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# Spatial and temporal patterns of changes in condition of southern elephant seals

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**Abstract:** The study of foraging success in marine predators is complicated by a lack of direct observations and relies mostly on proxy measures of foraging success. This study assessed spatial and temporal patterns of changes in body condition of southern elephant seals (*Mirounga leonina*) from Marion Island, based on changes in drift rates (which are related to gains and losses of blubber). Seals showed substantial individual variation in condition changes throughout migrations, which was not explained by age-, sex- or reproductive stages. Substantial variation was also evident in the spatial patterns of condition changes, although an area south of the Antarctic Polar Front (APF) between 10°E and 35°E was evidently associated with moderate, yet consistent gains in condition. Seals that foraged more distantly from Marion Island displayed more extreme gains and losses in condition, suggesting a possible risk/reward trade-off associated with foraging further afield versus closer to the island. Increased condition was consistently negatively related to sea surface temperature, suggesting that seals were generally improving their condition faster in cooler water masses. These results support previous studies predicting that continued warming of the Southern Ocean will result in changes to the habitat use patterns exhibited by southern elephant seals at sea.

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**Key words:** body condition, buoyancy, drift rate, foraging success, *Mirounga leonina*, satellite-relay data logger

## Introduction

In order to fully understand and model the energy flow and species interactions within an ecosystem it is important to investigate the behaviour and foraging ecology of top-level predators (Woodward & Hildrew 2002). In this context, it is useful to gain an understanding of where and when predators are foraging successfully. Although such information is critical to understanding the biology of an organism, the observation and collection of data from large marine predators has long posed a problem to scientists. Whales, seals and seabirds are often wide-ranging and spend large amounts of their time at sea. Further, in some cases, a large proportion of this time consists of diving to considerable depths, making direct observation impossible (Hooker *et al*. 2007).

Indicators of foraging success, such as changes in growth and body condition, can be obtained by direct measures on marine mammals that return to land. These can be compared to movement patterns while at sea to obtain estimates of the spatial distribution of successful foraging areas (Robinson *et al*. 2012). However, this provides only coarse data on changes in body condition over both large temporal and spatial scales, and no information related to prey encounter and successful foraging bouts. One way to obtain information about the at-sea behaviour and foraging strategies of marine mammals is through the use of bio-logging instruments. Most of these studies rely on the use of proxy behavioural data obtained from instruments such as time-depth recorders and accelerometers to infer foraging effort and/or success, although a few studies have also used more direct estimates of foraging success obtained from video imaging (McIntyre 2014).

An associated approach to inferring foraging success of marine predators, particularly elephant seals, is to use a measure of *in situ* body composition to estimate changes in body condition (Biuw *et al*. 2003). Marine predators, especially phocid seals, acquire large portions of lipids from their prey while at sea (Fedak *et al*. 1994). Most of the accumulated lipids are stored in the animal's blubber, and the ratio of lipids to lean body tissue determines an individual's buoyancy (Webb *et al*. 1998). While at sea, elephant seals (*Mirounga* spp.) perform dives (so-called 'drift dives') characterized by periods of active swimming to some depth followed by several minutes of passive drifting (Mitani *et al*. 2009). These dives probably play a role in food processing or rest (Crocker *et al*. 1997). If recorded, the buoyancy of seals can be assessed during these periods of passive drifting in the water column by calculating the rate of vertical displacement of the seals (Biuw *et al*. 2003). If a series of drift dives are recorded, changes in drift rate can be interpreted as changes in relative condition, where increased drift rates indicate increased buoyancy associated with higher blubber to lean muscle tissue ratios, and therefore, periods of successful foraging (Thums *et al*. 2008a). Such changes in drift rates have been widely used as indicators of foraging success in elephant seals (e.g. Biuw *et al*. 2003, Thums *et al*. 2008b, Robinson *et al*. 2010).

Previous studies on the movements and dive behaviour of southern elephant seals (*M. leonina L.*) from sub-Antarctic Marion Island showed variation in the vertical habitat use patterns between sexes, and different foraging strategies and dive patterns between females in different foraging phases (i.e. post-breeding and post-moult) (Jonker & Bester 1998, McIntyre *et al*. 2011a). Seals from this population potentially forage less efficiently in warmer water masses, where they tend to perform deeper dives characterized by comparatively shorter periods of time in the bottom phases (McIntyre *et al*. 2011b). In this study, we analysed temporal and spatial patterns of changes in drift rates of elephant seals from this population to increase our understanding of the distribution and nature of profitable foraging areas for elephant seals in the southern Indian Ocean.

## Methods

### *Animal handling*

Satellite-relay data loggers (SRDLs; Sea Mammal Research Unit, University of St. Andrews, Scotland) were attached to 84 southern elephant seals hauled out at Marion Island, in the southern Indian Ocean (46°53'S, 37°57'E), between April 2004 and February 2012. The animals were immobilized using a handheld syringe, extended by a length of drip-tubing, to deliver a calculated dose of ketamine (Bester 1988), and transmitters glued onto the fur of the heads of the animals using a quick-setting epoxy resin. All animals were of a known sex and age at the time of tag deployment and were part of a long-term mark-resighting programme on the island (Bester *et al*. 2011). We report on a subset (28 migrations) of the available dive dataset obtained from the 84 deployments, after retaining data from those migrations where we positively identified more than 20 drift dives (see below for details).

