Title: The role of eddies in the diving behaviour of female southern elephant seals

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Abstract

As the Antarctic Circumpolar Current crosses the South-West Indian Ocean Ridge it creates an extensive eddy field characterised by high sea level anomaly variability. We investigated the diving behaviour of female southern elephant seals from Marion Island during their post-moult migrations in relation to this eddy field in order to determine its role in the animals' at-sea dispersal. Most seals dived within the region significantly more often than predicted by chance, and these dives were generally shallower and shorter than dives outside the eddy field. Mixed effects models estimated reductions of 44.33 ± 3.00 m (maximum depth) and 6.37 ± 0.10 min (dive duration) as a result of diving within the region, along with low between seal variability (maximum depth: 5.5% and dive duration: 8.4%). U-shaped dives increased in frequency inside the eddy field, whereas W-shaped dives with multiple vertical movements decreased. Results suggest that Marion Island's adult female elephant seals' dives are characterised by lowered cost-of-transport when they encounter the eddy field during the start and end of their post-moult migrations. This might result from changes in buoyancy associated with varying body condition upon leaving and returning to the island. Our results do not suggest that the eddy field is a vital foraging ground for Marion Island's southern elephant seals. However, because seals preferentially travel through this area and likely forage opportunistically while minimising transport costs, we hypothesise that climate mediated changes in the nature or position of this region may alter the seals' at-sea dispersal patterns.

Keywords: Marion Island, Mirounga leonina, Antarctic Circumpolar Current, Mesoscale features, Energetics, Dive types , South-West Indian Ridge

Introduction

The Southern Ocean is characterised by the Antarctic Circumpolar Current (ACC) (Rintoul et al. 2001), which provides a crucial mechanism in driving regional biological productivity (Downes et al. 2011). While the ACC connects the global ocean basins via zonal mixing, it restricts meridional transport (Rintoul et al. 2001). However, poleward transport of water masses does occur through the formation of eddies (de Szoeke and Levine 1981), principally within frontal regions or where the ACC interacts with poleward extensions of western boundary currents or irregular bathymetry (Rintoul and Sokolov 2001). Some global climate models predict that increases in atmospheric CO_2 could lead to a southward migration and intensification of the region's westerly wind belt (Saenko et al. 2005). These changes may in turn lead to poleward shifts in the ACC's frontal systems (Downes et al. 2011) as well as increases in the region's eddy activity and poleward heat fluxes (Meredith and Hogg 2006). 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 Subantarctic fur seals (*Arctocephalus tropicalis)* (de Bruyn et al. 2009), grey-headed albatrosses (*Thalassarche chrysostoma)* (Nel et al. 2001), great frigate birds (*Fregata minor)* (Weimerskirch et al. 2004) and southern elephant seals (*Mirounga leonina*) (Campagna et al. 2006; Bailleul et al. 2010; Dragon et al. 2010).

The Prince Edward Islands are located south east of South Africa at 46.75°S and 37.92°E, directly in the path of the ACC (Duncombe Rae 1989; Ansorge and Lutjeharms 2002). The archipelago consists of Marion Island (270 km^2) and the smaller Prince Edward Island (45 km^2) (Pakhomov and Froneman 1999). Marion Island is home to over five million birds and seals (Ryan and Bester 2008) and forms one of the most northerly and isolated southern elephant seal colonies in the Southern Ocean. The nutritional energy necessary to sustain such vast numbers of top predators is derived from the close interaction between the oceanic environment and the islands themselves. Changes in the oceanic environment resulting in shifting prey distributions and availability have been earmarked as potential drivers of the observed population declines of Marion Island's southern elephant seals during the 20th century (McMahon et al. 2005).

The islands lie in the Polar Frontal Zone (PFZ), bounded to the north by the nearby sub-Antarctic Front (SAF) and to the south by the more distant Antarctic Polar Front (APF) (Ansorge and Lutjeharms 2002). While the frontal regions are highly productive (Guinet et al. 1997), productivity within the PFZ is more patchy (Weimerskirch et al. 1997). Areas of elevated nutrient concentration within the PFZ may therefore present important foraging areas. To the south-west of Marion Island lies an extensive corridor of high sea level anomaly variability corresponding to interactions between the ACC and the highly fractured South-West Indian Ridge (SWIR) (Ansorge and Lutjeharms 2003, 2005; Sclater et al. 2005; Durgadoo et al. 2010, 2011). This corridor, hereafter referred to as the eddy field, is comprised of cyclonic and anticyclonic eddies. The eddies are readily identified from satellite altimetry as sea level anomalies (SLAs) (Ansorge and Lutjeharms 2003, 2005; Ansorge et al. 2009) and result in elevated regional eddy kinetic energy (EKE) (Fig. 1). Cyclonic eddies (negative anomalies) are associated with enhanced productivity around their centres due to upwelling of nutrients into the photic zone and advection towards their turbulent edges (Bailleul et al. 2010). In contrast, anticyclonic eddies (positive anomalies) exhibit elevated productivity along their edges (Bailleul et al. 2010), due to increased turbulence across their outer density surfaces (Lévy et al. 2001). Interactions between eddies also result in interstitial jets, which can lead to enhanced localised biological activity (Lima et al. 2002). Eddies trap and redistribute nutrients leading to elevated localised productivity (Bailleul et al. 2010). As these features travel north-eastwards into the vicinity of the islands they are utilised as foraging grounds by breeding grey-headed albatrosses (Nel et al. 2001).

