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Horizontal Area-Restricted-Search and Vertical Diving Movements to Predict Foraging Success in a Marine Predator

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Abstract

With technical advances in wildlife telemetry, the study of cryptic predators' responses to prey distribution has been revolutionised. Considering marine predators, high resolution tagging devices were developed lately to collect long and precise diving datasets. In this study, we investigated, at fine temporal and spatial scales, changes in the horizontal movements and diving patterns of a marine predator, the southern elephant seal. Satellite tracking data collected on nine seals were processed with switching state-space models. Seals' body condition, as a proxy for foraging success, was estimated through changes in drift rate from Time Depth Recorder (TDR) data. We identified (1) statistically distinct behavioural modes along the

20 tracking data (intensive vs. extensive foraging modes) and (2) dive classes from the TDR diving
21 data (drift, exploratory, shallow active and deep active dives). Mass gain over the animals'
22 foraging trip was also linked with the proportions of intensive foraging zones and dive classes.
23 Active dives, associated with vertical foraging and chasing, were more numerous when the seals
24 were in intensive foraging mode. Improved body condition and mass gain of seals were also
25 associated with the occurrence of intensive foraging mode and, within the vertical dimension,
26 with sets of highly active dives. In conclusion, proportions of dive classes displayed by the seals
27 proved to vary according to their horizontal behaviour. The results allow us to conclude that
28 intensive foraging detected from surface tracking data is a good predictor of the diving activity
29 and foraging success occurring in the vertical dimension.

30 **Keywords:** area-restricted search, dive classification, drift dive, fine scale behaviour, movement
31 analysis

1 Introduction

Understanding the responses of predators to spatial and temporal variability of their prey distribution is fundamental for determining how animals may respond to global changes in their environment. The Southern Ocean is one of the most productive oceans (Smetacek & Nicol, 2005) and it has been shown that this circumpolar ocean has warmed more rapidly than the global ocean average (Gille, 2002). It has also been shown that winds over this ocean have strongly increased over the past few decades (Meredith & Hogg, 2006) causing an increase in eddy activity and number. This could have significant impacts on primary productivity (Le Quéré *et al.*, 2007) and hence on feeding opportunities for predators. Nonetheless, direct observations of how marine predators interact with their environment and their prey are very scarce. Because of the Southern Ocean remoteness, it is particularly challenging to obtain information on diet and the distribution of prey for long-ranging migrating species in those waters.

Acurate feeding indices are often difficult to obtain, and most studies instead use proxies such as changes in movement patterns and time spent within restricted areas (Weimerskirch *et al.*, 2007; Aarts *et al.*, 2008). Therefore, recent developments in animal-mounted loggers (Weimerskirch & Jouventin, 1990; Weimerskirch *et al.*, 2002) and indirect diet analyses (Bradshaw *et al.*, 2004) have significantly increased the amount of knowledge on cryptic marine predators' ecology. Especially, the recordings of predators' movements, diving behaviour and *in situ* oceanographic parameters have indirectly contributed in a better understanding of potential prey distribution otherwise difficult to observe.

By correlating movement patterns to environmental conditions, characteristics of the areas profitable for a predator can be revealed (Turchin, 1991). In various predator species, resource

57 acquisition has been linked to a type of free-ranging behaviour called the area-restricted search
58 (ARS) (Kareiva & Odell, 1987). In a prey-aggregated environment, such as in the open ocean,
59 an animal having already captured a first prey intensifies its foraging in the patch (Charnov,
60 1976; Parker & Stuart, 1976). Therefore, an ARS is characterised by a decrease in displacement
61 speed and an increase in the track sinuosity in areas with putative prey aggregation (Bovet &
62 Benhamou, 1988). Between two patches, the animal, on the contrary, travels more linearly and
63 at a faster pace. Natural environments are generally considered as hierarchical patch systems, in
64 which patches at small scales are nested in patches at larger scales (Kotliar & Wiens, 1990).
65 While foraging, predators often display movement patterns at multiple spatial and temporal
66 scales that are assumed to match the spatial structure of the hierarchical aggregations of prey
67 (Fauchald, 1999). Since predators likely adjust their foraging movements at small spatial scales,
68 especially within a dense patch, prey encounter rate is supposed to play a major role in
69 predator's foraging decisions. On the other hand, past experiences are expected to act mainly in
70 large-scale movements at a scale where prey distribution is more predictable (Hunt *et al.*, 1999).
71 With the latest technical advances in wildlife telemetry, it is now possible to examine
72 small-scale movements that are crucial to better understand scale-dependent adjustments of
73 long-ranging predators. By using high-precision locating system (GPS, Weimerskirch *et al.*
74 (2002)) together with high-resolution behavioural recorders (Time Depth Recorders (TDR)
75 Charrassin *et al.* (2001), stomach temperature sensors Austin *et al.* (2006)), it is now possible to
76 accurately study foraging decisions. However, to understand the effects of environmental
77 variability on foraging success of marine predators and, ultimately their fitness increase,
78 requires not only at-sea movement analyses, but also some method of identifying where and
79 when the animals actually improve their body condition.

