A statistical investigation of the behavioural responses of a deep diving predator to mesoscale oceanographic features

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Abstract

Marion Island lies directly in the path of the ACC and to the south-west of the island is an extensive region of high sea level anomaly variability (eddy field). Previous research has shown how southern elephant seals from Kerguelen Island and Peninsula Valdés have targeted eddies for foraging. These findings combined with the observed post-moult migrations of tagged female southern elephant seals from Marion Island which traverse the nearby eddy field suggest that they may exploit the eddy field for foraging. Overall the seals undertook significantly more of their dives (18.5%) within the eddy field than predicted ($p <$ 0.01). Eleven of the 16 seals dived within the eddy field region significantly more often than predicted. Dives were generally shallower and shorter within the eddy field. Mixed models estimated that a maximum depth reduction of 53.03 ± 5.30 m (LME: t=10.00, DF=24986, $p <$ 0.01) and a dive duration reduction of 6.17 ± 0.58 min (LME: t=10.70, DF=24986, $p < 0.01$) could be attributed to diving within the eddy field. Within the eddy field U-dives increased by 6.97%, W dives decreased by 7.18% and O-dives increased by 0.21%. Seven individuals' maximum dive depths were shallower and nine individuals dive durations were shorter as a result of diving within the eddy field. Ten individuals showed significant changes in the types of dives which they undertook inside of the eddy field with eight seals undertaking more U- and fewer W-dives and two seals undertaking more W- and fewer U-dives. Overall the effect of diving within the eddy field appeared to be biologically important to ten seals. While dive durations were significantly affected by changing sea level anomaly (SLA) (LME: 0.15 ± 0.01 min, t=11.72, DF=12372, $p <$ 0.01), maximum depths were not. The log-odds of switching from U- to W-dives within the eddy field were significantly affected by changing SLA (Multinomial: 0.00 ± 0.00, z=2.97, $p <$ 0.01). However all significant effects of SLA on dive parameters within the eddy field were very small in comparison to those of day-stage. The low magnitudes of the effects of SLA were similar for all individuals.

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Introduction and literature review

The Southern Ocean forms a vital link between the world's ocean basins, transferring energy across and between latitudes (Gille 2002, 2003). As a result of increasing atmospheric CO_2, the structure, transport and productivity distributions within the region are shifting with predictable and unpredictable knock-on effects throughout the ocean's trophic webs (Oke & England 2004; Böning et al. 2008; Ansorge et al. 2009; Downes et al. 2011). Near the apex of these webs, southern elephant seals *Mirounga leonina* have undergone severe population fluctuations during the 19th and 20th centuries (Hindell et al. 1994; McMahon et al. 2005). Information relating to the foraging grounds and dive behaviour of southern elephant seals are important for understanding issues surrounding population shifts and making informed management and conservation decisions (Hindell et al. 1991; Pistorius et al. 2004).

The physical nature of the Southern Ocean

The Southern Ocean is characterised by the powerful Antarctic Circumpolar Current (ACC) (Rintoul et al. 2001), which provides crucial mechanisms for driving regional biological productivity and transferring heat energy and dissolved atmospheric gasses around the planet (Downes et al. 2011). The current runs unimpeded by continental landmasses from west to east around the high southern latitudes, connecting the world's major oceans (Gille 2002, 2003). The ACC is at its most northerly extent in the southern Atlantic and most southerly in the eastern Pacific (Gille 2002). The sub-Antarctic Front (SAF), the Polar Front (PF) and the southern ACC front (SACCF) are the three primary convergences associated with the ACC (Sokolov & Rintoul 2009). The SAF defines the northern hydrographic boundary between the ACC and more temperate northerly sub-tropical flows (Orsi et al. 1995). Poleward of the SAF, between approximately 45°S and 55°S, the strongest westerly winds on the planet drive the ACC (Orsi et al. 1995; Rintoul et al. 2001; Oke & England 2004). The PF lies to the south of the SAF at around 49°S in the south western Indian Ocean, marking the southern extent of

water warmer than 2.2°C at 200 m (Belkin & Gordon 1996; Sokolov & Rintoul 2009). The position of the SACCF fluctuates around approximately 58.4°S, marking the southern limit of water warmer than 2.0°C (Sokolov & Rintoul 2002). The southern extents of the ACC are less clearly demarcated with no distinct hydrographic boundary between the current and the sub-polar regions (Orsi et al. 1995).

The Southern Ocean is the planet's largest high-nutrient low-chlorophyll region (Buesseler et al. 2004). The low primary productivity levels are attributed to iron limitation (de Baar et al. 1990), with productivity restricted to zones where iron is introduced from different water masses, icebergs or proximate shelf sediments (de Baar et al. 1990; Rintoul & Sokolov 2001), such as the Agulhas Retroflection, the Patagonian Shelf, the Tasman Sea and the shelf west of New Zealand (Sullivan et al. 1993). As a result, the Southern Ocean's patchy productivity distributions are determined both temporally and spatially by interactions involving the ACC and bathymetry or other water masses (Atkinson et al. 2004).

While the ACC connects the globe's ocean basins via zonal mixing, it also restricts heat transfer between sub-tropical and sub-polar latitudes (Rintoul et al. 2001). Some poleward heat flux does however occur, likely via the formation of eddies (de Szoeke & Levine 1981) which transfer heat and momentum polewards, across the ACC's density surfaces (Rintoul et al. 2001). The instabilities which result in vertical mixing and the formation of these eddies are strongest where the ACC interacts with poleward extensions of western boundary currents, irregular bathymetry and in frontal regions (Rintoul & Sokolov 2001).

Mesoscale Eddies

Eddies are rotating masses of water and are distinguished into two primary types based on the direction of their rotation. Cyclonic eddies rotate in a clockwise direction in the southern hemisphere, resulting in both Coriolis and centrifugal forces acting in an outward direction,

while a balancing pressure gradient force acts toward the centre of these structures (Bakun 2006). Therefore, these mesoscale structures have a depressed sea surface height and elevated thermoclines. The raised central thermocline and steepening isopycnals around these structures are generally indicative of upwelling processes. In contrast, anticyclonic eddies rotate anti-clockwise in the southern hemisphere, and the strong Coriolis force is directed toward the centre of the features (Bakun 2006). Along with the outward centrifugal force, the pressure gradient force balances the Coriolis force resulting in a surface elevation, and sub-surface thermocline depression in the centre of these features (Bakun 2006).

The central portions of eddies transport particles internally while the outer portions interact and mix with the surrounding environment (Olson 1991). Because of these properties, eddies are closely associated with nutrient fluxes in the open ocean (Ansorge et al. 2009) and are utilised as foraging grounds by many marine species, including sub-Antarctic fur seals *Arctocephalus tropicalis* (de Bruyn et al. 2009), grey-headed albatrosses *Thalassarche chrysostoma* (Nel et al. 2001), great frigatebirds *Fregata minor* and tuna (Weimerskirch et al. 2004; Tew-Kai & Marsac 2010).

Global climate change

Water has a higher specific heat capacity than the land or the atmosphere (Roemmich et al. 2012). As a result, the deep oceans are able to remove and store a great deal of heat from the ocean surface through mixing (Levitus et al. 2001; Roemmich et al. 2012). This stored heat has resulted in ocean temperature rise and presents a key indicator of global climate change (Levitus et al. 2001; Roemmich et al. 2012). While sea surface temperature change studies indicate little if any change between the 1870s and 1950s (Wunsch 1981), a recent global study comparing current Argo float temperature data with those from the 1800s revealed warming at 78% of the stations analysed (Roemmich et al. 2012). The warming extended

from the sea surface to below 1800 m and was estimated at 0.59 ± 0.12ºC across the Atlantic and Pacific Oceans (Roemmich et al. 2012).

Within the Southern Ocean, zonal transport between ocean basins means that oceanographic signals in one basin can be transported to and affect the climate in distant basins via teleconnections (Rintoul et al. 2001). Since the 1960s the ACC has shifted 50-70 km polewards (Swift 1995; Gille 2002; Sokolov & Rintoul 2009) along with an intensification of the regions westerly winds since the early 1990s (Downes et al. 2011). Global climate models predict that, as a result of ongoing increases in atmospheric CO_2, westerly winds in the southern hemisphere will continue to shift polewards and increase in intensity (Saenko et al. 2005). These changes are likely to result in a restructuring of the ACC and may impact aspects of the current's transport and flow as well as regional productivity distributions (Pakhomov & Chown 2003; Oke & England 2004; Böning et al. 2008; Ansorge et al. 2009; Downes et al. 2011).

Global ocean and atmospheric processes involving water mass formation, productivity variability as well as fluxes of heat and dissolved gasses are detectable within the ACC (Roemmich et al. 2012). Changes to the ACC's mean flow are predicted to have knock-on effects in terms of water mass subduction and transfer of heat and nutrients between the globe's ocean basins thereby influencing productivity distributions in remote parts of the Southern Ocean (Downes et al. 2011).

Data acquisition and analysis
Since the early 1990s, the use of small electronic tags attached to marine animals has substantially augmented traditional oceanographic observation tools such as vessel-borne instrumentation and remote sensing, providing the scientific community with a wealth of oceanographic (Fedak 2013) and biological data (e.g. Costa 1993; Boehlert et al. 2001;

Dragon et al. 2010). Technological advances in the miniaturisation and measurement accuracy of these tags have allowed the technology to be extended to a variety of marine animals including fish (e.g. Block et al. 2005), sea turtles (e.g. Polovina et al. 2001), marine mammals (e.g. Campagna et al. 2006), and seabirds (e.g. Nel et al. 2001; Bost et al. 2007).

Datasets retrieved from tagged animals have dramatically improved our capacity for understanding marine vertebrate habitat preferences and movement patterns (Boehlert 1997). Not only have we gained insights into the biology of the tagged species, but we have also been able to gather environmental data from remote parts of the ocean such as polar zones (Costa 1993; Fedak 2013). These data have allowed examination of the seasonal- and inter-annual oceanographic nature of these regions, as well as provided insights into the interplay between the biological and physical environments (e.g. Campagna et al. 2006; Biuw et al. 2007; Dragon et al. 2010). For example, studies have shown how seals (Campagna et al. 2006), birds (Nel et al. 2001) and turtles (Polovina et al. 2001) move between large scale (frontal systems and currents) and mesoscale (eddies and meanders) oceanographic features. These structures are associated with increased productivity, attracting mesopelagic fish and providing favourable feeding grounds for predators (Weimerskirch et al. 2004).

Data acquisition often requires recovery of the tag, which may necessitate the recovery of the tagged individual (Boehlert et al. 2001). In order to increase the likelihood of tag recovery, deployment is either required on a large, and expensive scale or the tagged animal needs to exhibit homing behaviour and have low mortality rates (McCafferty et al. 1999; Boehlert et al. 2001). Pop-up tags circumvent this problem by releasing themselves from the tagged animal after a prescribed time, floating to the surface and transmitting their stored data to a satellite (Boehlert et al. 2001). Some larger Argos satellite relay data loggers (SRDL) can provide not only location information, but time-depth dive profiles, as well as conductivity and temperature data at depth (Boehme et al. 2009a). The instruments housed within these

tags can collect information from data-sparse areas of the oceans, of a high enough quality to be included in the Global Ocean Observing System (Boehme et al. 2009b). Due to their circumpolar distribution, their role as top predators and their deep diving habits and expansive migrations, southern elephant seals are considered to be a useful indicator species for distributions of Southern Ocean prey resources (Hindell et al. 1991; Le Boeuf & Laws 1994).