There is evidence of a role for eddies in the foraging of southern elephant seals from colonies at Peninsula Valdés and the Kerguelen Islands (Campagna et al. 2006; Bailleul et al. 2010), but the behaviour of Marion Island's population within the archipelago's upstream eddy field has remained largely unexplored. This study assesses whether 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 (winter) migrations. As a result of localised elevated prey availability within the eddy field region we expected the elephant seals to (1) preferentially travel through the region on their migrations to more distant foraging areas; (2) increase their dive frequencies within the region; and (3) perform shallower and shorter dives which incorporate fewer underwater up-and-down movements (wiggles). To explore these questions we determined if seals dived more often than predicted by chance within the eddy field by developing a correlated random walk model. Metrics describing the diving parameters (maximum dive depth, dive duration and dive type) of adult post-moult female elephant seals tracked inside and outside of the region were then compared using a mixed effects modelling approach.

Materials and methods

Ethics statement

The research described conforms to Antarctic Treaty legislation and to the SCAR code of conduct. We adhere to the 'Guidelines for the use of animals in research' as published in Animal Behaviour (1990, 41, 183-186) and the laws of the country where the research was conducted. All flipper tagging and satellite-device deployment/retrieval procedures were reviewed and approved by the Animal Use and Care Committee of the University of Pretoria (AUCC 040827-024 and AUCC 040827-023) and fieldwork was performed under Prince Edward Island's Research Permits R8-04 and R04-08.

Data Processing

Between 26 October 2007 and 10 January 2010, 32 female southern elephant seals from Marion Island were tagged with satellite relay data loggers (SMRU/Series 9000 SRDL or SRDL/CTD, Sea Mammal Research Unit, University of St Andrews, UK). These devices record time and dive information which is transmitted via the Service Argos satellite system (Collecte Localisation Satellites (CLS) 2011) to the Sea Mammal Research Unit (Vincent et al. 2002). Track position estimates provided by Service Argos are filtered to remove points describing implausible elephant seal swimming speeds and the positions of the dives are estimated as interpolated points framed by Argos uplink position estimates (Boehme et al. 2009). These interpolations are based on uplink times in relation to the times at which the dives occurred and have an estimated accuracy of ± 2 km (Boehme et al. 2009).

The seal track data used for this study are available via the PANGEA information system (http://www.pangea.de). Each track was made up of consecutive dives for which the time, date, geographical position, total dive duration, maximum depth as well as 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. All subsequent data processing was undertaken in the R environment for statistical computing (R Core Team 2015).

Only data from the approximately eight-month long adult female post-moult migrations were included and, to ensure that overall dive behaviour was properly represented, tracks with at-sea durations of fewer than 30 days were excluded from the analysis (cf. Bailleul et al. 2007). Using the geosphere package (Hijmans et al. 2012), each dive's distance and absolute bearing relative to Marion Island was calculated along with distances, speeds, and relative bearings between successive dives. Distances were calculated using Vincenty's ellipsoidal formula. The data sets for three seal tracks (GG335 – 2009, GG335 – 2010, YY189 - 2010) contained unusually large numbers of dives with durations of exactly 5715 sec (201, 780, 167 respectively). These times were attributed to erroneous SRDL tag readings and the dives were excluded from further analysis. Using the maptools package (Bivand 2013) dives were classified as taking place during the day or night. If the dives took place within 30 min of sunrise or sunset they were classified as dawn or dusk dives respectively and excluded from further analysis (cf. McIntyre et al. 2011). Each dive was further categorised as to whether it occurred inside or outside of the eddy field. The data set at this point included a total of 107,376 dives within 22 tracks from 16 seals (Online Resource 1, Fig 2).

Dive types

Time-depth profiles based on four inflection points were used to categorize each dive into one of six types using the approach developed by M. Biuw (unpublished data) and used by Photopoulos (2007) (Online Resource 2). Two of these dive types are characterised in part by durations at depth exceeding one minute along with rapid ascent and descent rates (Hindell et al. 1991). The first of these two types includes large wiggles over a range of depths and are termed wiggle dives (W-dives) (Hindell et al. 1991; Photopoulos 2007). W-dives show some diurnal patterns which presumably are linked to the daily vertical migrations of pelagic prey (Hindell et al. 1991). Square dives (SQ-dives) are characterised by fewer wiggles and no diurnal pattern (Hindell et al. 1991).

The remaining four 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-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. 2011). These dives are terminated by a rapid ascent (Le Boeuf et al. 1988; Hindell et al. 1991;

Photopoulos 2007). During the first fortnight of their post-moult migrations the seals cover up to 120 km per day, primarily undertaking U-shaped dives (U-dives) (Hindell et al. 1991). Root dives (R-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 sixth dive type described by Photopoulos (2007) are V-shaped dives which are linked to travelling to and from foraging grounds.

Breiman’s random forest algorithm was used to classify each dive based on a training set. The training set is a 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 that a large number of dive profiles are visually assessed and classified according to the above mentioned dive types. This is a subjective process and so, in order to increase conformity of results between research studies we used an existing training set, previously used in studies involving the identification of dive types in seals from Marion Island (McIntyre et al. 2011).

Correlated Random Walks

Correlated random walk (CRW) distributions were generated using the adehabitatLE package (Calenge 2006). These CRWs were compared with the tracks of instrumented seals in order to determine whether tracked animals dived within the eddy field more often than might be expected by chance. The recorded 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 individually analysed in order to derive arguments for the simm.crw() function. The scaling parameter (h) for each outward track was estimated using the hbrown() function in adehabitatLE. Each seal’s outward-track turning angles were fitted to a wrapped normal distribution using the mde.wrappednormal() function from the wle library (Agostinelli 2013). These distributions were used to estimate concentration factor values (r) (Fig. 3). The individual seal’s number of outward bound steps and mean durations between successive steps were used to generate date ranges (dr).