80

81 Considering diving predators, buoyancy has been proved to directly depend on the animals'
82 body condition (Webb *et al.*, 1998; Aoki *et al.*, 2011). As a predator feeds and increases its body

83 condition, the relative proportion of adipose tissue increases thereby increasing its buoyancy
84 (Robinson *et al.*, 2010). Therefore, a predator species that performs dives during which the
85 animals drift passively in the water column can be considered as an ideal study model to inform
86 on *in situ* buoyancy *in situ* (Biuw *et al.*, 2003). Travelling thousands of kilometres per year in
87 the circumpolar waters of the Southern Ocean (McConnell *et al.*, 1992), southern elephant
88 seals, *Mirounga leonina*, are elusive marine predators that can spend as much as 85% of their
89 lifetime at sea (McIntyre *et al.*, 2010). They continuously dive during their extended stay at sea
90 and display behaviours qualified of “drift dives” along their track (Crocker *et al.*, 1997). They
91 regularly perform those dives during which they stop swimming and drift passively in the water
92 column (Biuw *et al.*, 2003; Mitani *et al.*, 2010). Vertical movements during these dives were
93 shown to be related to the seal’s body condition (Webb *et al.*, 1998): fat and positively buoyant
94 seals will follow an upward drift. Inversely, lean seals with negatively buoyant body condition
95 will sink during a drift dive. An increase in the drift rate over time is therefore an index of a
96 successful foraging activity (Biuw *et al.*, 2007; Bailleul *et al.*, 2007b; Thums *et al.*, 2008;
97 Robinson *et al.*, 2010). Although there are potential errors in the estimation of foraging success
98 from drift rate, they generally lead to an underestimation of the energy gain and foraging
99 success (Robinson *et al.*, 2010). Southern elephant seals represent therefore a unique
100 opportunity for studying, *in situ*, links between the foraging behaviour and the individual’s body
101 condition.

102

103 Horizontal foraging behaviour, from track-based analyses of low-resolution surface tracking
104 data, has been studied in detail (Bailleul *et al.*, 2008). However, southern elephant seals spend
105 little time at the surface between each dive (Hindell *et al.*, 1991) and feed on deep-ranging prey
106 (Cherel *et al.*, 2008). In addition, previous studies could only integrate the diving behaviour by
107 using indices estimated from low-resolution dive profiles (four depth-time points per dive, Biuw
108 *et al.* (2003); Bailleul *et al.* (2007a)). Recent studies have focused on the fine scale vertical

109 behaviour which is more likely to respond directly to prey abundance (Thums *et al.*, 2011).
110 However, fine scale vertical as well as horizontal foraging behaviour remain poorly known
111 which limits our understanding of the seals' responses to the variability in prey distribution.

112

113 In the Southern Ocean, mesoscale features, such as fronts and eddies, have been shown to have
114 a significant impact in structuring and enhancing primary productivity (Bakun, 2006). They are
115 likely to influence the spatial structure of prey patches and play a key role in the formation of
116 profitable foraging areas for oceanic predators (Bost *et al.*, 2009). The interfrontal zone,
117 between the Polar Front (PF) and the Subtropical Front (STF, see Figure 1), is especially
118 dynamic with locally productive eddies that are rich in prey. Within the Kerguelen population,
119 Bailleul *et al.* (2010a) work suggests that over two thirds of the southern elephant seal females
120 forage in the interfrontal zone. It is therefore likely to be a key habitat where those predators
121 interact with spatially and temporally heterogeneous oceanographic features (Dragon *et al.*,
122 2010). In this study, we used high resolution tracking and diving data to investigate fine-scale
123 temporal and spatial changes in horizontal movements and diving patterns of female elephant
124 seals in the interfrontal zone. We expected a good correspondence between the areas of
125 intensive foraging identified from horizontal tracking data and the areas with high proportions
126 of foraging dives, as determined from TDR data. Finally, using drift rate as a physiological
127 proxy of foraging success, we expected to monitor the gain or loss in the seals' body conditions
128 and to relate it with the observed diving behaviour.

2 Material & Methods

2.1 Logger Deployment

In October 2009, nine post-breeding southern elephant seal females, all about the same mass (296 ± 26 kg) and length (236 ± 14 cm), were captured on the Kerguelen Islands ($49^{\circ}20'S$, $70^{\circ}20'E$). They were anaesthetised using a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100) which was injected intravenously (McMahon *et al.*, 2000). Data loggers were glued on the head of the seals, using quick-setting epoxy (Araldite AW 2101), after cleaning the fur with acetone. Four seals were equipped with satellite-GPS loggers in combination with satellite-Argos and archival data loggers (MK10 Fast-Loc, Wildlife Computers, Washington, USA). MK10 devices transmitted Argos location data and collected GPS location data. To save battery life, the sampling interval of GPS locations was set to a minimum of 20 minutes, i.e. slightly shorter than the average dive duration of the species (Hindell *et al.*, 1991). The additional logger, Time-Depth Recorder (TDR), included in the MK10 devices collected and archived pressure and temperature levels every two seconds. Five other seals were equipped with Fluorometry - Conductivity - Temperature - Depth Satellite - Relayed Data Loggers (termed Fluo-CTD-SRDLs, designed and manufactured by the Sea Mammal Research Unit, University of St Andrews, Scotland) combined with MK9-TDR loggers (Wildlife Computers, Washington, USA). Fluo-CTD-SRDLs devices allowed the calculation and transmission of tag positions estimates of Argos quality. The MK9 devices combined with each Fluo-CTD-SRDL were set to sample and archive pressure and temperature levels every two seconds. After locating their respective haulout beaches via Argos locations, returning females were recaptured, weighed and loggers were retrieved.