### *Dive measurements*

The SRDLs provide abstracted time-depth profiles of individual dives that include the dive duration, the maximum depth reached during the dive and four time-depth points reflecting the greatest inflections, as calculated by a broken stick algorithm (Boehme *et al*. 2009). The information was relayed via Service Argos, which also provided position estimates for individual animals. All dive and track data are available via the PANGEA data archiving system (http://pangaea.de).

### *Data analyses*

Dive types were classified by an automated tree-building method using Breiman's random forest algorithm, implemented using the 'randomForest' package in R (Liaw & Wiener 2002). All dives were classified as one of six dive types, namely U-shaped, V-shaped, wiggle (W-shaped), drift, square, and root dives as detailed in McIntyre *et al*. (2011a). Accordingly, we created a training set of manually classified dives to inform the random forest algorithm. In order to minimize observer bias, two researchers (AD and TM) independently classified a random subset ($n = 1000$) of dives. We then included only dives where both researchers agreed on the type allocation (71%) for use to inform the random forest classification model. Eighteen derived parameters were used for the random forest classification as detailed in McIntyre *et al.* (2011a).

Drift dives were isolated from the entire dataset, and drift rates calculated as per Biuw *et al*. (2003). The resulting dataset was filtered to only include dives that were i) deeper than 100 m to account for air trapped in the airways affecting buoyancy (Biuw *et al*. 2003), ii) consisted of a drift phase that encompassed at least 40% of the dive duration, and iii) had drift rates between -0.3 and +0.3 m $s^{-1}$ (Biuw *et al*. 2003). Daily medians of drift rate for each animal were calculated from the filtered dives and a weekly average was then generated and combined with the track data for that week. Daily median values were chosen over mean values to minimize the influence of outlying drift rate values. A timespan of a week was chosen both for convenience, as well as the correlation of approximately seven days with the estimates of minimum time over which changes in predicted lipid content were detected by Thums *et al*. (2008a). Changes in drift rate ($\Delta DR$) were calculated as the difference between any given week and the preceding week. To visualize spatial changes in drift rate, we used an inverse distance weighting (IDW) interpolation of changes in drift rate. This was done in order to provide a representative average image of areas where datapoints overlap. The IDW interpolations assign greater weights to sampled points closer to the interpolated ones, explicitly assuming the existence of spatial autocorrelation. Interpolations were carried out in ArcMap 10, using a small fixed neighbourhood of 0.5° in order to minimize loss of detailed information in areas with no overlapping datapoints. Generalized additive models (GAM) were fit to time series of drift rates from each individual migration in order to assess temporal trends.

To examine correlates between the ocean environment and changes in drift rates of study animals, we extracted remotely sensed sea surface temperature (SST) (MODIS 4 km resolution), chlorophyll *a* (chl *a*) (merged SeaWiFS + MODIS aqua 9 km resolution), and sea floor depth (ETOPO1) estimates for each dive location within the weekly periods for which drift rate information was available. The SST and chl *a* products were merged temporally to correspond with post-moult (Mar–Oct) and post-breeding (Nov–Feb) migration periods of seals tracked using the 'Giovanni' web application (http://disc.sci.gsfc. nasa.gov/giovanni).

A series of linear mixed effects models were then used to assess the relationships between these environmental variables and the changes in drift rate recorded for tracked seals. Due to probable differences in tissue deposition rates between females on post-breeding (PB) and post-moult (PM) (when they mostly carry a developing foetus) migrations, as well as between sexes, we separated our models between sexes and between foraging migrations in females. Only six tracks (all PM) were retained for male seals (see below). These seals ranged in age between four and 11 years. Since growth rates are faster in sub-adult males (classified here as males between the ages of one and six), compared to adult males (classified here as males older than six years) (Clinton 1994), we incorporated age class as a nested effect within the random term. Therefore, our starting full models were:

For female seals on PM and PB migrations:

$$\Delta DR \sim SST + \text{chl}\, a + SF_{depth} + Sex + random = i_{seal},$$

For male seals:

$$\Delta DR \sim SST + \text{chl}\, a + SF_{depth} + Sex + random \\ = i_{seal}/age\_class,$$

where : $\Delta DR$ = change in drift rate $\left(\text{m s}^{-1}\right)$
$SST$ = sea surface temperature
$\text{chl}\, a$ = chlorophyll $a$
$SF_{depth}$ = sea floor depth (m)
$i_{seal}$ = individual seal (random term)
$age\_class$ = age class (adult or sub-adult).