Each seal’s unique combination of h, r and dr values was grouped together. One of these groups was selected at random for the generation of each CRW in order to render the random walks more realistic in comparison with the actual tracks. The ratio of simulated dives occurring within the eddy field domain converged on roughly 8.5% after approximately 5,000 CRWs. We conservatively used 10,000 CRWs for comparisons.

Oceanographic data processing

Daily, delayed time, 1/4 degree resolution zonal(u) and meridional(v) geostrophic current data for the period 1 January 2008 - 31 December 2010 were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/). These data were used to calculate eddy kinetic energy (EKE in cm^2/s^2) for the full extents of the seals migration tracks:

$$EKE = \frac{(u^2 + v^2)}{2}$$

The eddy field was defined as the area from 47.33° to 53° S and from 27.33° to 37.66° E (Fig. 1), where a large proportion of the ACC flow between the SAF and the APF is concentrated through the Andrew Bain Fracture Region of the South-West Indian Ridge (Ansorge and Lutjeharms 2005). Topographical interactions give rise to elevated sea surface height variability (Snaith and Robinson 1996; Pollard and Read 2001) and generate eddies which move downstream toward the Prince Edward Islands (Durgadoo et al. 2010). As defined here, the eddy field encloses both the core of the elevated EKE as well as a part of the downstream path of the region’s cyclonic and anticyclonic eddies.

Statistical analyses

Dive likelihood inside vs outside the eddy field

Exact binomial tests were run using the core stats package in R to determine whether the ratio of observed dives occurring outside vs inside the eddy field was significantly greater than the same ratio within the simulated CRWs. These tests were run for the grouped track data as well as for each of the 16 seals' 22 post-moult tracks. Further investigations included only tracks where individuals had dived within the eddy field significantly more frequently than predicted by the CRWs. This subsequent data set included 10 individuals, 13 tracks and 71,259 dives (Online Resource 1).

Mixed effects modelling procedures

In order to detect significant differences in maximum depth and dive duration as a result of diving within the eddy field or changing day-stage (day or night) along with individual seal's contributions to variance, linear mixed effects models were run using the nlme package (Pinheiro et al. 2013) in R. Where mixed effect model results are reported, values refer to estimated effect ± standard error. Before running mixed effects models, 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 model 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 and examined for each model.

Mixed effects models were run using the restricted maximum likelihood (REML) method and subsequently updated using first order autoregressive correlation structures with theta set to the lag-1 interval in order to account for autocorrelation (Pinheiro and Bates 2000). ACF plots and semivariograms were used to confirm autocorrelation reduction. Where mixed effects models were run on individual seals, constants were used for random effects.

Outside vs inside the eddy field

An initial investigation explored the impact of position (inside vs outside the eddy field), day-stage (day vs night) and time since departure (days at sea) on maximum depth and dive duration for the individuals which had dived more often inside the eddy field than might be expected by chance. The results of these models suggested that time at sea explained less than 1 m of depth and 1 min of dive duration variation. Moreover, inclusion of this variable necessitated limiting the data set to the first 150 days and as a result of this constraint and its small effect, time since departure was excluded from this report.

To assess the significant effects of the eddy field and day-stage on maximum depth and dive duration across the full data set, mixed effects models were run on the grouped data as well as on individual seal data using position relative to the eddy field (inside vs outside) and day-stage (day vs night) as fixed effects. This data set included only the dives from individuals which had dived within the eddy field more often than expected by chance.

Most dives, both inside and outside of the eddy field, were either U- or W-dives, together accounting for approximately 95% of the total number of dives. 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.

Results

Interactions between the ACC and a series of faults in the SWIR resulted in elevated mesoscale activity easily identified from elevated EKE in the region (Fig. 1). The 16 tracked adult female seals undertook 22 post-moult migrations between 2008 and 2010 (Fig. 2, Online Resource 1), making 94,771 dives outside of the eddy field and 12,605 dives inside the region. Of the outward bound dives, 77% took place in the sector south-west of Marion Island (between 195° and 255° from the island; Fig. 4). Twenty tracks traversed the eddy field region.

Dive frequencies

The seals performed significantly more dives (18.5%) within the eddy field than predicted by the CRWs (8.5%; $p < 0.01$; Fig. 3). On an individual level, 10 of the 16 seals dived within the eddy field region significantly more often than predicted (13 of 22 tracks; Online resource 1). Seal OO021 did not dive within the eddy field region during either tracked migration year (2008 or 2009) while seals PO043 (2008 and 2009) and YY189 (2008, 2009 and 2010) dived significantly more frequently within the eddy field during all tracked years. Seal GG335 dived significantly more often within the eddy field in 2008 but not in 2009 or 2010. Of the remaining 12 tracks undertaken by different seals, seven dived within the eddy field significantly more often than predicted.

Dive parameters

Considering the seals that dived significantly more often in the eddy field than predicted by the CRW model as a group, the recorded mean and maximum dive depths and durations were shallower and shorter inside the eddy field, regardless of day-stage (Table 1). Mixed effects models that included all tracks confirmed that maximum dive depths inside the eddy field were significantly shallower than dives outside of this region as a result of both position relative to the eddy field and day-stage (Table 2). The effects of day-stage were stronger than the eddy field on maximum depth, accounting for an estimated reduction of 149.30 ± 1.71 m. In terms of dive durations, diving within the eddy field had a stronger effect than day-stage, resulting in an estimated 6.37 ± 0.26 min reduction. Little variability in maximum depth (5.5%) or dive duration (8.4%) could be attributed to differences between individual seals, with most variation common to the group (Table 3).

