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

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14 **Abstract**

15 As the Antarctic Circumpolar Current crosses the South-West Indian Ocean Ridge it creates
16 an extensive eddy field characterised by high sea level anomaly variability. We investigated
17 the diving behaviour of female southern elephant seals from Marion Island during their post-
18 moult migrations in relation to this eddy field in order to determine its role in the animals' at-
19 sea dispersal. Most seals dived within the region significantly more often than predicted by
20 chance, and these dives were generally shallower and shorter than dives outside the eddy
21 field. Mixed effects models estimated reductions of 44.33 ± 3.00 m (maximum depth) and
22 6.37 ± 0.10 min (dive duration) as a result of diving within the region, along with low
23 between seal variability (maximum depth: 5.5% and dive duration: 8.4%). U-shaped dives
24 increased in frequency inside the eddy field, whereas W-shaped dives with multiple vertical
25 movements decreased. Results suggest that Marion Island's adult female elephant seals' dives
26 are characterised by lowered cost-of-transport when they encounter the eddy field during the
27 start and end of their post-moult migrations. This might result from changes in buoyancy
28 associated with varying body condition upon leaving and returning to the island. Our results
29 do not suggest that the eddy field is a vital foraging ground for Marion Island's southern
30 elephant seals. However, because seals preferentially travel through this area and likely
31 forage opportunistically while minimising transport costs, we hypothesise that climate
32 mediated changes in the nature or position of this region may alter the seals' at-sea dispersal
33 patterns.

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

36 **Introduction**

37 The Southern Ocean is characterised by the Antarctic Circumpolar Current (ACC) (Rintoul et
38 al. 2001), which provides a crucial mechanism in driving regional biological productivity
39 (Downes et al. 2011). While the ACC connects the global ocean basins via zonal mixing, it
40 restricts meridional transport (Rintoul et al. 2001). However, poleward transport of water
41 masses does occur through the formation of eddies (de Szoeke and Levine 1981), principally
42 within frontal regions or where the ACC interacts with poleward extensions of western
43 boundary currents or irregular bathymetry (Rintoul and Sokolov 2001). Some global climate
44 models predict that increases in atmospheric CO₂ could lead to a southward migration and
45 intensification of the region's westerly wind belt (Saenko et al. 2005). These changes may in
46 turn lead to poleward shifts in the ACC's frontal systems (Downes et al. 2011) as well as
47 increases in the region's eddy activity and poleward heat fluxes (Meredith and Hogg 2006).
48 Eddies are closely associated with nutrient fluxes in the open ocean (Ansorge et al. 2009) and
49 are utilised as foraging grounds by many marine species, including Subantarctic fur seals
50 (*Arctocephalus tropicalis*) (de Bruyn et al. 2009), grey-headed albatrosses (*Thalassarche*
51 *chrysostoma*) (Nel et al. 2001), great frigate birds (*Fregata minor*) (Weimerskirch et al. 2004)
52 and southern elephant seals (*Mirounga leonina*) (Campagna et al. 2006; Bailleul et al. 2010;
53 Dragon et al. 2010).

54 The Prince Edward Islands are located south east of South Africa at 46.75°S and 37.92°E,
55 directly in the path of the ACC (Duncombe Rae 1989; Ansorge and Lutjeharms 2002). The
56 archipelago consists of Marion Island (270 km²) and the smaller Prince Edward Island (45
57 km²) (Pakhomov and Froneman 1999). Marion Island is home to over five million birds and
58 seals (Ryan and Bester 2008) and forms one of the most northerly and isolated southern
59 elephant seal colonies in the Southern Ocean. The nutritional energy necessary to sustain
60 such vast numbers of top predators is derived from the close interaction between the oceanic

61 environment and the islands themselves. Changes in the oceanic environment resulting in
62 shifting prey distributions and availability have been earmarked as potential drivers of the
63 observed population declines of Marion Island's southern elephant seals during the 20th
64 century (McMahon et al. 2005).

65 The islands lie in the Polar Frontal Zone (PFZ), bounded to the north by the nearby sub-
66 Antarctic Front (SAF) and to the south by the more distant Antarctic Polar Front (APF)
67 (Ansorge and Lutjeharms 2002). While the frontal regions are highly productive (Guinet et
68 al. 1997), productivity within the PFZ is more patchy (Weimerskirch et al. 1997). Areas of
69 elevated nutrient concentration within the PFZ may therefore present important foraging
70 areas. To the south-west of Marion Island lies an extensive corridor of high sea level anomaly
71 variability corresponding to interactions between the ACC and the highly fractured South-
72 West Indian Ridge (SWIR) (Ansorge and Lutjeharms 2003, 2005; Sclater et al. 2005;
73 Durgadoo et al. 2010, 2011). This corridor, hereafter referred to as the eddy field, is
74 comprised of cyclonic and anticyclonic eddies. The eddies are readily identified from satellite
75 altimetry as sea level anomalies (SLAs) (Ansorge and Lutjeharms 2003, 2005; Ansorge et al.
76 2009) and result in elevated regional eddy kinetic energy (EKE) (Fig. 1). Cyclonic eddies
77 (negative anomalies) are associated with enhanced productivity around their centres due to
78 upwelling of nutrients into the photic zone and advection towards their turbulent edges
79 (Bailleul et al. 2010). In contrast, anticyclonic eddies (positive anomalies) exhibit elevated
80 productivity along their edges (Bailleul et al. 2010), due to increased turbulence across their
81 outer density surfaces (Lévy et al. 2001). Interactions between eddies also result in interstitial
82 jets, which can lead to enhanced localised biological activity (Lima et al. 2002). Eddies trap
83 and redistribute nutrients leading to elevated localised productivity (Bailleul et al. 2010). As
84 these features travel north-eastwards into the vicinity of the islands they are utilised as
85 foraging grounds by breeding grey-headed albatrosses (Nel et al. 2001).