151 **2.2 Tracking data and identification of horizontal foraging behaviour**

152 The GPS and Argos seal tracking data were both analysed with state-space models in order to
153 detect areas of restricted search (Jonsen *et al.*, 2003; Patterson *et al.*, 2008; Schick *et al.*, 2008;
154 Block *et al.*, 2011). Argos locations were first estimated using the observation model of a
155 switching-state-space model in order to take into account measurement errors (Jonsen *et al.*,
156 2003). Following preliminary studies based on the movement parameters distributions (not
157 displayed here), we used two behavioural modes for the analyses. The state-space models also
158 estimated the probability of being in a particular behavioural mode (intensive foraging, that is
159 when ARS behaviour is displayed, vs. extensive foraging, when the animal travels at a faster
160 and more linear pace) along the animals' paths (for details see Jonsen *et al.* (2007); Block *et al.*
161 (2011)). GPS tracks were analysed the same way: the switching state-space models discerned
162 two behavioural modes within the location data. All models were fitted with freely available
163 software *WinBUGS* (Bayesian Analysis Using Gibbs Sampler, Spiegelhalter *et al.* (1999)) called
164 from *R* (R Development Core Team, 2009) with the package *R2WinBUGS* (Sturtz *et al.*,
165 2005). As recommended by Dennis (1996), we used vague priors (Gamma and Uniform
166 distributions). Two Monte-Carlo Markov Chains (MCMC) were run for each model, with
167 50000 iterations following a 25000 burn-in (thin=2).

168 As female southern elephant seals from Kerguelen population are known to forage mostly in the
169 pelagic waters of the interfrontal zone (Bailleul *et al.*, 2010b; Dragon *et al.*, 2010), we focused
170 on the pelagic part of the tracks after having applied a bathymetric mask (1000 m depth from
171 Etopo mask 2' (NGDC, 2001)) to exclude all locations on the Kerguelen and Crozet plateaux,
172 and hence all benthic dives.

2.3 Diving Behaviour and dive classification

The following diving variables were derived from MK9 and MK10 TDR data (Table 1):

maximum depth, descent and ascent speeds, bottom-time duration (where the bottom phase

starts at the end of the descending phase and finishes at the beginning of the final ascent to the

surface) and bottom-time residuals (residuals of multiple regression of

$bottomtime \sim maximumdivedepth + diveduration$ Bailleul *et al.* (2008); calculated for each

dive within a path) and vertical sinuosity in the bottom phase (Equation 1, derived from

Weimerskirch *et al.* (2007)).

$$BottomSinuosity = \frac{BottomDistance_{observed}}{BottomDistance_{euclidean}} \quad (1)$$

where $BottomDistance_{observed}$ is the total vertical distance swum in the bottom of the dive,

and $BottomDistance_{euclidean}$ is the sum of the Euclidean distances from the depth at the

beginning of the bottom to the maximum depth and from the maximum depth to the depth at the

end of the bottom phase.

Vertical sinuosity takes a value of 1.0 when the animals swims in a straight path at the bottom of

its dive. Any deviation from a straight path increases the sinuosity value. The horizontal

distance travelled during each dive was also estimated from linearly interpolated GPS tracking

data. Drift dive identification was processed from the complete time-depth (TDR) data in 3

steps. (1) Instantaneous vertical speed was calculated from the time-depth data. (2) Vertical

speed was then smoothed by using a moving average filter (10 seconds window) in order to

compensate for abrupt changes in depth reading due to the sensor accuracy ($\pm 1m$). (3) Within

dives, drift phases were isolated using a custom-made function under R software (R

Development Core Team, 2009). Drift phases were detected as periods of time of more than 3

minutes during which the vertical speed was bounded between $[-0.6; 0.6]m.s^{-1}$ and with a low

variance ($s^2 < 0.005$) (for more details see the annotated R codes in the supplementary

196 material). For each drift dive, a drift rate was determined as the slope coefficient of a linear
197 regression between depth and time (Biuw *et al.*, 2003; Bailleul *et al.*, 2007a; Mitani *et al.*,
198 2010). Daily averaged drift rates were calculated for the 3-month tracks.
199 Following a preliminary analysis of diving behaviour (Table 1) and a literature review (Hindell
200 *et al.*, 1991; Schreer *et al.*, 2001; Hassrick *et al.*, 2007), four dive classes displayed by the seals
201 in pelagic waters were determined. A k-mean classification was then applied on the normalised
202 Principal Component Analysis (PCA, in this study with 4 principal components) scores from
203 the behavioural variables of all individuals in the pelagic part of their tracks (Forgy, 1965).
204 Transition matrices including the probabilities of dive class changing were then estimated. The
205 daily proportions of each dive classes for each individual were also calculated. Linear mixed
206 models, with individual as random effect, were used to evaluate the daily proportions of dive
207 class in intensive foraging vs. extensive foraging areas detected from the tracking data (in R,
208 nlme library from Pinheiro & Bates (2000) with REML method). Models' assumptions were
209 verified and no autocorrelation nor heterogeneity of variance of within-group residuals was
210 noticed (Pinheiro & Bates, 2000).

