LINKING FORAGING BEHAVIOUR OF POST-BREEDING ADULT FEMALE ELEPHANT SEALS FROM MARION ISLAND TO PHYSICAL DYNAMICS AND PRODUCTIVITY AT THE SOUTH-WEST INDIAN RIDGE.

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ABSTRACT

Advances in remote sensing and tagging technology have made it possible to investigate the relationship between oceanographic dynamics and the distribution of certain marine species. For this study, surface chlorophyll-a concentration was used as a proxy for underlying related productivity, rather than as a direct indicator of prey density. Post-breeding, adult female southern elephant seals from Marion Island were tagged with conductivity, temperature and depth satellite-relayed data loggers (CTD-SRDL's) and their foraging behaviour was examined in relation to different chlorophyll-a concentrations. Optimal foraging and area restricted search theories predict that travelling speed and turning frequency would be quantifiably affected by prey density, which is in turn affected by the underlying richness of primary producers. Ten female elephant seals from Marion Island, tracked between 2005 and 2009, decelerated and made sharper changes in orientation once chlorophyll-a peaked to between 0.30 mg/m^3 and 0.40 mg/m^3. Results indicate that seals significantly shift their behaviour from 'searching' to Brownian-type 'foraging' at an apparent threshold of 0.30 mg/m^3. This tipping point may denote the limit where underlying biomass is abundant enough to attract high densities of downstream prey species, encouraging adult female elephant seals to engage in area restricted foraging behaviour.

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1. RESEARCH REVIEW

In the Southern Hemisphere, apex predators in mid to high latitudes often have to forage in hostile and unpredictable environments (Dragon *et al.,* 2010). Southern elephant seals, *Mirounga leonina* (Linnaeus, 1758), travel vast distances within the circumpolar waters of the Antarctic in their search for prey species (McConnell *et al.,* 1992). By instrumenting these free-ranging marine predators with satellite-linked transmitters, their foraging and distribution patterns are starting to be expounded upon, as are the dynamics that drive them. The objective of this short study was to investigate a possible correlation between the complexities of the oceanic and biological environment around the Prince Edward Islands, and the foraging behaviour of tagged resident adult female southern elephant seals.

1.1 The Southern Ocean

The Southern Ocean is an extensive ocean, unique in that it flows unhindered around the globe and distinctive because, although it links the Atlantic, Indian and Pacific oceans, it does not conform to their dynamics (Tomczak and Godfrey, 1994). The Antarctic continent forms the southern boundary of the Southern Ocean. The northern border is not physiographically fixed and is conventionally considered to coincide with the geographic location of the Subtropical Convergence (STC) (Lutjeharms, 1985). On a global scale, the Southern Ocean is key to the thermohaline circulation and deep interior waters are continuously being overturned by surface waters from the high latitudes (Toggweiler and Russell, 2008). Because these exchanges play an important role in regulating global climate, sustained hydrographic observations are essential in order to describe and better understand the physical and dynamic processes responsible for the variability of the Antarctic Circumpolar Current (ACC).

1.2 The Antarctic Circumpolar Current

Circulation of the Southern Ocean is dominated by the ACC. This current is driven by dominant westerly winds prevailing between 30°S and 65°S, and extends unbroken around Antarctica (Trenberth *et al.,* 1990). Forming the southern stretch of the thermohaline conveyor belt, it is also the primary means by which salt and heat are transferred between different ocean basins. A major part of the flow associated with the ACC is concentrated at deep current cores of circumpolar fronts that act to separate zones of uniform water masses (Fig. 1.1) (Nowlin and Clifford, 1982; Nowlin and Klinck, 1986).

From north to south, the fronts and associated zones of the Southern Ocean are: the Subtropical Convergence (STC) or Subtropical Front (STF), the Subantarctic Zone (SAZ), the Subantarctic Front (SAF), the Polar Frontal Zone (PFZ), the Antarctic Polar Front (APF), the Antarctic Zone (AAZ) and the Antarctic Divergence (AAD) (Fig. 1.1) (Orsi *et al.,* 1995). Although all these fronts are circumpolar, they show strong temporal variability in latitudes between different oceanic sectors (Lutjeharms, 1985).

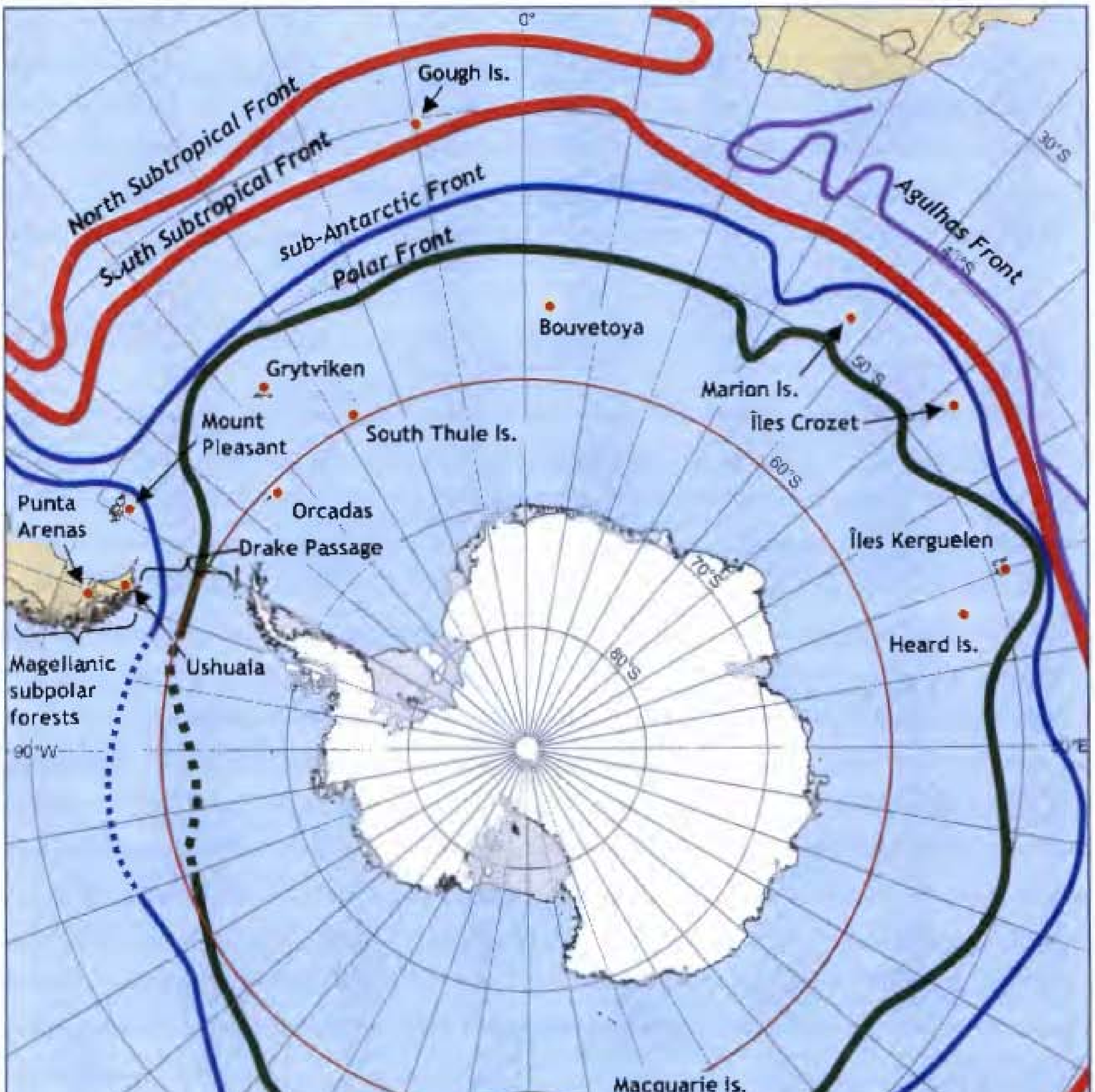

Fig. 1.1: Locations of the ACC fronts (Belkin and Gordon, 1996; Pendlebury and Barnes-Keoghan, 2007).

Having cognisance of the structure and location of the ACC fronts, despite their integral stochastic nature, is of vital importance nonetheless for understanding ecosystem processes (Boehme *et al.*, 2008).

Longhurst (2007) proposed that these frontal and zonal patterns form a platform for four distinct biogeochemical provinces. From north to south, these are: the South Subtropical Convergence Zone, a Subantarctic Water Ring (SANT), the Antarctic Province (ANTA) and the Austral Polar Province (APLR). ANTA is situated between the APF and the ADD, and it includes ice-free waters, the seasonally defined marginal ice zone and permanently ice-covered areas. It is relevant to this investigation because it shares an ecotone, or transition boundary, with SANT (Longhurst, 2007). The area of interest for this study is specifically the SANT province, as delineated by the STC and APF.

1.3 Influences of Bathymetry

The bathymetry of the Southern Ocean comprises of deep (>4000m) ocean basins broken up by numerous shallow mid ocean ridges and prominent plateaus where depths range from 2000m – 5000m. The two fronts that define the classical zonation of the ACC are the SAF and APF. However, closer inspection of their structures have suggested that each front is characterized by numerous eastward flowing jets that, together, constitute the total circumpolar flow (Sokolov and Rintoul, 2008). Indeed, these fronts display strong temporal variability in latitude and structure with large areas of substantial mesoscale eddy activity dominating the core of the ACC. Comparing these eddy "hotspots" with the underlying seafloor confirms that the current is topographically steered and implies that the ACC dynamics near topographic features are substantially altered from those in broad ocean basins (Gille *et al.,* 2004; Gille, 1997). Results from numerous measurements taken from early ship data (Gordon *et al.,* 1978; Lutjeharms and Baker, 1980), numerical model studies (Gille, 1997), satellite altimetry data (Sandwell and Zhang, 1989) and surface drifters (Hofmann, 1985) have confirmed that the mean kinetic energy associated with the ACC is almost nonexistent over deep ocean basins, where topographic constraint is weak, but surges on encountering prominent topographic features. This is true for the ACC in its entirety but, south of South Africa, at an area broadly influenced by the South West Indian Ridge (SWIR), the SAF and APF are particularly affected (Fig. 1.2) (Read and Pollard, 1993).

The SWIR is a deeply fractured divergent boundary that separates the African Plate from the Antarctic Plate. The SAF and APF, which carry the core of the ACC, become notably stochastic as they flow into this region (Fig. 1.3) (Lutjeharms *et al.,* 2002; Ansorge *et al.,* 2010). Occasionally, the SAF bifurcates into two branches and the southern split has been observed to merge with the APF at the SWIR to form a double front (Sokolov and Rintoul, 2002; Froneman *et al.,* 2002; Bernard and Froneman, 2003). Of particular importance is a tightly spaced set of fractures known as the Andrew Bain Fracture Zone (ABFZ) (Lemaux *et al.,* 2002). The ABFZ interacts directly with the eastward-flowing Antarctic waters, funnelling approximately 110 Sv of the ACC and effectively acting as a choke point (Fig. 1.3) (Pollard and Read, 2001; Ansorge and Lutjeharms, 2003). Disturbances to the mean flow appear to occur at the ridge, and then evolve with the eastward-flowing current in the form of mesoscale features such as meanders and eddies. Eddies serve to retain nutrients and biomass, transporting phytoplankton blooms downstream and providing potentially rich foraging grounds for birds and mammals (Jonker and Bester, 1998; Nel *et al.*, 2001; Sokolov, 2008; Bailleul *et al.*, 2010).

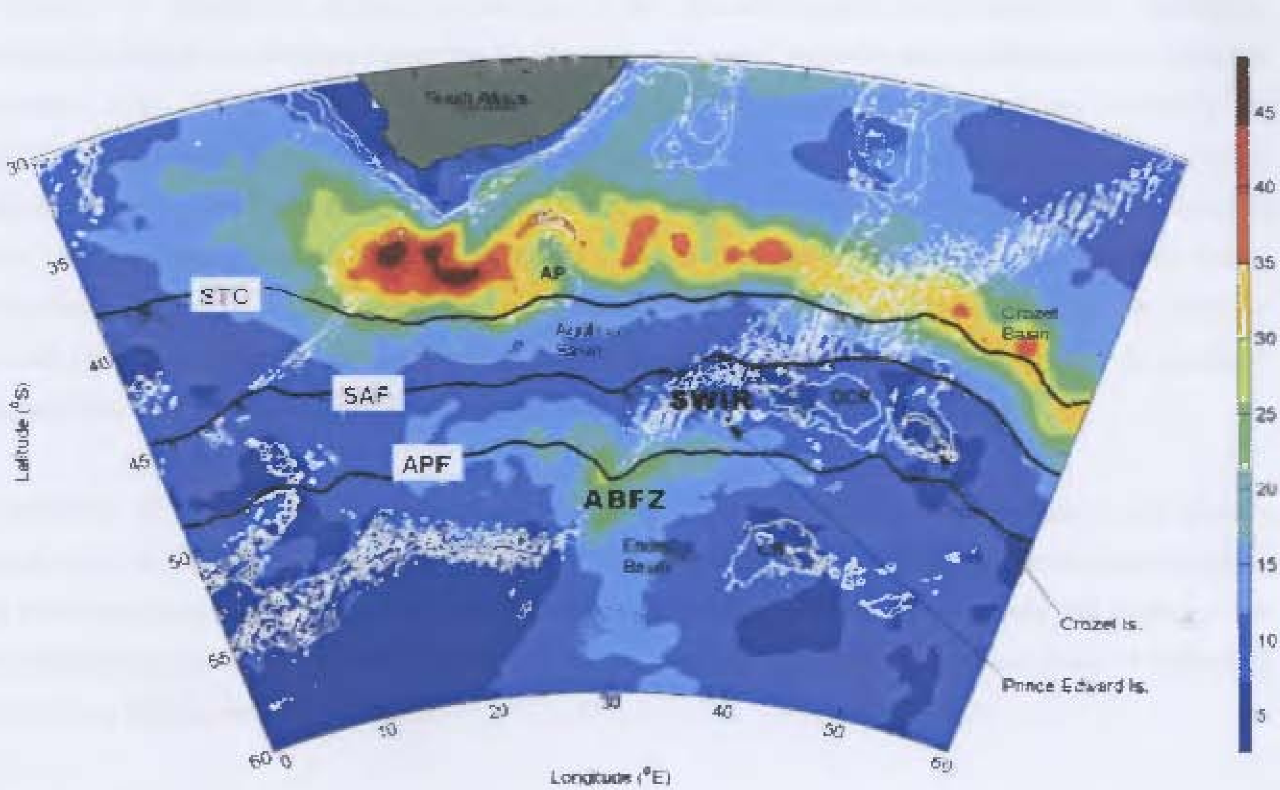

Figure 1.2: Positions of fronts relative to Root Square Mean of Sea Level Anomalies (cm) (Durgadoo, 2008).

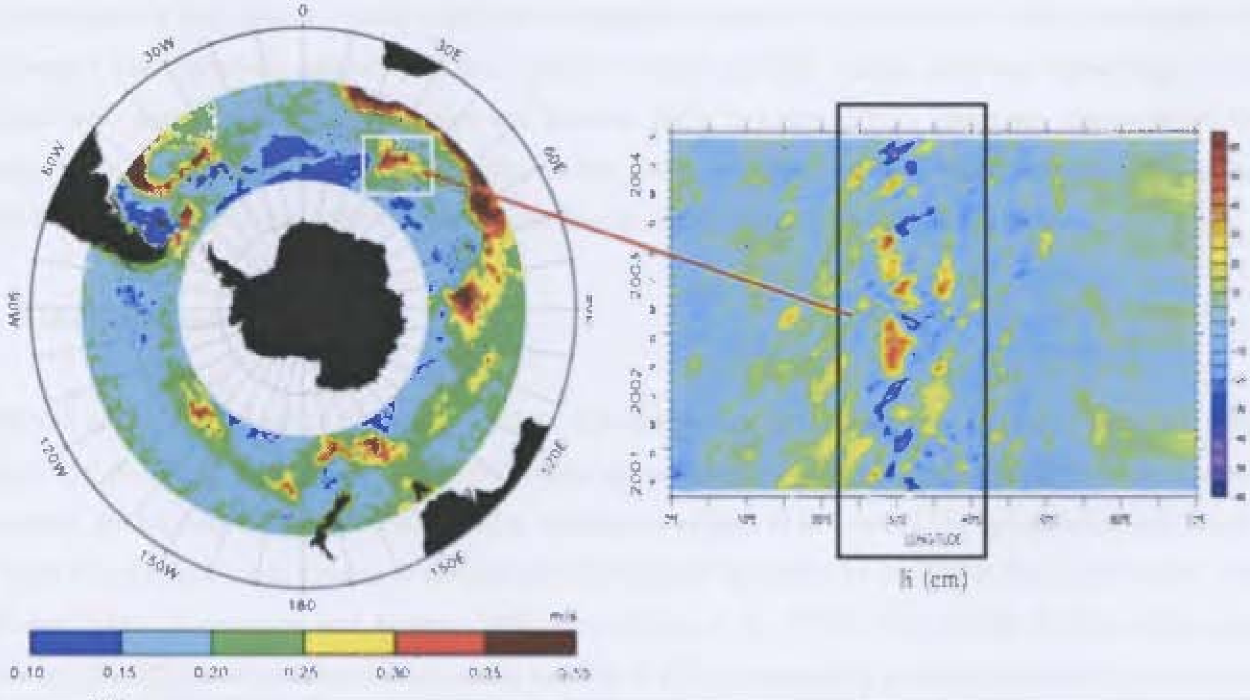

Figure 1.3: LHS: Highly elevated eddy kinetic energy (m/s); RHS: Hovmoller plot of the resultant cold and warm core eddies from 2001-2004 (Height in cm). Note the sudden increase in variability due to conservation of vorticity as the ACC is funnelled through the SWIR fracture zones.