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

101 **Materials and methods**

102 **Ethics statement**

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

110 **Data Processing**

111 Between 26 October 2007 and 10 January 2010, 32 female southern elephant seals from
112 Marion Island were tagged with satellite relay data loggers (SMRU/Series 9000 SRDL or
113 SRDL/CTD, Sea Mammal Research Unit, University of St Andrews, UK). These devices
114 record time and dive information which is transmitted via the Service Argos satellite system
115 (Collecte Localisation Satellites (CLS) 2011) to the Sea Mammal Research Unit (Vincent et
116 al. 2002). Track position estimates provided by Service Argos are filtered to remove points
117 describing implausible elephant seal swimming speeds and the positions of the dives are
118 estimated as interpolated points framed by Argos uplink position estimates (Boehme et al.
119 2009). These interpolations are based on uplink times in relation to the times at which the
120 dives occurred and have an estimated accuracy of ± 2 km (Boehme et al. 2009).

121 The seal track data used for this study are available via the PANGEA information system
122 (<http://www.pangea.de>). Each track was made up of consecutive dives for which the time,
123 date, geographical position, total dive duration, maximum depth as well as depths and times
124 of four inflection points were recorded. These data were collated with deployment records
125 from the Mammal Research Institute (MRI, University of Pretoria) so as to include each
126 individual's age class and sex, using Python 2.7.5 (<http://www.python.org/>) along with the
127 pyodbc (<http://code.google.com/p/pyodbc/>) and xlrd (<http://www.python-excel.org/>) libraries.
128 All subsequent data processing was undertaken in the R environment for statistical computing
129 (R Core Team 2015).

130 Only data from the approximately eight-month long adult female post-moult migrations were
131 included and, to ensure that overall dive behaviour was properly represented, tracks with at-
132 sea durations of fewer than 30 days were excluded from the analysis (cf. Bailleul et al. 2007).
133 Using the geosphere package (Hijmans et al. 2012), each dive's distance and absolute bearing
134 relative to Marion Island was calculated along with distances, speeds, and relative bearings

135 between successive dives. Distances were calculated using Vincenty's ellipsoidal formula.
136 The data sets for three seal tracks (GG335 – 2009, GG335 – 2010, YY189 - 2010) contained
137 unusually large numbers of dives with durations of exactly 5715 sec (201, 780, 167
138 respectively). These times were attributed to erroneous SRDL tag readings and the dives were
139 excluded from further analysis. Using the maptools package (Bivand 2013) dives were
140 classified as taking place during the day or night. If the dives took place within 30 min of
141 sunrise or sunset they were classified as dawn or dusk dives respectively and excluded from
142 further analysis (cf. McIntyre et al. 2011). Each dive was further categorised as to whether it
143 occurred inside or outside of the eddy field. The data set at this point included a total of
144 107,376 dives within 22 tracks from 16 seals (Online Resource 1, Fig 2).

145 *Dive types*

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

155 The remaining four dive types are distinguished by slower ascent and descent rates along
156 with durations of less than one minute in their deepest sections (Hindell et al. 1991). Drift
157 dives (DR-dives) incorporate a rapid initial descent to around 200 m followed by a longer,
158 slower descent lasting most of the remainder of the dive (Hindell et al. 1991; McIntyre et al.
159 2011). These dives are terminated by a rapid ascent (Le Boeuf et al. 1988; Hindell et al. 1991;

160 Photopoulos 2007). During the first fortnight of their post-moult migrations the seals cover
161 up to 120 km per day, primarily undertaking U-shaped dives (U-dives) (Hindell et al. 1991).
162 Root dives (R-dives) constitute a combination of several unclassified dive shapes and are
163 thought to be associated with exploratory diving (Hindell et al. 1991; Photopoulos 2007). The
164 sixth dive type described by Photopoulos (2007) are V-shaped dives which are linked to
165 travelling to and from foraging grounds.

166 Breiman's random forest algorithm was used to classify each dive based on a training set.
167 The training set is a subset of dives with which proportions of dive time, vertical direction of
168 travel and rates of ascent or descent between inflection points could be compared for
169 classification. Generation of a training set requires that a large number of dive profiles are
170 visually assessed and classified according to the above mentioned dive types. This is a
171 subjective process and so, in order to increase conformity of results between research studies
172 we used an existing training set, previously used in studies involving the identification of
173 dive types in seals from Marion Island (McIntyre et al. 2011).

