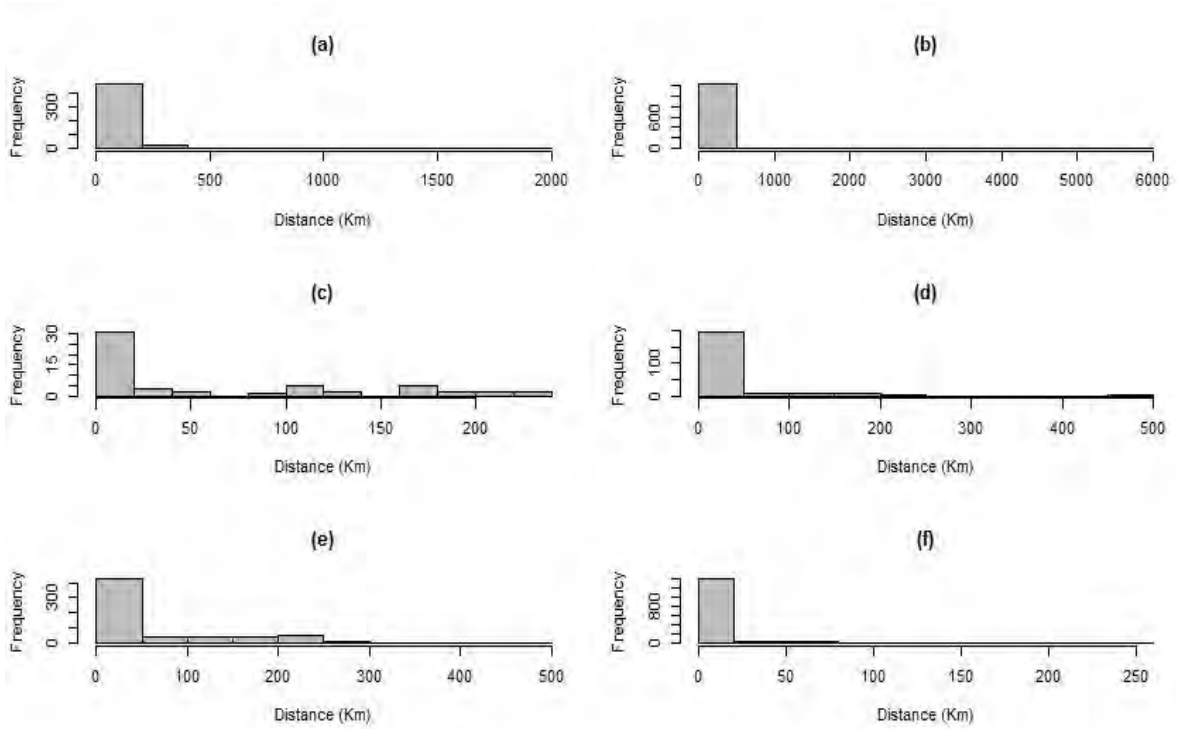


Figure 7c. Distance travelled during foraging trips (<< 10 km/hr) with respect to each annual breeding stage. Left panel – *P. fusca* (a) Nest construction, (c) Incubating, and (e) Chick-provisioning period. Right panel – *P. palpebrata* (b) Nest construction, (d) Incubating, (f) Chick-provisioning period

Tracked seabird movements in relation to oceanographic features

Tracked individuals of *P. fusca* concentrated their foraging activities in dynamic regions of high mesoscale variability such as regions around the Agulhas Return Current, fronts and mesoscale eddies. The results demonstrate that tracked individuals of *P. fusca* foraged in the mesoscale features to the north of the islands created as a result of Agulhas Return Current and their foraging activities were distributed along the trajectory of this current (Fig. 8a). These foraging activities were concentrated within the Subtropical Convergence (STC) in waters $>> 15\text{ }^{\circ}\text{C}$ and characterised by high mesoscale variability (mean EKE $>> 1600\text{ cm}^2/\text{s}^2$, Fig. 8a & 9a).

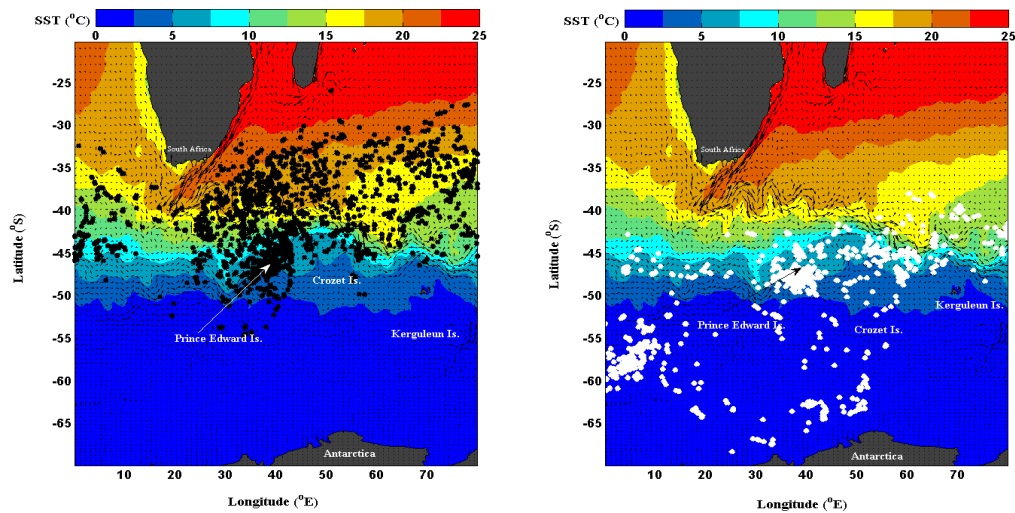


Figure 8a. Monthly SSTs delineating foraging locations south of the African continent during the nest construction period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

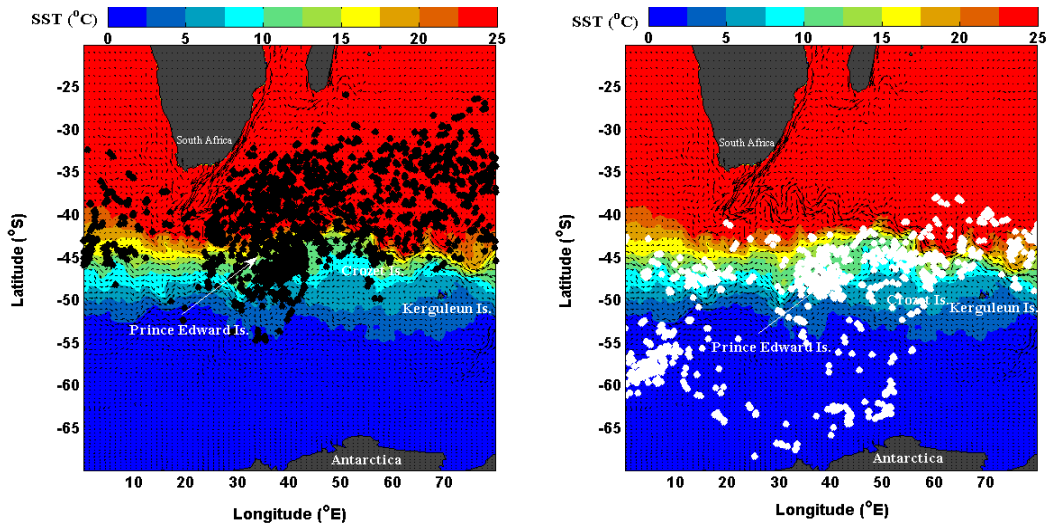


Figure 8b. Monthly SSTs delineating foraging locations south of the African continent during the incubating period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

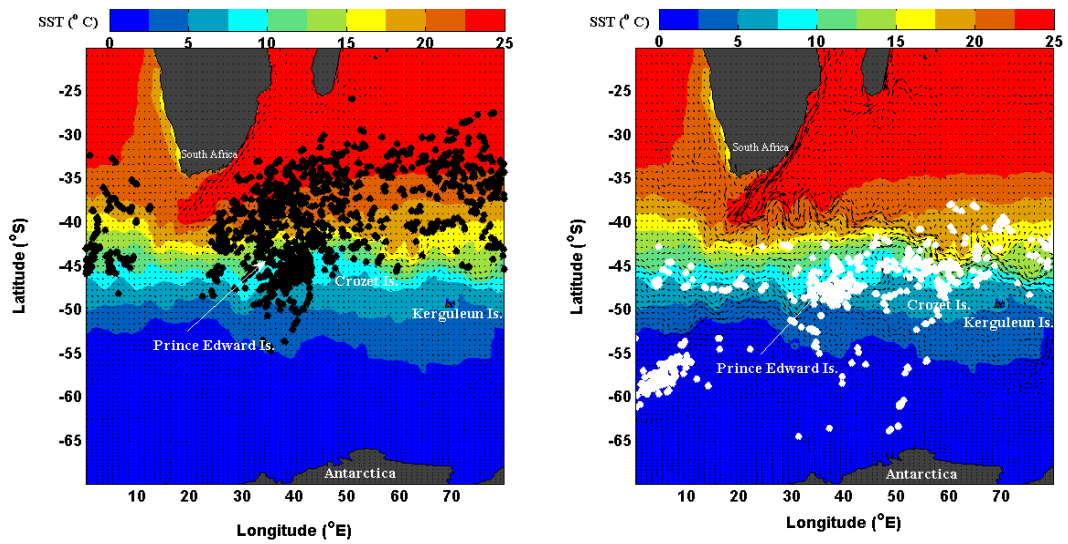


Figure 8c. Monthly SSTs delineating foraging locations south of the African continent during the chick-provisioning period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

Tracked individuals of *P. fusca* demonstrated a positive association of mesoscale features created as a result of Agulhas Return Current as expressed by sea surface temperatures (Fig. 8a & 12a). Interestingly, these foraging activities were concentrated to the north at distances >> 500 km away from breeding islands during nest construction period.