1.4 Regional Productivity

'Hotspots' of upregulated primary productivity in the characteristically high-nutrient, low chlorophyll (HNLC) waters of the Southern Ocean can be observed and studied remotely using chlorophyll-a as a marker (Henson *et al.,* 2009). Monitoring concentrations by passive spectroradiometer requires measuring the relatively small proportion of incident radiation not absorbed or scattered by the ocean waters, observed as the water-leaving irradiance (Longhurst, 2007). Satellite analysis of world ocean colour using chlorophyll-a has revealed complicated variability on a global scale in both space and time. In the Southern Ocean specifically, chlorophyll-a concentrations are relatively modest and phytoplankton blooms are generally traced along the marginal ice zone, observed near certain fronts of the ACC, and linked to dominant bathymetric features and islands (Sokolov and Rintoul, 2007).

Availability of light and the presence of trace nutrients are key "bottom-up" factors that control primary productivity in HNLC Antarctic waters (Sokolov, 2008). Chlorophyll-a is a useful biogeochemical indicator of underlying productivity (Falkowski *et al.,* 1998) and ocean colour studies have shown that surface levels are elevated along the PF during the high-light austral summer, but are persistent over areas of distinctive bathymetry (Moore and Abbott, 2002).

Where the ACC interacts with complex bathymetry, bottom torque destabilizes vertical coherence of the water column, upwelling nutrients from the ocean bed into surface waters (Sokolov and Rintoul, 2007). Increased turbidity would then also generate the formation of regional meandering and eddy processes. This phenomenon is not unusual – every significant topographic feature in the Southern Ocean is associated with enhanced chlorophyll-a; inherently, where nonzero bottom pressure torque generates upwelling of iron, silicic acid and other nutrients (Sokolov and Rintoul, 2007; Sokolov, 2008). Important topographical 'hot spots' include the SWIR, the Southeast Indian Ridge, South and North Scotia Ridges, Kerguelen Plateau and the Pacific Antarctic Ridges (Holm-Hansen and Hewes, 2005; Sokolov and Rintoul, 2007).

1.5 Marion Island

Marion Island, the largest of the volcanic Prince Edward Islands (PEI), rises to prominence along the SWIR at 46° 54' S, 37° 45' E (Durgadoo, 2008). The area surrounding the PEI is characterised by enhanced marine primary productivity but until the late 1980's, uncertainty existed as to whether the upregulation was due to a "mass island effect" or as a result of the complicated physical dynamics of the SWIR (Doty and Oguri, 1965; Boden, 1988; Perissinotto and Boden, 1989; Perissinotto *et al.,* 1990). The Marion Offshore Ecological Survey (MOES-II), undertaken in the austral autumn of 1989, successfully gathered physical information on the spatial parameters of the region. Results confirmed the meandering nature of the SAF and established that, downstream of the island, conditions differed from the upstream oceanography (Perissinotto *et al.,* 1990). Notably, a warm core eddy was identified in this downstream area (Ansorge *et al.,* 1999). The Marion

Island Oceanographic Survey II (MIOS-II) covered a wider geographic range and eddy processes appeared to be flanking feature of the Prince Edward Island group. The upregulated primary productivity characteristic of the area was found to be a consequence of the complex physical dynamics of the SWIR, as well as the resultant mesoscale features (Ansorge *et al.*, 1999; Froneman *et al.*, 1999; Ansorge and Lutjeharms, 2002).

Meanders and eddies have a marked impact on community structure and productivity throughout the Southern Ocean (Ansorge *et al.*, 2010; Dragon *et al.*, 2010). During the light-limited months over austral winter, there is persistent above-average primary productivity in areas where the ACC interacts with islands, ridges and plateaus. Intense blooms generated by these interactions are often carried downstream for hundreds to thousands of kilometres, implying that horizontal transport of biomass and nutrients along ACC jets is a significant factor in phytoplankton productivity dynamics (Sokolov, 2008).

These areas of upregulated productivity attract swarms of zooplankton, which, in turn attract predators ranging from krill and fish, to squid, seabirds and baleen whales. Higher predators targeting the squid and fish are, however, less correlated to the mesoscale features and spatial-temporal disconnections may mask habitat association (Longhurst, 2007; Bailleul *et al.*, 2010). Advances in remote sensing and tagging technology have made it more accessible to investigate the relationship between primary productivity and the distribution of instrumented marine species (Bailleul *et al.*, 2010). Although top predators are not passive tracers of water movement and spatial and temporal lags make it difficult to correlate their foraging distribution with chlorophyll-a levels, optimal foraging theory predicts that speed and turning frequency of these animals would be measurably affected by prey density (Longhurst, 2007; Dragon *et al.*, 2010).

Southern elephant seals, *Mirounga leonina*, from Marion Island have been extensively studied during their terrestrial phases, largely through a long-term mark re-sighting study (Bester, 1998; Pistorius *et al.*, 1999; de Bruyn *et al.*, 2008; McIntyre *et al.*, 2010b). All foraging, however, takes place at sea and questions remain unanswered about which oceanographic cues, if any, are exploited in the search for prey species.

2. INTRODUCTION

Marine predators are compelled to make foraging decisions based on little to no knowledge of the current resource distribution, however, near-distance and broad scale clues may be exploited (Sims *et al.,* 2008). Despite the dynamic distributions of prey species such as phytoplankton, shoaling fish and squid, free-ranging marine predators may be able to fine tune foraging decisions using seasonal, geographical and physical information (Sims *et al.,* 2008; Humphries *et al.,* 2010). Optimal foraging theory and area-restricted search (ARS) predicts that marine predators will decrease speed and increase turning frequency as they encounter higher densities of prey species (MacArthur and Pianka, 1966; Kareiva and Odell, 1987; Dragon *et al.,* 2010). Specialised random walks producing fractal trajectories are widespread among a range of organisms, including marine top predators, and have possibly evolved as a mechanism of exploiting patchily distributed resources (Viswanathan *et al.,* 2000; Sims *et al.,* 2008; Reynolds, 2009; Humphries *et al.,* 2010). These Lévy walks comprise of long orientation steps (search for prey), punctuated by switches to Brownian motion (foraging within a patch) (Humphries *et al.,* 2010).

2.1 Southern Elephant Seals

Southern elephant seals (*Mirounga leonina*) are the quintessential marine predator. They inhabit the mid to high latitudes of the Southern Ocean and successfully exploit a highly stochastic environment defined by patchily distributed resources. These mammals have been extensively studied from a biological and behavioural perspective so there is a significant amount of information available on their terrestrial dynamics (Le Boef and Laws, 1994; McIntyre *et al.,* 2010b). Adult southern elephant seals typically haul out onto land twice a year, once to breed (September - October) and once for the obligatory annual moult (December - February). Feeding takes place exclusively during the less well elucidated pelagic phase and southern elephant seals spend approximately 80% of their lives at sea (Le Boeuf and Laws, 1994; McIntyre *et al.,* 2010a).

The post-breeding foraging phase is short and intensive, taking place during the early austral summer. Because of the time limitations faced during this migration, focused and directed foraging along or parallel to the SWIR is observed more commonly than exploratory distributions (Fig. 2.1) (Tosh, 2010). The post-moult migration, on the other hand, takes up to 8 months and spans over autumn, winter and early spring. Tagged adult females from Marion Island have been tracked as far south as 69°S, when winter ice cover allows, and individual variation is frequently observed (Fig. 2.2).

Throughout each migration, while foraging in the Southern Ocean, southern elephant seals dive for approximately 20 - 30 minutes to their preferred depth of between 300 – 400m, surfacing for short periods of approximately 2 - 3 minutes (Boyd and Arnbom, 1991; McIntyre *et al.,* 2010a). Individuals exhibit significant variability in the targeted foraging depths.

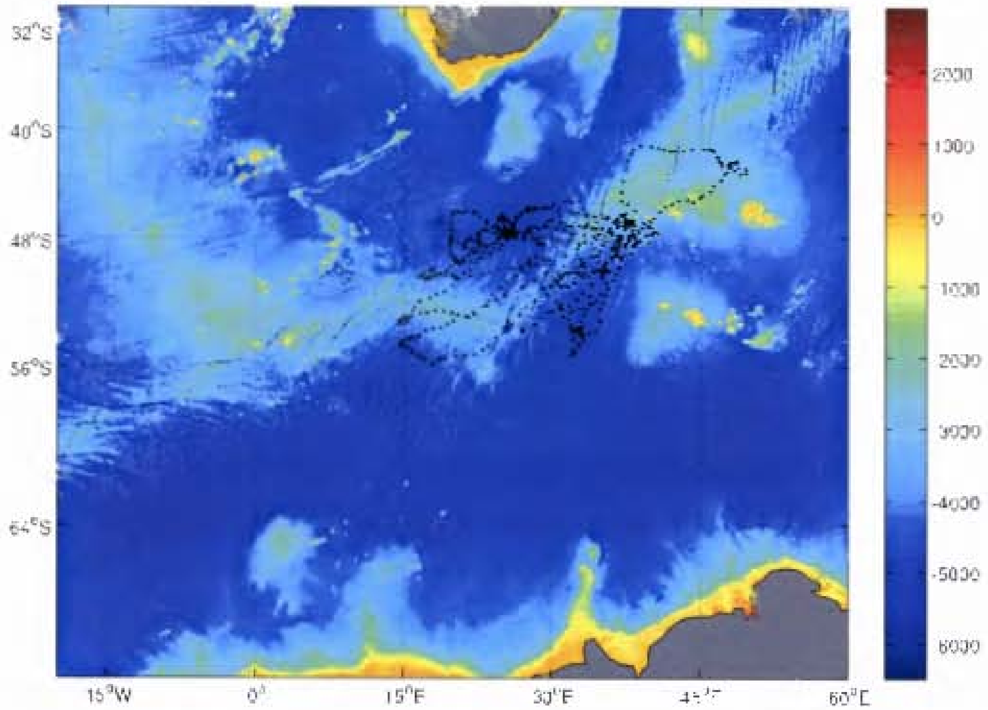

Fig. 2.1: Post-breeding summer dispersal of tagged female elephant seals from Marion Island showing how most individuals focus their foraging distribution along, or parallel to, the SWIR (2004 – 2009).

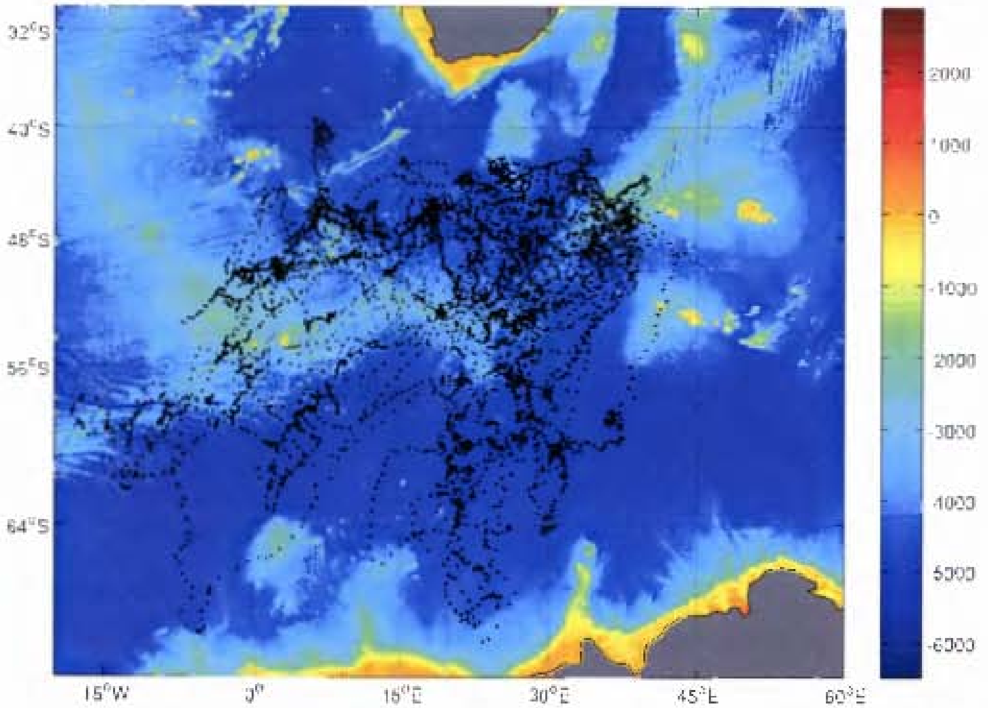

Fig. 2.2: The extensive post-moult winter distribution of tagged female elephant seals from Marion Island showing high individual variation and less directed foraging distribution (2004 – 2009).

Male elephant seals can grow up to ten times bigger than their female counterparts, and large adult bulls are able to dive to an excess of 2000m to forage benthically (Le Boeuf & Laws 1994). They are the deepest diving air-breathing non-cetaceans and have been recorded at a maximum of 2 133m (McIntyre *et al.*, 2010a).

2.2 Tagging

Advances in tagging technology have made it possible to instrument southern elephant seals and track their pelagic phases using custom-built conductivity, temperature and depth satellite-relayed data loggers (CTD-SRDL's) (Sea Mammal Research Unit, University of St. Andrews, Scotland). These tags are glued to the fur on seals' head to allow for the Argos-linked aerial to emerge when the seal surfaces to breathe (Fedak *et al.*, 1983), and they fall off for retrieval during the annual moult. CTD-SRDL's are capable of transmitting vertical profiles of salinity, temperature and pressure to depths of approximately 2000m, accurate to 2mK and 0.003 mS/cm in conductivity and temperature, respectively (Boehme *et al.*, 2008).

Studies seeking to combine satellite-derived oceanographic information with tracking data have elucidated the importance that mesoscale and broad scale features have in creating rich feeding pockets for top predators (Tosh, 2010; Dragon *et al.*, 2010). Variations in marine predator behaviour and distribution can now possibly be linked to physical dynamics such as sea surface temperature, ocean colour, sea-ice extent and concentration, and bathymetry (Bornemann *et al.*, 2000; Charrassin *et al.*, 2008; Hindell *et al.*, 1991; Sokolov and Rintoul, 2007). However, despite the precise information that CTD-SRDL's collect and relay, there are still many unanswered questions relating to the foraging behaviour of southern elephant seals, and the possible oceanographic clues, if any, that they exploit. Furthermore, variations in tactics and patterns have been reported between sexes, age classes and populations (McIntyre *et al.*, 2010 a,b).

Female elephant seals are characteristically philopatric (Hofmeyr, 2000), returning to the island of their birth for annual breeding and moulting haul-outs. This allows for limited genetic exchange between geographically isolated populations, resulting in *Mirounga leonina* being divided into four genetically distinct populations. The home groups are South Georgia, Peninsula Valdés, Macquarie and Kerguelen Islands (Slade *et al.*, 1998; Hoelzel *et al.*, 2001), with smaller satellite islands adding to the stock numbers (Fig. 2.3).

2.3 South Georgia Islands

Seals from the South Georgia group tend to stay within the ACC, exploiting the destabilised current as it is funnelled through the Drake Passage (Biuw *et al.*, 2007). Three female elephant seals tagged in the early 1990's travelled south-west over deep water to the Antarctic coastal shelf during their post-breeding trip. One dived repeatedly to the sea floor, possibly feeding benthically (McConnell *et al.*, 1992). In a separate study attempting to measure sea-ice formation rates, tagged seals were monitored as they explored the Scotia sea during their post-moult migration (Charrassin *et al.*, 2008). Boehme *et al* (2008) successfully tagged 21 seals to observe their winter foraging trip. Several travelled west from S. Georgia directly to the Antarctic Peninsula and two perpendicularly crossed the Drake Passage (Boehme *et al.*, 2008).