The southern elephant seal

Southern elephant seals breed on islands throughout the Southern Ocean, with their highest concentrations on sub-Antarctic islands (Laws 1994). Due to their large, robust nature southern elephant seals are able to carry heavier, more complex SRDLs (Boehlert et al. 2001), evidently without any consequences to their fitness or survival (McMahon et al. 2008). Moreover, due to declines in numbers in several southern elephant seal populations during the 20th century, the species has been a focus for SRDL based conservation research since about 1990 (Le Boeuf & Laws 1994; Dragon et al. 2010).

Population status

The global southern elephant seal population is generally considered to be comprised of three stocks: the South Georgia, Kerguelen- and Macquarie Island stocks (Laws 1960 in Le Boeuf & Laws 1994). Overall the South Atlantic (South Georgia) stocks have fared better than the South Indian (Kerguelen) and South Pacific (Macquarie) stocks during the 20th century, either remaining stable or increasing (Laws 1960; Gales & Burton 1989; Guinet et al. 1992; Pistorius et al. 1999a). The South Georgia stock is the largest and includes colonies in South America, on South Georgia and the South Sandwich Islands, the South Orkney Islands, the South Shetland Islands, the Falkland/Malvinas Islands as well as on Gough and Bouvet Islands (Laws 1960). Individuals from this stock were hunted for their oil in the 19th and 20th centuries and in 1899 the Falklands government introduced the Seal Fishery Ordinance with

the goal of continuing the sealing industry on a more sustainable, rotational basis (Le Boeuf & Laws 1994). Despite such control measures, exploitation continued to reduce seal stocks and in 1964, along with the collapse of the whaling industry in South Georgia, licensed sealing came to a stop (Le Boeuf & Laws 1994). In 1951 the South Georgia stock was estimated at between 328,000 and 357,000 individuals. Numbers of adult males are thought to have recovered by 1970, and in 1985 the stock was estimated at 397,000 seals (Le Boeuf & Laws 1994).

The Kerguelen stock includes colonies at Kerguelen-, Heard-, Marion-, Prince Edward- and the Crozet Islands, as well as the Vestfold Hills in Antarctica (Laws 1960). All of these colonies experienced population declines in the 20th century. The Kerguelen population decreased by 44% between 1956 and 1989 and the colony on Heard Island by 50% between 1949 and 1990 (Burton 1986). A decrease of 70% was experienced between 1966 and 1992 by the Crozet population and this trend appears to be ongoing (Guinet et al. 1992). Antarctica's Vestfold Hills population decreased by 50-75% between 1958 and 1989 (Gales & Burton 1989). Marion Island's seals underwent a severe decrease of approximately 83% between 1951 and 1990 which has been linked to reduced adult female survival (Pistorius et al. 1999a, 1999b). However, this population stabilised during the mid-1990s and seems to be showing signs of slow recovery (Pistorius et al. 1999a, 1999b, 2004; McMahon et al. 2009).

The Macquarie Island stock is comprised of colonies at Macquarie-, Campbell-, Auckland- and the Antipodes Islands (Laws 1960). Macquarie Island, which supports 99% of this stock (McMahon et al. 2005), was heavily exploited by the sealing industry during the early 19th century leading to a decline of approximately 70% (Hindell & Burton 1988). By the early 1900s however the population was thought to have recovered to pre-sealing numbers as a result of more sustainable levels of oil harvesting (Hindell & Burton 1988). The stock

however went on to decrease by 59% between 1949 and 2001 and the decrease seems to be continuing (McMahon et al. 2005).

Drivers of population decline

When comparing the declining Macquarie Island stock with the relatively stable South Georgia stock some patterns were evident (Hindell et al. 1994): South Georgia stock growth rates were higher and age at first breeding was one year earlier than those at Macquarie Island and Macquarie Island survivorship was lower across all age cohorts than at South Georgia. In addition, Macquarie Island male and female populations were declining at roughly the same rate as one another. A number of explanations for the declines have emerged including intrinsic and extrinsic factors (Hindell et al. 1994; McMahon et al. 2005).

Density dependent pup mortality as a result of beach overcrowding (Reiter et al. 1978) has been suggested as an intrinsic mechanism for population declines, but fails to account for the stability of the South Georgia stock (Hindell et al. 1994). Increased juvenile predation by killer whales (*Orcinus orca*) has also been suggested but there is no evidence for increased numbers of killer whales in the Southern Ocean during the second half of the 20th century (Hindell et al. 1994).

Reduced availability of food based on increased competition, population equilibration or environmental shifts may have played a role in the stocks' failure to recover (Hindell et al. 1994; McMahon et al. 2005). Whilst foraging on the Antarctic shelf there may be some degree of competition with Weddell seals *Leptonychotes weddellii*, but in most of their foraging grounds southern elephant seals' only mammalian competitors are sperm whales *Physeter macrocephalus* (Hindell et al. 1991). Sperm whale diets are however dominated by chranchiid squid (Cranchiidae), which are likely to be too large for female elephant seals whose diets are dominated by, but not limited to, myctophid fishes (Hindell et al. 1991;

Cherel et al. 2008). Commercial fishing, particularly for Patagonian toothfish *Dissostichus eleginoides* (Lombard et al. 2007) may also result in some competition for food resources (Boyd et al. 1994). As of 1994 however, fishing pressure did not overlap with Macquarie Island seal foraging grounds (Hindell et al. 1994).

Recovering elephant seal stocks may show population fluctuations as they approach an equilibrium (Hindell et al. 1994). It is possible that during the years of heavy exploitation by sealers, populations of the seals' prey items would have increased. With the release of sealing pressure in the early 20th century the seal stock may have increased beyond the carrying capacity of its resource. This overshoot would have been followed by population declines due to resource limitation. The 'overshoot' hypothesis does not however adequately explain population decreases in smaller colonies which were never heavily exploited (e.g. Marion Island), nor synchronous declines in multiple populations across a broad geographical range (e.g. southern Indian and Pacific Oceans) (Hindell et al. 1994).

Another possible cause for the recent decreases has to do with environmental and prey distribution shifts linked to climate change (McMahon et al. 2005). The effects of global climate change on the Southern Ocean environment have been briefly covered above. Persistent high altitude weather patterns over Southern Australia have expanded and now encompass foraging areas of Macquarie Island elephant seals (Hindell et al. 1994). This climate shift appears to correspond with an increase in first year pup mortality (Hindell et al. 1994). Where Marion Island supported a permanent ice cap in the 1950s and 60s, increased temperatures, decreased precipitation and an increase in the number of sunshine hours have resulted in the melting of this ice cap (Sumner et al. 2004). These changes have been accompanied by an increase in regional ocean temperatures (A. Blair, unpublished data) and a southward shift of the SAF in the vicinity of Marion Island over the same period (Gille 2002). It is likely that these environmental changes have been accompanied by regional prey

distribution shifts impacting the foraging grounds and survivorship of southern elephant seals. Moreover these types of environmental impacts are unlikely to have occurred to the same degree throughout the sub-Antarctic region, which may account for the differences in recovery between stocks (Atkinson et al. 2004). Nevertheless, linking the population shifts in southern elephant seals to global climate shifts is, at this stage, highly speculative (Hindell et al. 1994).

Diving behaviour of southern elephant seals

The diving behaviour of southern elephant seals was first described by Hindell et al. (1991) who investigated dive profiles of adult males and females from Macquarie Island. Adult elephant seals generally haul out onto land twice a year – once for a breeding period when females give birth, nurse their young and mate before returning to sea; and a second time for an obligatory moult (Le Boeuf & Laws 1994). During their at-sea migrations southern elephant seals spent almost 90% of their time diving (Hindell et al. 1991; Boyd et al. 1994). Bottom time accounted for 42% of their dive time and was assumed to be spent foraging, although not necessarily feeding (Hindell et al. 1991). The seals maintained a frequency of 2.5 dives per hour for the duration of their migrations. Foraging dives were relatively uncommon in the first two weeks of migration suggesting that during this time the animals were en route to distant foraging grounds. During this initial period female foraging dive frequencies increased steadily, levelling off after the second week.

Hindell et al.'s (1991) analysis revealed that 71% of the variance between dives was described by rates of ascent and descent as well as the number of vertical fluctuations (wiggles) while at depth. Based on this variance, Hindell et al. (1991) resolved six distinct dive types (Types 1-6). Photopoulos (2007) revisited these categorizations, also deriving six types (W-, U-, V-, Dr- and SQ-dives) based on a technique developed by M. Buiw (unpublished data). While five of these dive types were similar between studies, Hindell et al.

(1991) described a very short shallow type (Type 5), excluded by Photopoulos (2007) in favour of V-shaped dives, to which the authors attributed travelling. For the purposes of this study I use the more recent interpretation of Photopoulos (2007) and M. Buiw (unpublished data).

Two of these dive types are characterised in part by having durations at depth of greater than one minute along with rapid ascent and descent rates (Hindell et al. 1991). The first of these dive types includes large wiggles over a range of depths and are termed wiggle dives (W- or Type 1 dives) (Hindell et al. 1991; Photopoulos 2007). The wiggles may be associated with predator avoidance or with vertical zigzagging through schools of prey (Hindell et al. 1991). W-dives show some diurnal patterns which presumably are linked to the daily vertical migrations of pelagic prey (Hindell et al. 1991; Photopoulos 2007). Square dives (SQ- or Type 2 dives) are characterised by having fewer wiggles and no diurnal pattern (Hindell et al. 1991). These dives are linked to benthic foraging as their depths correlate with regional bathymetry.

The remaining dive types are distinguished by slower ascent and descent rates along with durations of less than one minute in their deepest sections (Hindell et al. 1991). Drift dives (DR- or Type 3 dives) incorporate a rapid initial descent to around 200 m followed by a longer, slower descent lasting most of the remainder of the dive (Hindell et al. 1991; McIntyre et al. 2011b). During this part of the dive, elephant seals assume a belly up position and drift deeper tracing large slow circles (Mitani et al. 2010). This period is thought to be associated with either resting and digesting food or searching for prey (Mitani et al. 2010). The drifting period is thought to only ensue once the animals reach a depth beyond that generally frequented by their predators (Mitani et al. 2010). These dives are terminated by a rapid ascent (Le Boeuf et al. 1988; Hindell et al. 1991; Photopoulos 2007). Some individuals

undertake DR-dives on a daily basis while others carried them out less frequently (Hindell et al. 1991).

During the first fortnight of their migrations the seals cover up to 120 km per day, primarily undertaking U-shaped dives (U- or Type 4 dives) (Hindell et al. 1991). While these dives are thought to be mainly associated with travelling, they are deeper than other non-foraging dive types and may include some exploratory and opportunistic foraging (Hindell et al. 1991; Photopoulos 2007). This assertion is supported by the dominance of this dive type during Marion Island elephant seal migrations (McIntyre et al. 2011b) as well as accelerometry data collected from seals in other populations (Gallon et al. 2013; Naito et al. 2013). Root dives (R- or Type 6 dives) constitute a combination of several unclassified dive shapes and are thought to be associated with exploratory diving (Hindell et al. 1991; Photopoulos 2007). The short, shallow Type 5 dives described by Hindell et al. (1991) typically last less than two minutes and reach depths <7 m. These dives might be attributed to tag malfunctions because they tended to occur in bursts. The sixth dive type described by Photopoulos (2007) are V-shaped dives which are linked to travelling to and from foraging grounds.