U-dives were the most common both inside- (70.4%) and outside (64.3%) of the eddy field, followed by W- (inside: 23.8%, outside: 29.9%) and O- (inside: 5.8%, outside: 5.7%) type dives. These values represented statistically significant changes in the frequencies of each dive type (U dives: +6.07%, W dives: -6.17%, O dives: 0.10%) within vs outside of the eddy field.

Mixed effects models estimated that diving within the eddy field accounted for significantly shallower dives in five of the ten cases where seals dived more frequently in the eddy field than expected (Table 4). However, day-stage had a stronger effect on maximum depth in all but one cases (OO418). In terms of dive durations, the effects of the eddy field were closer to those of day-stage; nine seals' dive durations were shorter in the eddy field and in seven of these cases, the eddy field effects were stronger than those of day-stage.

Nine individuals showed significant changes in the types of dives which they undertook inside the eddy field. Within the eddy field, seven 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 for all but one individual (PO043) whose proportional change in dive type use was low across all dive types. Four seals' dive type choices changed by more than 10% within the eddy field.

Discussion

The southern elephant seals in this study showed a strong preference for dispersing south-west from Marion Island during their post moult migrations (Figs 2, 4). Given the expansive nature of these migrations, it appears that the seals were primarily traversing the region en route to more distant, preferred foraging grounds (Jonker and Bester 1998; McIntyre et al. 2011; Tosh et al. 2012). Any foraging activity within the eddy field was therefore likely to have been opportunistic, explaining the variation in individual responses. Nevertheless, the potential biological relevance of the group response seems to be reinforced by the number of individuals which dived more frequently within the region than expected.

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

Compared to female seals from Peninsula Valdés and Macquarie island (Hindell et al. 1991; Campagna et al. 1995), female southern elephant seals from Marion Island dive both deeper and longer (McIntyre et al. 2011). It is likely that the increased depth and duration pushes the animals closer to their physiological limits (Hindell et al. 2000). This 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.

The reasonably low measure of between-seal variance in maximum depths and dive durations may suggest that, to some extent, this study's seals were behaving in similar ways to one another (Table 3). Although maximum depth was more strongly affected by day-stage than by the eddy field, the effect of the latter was still relatively large for half of the seals (Table 4). Moreover dive durations were affected to very similar degrees by both day-stage and the eddy field and may account for important energy savings for eight seals.

Southern elephant seals show reasonably high levels of at-sea fidelity (Bradshaw et al. 2004). This may suggest a selective pressure to preferentially traverse the eddy field although this has yet to be tested. Within such a framework of distribution fidelity, a presumed increase in physiological stress associated with deeper diving (McIntyre et al. 2010) and the established biological importance of day-stage (McIntyre et al. 2011) to Marion Island's southern elephant seals, diving within the eddy field may have had biologically important impacts on both dive depth and duration for five and eight of the seals respectively.

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. Given their dominance during elephant seal migrations, U-dives are necessarily associated with both travelling and exploration (McIntyre et al. 2011). Furthermore, accelerometry data gathered from jaw and head movements suggest that, like W-dives, U-dives also appear to include foraging components (Gallon et al. 2013; Naito et al. 2013). U-dives however 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 in turn suggests a change in prey type or foraging strategy within the eddy field region. Alternatively, the increase in U-dives within the eddy field may indicate an increase in travelling, along with reduced foraging. Nevertheless, W-dives with their diurnal patterns made up almost 24% of the within-eddy field dives. W-dives are associated with foraging for prey which undertake daily vertical migrations (Hindell et al. 1991). The high proportion of this dive type suggests that these prey items were still important foraging targets within the region. Characteristic differences between dive types suggest that the reported proportional changes in type choice seem likely to have important impacts for a number of individual seals.

Overall, the effects of diving within the eddy field appear statistically and biologically significant to varying degrees for nine of the ten seals. Four seals' dive parameters within the eddy field combined shallower with shorter dives and two of these also included fewer energetically costly dive types. The individual results seem to confirm the group result suggesting that dives within the eddy field were energetically less costly and physiologically less demanding for the majority of the seals.

Energetics

Before the female seals embark on their post-moult migrations they undergo an energetically costly moult accounting for around 10.8% of their annual energy budget (Boyd et al. 1994). During this period Marion Island's females lose on average 34% of their body mass (Postma et al. 2013). Females from Marion Island are not only typically smaller, but also lose a greater proportion of their body mass during their post-moult migrations, when compared to their equivalents from King George Island, South Georgia or Macquarie Island (Postma et al. 2013). As a result, when the post-moult animals leave the island they are comparatively lean and negatively buoyant as a result of their loss of fatty tissue. In these periods the seals are able to glide to depth with their energy expenditure at a basal level, but require active swimming to return to the surface, thereby expending more energy (Miller et al. 2012). On their homeward leg the animals are generally carrying more fatty tissue and are more positively buoyant as a result. In this state the seals' descents incur the costs of overcoming their positive buoyancy, particularly during the initial parts of their dives (Williams et al. 2000; Miller et al. 2012). Elephant seals tend to approach neutral buoyancy mid-migration, expending smaller amounts of energy during both diving and surfacing, thereby minimising their cost-of-transport (Miller et al. 2012) .

Female seals from Marion Island tend 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).