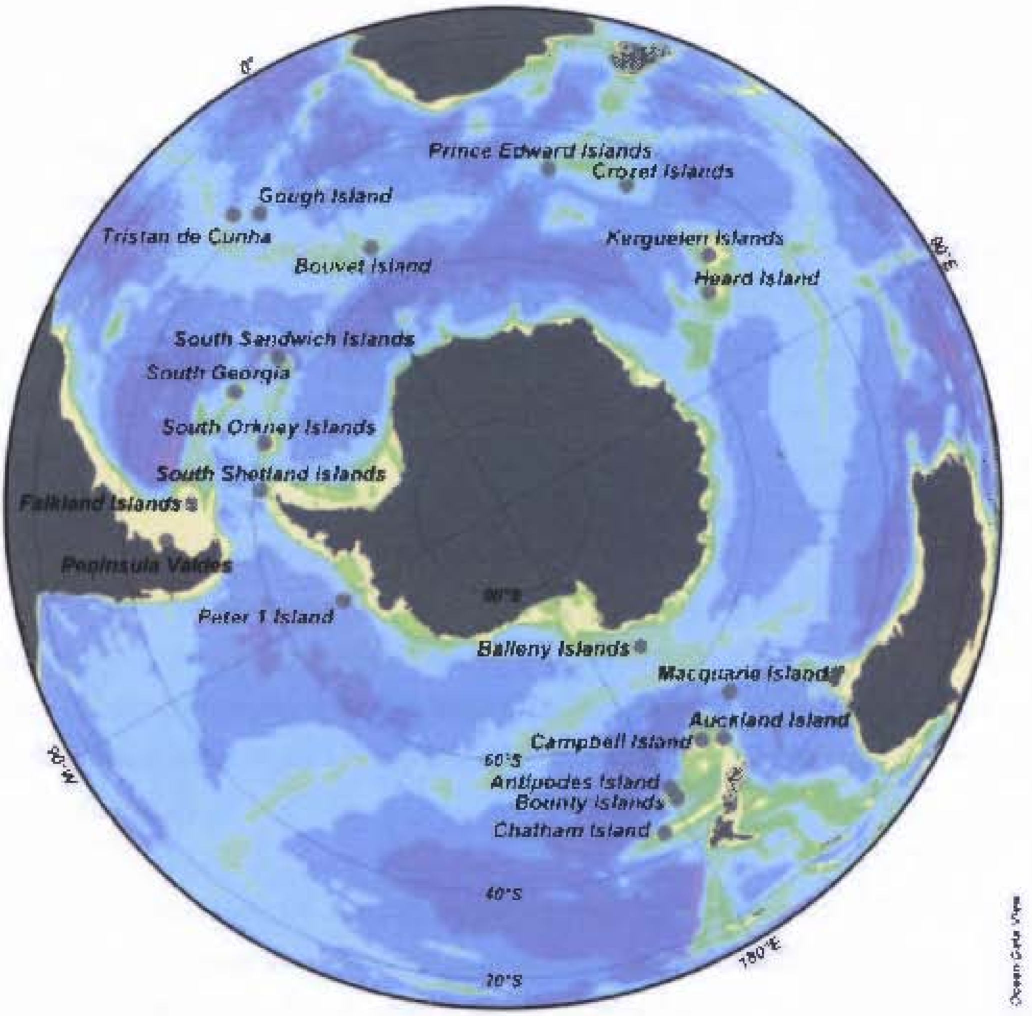

Fig. 2.3: Circumpolar distribution of *M. leonina* populations (Tosh, 2010; McMahon *et al.*, 2005)

2.4 Kerguelen Island

Southern elephant seals from Kerguelen are able to take advantage of the shallow plateau that circles the island and extends towards the Antarctic landmass. Within the population, three distinct foraging zones have been identified (Dragon *et al.*, 2010). After moulting in the late summer (around February), the majority of seals tend to swim directly from their island to the continental shelf, focusing their foraging activities on the Antarctic slope and plateau (Bailleul *et al.*, 2007a,b). Both sexes dive deeper and remain at depth for longer when foraging here, suggesting benthic hunting (Hindell *et al.,* 1991; Bailleul *et al.,* 2007b). As the season progresses into late austral winter, building sea ice steadily encroaches northwards and outwards from the continent. Male elephant seals and juveniles remain on the shelf area while the females move with the migrating marginal ice zone, shifting from benthic to pelagic feeding as they are forced back into the open sea (Bailleul *et al.,* 2007a). Similar behaviour has been observed in adult females from South Georgia (McConnell and Fedak, 1996) and Macquarie Island (Hindell *et al.,* 1991).

2.5 Marion Island

Southern elephant seals from Marion Island genetically augment the Kerguelen population (McMahon *et al.,* 2005) but perhaps due to the unique regional bathymetry and physical dynamics, they exhibit different foraging patterns. The Marion Island population is one of the northernmost breeding aggregations and their distance from large land masses and the ice edge encourages its inhabitants to adopt pelagic-dominant foraging patterns and, by extension, a more extreme lifestyle than populations from other islands (McIntyre *et al.,* 2010a).

According to a study undertaken by McIntyre *et al.*(2010a), targeting only re-sighted and known individuals, Marion southern elephant seals spend an average of 85% of their lives in the ocean, diving most of that time. On a horizontal scale, resident seals have been observed travelling as far as the Antarctic continental shelf to predate upon the resources associated with the encroaching or melting sea ice. Most, however, do not follow this strategy, choosing to remain in ice-free waters (Jonker and Bester, 1998). On a vertical scale, adult bulls dived to the greatest mean depths (550m) while adult females remained at shallower mean depths (450m) (McIntyre *et al.,* 2010a).

Differences between the sexes are also apparent when observing the proportion of time spent on the shorter post-breeding and extensive post-moult migrations, with females spending less time in the water after breeding than the males. Furthermore, adult bulls spend more time on land due to the fact that they have to establish and maintain their harem territories. Most seals from Marion Island, however, regardless of sex, appear to focus their post-breeding foraging activities along the SWIR (Tosh, 2010; McIntyre *et al.,* 2010a).

2.6 Selection Criteria

Ostensibly, female elephant seals from Marion Island conform to more predictable patterns than the males and, consequently, may display a clearer correlation to the physical oceanography while at sea (Le Boeuf and Laws, 1994; Tosh, 2010). Before the post-breeding foraging trip, adult females give birth and wean a single pup. In order to regain the body condition lost during this terrestrial phase, foraging and feeding success over the few short weeks between breeding and moulting needs to be substantial (Le Boeuf and Crocker, 2005). Despite this, they spend less time in the water than the males, with bulls staying closer to the island and possibly exploiting benthic hunting grounds inaccessible to their small-bodied counterparts (Tosh, 2010). Because adult female elephant seals have less time to forage, they are less able to adopt exploratory hunting distributions and conform instead to directed and more predictable distributions. Furthermore, being less adept at exploiting the deeper benthic resources, they have to follow the physical and biological clues that lead them away from Marion Island and southeast along the SWIR. For these reasons, only data transmitted from adult female elephant seals tagged on Marion Island were used for this study.

Once weaned, both male and female pups have to immediately fend for themselves and gain foraging experience in order to learn about underlying prey distributions. Mortality in the first year tends to be high due to a combination of predation and unsuccessful foraging tactics (Pistorius *et al.,* 2001; Pistorius and Bester, 2002). Potential "trial and error" foraging behaviour is not strictly useful for elucidating overarching patterns and female seals under 3 years old (approximate age at sexual maturity) were excluded from this investigation.

2.7 Summary

Location patterns of prey species are often dynamic but areas of enhanced primary productivity tend to attract strings of downstream foodchains, and top predators such as southern elephant seals may exploit the related seasonal, geographical and physical clues (Sims *et al.,* 2008). Chlorophyll-a is a convenient marker of underlying productivity, biogeochemistry and physical processes (Falkowski *et al.,* 2008) though a clear link between these features and the foraging distribution of adult female elephant seals from the Marion Island population has not yet been shown.

This study aimed to investigate whether chlorophyll-a, as a marker of underlying regional processes and productivity, influences the foraging distribution patterns of adult female elephant seals from Marion Island during their post breeding migrations.

Specific research questions for this investigation include:

1. Using reduced speed as a measure of foraging activity, is the distribution pattern of adult female elephant seals independent of chlorophyll-a levels during their short post-breeding migration over December and January?

2. Based on turning frequency as an indicator of foraging activity, can we link distribution patterns of elephant seals to chlorophyll-a levels during the intensive post-breeding feeding that takes place over December and January?

3. MATERIALS AND METHODS

Data

3.1 Tag Deployment

Between 2005 and 2008, 10 adult female southern elephant seals were tagged with CTD-SDRLs (Table 3.1) (Sea Mammal Research Unit, University of St. Andrews, Scotland).

Table 3.1: The ten female elephant seals tagged and monitored over their post-breeding foraging trip.

Seal Designation	Year	First transmission	Last transmission	Days of Dive Data
PE791	2005	10/11/2005	15/01/2006	66
RR483	2007	03/11/2007	07/01/2008	65
YY070	2007	02/11/2007	25/12/2007	53
YY193	2007	04/11/2007	07/01/2008	64
YY240	2007	30/10/2007	03/01/2008	65
YY264	2007	12/11/2007	16/01/2008	65
YY348	2007	04/11/2007	12/01/2008	69
GG380	2008	08/11/2008	24/11/2008	16
WR336	2008	08/11/2008	06/01/2009	59
BB246	2008	08/11/2008	22/01/2009	75

Animals were immobilized with ketamine using an established remote injection method and tags were then glued to the fur on the head using a quick-setting epoxy resin (Bester, 1998; McIntyre *et al.*, 2010a). The instruments transmitted information on seal locations and distributions during the short summer foraging expeditions – ranging from early November to January of the following year. Location estimates are calculated by Service Argos from Doppler Shift Measurements between uplinks. Raw data were downloaded from the SMRU website (http://www.smru.st-andrews.ac.uk/). Salinity, temperature and depth information were not used for this particular study but all data are available through the PANGAEA system (http://www.pangaea.de).

Only information from the summer (post-breeding) foraging migration was used for this study. Female elephant seals from Marion Island tend to move southeast along the SWIR, returning back to the island after a few short weeks in order to moult (Tosh, 2010).

3.2 Study Area

The area selected for investigation extends from -30°S to -70°S, and from 20°W to 55°E. This selection encompasses all the ACC fronts and zones between South Africa and the Antarctic continent, and also includes the highly fractured SWIR (Fig. 3.1).

3.3 Bathymetry

In order to visualize horizontal seal distribution in relation to the SWIR, bathymetry data was downloaded in netCDF format via the NOAA National Geophysical Centre platform. The ETOPO bathymetry product was extracted with function etopo2v2.m at spatial resolution of 2' (Fig. 3.1). http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO2/ETOPO2v2-2006/ETOPO2v2g/netCDF

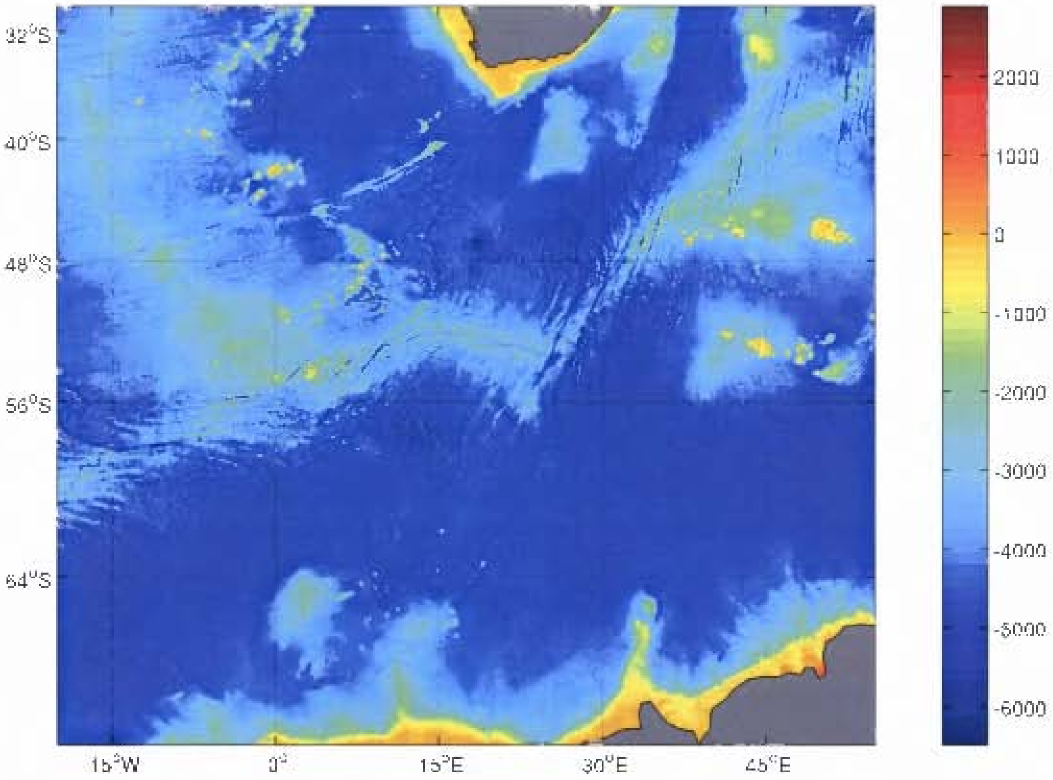

Fig. 3.1: The study area as it extends from South Africa to the Antarctic Continent, showing the bottom topography (approximately -5 km – sea level)

3.4 Chlorophyll-a

Conceivably, top marine predators such as southern elephant seals may recognize a suite of individual or coupled environmental and physical cues. However, phytoplankton are the foundation of the marine food web and shifts in the abundance and distribution of primary producers would be expected to impact on all these networks (Henson *et al.*, 2009). Ocean colour studies allow for an inference of downstream connections to food chains at practical spatio-temporal scales. Specifically, chlorophyll-a concentration can be used as an approximation of phytoplankton production and biological richness (Platt and Sathyendranath, 2008). Due to its usefulness as a marker of underlying oceanographic factors, remotely measured chlorophyll-a concentrations were selected as the chief indicator of system dynamics.

Merging all available data within a chosen period of time generates one image that is representative of conditions during that interval (Fig. 3.2). Creating composite images reduces the number of missing data points resulting from cloud cover or other interferences. For this study, bi-monthly binned level 3 data from the ESA GlobColour project were used. GlobColour is merged ocean color data from ENVISAT's Medium Resolution Imaging Spectrometer Instrument (MERIS), the Moderate Imaging Spectrometer (MODIS) on the Aqua Earth Observing System (EOS), and the Sea-viewing Wide Field of view Sensor (SeaWiFS) on board OrbView-2 (ESA Globcolour Project). The chlorophyll-a data has been spatially interpolated onto a regular ¼ degree grid and provided in mg/m^3. This is in order to make for easier comparison with satellite altimetry products, which are mapped to the same spatial resolution. The Globcolour data used in this study covers the austral summers from 2005 to 2009.

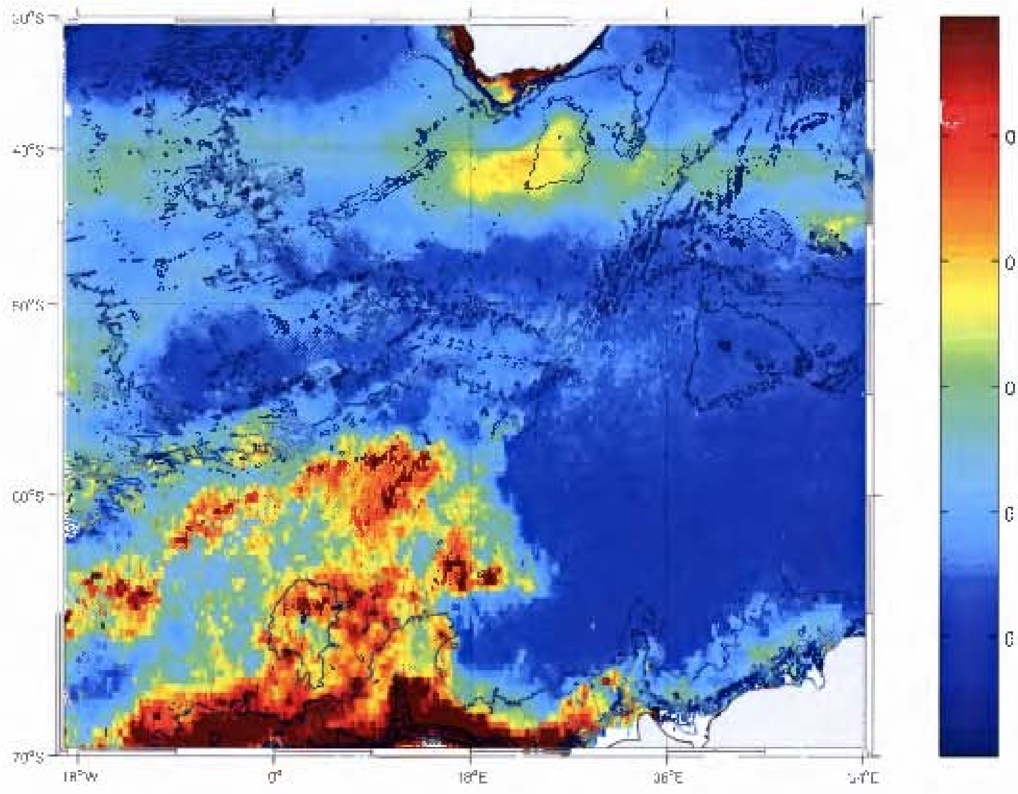

Fig 3.2: Overlayed onto ETOPO bathymetry data; composite GlobColour data of chlorophyll-a values from 2005 – 2009. Colorbar values are presented as $\log_{10}(\text{mg/m}^3) + 1$.

A box-and-whisker plot was generated to descriptively depict the minimum chlorophyll-a value, the lower quartile, the median value, the upper quartile and the maximum chlorophyll-a concentration of the waters the adult female seals travel and forage within. As a graphical tool, differences in concentrations were displayed without assumptions being made about the underlying relationships.

3.5 Seal Movements

Raw distribution data were processed with a filter that removes locations exhibiting unrealistic swim speeds and turning angles as per the methodology from Freitas *et al* (2008) (Fig. 3.3). "False" location estimates are identified based on the premise that swim-speeds higher than 3.5 m/s or 10 km/hr are improbable (Gaspar *et al.,* 2006). Furthermore, locations creating a 'spike' in the track line with angles smaller than 15° and 25° were flagged as erroneous, as were the associated extensions greater than 2500m and 5000m, respectively (Fig. 3.3). Filtering out of these values was carried out in the R computing environment (R Development Core Team, 2008). Erroneous data are generally due to interruptions to the communication uplink with the Argos receiver during a surfacing event – data collected via satellite are, in fact, only subsets of the information recorded by the devices themselves (McIntyre *et al.,* 2010a).

While at sea, seals surface many times per day to breathe. Only some surfacing events will result in a successful communication uplink to Argos satellites, though there are normally at least several position estimates obtained per day. After applying the velocity filter, remaining "true" data points were processed to generate daily locations for each seal.

The principal reason for taking daily latitudes and longitudes instead of working with several position points per day is that the accompanying oceanographic data is not available at finer temporal resolutions. Because chlorophyll-a concentrations do not vary as quickly or as powerfully in the open ocean as they do in coastal or near-coastal regimes (Clarke and Leakey, 1996), behavioral changes relative to changes in the chlorophyll-a can still be comprehensively studied at daily time intervals.