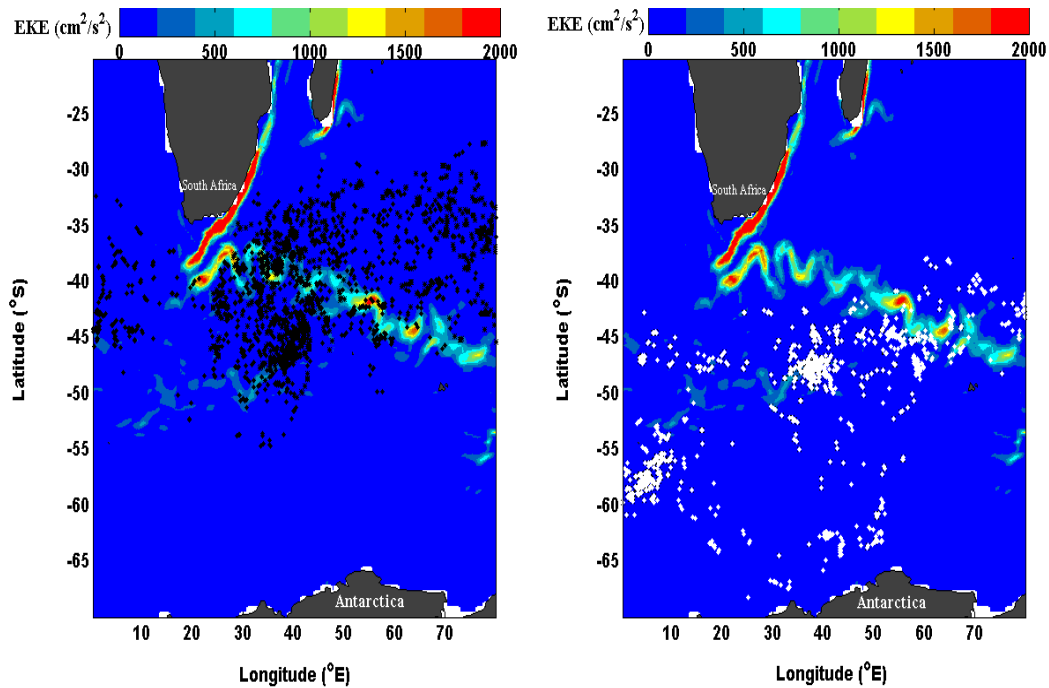


Figure 9a. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability south of the African continent during the nest construction period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

Moreover, foraging activities of tracked *P. fusca* were also conducted within this frontal region were concentrated in waters between 10 – 15 °C to the north of the breeding islands (Fig. 15). Altimetry results demonstrate that tracked individuals of *P. fusca* preferred the section to the south of the front characterised by low mesoscale variability (mean EKE << 1600 cm^2/s^2 , Fig. 15).

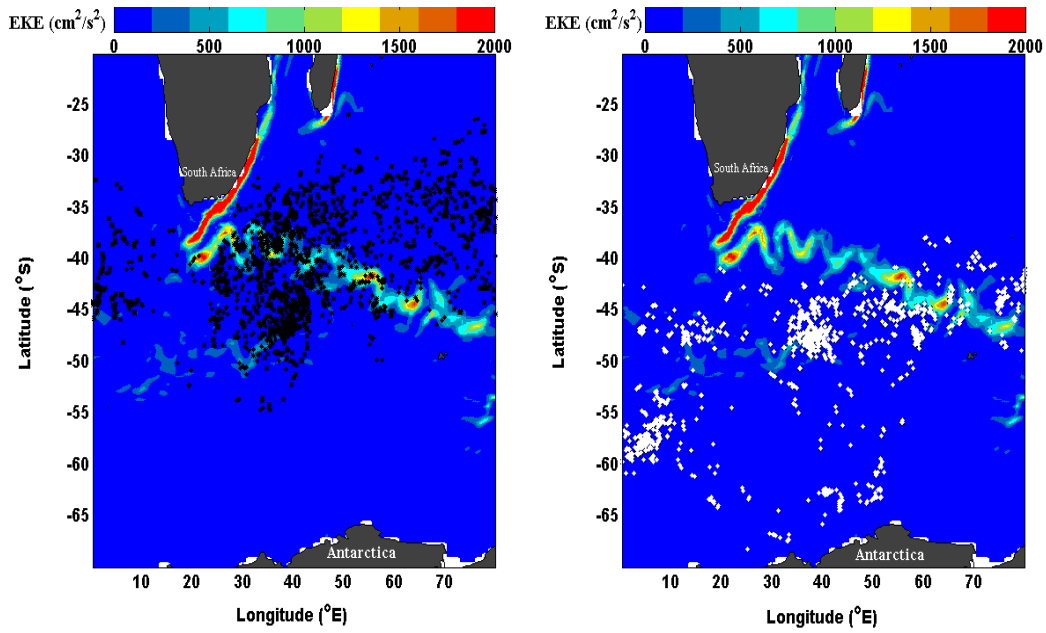


Figure 9b. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability south of the African continent during the incubating period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

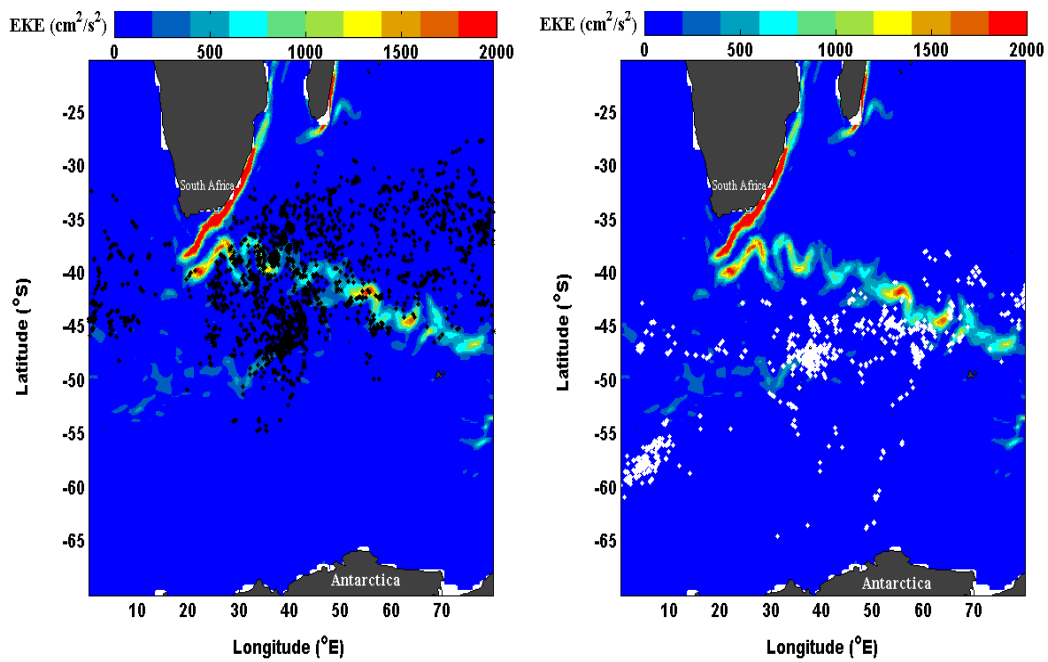


Figure 9c. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability south of the African continent during chick-provisioning period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

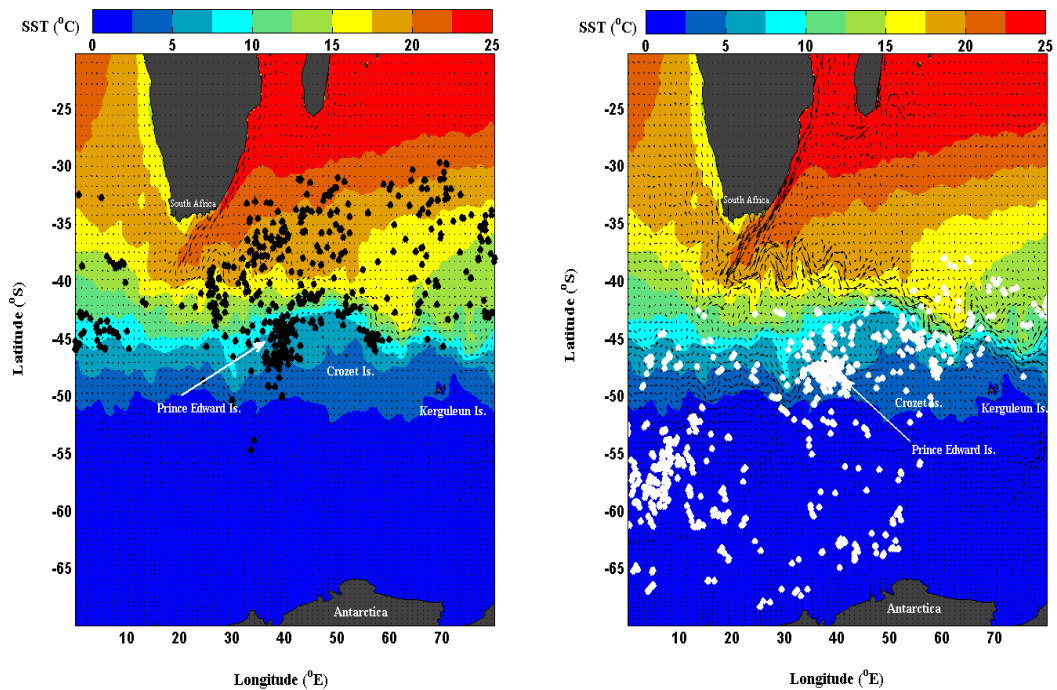


Figure 10a. Monthly SSTs delineating travelling locations south of the African continent during the nest construction period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

Contrastingly, tracked individuals of *P. palpebrata* concentrated foraged further to the south of the Agulhas Return Current in waters $\ll 10^\circ\text{C}$ (Fig. 8a, 10a & 11a). They foraged in regions of low mesoscale variability (mean EKE $\ll 800\text{ cm}^2/\text{s}^2$, Fig. 9 & 11b). The altimetry results demonstrate that tracked *P. palpebrata* did not show any positive association with mesoscale features as expressed by sea surface temperatures in the frontal region to the south of the Agulhas Return Current (Fig. 15).