Post-moult and post-breeding individuals from Macquarie Island spend approximately the same amount of time on both foraging and non-foraging dives (Hindell et al. 1991). Dive depth, bottom time, wiggle magnitude and proportion of each dive type are also similar between the sexes. Despite the lack of significant differences between the female post-moult and post-breeding bottom times, their overall post-moult dive times are longer, suggesting generally slower descent and ascent rates. Hindell et al. (1991) attributed these differences to changing foraging strategies resulting from variations in prey distributions between seasons and foraging grounds.

Foraging grounds

The foraging patterns of the seals reflect the Southern Ocean's patchy and highly variable prey abundances (Bornemann et al. 2000; Field et al. 2001). Individuals from South Georgia, Macquarie-, Marion- and the Kerguelen islands forage in various regions of the SAF, the PF, the interfrontal zones, the ACC and over the Antarctic continental shelf (McConnell et al. 1992; Jonker & Bester 1998; van den Hoff et al. 2002; Bailleul et al. 2010; Dragon et al. 2010). Adult female seals from Macquarie Island foraged almost exclusively pelagically (Hindell et al. 1991) as did those from Peninsula Valdés (Campagna et al. 1995), while a single female seal from South Georgia was recorded undertaking repeated benthic dives (McConnell et al. 1992). Both males and females from Kerguelen appear to prefer benthic foraging in the vicinity of the Antarctic continent (Bailleul et al. 2007). However, as the seasonal sea-ice extends equatorwards during winter, the females move north, switching to pelagic foraging while the males remain in the south, continuing to forage benthically (Bailleul et al. 2007). Both males and females from the Kerguelen Islands also forage pelagically around eddies downstream of the islands (Bailleul et al. 2007).

The role of eddies for southern elephant seal foraging

The dynamic Polar Frontal Zone (PFZ) between the SAF and PF to the east of the Kerguelen Islands is an important foraging ground for female elephant seal from this archipelago's population (Bailleul et al. 2010; Dragon et al. 2010). Phytoplankton blooms occur in the islands' shelf waters, spreading eastward along the Antarctic circumpolar current (Bailleul et al. 2010). These blooms can become trapped and concentrated by interfrontal eddies and may account for the easterly direction of the animals' outward foraging trips (Bailleul et al. 2010). While some animals exhibit foraging/searching behaviour when in proximity to both cyclonic (cold) and anticyclonic (warm) eddies, others do not (Bailleul et al. 2010; Dragon et al. 2010)

illustrating variability in individual response to oceanographic conditions (Bailleul et al. 2010; Dragon et al. 2010).

Adult southern elephant seal males and females from the Patagonian colony at Peninsula Valdés, Argentina, typically forage along the edge of the Patagonian Shelf and in the Argentine Basin (Campagna et al. 2006). However, a 2006 study revealed how juvenile southern elephant seals preferentially foraged around cold- and warm core eddies which formed at the confluence of the Malvinas and Brazil Currents (Campagna et al. 2006). This study was accomplished by comparing elephant seal satellite tag position information with data from surface drifters (Campagna et al. 2006). The authors suggested that both the positive and negative sea level anomalies may present areas of predictable productivity with reduced foraging congestion, a reasonably common strategy for species reliant on patchy food availability in large areas (Campagna et al. 2006).

Marion Island

The Prince Edward Islands consist of Marion Island (270 km^2) and the smaller Prince Edward Island (45 km^2) (Pakhomov & Froneman 1999). The islands are located at 46.75°S and 37.92°E, south east of South Africa, directly in the path of the ACC (Duncombe Rae 1989; Ansorge & Lutjeharms 2002). The islands are situated in the PFZ, bounded to the north by the SAF and to the south by the APF (Ansorge & Lutjeharms 2002). While the frontal regions have high phytoplankton concentrations, the PFZ itself has low nutrient concentrations characteristic of the Southern Ocean (Balarin 1999). The PFZ's northern and southern boundaries are prone to greater meridional variability in this region than elsewhere in the Southern Ocean (Ansorge & Lutjeharms 2002) as a result of interactions with the Agulhas Return Current to the north. These interactions are thought to result in increased exchange of water between the subtropics and the PFZ (Miller et al. 1984).

The role of eddies in Prince Edward Island ecosystems

The meridional position of the SAF plays an important role in the macro- and mesoscale oceanographic conditions around the Prince Edward Islands (Pakhomov et al. 2000; Ansorge & Lutjeharms 2002), ultimately affecting the ecology of the islands' top predators (Pakhomov & Froneman 1999). When the SAF is near its northern-most extent, the ACC flow rate around the islands is relatively slow (Ansorge & Lutjeharms 2002). Eddies which form as a result of frictional interactions between the ACC and the islands may become trapped in the lee of the islands (Perissinotto & Duncombe Rae 1990). These eddies can concentrate macro nutrients and iron introduced from island freshwater runoff leading to localised phytoplankton blooms (Boden 1988; Perissinotto & Duncombe Rae 1990). Such blooms are dominated by large diatoms as opposed to the nano- and picophytoplankton, which are more typical of the region (Balarin 1999). This mechanism is known as the 'Island Mass Effect" (Boden 1988) and represents the autochthonous mode of the Prince Edward Islands' life support system (Pakhomov & Froneman 1999).

By comparison, when the SAF is near its southern-most extent the Prince Edward Islands' ecosystems rely on allochthonous nutrient supplies (Pakhomov & Froneman 1999). Under these conditions the flow rate of the ACC around the islands is far faster, preventing the retention of eddies in the vicinity of the islands (Perissinotto et al. 2000). The island ecosystems then utilise zooplankton and nekton advected by the ACC from upstream of the islands (Pakhomov & Froneman 1999). Interactions between the ACC and the South West Indian Ridge (SWIR) can result in deep mixing (Rintoul & Sokolov 2001). This mixing may lead to increased surface concentrations of nutrients and iron as well as the formation of warm- and cold core eddies which transport not only heat, but various species of plankton into the PFZ (Bernard et al. 2007). As a result the species assemblages found in the PFZ have

highly variable geographic affinities including Subtropical, sub-Antarctic and Antarctic waters (Hunt et al. 2001; Bernard & Froneman 2002, 2003).

Origin of the upstream eddies

The deep basins of the Southern Ocean are associated with very low levels of eddy kinetic energy, while in areas where the ACC interacts with topography such as chokepoints and bathymetry, high levels of mesoscale activity are observed (Phillips & Rintoul 2000; Sokolov & Rintoul 2009). To the south-west of the Prince Edward Islands is an extensive region of high sea level anomaly variability overlying the SWIR (Ansorge & Lutjeharms 2003, 2005; Durgadoo et al. 2010, 2011) (Figure 1). The SWIR is divided into two, almost equally long parts, by a series of four transform faults (Sclater et al. 2005), and interactions between the ACC and this irregular bathymetry result in the eddy field as well as downstream jet fragmentation (Pollard & Read 2001). This eddy field also coincides with a southward deflection and intensification of the ACC (Ansorge et al. 2012). The eddies concentrate and transport nutrients, plankton and associated trophic food webs in the direction of the islands and are known to be utilised as foraging grounds by grey-headed albatrosses and sub-Antarctic fur seals (Nel et al. 2001; de Bruyn et al. 2009).

In April 2013 a marine protected area (MPA) was declared within the economic exclusion zone (EEZ) around the Prince Edward Islands (Lombard et al. 2007; Ansorge et al. 2014). The planning process took into account foraging areas of southern elephant seals as well as wandering *Diomedea exulans* and grey-headed albatrosses (Lombard et al. 2007). While the conservation plan acknowledged the importance of mesoscale processes such as eddies spawned at the SWIR to the health of the Prince Edward Islands ecosystems, the EEZ does not extend to the SWIR south west of the islands (Lombard et al. 2007).

Marion Island's female southern elephant seals

The majority of tagged adult post-moult female southern elephant seals from Marion Island move from the islands towards foraging grounds to the west and south-west, traversing the eddy field en route (Figure 2) (Jonker & Bester 1998; Tosh 2010). These individuals appear to forage preferentially either adjacent-to or to the west of the SWIR (Jonker & Bester 1998; McIntyre et al. 2011b). The post moult migration tracks of the female southern elephant seals (McIntyre et al. 2011b) extend far beyond the reach of the Prince Edward Islands MPA, suggesting that for this species at least, the efficacy of the MPA may be limited.

The proximity of the seal tracks to the SWIR suggests a role for oceanographic cues in determining the animals' outward trajectories (Jonker & Bester 1998). Except for the seals' comparable initial migratory directions however, there is little similarity between individuals in terms of the foraging areas they target or the strategies they display (Tosh 2010; McIntyre et al. 2011b). Female elephant seals from Marion Island dive almost exclusively pelagically (McIntyre et al. 2010) although post-moult dives are typically deeper and longer than post-breeding dives (McIntyre et al. 2011b). Pelagic foraging appears to primarily take place to 360–560 m (McIntyre et al. 2011b). Not only are elephant seal's eyes well suited to the low light levels found at these depths (Levenson & Schusterman 1999), but some of their cephalopod and deep water fish prey items bioluminesce (Rees et al. 1998). Prey species which undergo daily vertical migrations move closer to the surface at night and the targeting of these species explains the diurnal variation in the seals diving patterns (Hindell et al. 1991; McIntyre et al. 2011b).

Southern elephant seal behaviour within the eddy field has, until this point, remained largely unexplored. Like other regions in the Southern Ocean the eddy field shows signs of already having undergone shifts as a result of anthropogenic climate change, and these changes seem

likely to intensify in the future. Given evidence of a role for eddies in the foraging of southern elephant seals from other colonies in conjunction with Marion Island's historic population decreases and comparatively low current elephant seal numbers, it is important to investigate the nature of the animals' foraging behaviour in the nearby eddy field.

Aims of this study

The goal of this study is to determine whether or not the eddy field to the south-west of Marion Island represents an important foraging ground for adult female southern elephant seals during their post-moult migrations. To answer this overarching question I analyse the diving patterns of the seals within and outside of the region at two spatial scales. The first question asks whether the seals dive within the eddy field more often than might be predicted by random chance. The hypothesis is that due to elevated productivity associated with the eddies, dive frequencies will be higher in this region. The second question asks whether the dive characteristics of the seals (maximum dive depth, dive duration and dive type) differ significantly within the eddy field compared to outside areas. My hypothesis is that the expected increase in prey availability in the eddy field region will result in shallower, shorter dives incorporating fewer underwater wiggles. The final question investigates potential correlations between eddy activity and the same dive characteristics inside of the eddy field. I expect in this case that dives will be shallower and shorter in proximity to elevated- and depressed sea level anomalies.

Methods

Data Processing

Between 26 October 2007 and 10 January 2010, 32 female southern elephant seals from Marion Island were tagged with SMRU/Series 9000 SRDL or SRDL/CTD satellite relay data loggers (Sea Mammal Research Unit, University of St Andrews, UK). These devices record time and dive information which is then transmitted along with global position estimates via the Service Argos satellite system (Argos 1996) to the Sea Mammal Research Unit (Vincent et al. 2002). Tracks are filtered to remove points describing implausible elephant seal swimming speeds and the positions of each dive are estimated as interpolated points framed by Argos uplink position estimates (Boehme et al. 2009b). These interpolations are based on uplink times in relation to the times at which the dives occurred and have an estimated accuracy of around 2 km (Boehme et al. 2009b).