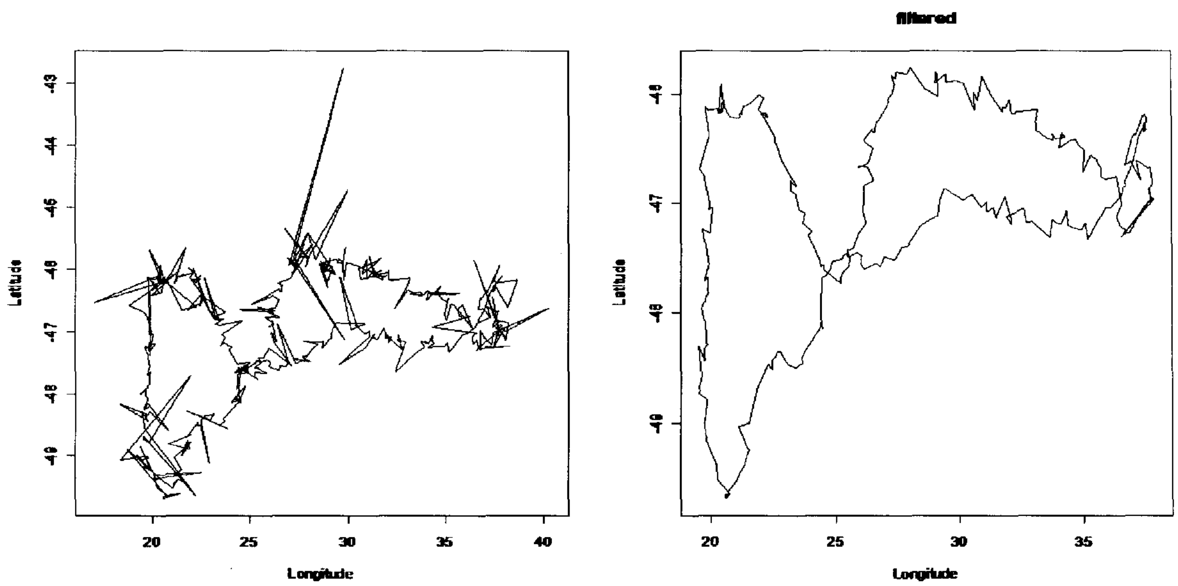

Fig. 3.3: Raw tracks are filtered to remove "false" data using the R statistical computing program (Data from tagged adult female elephant seal YY348 tracked in 2007).

Statistical Analysis

Data processing was executed off-line using a commercial software package (MATLAB 6.1, The MathWorks Inc., Natick, MA, 2000). MATLAB is a general-purpose scientific programming language that provides a tool for manipulating matrix data and creating visual representations such a plots. Scripts and functions were created (M-files) to process the R-filtered data. As a first step, average latitudes and longitudes were generated for each day so as to provide a daily mean position, then overlaid onto the GlobColour two-weekly binned (level 3) merged data.

3.6 Linking Chlorophyll-a and Speed

One of the most challenging aspects of linking daily seal positions to a chlorophyll-a value arises from the temporal disconnection. Day-to-day satellite snapshots of the foraging grounds that adult female elephant seals exploit are available for fine-scale analysis but only small areas, or windows, are not blanketed out by cloud. Fortunately, relative to coastal waters, open ocean phytoplankton blooms do not shift and change over rapid time-scales.

GlobColour data merged over one week was unfortunately overly patchy and too few daily seal positions were assigned a chlorophyll-a reading. Using monthly-merged data, the majority of seal positions then had a value attached but the temporal gap became too large to capture spatial changes in bloom dynamics and variations in chlorophyll-a concentrations. The compromise was a two-weekly merged product where some daily positions were lost, but where mesoscale shifts in productivity and richness were still captured. Each final chlorophyll-a concentration assigned to the daily seal position is thus a merged value calculated from all concentrations from the week before and the week after.

From each of these daily positions, a swim-speed (km/day) was calculated by computing the distance between successive daily averaged latitudes and longitudes. Essentially, longer track lengths between days imply greater speeds and, by extension, travelling behaviour. Conversely, short track lengths show reduced swim rates and, with ARS in mind, imply foraging.

Descriptive analysis:

Box and whisker plots

Boxplots of the travelling speeds at different chlorophyll-a concentrations were generated to graphically represent the minimum swim rates, the lower and upper quartiles (the spread of the data), medians and the maximum swimming rates. As a descriptive tool, the boxplots served to graphically represent the spread of travelling speeds at varying chlorophyll-a concentrations without making assumptions about any relationships between the variables.

Test for nominal variables:

Chi-square test of independence

A chi-squared (X^2) test of homogenity was performed to detect if chlorophyll-a concentrations have a measurable effect on the travelling speeds of adult female southern elephant seals from Marion Island. The 3x3 contingency table was generated in STATISTICA (StatSoft, 2010).

Chlorophyll-a bins of low, medium and high concentrations were tested against low, medium and high daily swimming speeds (see Table 3.2 for bin designations). The null hypothesis was that the probabilities for each outcome (low, medium or high swimming speed) are independent of primary productivity (low, medium or high chlorophyll-a). The X^2 test is then applied to compare the expected contingency table of independent probabilities to the observed contingency table. Finally, the X^2 value is measured at a confidence interval of 95% on the chi-square probabilities table to determine the level of significance. Statistical significance for all analyses was set at $p < 0.05$.

Table 3.2: Predefined bins of chlorophyll-a concentrations and travel speeds (swim rate)

	Low	**Medium**	**High**
Chlorophyll-a (mg/m3)	0.05 – 0.2	0.2 – 0.35	0.35 – 0.5
Travel Speed (km/day)	0 - 50	50 - 100	100 - 150

Binning is a useful tool for aggregating data to test the possible effects of one variable on another, but it can be a bulky method of manipulating diffuse data and invariably some information is lost.

Test for multiple measurement variables:

Correlation and linear regression

Using the same matrix of speed and attached values of chlorophyll-a concentrations, an exploratory methodology was implemented to statistically quantify the link between the two variables (Legendre and Legendre, 1998). As with the chi-square test of homogeneity or independence, chlorophyll-a concentration, as an indicator of marine productivity, stood as the independent variable. Travelling speed, as calculated from the distance between daily averaged latitudes and longitudes, was again the dependent variable (table 3.2).

A linear regression was selected merely as a method of broadly visualising if the dependent variable (speed) changes when the independent variable (chlorophyll-a concentration) varied. Furthermore, Pearson's Coefficient of Correlation was computed to quantify the strength of this relationship. Where the P-value falls below 0.05, the relationship may be considered significant and the null hypothesis of independence may be disregarded. Testing was done in MATLAB and STATISTICA (2010).

Simple moving median

Egerton *et al.* (1999) showed that using a simple moving median on raw information significantly reduces noise and filters outliers. A successive moving median is particularly useful for detecting the core relationship between two variables, speed and chlorophyll-a concentration. Furthermore, an assumption of normality is not required.

Due to the high dispersion of the seal data, this filtering technique was applied to R-filtered information that still contained the outliers previously removed for the chi-square test, correlation and regression analyses. The filtering method was calculated as follows (Legendre & Legendre, 1998):

$$X_i = \text{median}\ (X_{i-n}, \ldots, X_i, \ldots, X_{i+n})$$

The value of the average speed (Xi) at chlorophyll-a concentration i is equal to the median of the speed in a "window" of chlorophyll-a concentration. This window sits between chlorophyll-a concentrations $i-n$ and $i+n$ where n is the order of the moving median. Intervals of chlorophyll i ranging from 0 to n were filtered in MATLAB using only raw data between i to $i+n$ (Legendre & Legendre, 1998).

A successive moving median method automatically removes the outliers of the dataset and displays a maximum amount of information on the trend of the relationship (Legendre & Legendre, 1998). Successive moving median tests were performed until the data plateaued; in this case, after six repeats.

3.7 Linking Chlorophyll-a and Change in Orientation

Optimal foraging theory and area-restricted search (ARS) predict that top marine predators would increase turning frequency as they encounter patches of higher prey density (MacArthur and Pianka, 1966; Kareiva and Odell, 1987; Dragon *et al.,* 2010). This increase of turning frequency would be representative of Brownian motion type foraging, as opposed to bouts of long step lengths indicative of Lévy-type active searching (Reynolds, 2008; Reynolds, 2009).

In this study, the limiting factor has consistently been the availability of reliable temporal and spatial chlorophyll-a data. Due to the difficulties in obtaining 'clean' daily ocean colour data, two-weekly merged GlobColour values of chlorophyll-a were linked to the corresponding daily seal positions. By using this daily average, relationships to chlorophyll-a could be broadly tested and observed, but very fine-scale resolution was lost. In order to test for the frequency of turning behaviour, however, this fine-scale data is a necessity.

Without being able to accurately utilize several seal positions per day for studying frequency, changes in orientation from one day to the next were used as a potential proxy.

Exploratory Analysis

Polar coordinate system

As before, daily seal positions were generated in MATLAB by averaging latitudes and longitudes within 24-hour windows. Each position was then assigned a corresponding chlorophyll-a value from the merged GlobColour product. In addition, each daily location was projected onto a polar coordinate system with East represented as 0°, North as 90°, West as 180° and South as 270° (Fig. 3.4). The angles, or differences in orientation between two successive daily positions were thus computed in degrees. The final change in orientation was calculated by subtracting each successive daily angle from that of the day before. Any nonzero values (1° - 180°) would signify that there had been a change in swim direction from one day to the next. Acute values (<90°) would imply abrupt and sharp changes in orientation, while obtuse (90° - 180°) would be indicative of wider turns.

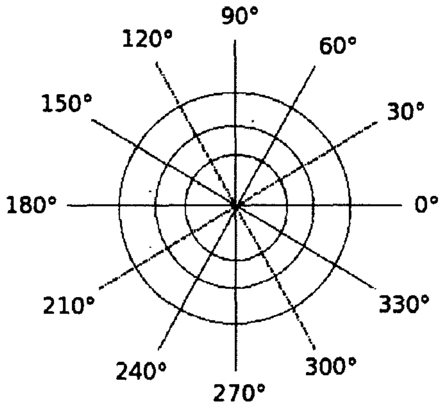

Fig. 3.4: The Polar Grid layout for measuring changes in orientation.

Descriptive analysis:

Box and whisker plots

Boxplots of the changes in orientation at different chlorophyll-a concentrations were generated to graphically represent the median, the lower and upper quartiles (the dispersion or spread), the minimum and the maximum turning angles. As a descriptive tool, the boxplots served to graphically represent the spread of changes in orientation at varying chlorophyll-a concentrations without making assumptions about any relationships between the variables.

Test for multiple measurement variables:

Correlation and linear regression

Using the same matrix of change in orientation and chlorophyll-a, a linear regression was done to broadly visualise if the dependent variable (speed) changed when the independent variable (chlorophyll-a concentration) varied. Furthermore, Pearson's Coefficient of Correlation was computed to quantify the strength of this relationship. Where the P-value falls below 0.05, the relationship may be considered significant and the null hypothesis of independence may be disregarded. All testing was done in MATLAB and STATISTICA (2010).

4 RESULTS

Advances in remote sensing and tagging technology have made it possible to investigate the relationship between oceanographic dynamics and the distribution of certain marine species (Bailleul *et al.,* 2010). For this study, surface chlorophyll-a concentration is used as a biomarker of the underlying dynamics and of the productivity rather than as direct indicator of prey density (Park *et al.,* 2002; Dragon *et al.,* 2010). Top predators such as elephant seals are not passive tracers of water movement and spatial and temporal lags make it difficult to correlate their foraging distribution with chlorophyll-a levels. However, optimal foraging theory predicts that travelling speed and turning frequency would be measurably affected by prey density, which is in turn affected by the spatial and temporal richness of phytoplankton (Longhurst, 2007; Dragon *et al.,* 2010).

Using remotely measured chlorophyll-a concentration as a biomarker of underlying biological richness; a question arises whether adult female southern elephant seals reduce travelling speed when encountering waters exhibiting higher chlorophyll-a concentrations? Furthermore, is it possible that changes in the daily orientation could be related to changes in productivity?

4.1 Tagging

Thanks to a dedicated group of scientists working under extreme conditions, a total of 70 elephant seals were successfully instrumented with satellite-relay data loggers (SRDLs) on Marion Island between 2004 and 2009. Twenty-seven of those tagged were male, 21 were yearlings or sub-adults, and 51 were instrumented for their lengthy post-moult migration only. Of the total number of animals tagged, 10 elephant seals fitted the criteria of being both post-breeding and adult female.

4.2 Distribution Data

Animals were tracked for a mean period of 59.7 days. Seal BB246 transmitted the longest post-breeding foraging trip of 75 days during the summer of 1998/1999. The shortest transmission of 16 days was due to an incomplete migration – either the tag failed or seal GG380 died at sea. Bar one, all adult females remained north of 56° S and east of 14° E, most moving directly southwest along or parallel to the SWIR (Fig. 4.1).

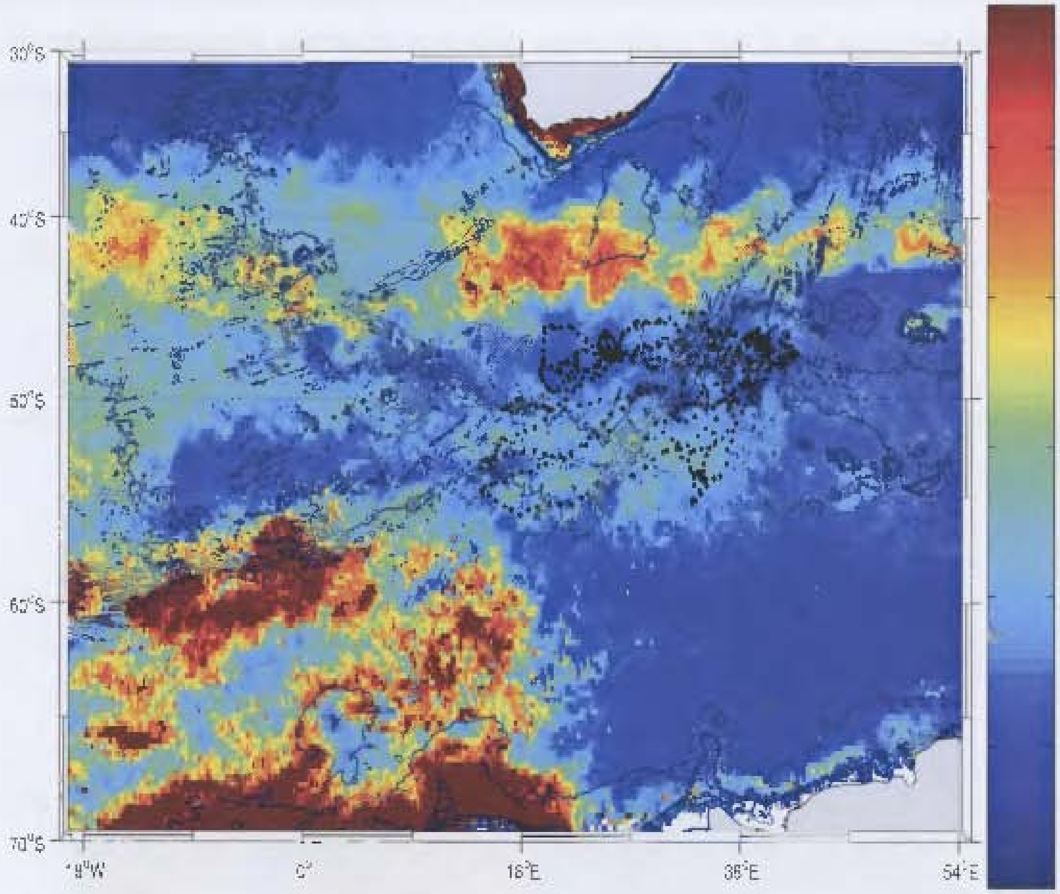

Fig. 4.1: Chlorophyll-a patterns (log$_{10}$ (mg/m^3) −1) and distribution of all adult female elephant seal except BB246 during their post-breeding foraging migration (November 2008 – January 2009).

One seal exhibited an alternate foraging distribution, swimming northeast instead of southwest (See Fig. 4.2 and 4.3 for overall perspective and zoom-in picture, respectively). This is the same seal that transmitted the most number of days at sea, namely BB246.