174 *Correlated Random Walks*

175 Correlated random walk (CRW) distributions were generated using the adehabitatLE package
176 (Calenge 2006). These CRWs were compared with the tracks of instrumented seals in order
177 to determine whether tracked animals dived within the eddy field more often than might be
178 expected by chance. The recorded seal tracks were first split into outward and homeward legs
179 using their furthest dives from Marion Island as turning points. The 22 outward legs were
180 then individually analysed in order to derive arguments for the `simm.crw()` function. The
181 scaling parameter (h) for each outward track was estimated using the `hbrown()` function in
182 `adehabitatLE`. Each seal's outward-track turning angles were fitted to a wrapped normal
183 distribution using the `mde.wrappednormal()` function from the `wle` library (Agostinelli 2013).
184 These distributions were used to estimate concentration factor values (r) (Fig. 3). The

185 individual seal's number of outward bound steps and mean durations between successive
186 steps were used to generate date ranges (dr).

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

192 *Oceanographic data processing*

193 Daily, delayed time, 1/4 degree resolution zonal(*u*) and meridional(*v*) geostrophic current
194 data for the period 1 January 2008 - 31 December 2010 were produced by Ssalto/Duacs and
195 distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>).

196 These data were used to calculate eddy kinetic energy (EKE in cm²/s²) for the full extents of
197 the seals migration tracks:

$$198 \quad EKE = \frac{(u^2 + v^2)}{2}$$

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

207 **Statistical analyses**

208 *Dive likelihood inside vs outside the eddy field*

209 Exact binomial tests were run using the core stats package in R to determine whether the ratio
210 of observed dives occurring outside vs inside the eddy field was significantly greater than the
211 same ratio within the simulated CRWs. These tests were run for the grouped track data as
212 well as for each of the 16 seals' 22 post-moult tracks. Further investigations included only
213 tracks where individuals had dived within the eddy field significantly more frequently than
214 predicted by the CRWs. This subsequent data set included 10 individuals, 13 tracks and
215 71,259 dives (Online Resource 1).

216 *Mixed effects modelling procedures*

217 In order to detect significant differences in maximum depth and dive duration as a result of
218 diving within the eddy field or changing day-stage (day or night) along with individual seal's
219 contributions to variance, linear mixed effects models were run using the nlme package
220 (Pinheiro et al. 2013) in R. Where mixed effect model results are reported, values refer to
221 estimated effect \pm standard error. Before running mixed effects models, residual histograms
222 were inspected to ensure that the data were approaching normal distributions (Zuur et al.
223 2009). In order to account for heterogeneity, scatter plots of model residuals were checked for
224 funnelling (Zuur et al. 2009). No data transformations were applied during the data
225 preparation. To check for independence, autocorrelation function (ACF) plots and
226 semivariograms were generated and examined for each model.

227 Mixed effects models were run using the restricted maximum likelihood (REML) method and
228 subsequently updated using first order autoregressive correlation structures with theta set to
229 the lag-1 interval in order to account for autocorrelation (Pinheiro and Bates 2000). ACF

230 plots and semivariograms were used to confirm autocorrelation reduction. Where mixed
231 effects models were run on individual seals, constants were used for random effects.

232 *Outside vs inside the eddy field*

233 An initial investigation explored the impact of position (inside vs outside the eddy field), day-
234 stage (day vs night) and time since departure (days at sea) on maximum depth and dive
235 duration for the individuals which had dived more often inside the eddy field than might be
236 expected by chance. The results of these models suggested that time at sea explained less than
237 1 m of depth and 1 min of dive duration variation. Moreover, inclusion of this variable
238 necessitated limiting the data set to the first 150 days and as a result of this constraint and its
239 small effect, time since departure was excluded from this report.

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

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

252 **Results**

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

260 **Dive frequencies**

261 The seals performed significantly more dives (18.5%) within the eddy field than predicted by
262 the CRWs (8.5%; $p < 0.01$; Fig. 3). On an individual level, 10 of the 16 seals dived within the
263 eddy field region significantly more often than predicted (13 of 22 tracks; Online resource 1).
264 Seal OO021 did not dive within the eddy field region during either tracked migration year
265 (2008 or 2009) while seals PO043 (2008 and 2009) and YY189 (2008, 2009 and 2010) dived
266 significantly more frequently within the eddy field during all tracked years. Seal GG335
267 dived significantly more often within the eddy field in 2008 but not in 2009 or 2010. Of the
268 remaining 12 tracks undertaken by different seals, seven dived within the eddy field
269 significantly more often than predicted.

270 **Dive parameters**

271 Considering the seals that dived significantly more often in the eddy field than predicted by
272 the CRW model as a group, the recorded mean and maximum dive depths and durations were
273 shallower and shorter inside the eddy field, regardless of day-stage (Table 1). Mixed effects
274 models that included all tracks confirmed that maximum dive depths inside the eddy field
275 were significantly shallower than dives outside of this region as a result of both position
276 relative to the eddy field and day-stage (Table 2). The effects of day-stage were stronger than

277 the eddy field on maximum depth, accounting for an estimated reduction of 149.30 ± 1.71 m.
278 In terms of dive durations, diving within the eddy field had a stronger effect than day-stage,
279 resulting in an estimated 6.37 ± 0.26 min reduction. Little variability in maximum depth
280 (5.5%) or dive duration (8.4%) could be attributed to differences between individual seals,
281 with most variation common to the group (Table 3).