All possible combinations of fixed variables were then compared in order to select the most parsimonious models. Model selection was undertaken based on maximum likelihood and using second-order AIC (AICc) and corresponding AIC weights to select the most parsimonious models (Burnham & Anderson 2002). All analyses were undertaken in the R statistical environment (Version 2.15.2, R Core Team 2012). We used the package nlme (Pinheiro *et al.* 2012) for mixed effect model analyses, and mgcv (Wood 2006) for GAMs. Unless otherwise stated, mean values ± standard deviation are reported. Statistical significance was set at $P \leq 0.05$.

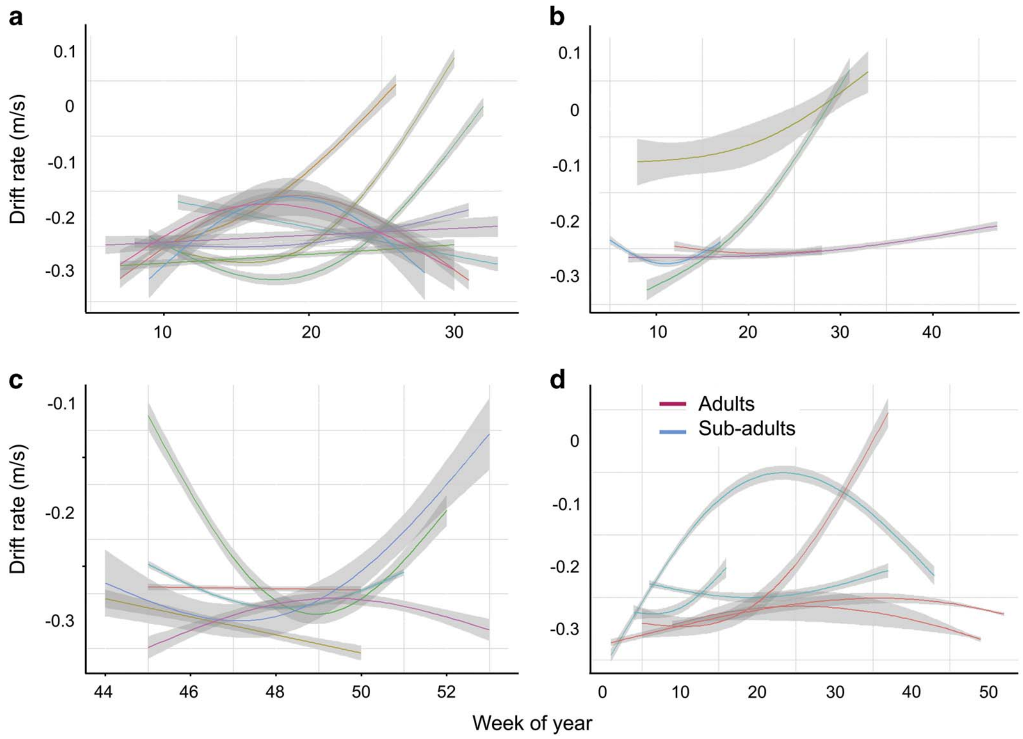

**Fig. 1.** Temporal trends, displayed by generalized additive models, in drift rates (m s$^{-1}$) for **a.** known pregnant female seals during post-moult migrations, **b.** females of unknown reproductive status during post-moult migrations, **c.** female seals during post-breeding migrations, and **d.** adult and sub-adult male seals.