211 **2.4 Detection of successful foraging areas with drift rate increases and** 212 **mass gain models**

213 Positive variations of drift rate are supposed to indicate an improvement of the seal's body
214 condition and buoyancy (Crocker *et al.*, 1997; Biuw *et al.*, 2003). We used increases in drift rate
215 as a physiological index of successful foraging activity along the seals' tracks. The overall drift
216 rate increase was calculated as the difference between the mean drift rate over the last 10% of
217 the track, hereafter referred as the final drift rate, and the one over the first 10% of the track.
218 Final drift rate before the animal's hauling out and percentage of time spent in intensive
219 foraging were also considered. Finally, we also calculated the respective proportions of the four

220 dive classes while the animal was displaying intensive, or extensive, foraging behavioural mode.
221 For all individuals, mass gain (kg) over the foraging trip was related, using linear models, to
222 overall drift rate, final drift rate and the proportions of dive classes while in intensive foraging.
223 In the end, we used linear models to estimate the mass gain from multiple regressions of the
224 variables listed above. Model selection was based on Akaike Information Criterion (AIC,
225 Akaike (1973), with a correction for small sample sizes Burnham & Anderson (2002)) to find
226 the best linear model (Venables & Ripley, 2002).

227 **3 Results**

228 **3.1 Statistics of the horizontal tracking data**

229 Argos tags transmitted in average (*mean* \pm *s.d.*) 6.86 ± 4.31 locations per day whereas GPS tags
230 collected an average of 38.28 ± 10.57 daily locations. The 9 animals equipped for this study
231 spent an average of 79 ± 6 days at sea with 69 ± 9 days in the pelagic area. They covered an
232 average of 4399 ± 622 km, including 3822 ± 763 km in pelagic waters (Figure 1). All but one
233 individual foraged exclusively within the interfrontal zone east of Kerguelen Island. The last
234 one went to the western interfrontal zone, near Crozet plateau. Individual seals dived on average
235 64 times per day which is consistent with the literature (Boyd & Arnborn, 1991). This provided
236 5059 ± 700 dives, per seal, of which 4529 ± 909 were in pelagic waters. From the state-space
237 model analysis, seals displayed two statistically distinct behavioural movement modes:
238 intensive, which corresponds to the display of ARS behaviour, and extensive foraging. Intensive
239 foraging mode was estimated on average during 33 % of their time ($33 \pm 12\%$; 28 ± 8 days)
240 including in pelagic waters (23 ± 9 days).

241 **3.2 Characterisation and localisation of the dive classes**

242 For all individuals, four dive classes were detected and defined as: drift, exploratory,
243 shallow-active and deep-active dives. The biological meanings of the dive classes will be
244 discussed in detail in the first part of the discussion. Characteristics of the four dive classes are
245 illustrated in Figure 2 and Table 2. Although their relative proportions varied, with for instance
246 deep active dives being more numerous by day than by night, all dive classes were observed by
247 day and night time (Figure 2b). Drift dives were the least sinuous in the bottom (Figure 2d),
248 presented the longest bottom time durations (Figure 2a,c) and low horizontal distances (Figure
249 2f). While “drift-diving”, the animals displayed low descent (Figure 2e) and ascent speeds
250 (Figure 2d) and performed this class of dive at average depths (Figure 2c and Table 2). On the

251 contrary, deep active and shallow active dive classes exhibited high sinuosity ratio during their
252 bottom phases (Figure 2d). The deep active dive class was the most sinuous of all dive classes.
253 Both shallow and deep active classes also exhibited high descent and ascent speeds (Figure
254 2d,e). Deep active dive presented also the lowest horizontal distance travelled between two
255 dives of this class (Figure 2f). Finally deep active dive class was also characterised by negative
256 bottom-time residuals that is bottom times lower than expected. Considering the exploratory
257 dive class, they were characterised by large horizontal distance (Figure 2f), medium vertical
258 sinuosity at the bottom of the dives (Figure 2d) and low descent speed (Figure 2e). Figure 3a
259 presents the typical profiles of the four dive classes.

260 The proportions of dive classes along the pelagic part of the individual tracks are presented on
261 Table 3. Deep active dives represent the majority of the dives along the animal path (46.1 % in
262 average) while shallow active and exploratory dives are the second and third classes with
263 respectively 31.3% and 14.9% of the dives. Finally, drift dives are sparsely displayed (7.7%).
264 The combination of deep and shallow active classes (from now on referred as active dives)
265 represents over three quarters of the whole set of dives (77.4 %). All dive classes occurred all
266 along the tracks (Figure 3b). On the other hand, observed probabilities of dive class changing
267 from dive at time t to dive at time $(t+1)$ revealed a high temporal persistence, i.e. temporal
268 auto-correlation, in the animals behaviour and a hierarchy in the dive classes activity (Table 4).
269 An animal displaying a shallow active dive is more likely to continue displaying this class of
270 dive or to change most likely for a deep active dive or an exploratory dive.

271 **3.3 Combining horizontal foraging behaviour identified from tracking data** 272 **to fine scale vertical behaviour**

273 The most parsimonious linear mixed model on the daily proportions of shallow active dives
274 showed a positive intercept ($intercept = 42.11 \pm 5.42$, $p.value = < 0.0001$), a negative link with

275 the daily horizontal distance travelled ($slope(Hor.Dist) = -0.26 \pm 0.03$, $p.value = < 0.0001$)
276 and a positive link with the intensive foraging mode ($slope(ARS) = 5.32 \pm 2.35$, $p.value =$
277 0.02). Furthermore, the most parsimonious linear mixed model on the daily proportions of drift
278 dives showed a positive intercept ($intercept = 5.91 \pm 1.28$, $p.value = < 0.0001$), a positive link
279 with the proportions of shallow dives ($slope(Shallow.Active) = 0.03 \pm 0.01$, $p.value = 0.03$)
280 and with the intensive foraging mode ($slope(ARS) = 1.37 \pm 0.73$, $p.value = 0.05$). Figure 4(a,
281 b) confirm the variations of proportions of the four dive classes between the 2 behavioural
282 movement modes detected on the tracking data: extensive (a) and intensive (b) foraging. The
283 proportion of exploratory dives almost doubles in extensive foraging areas compared to
284 intensive ones. Meanwhile, drift dives number is reduced nearly 50% in extensive foraging
285 areas. The proportion of deep active dives remains identical while the proportion of shallow
286 active dives increases with the intensification of the foraging behaviour. Therefore, the
287 proportion of active dives, combination of deep and shallow active dives, is more important in
288 intensive foraging areas than in extensive ones.