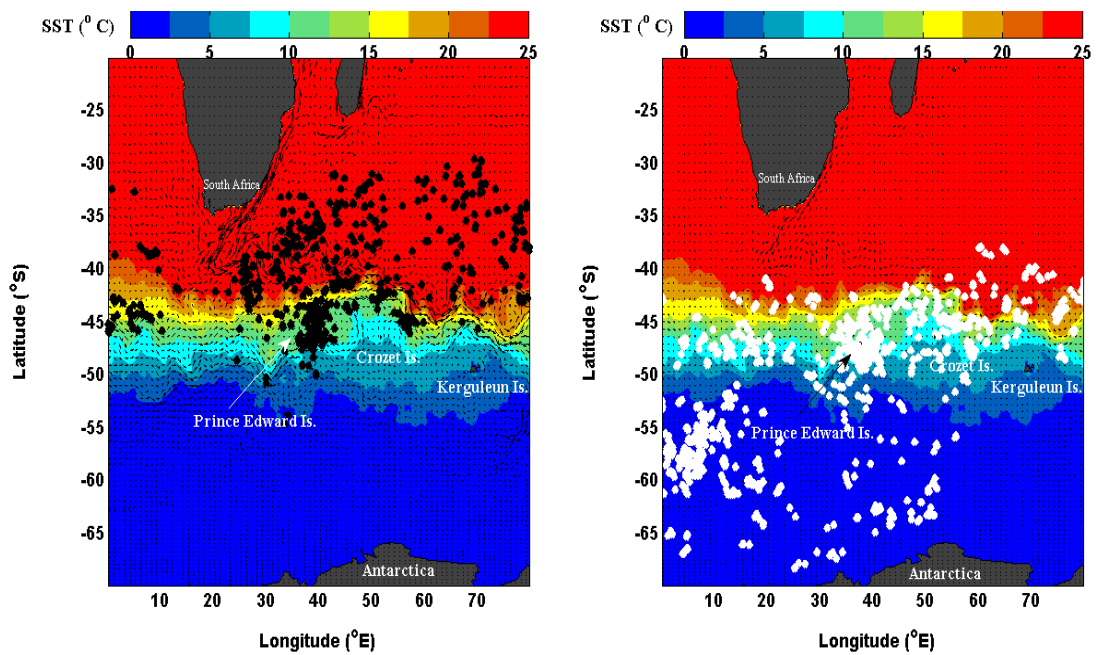


Figure 10b. Monthly SSTs delineating travelling locations south of the African continent during the incubating period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

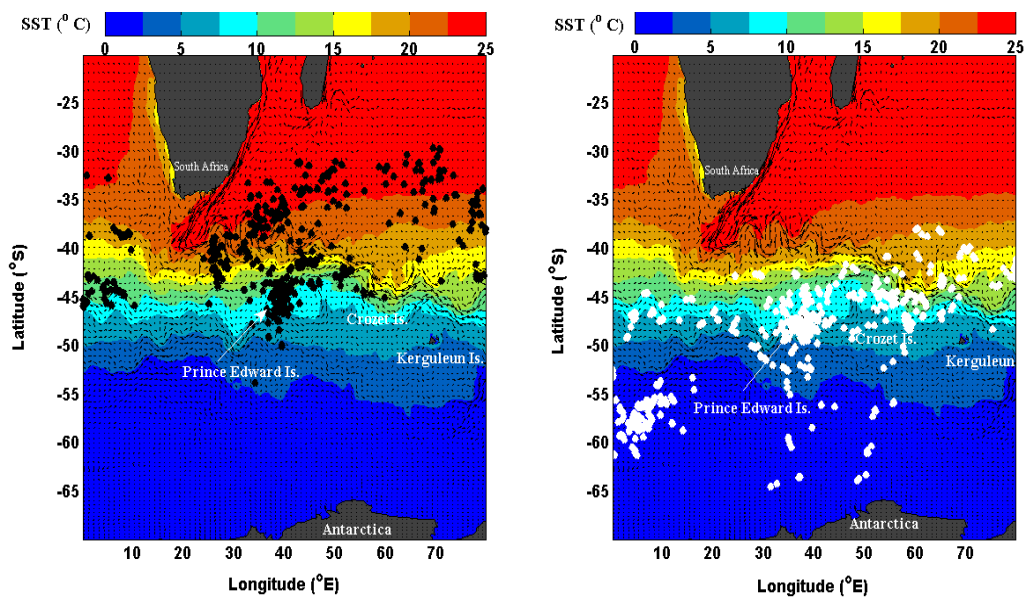


Figure 10c. Monthly SSTs delineating travelling locations south of the African continent during the incubating period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

Ecological response of the two *Phoebetria* albatrosses to seasonal variability

Phoebetria albatrosses are biennial breeders on subantarctic islands and they forage in Antarctic waters (ACAP 2010). They are known to optimise foraging efficiency by concentrating effort on specific foraging zones in order to minimise time spent commuting (Weimerskirch 1986). This foraging strategy ensures they minimise effort and maximise return. Seasonality plays a role in the ecology of the two tracked *Phoebetria* albatrosses. They conduct their breeding activities in accordance with seasonality. *Phoebetria fusca* conducts its incubating period from 16 September – 31 December and subsequently, conduct chick-provisioning activities from 1 January – 31 May. Nest construction is done from 1 June – 15 September (ACAP 2010). Similarly, *Phoebetria palpebrata* conducts its incubating period from 16 October – 31 December and subsequently, conducts its chick-provisioning season from 1 January – 15 June. Nest construction activities are conducted from 16 June – 15 October (ACAP 2010).

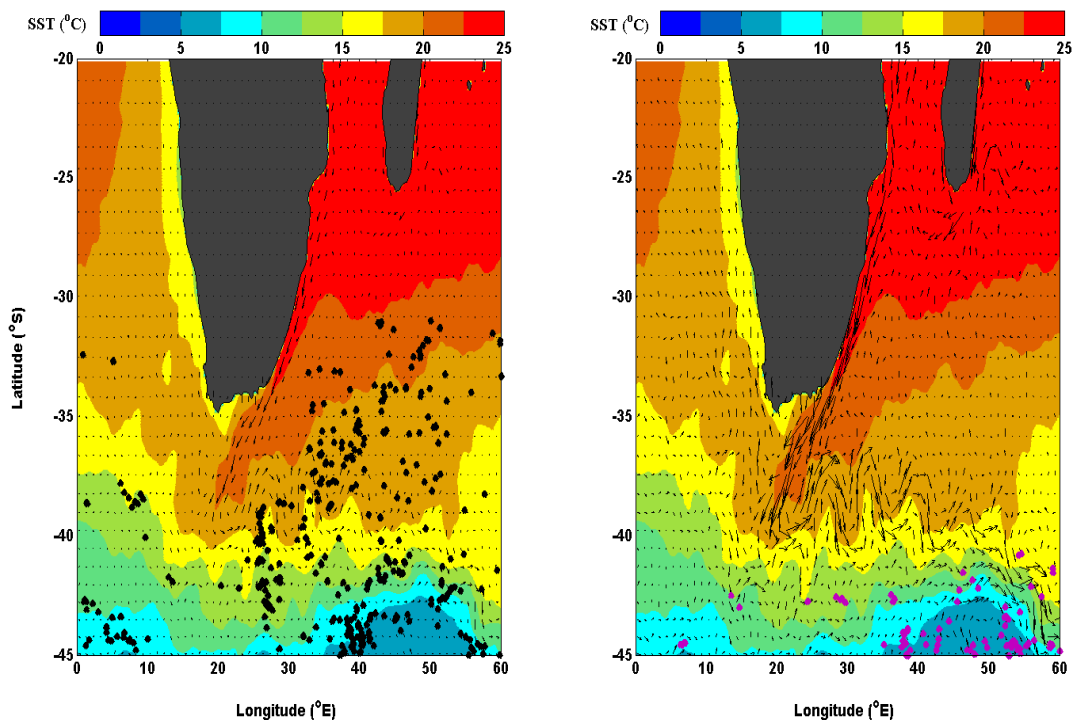


Figure 11a. Monthly SSTs delineating foraging locations within the current south of the African continent during nest construction period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (pink dots).

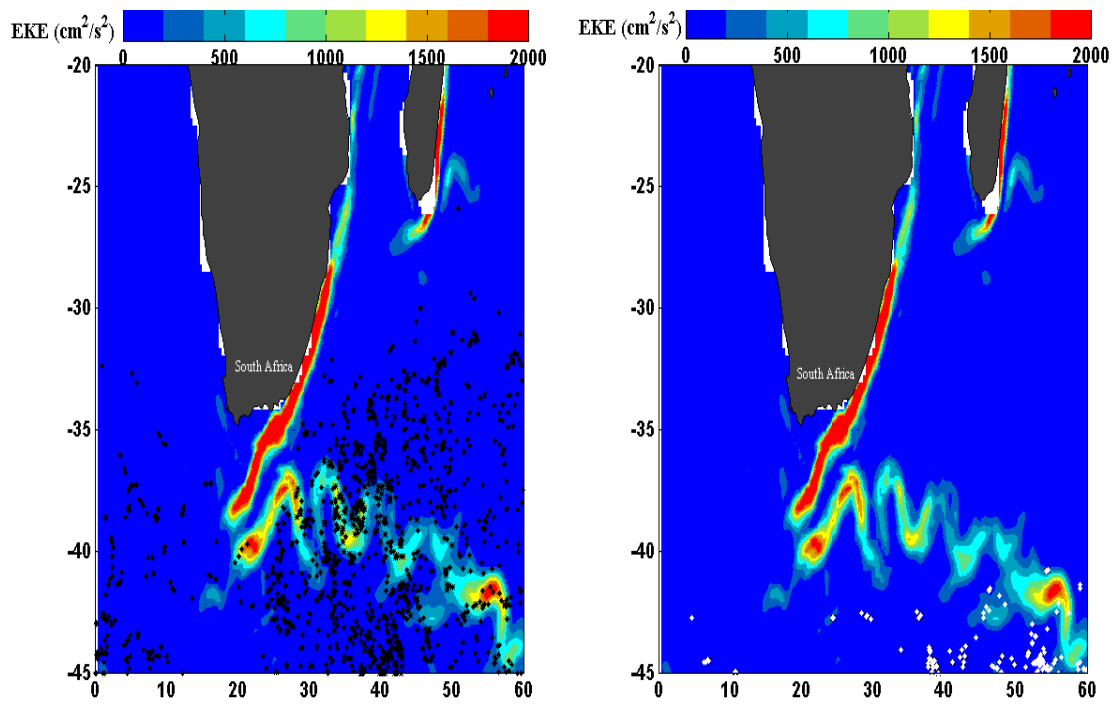


Figure 11b. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability within the current south of the African continent during nest construction period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