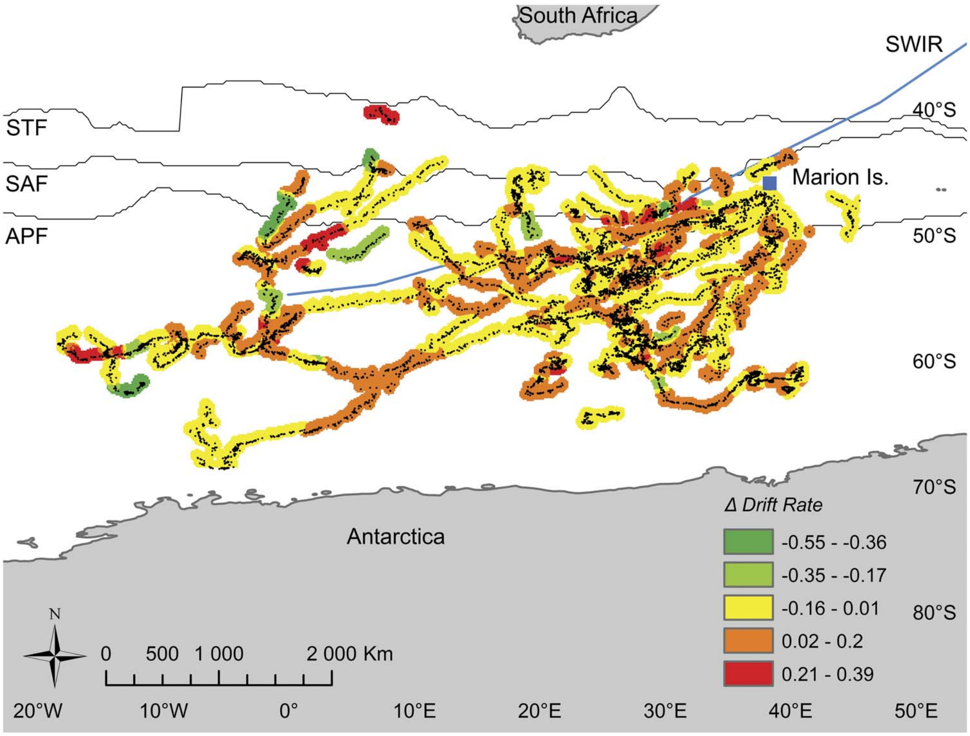

**Fig. 2.** Interpolated trends of changes in drift rate (*Δ Drift Rate*) during post-moult migrations of female southern elephant seals from Marion Island. SWIR = Southwest Indian Ridge, STF = Subtropical Front, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front. Frontal locations are based on Swart *et al.* (2010).

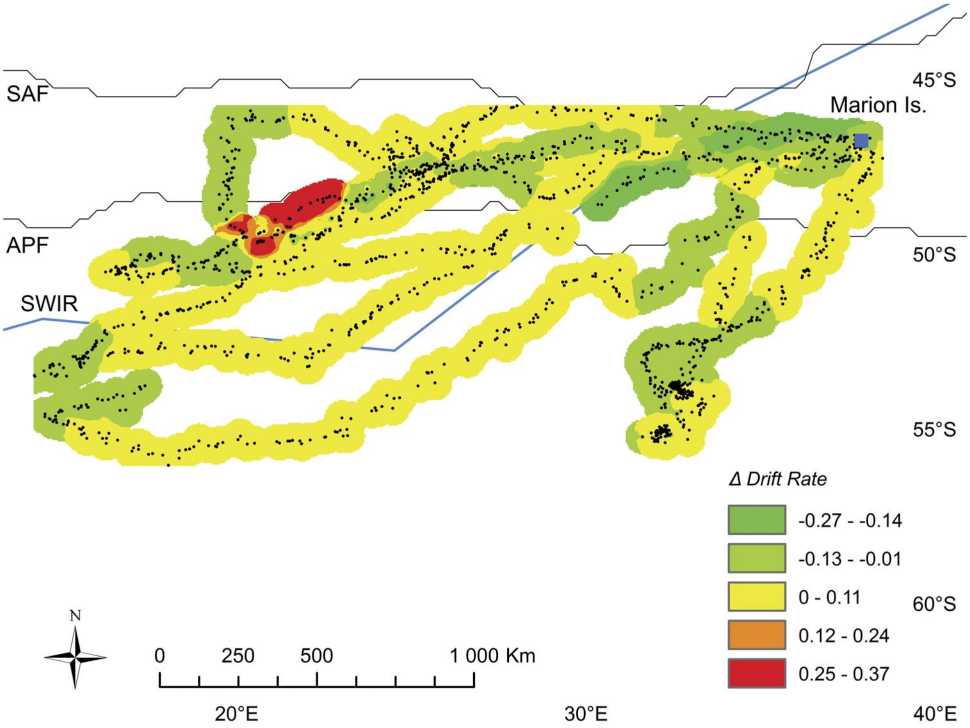

**Fig. 3.** Interpolated trends of changes in drift rate (*Δ Drift Rate*) during post-breeding migrations of female southern elephant seals from Marion Island. SWIR = Southwest Indian Ridge, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front. Frontal locations are based on Swart *et al.* (2010).