289 **3.4 Mass Gain related to an increase in drift rate and active dives**

290 Mass gain ranged from -60 to 120 kg (Figure 5) and was positively related to four variables.
291 The overall change in drift rate along the track, referred as the gain in drift rate
292 ($\rho = 0.83$, $p.value = 0.006$, Figure 5a), and the final drift rate ($\rho = 0.78$, $p.value = 0.013$,
293 Figure 5a) were positively related to the mass gain. The proportion of time spent in intensive
294 foraging ($\rho = 0.67$, $p.value = 0.049$, Figure 5b) and the proportion of active dives realised
295 while the animal was in intensive foraging ($\rho = 0.80$, $p.value = 0.009$, Figure 5b) were also
296 positively related to the mass gain. The drift rate gain was the variable best correlated with mass
297 gain. The model selection, based on small sample size corrected AIC, that applied to the
298 multiple regressions (table 5) highlighted the most parsimonious model: $Mass\ Gain \sim Drift$
299 $Rate\ Gain$ ($AICc = 65.99$, $R^2 = 0.685$, with $slope = 708.26 \pm 181.54$ and

300 *intercept* = -110.75 ± 42.82). It is to be noted that the second most parsimonious is: Mass
301 Gain \sim Drift Rate Gain + Proportion Active Dives in ARS ($AICc = 69.47$ and $R^2 = 0.728$).

302 **4 Discussion & Perspectives**

303 In this study, we showed that intensive foraging detected from surface tracking data is a good
304 predictor of the diving activity and foraging success occurring in the vertical dimension.

305 Previous studies have shown that southern elephant seals display several dive classes during the
306 pelagic parts of their foraging trips (Hindell *et al.*, 1991; Schreer *et al.*, 2001; Thums *et al.*,
307 2008). However, only few studies linked the fine scale diving patterns with the horizontal
308 movements detected from high resolution tracking data e.g. Thums *et al.* (2011). Our results
309 suggest that proportions of active dives are more important when seals are displaying
310 area-restricted search behaviour than when they are extensively foraging. Our study also
311 highlights that the mass gain over the animals' foraging trip is positively correlated to the gain
312 in drift rate and to the proportions of active dives and intensive foraging detected from tracking
313 data.

314 **4.1 Characterisation and ecological role of dive classes**

315 In the pelagic waters of the interfrontal zone, all individuals displayed four distinct dive classes.
316 For all individuals but one (09-78524, Table 3), the drift dives were the least abundant dives. As
317 first mentioned by Hindell *et al.* (1991), drift dives occurred in bouts generally in the early
318 hours of the morning and are thought to be resting and/or food processing dives (Crocker *et al.*,
319 1997; Mitani *et al.*, 2010). For some individuals, we also noticed a high occurrence of drift
320 dives after long sets of deep active dives (results not shown). Thums *et al.* (2008) observed a
321 tendency of positively buoyant seals to display upwards drift phases in their foraging dives
322 leading to their misclassification as drift dives. Because our study was based on post-breeding

323 foraging trips that are much shorter (ca. 2 months) than post-moulting ones (ca. 8 months), only
324 one seal reached positive buoyancy. Therefore, misclassification of the dives was not
325 problematic in our study.

326 High sinuosity, corresponding to wiggle displays in the bottom phase, combined with a
327 maximisation of the time spent at the bottom of the dive (i.e. high descent and ascent speeds)
328 can be associated with intensively active foraging (Fedak *et al.*, 2001). Both deep and shallow
329 active dives are very abundant, occur in bouts or series and generally have a uniform depth
330 within a bout. Finally, deep active dives were characterised by negative bottom-time residuals
331 corresponding to dives with short bottom duration in regards to their maximum depths. Large
332 vertical sinuosity, fast descending and ascending speeds combined to negative bottom-time
333 residuals highlight the very high energetic demand of this dive class. Shallow active dives
334 presented slightly positive bottom-time residuals that is a longer time than expected at the
335 bottom phase which was presented in previous studies as a proxy for intensive foraging
336 (Bailleul *et al.*, 2007b). Considering the time spent at the bottom, female elephant seals seem to
337 display a trade-off between foraging intensity and depths at which foraging occurs. Since
338 bottom-time residuals are calculated with a linear multiple regression (Bailleul *et al.*, 2007b,
339 2008), it seems plausible that at deep depths, where the deep active dives occur, the relation
340 between dive duration and maximum depth changes. The inflexion of this relation would
341 therefore lead to the sign inversion observed in bottom-time residuals between the deep and
342 shallow active dives. In shallow active dives, seals would optimise their efficient hunting time in
343 maximizing the proportion of time spent at the bottom of their dives where prey may be
344 encountered, hence displaying positive bottom-time residuals (Schreer *et al.* 2001). While
345 deep-diving, the seals' abilities for bottom-time adjustment, on the contrary, are reduced by
346 long descending and ascending durations. In the end, both active dive classes are likely to
347 represent intensive foraging activity as square dives were described in previous studies on
348 various diving predators (LeBoeuf *et al.*, 1988; Hindell *et al.*, 1991; Schreer & Testa, 1996;