The data used for this study initially included 170,904 dives. Each track was made up of consecutive dives for which the time, date, geographical position, total dive duration, maximum depth and the depths and times of four inflection points were recorded. These data were collated with deployment records from the Mammal Research Institute (MRI, University of Pretoria) so as to include each individual's age class and sex, using Python 2.7.5 (http://www.python.org/) along with the pyodbc (http://code.google.com/p/pyodbc/) and xlrd (http://www.python-excel.org/) libraries. Except where otherwise indicated, all subsequent data processing were undertaken in the R environment for statistical computing (R Core Team 2013).

The decision to study only adult females was based on their spending more time at sea per year than the males, as well as their extensive post-moult migrations which can last up to eight months (Le Boeuf & Laws 1994). Adult females spend up to 88% of their time diving, more than that of males or females in any other age-class (Boyd et al. 1994). Only data from

the approximately eight-month long adult female post-moult migrations (n=16) were included; tracks which ended before the animal had returned to Marion Island and covered less than 30 days at sea were excluded from the analysis (cf. Bailleul et al. 2010). The region of enhanced mesoscale oceanographic activity was determined to fall into the region defined from 47.33° to 53° S and 27.33° to 37.66° E (Figure 1) (I. Ansorge pers. comm.).

Using the geosphere libraries (Hijmans et al. 2012), each dive's distance and absolute bearing from Marion Island was calculated along with distances, speeds, and relative bearings between successive dives. These calculations were undertaken on a seal by seal basis and distances were derived using Vincenty's ellipsoidal formula (Vincenty 1975). The data sets for three seal tracks (GG335 – 2009, GG335 – 2010, YY189 - 2010) contained unusually large numbers of dives (201, 780, 167 respectively) with durations of exactly 5715 sec. These times were attributed to erroneous tag readings and excluded from further analysis. In order to determine whether a dive occurred during a post-breeding or post-moult migration, dive distances from Marion Island were used. This technique allowed me to avoid inadvertently excluding dives undertaken by individuals who might have left the island earlier or arrived later than typical seals. On an individual basis, consecutive dive distances from Marion Island were plotted as a function of date. These plots were inspected visually and distance minima were used as transition points between migrations. The data set at this point included a total of 116,568 dives within 22 individual tracks from 16 seals as data were collected for some seals over multiple years (Table 1). Using the maptools library (Bivand & Lewin-Koh 2013) dives were classified as taking place during the day or night. Because this analysis involved clearly distinguishing between dive parameters occurring during the day and night, if a dive took place within 30 minutes of sunrise or sunset it was classified as a dusk dive and excluded from further analysis (cf. McIntyre et al. 2011b). Each dive was further categorised as to whether it occurred within or outside of the eddy field domain.

Time-depth profiles were used to categorize each dive into one of six categories using the approach developed by M. Biuw (unpublished data) and used by Photopoulos (2007). Breiman's random forest algorithm was used to classify each dive based on a training set. The training set is a visually categorised subset of dives with which proportions of dive time, vertical direction of travel and rates of ascent or descent between inflection points could be compared for classification. Generation of a training set requires subjective dive type classifications and as such it was determined that an existing training set, provided courtesy of the MRI, would increase conformity of results between research studies.

Correlated Random Walks

I first tested whether the seal tracks approximated Lévy walks (see Appendix A). Since my results provided no evidence of such movement patterns, a correlated random walk (CRW) distribution was generated with which to compare the seals' use of the eddy field. The CRW function simm.crw() from the adehabitatLE library (Calenge 2006) requires three arguments, a date range, a scaling parameter (h) for resolving the distance travelled during each step, and a concentration factor (r) which determines the range of possible turning angles available to each successive step. The observed seal tracks were first split into outward and homeward legs using their furthest dives from Marion Island as turning points. The 22 outward legs were then analysed in order to derive values for these arguments. The scaling parameter for each outward track was estimated using the hbrown() function in adehabitatLE. Each seal's outward-bound turning angles were fitted to a wrapped normal distribution using the wle library (Agostinelli 2012) in order to estimate a value for r. Individual seals' number of outward bound steps along with mean step durations were used to generate their date range.

Each seal's unique combination of date range, h and r values were grouped together. During the generation of the CRWs, one of these groups of values was selected at random for each CRW in order to render the random walks more realistic. Unfortunately the value for r was

consistently over- or under-estimated, resulting in unrealistically long and straight or short and scattered random walks. After visually assessing the random walks, a static value of 0.96 was chosen for r, generating tracks which resembled those recorded from the seals CRWs (Figure 2 ii). A total of 5,000 CRWs were produced. The ratio of dives occurring within the eddy field domain converged on 7.9% after approximately 4,000 CRWs, so the full complement of 5,000 CRWs was used for comparisons.

Oceanographic data processing

Daily, delayed time, mean sea level anomaly (SLA) for the period 1 January 2008 to 31 December 2010 were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/). All the data processing for SLA anomaly were carried out in MATLAB® R2011b (http://www.mathworks.com). SLA data were gridded to 1/3° latitude blocks to match their native longitude resolution, and subsampled to include only the eddy field region.

Statistical analyses

Exact binomial tests were run using the core stats package in R to determine whether the ratio of observed dives occurring outside vs inside of the eddy field was significantly greater than the same ratio within the simulated CRWs. These tests were run for all dives as well as for each of the 16 seals' 22 post-moult tracks. After this initial analysis, further investigations included only the tracks of individuals who had dived within the eddy field significantly more frequently than predicted by the CRWs. This subsequent data set included 11 individuals, 14 tracks and 77,045 dives (Table 2).

Changes in maximum depth and dive duration

In order to detect significant differences in maximum depth and dive duration as a result of diving within the eddy field, changing day-stage or changing SLA, linear mixed effects (LME) models were run using the nlme (Pinheiro et al. 2013) package in R. Mixed effects

models were chosen so that individual seals could be included as random effects and the contribution of individual variance determined (Pinheiro & Bates 2000). Where mixed effect model results are reported, values refer to estimated effect ± standard error. Except where otherwise indicated, these models were initially run with the maximum likelihood (ML) method so that best fit models could be determined using Akaike's information criterion (AIC) values. The dredge function in the MuMIN library (Barton 2013) was used to determine the best fit combination of predictors, and models were updated accordingly.

Residual histograms were inspected to ensure that the data were approaching normal distributions (Zuur et al. 2009). In order to account for heterogeneity, scatter plots of residuals were checked for funnelling (Zuur et al. 2009). No data transformations were applied during the data preparation. To check for independence, autocorrelation function (ACF) plots and semivariograms were generated for each model. Where data were found to be autocorrelated (all cases), models were updated with best fit correlation structure functions (Pinheiro & Bates 2000).

For larger data sets, best fit correlation structure functions were determined by analysing models of 5,000 dive subsets while for the smaller data sets these analyses were run on full sets of dives. This analysis included updating initial autocorrelated models with spherical, exponential, Gaussian, rational quadratic and first order autoregressive correlation structure functions (Pinheiro & Bates 2000). AIC values were compared in order to find the best fit models. ACF plots and semivariograms were used to confirm that selected correlation structure functions had successfully reduced the autocorrelation (A. Amar pers. comm.; T. McIntyre pers. comm.). For the larger data sets, final models were run on 25,000 dive subsets and then updated using the optimal correlation structure functions and restricted maximum likelihood (REML) method. Final mixed effects models run on individuals used each seals full data set and included seal IDs as a dummy random effects.

In order to check for significant effects of the eddy field and day-stage on maximum depth and dive duration, mixed models were run on the group data as well as on individual seals. Autocorrelation function selection and final models for the grouped data were run as outlined above. Individual models included each seals full data set. Due to model complexity these individual models did not undergo correlation structure function selection and were all updated with first order autoregressive correlation structure functions in order to account for autocorrelation (Pinheiro & Bates 2000).

To check for significant effects of SLA and day-stage on maximum depth and dive duration within the eddy field, mixed models were again run on the group data as well as on individual seals. The group data set within the eddy field included 12,386 out of the 77,045 dives, each of which was paired with an SLA value corresponding to the date of the dive. Autocorrelation function selections for the grouped data were run as outlined above. The final models included the full data set and were updated as before. This process was repeated for each individual which dived within the eddy field. In these cases however each individual's model was updated to the REML method before selecting the best autoregressive correlation structure functions. These selections were therefore based on Bayesian information criterion (BIC) as opposed to AIC values.

Changes in dive types

The majority of dives, both inside and outside of the eddy field, were either U- or W-dives, together accounting for approximately 95% of the total. For this reason the remaining dive types (SQ-, DR-, R- and V-dives) were grouped into a third type called other dives (O-dives). To assess whether the proportions of dive types used by the seals differed significantly outside vs inside of the eddy field, the binomial regression analysis function from the EMT library (Menzel 2013) was used. These analyses were run for all the seals together as well as separately for each individual seal and included the full data set.

In order to explore relationships between the dive types used by the seals and the oceanographic variables within the eddy field, multinomial regression analyses were then run using the nnet libraries (Venables & Ripley 2002). These models predicted statistically significant log-odds of switching from U-dives (the most common) to either W- or O-dives in the context of changing SLA or day-stage.

Results

Interactions between the ACC and a fault region in the SWIR result in elevated mesoscale activity easily identified from the mean absolute SLA in the region (Figure 1). Overall 20 tracks, undertaken by 15 seals traversed the eddy field region to the south west of the island (Figure 2 i). The tracked female seals undertook 22 post-moult migrations between 2008 and 2010 (Table 1), making 102,841 dives outside of the eddy field and 13,727 dives inside the region.
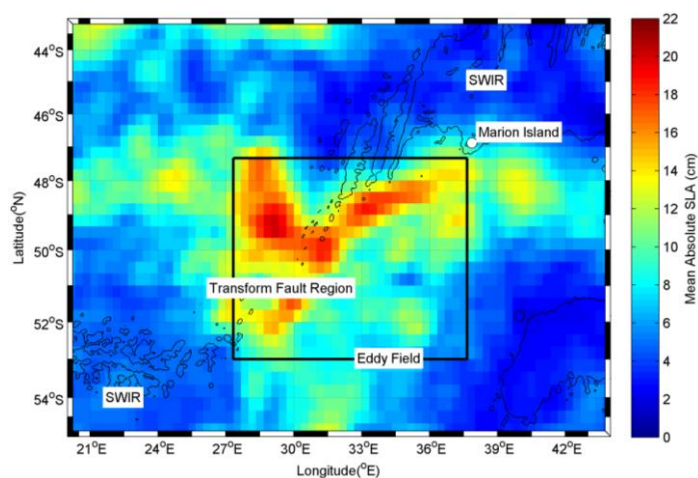
Figure 1: The region of elevated mean absolute sea level anomaly, or eddy field (black rectangle) to the south west of Marion Island (white dot) for the period 2008-2010. The isobaths show the 3000 m contour and the series of faults cross-cutting the South West Indian Ridge.
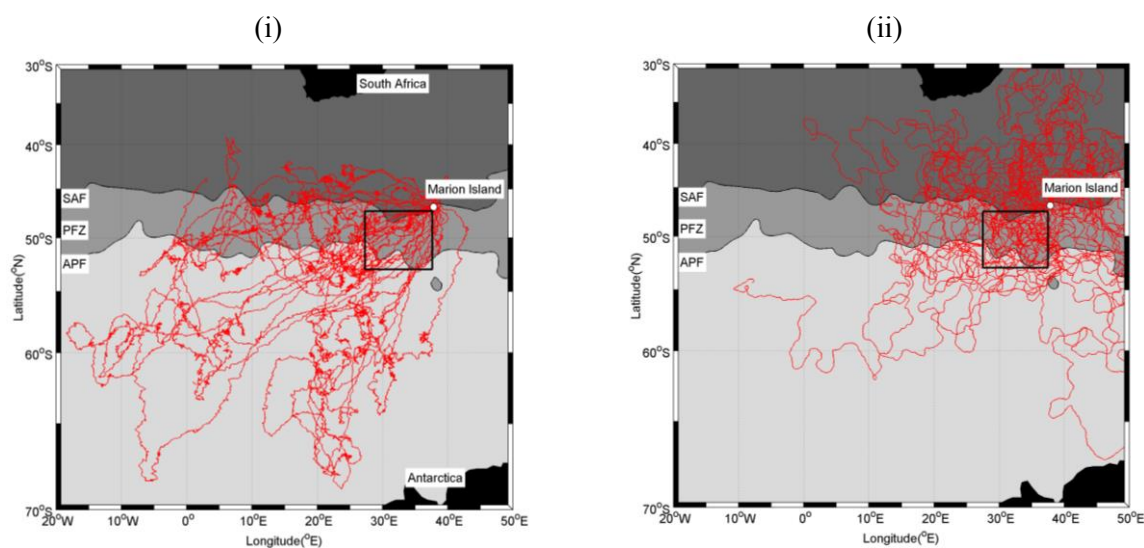
Figure 2: The position of Marion Island in relation to South Africa, Antarctica, the sub-Antarctic front (SAF), the Antarctic Polar Front (APF) and the Polar Frontal Zone (PFZ). The eddy field is demarcated by a black square. Red lines indicate post-moult dive locations of the 22 females referenced in this study (i) and a subset of the CRWs with which they were compared (ii).