On the one hand, these findings highlight 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. However, the increased energetic costs incurred by the elephant seals' buoyancy states may themselves partially account for the significant maximum depth reduction in half of the seals, with the significantly shorter dives undertaken by 80% of the seals as well as the switch from W- to energetically less costly U-dives by 70% of the animals within the eddy field. Based on these findings, we propose that the occurrence of energetically expensive W-dives could peak during stages of seal migrations when the buoyancy of seals are closest to neutral and their vertical drift rates approach zero. This hypothesis however requires further investigation in order to articulate cost of transport costs associated with W-dives, foraging success attributed to different dive types, as well as any other factors which may influence dive type choices.

Conclusions

Interactions between the ACC and the SWIR to the south-west of Marion Island generate an enhanced eddy field (Ansorge and Lutjeharms 2005). Previous research showed 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. In order to investigate this question, dive metrics from Marion Island's post-moult female southern elephant seals were statistically evaluated within and outside of the eddy field. 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 potential energy savings as well as possible changes in foraging strategies in comparison to those outside of the region.

Comparing the southern elephant seals from Marion Island's dive parameters outside vs inside the eddy field suggests that the region may be an energetically inexpensive area in which to forage. In light of the historic and projected effects of climate change on the ACC and its frontal systems, the eddy field may be spawning an increasing number of warm core anticyclonic features as the SAF shifts further south (Gille 2002). Potential direct effects of changes in the character of the eddy field on the far ranging animals remain unclear. 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. Future investigations could benefit from using newer biologging technologies (e.g. jaw accelerometers and/or cameras) to better inform the likely use of the eddy field for foraging purposes by southern elephant seals from Marion Island.

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Figure captions and Tables

Fig. 1 The region of elevated mesoscale activity, or eddy field (dashed rectangle), to the south-west of Marion Island. Mean eddy kinetic energy values for the period 2008-2010 are plotted and the 3000 m isobaths show the series of faults cross-cutting the South-West Indian Ridge (SWIR).

Fig. 2 The position of Marion Island (white circle) 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 the shaded rectangle. Black lines represent the 22 post-moult migration tracks and dive locations referenced in this study. Frontal position estimates from Swart et al (2008).

Fig. 3 The position of Marion Island (white circle) 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 the shaded rectangle. Black lines represent a 22 track subset of the 10 000 outward leg correlated random walks with which the recorded dive locations were compared.

Fig. 4 Frequencies of post moult migration dive position bearings relative to Marion Island for the 22 post moult migrations referenced in this study.

Online Resource 1: Tagged post-moult female southern elephant seals from Marion Island included in this study along with deployment ages, years, dates of the first dives, track durations, numbers of recorded dives (excluding those within 30 min of sunrise or sunset). Percentage of recorded, outward leg dives which occurred within the eddy field for the 10,000 CRW simulations as well as for the grouped and individual post-moult tracks (n=22) of adult female southern elephant seals from Marion Island included in this study (n=16). Significant differences between observed and predicted values are indicated by * ($p < 0.01$).

Online Resource 2: Characteristic profiles of the six dive types identified in this study. The four inflection points (D1-D4) as well as start and end times used to categorise the dive types are shown. R root dive, V V-shaped dive, DR drift dive, U U-shaped dive, W wiggle dive, SQ square dive.

Figure 1

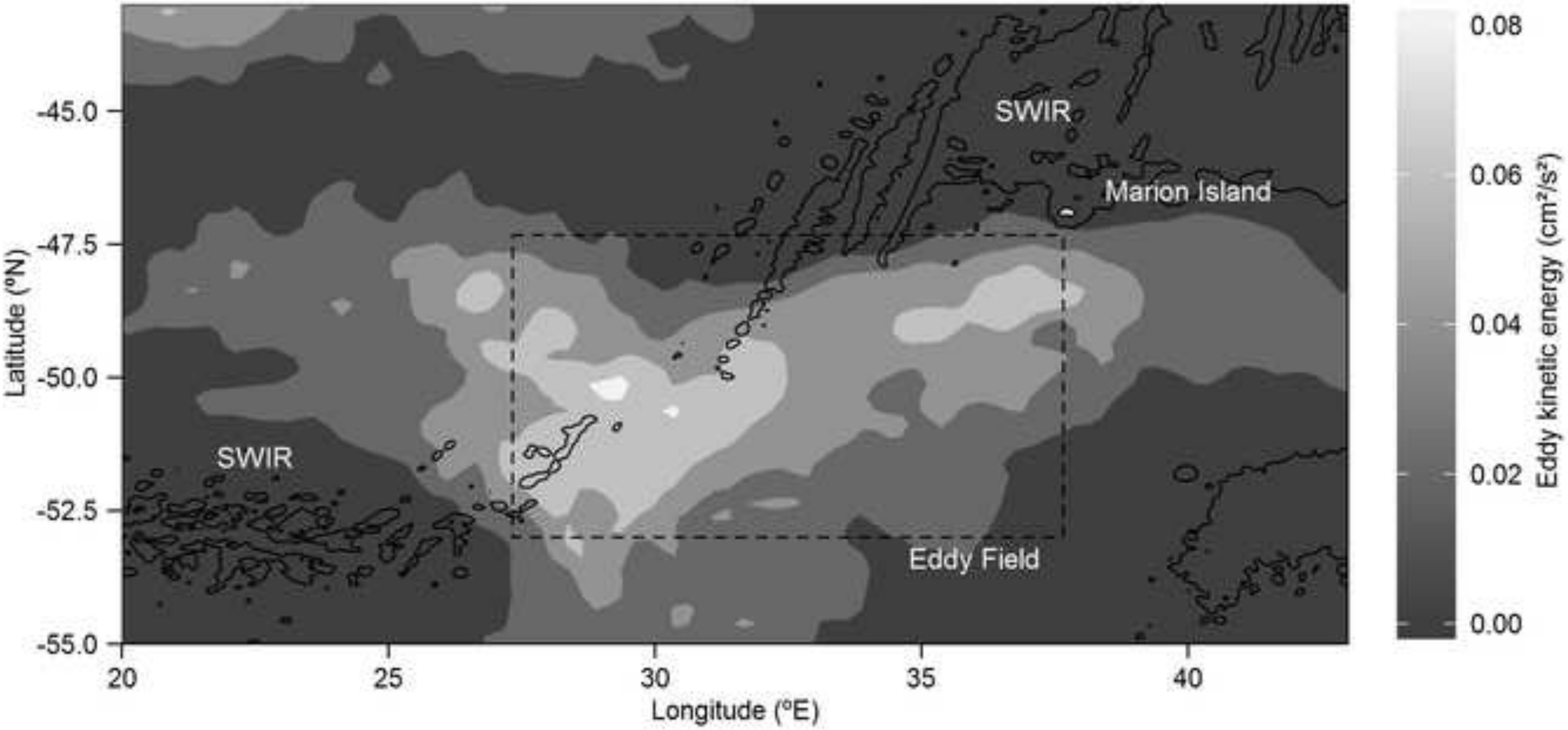
SWIR
Marion Island
SWIR
Eddy Field
-45.0
-47.5
-50.0
-52.5
-55.0
Latitude (ºN)
20
25
30
35
40
Longitude (ºE)
0.08
0.06
0.04
0.02
0.00
Eddy kinetic energy (cm²/s²)