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

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

293 Nine individuals showed significant changes in the types of dives which they undertook
294 inside the eddy field. Within the eddy field, seven seals undertook more U- and fewer W-
295 dives while two seals undertook more W- and fewer U-dives. Percentage changes in O-dive
296 occurrence were low in comparison to changes in U- and W-dives for all but one individual
297 (PO043) whose proportional change in dive type use was low across all dive types. Four
298 seals' dive type choices changed by more than 10% within the eddy field.

299 **Discussion**

300 The southern elephant seals in this study showed a strong preference for dispersing south-
301 west from Marion Island during their post moult migrations (Figs 2, 4). Given the expansive
302 nature of these migrations, it appears that the seals were primarily traversing the region en
303 route to more distant, preferred foraging grounds (Jonker and Bester 1998; McIntyre et al.
304 2011; Tosh et al. 2012). Any foraging activity within the eddy field was therefore likely to
305 have been opportunistic, explaining the variation in individual responses. Nevertheless, the
306 potential biological relevance of the group response seems to be reinforced by the number of
307 individuals which dived more frequently within the region than expected.

308 Given that the adult female southern elephant seals from Marion Island appeared to dive
309 more often than expected within the eddy field, we predicted that these animals' maximum
310 dive depths, their dive durations and the dive types they preferentially used would also differ
311 within the region. The dives of female elephant seals tend to be shorter and shallower at night
312 than during the day, most likely in response to vertically migrating prey (McIntyre et al.
313 2011). For this reason, day-stage (day or night) was included in this study as a comparative
314 measure of biological importance.

315 Compared to female seals from Peninsula Valdés and Macquarie island (Hindell et al. 1991;
316 Campagna et al. 1995), female southern elephant seals from Marion Island dive both deeper
317 and longer (McIntyre et al. 2011). It is likely that the increased depth and duration pushes the
318 animals closer to their physiological limits (Hindell et al. 2000). This extreme diving
319 behaviour of Marion Island elephant seals, combined with their relatively short lifespans
320 (rarely extending past 12-14 years at Marion Island) (de Bruyn et al. 2009), prompted
321 McIntyre et al.'s (2010) "deeper diving-shorter life" hypothesis.

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

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

335 Because of the small changes in O-dive occurrence in both the group and individual results,
336 biological importance of dive type choice was based on changes between U- and W-dives.
337 Given their dominance during elephant seal migrations, U-dives are necessarily associated
338 with both travelling and exploration (McIntyre et al. 2011). Furthermore, accelerometry data
339 gathered from jaw and head movements suggest that, like W-dives, U-dives also appear to
340 include foraging components (Gallon et al. 2013; Naito et al. 2013). U-dives however lack
341 the uniform wiggles of W-dives. The observed reduction in underwater wiggles may imply
342 less searching and more targeted foraging of prey items trapped by an eddy's density
343 boundaries. This in turn suggests a change in prey type or foraging strategy within the eddy
344 field region. Alternatively, the increase in U-dives within the eddy field may indicate an
345 increase in travelling, along with reduced foraging. Nevertheless, W-dives with their diurnal
346 patterns made up almost 24% of the within-eddy field dives. W-dives are associated with

347 foraging for prey which undertake daily vertical migrations (Hindell et al. 1991). The high
348 proportion of this dive type suggests that these prey items were still important foraging
349 targets within the region. Characteristic differences between dive types suggest that the
350 reported proportional changes in type choice seem likely to have important impacts for a
351 number of individual seals.

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

358 **Energetics**

359 Before the female seals embark on their post-moult migrations they undergo an energetically
360 costly moult accounting for around 10.8% of their annual energy budget (Boyd et al. 1994).
361 During this period Marion Island's females lose on average 34% of their body mass (Postma
362 et al. 2013). Females from Marion Island are not only typically smaller, but also lose a
363 greater proportion of their body mass during their post-moult migrations, when compared to
364 their equivalents from King George Island, South Georgia or Macquarie Island (Postma et al.
365 2013). As a result, when the post-moult animals leave the island they are comparatively lean
366 and negatively buoyant as a result of their loss of fatty tissue. In these periods the seals are
367 able to glide to depth with their energy expenditure at a basal level, but require active
368 swimming to return to the surface, thereby expending more energy (Miller et al. 2012). On
369 their homeward leg the animals are generally carrying more fatty tissue and are more
370 positively buoyant as a result. In this state the seals' descents incur the costs of overcoming

371 their positive buoyancy, particularly during the initial parts of their dives (Williams et al.
372 2000; Miller et al. 2012). Elephant seals tend to approach neutral buoyancy mid-migration,
373 expending smaller amounts of energy during both diving and surfacing, thereby minimising
374 their cost-of-transport (Miller et al. 2012) .

375 Female seals from Marion Island tend to encounter the eddy field area during the early stages
376 of their outward- and late stages of their homeward post-moult migration legs. As a result,
377 dives in the region are likely to have occurred when the animals were close to the extremes of
378 their buoyancy states, increasing the energetic costs associated with their dives (Miller et al.
379 2012).