Table 1: Tagged female southern elephant seals from Marion Island included in this study along with deployment ages and years, dates of the first post-moult dives and the number of days spent at sea during each post-moult track. Numbers of dives are split into those occurring inside and outside of the eddy field region to the south west of Marion Island.

Seal ID	Age at deployment (days)	Event year	Track start date	Days at sea	Dives inside eddy field	Dives outside eddy field
OO021	2289	2007	2008/02/02	225	0	5330
OO418	2308	2007	2008/02/22	97	318	3077
PO043	3403	2007	2008/02/15	258	686	4810
WW058	2654	2007	2008/01/27	232	433	7667
WW061	2654	2007	2008/02/07	234	342	5974
10755	1929	2007	2008/01/28	102	1016	1860
GG335	3039	2007	2008/02/14	293	624	7849
YY189	1564	2007	2008/02/04	241	1817	4725
YY039	1588	2008	2008/02/29	168	840	3526
YY193b	1578	2008	2008/02/13	179	214	5682
YY264b	1588	2008	2008/02/21	159	295	4163
YY348b	1581	2008	2008/02/19	187	287	4214
BB246	2314	2009	2009/02/21	228	330	5125
BB349	2317	2009	2009/02/23	223	491	5295
RR217	1578	2009	2009/02/09	195	105	4550
RR435	1587	2009	2009/02/21	230	1135	4507
GG335	3387	2009	2009/01/24	129	94	1555
OO021	2642	2009	2009/01/23	67	0	1075
PO043	3769	2009	2009/02/10	233	3210	5305
YY189	1934	2009	2009/02/03	241	414	6536
YY189	-	2010	2010/02/01	82	868	1907
GG335	-	2010	2010/02/13	237	208	8109

Dive frequencies outside vs inside of the eddy field

Altogether, the seals undertook significantly more of their dives (18.5%) within the eddy field than the 7.9% predicted by the CRWs ($p < 0.01$; Table 2, Figure 2 ii). On an individual level, 11 of the 16 seals dived within the eddy field region significantly more often than predicted by the CRWs during 14 out of 22 tracks (Table 2). While seals YY189 and PO043 dived significantly more frequently within the eddy field during all tracked years, seal GG335 dived more often within the eddy field during all three tracked years but significantly so in

only one. The remaining 14 tracks were undertaken by different seals and included eight tracks where the seals dived within the eddy field more often than predicted and two tracks which took place outside of the eddy field. Two tracks were comprised of more eddy field dives than predicted but not significantly so and two contained fewer eddy field dives than predicted.

Table 2: Observed percentage of dives which occurred within the eddy field for the 5,000 CRW simulations, for the grouped post-moult tracks of adult female southern elephant seals from Marion Island included in this study (n=16) as well as for individual tracks (n=22). Significant differences between observed and predicted values are indicated by * ($p < 0.01$).

Seal ID	Deployment year	Observed percentage of dives occurring within the eddy field
CRW	-	7.9%
All seals	2007-2010	18.5% *
OO021	2007	0.0%
OO418	2007	16.5% *
PO043	2007	22.5% *
WW058	2007	5.0%
WW061	2007	12.0% *
10755	2007	42.5% *
GG335	2007	10.8% *
YY189	2007	35.9% *
YY039	2008	24.4% *
YY193b	2008	7.0%
YY264b	2008	14.6% *
YY348b	2008	7.0%
BB246	2009	9.5% *
BB349	2009	9.6% *
RR217	2009	4.5%
RR435	2009	24.2% *
GG335	2009	6.9%
OO021	2009	0.0%
PO043	2009	57.2% *
YY189	2009	12.4% *
YY189	2010	46.4% *
GG335	2010	4.7%

Dive parameters outside vs inside of the eddy field

Considering all the seals together, the recorded maximum dive depths reached 1678 m outside of the eddy field and 1189 m inside of the region with mean maximum depths and dive durations being shorter and shallower within the region regardless of day-stage (Table 3). Mixed effects models confirm that overall, mean maximum dive depths inside of the eddy field were significantly shallower than dives outside of the region as a result of both position relative to the eddy field and day-stage (Table 4). A maximum depth reduction of 53.03 ± 5.30 m could be attributed to diving within the eddy field. However, the effects of day-stage were stronger, with night-time accounting for dives which were shallower by an estimated 161.01 ± 2.21 m.

Mixed effects models confirm that position played a significant role in the shorter dive durations within the eddy field (Table 4). Dives were approximately 6.17 ± 0.58 min shorter as a result of occurring inside of the eddy field rather than outside of the region. Compared to position relative to the eddy field, day-stage was a stronger predictor of dive duration resulting in night-time dives of up to 7.38 ± 0.12 min shorter than daytime dives. Little variability in maximum depth (5.5%) and dive duration (7.5%) could be attributed to differences between individual seals, with most variation occurring within individuals (Table 5).

U-dives were the most common both inside- and outside of the eddy field, followed by W- and O- type dives (Figure 3). There was a statistically significant increase in the frequency of U dives, along with decreases in W and O dives inside of the eddy field in the combined dataset from the 16 seals that dived more frequently within the eddy field. Inside the eddy field U-dives increased by 6.97%, W dives decreased by 7.18% and O-dives increased by 0.21%.

Table 3: Post-moult dive maximum depth and dive duration statistics for the adult female southern elephant seals from Marion Island which dived more frequently within the eddy field (EF) than predicted (n = 11) between 2008 and 2010. Values are grouped by position relative to the eddy field and day-stage (day or night).

Maximum depth (m)	Day dives (mean ± sd)	Night dives (mean ± sd)	Maximum
Inside EF	514.80 ± 160.74	380.64 ± 138.18	1189.0
Outside EF	555.42 ± 176.29	409.07 ± 169.21	1678.0
Dive duration (min)			
Inside EF	23.68 ± 9.55	20.56 ± 8.85	88.25
Outside EF	31.61 ± 12.18	26.30 ± 10.67	95.25

Table 4: Estimated mixed effects model impacts of the eddy field and day-stage on maximum depth and dive duration for the adult female southern elephant seals from Marion Island which dived more frequently within the eddy field (EF) than predicted (n=11) between 2008 and 2010.

	Max depth (m ± se)	DF	t-value	p-value
Inside EF	-53.03 ± 5.30	24986	10.00	< 0.01
Night	-161.01 ± 2.21	24986	-72.98	< 0.01
	Dive duration (min ± se)			
Inside EF	-6.17 ± 0.58	24986	10.70	< 0.01
Night	-7.38 ± 0.12	24986	-60.70	< 0.01

Table 5: Mixed effects model estimates of variability in maximum depth and in dive duration, between (τ^2) and within (σ^2) individual adult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n=11), during their post-moult migrations between 2008 and 2010.

	Variance (τ^2 ± SD)	Residual (σ^2 ± SD)	Between seal variability
Maximum depth	1410.09 ± 37.55	24117.02 ± 155.30	5.5%
Dive duration	8.83 ± 2.97	108.33 ± 10.41	7.5%
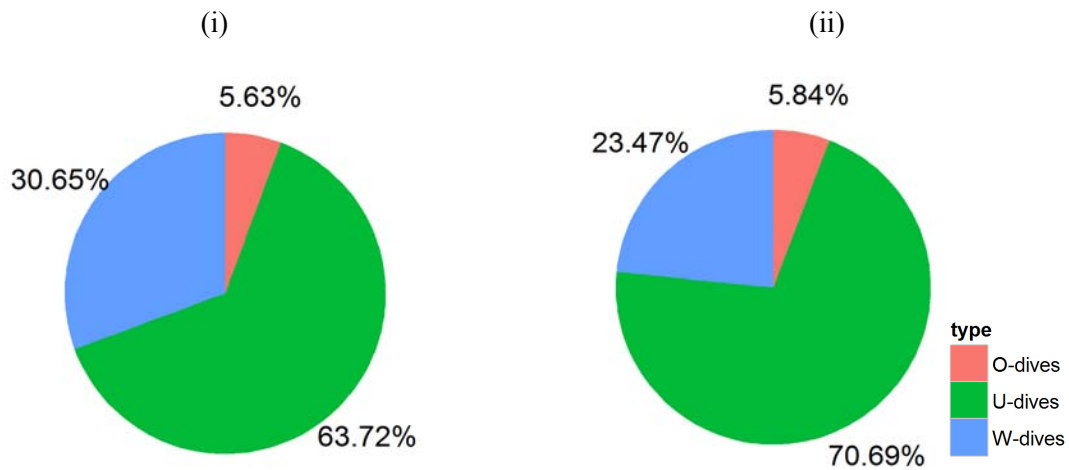
Figure 3: Binomial regression estimates of statistically significant changes in dive type usage by post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010, outside (i) vs inside (ii) of the upstream eddy field.

Of the 11 seals which dived more frequently than predicted inside the eddy field, eight individuals' maximum dive depths were shallower inside- vs outside of the eddy field (Table 6). Ten individuals' dive durations were shorter within the eddy field (Table 6). Diving at night accounted for shallower dives all 11 cases while eddy field diving accounted for shallower dives in seven cases (Table 7). Two individuals' maximum depths were more strongly reduced by eddy field diving than by day-stage. One individuals' best fit model did not include eddy field diving (BB246) while for two seals diving in the eddy field was not a significant predictor of maximum depth (RR435, 10755). Dive durations of nine individuals were reduced as a result of eddy field diving (Table 7). The dive durations of eight seals were more strongly reduced by diving within the eddy field than day-stage. Two seals' dive durations were more substantially reduced by day-stage resulting in shorter dives at night. One individual dived both deeper and longer as a result of the eddy field.

Table 6: Mean maximum depths and dive durations outside and within the eddy field for post-moult adult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010.