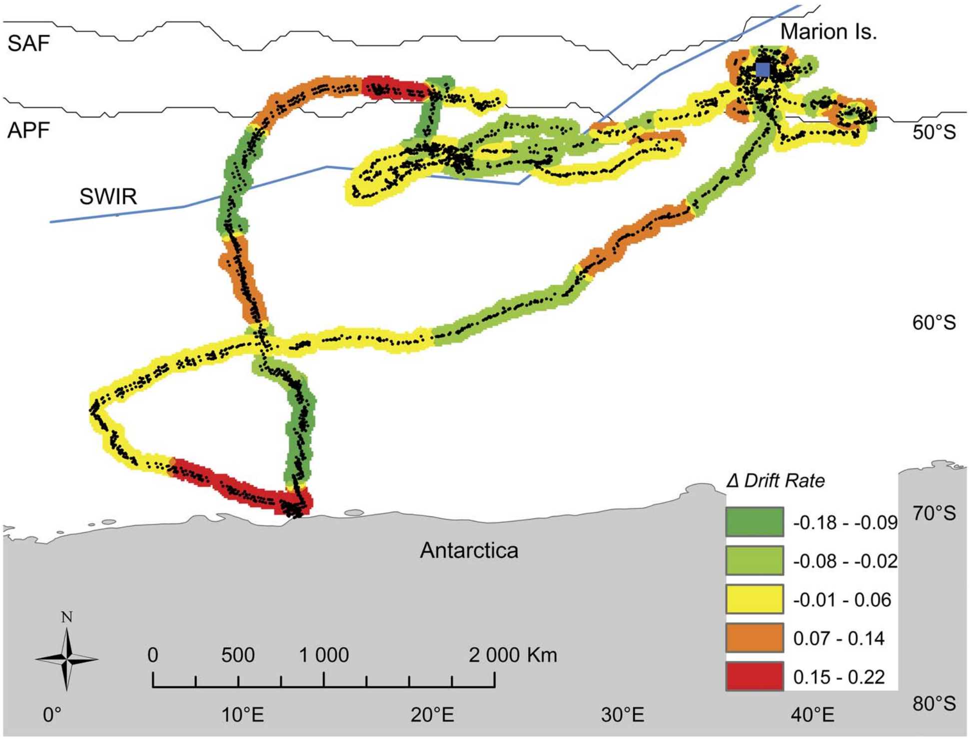

**Fig. 4.** Interpolated trends of changes in drift rate (*Δ Drift Rate*) during migrations of male southern elephant seals from Marion Island. SWIR = Southwest Indian Ridge, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front. Frontal locations are based on Swart *et al.* (2010).

## Results

We retained six PB and 15 PM tracks from adult females, as well as three tracks from sub-adult and three tracks from adult males, each of which contained more than 20 drift dives. These included a total of 1462 drift dives identified from 129 950 recorded dives.

### *Temporal changes in drift rates*

We observed substantial variation in temporal trends of drift rates during individual migrations (Fig. 1). Two trend patterns were evident during PM migrations of females observed to have pupped on their return to the island (Fig. 1a): initial decreases in drift rate followed by continual increases, and patterns that showed an initial increase in drift rates, followed by a decline in drift rates towards the end of the migrations. Three females did not return to Marion Island for the breeding season haulout after being instrumented (Fig. 1b). Of these, two hauled out on neighbouring Prince Edward Island and one device failed prematurely resulting in the seal's location being unknown. One female did not complete her PM migration and has subsequently not been resighted at Marion Island. One female remained at-sea during the breeding season and returned to Marion Island only for the following moult haulout. This female displayed a pattern of consistent, but slow, increased drift rates throughout her extended foraging migration (Fig. 1b).

Females displayed higher drift rates during PM migrations compared to PB migrations (Kruskal-Wallis = 221.2, df = 1, $P < 0.001$). The temporal trends in PB drift rates of females were similarly variable between

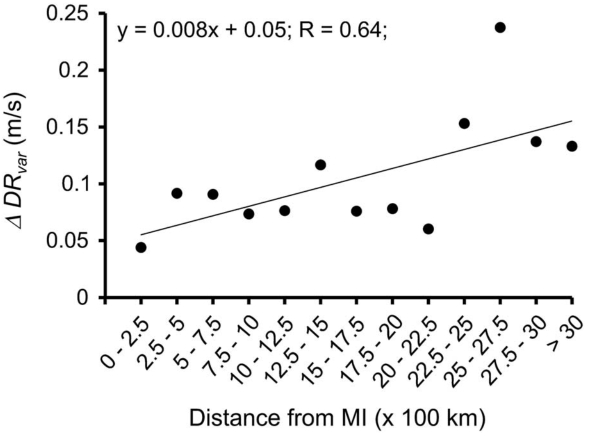

**Fig. 5.** Relationship between distance from Marion Island (MI) and variance in drift rates displayed by elephant seals ($\Delta DR_{var}$). $\Delta DR_{var}$ is defined here as the difference between the 75th and 25th percentiles of drift rates measured within the distance categories displayed.

**Table I.** Akaike Information Criterion (AIC) ranking results for candidate models assessing environmental correlates with changes in drift rates of tracked elephant seals. Bold faced models indicate the top-ranked models.