During foraging trips

The results demonstrate that during nest construction period, tracked individuals of *P. fusca* travelled a few 100 km up to 2000 km (Fig. 7c) reaching foraging grounds with water temperatures ranging from 5 – 20 °C (Fig. 7a & 8a). Contrastingly, tracked individuals of *P. palpebrata* travelled a few 100 km up to 6000 km (Fig. 7c) reaching foraging grounds characterised by water temperatures ranging from 8 – 12 °C during the same period (Fig. 7a & 8a).

During incubating period, tracked *P. fusca* travelled a few 10 km up to 200 km (Fig. 7c) reaching foraging grounds with water temperatures ranging from 20 - 25 °C (Fig. 7a & 8b). Contrastingly, tracked *P. palpebrata* travelled a few 10 km up to 500 km (Fig 7c) reaching foraging localities with water temperatures ranging from 4 – 9 °C (Fig. 7a & 8b) during the same period. With the APF located just < 400 km from Marion Island (Fig. 1), the results demonstrate that tracked *P. palpebrata* could easily forage up to the south of the APF.

During chick-provisioning period, tracked individuals of *P. fusca* travelled a few 10 km up to 250 km (Fig. 7c) reaching foraging grounds with water temperatures ranging from 15 – 20 °C (Fig 7a & 8c) to the north of breeding islands in the frontal region as well as in the Agulhas Return Current region. They foraged in dynamic regions which were characterised by high mesoscale variability ($EKE \gg 1400 \text{ cm}^2/\text{s}^2$, Fig. 9c) and are known for their high predictability of prey availability (Schneider 1990). Similarly, tracked *P. palpebrata* travelled a few 10 km up to 250 km (Fig. 7c) to water temperatures ranging from 0 – 5 °C (Fig. 7a & 8c) to the south of breeding islands in regions of less mesoscale variability ($EKE \ll 800 \text{ cm}^2/\text{s}^2$, Fig. 9c).

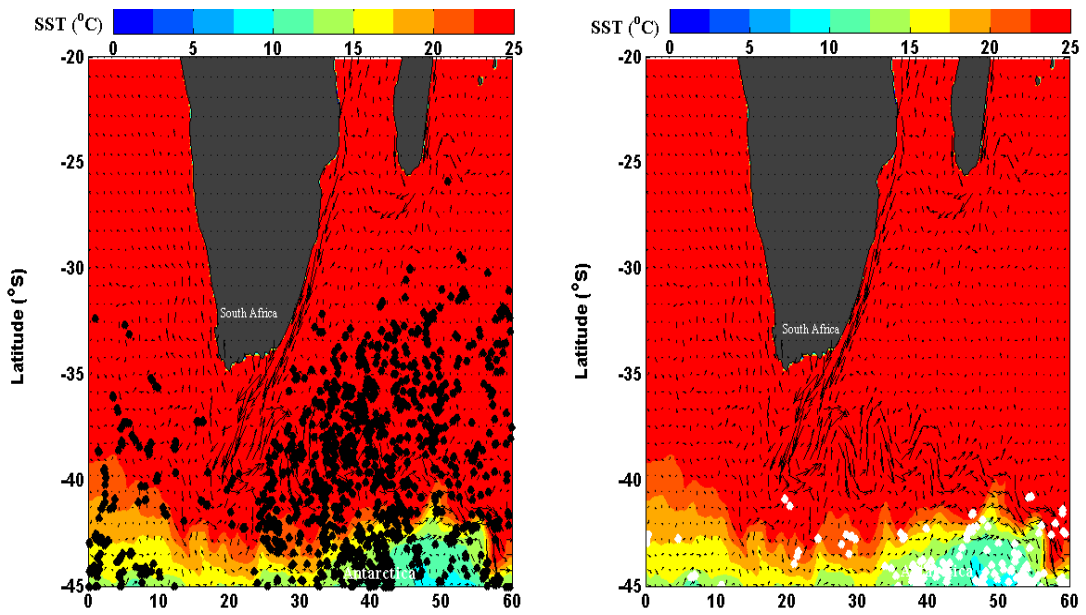


Figure 12a. Monthly SSTs delineating foraging locations within the current south of the African continent during incubating period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (pink dots).

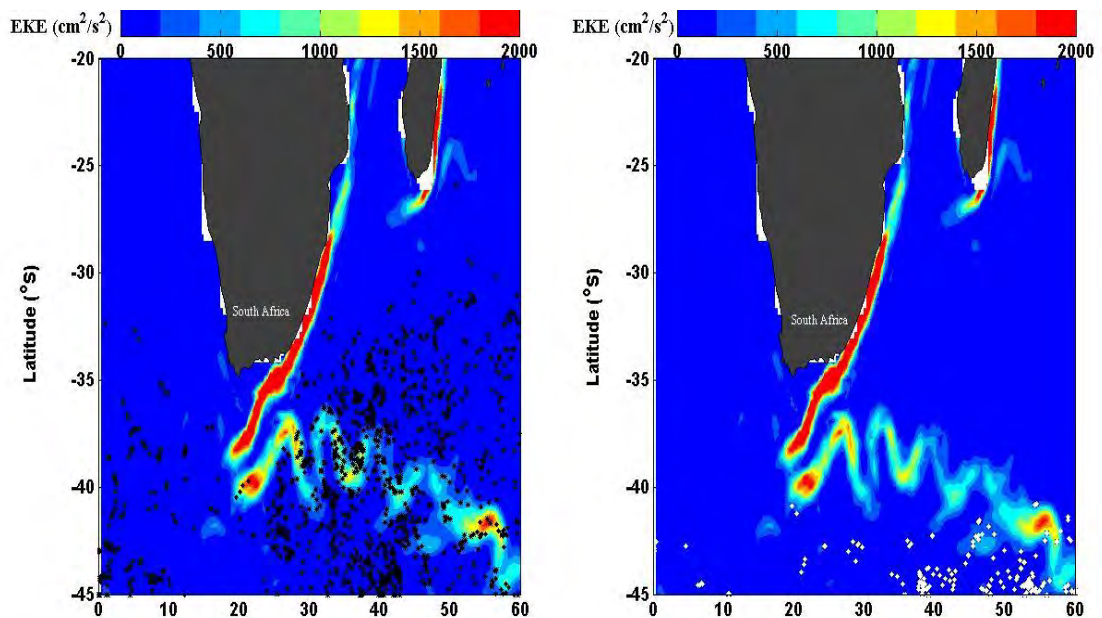


Figure 12b. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability within the current south of the African continent during incubating period of the two sympatric *Phoebastria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

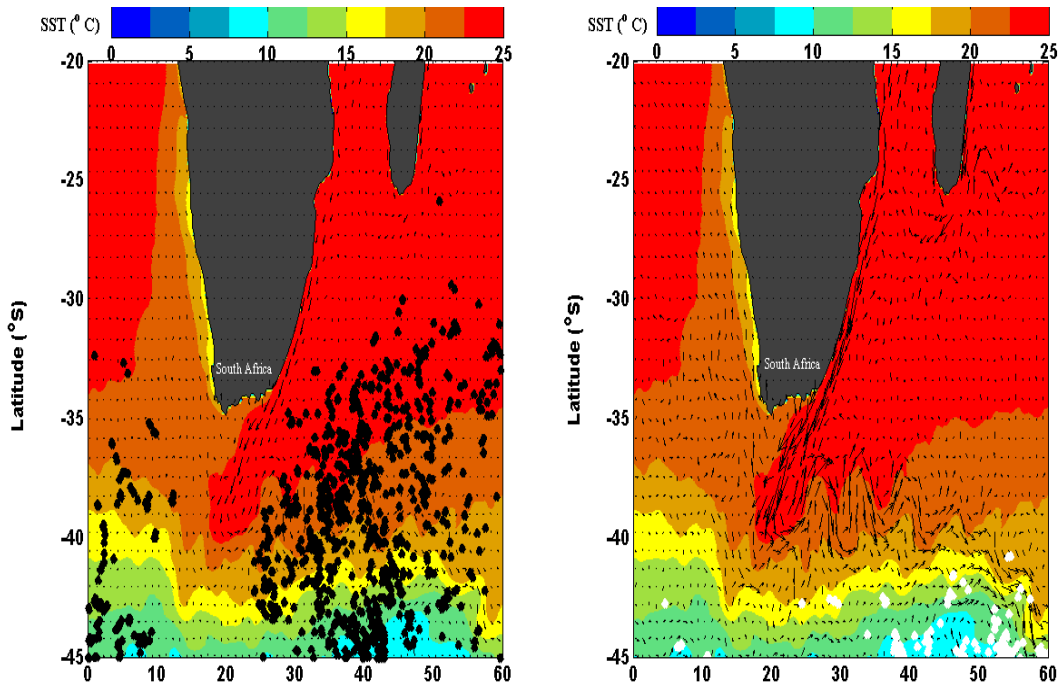


Figure 13a. Monthly SSTs delineating foraging locations within the current south of the African continent during chick-provisioning period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (pink dots).