Figure 2

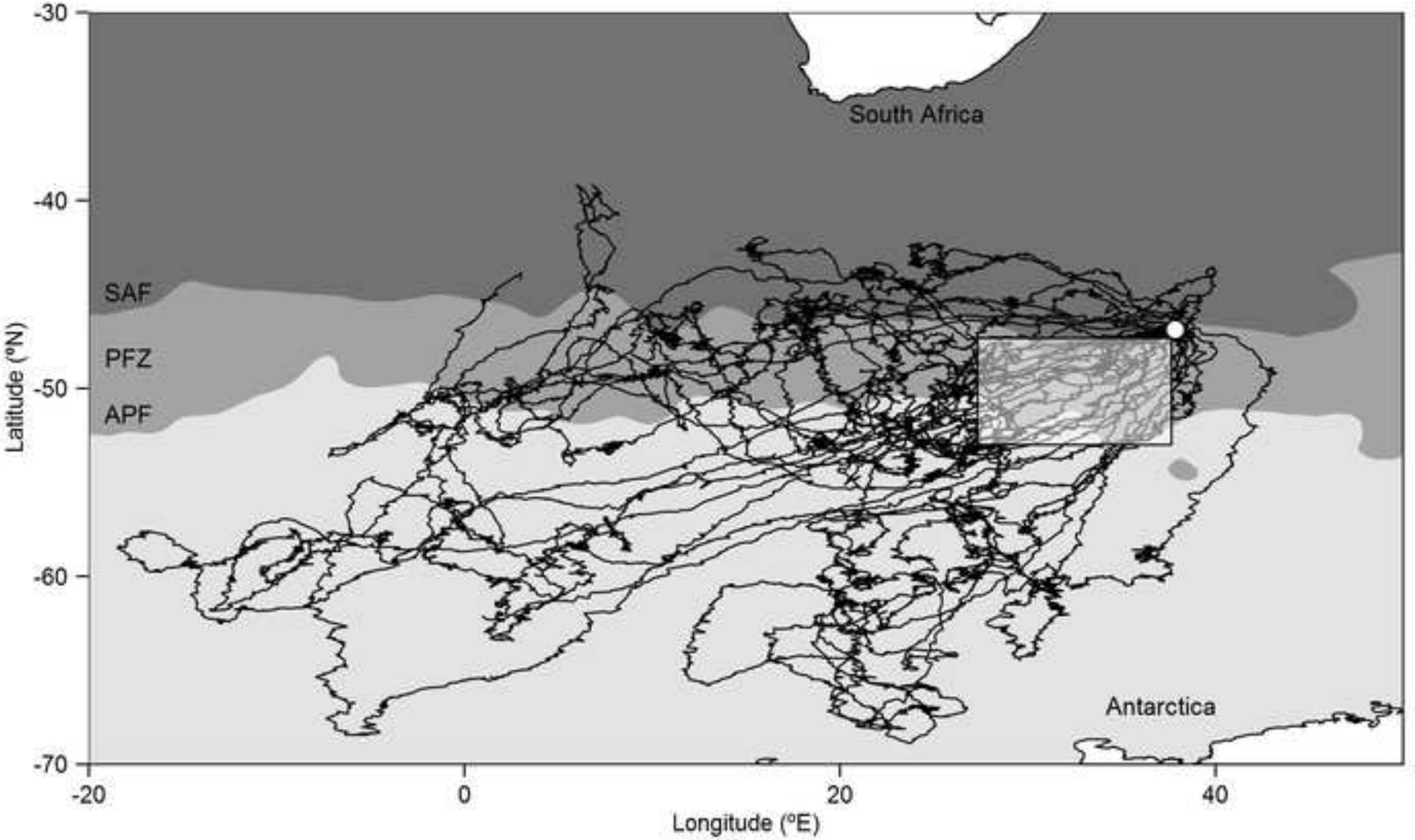
-30
-40
-50
-60
-70
-20
0
20
40
Latitude (°N)
Longitude (°E)
South Africa
SAF
PFZ
APF
Antarctica