380 On the one hand, these findings highlight the potential value to Marion Island's female post-
381 moult elephant seals of being able to potentially access prey items during less energetically
382 costly shallower and shorter dives. These savings may be compounded by a switch to more
383 efficient foraging techniques within the eddy field. However, the increased energetic costs
384 incurred by the elephant seals' buoyancy states may themselves partially account for the
385 significant maximum depth reduction in half of the seals, with the significantly shorter dives
386 undertaken by 80% of the seals as well as the switch from W- to energetically less costly U-
387 dives by 70% of the animals within the eddy field. Based on these findings, we propose that
388 the occurrence of energetically expensive W-dives could peak during stages of seal
389 migrations when the buoyancy of seals are closest to neutral and their vertical drift rates
390 approach zero. This hypothesis however requires further investigation in order to articulate
391 cost of transport costs associated with W-dives, foraging success attributed to different dive
392 types, as well as any other factors which may influence dive type choices.

393 **Conclusions**

394 Interactions between the ACC and the SWIR to the south-west of Marion Island generate an
395 enhanced eddy field (Ansorge and Lutjeharms 2005). Previous research showed how
396 southern elephant seals target eddies for foraging (Campagna et al. 2006; Bailleul et al. 2010;
397 Dragon et al. 2010), suggesting that elephant seals might exploit the eddy field upstream of
398 Marion Island. In order to investigate this question, dive metrics from Marion Island's post-
399 moult female southern elephant seals were statistically evaluated within and outside of the
400 eddy field. Dive behaviours appear to change within this region, with the seals diving more
401 frequently within the eddy field. Dive parameters within the eddy field suggest potential
402 energy savings as well as possible changes in foraging strategies in comparison to those
403 outside of the region.

404 Comparing the southern elephant seals from Marion Island's dive parameters outside vs
405 inside the eddy field suggests that the region may be an energetically inexpensive area in
406 which to forage. In light of the historic and projected effects of climate change on the ACC
407 and its frontal systems, the eddy field may be spawning an increasing number of warm core
408 anticyclonic features as the SAF shifts further south (Gille 2002). Potential direct effects of
409 changes in the character of the eddy field on the far ranging animals remain unclear.
410 However, if efficient, opportunistic foraging within the eddy field plays a role in the decision
411 of the seals to leave Marion Island in a generally south-westerly direction then regional
412 climate mediated changes may indirectly alter the elephant seals' dispersal patterns via
413 changes in the nature of the eddy field. Future investigations could benefit from using newer
414 biologging technologies (e.g. jaw accelerometers and/or cameras) to better inform the likely
415 use of the eddy field for foraging purposes by southern elephant seals from Marion Island.

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605

606 **Figure captions and Tables**

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

611 **Fig. 2** The position of Marion Island (white circle) in relation to South Africa, Antarctica, the
612 sub-Antarctic front (SAF), the Antarctic Polar Front (APF) and the Polar Frontal Zone (PFZ).
613 The eddy field is demarcated by the shaded rectangle. Black lines represent the 22 post-moult
614 migration tracks and dive locations referenced in this study. Frontal position estimates from
615 Swart et al (2008).

616 **Fig. 3** The position of Marion Island (white circle) in relation to South Africa, Antarctica, the
617 sub-Antarctic front (SAF), the Antarctic Polar Front (APF) and the Polar Frontal Zone (PFZ).
618 The eddy field is demarcated by the shaded rectangle. Black lines represent a 22 track subset
619 of the 10 000 outward leg correlated random walks with which the recorded dive locations
620 were compared.

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

623 **Online Resource 1:** Tagged post-moult female southern elephant seals from Marion Island
624 included in this study along with deployment ages, years, dates of the first dives, track
625 durations, numbers of recorded dives (excluding those within 30 min of sunrise or sunset).
626 Percentage of recorded, outward leg dives which occurred within the eddy field for the
627 10,000 CRW simulations as well as for the grouped and individual post-moult tracks (n=22)
628 of adult female southern elephant seals from Marion Island included in this study (n=16).
629 Significant differences between observed and predicted values are indicated by * ($p < 0.01$).