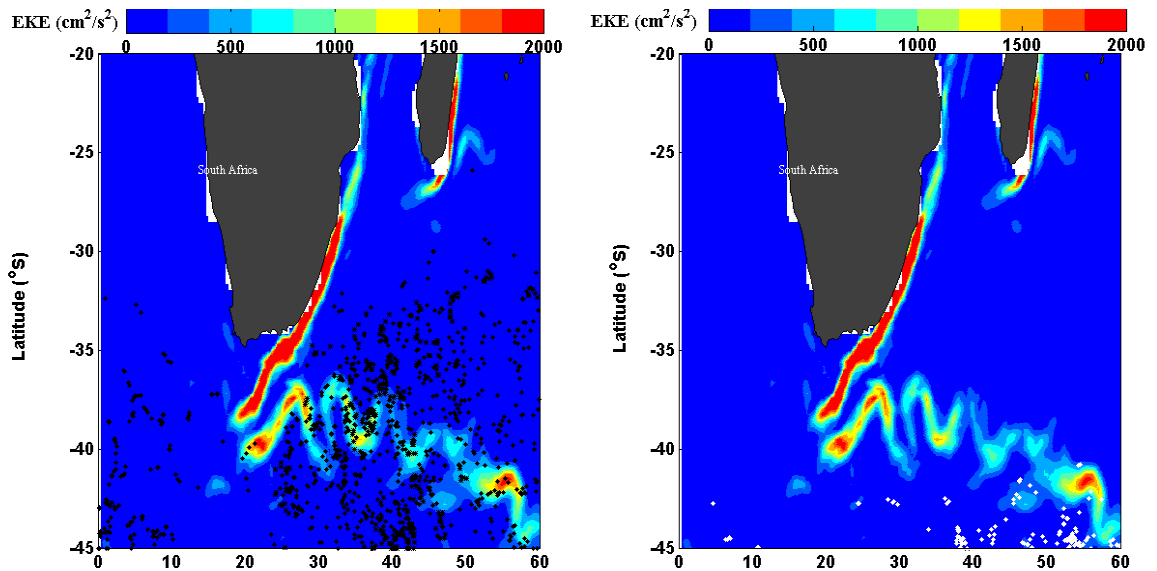


Figure 13b. Mean Eddy Kinetic Energy (cm^2/s^2) delineating foraging areas of mesoscale variability within the current south of the African continent during chick-provisioning period of the two sympatric *Phoebetria* albatrosses, respectively. Left panel – *P. fusca* (black dots) and Right panel – *P. palpebrata* (white dots).

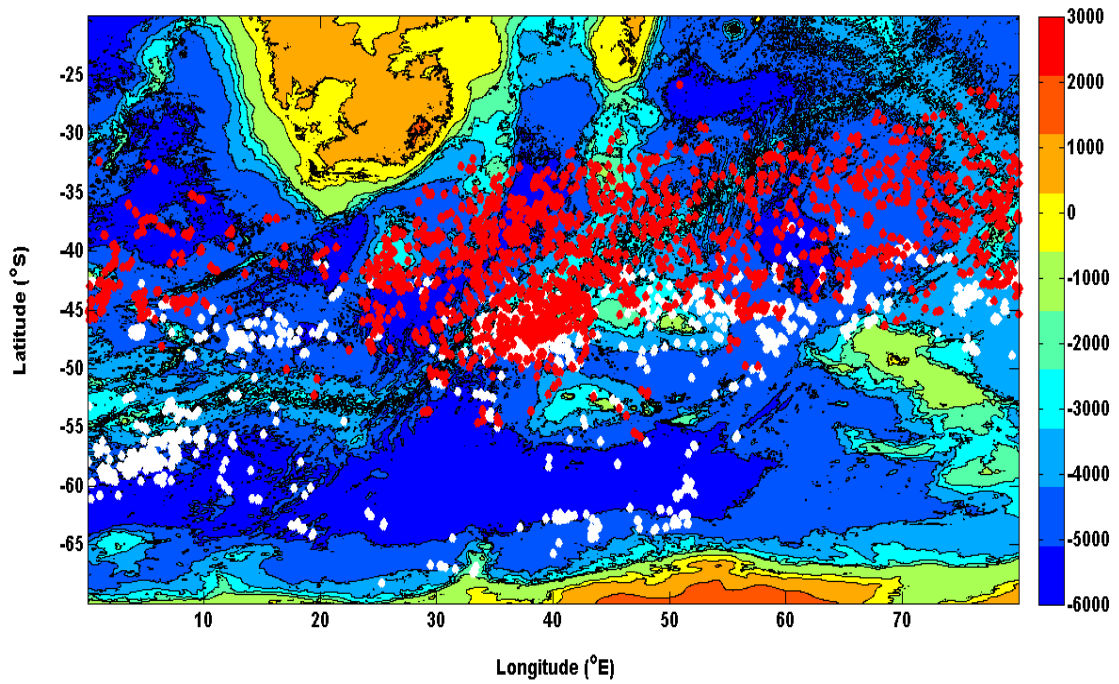


Figure 14a. At-sea distribution during foraging trips ($\ll 10 \text{ km/hr}$) of the two *Phoebastria* albatrosses in relation to bathymetry (ocean depths in metres). Tracked *individuals* of *P. fusca* (represented by red dots) and *palpebrata* (represented by white dots).

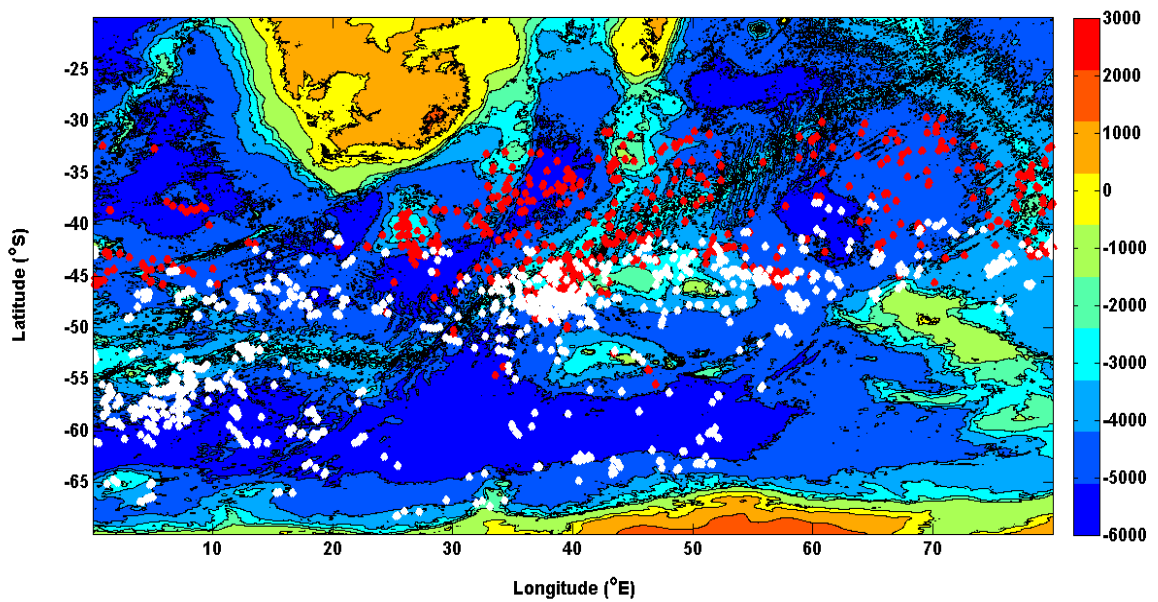


Figure 14b. At-sea distribution during traveling trips ($> 10 \text{ km/hr}$) of the two *Phoebastria* albatrosses in relation to bathymetry (ocean depths in metres). Tracked *individuals* of *P. fusca* (represented by red dots) and *palpebrata* (represented by white dots).

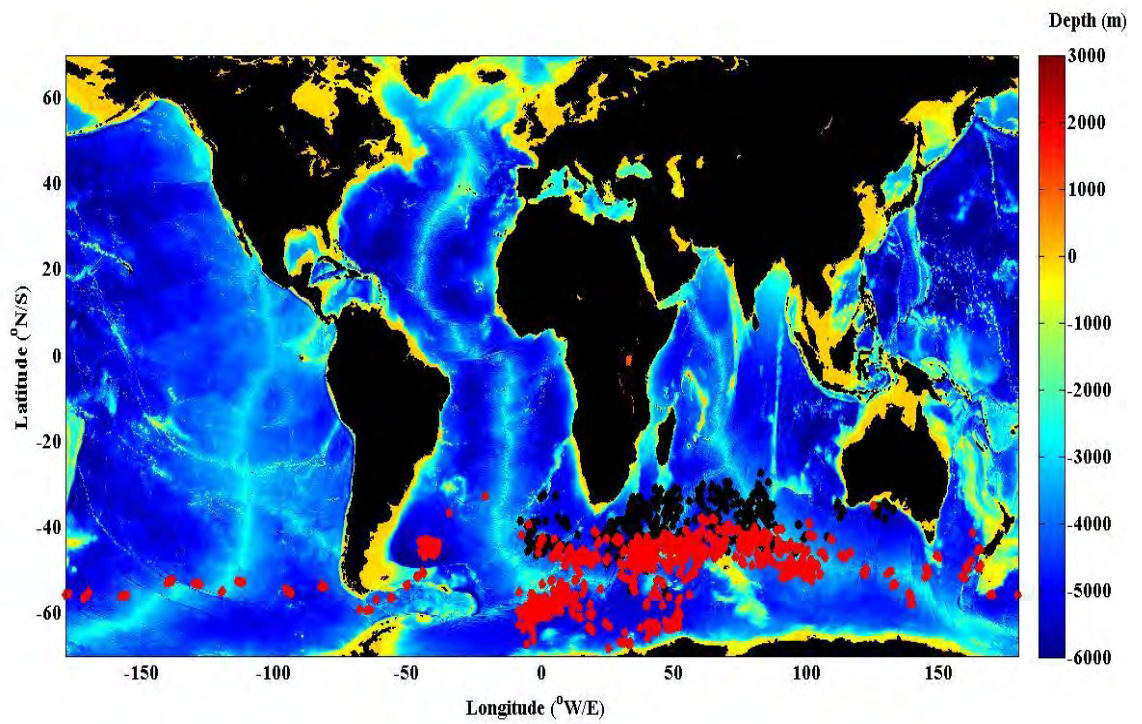


Figure 14c. At-sea distribution of the two *Phoebetria* albatrosses in relation to bathymetry (ocean depths in metres). Tracked *individuals* of *P. fusca* (represented by black dots) and *palpebrata* (represented by red dots).