	Mean maximum depth (m ± sd)		Mean dive duration (min ± sd)	
Seal ID	Inside	Outside	Inside	Outside
WW061	471.35 ± 136.14	500.28 ± 172.77	21.94 ± 5.42	29.28 ± 9.12
PO043	451.66 ± 148.42	515.93 ± 180.64	21.44 ± 8.24	29.57 ± 10.23
OO418	252.73 ± 154.38	455.54 ± 174.83	20.13 ± 9.02	24.64 ± 8.61
YY264b	389.68 ± 123.12	391.48 ± 179.63	18.67 ± 4.38	27.30 ± 11.14
YY039	379.52 ± 136.32	441.34 ± 147.24	19.96 ± 6.58	27.78 ± 10.38
BB246	458.25 ± 160.2	455.25 ± 188.87	17.14 ± 7.17	29.01 ± 13.15
RR435	528.07 ± 187.1	502.67 ± 193.65	34.56 ± 13.32	33.58 ± 11.64
BB349	402.18 ± 184.72	553.05 ± 167.68	25.46 ± 8.21	34.36 ± 11.17
YY189	454.46 ± 153.20	455.61 ± 155.99	19.92 ± 7.98	26.94 ± 9.66
10755	458.13 ± 145.67	459.74 ± 158.85	22.33 ± 7.96	24.62 ± 9.18
GG335	495.35 ± 189.85	493.53 ± 192.58	26.87 ± 10.33	32.63 ± 13.23

Table 7: Mixed effects model estimates of significant individual maximum depth and dive duration effects attributed to diving within the eddy field and day-stage for post-moult adult female southern elephant seals from Marion Island which dived more frequently within the eddy field (EF) than predicted (n = 11) between 2008 and 2010. Reported values are significant at $p < 0.05$ where marked with *.

	Maximum depth (m ± se)		Dive duration (min ± se)	
Seal ID	Inside EF	Night-time	Inside EF	Night-time
WW061	-55.12 ± 14.21	-173.29 ± 7.08	-7.83 ± 1.03	-5.17 ± 0.35
PO043	-79.75 ± 5.52	-165.06 ± 4.66	-8.72 ± 0.39	-8.75 ± 0.25
OO418	-212.00 ± 17.76	-143.48 ± 10.36	-4.81 ± 1.12	-4.43 ± 0.50
YY264b	-34.05 ± 16.59 *	-198.48 ± 7.74	-9.18 ± 1.53	-7.43 ± 0.46
YY039	-74.12 ± 9.49	-109.17 ± 7.98	-6.57 ± 0.94	-6.19 ± 0.40
BB246	-	-175.76 ± 6.75	-10.11 ± 1.68	-5.96 ± 0.49
RR435	-	-126.65 ± 9.32	-	-6.15 ± 0.40
BB349	-152.59 ± 14.91	-121.50 ± 6.59	-6.78 ± 1.39	-3.90 ± 0.33
YY189	15.94 ± 4.73	-112.30 ± 3.44	4.87 ± 0.45	-2.40 ± 0.43
10755	-	-125.24 ± 7.83	-2.16 ± 0.84	-2.29 ± 0.51
GG335	-29.39 ± 13.73 *	-167.94 ± 13.73 *	-5.62 ± 1.36	-4.99 ± 0.37

Ten individuals showed significant changes in the types of dives which they undertook once inside of the eddy field (Table 8). Within the eddy field eight seals undertook more U- and

fewer W-dives while two seals undertook more W- and fewer U-dives. Percentage changes in O-dive occurrence were low in comparison to changes in U- and W-dives.

All 11 seals displayed some significant differences in dive parameters associated with the eddy field (Table 9). Three seals displayed substantial effects in all three measured dive parameters as a result of diving within the eddy field. The impacts of diving within the eddy field were also evidently important to three individuals in terms of only their maximum depths and dive durations, although two seals' dives were shorter and shallower while one dived longer and deeper. For one seal only dive durations and dive types were substantially different inside the eddy field. Diving inside of the eddy field had large impacts on only the dive durations for two individuals while one seal did not appear to be affected by the eddy field in terms of any dive parameters.

Table 8: Binomial regression estimates based estimates of significant proportional change in dive type occurrence within the eddy field for individual adult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted(n = 11) between 2008 and 2010. Reported values are significant at $p < 0.05$ where marked with *.

| Seal ID	Proportional change in dive type use (%)		
	U-dives	W-dives	O-dives
WW061	30.17	-26.35	-3.83
PO043 *	1.68	-1.91	0.21
OO418	27.21	-26.97	-0.23
YY264b	17.34	-18.03	0.69
BB246	-5.83	7.58	-1.75
RR435	14.33	-13.13	-1.20
BB349	25.27	-25.62	0.36
YY189	6.33	-9.25	2.92
10755	6.84	-4.67	-2.15
GG335	-6.24	7.03	-0.78

Table 9: Multinomial regression based estimates of statistically significant effects on dive parameters of adult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010, attributed to diving within the eddy field. Dive type variation refers to switches between U- and W-dives.

Seal ID	Max. Depth	Dive duration	Dive type
WW061	-11%	-27%	> 10%
BB349	-28%	-20%	> 10%
PO043	-15%	-29%	< 10%
YY039	-17%	-24%	-
OO418	-47%	-20%	> 10%
YY264b	-9%	-34%	> 10%
YY189	+25%	+18%	< 10%
GG335	-6%	-17%	< 10%
BB246	-	-35%	< 10%
RR435	-	-	> 10%
10755	-	-9%	< 10%

Dive parameters within the eddy field

Both dive depth and dive durations within the eddy field clustered around moderate SLA (Figure 4). R^2 values were very low in both cases. Mixed effects models estimated that maximum dive depths within the eddy field were significantly affected by day-stage while SLA was not a significant predictor (Table 10). Both SLA and day-stage were statistically significant predictors for dive duration with elevated SLA resulting in longer dives and dives tending to be shorter at night (Table 10). With regards to dive type choice, the log-odds prediction was that that a unit increase in SLA was a significant predictor for a change from U- to W-dives, but not to O-dives (Table 10). Day-stage was a stronger, significant predictor for changing from U- to both W- and O-dives. The model output suggested that 19.30% of the variance in maximum dive depth and 16.83% of variance in dive duration was the result of variance between individuals (Table 11).

(i)   (ii)
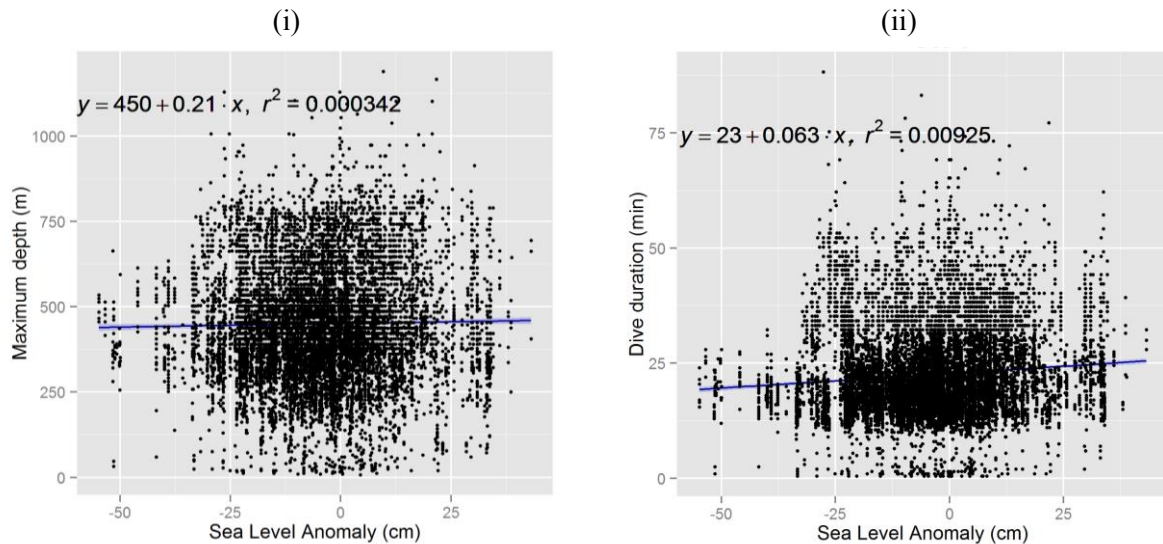
Figure 4: Relationships between maximum depths (i) and dive durations (ii) vs SLA within the eddy field, for adult post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010.

Table 10: Mixed effects model predictions for adult post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010, comparing the effects attributed to changing SLA and day-stage on maximum depth, dive duration and dive type likelihood within the eddy field. Dive type values represent the log-odds of changing between U-dives and either W- or O-dives as a result of changing SLA or day-stage.

	Max depth (m ± se)	DF	t-value	p-value
SLA	-0.04 ± 0.20	12372	0.21	> 0.05
Night	-138.17 ± 3.54	12372	-39.00	< 0.01
	Dive duration (min ± se)			
SLA	0.15 ± 0.01	12372	11.72	< 0.01
Night	-4.31 ± 0.16	12372	-26.82	< 0.01
	W-dives (Log-odds ± se)		z-value	
SLA	0.00 ± 0.00	-	2.97	< 0.01
Night	0.56 ± 0.05	-	12.33	< 0.01
	O-dives (Log-odds ± se)			
SLA	0.00 ± 0.00	-	-1.55	> 0.05
Night	0.27 ± 0.08	-	3.28	< 0.01

Table 11: Mixed effects model estimates of variability in maximum depth and in dive duration, between (τ^2) and within (σ^2) individual seals, inside of the eddy field. Values are estimated by mixed effects models and include adult post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010.

	Variance ($\tau^2 \pm SD$)	Residual ($\sigma^2 \pm SD$)	Between seal variability
Maximum depth	4985.45 ± 70.61	20844.57 ± 144.38	19.30%
Dive duration	58404.13 ± 241.67	288580.83 ± 237.20	16.83%

SLA was a significant predictor of maximum depth for two seals (Table 12). Day-stage was estimated to be significant for all 11 individuals. In both cases the effect of elevated SLA (0.55 ± 0.20 m to 0.82 ± 0.30 m) was much smaller than that of day-stage (-73.03 ± 12.65 m to -218.76 ± 20.98 m). In terms of dive durations, SLA was a significant predictor in four cases (-0.05 ± 0.02 min to 0.27 ± 0.05 min) but once again day-stage was the stronger predictor (-2.02 ± 0.54 min to -8.92 ± 0.59 min) (Table 12).

The log-odds likelihood of switching between U- and W- dives were significant for ten seals, but SLA only accounted for four of these (Table 13). SLA related log-odds ranged from -0.01 ± 0.00 to 0.02 ± 0.01 while day-stage estimates accounted for nine seals and ranged from -0.43 ± 0.20 to 2.03 ± 0.50. In terms of switching from U-dives to O-dives, the log-odds estimate of a one unit change in SLA resulting in a change in dive type was significant for one seal (-0.01 ± 0.00) while day-stage was significant for three individuals (0.43 ± 0.16 to 1.61 ± 0.64) (Table 13).

Table 12: Mixed effects model estimates of significant individual maximum depth and dive duration effects attributed to changing SLA and day-stage for adult post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010. Reported values are significant at p < 0.05 where marked with *.