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

634

Figure 1

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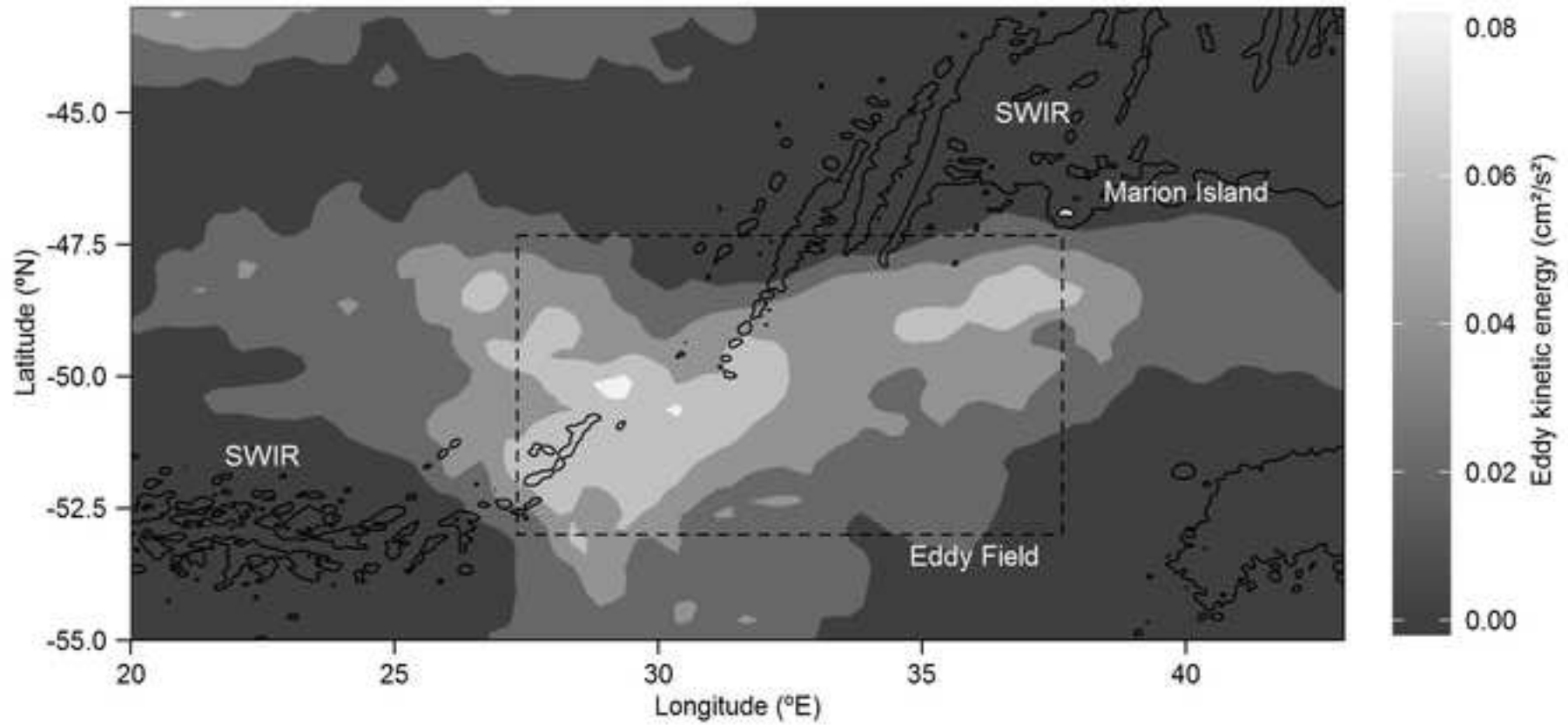


Figure 2

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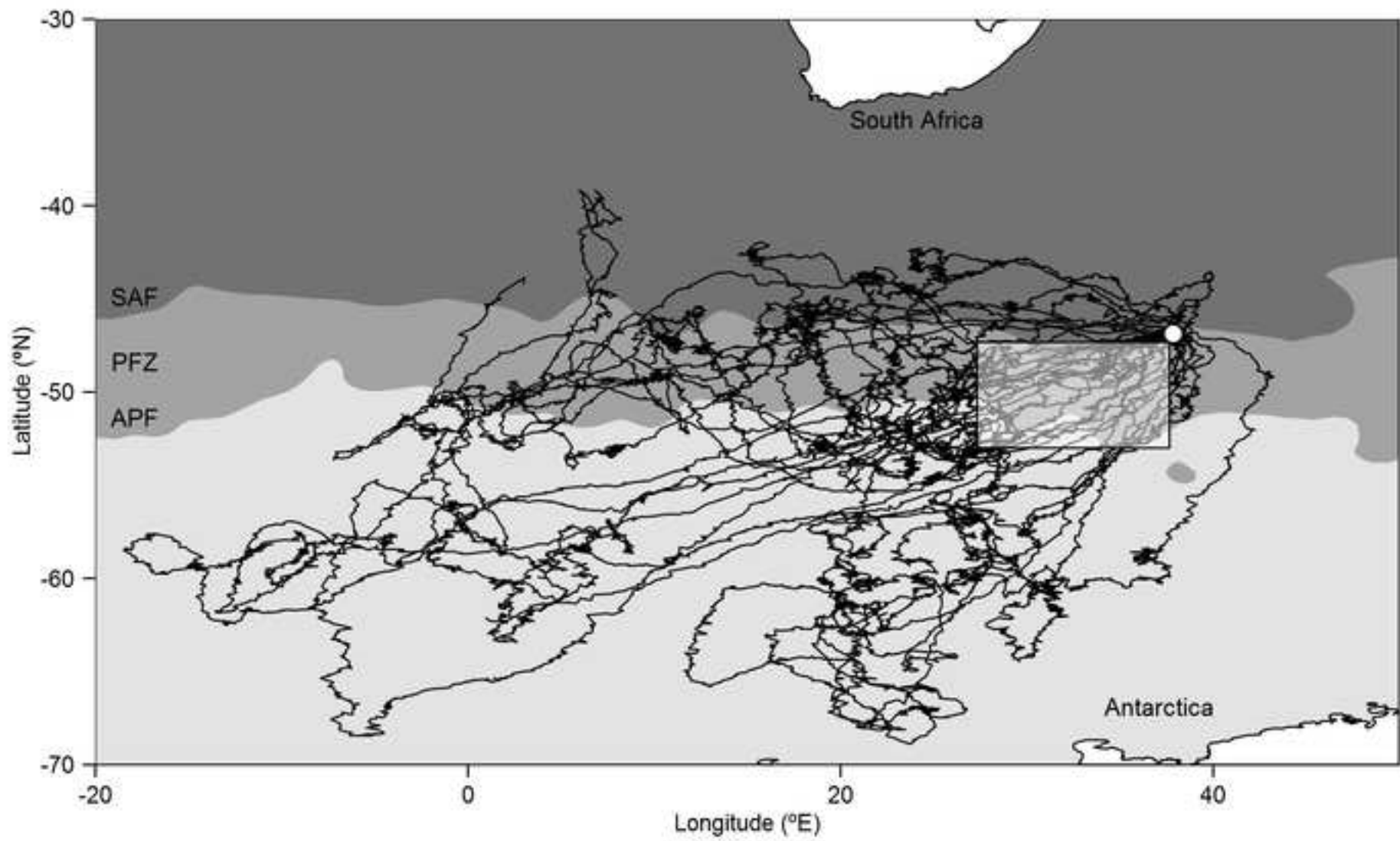