349 Fedak *et al.*, 2001; Schreer *et al.*, 2001; Hassrick *et al.*, 2007). Therefore, the vertical sinuosity
350 at the bottom was an important predictor of the dive class as speed and depth were in other
351 classification studies on southern elephant seals (Hindell *et al.*, 1991; Thums *et al.*, 2008).
352 Exploratory dives exhibited large horizontal distances and low bottom time residuals. These
353 dives are thought to be travelling dives because the seals dive at average depths, without
354 displaying much wiggle activity (low sinuosity in the bottom), with low-speed descent and
355 ascent phases and potentially travelling in a straight direction (high horizontal distance). All
356 these characteristics also describe the V-shape dives detected in previous studies (Schreer *et al.*,
357 2001).
358 Although southern elephant seal females from Kerguelen forage mainly in pelagic waters
359 (Dragon *et al.*, 2010; Bailleul *et al.*, 2010b), it has been shown that females of this species can
360 dive and forage over continental shelves (Hindell *et al.*, 1991). In this case, they can interact
361 with different oceanographic conditions and display other foraging behaviours resulting in
362 additional dive classes. As a result, our data correspond to a subset of the dive classes spectrum
363 displayed by foraging seals. All seals in this study were females, so additional work on the
364 fine-scale diving behaviour of males is needed.

365 **4.2 Association of horizontal foraging patterns with vertical behaviour and** 366 **overall successful foraging**

367 Our results indicate that southern elephant seals display ARS over 30% of their time spent at sea
368 and mainly within pelagic waters. From previous tracking studies, southern elephant seals are
369 known to be predators that prospect continually within and between prey patches (Bailleul
370 *et al.*, 2008; McIntyre *et al.*, 2011). This may be especially true for pregnant phocid females
371 that exhibit a capital-breeding strategy. Phocids accumulate energy stores prior to fasting during
372 month-long hauling-out for parturition or moult (Berta *et al.*, 2006). Between fasting periods

373 during parturition and moult, pregnant southern elephant seal females, on their 3-month
374 post-breeding foraging trip, potentially optimise their foraging to recover from breeding and
375 prepare the next energetically demanding period of hauling-out. All seals in this study showed a
376 large proportion of active dives that occur all along the pelagic parts of the tracks by day and
377 night time. This confirms that seals are foraging and probably feeding all along their tracks and
378 that the typical intensification of their search in a zone may therefore correspond to encounters
379 with high quality prey patches. Seals were also found to modify their proportions of dive classes
380 according to the movement behavioural mode: while intensively foraging, the active dive
381 classes were more represented, e.g. most energetically demanding dives (high vertical sinuosity
382 and high ascent speed). The adjustment between intensive and extensive foraging behaviour
383 was not observed on the proportion of deep active dives but on the shallow active ones. From a
384 physiological point of view, numerous deep dives that require intense foraging activity could be
385 too demanding in terms of recovery time (Costa *et al.*, 2004) as suggested by the fact that sets of
386 deep active dives are followed, for some individuals, by sets of drift dives. Therefore, the
387 proportion of deep active dives in intensive and extensive foraging areas (ca. 45%) could be an
388 average threshold of southern elephant seals' ability to dive deeply and actively without
389 energetic pay-off (Davis *et al.*, 2001; Costa *et al.*, 2004).

390 Regarding the existence of two active dive classes, differences in their proportions were
391 observed between day and night. But since deep and shallow active dives are both displayed
392 during day and night time, a diel pattern cannot be the only explanation for their display.
393 Besides diving physiology, a combination of biologic and oceanographic reasons can explain the
394 existence of two distinct types of active dives. Previous studies have shown that female southern
395 elephant seals feed on myctophids in the interfrontal zone (Ducatez *et al.*, 2008; Cherel *et al.*,
396 2008). Myctophids are bioluminescent cryptic fish and their habitat is highly dependent on light
397 level (Widder, 2010). They adjust their habitat depth according to the light intensity and display
398 not only nycthemeral migrations but also migrations in the water column depending on the local