Figure 3

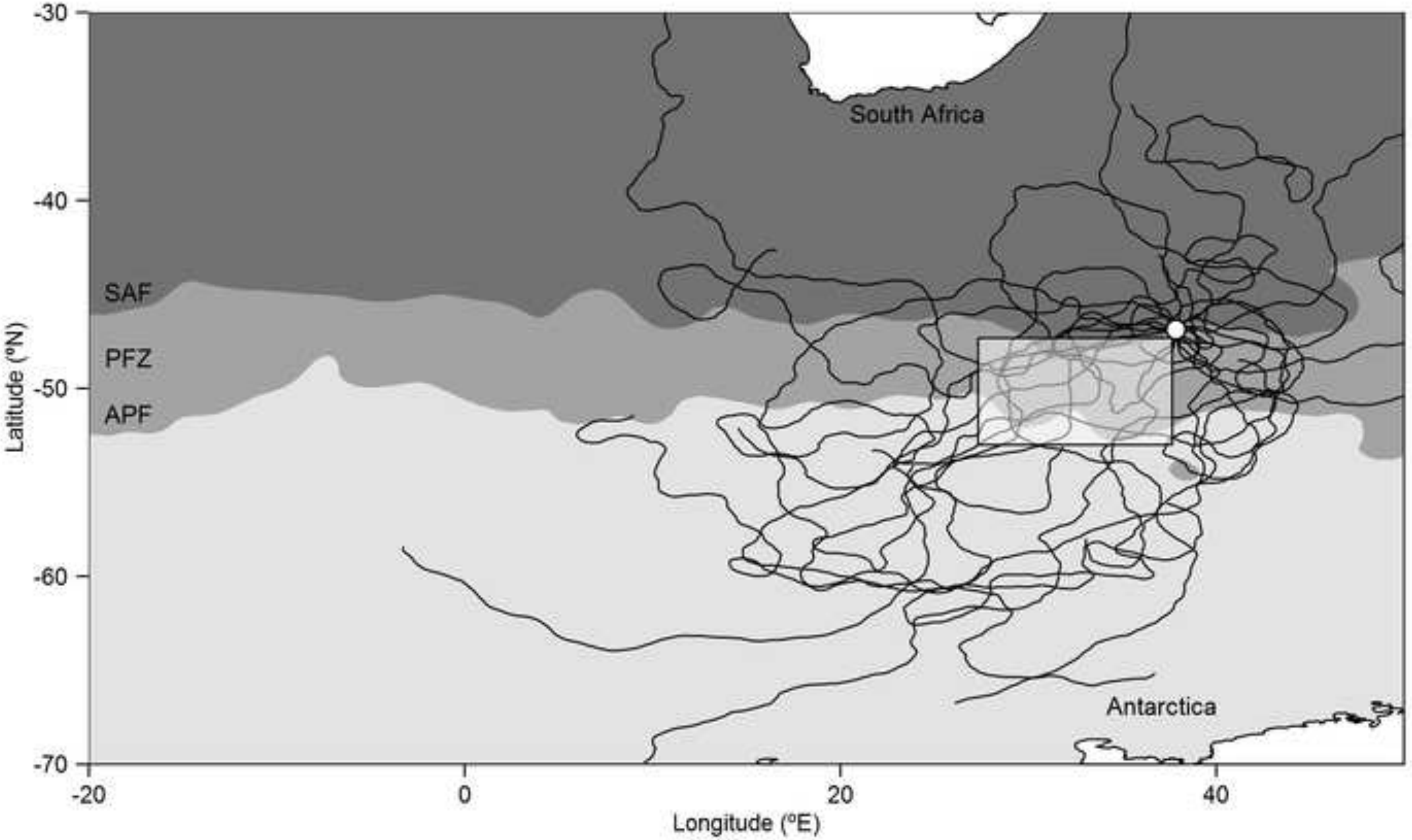
-30
-40
-50
-60
-70
Latitude (°N)
-20
0
20
40
Longitude (°E)
South Africa
SAF
PFZ
APF
Antarctica