Figure 3
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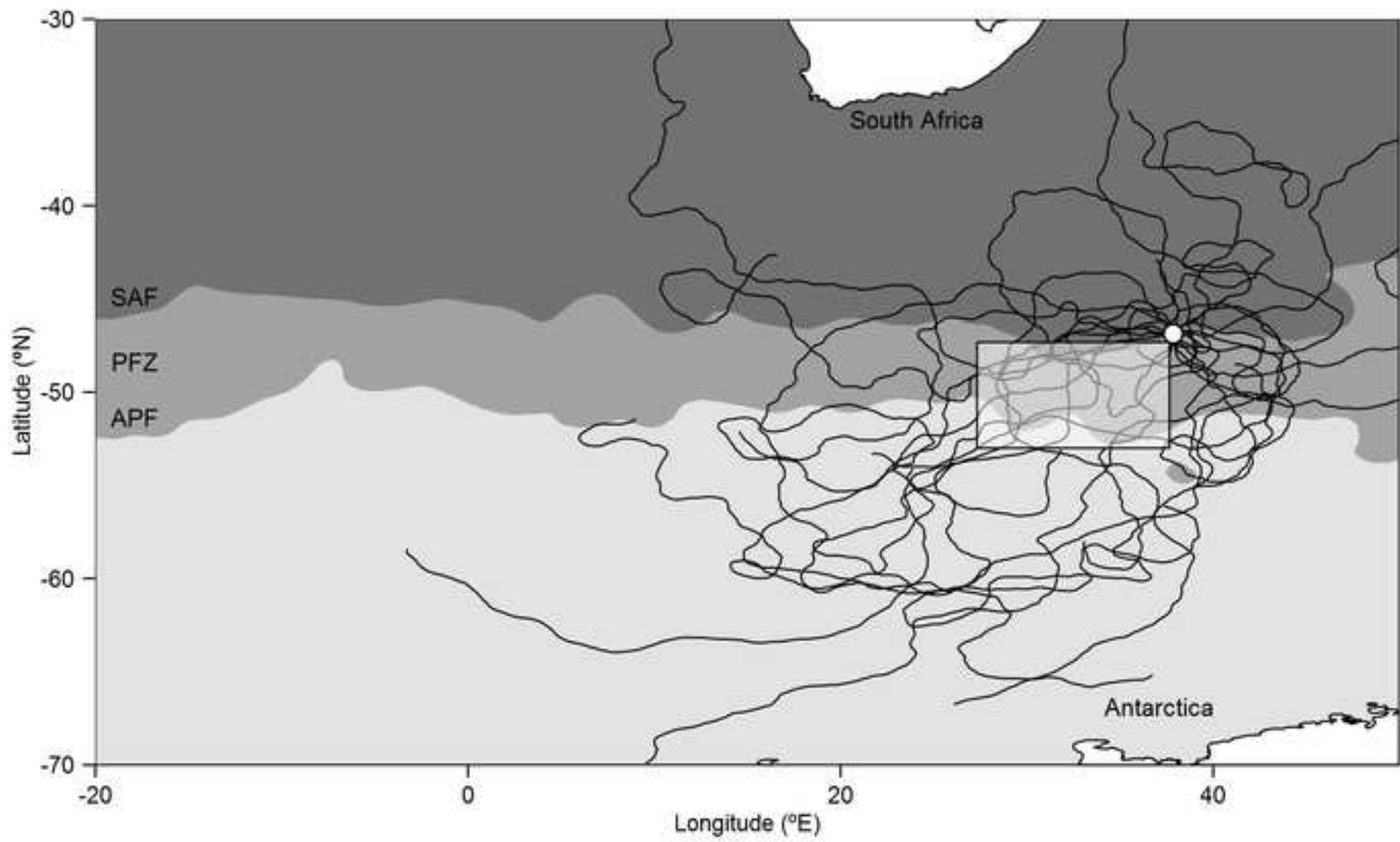