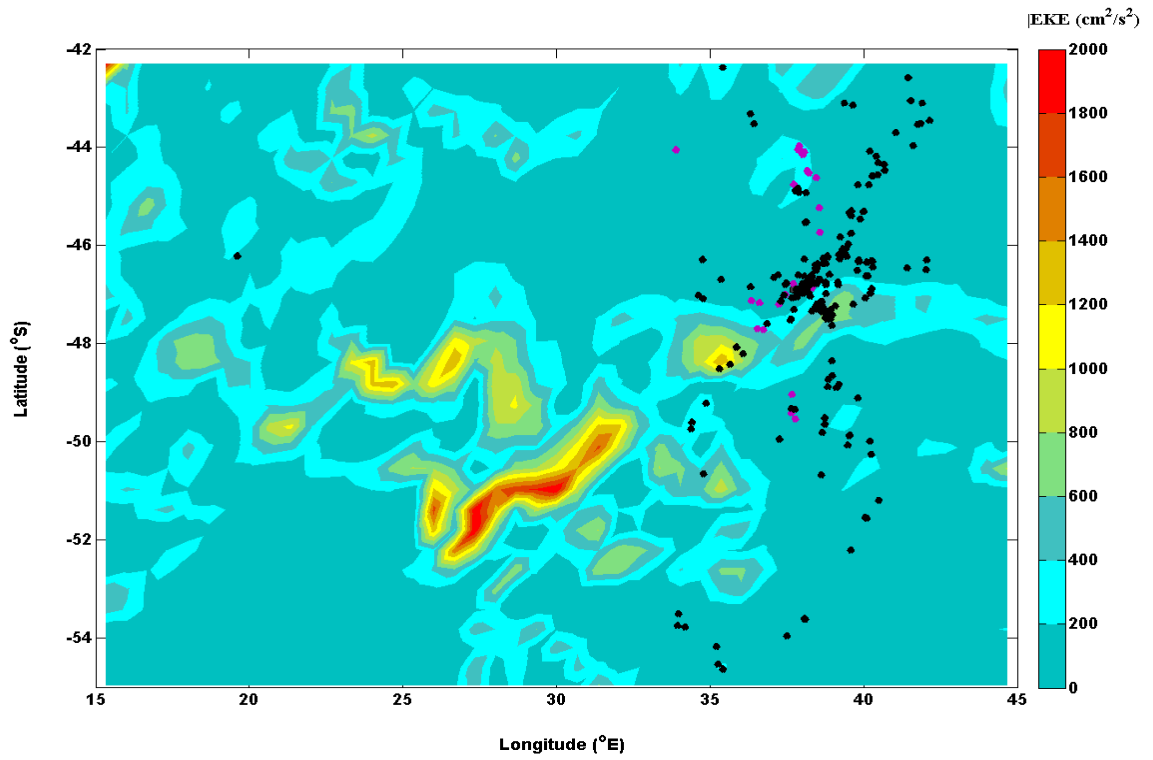


Figure 15. Mean Eddy Kinetic Energy (cm^2/s^2) delineating areas of mesoscale variability within the frontal region exploited tracked individuals of *Phoebastria albatrosses* south of the African continent during chick-provisioning stage. Black and pink dots represent tracked *P. fusca* and *palpebrata*, respectively.

During travelling trips

Tracked individuals of *P. fusca* conducted their traveling trips over high seas in the Sub-Tropical Convergence Zone of the South Indian Ocean (Fig 14b-c). Some individuals travelled across the dynamic Agulhas Return Current (Fig. 12a – b). The results demonstrate that during energy-demanding periods such as chick-provisioning, tracked individuals flew over relatively warmer waters 20 – 22 °C to the north of breeding islands in areas of high mesoscale variability (Fig. 7b, 10a – c).

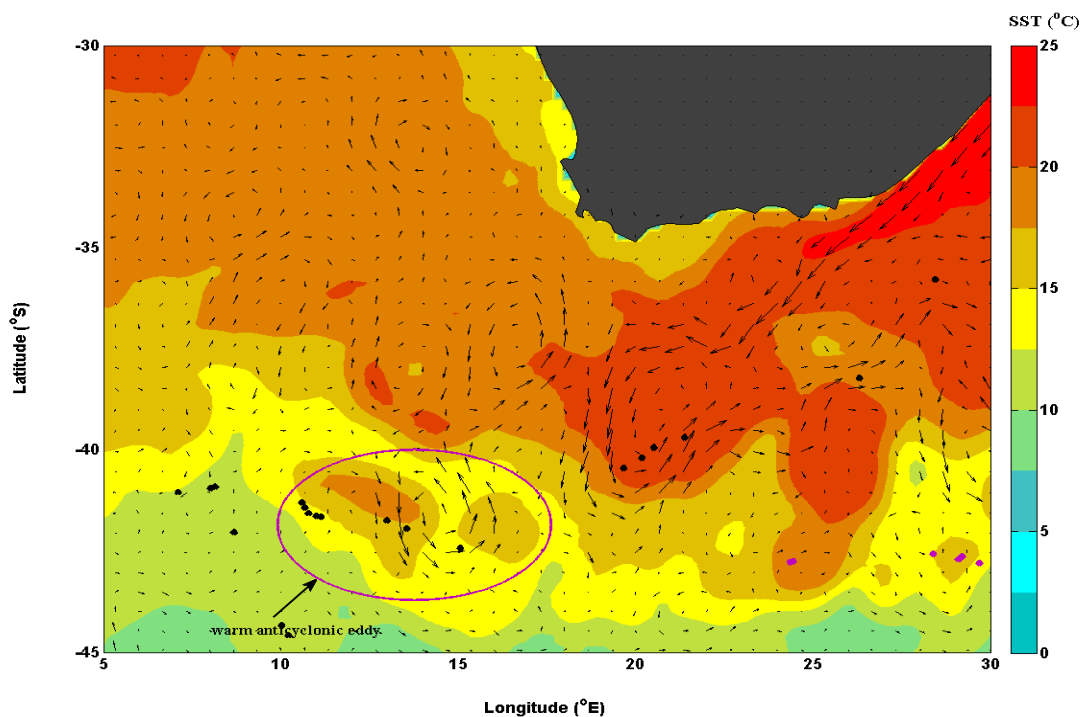


Figure 16. Monthly mean sea surface temperatures demonstrating interaction of tracked individuals of *P. fusca* with warm anticyclonic eddies during May 2011. Geostrophic velocities are represented by black arrows whereas black and pink dots represent tracked *P. fusca* and *palpebrata*, respectively.

Contrastingly, tracked individuals of *P. palpebrata* travelled over cold high seas in the south Indian and Atlantic Oceans (Fig. 14b-c). Some individuals travelled as far south as the Antarctic continent as well as some cold waters near the Bouvet Island $<< 10$ °C (Fig. 7b, 10 a-c). Moreover, the results demonstrate that during energy-demanding periods such chick-provisioning, some individuals travelled to the south and southwest of the breeding islands in waters between 5 – 10 °C. During incubating period, tracked individuals travelled to the

cold waters of the Antarctic indicating that these individuals could afford to travel that far south – as they had only themselves to feed.

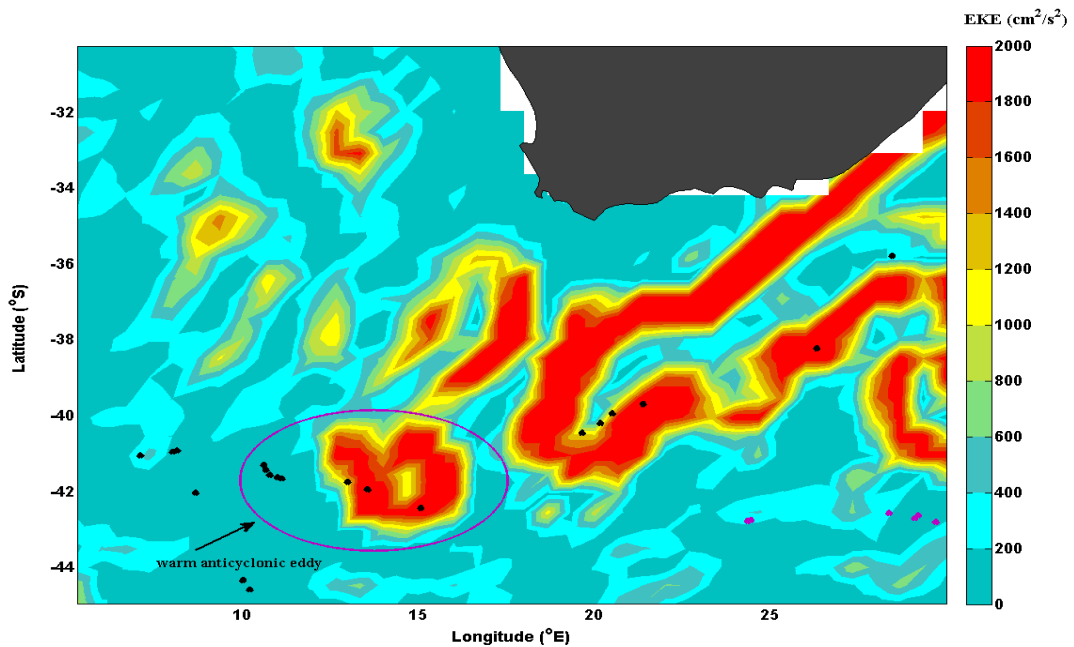


Figure 17. Mean Eddy Kinetic Energy (cm^2/s^2) indicating regions of mesoscale variability off the south of the continent during May 2011. Black and pink dots represent tracked *P. fusca* and *palpebrata*, respectively.