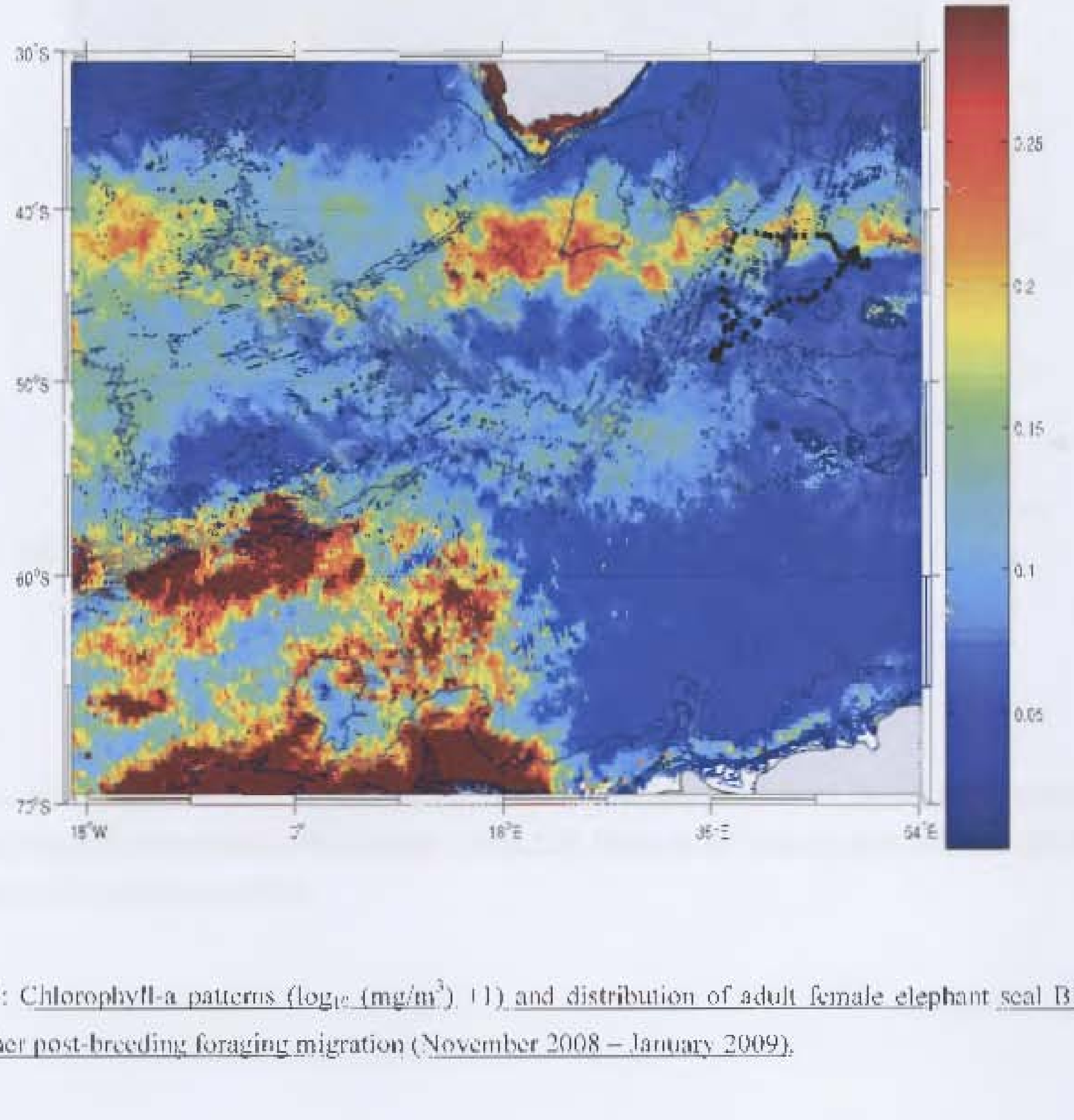

Fig. 4.2: Chlorophyll-a patterns ($\log_{10}$ (mg/m^3) +1) and distribution of adult female elephant seal BB246 during her post-breeding foraging migration (November 2008 – January 2009).

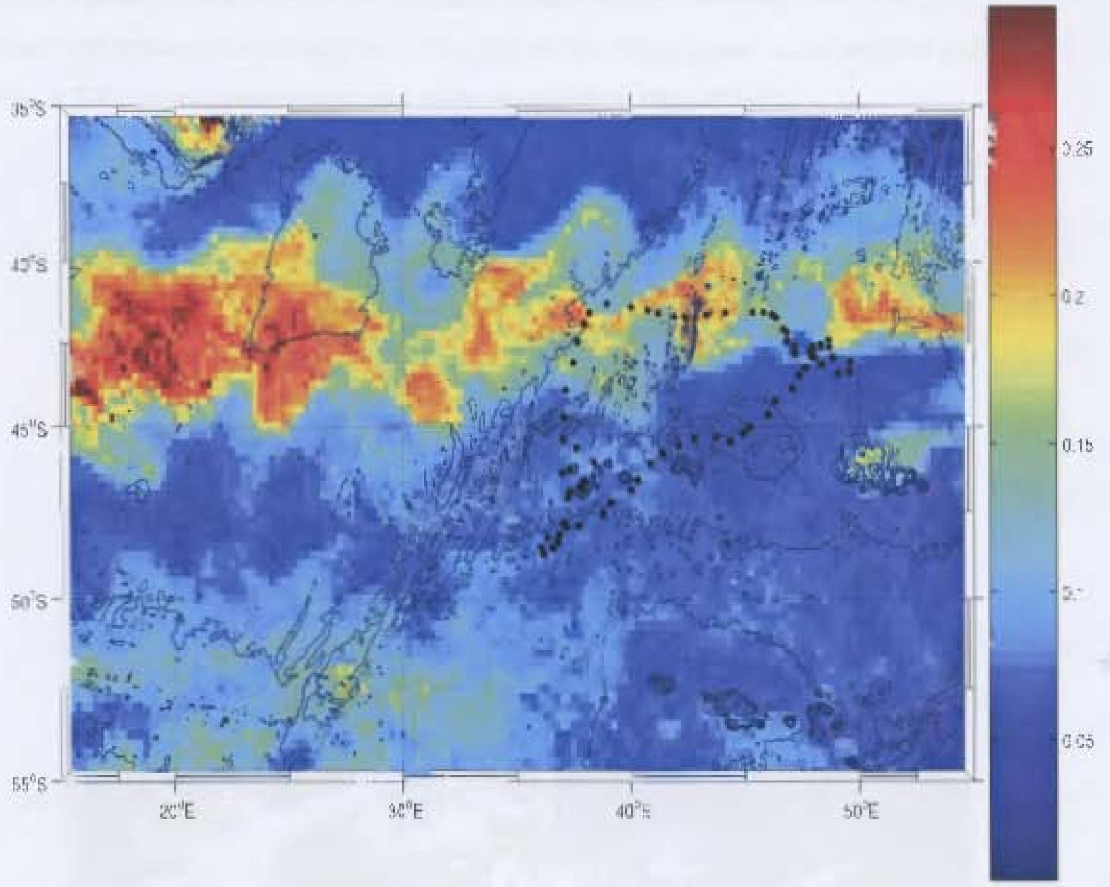

Fig. 4.3: Chlorophyll-a patterns (log$_{10}$ (mg/m^3) +1) and distribution of BB246 during her post-breeding foraging migration (November 2008 – January 2009) with focus on the areas of enhanced chlorophyll-a at the subtropical convergence (STC).

Over the same months (November 2008 – January 2009) that BB246 made the unusual foraging trip to the northwest of Marion Island, the only other adult female tagged and monitored that year moved along the SWIR Plumes of enhanced chlorophyll-a to the east of the ridge appear to be targeted and circled (See Fig. 4.4 and Fig. 4.5 for overall perspective and zoom-in snapshot, respectively).

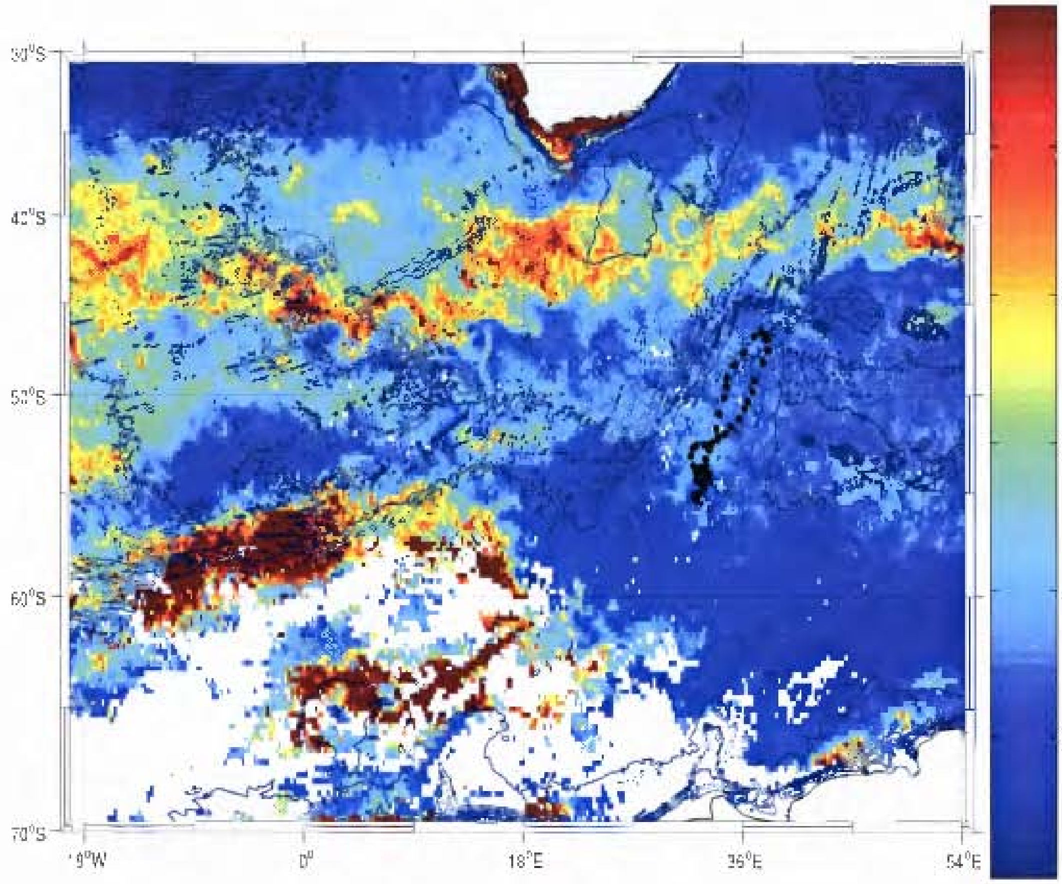

Fig. 4.4: Chlorophyll-a patterns ($\log_{10}$ (mg/m^3) +1) and distribution of adult female elephant seal WR336 during her post-breeding foraging migration (November 2008 – January 2009).

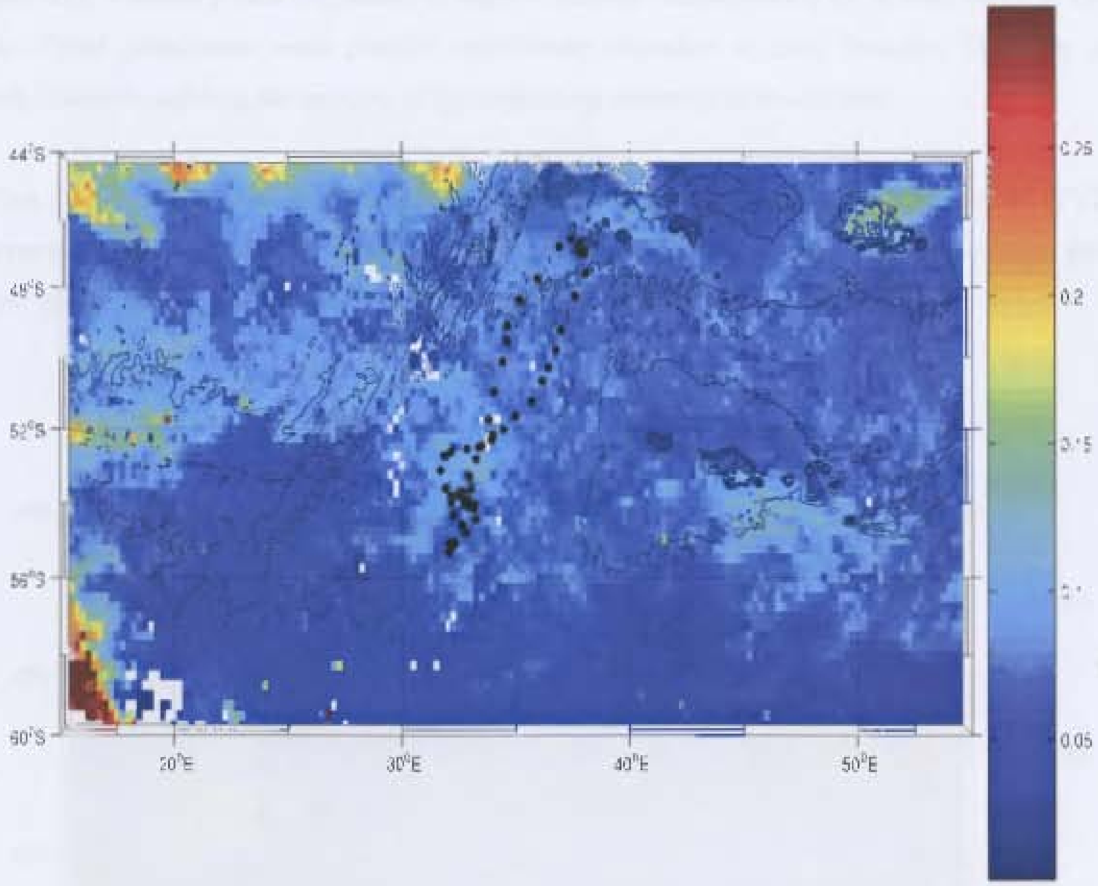

Fig. 4.5: Chlorophyll-a patterns ($\log_{10}$ (mg/m^3) +1) and distribution of WR336 during her post-breeding foraging migration (November 2008 – January 2009) with focus on the area of enhanced chlorophyll-a concentrations to the east of the SWIR

Two adult female elephant seals tagged and tracked for the duration of their summer foraging trip (November 2007 – January 2008) appeared to target mesoscale features along the western edge of the SWIR (Fig. 4.6). These phenomena were possibly small-scale meanders or eddy features. This may only be speculated, however, pending the analysis of the supporting altimetry or *in-situ* data.

GlobColour data shows plumes of enhanced productivity in the areas flanking the SWIR. Seals YY240 and RR483 appear to direct their foraging efforts along the edges of these plumes, circling the target areas (See Fig. 4.7 to "zoom-in" to the relevant mesoscale features of enhanced chlorophyll-a).

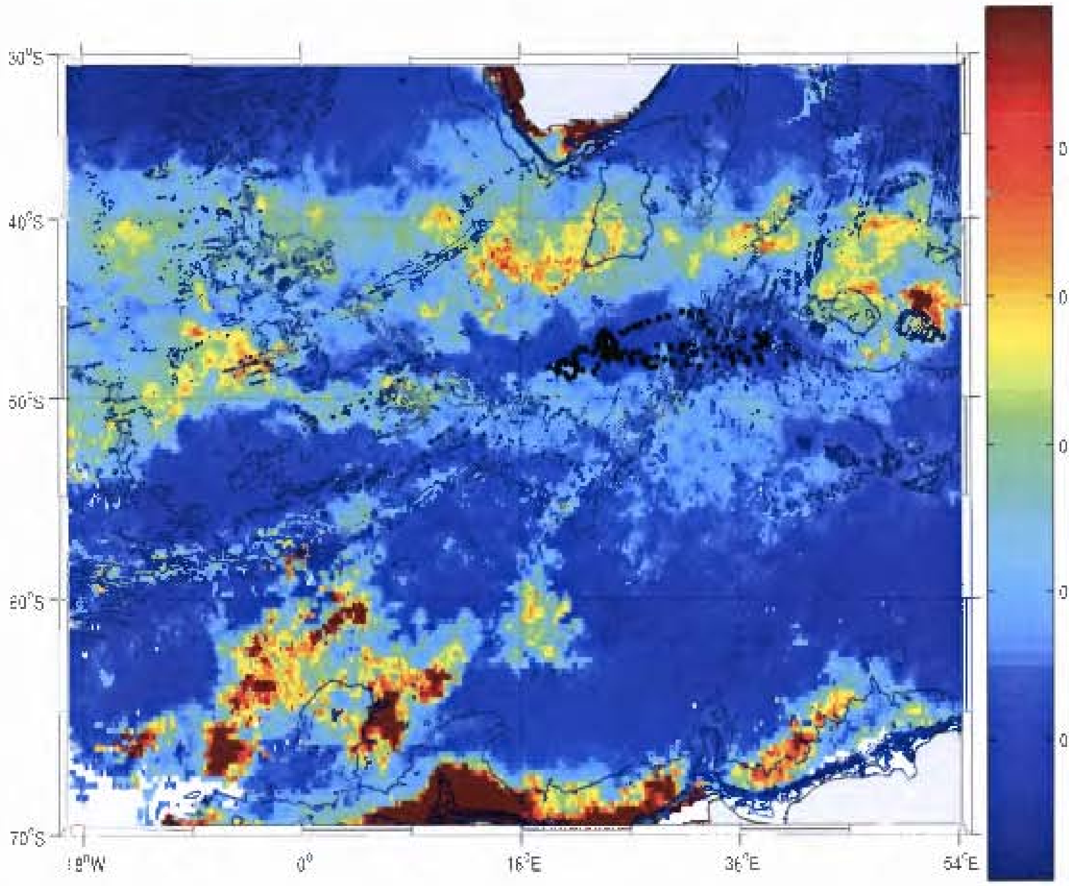

Fig 4.6: Chlorophyll-a patterns ($\log_{10}$ (mg/m^3) +1) and distribution of adult female elephant seals YY240 and RR483 during their post-breeding foraging migration (November 2007 – January 2008).