Figure 4

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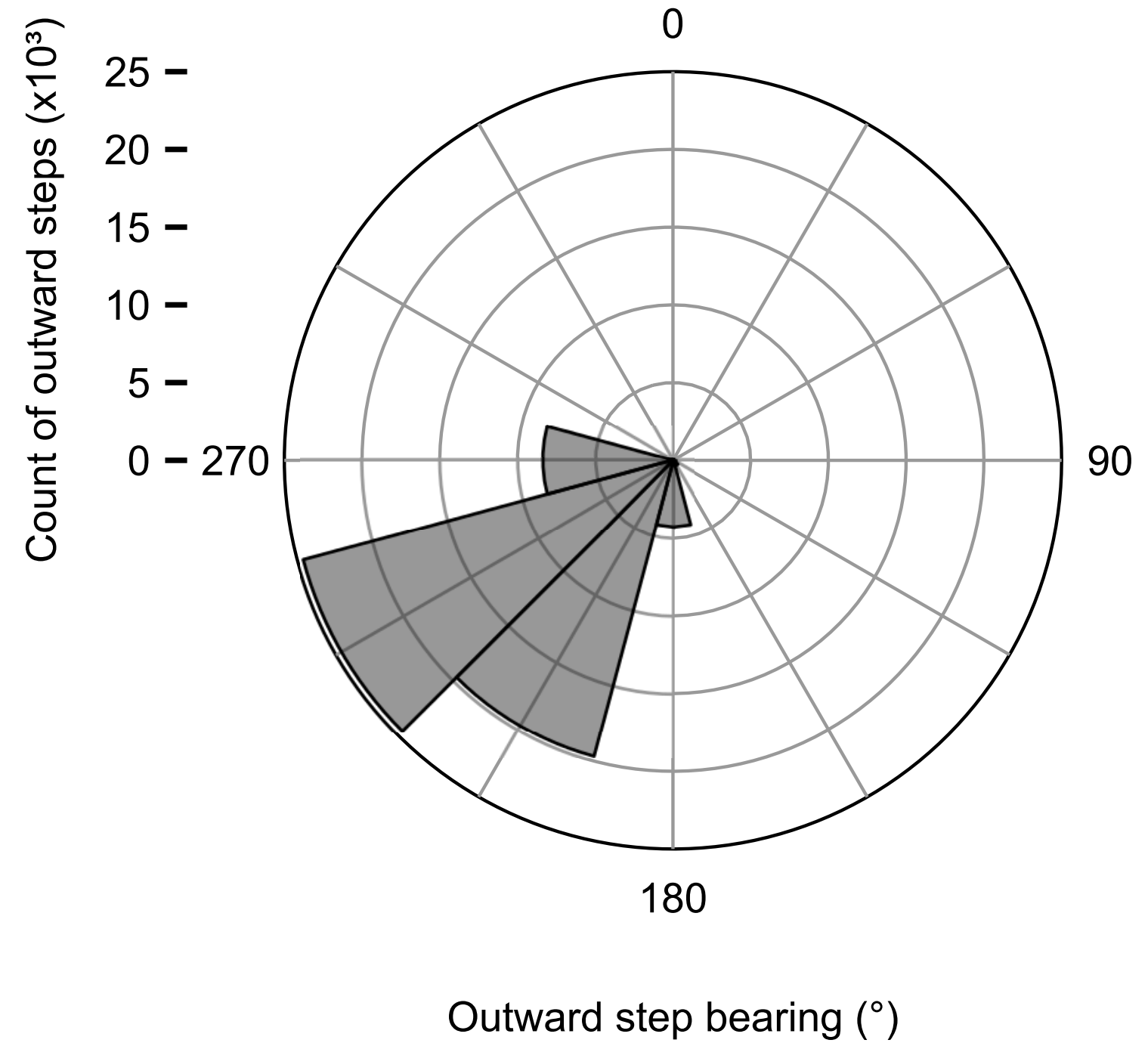


Table 1: Post-moult dive maximum depth and dive duration statistics for the adult female southern elephant seals from Marion Island which dived more frequently within the eddy field (EF) than predicted ($n = 9$) between 2008 and 2010. Values are grouped by position relative to the eddy field and day-stage (day or night).

Maximum depth (m)	Day dives (mean \pm sd)	Max (day)	Night dives (mean \pm sd)	Max(night)
Inside EF	520.34 \pm 158.81	1188.8	385.04 \pm 136.09	1128.8
Outside EF	575.28 \pm 171.52	1678.0	410.61 \pm 154.70	1486.0
Dive duration (min)				
Inside EF	23.88 \pm 9.87	88.25	20.80 \pm 9.12	73.25
Outside EF	32.93 \pm 12.11	95.25	26.31 \pm 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 \pm se)	DF	t-value	p-value
Inside EF	-44.33 \pm 3.00	65639	-14.77	< 0.01
Night	-149.30 \pm 1.71	65639	-87.40	< 0.01
	Dive duration (min \pm se)			
Inside EF	-6.37 \pm 0.26	65639	-24.25	< 0.01
Night	-5.86 \pm 0.10	65639	-57.60	< 0.01

Table 3: 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=9), during their post-moult migrations between 2008 and 2010.

	Variance ($\tau^2 \pm \text{SD}$)	Residual ($\sigma^2 \pm \text{SD}$)	Between seal variability
Maximum depth (m)	1407.48 \pm 37.52	24245.23 \pm 155.71	5.5 %
Dive duration (min)	9.37 \pm 3.06	102.68 \pm 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 *.

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

ESM 1

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ESM 2

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