399 light attenuation (e.g. depending on the particles concentration in the surface water layers, cloud
400 cover, moonlight intensity etc.). Furthermore, the pelagic waters of the interfrontal zone include
401 a variety of water masses (subtropical, subantarctic, polar water masses etc.) that host different
402 prey species for southern elephant seals. The variety in prey, and their respective habitats,
403 potentially drives different foraging behaviours. Interfrontal zones are major components in
404 terms of biological production and are frequently populated with intense mesoscale eddies
405 (Bakun, 2006). Vertical movement of water masses associated with cold-core eddies can induce
406 isopycnal shoaling that is likely to influence prey behaviour, driving upward migrations to
407 remain at preferred densities and temperatures (Wiebe, 1982). Cold water and high biomass in
408 the surface layers may cause a decrease of luminosity contributing to the presence of the cryptic
409 myctophids species at shallower depths (Flierl & McGillicuddy, 2002). Upward cold water
410 masses, often from cyclonic eddies' cores and anticyclonic eddies' edges (Bakun, 2006), have
411 been found to be preferential marine structures for foraging predators (Bost *et al.*, 2009; Bailleul
412 *et al.*, 2010b; Dragon *et al.*, 2010). Female southern elephant seals were shown to clearly
413 intensify their diving effort and decrease their diving depth in rich upwelling areas (Dragon
414 *et al.*, 2010). Therefore, the existence of two active dive classes can be interpreted as a direct
415 adaptation to the highly dynamic and heterogeneous pelagic waters where the seals forage.
416 On the other hand, the increase of shallow active dives in areas of intensive foraging likely
417 highlight the increased accessibility of prey in the water column as observed in previous studies
418 (Dragon *et al.*, 2010). In cyclonic cores and anticyclonic edges where myctophids migrate to
419 shallower depths, we can therefore expect the seals to display higher proportions of shallow
420 active dives. Proportions of drift dives also varied accordingly: while intensively foraging, the
421 seals displayed more drift dives. This could highlight their need, after displaying numerous
422 active dives, either for resting or for food processing (Biuw *et al.*, 2003). In contrast, when the
423 seals are extensively foraging and abundantly displaying exploratory dives, the diminution of
424 drift dive proportions suggests either a low energy consumption prospective mode adopted

425 during the exploratory dives or, simply, less need for food processing. Either way, the ultimate
426 proxy of the seals overall successful foraging, the mass gain, was significantly correlated with
427 the percentage of intensive foraging mode and of active dives while in intensive foraging: the
428 more numerous the active dives while intensive foraging, the more successful the foraging seals.
429 Although we worked on a 1-year sample, similar results were found on numerous post-moulting
430 and post-breeding tracks of northern elephant seals by Robinson *et al.* (2010). It should finally
431 be noted that these significant correlations highlight the proxies' pertinence to predict, at the
432 track scale, the foraging success of seals. Our sample of post-breeding females was selected to
433 be homogeneous in mass and length so that the females could be supposed to have similar age
434 and amount of experience. All went to forage in the interfrontal zone but displayed, in the end, a
435 variety of mass gain, ranging from a loss of 60 kg to the gain of more than 100 kg in only 3
436 months. This high inter-individual variability in mass gain probably drives a fitness variability
437 related to inter-individual variations in foraging behaviour and/or differences in prey selection
438 (Field *et al.*, 2004, 2007). This confirms the importance of the individual foraging efficiency,
439 and past experiences, in this dynamic and unpredictable oceanographic environment (Hindell
440 *et al.*, 1999; Bradshaw *et al.*, 2004).

441 **4.3 Methodological perspectives**

442 Direct information on prey distribution remains very scarce in the Southern Ocean. Therefore,
443 identifying periods of intensive foraging appears to be an efficient way to investigate the prey
444 distribution of marine predators. Animal behaviour, in the horizontal and the vertical
445 dimension, can be modeled as a dynamic variable changing in relation to the animal's internal
446 state and/or its environment (Morales *et al.*, 2004; Jonsen *et al.*, 2007). Track-based analyses of
447 the fine scale vertical behaviour could be an interesting next step to investigate relationships
448 between seals behaviour and their environment. This could be used to systematically detect
449 behavioural transitions along the dive profiles, associate them with the animal's direct

450 surroundings and infer information on prey distribution.

451 On the other hand, there are difficulties of interpretation of 2-dimensional data (time and depth)
452 into a behaviour occurring in 4-dimensions (time-longitude-latitude-depth, Thums *et al.*
453 (2008)). Brillinger & Stewart (1997) have shown that a time-depth curve can actually
454 correspond to different possible 4D paths. We can therefore expect the same differences
455 between the observed horizontal trajectory (longitude-latitude) and the actual path of a diving
456 animal. Other studies have also questioned the validity of behavioural interpretations based on
457 dataset with reduced dimensions (Harcourt *et al.*, 2000; Davis *et al.*, 2003). New technological
458 devices, such as 3D-accelerometers and video cameras, are promising to solve those issues. In
459 free-ranging Weddell seals (*Leptonychotes weddellii*) for instance, studies using video
460 recordings have proved the encounter of prey within the foraging dives (Davis *et al.*, 2003). In
461 Weddell seals and also in captive Steller sea lions (*Eumetopias jubatus*), accelerometers were
462 able to precisely detect the mouth opening events linked with prey capture attempts (Naito
463 *et al.*, 2010; Viviant *et al.*, 2010). Such *in situ* recording devices will indicate the real
464 behavioural activity and also help to identify accurate 2-dimensional proxies of the foraging
465 effort. Uses of such new devices could therefore validate our findings on active dives being the
466 most successful foraging dives. It is our intention to examine this in future work.

467 **5 Conclusion**

468 Previous studies have shown that southern elephant seals display various behavioural modes
469 detected from tracking data (Bailleul *et al.*, 2008) and various dive classes during their foraging
470 trip (Hindell *et al.*, 1991; Thums *et al.*, 2008). Here we have shown that proportions of dive
471 classes displayed by southern elephant seal females varied according to their horizontal
472 behaviour. It is probable that by going to the polar frontal zone where resources are both
473 spatially and temporally highly variable, female elephant seals can concentrate their foraging

474 searching activity in the most productive parts of the zone and maximise feeding success. They
475 repeatedly adapt their diving behaviour to prey accessibility in the water column and seem to
476 display a trade-off between diving depth and recovery time. Mass gain over the animals'
477 foraging trip was also highly correlated to the proportions of intensive foraging detected with
478 track-based analyses. Improved body condition of seals was finally associated with the
479 occurrence, within the vertical dimension, of sets of highly active dives. The classification of
480 diving behaviour is not an end in itself, but rather a tool that allowed us to conclude that
481 intensive foraging detected from surface tracking data is a good predictor of the diving activity
482 and foraging success occurring in the vertical dimension. However, in changing environments,
483 the addition of fine-scale monitoring of *in situ* oceanographic conditions to high resolution
484 behavioural datasets is an interesting further step in research on foraging behaviour in relation
485 to prey distribution.