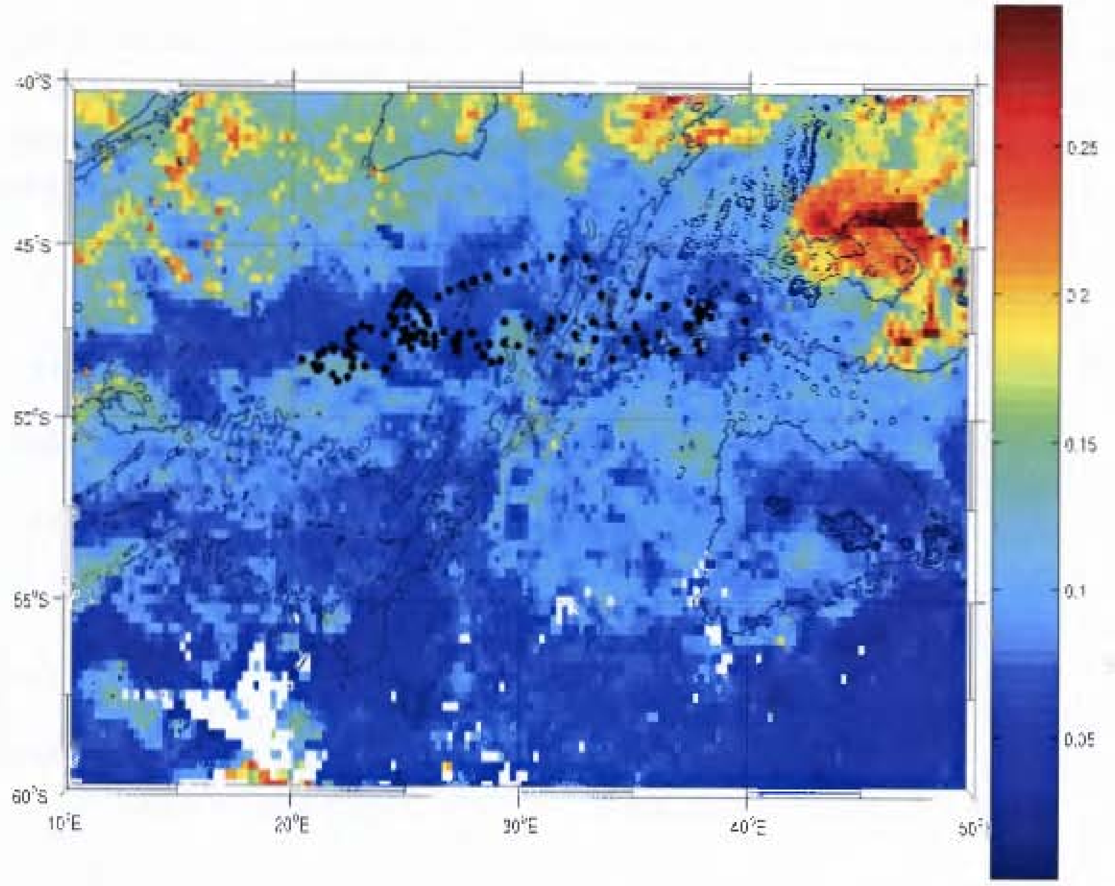

Fig. 4.7: Chlorophyll-a patterns (log$_{10}$ (mg/m^3) +1) and distribution of YY240 and RR483 during their post-breeding foraging migration (November 2007 - January 2008) with focus on the areas of enhanced chlorophyll-a at the SWIR.

4.3 Chlorophyll-a concentrations of Southern Ocean foraging grounds

The median of chlorophyll-a concentration of the waters that these seals travelled through and possibly foraged within is approximately 0.19 mg/m^3 (Fig. 4.8: red line). The minimum value of chlorophyll-a does not fall below 0.05 mg/m^3 (bottom black whisker) but the majority of concentrations are spread between 0.15 mg/m^3 and 0.27 mg/m^3 (the 25th and 75th quartiles, respectively) (bottom and top blue lines of the box).

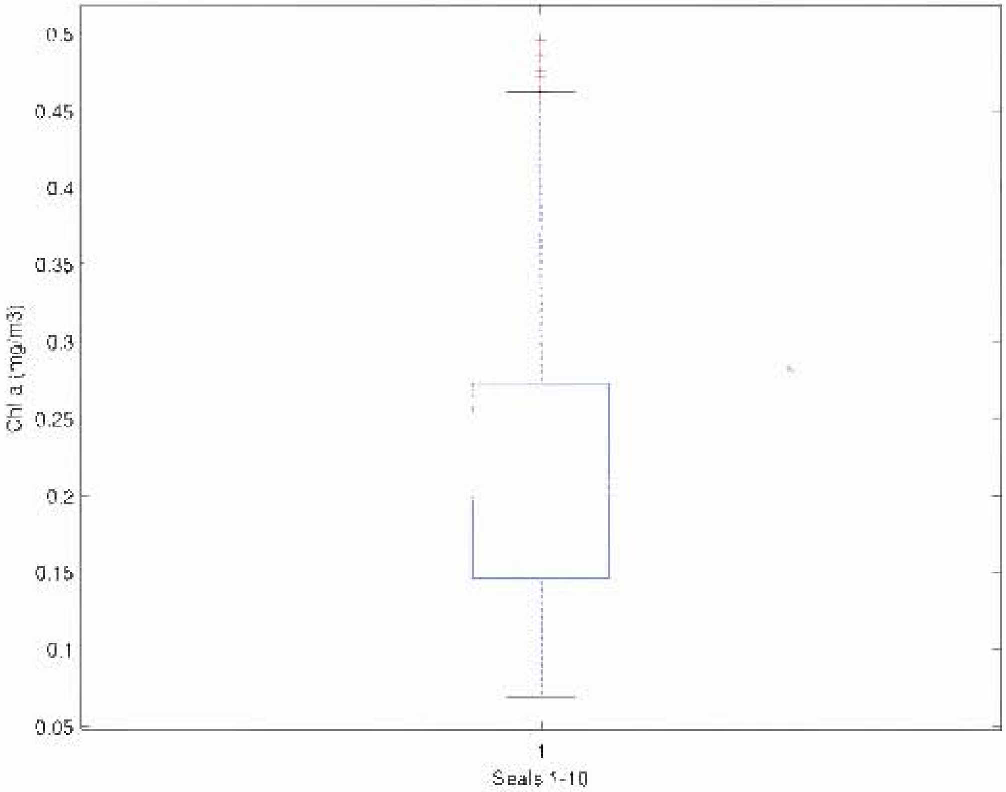

Fig. 4.8: Box and whisker plot of chlorophyll-a concentrations in the environments all 10 adult female elephant seals experienced throughout their foraging migration (2004 – 2009).

The maximum chlorophyll-a concentration that the tagged adult female elephant seals from Marion Island experienced was approximately 0.46 mg/m^3 (top black whisker). Values of chlorophyll-a above 0.5 mg/m^3 (Fig. 4.8: red crosses) were marked as outliers and were disregarded for the chi-squared test, and the correlation and regression analyses.

4.4 Swim Speeds and Chlorophyll-a Concentrations

As seen from Fig. 4.9, adult female southern elephant seals are able to maintain speeds of up to 150 km/day while travelling and searching for productive foraging grounds.

In waters exhibiting chlorophyll-a values between 0.1 mg/m^3 and 0.3 mg/m^3, the majority of travel speeds are spread between 35 km/day and 85 km/day. In line with optimal foraging and ARS theory, where chlorophyll-a concentrations remained below 0.15 mg/m^3, the tagged adult female seals showed highest swim speeds, with the bulk of data spread between 45 km/day and 85 km/day (lower and upper quartiles, respectively).

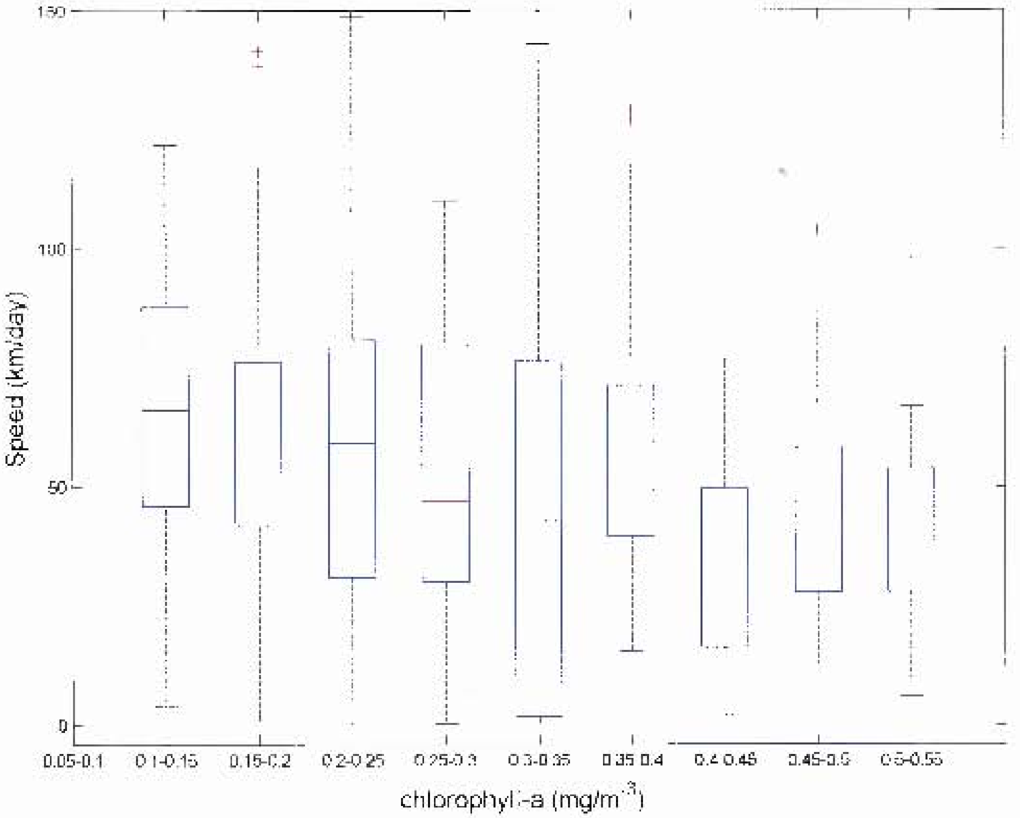

Fig. 4.9: Box and whisker plots of the different speeds travelled by adult female elephant seals moving through varying chlorophyll-a waters

The most variation in speeds coincides within a narrow band of chlorophyll-a concentrations between 0.3 mg/m^3 and 0.35 mg/m^3 (Fig. 4.9). It is also within this narrow range that the seals travel the slowest approximately 5 km/day at the lowest quartile.

In waters with chlorophyll-a values above 0.35 mg/m^3, the spread of data narrows and the upper quartiles of swim speeds do not exceed 60 km/day. In other words, the variance appears to decrease with an increase in chlorophyll-a concentration.

At the highest chlorophyll-a concentrations between 0.4 mg/m^3 and 0.55 mg/m^3, the tagged adult female southern elephant seals consistently slowed their swim speeds to between 15 km/day to 30 km/day. The slowest median of speed was found at between 0.45 mg/m^3 and 0.50 mg/m^3.

Chi-squared analysis

In order to statistically test whether chlorophyll-a and speed were impacting on each other's distribution, a chi-squared contingency table was generated using low, medium and high bins of speed (Table 4.1: rows) and chlorophyll-a concentrations (Table 4.2: columns).

Table 4.1: Contingency Table of observed speed against chlorophyll-a concentration data

	0.05 - 0.2	0.2 - 0.35	0.35 - 0.5	
0 - 50	108	89	42	239
50 - 100	143	56	21	220
100 - 150	20	15	1	36
	271	160	64	**495**

Table 4.2: Contingency Table of expected data

	0.05 - 0.2	0.2 - 0.35	0.35 - 0.5
0 - 50	131	77.3	30.9
50 - 100	120	71.1	28.4
100 - 150	19.7	11.6	4.65

Chi-square value = 23.0
Degrees of freedom = 4
Significance < 0.001

We reject the null hypothesis of independence because $p < 0.05$

Correlation and regression

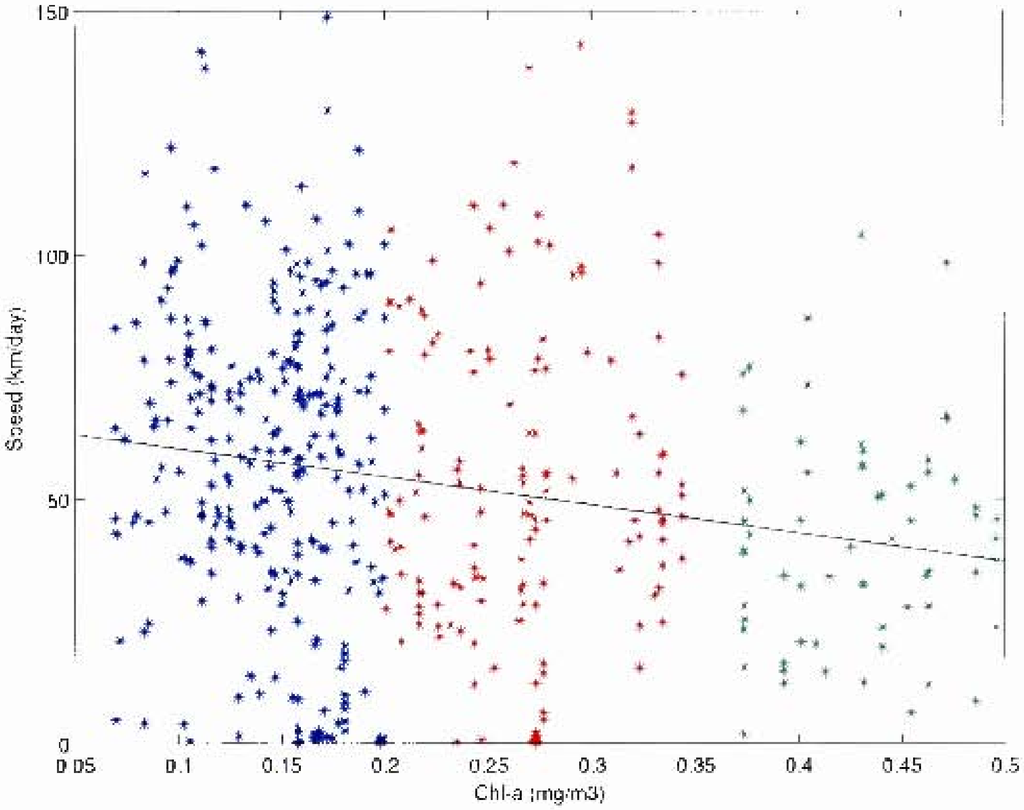

Fig. 4.10: Scatter plot of travel speed correlated to chlorophyll-a concentration with linear regression.

Number of data points:	N	= 226
Correlation coefficient:	r	= -0.188
Coefficient of determination:	r^2	= 0.035
Significance:	p	< 0.001

Results indicate a negative relationship between the two variables with 3.5% of the variance of the data cloud explained by this analysis ($r^2 = 0.035$). Despite the wide scatter of data, the correlation of swim rate and chlorophyll-a concentration is significant ($p<0.05$) and the null hypothesis of independence may thus be disregarded.

Speed-associated chlorophyll-a concentrations have been highlighted in blue (0.05 mg/m^3 – 0.2 mg/m^3), red (0.2 mg/m^3 - 0.35 mg/m^3) and green (0.35 mg/m^3 – 0.5 mg/m^3) for visualization of how the data cloud was binned into the three concentrations (Fig. 4.10). In agreement with the box and whisker plot of the chlorophyll-a concentrations experienced by the tagged seals as they forage within the waters of the Southern Ocean (Fig. 4.8), the data cloud is most concentrated between 0.15 mg/m^3 (blue) and 0.27 mg/m^3 (red).

Note that the linear regression line in Fig. 4.10 is simply a visual summary of the association between the variables. In order to improve the accuracy of the coefficient, the large and diffuse data cloud was filtered (moving median filter) to achieve a simple running median.

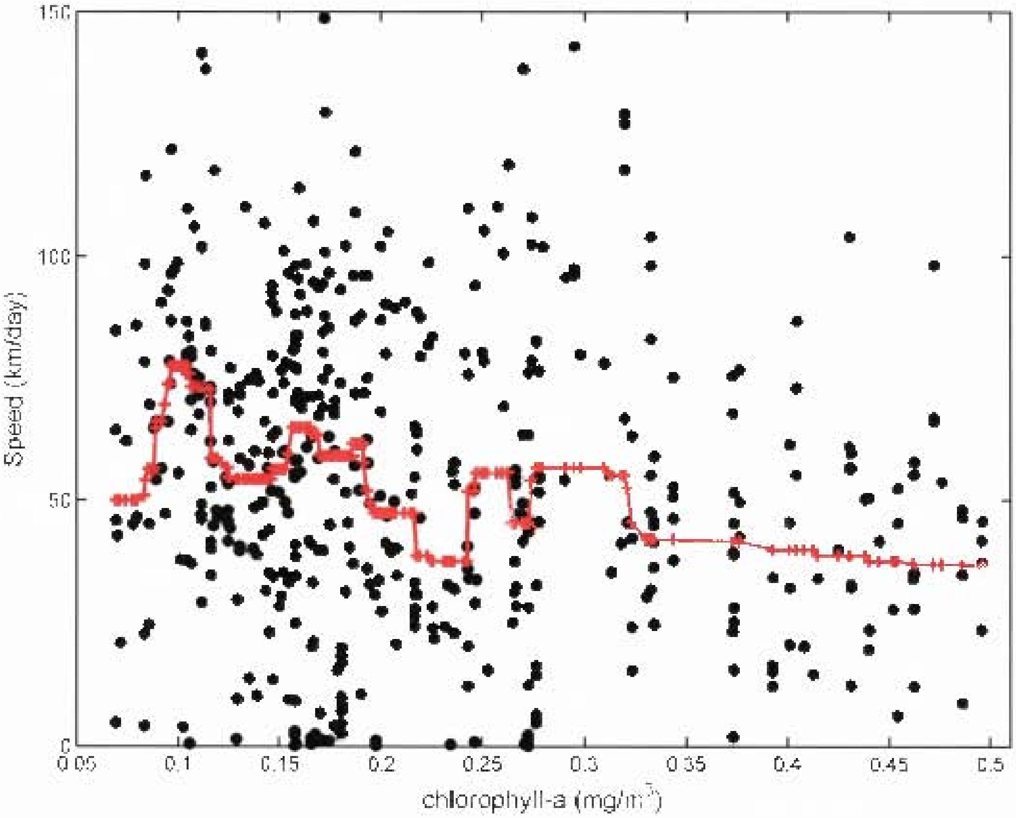

Fig. 4.11: Scatter plot of the filtered data cloud with the running median line shown in red (6th repeat)

The running median does not show linearity between speed and chlorophyll-a until concentrations reach approximately 0.33 mg/m^3. At the lowest chlorophyll-a values, travel speed moves step-wise from 75 km/day at 0.1 mg/m^3 to 55 km/day at 0.15 mg/m^3. Speed continues to adjust in a step-wise fashion, dropping and rising, until the apparent threshold of approximately 0.33 mg/m^3.