| Rank | Candidate models | Coefficients | | | df | AICc | $\Delta$ AIC$_c$ | AIC weight |
|---|---|---|---|---|---|---|---|---|
| | | $SF_{depth}$ | chl $a$ | $SST$ | | | | |
| *Post-moult females* | | | | | | | | |
| **1** | **$SST$** | | | **-0.003** | **4** | **-8049.6** | **0** | **0.876** |
| 2 | - | | | | 3 | -8044.3 | 5.36 | 0.06 |
| 3 | $SST$ + chl $a$ | | 0.02 | -0.003 | 5 | -8043.6 | 6 | 0.044 |
| 4 | chl $a$ | | -0.088 | | 4 | -8042.1 | 7.51 | 0.021 |
| 5 | $SST + SF_{depth}$ | $< 0.001$ | | -0.003 | 5 | -8028.9 | 20.74 | 0 |
| 6 | $SST$ + chl $a$ + $SF_{depth}$ | $< 0.001$ | 0.026 | -0.003 | 6 | -8023 | 26.63 | 0 |
| 7 | $SF_{depth}$ | $< 0.001$ | | | 4 | -8022.3 | 27.36 | 0 |
| 8 | *chl a* + $SF_{depth}$ | $< 0.001$ | -0.087 | | 5 | -8020.1 | 29.57 | 0 |
| *Post-breeding females* | | | | | | | | |
| **1** | **$SST$** | | | **-0.014** | **4** | **-2945.5** | **0** | **0.923** |
| 2 | $SST$ + chl $a$ | | -0.055 | -0.015 | 5 | -2940.6 | 4.96 | 0.077 |
| 3 | $SST + SF_{depth}$ | $< 0.001$ | | -0.014 | 5 | -2921.6 | 23.88 | 0 |
| 4 | $SST$ + chl $a$ + $SF_{depth}$ | $< 0.001$ | -0.056 | -0.014 | 6 | -2916.7 | 28.81 | 0 |
| 5 | - | | | | 3 | -2852 | 93.5 | 0 |
| 6 | chl $a$ | | -0.033 | | 4 | -2846.4 | 99.15 | 0 |
| 7 | $SF_{depth}$ | $< 0.001$ | | | 4 | -2836 | 109.5 | 0 |
| 8 | chl $a$ + $SF_{depth}$ | $< 0.001$ | -0.036 | | 5 | -2830.4 | 115.09 | 0 |
| *Males* | | | | | | | | |
| **1** | **$SST$ + chl $a$ + $SF_{depth}$** | **$< 0.001$** | **-0.328** | **-0.007** | **7** | **-4816.4** | **0** | **0.999** |
| 2 | $SST + SF_{depth}$ | $< 0.001$ | | -0.01 | 6 | -4802.1 | 14.3 | 0.001 |
| 3 | chl $a$ + $SF_{depth}$ | $< 0.001$ | -0.514 | | 6 | -4792.6 | 23.8 | 0 |
| 4 | $SST$ + chl $a$ | | -0.428 | -0.007 | 6 | -4774.5 | 41.87 | 0 |
| 5 | chl $a$ | | -0.625 | | 5 | -4751 | 65.4 | 0 |
| 6 | $SST$ | | | -0.011 | 5 | -4745.7 | 70.69 | 0 |
| 7 | $SF_{depth}$ | $< 0.001$ | | | 5 | -4744.9 | 71.47 | 0 |
| 8 | - | | | | 4 | -4677.6 | 138.75 | 0 |

tracks. Some showed initial decreases in drift rates, followed by increased drift rates between the middle and the end of the migrations, while others initially displayed increasing drift rates, followed by decreases towards the end of their migrations (Fig. 1c). Male seals tended to display slightly higher drift rates on average, compared to females (Kruskal-Wallis = 8.9, df = 1, $P = 0.003$), but there was also much variation between individuals (Fig. 1d). The only adult male that displayed substantial increases in drift rate was also the only male, other than one sub-adult male, to return to the island for the breeding season after their PM migrations (the others either remained at sea, or suffered tag failure during their PM migrations).

### *Spatial changes in drift rates*

Tracked seals utilized a large area, totalling approximately 9.8 million km$^2$, during PM and PB migrations. Seals travelled predominantly to the south-west of Marion Island, using an area extending from the Sub-Antarctic Front (SAF) in the north, south towards the Antarctic continent (Figs 2–4). The spatial locations of areas where seals displayed more positive, as well as negative, drift rates were varied and scattered throughout foraging ranges for female PM and PB migrations, as well as male migrations.

Female seals generally showed increased drift rates during PM migrations between ~15° and ~35°E, south of the SAF. A similar area of increased drift rates was evident during female PB migrations, but restricted mainly to areas south of the Antarctic Polar Front (APF) and west of ~30°E, over the Southwest Indian Ridge (Figs 2 & 3). Male seals also used this area, but displayed more stable, and slightly decreasing drift rates here (Fig. 4). A few areas were consistently associated with decreased drift rates between the identified migration groups, particularly the inter-frontal area (between the SAF and APF) east of 30°E. Areas where seals displayed more extreme changes (both positive and negative) in drift rates were mostly located further away from Marion Island (Figs 2–4), and distance from Marion Island was positively correlated with increased variability in drift rate changes (Pearson's product-moment correlation = 0.64, $t = 2.73_{(11)}$, $P = 0.02$; Fig. 5).

### *Environmental correlates with $\Delta DR$*

All top-ranked models (for males and females) showed significant negative relationships between SST and $\Delta DR$ (Table I), suggesting increased buoyancy associated with colder waters. The coefficients of the modelled relationships between $\Delta DR$ and SST was strongest for female seals on PB migrations (-0.014), followed by male seals (-0.007) and females on PM migrations (-0.003). No other environmental variables were retained in the top models for female migrations. Both sea floor depth and chl *a* concentrations were retained (i.e. the full starting model) in the top-ranked model for male migrations, suggesting that male seals performed dives consistent with increased buoyancy in areas characterized by lower surface chlorophyll concentrations and deeper sea floors (Table I).

## Discussion

Our study aimed to firstly determine the spatial and temporal trends of changes in buoyancy of elephant seals from Marion Island, and secondly to relate such changes to a series of environmental covariates. Since changes in buoyancy is a proxy for foraging success (e.g. Biuw *et al.* 2007), our results provide important insights into the spatial distribution and environmental characteristics of productive areas in a relatively little-known sector of the Southern Ocean.