Seal	Maximum depth (m ± se)		Dive duration (min ± se)	
	SLA	Night	SLA	Night
WW061		-124.39 ± 19.23		-4.59 ± 0.86
PO043	0.55 ± 0.20	-157.26 ± 6.41		-2.84 ± 0.56
OO418		-76.34 ± 20.16		-7.02 ± 1.34
YY264b		-154.83 ± 17.94	-0.05 ± 0.02 *	-5.24 ± 0.63
YY039		-73.03 ± 12.65		
BB246		-218.76 ± 20.98		-7.81 ± 0.81
RR435		-127.68 ± 11.11	-0.17 ± 0.06	-8.92 ± 0.59
BB349		-197.50 ± 20.77		-3.06 ± 1.07
YY189	0.82 ± 0.30	-121.17 ± 7.70	0.14 ± 0.02	-2.34 ± 0.45
10755		-112.17 ± 12.45	0.27 ± 0.05	-2.02 ± 0.54
GG335		-119.11 ± 18.60		

Table 13: Mixed effects model estimates of significant individual log-odds of changing from U- to W- or O-dives, attributed to changing SLA and day-stage for adult post-moult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n = 11) between 2008 and 2010. Reported values are significant at p < 0.05 where marked with *.

Seal	Change to W-dives (log-odds ± se)		Change to O-dives (log-odds ± se)	
	SLA	Night	SLA	Night
WW061		2.03 ± 0.50		
PO043	0.01 ± 0.00	0.51 ± 0.08	-0.01 ± 0.00 *	0.43 ± 0.16
YY264b		0.69 ± 0.39 *		
YY039	-0.01 ± 0.01 *			
BB246		1.91 ± 0.32		1.59 ± 0.6
RR435	0.02 ± 0.01	0.67 ± 0.25		
BB349		0.85 ± 0.26		1.61 ± 0.64
YY189	0.01 ± 0.00 *	0.81 ± 0.1		
10755		0.78 ± 0.19		
GG335		-0.43 ± 0.20 *		

Discussion

Marion Island is home to one of the most northerly southern elephant seal populations and its long distance from many preferred elephant seal foraging areas means that its seal population may be more vulnerable to changing prey distributions than other more southerly populations (McIntyre et al. 2011a). Previous research has confirmed the role of eddies as foraging grounds for sub-Antarctic fur seals and grey-headed albatrosses from Marion Island (Nel et al. 2001; de Bruyn et al. 2009) as well as for southern elephant seals from Peninsula Valdés and the Kerguelen Islands (Campagna et al. 2006; Bailleul et al. 2010). The eddy field to the south west of Marion Island in the vicinity of the Andrew Bain Fault Region is mostly generated by interactions between the ACC and the region's irregular bathymetry (Ansorge & Lutjeharms 2003, 2005, Ansorge *et al.* 2009). The SAF of the ACC has gradually been shifting southwards over the past 60 years (Swift 1995; Gille 2002; Sokolov & Rintoul 2009), and this shift is expected to result in increased generation of warm eddies (Gille 2003). Should this eddy field be a biologically important foraging area for Marion Island's southern elephant seals, changes in prey distributions resulting from shifts in the nature of the eddy field may be contributing to the species' failure to recover from 20th century population declines.

This study incorporated the dive- and track data of 16 adult female southern elephant seals from the Marion Island population (Table 1). Out of the 22 tracks only two from a single individual seal during different years moved west of Marion Island and didn't encounter the eddy field (Figure 2 i). The remaining 20 tracks moved predominantly south west from the Island, traversing the eddy field during their outward and homeward legs.

Dive frequencies outside vs inside of the eddy field

In order to determine whether Marion Island's southern elephant seals dive within the eddy field region more often than might be expected by chance, I evaluated the observed track data

against simulated random walk distributions. Analyses of the track data in terms of both distance and speed confirmed that the seals were not undertaking Lévy walks (see Appendix A). I therefore compared the observed tracks with distributions of correlated random walks (CRWs) (Figure 2 ii). The value of these 'classical' random walks for modelling animal movements is well established (Turchin 1998). The CRWs suggested that the seals would encounter the eddy field region during 7.9% of their outward leg post-moult dives. Analyses of the animals' outward post-moult migration legs revealed that 18.5% of the observed dives occurred within the eddy field. On an individual level, 69% of the seals dived statistically more frequently than expected within the eddy field during 64% of the post-moult migrations (Table 2). Results for these 14 tracks were fairly widely spread, with between 9.5% and 57.5% of their dives occurring within the eddy field.

Southern elephant seals forage in widely disparate regions and Marion Island's adult females are no exception (McIntyre et al. 2011b). The majority of adult females have been observed moving to the west and south-west of the Prince Edward Islands (Jonker & Bester 1998; Tosh 2010; McIntyre et al. 2011b). Their preferred foraging regions were generally to the west of the Andrew Bain Fracture Zone of the SWIR (McIntyre et al. 2011b). Individual variation has been observed in adult female post-moult migrations (McIntyre et al. 2011b), possibly as a result of the exploratory nature of such far ranging migrations (Tosh 2010). Two broad post-moult strategies were described by Tosh (2010). One group of females stayed relatively close (<1,900 km) to the islands, concentrating their movements around the nearby fault region of the SWIR (Tosh 2010). These animals' searching behaviour appeared to coincide with cyclonic and anticyclonic features. The second, more expansive group (moving >2,500 km from the island) foraged on the SWIR, the SAF or travelled south to the Antarctic ice pack, although the latter was a comparatively rare occurrence (Jonker & Bester 1994; Tosh 2010; McIntyre et al. 2010, 2011b).

In light of their expansive migrations, it is likely that this study's seals were primarily travelling through the region en route to more distant, preferred foraging grounds. Any foraging activity within the eddy field was therefore likely to have been opportunistic, explaining the variation in individual responses. Nevertheless, the biological importance of the group response seems to be reinforced by the individual results.

Dive parameters outside vs inside of the eddy field

Given that the southern elephant seals from Marion Island appeared to dive more often than expected within the eddy field, I predicted that their maximum dive depths, their dive durations and the dive types they preferentially used would also differ within the region. This investigation was restricted to the 11 animals which had dived more frequently within the eddy field. The dives of adult female seals from Marion Island are shorter and shallower at night than during the day, most likely in response to vertically migrating prey (McIntyre et al. 2011b). For this reason, day-stage (day or night) was included in this study as a comparative measure of biological importance.

Overall, maximum depths were shallower and dive durations were shorter within the eddy field and at night (Table 3). Day-stage however contributed more to the observed variance in both parameters than did diving within the eddy field (Table 4). Nevertheless the changes in dive durations as a result of night diving were similar to those attributed to diving within the eddy field. The mixed model results suggested that 5.5% of the variance in maximum depths and 7.5% of the variance in dive durations could be attributed to differences between individuals (Table 5). This reasonably low measure of between-seal variance implies that the bulk of variability in maximum depth and duration occurred within individual seals and that, to some extent, the seals were behaving in a similar way to one another. In terms of dive types the number of U-dives increased within the eddy field by a statistically significant 6.97% (Figure 3). This increase was principally at the expense of W-dives with very little

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change in the occurrence of O-dives. Within the eddy field however W-dives still comprised almost a quarter of the total dives.

Most individuals dived both shallower and shorter within the eddy field (Table 6). Diving within this region was a significant predictor of maximum depth for eight seals although day-stage had a larger effect in all cases (Table 7). Conversely, in terms of dive duration, the eddy field was a stronger predictor than day-stage for the majority of the animals although, as with the group result, the magnitudes of the effects were similar in many cases (Table 7). Most of the seals increased their proportional use of U-dives within the eddy field primarily at the expense of W-dives (Table 8). Changes in O-dive occurrences were relatively low for all seals.

Female southern elephant seals from Marion Island dive deeper and longer than females from other populations (Hindell et al. 1991; Campagna et al. 1995; McIntyre et al. 2011b). It is likely that this increased depth and duration pushes the animals closer to their physiological limits (Hindell et al. 2000). The extreme diving behaviour of Marion Island elephant seals, combined with their relatively short lifespans (rarely extending past 12-14 years at Marion Island) (de Bruyn et al. 2009), prompted McIntyre et al.'s (2010) "deeper diving-shorter life" hypothesis. In light of their diving habits and the associated stress, it seems likely that a 10% reduction in depth or duration would be biologically important to the animals from Marion Island. Unlike dive duration, the maximum depth reduction associated with diving inside the eddy field was substantially less than that attributed to diving at night (Table 4). Diving within the eddy field nevertheless accounted for a greater than 10% maximum depth reduction for five of the 11 seals (Table 9). For instance, diving within the eddy field accounted for a depth reduction of 55.12 m (Table 7) within the eddy field for seal WW061 whose mean depth outside of the region was 500.28 m (Table 6). Given the established biological importance of day-stage (McIntyre et al. 2011b) and based on the magnitude of its

effect on dive durations, diving within the eddy field had biologically important dive duration effects for nine seals (Table 9).

Because of the small changes in O-dive occurrence in both the group and individual results, biological importance of dive type choice was based on changes between U- and W-dives. Both of these dive types have been linked to foraging (Hindell et al. 1991; McIntyre et al. 2011b) although one study has suggested that U-dives may involve travelling along with opportunistic feeding (Photopoulos 2007). U-dives are not associated with diurnal depth patterns and lack the uniform wiggles of W-dives. The observed reduction in underwater wiggles may imply less searching and more targeted foraging of prey items trapped by an eddy's density boundaries. This suggests a change in prey type or foraging strategy within the eddy field region (Hindell et al. 1991). Nevertheless, W-dives made up around 25% of the within-eddy field dives, suggesting that vertically migrating prey were still important foraging targets. The small changes in the O-dives reinforce the idea of a change in foraging strategy as opposed to the amount thereof. The percentage changes in U- and W-dives within the eddy field were relatively large for five of the seals ranging from 14.33% to 30.17% (Table 8). Because of the differences in characteristics between these dive types, changes of this magnitude seem likely to have important impacts. As a result five seals' dive type choices were deemed to be altered to a biologically significant extent as a result of diving within the eddy field (Table 9).

The ratio of night to day dives within the eddy field was lower inside the eddy field (1.01 inside vs 1.74 outside). Superficially, this suggests that the shorter, shallower dives weren't associated with an increased occurrence of night dives, but more likely with changes in foraging strategies. With the onset of the austral winter however, day lengths become increasingly short. When combined with the high latitudes of many of the seals post-moult

dives these seasonal and latitudinal shifts may account for the lower proportion of night dives while inside of the eddy field.

Before the animals embark on their post-moult migrations they undergo an energetically costly moult wherein they shed both their hair and skin (Fedak et al. 1994). The moult typically lasts around 28 days for females (Boyd et al. 1994) and during this time they lose between 112 kg and 140 kg, 70% of which is fatty tissue (Fedak et al. 1994). This may represent as much as 37% of the animals' body mass and account for 10.8% of their annual energy budget (Boyd et al. 1994). As is the case with their breeding haul-outs the animals fast during their moults (Fedak et al. 1994), relying on subsequent migrations to regain the energy expended during their time on land. During their migrations the animals spend as much as 88% of their time diving (Boyd et al. 1994). Due to their swimming technique and comparatively large size, the animals have more drag than smaller phocids (Williams & Kooyman 1985; Feldkamp 1987) and need more energy to propel themselves through the water (Boyd et al. 1994). Foraging therefore accounts for 68.2% of adult female southern elephant seals' annual energy budget (Boyd et al. 1994).

When the seals leave the island after their moult they are likely to be negatively buoyant as a result of their loss of fatty tissue (Miller et al. 2012). On their homeward leg the animals are generally carrying more fatty tissue and are more positively buoyant as a result. Mid-migration, as elephant seals approach neutral buoyancy the animals need to expend energy during their downward and upward travel directions. In this state the cost-of-travel of their dives is at a minimum (Miller et al. 2012). However, as the animals buoyancy state extends further from neutral, the energy requirements of overcoming their state increases sharply. Elephant seals exhale before diving and so air-spaces associated with lung volume are unlikely to play a role in their buoyancy (Webb et al. 1998).