4.5 Changes in orientation and Chlorophyll-a Concentrations

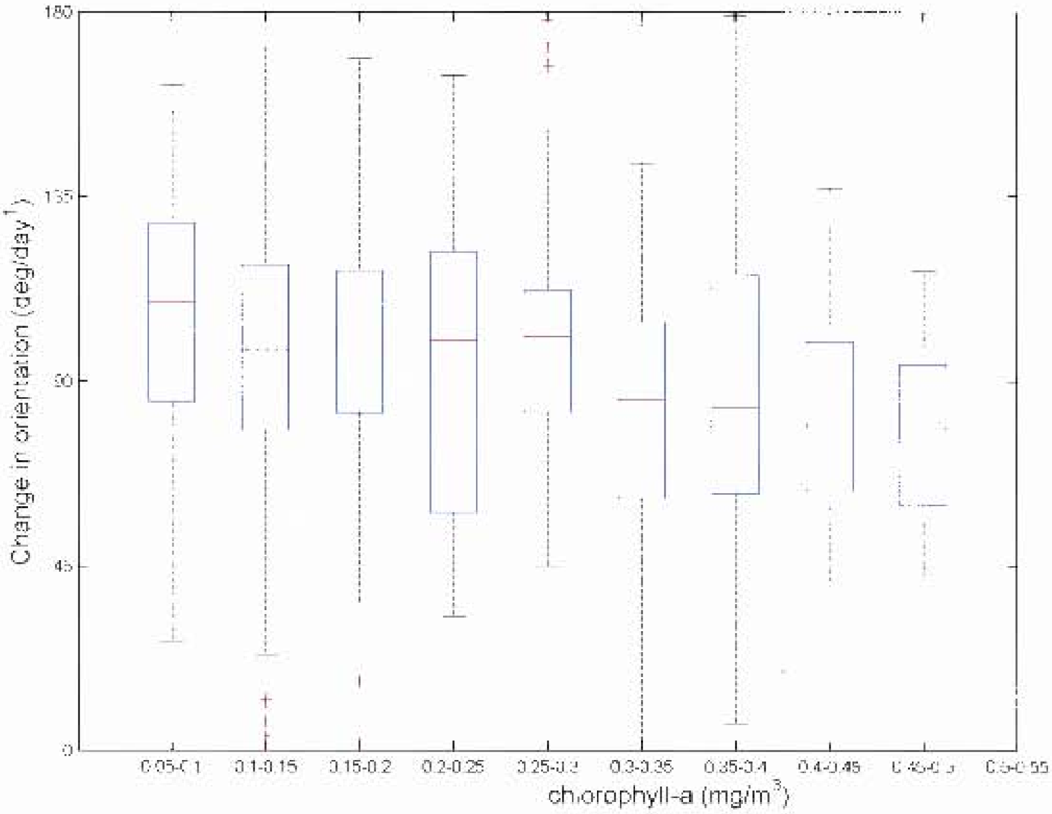

Fig. 4.12: Turning frequency, as measured by change in orientation, of seals moving through varying chlorophyll-a waters

Larger changes in orientation (medians of between 100°/day and 110°/day) occurred in waters exhibiting the lowest chlorophyll-a values (0.05 mg/m^3 to 0.3 mg/m^3). As soon as chlorophyll-a concentrations peaked above this apparent threshold of approximately 0.3 mg/m^3, median changes in orientation consistently dropped to below 90°/day.

Generally, the spread of data is large and ranges from acute (50°/day) to obtuse (130°/day) across the different chlorophyll-a concentrations.

Adult female southern elephant seals exhibit obtuse angles of direction change in low chlorophyll waters, shifting down to acute changes in orientation only once the threshold of approximately 0.3 mg/m^3 is surpassed.

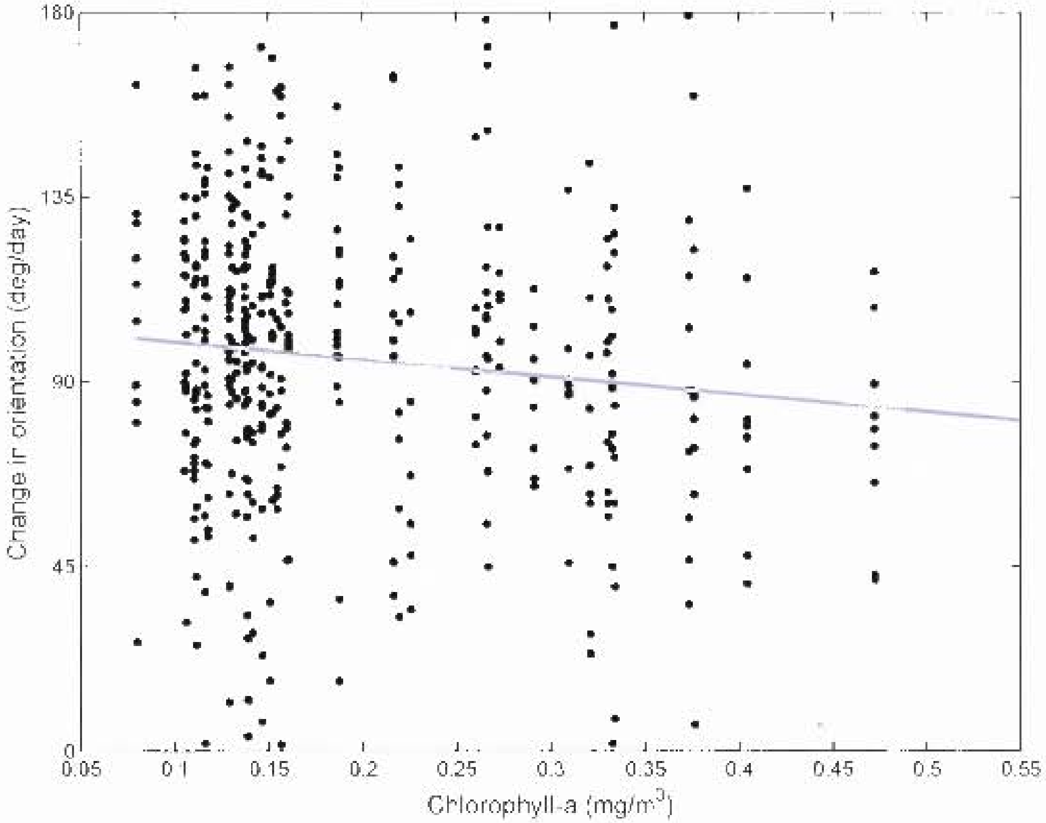

Fig. 4.13: Scatter plot of the change in orientation correlated to chlorophyll-a concentration with linear regression line

Number of data points:	N	= 776
Correlation coefficient:	r	= -0.0137
Coefficient of determination:	r^2	= 0.019
Significance:	p	= 0.005

Results indicate a negative relationship between the two variables but only 1.3% of the variance is explained by this analysis ($r^2 = 0.019$). In spite of the wide scatter of data, the correlation between change in orientation and chlorophyll-a concentration is significant ($p<0.05$) and the null hypothesis of independence may thus be disregarded.

In order to reduce the noise generate by the wide cloud scatter, data was processed using a moving median filter.

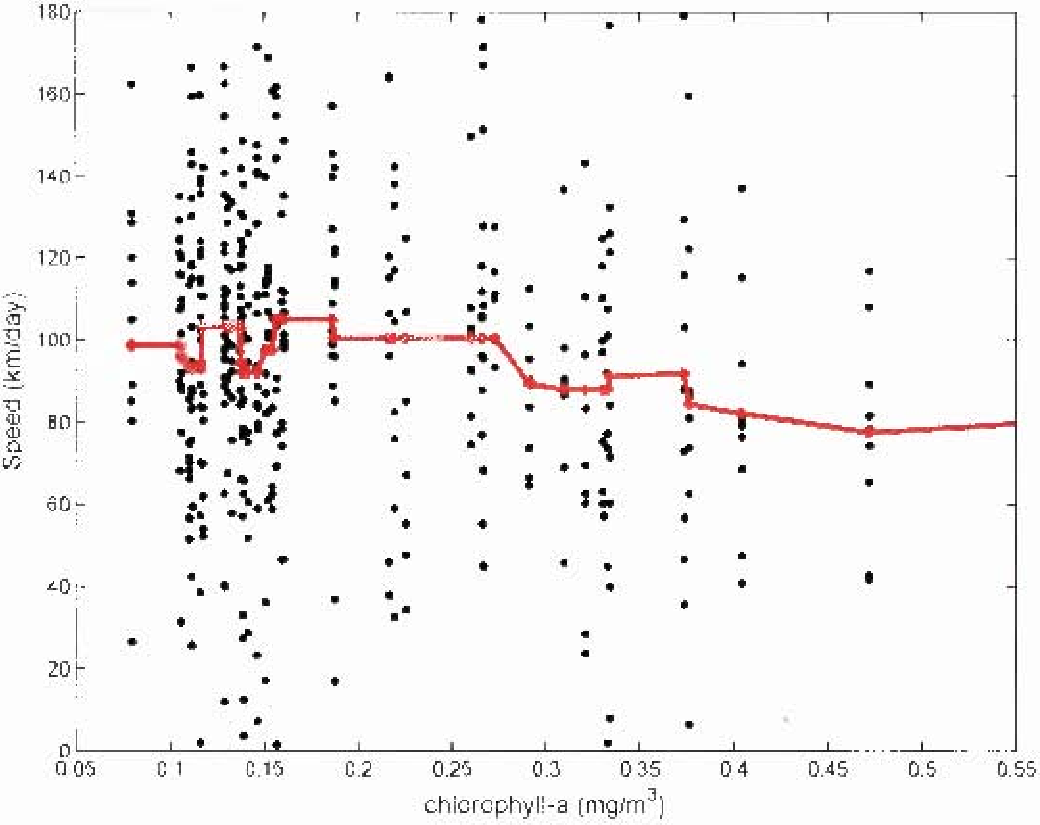

Fig. 4.14: Scatter plot of the filtered data cloud with the running median line shown in red (3rd repeat)

Due to the high density of data between 0.1 mg/m^3 and 0.15 mg/m^3, the variability is naturally more sensitive and so the running median drops and rises in a step-wise manner. At approximately 0.18 mg/m^3, the running median drops to 100° and remains below that threshold as the chlorophyll-a concentrations steadily increase. The second noticeable drop to below 90° occurs between 0.27 mg/m^3 and 0.35 mg/m^3. After this threshold range, the running median appears to smooth out into a more linear trend, though the number of data points within this range is also smaller.

The phenomenon of a chlorophyll-a concentration threshold between approximately 0.3 mg/m^3 to 0.4 mg/m^3 appears to be true for both change in orientation, as a proxy for turning frequency, and swim speed.

From the correlation and regression analyses, and perhaps as a consequence of the expected spatio-temporal lag between primary productivity and predator distribution, only a fraction of the behavioural variance is explained by chlorophyll-a concentration. Despite this, and notwithstanding the fact that the data clouds of both speed and change in orientation are so widely scattered, statistically significant relationships to chlorophyll-a are still apparent.

5. DISCUSSION

'Hotspots' of upregulated primary productivity in the characteristically high-nutrient, low chlorophyll (HNLC) waters of the Southern Ocean can be observed remotely using chlorophyll-a as a marker (Henson *et al.*, 2009). For this study, surface chlorophyll-a concentration is used only as an indicator of the underlying physical dynamics and biological richness rather than a direct indicator of prey density (Park *et al.*, 2002; Dragon *et al.*, 2010). However, areas of upregulated productivity attract swarms of zooplankton, which in turn attract predators ranging from zooplankton to fish and squid, to southern elephant seals. Top predators targeting fish and squid may not exhibit close correlations to mesoscale features due to the spatio-temporal disconnections that mask such relationships (Longhurst, 2007; Bailleul *et al.*, 2010). However, optimal foraging and area restricted search (ARS) theory predicts that speed and turning frequency of these animals would be measurably affected by the presence/absence of such mesoscale features (Longhurst, 2007; Dragon *et al.*, 2010).

This short study aimed to investigate whether chlorophyll-a, as a proxy for productivity, influenced the speed and turning frequency of adult female elephant seals from Marion Island during their post-breeding migration.

5.1 Distribution Patterns

Southern elephant seals, as with most marine predators, have to balance their "free will" to forage according to individual impulse with positively reinforced, successful ontogenetic behavioural patterns (Viswanathan, 2000). Kareiva and Odell (1987) were able to show from model and experimental work that when many animals engage in area restricted search behaviour, the phenomenon of 'preytaxis' – the targeted movement of predators in response to prey – may manifest.

Post-breeding adult female southern elephant seals leave Marion island within a few days of one another and, following typical area restricted search (ARS) patterns, may generate group behaviour where they swarm toward regions of high biological richness (Kareiva and Odell, 1987). In this region of the Southern Ocean, the ACC interacts directly with the dominant bottom topography to generate meanders and eddies. These mesoscale features serve to entrain upwelled nutrients and phytoplankton blooms, making the SWIR a targeted area of enhanced productivity and downstream prey density. In agreement with this phenomenon, all post-breeding adult female seals tracked from 2005 to 2009 showed similar movement patterns and distributions to the SWIR, bar one (Fig. 4.1).

Seal BB246 anomalously moved northwest to the Subtropical Convergence (STC) and appeared to focus foraging energy on the edges of a high chlorophyll-a concentration mesoscale feature, possibly an eddy (Fig. 4.2 and 4.3). Unfortunately, it was the only time this seal had been tagged and tracked, so it is not yet possible to determine whether this particular adult female reliably follows an unusual foraging distribution or ordinarily conforms to the expected pattern. It is not improbable that, as a pup, seal BB246 discovered biologically rich hunting grounds away from the SWIR and continued to exploit the STC as an adult. Only by re-tagging BB246 and monitoring successive post-breeding trips would this be shown with any certainty.

It is also possible that resources were patchier than normal at the SWIR over the November 2008 – February 2009 summer period, inducing a change in foraging pattern direction from southwest to northeast. Longhurst (2007) has proposed that the area between the STC and the APF is one distinct biogeochemical province. It is therefore plausible that the same chemical and/or biological cues exist to the north and south of Marion Island, within the borders of SANT (Longhurst, 2007). Spatially, seal BB246 covered a similar area range but spent 75 days at sea – a full 6 days longer than any other adult female seal tracked between 2005 and 2009. Over the same period, seal GG380 moved southwest from Marion Island to forage along the east of the SWIR but transmission terminated after 16 days (data not shown). The CTD-SDRL either failed or, in line with the theory that food resources were unusually scarce that season, the seal died from starvation. However, another adult female seal WR336 followed the 'conventional' pattern over the same summer months, foraging to the east of the SWIR and circling plumes of enhanced chlorophyll-a (Fig. 4.4 and 4.5) before successfully hauling out to moult after 59 days at sea.

These differences are not fully understood but may simply result from each individual seal's past experiences (Bradshaw *et al.,* 2004). On balance, despite the group behaviour described by Kareiva and Odell (1987) and seen in this study, past successes should act to positively reinforce 'unusual' foraging patterns. The nine adult female southern elephant seals that followed the SWIR do not necessarily represent convention and atypical migration tracks may become less anomalous as more seals are tagged and tracked. Enhanced chlorophyll-a at the SWIR is perhaps as much an indicator of biological richness as it is at the STC. The underlying physical dynamics, however, are very different.

5.2 Productivity around Marion Island

Enhanced productivity in the region of the Prince Edward Islands appears to be a phenomenon of the topography of the SWIR (Perissinotto *et al.,* 1990; Lutjeharms, 1990; Ansorge and Lutjeharms, 2000; McQuaid and Froneman, 2004). Where the ACC interacts with complex bathymetry, bottom torque destabilizes vertical coherence of the water column, upwelling nutrients and generating the formation of meanders and eddies (Sokolov and Rintoul, 2007). As the ACC is funnelled through the SWIR, nutrients are injected into surface waters, vorticity is enhanced and productive eddies form. These mesoscale features serve to retain nutrients and biomass, transporting phytoplankton blooms downstream and providing potentially rich foraging grounds for birds and mammals (Jonker and Bester, 1998; Nel *et al.,* 2001; Sokolov, 2008; Bailleul *et al.,* 2010). Eddies formed at the SWIR also play an important role in transporting Antarctic euphausiid species downstream, and contribute to the spatial mixing of zooplankton communities within the region (Bernard *et al.,* 2007).

Plumes of upregulated chlorophyll-a appear to flank both sides of the SWIR and productive 'hotspots' do not seem to be limited to downstream areas as originally thought (Ansorge and Lutjeharms, 2003) (Fig. 4.6). Over the post-breeding migration of November 2007/January 2008, seal YY240 and seal RR483 directed their foraging energy to the west of the SWIR, both circling plumes of upregulated chlorophyll-a (Fig. 4.7) and successfully returning to Marion Island after 65 days at sea to moult.