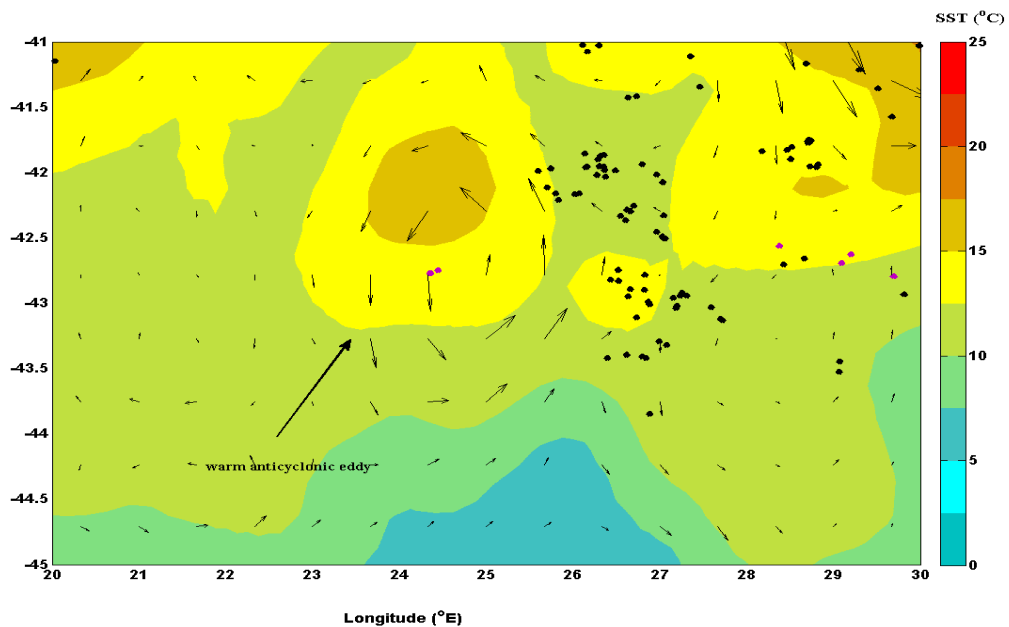


Figure 18. Interaction of tracked individuals of *P. fusca* with warm anticyclonic eddies off the coastline of South Africa during the August 2011 period. Black and pink dots represent tracked *P. fusca* and *palpebrata*, respectively.

Latitudinal distribution and segregation in foraging areas of the two Phoebetria albatrosses

The results demonstrate that the two tracked *Phoebetria* albatrosses have dissimilar latitudinal distribution (Fig. 14a-c). They have demonstrated different pelagic distributions with the tracked *P. palpebrata* having a more southerly distribution of the two. Although, they breed on subantarctic islands, they forage in high waters of the Antarctic (ACAP 2010). Tracked individuals of *P. fusca* were widely distributed to the north of the breeding islands within the Subtropical Convergence in the Southern Indian Ocean in relatively warmer waters $>> 15\text{ }^{\circ}\text{C}$ (Fig. 7).

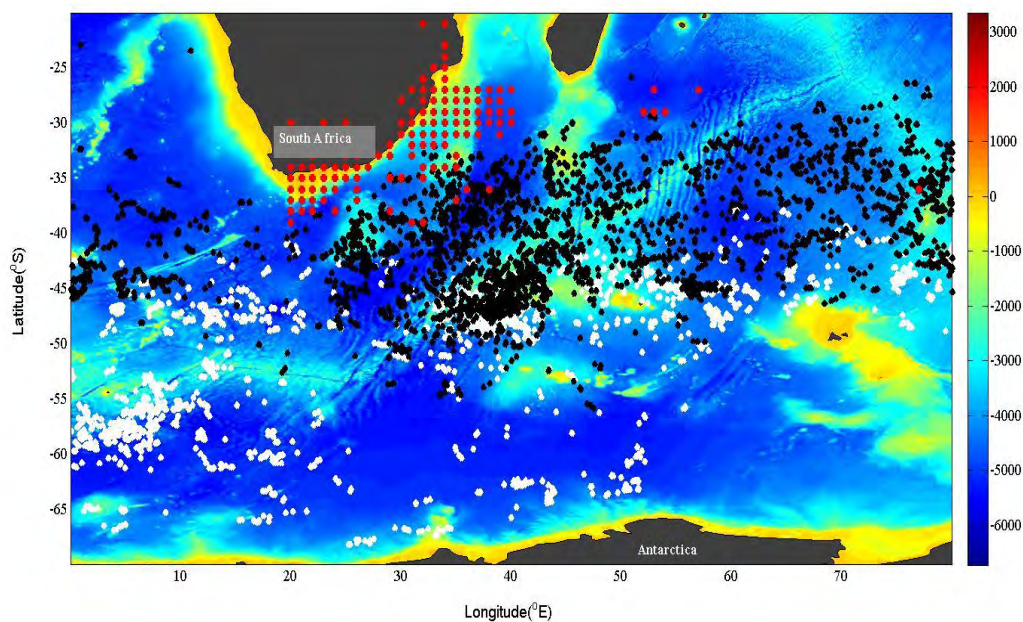


Figure 19. Interaction of the two *Phoebetria* albatrosses with Indian Ocean Tuna Commission tuna longline fisheries in the Southern Indian Ocean. Bathymetry is expressed in metres, tracked *P. fusca* (black dots) and *palpebrata* (white dots), fisheries activities (in red dots).

Tracked individuals of *P. fusca* have demonstrated an extensive distribution within the South Indian Ocean which unfortunately overlaps with high seas longline fisheries. This means that tracked individuals would possibly be vulnerable to incidental capture from fisheries as they overlap with seabird bycatch hotspots of the Indian Ocean Tuna Commission (IOTC) Convention area. Such extensive overlap with bycatch hotspots has serious implications to the conservation of this species (Fig. 19).

Contrastingly, tracked individuals of *P. palpebrata* has demonstrated a more circumpolar distribution in the Southern Ocean (Fig. 14a-c). Tracked individuals of *P. palpebrata* foraged to the south of breeding islands in waters << 15 °C (Fig.7 & 9). Tracked individuals remained in the front to the north of the breeding islands with a few individuals making it as far south as the Antarctic Polar Front (Fig. 14a-c, 19). Interestingly, tracked individuals of *P. palpebrata* confined their foraging activities south of the 40 °S. The results demonstrate that their foraging distribution does not overlap with seabird bycatch hotspots of the IOTC Convention area in the Southern Indian Ocean (Fig. 19).

Statistical model results

We fitted negative binomial Generalised Linear Models with a response variable of species distribution tested against explanatory variables such as the SST, annual breeding stage (nest construction, incubating and chick-provisioning periods) and activity (i.e. foraging and travelling). These models, however, did not treat the two species individually but instead included both species as a response variable. The objective of fitting such models was to determine the best-fit model with explanatory variables.

The models followed the following linear formula – and the best-fit model was chosen based on its lowest AIC and if it passed the Hoslem & Lemeshow Goodness of Fit test.

Model < - glm.nb (y ~ x + xa + xb, data = new)

Table 4. Different GLMs tested for Goodness of Fit using both species as response variable.

Model	AIC	Hoslem & Lemeshow GOF
M1<- spp ~ annual breeding stage + sst + activity + distance	10436	P << 0.05
M2<- spp~ annual breeding stage + sst + activity	10435**	P << 0.05
M3<- spp~ annual breeding stage + sst	10440	P << 0.05
M4<- spp~ annual breeding stage	15542	P << 0.05
M5<- spp~ sst	10443	P << 0.05
M6 <- spp ~ 1	10448	P << 0.05

* **M2 – was chosen as the best-fit model given its lowest AIC.

Model results demonstrate that the best GLM model was model M2 based on its lowest AIC (Table 4). This best-fit model included variables annual breeding stage, SST and activity are very important in fitting the best model to simulate the species distribution of the two sympatric *Phoebetria* albatrosses.

Table 5. Coefficients for the Best Fit Model – both species as response variable

	Estimate	Std. Error	Z-value	Pr (> z)
Intercept	3.72	0.092	40.61	< 2e – 16 ***
Annual breeding stage	-0.0045	0.022	-2.03	0.042 **
SST	-0.32	0.0068	-47.58	<2e – 16 ***
Activity	-0.085	0.031	-2.77	0.0056 **

<< 0.05 are significant ***

The study demonstrates that the most significant variable is sea surface temperature ($P << 2e-16$, Table 5) in simulating the species distribution of the two *Phoebetria* albatrosses. The negative coefficient of annual breeding stage of 0.0045 which is statistically significant implies that annual breeding stage, has a statistically negative effect on the aggregation of these tracked birds. Additionally, it must be noted that negative coefficient of SST of 0.32 is not statistically significant, indicating that a one-unit increase in SST, the expected log count of species decreases by 0.3. However, the effect of SST on either of the two albatrosses will be further investigated the analysis at later stage.

Table 6. Different GLMs tested for Goodness of Fit using *P. fusca* as response variable.

Model	AIC	Hoslem & Lemeshow GOF
M1<- spp ~ annual breeding stage + sst + activity + distance	10010	P << 0.05
M2<- spp~ annual breeding stage + sst + activity	10008	P << 0.05
M3<- spp~ annual breeding stage + sst	10006**	P << 0.05
M4<- spp~ annual stage	10011	P << 0.05
M5<- spp~ sst	10598	P << 0.05
M6 <- spp ~ 1	10945	P << 0.05

* *M3 – was chosen the best-fit model given its lowest AIC.