Our results showed substantial variation in the temporal changes in drift rate displayed by tracked seals during their foraging migrations (Fig. 1). While some individuals displayed similar temporal trends to that reported by Thums *et al.* (2008a), the seals typically did not display initial decreases in drift rate, followed by recovery as illustrated in Biuw *et al.* (2003). Continuous increases in drift rate throughout PM migrations, followed by decreases towards the end of the migrations, are possibly typical of pregnant female seals foraging successfully throughout their migrations, but displaying decreased drift rates towards the end of their migrations as a result of variable tissue deposition associated with the developing foetus (e.g. Robinson *et al.* 2010). However, while some known pregnant females in our sample did display similar temporal patterns, some pregnant females continued to display increasing drift rates for their entire migrations (Fig. 1a). The one female that remained at-sea throughout the breeding period displayed a temporal trend indicating continued increasing drift rates (Fig. 1b). This seal was assumed not to be pregnant throughout the tracked migrations, although the possibility that she aborted sometime during the migration cannot be excluded. Female seals from this population often skip breeding seasons on the island altogether, returning in subsequent years to pup and breed again (de Bruyn *et al.* 2011). Temporal trends in the drift rates of female seals on PB migrations, as well as males on migrations throughout the year, were similarly variable, not showing the consistent patterns previously reported by other authors (e.g. Thums *et al.* 2008b). Interestingly, the only two male seals in our sample to show substantial increases in condition (as inferred from an increased drift rate) are also the only males to have returned to the island for the breeding season following instrumentation. The other males, including two adult males, did not return in time for the breeding season but remained at sea during this time period (past week 35; Fig. 4). Unfortunately our limited sample precluded the testing for any possible effects of foraging success on the probability of returning to the island for the breeding season.

Similarly, no obvious spatial patterns were evident in terms of where seals were generally increasing or decreasing drift rates (Figs 2–4). However, one area located approximately between 15°E and 35°E, south of the APF, was characterized by reasonably consistent increases in drift rates of tracked seals. In contrast, seals from Macquarie Island and the Kerguelen Archipelago showed distinct decreases in drift rates in the corresponding frontal zone (between the APF and the Southern Antarctic Circumpolar Front), especially around the Kerguelen Plateau (Biuw *et al.* 2007). Despite this, the Kerguelen Plateau is often targeted by elephant seals, particularly during the summer and autumn (O'Toole *et al.* 2014).

Much of the area used by Marion Island elephant seals to the south-west of the Prince Edward Islands coincides with the location of the Southwest Indian Ridge, a prominent bathymetric structure that is responsible for generating mesoscale eddies through interactions with the Antarctic Circumpolar Current (Ansorge & Lutjeharms 2003). These eddies, in turn, are often exploited by other predators breeding on Marion Island (e.g. Nel *et al.* 2001). Previous studies attempting to quantify relationships between changes in the condition of seals estimated from drift rates and remotely sensed environmental covariates reported mixed results, from suggesting that elephant seals are targeting mesoscale eddies (Bailleul *et al.* 2010), to not finding any considerable correlates (Schick *et al.* 2013). We did not test for any specific relationships between changes in drift rates and the presence and/or characteristics of mesoscale oceanographic features, but best fit models suggested generally poor relationships between changes in drift rate and surface chlorophyll levels. Where there was evidence for an influence of chlorophyll concentration (drift rate changes in males), this relationship was negative, suggesting that male seals tended not to deposit substantial blubber tissue in areas associated with increased surface productivity. Preliminary studies suggest that the seals from Marion Island apparently opportunistically exploit mesoscale features, with eddies not specifically targeted, but often encountered during transit phases of migrations (Massie *et al.* 2015).

Previous studies on the dive behaviour of elephant seals from Marion Island suggested that males tend to perform dives associated with increased foraging effort in areas associated with the Southwest Indian Ridge

(McIntyre *et al.* 2012), although no such trend is evident for females (McIntyre *et al.* 2011a). While elephant seals are known to occasionally forage benthically on seamounts, seals from Marion Island typically do not perform dives within reach of the estimated depths of the Southwest Indian Ridge. Therefore, it is likely that this area is rather targeted due to comparatively high levels of productivity in mid-water depth layers associated with increased upwelling and mixing (Sokolov & Rintoul 2007). Our model outputs also suggested a statistically significant influence of sea floor depth on changes in the drift rates of tracked seals. Positive changes in drift rates of male seals were evidently associated with slightly deeper sea floor depths. However, the modelled effect size here was negligible, suggesting it is not likely to be biologically meaningful.