Feeding success over the few weeks between breeding and moulting needs to be substantial enough to regain body condition, as seal weight drops dramatically (up to 40%) over the breeding season (Arnbom *et al.,* 2007). However, southern elephant seals are compelled to make foraging decisions based on little knowledge of the current resource distribution (Sims *et al.,* 2008). Despite the patchy and dynamic distribution of prey species in the Southern Ocean, adult females may be able to fine-tune their foraging decisions using physical, geographical and seasonal clues (Humphries *et al.,* 2010). Monitored remotely, chlorophyll-a concentration is a useful indictor of these underlying factors (Falkowski *et al.,* 2008)

The median surface chlorophyll-a concentration of the waters that the 10 tagged adult female elephant seals experienced around Marion Island was approximately 0.19 mg/m^3. The highest values of chlorophyll-a concentration peaked at around 0.46 mg/m^3; however, values mostly remained within a modest range of 0.15 mg/m^3 to 0.27 mg/m^3. Despite these characteristically moderate measurements of chlorophyll-a, female elephant seals appear to benefit from intense feeding success over their short summer foraging migration, regaining enough body condition to haul out onto land for the obligatory moult. Using ocean colour data from SeaWiFS, Moore and Abbott (2000) showed that mean chlorophyll concentrations remained well below 0.30–0.40 mg/m^3 for most of the Southern Ocean. Either modest gradients of change in surface chlorophyll-a values reflect large shifts in underlying biological richness, or remotely measured chlorophyll-a is an inaccurate gauge of actual productivity. As the most commonly used SeaWiFS chlorophyll-a algorithms aim to retrieve concentrations to ±35% accuracy (McClain *et al.*, 2009), trends suggested in this study could be further confirmed by validation with *in situ* data. Additionally, as ocean colour data only records surface features, *in situ* studies would confirm if this causes misrepresentation of potentially important features deeper than 1 optical depth (e.g.: sub-surface chlorophyll-a maxima).

Availability of light and nutrients are key "bottom-up" factors that control primary productivity in the high-nutrient, low chlorophyll (HNLC) waters of the Southern Ocean (Sokolov, 2008). The seasonal pattern of incoming solar radiation over the Southern Ocean entails winter darkness south of 66°S and an extensive midsummer daylength (Longhurst, 2007). In sections of the SANT biogeochemical province delineated by Longhurst (2007), total irradiance received at the sea surface in high summer is greater than in the central gyres. As a consequence, surface phytoplankton in the zone flanked by the STF and PF may become *light* saturated and, by late summer, subsurface primary production may be more significant (Longhurst, 2007).

Sub-surface chlorophyll maxima (SCM) are usually found between 40m - 60m, representing a layer of high biomass that cannot be accurately quantified by satellite (Revelante and Gilmartin, 1995). Most reports of subsurface chlorophyll-a in Southern Ocean waters have supported Longhurst's hypothesis of photo-inhibition (Holm-Hansen and Hewes, 2004). However, data collected by the US Antarctic Marine Living Resources (AMLR) program indicates that sub-surface biomass develops due to a number of contributing factors. These include the depletion of nutrients in the upper mixed layer (UML) as summer progresses, and growth of phytoplankton at a depth where iron concentrations and sunlight levels are both sufficient (Holm-Hansen and Hewes, 2004). Adult female elephant seals undertake their post-breeding foraging trip during the high to late austral summer, and this period of intense feeding may coincide with development of a SCM. The presence of a sub-surface biomass would not invalidate surface chlorophyll-a as an indicator of underlying processes and dynamics, but the available biological richness would certainly be under-reported. Without supporting *in situ* data, the presence of additional phytoplankton and the downstream impacts this would have on density of prey species and distribution of predators may only be speculated.

5.3 Optimal Foraging Theories

Apex predators are not passive tracers of water movement and spatio-temporal lags make it difficult to correlate their foraging distribution with chlorophyll-a levels; however, optimal foraging and ARS theory predicts that speed and turning frequency of such animals would be measurably affected by prey density (Longhurst, 2007; Dragon *et al.,* 2010).

Lévy-flight, an optimal foraging theory, predicts that Lévy walks would be adopted when prey is scarce (Sims *et al.,* 2008). Lévy behaviour is described as a movement pattern of many small steps connected by longer relocation walks, and it is theorised as the most effective method for finding patchily distributed resources on spatial scales beyond a predator's sensory range (Viswanathan, 2000). Slower swim speeds and increased turning frequency characteristic of Brownian movement would only be effective when productive patches are encountered. A range of marine predators including sharks, tuna, marlin and sunfish have been shown to switch between Lévy and Brownian movement patterns, depending on whether they are searching or feeding (Humphries *et al.,* 2010). With regard to vertical search strategies, southern elephant seals do not appear to conform to Lévy foraging (Sims *et al.,* 2008). Information of this kind currently appears to be limited on their horizontal movements. However, if reduced swim speed and increased turning frequency are used as a proxy for Brownian behaviour (this study), there is preliminary support for further study of this optimal foraging theory for adult female elephant seals.

5.4 Linking Chlorophyll-a Concentrations to Changes in Speed

Using remotely measured chlorophyll-a used as a biomarker of underlying biological richness, do adult female southern elephant seals reduce travelling speed when encountering waters exhibiting higher chlorophyll-a concentrations? While at sea, foraging seals are conceivably opportunistic, hunting even as they travel between patches. Adult females are able to maintain speeds of between 100 km/day to 150 km/day and they do so until the waters they're swimming in exhibit chlorophyll-a concentrations higher than 0.40 mg/m^3 (Fig. 4.9) Whether the tagged elephant seals moved to the STC, or to the east or west of the SWIR, as soon as chlorophyll-a values peaked above 0.40 mg/m^3, the maximum swim rate dropped to below 100 km/day and the median swimming speed fell to less than 50 km/day. By implication, once seals have encountered a patch, a plume or a mesoscale feature such as an eddy, they decelerate in order to remain in the region of biological richness.

The highest variation in seal swimming speeds occurs at an apparent threshold of between 0.30 mg/m^3 and 0.40 mg/m^3 (Fig. 4.9). It is possible that this level of chlorophyll-a is recognised as a gradient limit or productivity edge so seals respond by essentially 'shifting gears'. Those seals that increase speed may do so as they rapidly follow the gradient up into the densest region of prey. However, most of the speeds are spread between almost stationary to approximately 75 km/day and the median swim rate is below 50 km/day. Despite the wide distribution of swim speeds, the trend is one of slowing, implying a change from travelling to foraging behaviour at a chlorophyll-a concentration of around 0.35 mg/m^3.

The chi-squared test was implemented to determine whether chlorophyll-a and speed were independent. This test is a useful tool for scenarios where two categorical variables, each with two or more values, need to be examined against one another. In this example the two categories were Chlorophyll-a Concentration (mg/m^3) and Swim Speed (km/day). The values of both were binned into 'high, 'medium' and 'low' categories, and the observed frequencies (Table 4.1) were then measured against expected frequencies (Table 4.2). The null hypothesis is that the observed would not differ significantly from the expected – in other words, that the proportion of high, medium and low swim speeds would be the same at all three concentrations of chlorophyll-a. This hypothesis of independence was disregarded because the p-value was below 0.05 and the chi-squared test served to show that a statistically significant relationship did indeed exist between swimming speed and chlorophyll-a concentration.

A correlation analysis was implemented to reiterate covariance between chlorophyll-a concentration and swimming speed, and to measure the strength of this relationship (Fig. 4.10). As anticipated after the chi-squared test, the results of the correlation analysis showed that the relationship between the two variables was significant ($p<0.05$). The second result of any correlation analysis, the coefficient of determination, describes 'goodness-of-fit' and always falls between 0 (no correlation) and 1 (perfect correlation). In this case, only a minor percentage of the variance was actually explained by the relationship ($r^2 = 0.035$).

The food chain between phytoplankton and adult female elephant seals has many downstream links – elephant seals mainly foraging on varying ratios of squid and fish (Bradshaw *et al.*, 2003; Cherel *et al.*, 2008; Bailleul *et al.*, 2010). Furthermore, marine top predators are not known to be passive tracers of water movement. Both these factors would result in spatial and temporal lags, making it difficult to tightly associate foraging distribution patterns with chlorophyll-a levels. It is conceivably due to these decouplings that so little of the variance is explained by the correlation to productivity. Despite this, and notwithstanding the wide scatter of data (Fig. 4.10), the relationship is statistically significant.

In order to trim the diffuse data cloud and remove inherent noise that may obscure any underlying signal, a simple moving median filter was applied. The result was a running median (Fig. 4.11). Despite a total of 6 filtering runs, the wide scatter of data between 0.10 mg/m^3 and 0.27 mg/m^3 makes the running median sensitive to variation, and speed is seen to respond step-wise up to this point. The running median stabilises and drops without rising again at the apparent threshold of between 0.30 mg/m^3 and 0.35 mg/m^3, becoming more linear thereafter.

The concept of a chlorophyll-a threshold is a recurring phenomenon in the analyses of speed against concentration. Using chlorophyll-a as a proxy for underlying dynamics and productivity, a concentration of around 0.33 mg/m^3 may be the tipping point where the biomass becomes abundant enough to attract swarms and schools of the downstream prey species. In other words, above this apparent threshold of chlorophyll-a, fish and squid may accumulate in high enough densities to warrant a deceleration of swim speed, and Brownian-type foraging behaviour.

5.5 Linking Chlorophyll-a Concentrations to Changes in Orientation

Lévy-flight foraging predicts that marine predators searching for patchily distributed resources would take short steps punctuated by long reorientation steps (Reynolds, 2009). When an area of sufficient prey density is encountered, however, predators would conceivably switch to more Brownian-type movements by decreasing speed and increasing their turning frequency. A significant relationship between swim speed and chlorophyll-a has already been established in adult female southern elephant seals (this study). Would changes in orientation, as a proxy for turning frequency, also be measurably affected by higher chlorophyll-a concentrations?

By subtracting successive daily seal positions projected onto polar coordinates, changes in orientation were measured in degrees between 0° and 179°. Acute reorientations were those calculated between 0° and 90°, representing sharp changes in direction from one day to the next. Obtuse adjustments in orientation, on the other hand, fell between 90° and 179°.

Interestingly, the median changes in direction shifted definitively from obtuse to acute as soon as chlorophyll-a concentrations of between 0.30 mg/m^3 – 0.35 mg/m^3 had been reached (Fig. 4.12). By implication, adult female elephant seals appear to have remained on relatively straighter trajectories in waters exhibiting chlorophyll-a concentrations below 0.30 mg/m^3. Once the threshold range of chlorophyll-a had been surpassed, changes in orientation from one day to the next became sharp and sudden. Coinciding with a deceleration of swimming speed, the shift from obtuse to acute at 0.3 mg/m^3 may imply changes from travelling/searching behaviour, to active feeding. Without supporting *in situ* data, however, this apparent tipping point of chlorophyll-a concentration may only be speculated as a threshold between low and high phytoplankton biomass and prey density.

Variance of the data is high across all ranges of chlorophyll-a, narrowing only after concentrations had surpassed 0.40 mg/m^3 (Fig. 4.12). Before filtering this wide scatter with a running median, a correlation and regression analysis was done to broadly visualise the relationship between chlorophyll-a and change in orientation (Fig. 4.13), and to test the significance of the shifts from obtuse to acute. Results of the correlation analysis showed that the relationship between change in orientation and chlorophyll-a concentration was significant ($p<0.05$), invalidating the null hypothesis of independence. As with the previous analysis of speed and chlorophyll-a, only a fraction of the variance was actually explained by this link ($r^2 = 0.019$).

Because only two-weekly ocean colour data was available at sufficient resolution, daily averages of seal positions were used instead of the finer-scale information recorded by the SRDLs. Daily data are reasonably less accurate than what could be resolved from several data points per day, and changes in orientation were used merely as a proxy for turning frequency. It is conceivable that for this reason, as well as due to the spatial and temporal lags between the bottom and the top of the food chain, that so little of the variance is explained by the correlation to chlorophyll-a concentration. Despite these factors and the wide scatter of data (Fig. 4.13), the relationship is still statistically significant.

The simple moving median filtered out a fair proportion of this scatter after three runs. At a similar chlorophyll-a threshold of approximately 0.30 mg/m^3 to 0.37 mg/m^3, the running median of orientation changes shifted from obtuse to acute, and remained below 90° as the chlorophyll-a concentrations increased (Fig 4.14).

5.6 Summary

The tipping point observed with speed and chlorophyll-a, and change in orientation and chlorophyll-a, is really a narrow range of concentrations that suggest threshold changes in underlying biological richness. Until ship-based and drifter investigations can be carried out to determine what changes, if any, occur as chlorophyll-a values increase from below 0.30 mg/m^3 to 0.40 mg/m^3, speculation can only be made about related prey densities.

It is still unknown if adult female elephant seals from Marion Island are seeking out certain oceanographic conditions to find prey species, or acting in response to changes in prey densities, which are coupled to the oceanographic features (Sims *et al.,* 2008, Dragon *et al.,* 2010). Nonetheless, chlorophyll-a is a useful indicator of underlying physical dynamics and biological richness, and adult female elephant seals from Marion Island respond significantly to increasing concentrations by decelerating and shifting orientation from obtuse to acute. In line with optimal foraging and ARS theory, as well as the Lévy-flight foraging hypothesis, travelling and searching swim behaviour (short steps interspersed with long walks) can be differentiated from foraging and feeding behaviour (Brownian-type movements). The activities of adult female elephant seals show high variability and, despite the fact that very little is explained by the link to chlorophyll-a concentrations, the relationship is statistically significant.

6. Conclusion

The Southern Ocean is an extensive world ocean, distinctive in that it flows unhindered around the globe. These waters serve to link the Antarctic, the pacific and the Indian oceans, and form the southern stretch of the thermohaline circulation. This is the primary means by which salt and heat are transferred between different basins, and these exchanges play an important role in regulating global climate.

Mirounga leonina from Marion Island spend more than 85% of their lives at sea. After losing almost half their body weight during the breeding season, females have to forage intensively and successfully over the austral summer migration (December to February). Unlike their male counterparts, they cannot exploit deep benthic resources but, due to time limitations, nor can they move as far as the Antarctic continent to take advantage of productivity at the melting ice edge (Sokolov and Rintoul, 2007). Seals leaving Marion Island to forage are compelled to make decisions based on little to no knowledge of the current distribution of their prey species (Sims *et al.,* 2008). However, by following geographical and physical clues, elephant seals may be able to fine-tune their tracking and foraging patterns.

In line with observations made by McIntyre *et al.* (2010), nine out of the ten tagged adult females in this study directed their foraging activities along the SWIR. This deeply fractured bathymetric feature is well recognised for the role it plays in generating intense disturbances to the mean flow of the ACC. Satellite and *in situ* studies have highlighted how these downstream mesoscale features entrain nutrients and phytoplankton, providing abundant foraging grounds for higher trophic consumers from Marion Island. Productivity can be monitored via ocean colour studies and, because areas of high phytoplankton tend to attract strings of downstream foodchains, remotely measured surface chlorophyll-a is an effective indicator of underlying biological richness (Falkowski *et al.,* 2008).

Optimal foraging and area restricted search (ARS) theory predicts that top predators such as elephant seals will alter their behaviour upon encountering patches of high prey density. Conceivably, in order to remain in the biologically rich area, seals would demonstrably reduce their velocity and turn more frequently. In line with this, Lévy-flight foraging hypothesis predicts that predators would shift from Lévy walks (searching for prey) to Brownian-type behaviour (foraging) once abundant prey is located (Humphries *et al.,* 2010).

Adult female elephant seals from Marion Island appear to conform to optimal foraging and ARS behaviour during their post-breeding migration (this study). Interestingly, an apparent threshold of chlorophyll-a concentration appears to act as a tipping point between search tactics and Brownian-type foraging behaviour. At chlorophyll-a concentrations falling within a narrow range of between 0.30 mg/m^3 and 0.40 mg/m^3, seals decelerate significantly. At this same band of concentrations, seals also shift their daily changes in orientation from obtuse to acute, implying that they turn back on themselves and tighten their distribution in order to remain within the productive patch.

Despite the fact that little of the variance in foraging behaviour is explained by the link to surface chlorophyll-a, the relationship is statistically significant and foraging behaviour is definitively not independent of this bio-indictor. A concentration of around 0.33 mg/m^3 may be the tipping point where the biomass accumulates in high enough densities to warrant a measurable change in foraging behaviour.

Future Work

Without supporting *in situ* data, chlorophyll-a concentration is still only a proxy for primary productivity. For the month of March (2011), I will be part of a cruise steaming to Marion Island on the Africana. This scientific undertaking aims to provide more precise information on the mesoscale oceanographic features characteristic to this region of the Southern Ocean. We will use this data for investigations into the impacts of eddies on the distribution of southern elephant seals and other high trophic consumers from the Prince Edwards Island group. The phenomenon of a chlorophyll-a threshold will also be investigated *in situ.*

Modelling work would also be an essential contribution to resolving the eddy processes in the region. To study these regional mesoscale features relative to predator distributions in the Southern Ocean, ROMS would be applied at horizontal resolution of 1/12°. The model will be forced by QuikSCAT winds and NCEWP heat fluxes interpolated to the model grid, and receive boundary conditions from SODA (Ansorge, Pers Comm).

By applying interannually varying forcing to the model, the sensitivity of regional eddies to the Southern Annular Mode (SAM) could also be investigated. The SAM is the dominant mode of climate variability south of 20°S and has tended to be in its positive phase in recent decades (Ansorge, Pers Comm). Whether this tendency is a phenomenon of climate change processes or part of a long-term natural cycle remains to be elucidated. Ultimately, evidence is growing that the Southern Ocean is warming more swiftly than the world ocean average (Charrassin *et al.,* 2008). It is anticipated that the impacts of warmer oceans on higher trophic consumers will be generated primarily through changes in the distribution and abundance of their prey. In due course, by studying and understanding the links between modelled and measurable oceanographic parameters, as well as the effects of climate variability on regional productivity and the behaviour of top predators, southern elephant seals may be monitored as indicators of regional environmental changes.

Finally, despite work done by Sims *et al.* (2008) showing that southern elephant seals do not adopt Lévy-like search strategies when foraging on a vertical scale. It may be feasible to model the distribution data from this study, as well as from future studies, to determine whether Lévy-flight foraging behaviour applies to adult females on a horizontal scale.

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