We conducted more negative binomial GLMs to ascertain which of the aforementioned variables best represent the distribution of each individual species. We fitted different models with the response variable being either *P. fusca* or *palpebrata*.

Table 7. Coefficients for the Best Fit Model of *P. fusca*

	Estimate	Std. Error	Z-value	Pr (> z)
Intercept	-1.91	0.54	-3.56	0.004 **
Annual breeding stage	0.64	0.026	24.42	< 2e – 16 ***
SST	0.064	0.025	2.53	0.011 **

<< 0.05 are significant ***

The statistical model results demonstrate that a negative binomial GLM with explanatory of annual breeding stage and SST can best represent the spatial distribution of tracked *P. fusca* (Table 6). Such a negative binomial GLM resulted with a low AIC and passed the Hoslem & Lemeshow GOF test, and thus chosen the best fit model to represent species distribution of tracked *P. fusca*. The annual stage and SST are the most important factors one has to take care when modelling the species distribution of these tracked birds (Table 6).

Table 8. The 95 % Confidence Intervals for the Best Fit Model variables – *P. fusca*

	2.5 %	97.5 %
Intercept	-2.96	-0.86
Stage	0.59	0.69
SST	0.014	0.111

Model results demonstrate that the species distribution of tracked individuals of *P. fusca* was controlled mostly by its annual stages ($P \ll 0.05$, Table 7). However, SST also played a role in the species distribution of tracked *P. fusca* even though that even wasn't hugely significant ($P = 0.01$, Table 7). A positive coefficient of SST (Table 7) indicates that a one-unit in SST will imply that the expected log count of *P. fusca* species to increase by 0.06. These model results are consistent with the in-situ spatial distribution in Figure 7a, and 8.

Table 9. Different GLMs tested for Goodness of Fit using *P. palpebrata* as response variable.

Model	AIC	Hoslem & Lemeshow GOF
M1<- spp ~ annual stage + sst + activity + distance	10928	$P \ll 0.05$
M2<- spp~ annual stage + sst + activity	10926	$P \ll 0.05$
M3<- spp~ annual stage + sst	10922 **	$P \ll 0.05$
M4<- spp~ annual stage	10924	$P \ll 0.05$
M5<- spp~ sst	12053	$P \ll 0.05$
M6 <- spp ~ 1	12054	$P \ll 0.05$

* *M3 – was chosen the best-fit model given its lowest AIC.

A fitted model for tracked *P. palpebrata* demonstrates that a negative binomial GLM with annual stage and SST as explanatory can best represent the distribution of this species. Such certainty is given by the lowest AIC obtained for such a model (Table 9). Similarly with tracked *P. fusca* (Table 6), these results demonstrate that annual stage has a statistical significant effect on the distribution of the *P. palpebrata* ($P \ll 0.05$, Table 10). A positive coefficient of SST implies that a one-unit increase in SST, the expected log count of species increases by 0.005. However, it must be noted that one-unit increase in SST is statistically not significant ($P \gg 0.05$, Table 10).

Table 10. Coefficients for the Best Fit Model of *P. palpebrata*

	Estimate	Std. Error	Z-value	Pr (> z)
Intercept	-0.58	0.093	-6.26	$<3.9e - 10$ ** **
Annual breeding stage	0.57	0.017	34.54	$< 2e - 16$ ***
SST	0.0045	0.0077	0.58	0.56

$\ll 0.05$ are significant ***

Chapter 4. Discussion

Seabird movements in relation to physical oceanographic features

Tracked individuals of *P. fusca* from Marion Island demonstrated a strong association ($P < 0.05$, Table 7) with physical oceanographic features expressed as sea surface temperatures both during breeding and post-breeding seasons (Fig. 8a-c, & 12a-b). Interestingly, most foraging activities of tracked individuals of *P. fusca* were concentrated at the interfaces and around mesoscale features (Fig. 16, 17 & 18) perhaps due to their productivity and high predictability of prey availability (Schneider 1990).

During incubating period, tracked individuals of *P. fusca* travelled shorter distances despite them having no chicks to feed, possibly due to the availability of food and proximity of foraging localities (Fig. 7c). During chick-provisioning, they travelled shorter distances possibly to maximise returns for their chicks (Weimerskirch 1999). During nest construction periods, tracked *P. fusca* travelled greater distances suggesting their ability to forage at distant foraging grounds as they have no parental responsibilities to return to the colony to provide the chicks.

Contrastingly, tracked individuals of *Phoebastria palpebrata* did not demonstrate any association ($P > 0.05$, Table 7) with oceanographic features expressed as sea surface temperatures both during breeding and non-breeding seasons (Fig. 8a-c, & 12a-b). Unlike its sympatric *Phoebastria albatross*, tracked *P. palpebrata* foraged to the south of the 40°S latitude indicating a more southerly distribution (ACAP 2010). The model results demonstrate that foraging activities of this species were conducted in relation to their annual breeding stages.

During incubating period, tracked individuals of *P. palpebrata* travelled relatively greater distances to the south of the Antarctic Polar Front (APF) possibly due to interspecific competition with the sympatric *P. fusca*. In addition, this may possibly be due to the fact that during incubating period, tracked *P. palpebrata* have only themselves to feed and were therefore not forced to confine their foraging to those localities close to breeding islands (Fig. 7c). During chick-provisioning, tracked *P. palpebrata* travelled shorter distances possibly to maximise returns for their chicks while minimise effort (Weimerskirch 1999). During nest

construction periods, tracked *P. palpebrata* travelled greater distances suggesting their ability to travel to distant foraging grounds when they are no breeding responsibilities to attend to at the colony.

Commonalities and differences in the two *Phoebetria* species.

The two *Phoebetria* species, *fusca* and *palpebrata* breed sympatrically on the Prince Edward Islands in the Southern Indian Ocean (Berutti 1979). Both are biennial breeders with a capacity of re-laying if the first breeding attempt is unsuccessful (Marchant and Higgins, 1990). They both have relatively similar body size (ACAP 2010). They both have three annual breeding stages which include nest construction, incubating and chick-provisioning periods.

The results demonstrate that tracked *P. fusca* was far more abundant to the north of the Antarctic Polar Front (APF) whereas tracked *P. palpebrata* has a more southerly distribution. These results are consistent with the findings of Ryan et al. (2009). This latitudinal segregation as indicated by pelagic distribution suggests some interspecific competition of foraging habitats in the two species (Figure 14a-c). Our results suggest that tracked *P. palpebrata* travelled farther distance in search of prey and has greater maximum ranges suggesting lower chick-provisioning frequencies (Figure 7c). These results are consistent with those found by Phillips et al. (2005).

The interspecific differences in shifts of incubation and brooding suggest an interspecific competition for these two sympatric species. This is perhaps due to the chick-provisioning strategy adopted by tracked *P. palpebrata* which necessitates travelling great distances with an object of maximising returns. *P. palpebrata* has shorter incubation period than *P. fusca* indicating the localities and availability of these species and these results are consistent with those found at the Crozet Island (Weimerskirch et al. 1986).

Some studies have demonstrated that although the Antarctic Polar Front lies just < 400 km from Marion Island, *P. fusca* must cross it based on some prey species but not as much as the *P. palpebrata*. Studies conducted at the South Georgia Island have shown that *P. palpebrata* undertook frequent chick-provisioning activities than at Marion Island (Thomas et al. 1983)

suggesting that shorter foraging trips could be achieved with minimal effort while ensuring maximum returns.

Implications of conservation of the two *Phoebetria* albatrosses

The important foraging areas of this vulnerable species of *P. fusca* as listed on the IUCN Red List during non-breeding period were widely distributed across the Southern Ocean. The areas of importance overlapped mainly with international waters with the rest being in several Exclusive Economic Zones (EEZs). This suggests the importance of international collaboration for the conservation of seabirds, particularly albatrosses. It is worth noting that the IOTC Convention areas south of South Africa appeared to play an important role for individuals of *P. fusca* tracked at Marion Island (Fig. 19) that tended to spend most of the post-breeding period in the Southern Indian Ocean.

The results demonstrate that there is an overlap between seabird bycatch hotspots reported for the IOTC Convention area (Delord and Weimerskirch 2011) and distribution of *Phoebetria* breeding on islands in the Southern Indian Ocean. The results demonstrate that this species is at high risk of incidental bycatch from high seas longline fisheries because of their overlap with areas of high bycatch levels.

Similarly, the important foraging areas of the tracked individuals of *P. palpebrata* during non-breeding period were widely distributed across the Southern Ocean making it vulnerable to conflict with international high seas fisheries. Although, this species demonstrated a more southerly distribution than tracked *P. fusca*, its foraging movements overlapped with international high seas fisheries. This suggests that although it is still listed as near-threatened on the IUCN Red List, *P. palpebrata* may still be vulnerable to incidental bycatch due to its overlap with major IOTC bycatch hotspots.

Conclusions

The study demonstrated the ability of the two tracked *Phoebetria* albatrosses to effectively exploit oceanographic features with minimal effort while maximising returns during chick-provisioning and incubating periods. Most importantly, the study highlighted the fact that their important foraging areas overlap with IOTC Convention area, thus, putting them at high risks of incidental capture from high seas longline fisheries.

The study highlighted the crucial and urgent need to have access to quality-controlled fishery data and bycatch estimates at these specific bycatch hotspots in order to enable effective management of fisheries and vulnerable seabird populations. It emphasised the need to have a multi-faceted approach on fisheries management particularly on seabird bycatch mitigation in areas of concern. Such multi-faceted approach should be aimed at minimising conflicts between seabirds and high seas fisheries.

Although, the study would have preferred a long time series of these two tracked *Phoebetria* albatrosses coupled with longline fisheries data to account for their sabbatical period of these species as well as the extent of the impact of longline fisheries to these seabirds. Future studies should include a multi-faceted and thorough analysis of the impact of longline fisheries on the populations of these seabirds backed by robust statistical models.

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