Figure 4

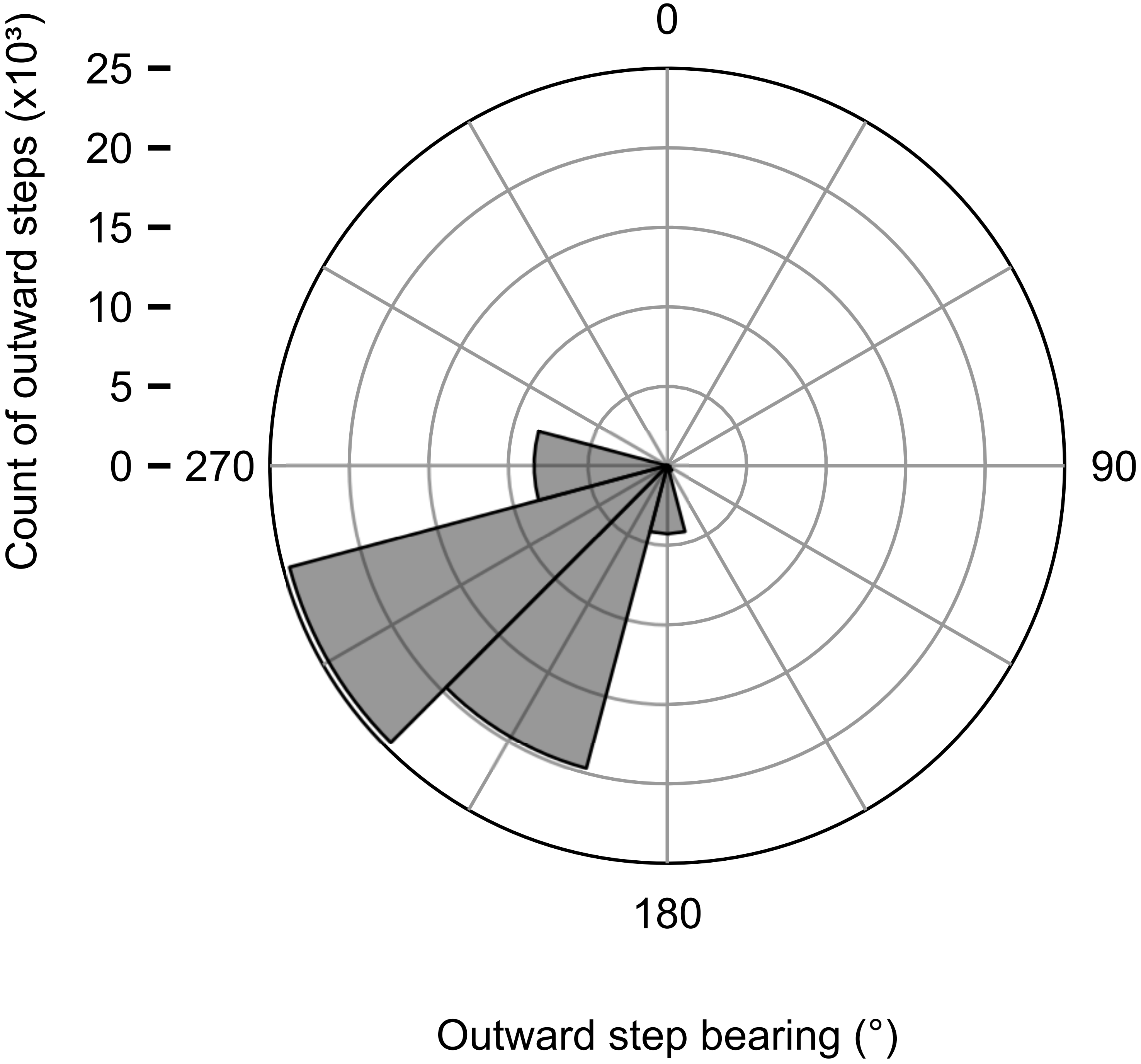
0
90
180
270
25
20
15
10
5
0
Count of outward steps (x10³)
Outward step bearing (°)

Table 1: 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 = 9) 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)	Max (day)	Night dives (mean ± sd)	Max(night)
Inside EF	520.34 ± 158.81	1188.8	385.04 ± 136.09	1128.8
Outside EF	575.28 ± 171.52	1678.0	410.61 ± 154.70	1486.0
Dive duration (min)				
Inside EF	23.88 ± 9.87	88.25	20.80 ± 9.12	73.25
Outside EF	32.93 ± 12.11	95.25	26.31 ± 9.68	83.25

Table 2: Mixed effects model estimates of the 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=9) between 2008 and 2010.

	Max depth (m ± se)	DF	t-value	p-value
Inside EF	-44.33 ± 3.00	65639	-14.77	< 0.01
Night	-149.30 ± 1.71	65639	-87.40	< 0.01
	Dive duration (min ± se)			
Inside EF	-6.37 ± 0.26	65639	-24.25	< 0.01
Night	-5.86 ± 0.10	65639	-57.60	< 0.01

Table 3: Mixed effects model estimates of variability in maximum depth and in dive duration, between (τ2) and within (σ2) individual adult female southern elephant seals from Marion Island which dived more frequently within the eddy field than predicted (n=9), during their post-moult migrations between 2008 and 2010.

	Variance (τ^2 ± SD)	Residual (σ^2 ± SD)	Between seal variability
Maximum depth (m)	1407.48 ± 37.52	24245.23 ± 155.71	5.5 %
Dive duration (min)	9.37 ± 3.06	102.68 ± 10.13	8.4%

Table 4: Mixed effect 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 ($n = 9$) between 2008 and 2010. Reported values are significant at $p < 0.01$ or $p < 0.05$ where marked with *.

	Maximum depth (m ± se)		Dive duration (min ± se)	
Seal ID	Inside EF	Night-time	Inside EF	Night-time
WW061	-56.79 ± 14.75	-174.71 ± 5.42	-7.79 ± 1.05	-4.98 ± 0.29
PO043	-77.66 ± 5.51	-159.37 ± 3.71	-8.49 ± 0.37	-8.54 ± 0.21
OO418	-210.33 ± 18.77	-147.71 ± 8.36	-4.55 ± 1.14	-3.87 ± 0.43
YY264b	-	-201.03 ± 6.48	-8.80 ± 1.56	-7.26 ± 0.42
YY039	-75.43 ± 9.86	-110.51 ± 6.12	-6.38 ± 0.92	-5.73 ± 0.35
BB246	-	-180.22 ± 6.32	-10.19 ± 1.67	-6.46 ± 0.43
RR435	-	-130.78 ± 6.94	-	-6.47 ± 0.36
YY189	-14.74 ± 4.80	-112.92 ± 3.22	-7.37 ± 0.45	-4.90 ± 0.20
BB191	-	-128.55 ± 7.44	-2.02 ± 0.85*	-2.16 ± 0.43
GG335	-	-169.99 ± 5.49	-5.64 ± 1.38	-5.03 ± 0.36

ESM 1

ESM 2