Dives characterized by increased drift rates were generally associated with colder surface water temperatures. The effect size was greatest in females on PB migrations, with smaller effect sizes for male and female seals tracked during winter months (on PM migrations). These differences may relate to seasonal differences in SST, which potentially result in seals directing their foraging efforts more strongly towards available colder water in the summer months; and displaying less focus on colder water in the cold winter months. The overall association of changes in condition with SST agrees well with previous studies suggesting increased foraging activity associated with cooler water masses (McIntyre *et al.* 2011b, Guinet *et al.* 2014). It also fits well with the overall distribution of foraging migrations (Figs 2 & 3), with seals generally travelling in a south-western direction from the island, and evidently targeting inter-frontal zones south of the SAF (Jonker & Bester 1998). Tracked seals from Macquarie Island and the Kerguelen Archipelago tend to switch to foraging modes (from travelling modes, as qualified using state-space models) when they enter cold Antarctic shelf and surface waters (Bestley *et al.* 2013), subsequently performing dives with increased periods spent during the bottom phases and characterized by fast descent rates. This area is typically targeted by seals from these populations (e.g. Bailleul *et al.* 2007), but not used as often by seals from Marion Island (e.g. McIntyre *et al.* 2011a). Previous work illustrated that elephant seals from Marion Island alter their dive behaviour in relation to the temperature of the water columns they dive in, probably performing less successful foraging dives in warmer waters, compared to the colder (and more productive) water masses of the Southern Ocean (McIntyre *et al.* 2011b). The modelled relationships we report here between the foraging success of elephant seals (as indicated by changes in drift rate) and the SST provide further support for the premise that these seals rely on the colder, more productive water masses for successful foraging and forage less successfully in slightly warmer waters. As a result, continued warming of the Southern Ocean (Roemmich *et al.* 2015) may result in the elephant seals, particularly those from the northern populations such as Marion Island, having to extend their foraging migrations poleward or adopt deeper diving strategies to follow expected changes in prey distribution.

Seals tended to display more extreme changes in drift rates (both positive and negative) at greater distances away from Marion Island (Fig. 5). This was most obvious for female PM migrations, when females also tended to travel greater distances away from the island. The trend of more extreme changes in drift rates in areas further away from the island may, therefore, be indicative of elephant seals facing a ‘high risk, high reward – moderate risk, moderate reward’ situation, whereby targeting potential foraging patches further afield (e.g. > 2500 km) from the Prince Edward Islands may sometimes result in above-average fitness gains associated with blubber gains, and other times above-average losses in fitness. On the other hand, foraging in inter-frontal areas closer to the islands may be more predictable, but result in average, yet more consistent, foraging success. One possible explanation for such a scenario may be related to influences of both inter- and intra-species competition for food resources. The Prince Edward Islands is an isolated archipelago that hosts large numbers of breeding marine predators (e.g. penguins, albatrosses, fur seals and elephant seals). Therefore, levels of competition for food resources are likely to be higher in closer proximity to the islands due to the increased concentrations of predators present. The general decrease in drift rates in the inter-frontal area (between the SAF and APF) east of 30°E is perhaps also related to inter-specific composition, since lactating fur seals (both Antarctic and sub-Antarctic fur seals) occasionally forage within this area (e.g. Arthur *et al.* 2015), and presumably also avian predators. Alternatively, high predation pressure closer to the island (from fur seals, penguins and other seabirds) may result in lower concentrations of prey available to elephant seals. Future studies incorporating more at-sea habitat use patterns of other marine predators are likely to clarify the importance of this area for the marine predator community of Marion Island. However, our results suggest a likelihood that such a high risk, high reward – moderate risk, moderate reward trade-off may play a role in the decisions of seals to use specific foraging areas. We did not specifically account for likely influences on drift rates associated with the developing foetus in most of the female seals on their PM migrations. While unknown, such influences are expected to be substantial, possibly offsetting changes in drift rates associated with the deposition of more than 30% of the total adipose stores accumulated over a migration (Robinson *et al.* 2010). Influences on drift rates associated with a developing foetus are expected to be most significant at the beginning and end of foraging migrations (Robinson *et al.* 2010), and as such, may have concealed larger changes in drift rates at locations closer to the island in our study.

Our study was generally hampered by the coarse-scale nature of the dive data obtained from SRDLs, and the associated lack of velocity measurements (such as used by Thums *et al.* 2008a). This necessarily impacted on the successful identification of drift dives in the dataset, and some dives were undoubtedly misclassified. However, previous validation experiments on a dive classification approach similar to ours suggested a likely error rate of between 2% and 4% (Thums *et al.* 2008b) and similar approaches were previously successfully used on similar low-resolution data (Bailleul *et al.* 2007, Biuw *et al.* 2007).

## Conclusion

Our results illustrate substantial individual variation in both temporal as well as spatial patterns of changes in buoyancy of southern elephant seals associated with changes in overall condition. While some areas were associated with consistent, but moderate improvements in condition of the tracked seals, more distant areas were characterized by more extreme gains and losses in condition, suggesting a possible risk-reward trade-off for seals pursuing foraging strategies further west than approximately 10°E. We also describe a consistent negative relationship between SST and changes in condition, suggesting that seals generally improve condition in cooler (probably more productive) areas. This provides support for previous work that suggested continued warming of the Southern Ocean may force elephant seals from northern populations to forage increasingly poleward and/or to exploit deeper water layers.

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## Author contribution

TM designed the research; TM and AD analysed the data; and TM, AD and MNB wrote the paper.

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