During lean, negatively buoyant periods the animals are able to glide to depth with their energy expenditure at a basal level (Miller et al. 2012). Swimming up to the surface however entails active swimming against their negative buoyancy requiring them to expend more energy. During their heavier periods, their descents incur the costs of overcoming their positive buoyancy, particularly during the initial parts of their dives (Williams 2000; Miller et al. 2012). While positively buoyant ascents may include active swimming (Williams 2000), they are nevertheless associated with low costs-of travel (Miller et al. 2012). The energy savings associated with positive buoyancy ascents and negative buoyancy descents are however comparatively small and do not offset their related costs (Miller et al. 2012). Moreover, once at depth, moving vertically up and down in the characteristic wiggles of W-dives is likely to compound the energetic costs of diving for the non-neutrally buoyant seals.

The tagged female seals from Marion Island tended to encounter the eddy field area during the early stages of their outward and late stages of their homeward post-moult migration legs. As a result, dives in the region are likely to have occurred when the animals were close to the extremes of their buoyancy states, increasing the energetic costs associated with their dives (Miller et al. 2012). This highlights the potential value to Marion Island's female post-moult elephant seals of being able to potentially access prey items during less energetically costly shallower and shorter dives. These savings may be compounded by a switch to more efficient foraging techniques within the eddy field. Overall, the effects of diving within the eddy field appear statistically and biologically significant to varying degrees for 10 of the 11 seals (Table 9). Reduced dive duration alone may account for important energy savings for eight seals. Two seals' dive parameters within the eddy field combined shallower with shorter dives while another three also included fewer energetically costly dives. Overall the individual results seem to confirm the group result suggesting that dives within the eddy field were less energetically costly and physiologically demanding for the majority of the seals.

Dive parameters within the eddy field

In order to further understand the shorter, shallower and less energetic dives within the eddy field region, the same dive parameters were investigated in relation to eddy field SLA and the occurrence of cyclonic or anticyclonic features. Interactions between the SAF and APF in the fault region of the SWIR generate an enhanced eddy field comprised of predominantly cyclonic (Durgadoo et al. 2010) as well as anticyclonic eddies, which are readily identified from satellite altimetry as negative and positive SLAs respectively (Ansorge & Lutjeharms 2003, 2005, Ansorge *et al.* 2009). Cyclonic eddies are associated with enhanced productivity around their centres due to upwelling of nutrients into the photic zone and advection toward their turbulent edges (Bailleul et al. 2010). Anticyclonic eddies can result in increased productivity along their edges as a result of weaker upwelling in these areas (Bailleul et al. 2010) and increased turbulence across their outer density surfaces (Lévy et al. 2001). Interactions between eddies also result in jets which can result in enhanced localised biological activity (Lima 2002).

There appeared to be some clustering of dives in regions with sea level anomaly values close to zero (Figure 4), suggesting that most dives occurred at the interfaces between eddies or in regions with low eddy activity. SLA was not a significant predictor of maximum dive depth but was significant with regards to dive duration accounting for a 0.7% change in eddy field dive durations (Table 10). When compared to the 19% effect of day-stage, SLA's lack of biological importance is confirmed. In order to explore associations between dive types and SLA, I modelled the estimated likelihood of switching from U-dives (the most common dive type) to either W- or O-dives in response to changing SLA. Similar to the dive duration results, the log-odds of switching between U- and W-dives as a result of change in SLA, while statistically significant, were substantially less than those attributed to change in day-stage (Table 10). Switching between U- and O-dives was not significantly impacted by SLA.

The mixed effects models for both maximum depths and dive durations suggested that much of the observed variance could be attributed to variation within individual seals (Table 11). On an individual level, day-stage accounted for most for the estimated change in both maximum depth and dive duration (Table 12). The significant estimated effects of SLA were very small in comparison to those of diving at night. Analyses of dive types revealed similar results, with SLA related log-odds of switching between U- and either W- or O-dives far lower than those associated with day-stage (Table 13).

No patterns were evident in any individuals' responses to changing SLA. For the two seals that displayed significant changes in maximum depths associated with elevated SLA, estimated depth changes were less than one meter, and of the four seals that displayed significant changes in dive durations associated with elevated SLA, two dived longer and two dived shorter (Table 12). In all cases however, diving at night accounted for shallower, shorter dives, consistent with previous findings. The odds of switching from U- to W dives increased in three cases and decreased in one case as a result of elevated SLA while only one seal was significantly less likely to undertake O-dives (Table 13). The group results are therefore confirmed in the individual results with no seals dive parameters appearing to be associated with variations in SLA.

Limitations of this study

One potential influence limiting my results is that the initial CRW distributions may not accurately represent the seals estimated dive locations, leading to an over estimate of eddy field use. The CRW function used in this study did not allow for an initial angle restriction resulting in widely disparate angles of departure, while the seals tend to leave the island in a south-westerly direction. Nor did the function allow for exclusion of regions leading to tracks which intersected land masses. A better technique might be to generate a set of random walks between Marion Island and the animals' preferred foraging grounds for this initial

investigation. From a modelling perspective, due to computational restrictions, when comparing diving parameters of all animals outside vs inside of the eddy field I chose a random subset of 25,000 of the initial 116,568 dives. It is difficult to estimate exactly how representative this subset was of all the variability within the original sample.

The diving parameters themselves may have been too coarse to resolve fine scale interactions. The dive types were dominated by two foraging classifications, with only a very small percentage associated with travelling or resting. These dive type classifications were based on four inflection points per dive, gathered via satellite. Although higher resolution data are stored on the tags themselves, these data are too large for satellite transmission, requiring instead manual connection and were not therefore available for this study. It is likely that higher resolution dive profiles, along with recent technological advances such as accelerometers (e.g. Mitani et al. 2010) would allow for finer scale dive classification. Detecting enhanced foraging in the region may be better achieved by analysing track data with first passage time analysis (Wilson et al. 2007), state-space modelling (Breed et al. 2009) or kernel density analysis (Robinson et al. 2010).

It is also possible that while en route to either their foraging grounds or their breeding destinations, the seals are not easily distracted by opportunistic foraging. This analysis compared undersea diving parameters with sea surface variability. While SLA is indicative of localised underwater turbulence such as upwelling, I did not include any underwater measures of these aspects such as stretch, shear or deformation. Furthermore, this study did not take into account the likely spatial and temporal offsets between eddy-associated primary productivity and increased southern elephant seal prey availability (Bailleul et al. 2010) or bathymetric structures which may influence the animals diving behaviour.

Conclusions

Interactions between the ACC and the SWIR to the south-west of Marion Island generate an eddy hotspot (Ansorge & Lutjeharms 2005). Previous research has shown how southern elephant seals target eddies for foraging (Campagna et al. 2006; Bailleul et al. 2010; Dragon et al. 2010), suggesting that elephant seals might exploit the eddy field upstream of Marion Island. Dive behaviours appear to change within this region, with the seals diving more frequently within the eddy field. Dive parameters within the eddy field suggest substantial energy savings as well as a change of foraging strategies in comparison to those outside of the region. The same dive parameters within the eddy field do not correlate with regions of enhanced mesoscale activity. This finding is surprising considering the elevated productivity associated with eddy activity (Bakun 2006) and prominent bathymetry such as the South West Indian Ridge (Sokolov & Rintoul 2009) in contrast to the oligotrophic nature of the deep abyssal plains of the Southern Ocean (Buesseler et al. 2004).

The results of this study are largely inconclusive in terms of providing further explanations for the late 20th century population declines in the Marion Island elephant seal populations. While the lack of correlations between dive parameters and SLA within the eddy field superficially suggest little opportunistic eddy-linked foraging, the same parameters indicate that the region is an efficient area in which to forage. Foraging has been associated with both cyclonic and anticyclonic features (Campagna et al. 2006; Bailleul et al. 2010; Dragon et al. 2010), but increased productivity is more strongly linked to the cyclonic upwellings (Bakun 2006). In light of the historic and projected effects of climate change within the ACC the eddy field may be spawning an increasing number of warm core features as the SAF shifts further south (Gille 2002). Should the position of the eddy field shift somewhat it seems unlikely to have much impact on the far ranging animals. However, if efficient, opportunistic foraging within the eddy field plays a role in the decision of the seals to leave Marion Island

in a generally south westerly direction then regional climate mediated changes may indirectly alter the elephant seals' dispersal patterns via changes in the nature of the eddy field. Should these changes occur, the viability of the Marion Island southern elephant seal population may once more come into question.

Acknowledgements

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Appendix A

Lévy walk tests

In order to determine whether seals dived in the eddy field more often than expected, the positions of dives were compared with random walk distributions. I began this investigation by trying to determine whether or not the seals were undertaking Lévy walks. This type of random walk has been proposed, over more traditional random walks, to more accurately describe the movement patterns of a number of species including wandering albatrosses (Viswanathan et al. 1996), grey seals *Halichoerus grypus* (Austin et al. 2004) and spider monkeys *Ateles geoffroyi* (Ramos-Fernández et al. 2004). The distances travelled between steps in these types of random walks follow power law distributions, resulting in many short steps and few long steps, as oppose to simpler correlated random walks where step lengths are constant. Recent studies have however called into question the use of Lévy walks, showing that composites of Brownian random walks may be significantly more efficient than Lévy walks (Benhamou 2007; Plank & James 2008). Edwards et al. (2007) revisited the flight path data of wandering albatrosses showing that the animals were not in fact undertaking Lévy walks.

In order to test for Lévy walks in the elephant seal data, individuals' tracks were analysed according to the methodology developed by Edwards et al. (2007) (Eq. 1). This statistical method estimates a value for μ, which, for the Lévy walk to be valid, needs to be greater than 1 and less than or equal to 3. The value for α, the start of the distributions heavy tail, was calculated from equation 5 in Newman (2005) (Eq. 2). The method developed by Edwards et al. (2007) is considered more robust than the more traditional technique of producing log-log histograms of the data, fitting a straight line across some or all of the data and using the inverse slope of the line as μ (Edwards et al. 2007).

The track data analysed by Edwards et al. (2007) differed from this study's data in that Edwards et al.'s (2007) tracks were comprised of points separated by constant time intervals with varying distances and directions. A limitation for the Southern Ocean is the frequent cloudiness and the short durations which diving mammals spend at the surface (Boehlert *et al.* 2001). As a result the time intervals between track steps are not uniform. From a spatial point of view therefore seal tracks may not always be representative of the types of movements the animals are undertaking. In short, a leg covering a vast distance may not always represent an animal travelling rapidly between points. I therefore considered not only the distance travelled but also the mean speed achieved between track points predicting that the latter measure would more likely fit a power-law distribution should the animal be undertaking Lévy walks (T. Reid pers. comm.). Analyses of the track data using the techniques outlined by Edwards et al. (2007) in terms of both distance and speed confirmed that the seals were not undertaking lévy walks with no μ values falling within the required range.

$$\mu = {1 - n}\big/{\left(n \log a - \sum_{j=1}^{n} \log x_j\right)} \qquad \text{(Eq. 1)}$$

$$\alpha = 1 + n \left[\sum_{i=1}^{n} \ln \frac{x_i}{x_{min}}\right]^{-1} \qquad \text{(Eq. 2)}$$