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Variable	Abbreviation	Definition	Source
Bottom-Time (mn)	Bott.Time	descent end to ascent start	TDR
Bottom-Time Residuals (mn)	Res.Bott.Time	residuals of multiple regression	TDR
Maximum diving depth (m)	Max.Depth	-	TDR
Sinuosity	-	derived from Weimerskirch <i>et al.</i> (2007)	TDR
Ascending Speed (m/s)	Asc.Speed	-	TDR
Descending Speed (m/s)	Des.Speed	-	TDR
Horizontal Distance (km)	Horiz.Dist	distance travelled between 2 dives	GPS

Table 1: Behavioural variables: unit, abbreviation name, definition and source.

	Drift	Exploratory	Shallow Active	Deep Active
N =	2846	6221	12482	17656
Bott.Time (mn)	15.8 ± 6.0	11.3 ± 4.8	13.2 ± 3.3	10.1 ± 3.6
Res.Bott.Time (mn)	2.6 ± 5.9	-0.6 ± 4.7	0.7 ± 2.8	-1.2 ± 3.2
Max.Depth (m)	424 ± 118	348 ± 156	324 ± 127	698 ± 131
Sinuosity	0.29 ± 0.05	0.35 ± 0.08	0.41 ± 0.06	0.52 ± 0.04
Asc.Speed (m/s)	1.21 ± 0.22	1.31 ± 0.24	1.77 ± 0.19	1.56 ± 0.15
Des.Speed (m/s)	1.18 ± 0.37	1.22 ± 0.27	1.74 ± 0.26	1.76 ± 0.25
Horiz.Dist (km)	0.98 ± 0.74	1.57 ± 0.67	1.20 ± 0.32	0.97 ± 0.54

Table 2: Characteristics of dive classes for all individuals. All differences, between the dive classes, are statistically significant ($p < 0.001$). Bott.Time stands for bottom time and Res.Bott.Time for bottom time residuals (both in minutes). Max.Depth corresponds to the maximal depth of the dive. Asc.Speed and Des.Speed stand respectively for ascent and descent speeds. Finally Horiz.Dist corresponds to the horizontal distance travelled by the animal during its dive estimated from the tracking data.

ind	N	%Drift	%Exploratory	%Shallow Active	%Deep Active	% Active
09-78524	2605	14.8	9.6	2.5	73.1	75.6
09-78525	4169	9.4	12.2	28.8	49.6	78.4
09-86372	5778	5.3	15.5	41.4	37.8	79.2
09-86373	4325	9.2	12.2	47.3	31.3	78.6
ft03-Cy1-09	4219	4.6	24.6	34.2	36.6	70.8
ft03-Cy2-09	4843	5.9	6.7	41.5	45.9	87.4
ft03-Cy4-09	4889	5.9	12.5	42.9	38.7	81.6
ft03-Cy5-09	5450	5.6	31.3	32.9	30.2	63.1
ft03-Cy11038-09	4485	8.1	9.8	10.2	71.9	82.1
all ind	40763	7.7 ± 3.2	14.9 ± 7.9	31.3 ± 15.4	46.1 ± 16.1	77.4 ± 7.0

Table 3: Proportions of dive classes for all individuals (%) equipped in October 2009. Only dives located in the pelagic part of the tracks were classified. Overall, inter-individual variability can be noticed. But deep active dives tend to always be the most important dive class and active dives, combined deep and shallow classes, represent for each individual over two thirds of the whole dives. Drift dive class rarely reach 10% of the whole dives.

Dive Class (t)	Drift (t+1)	Exploratory (t+1)	Shallow Active (t+1)	Deep Active (t+1)
Drift	0.70	0.12	0.05	0.13
Exploratory	0.06	0.60	0.19	0.15
Shallow Active	0.01	0.09	0.76	0.14
Deep Active	0.02	0.05	0.11	0.82

Table 4: Observed probabilities of dive class changing from dive at time t to dive at time $(t+1)$. High temporal persistence in the dive classes can be noticed and the second highest probabilities of dive class changing always correspond to the nearest dive class in terms of activity. Probabilities of changing reveal thus the hierarchy in the dive classes activity: an animal displaying a deep active dive is more likely to continue displaying this class of dive or to change for a shallow active dive and vice versa.

Model Formula	AICc
$MassGain \sim MassStart + DriftRateGain + FinalDriftRate + PropARS + PropActiveARS$	111.25
$MassGain \sim MassStart + DriftRateGain + PropARS + PropActiveARS$	87.27
$MassGain \sim MassStart + DriftRateGain + PropActiveARS$	75.61
$MassGain \sim DriftRateGain + PropActiveARS$	69.47
$MassGain \sim DriftRateGain$	65.99

Table 5: Model selection based on small sample sizes corrected AIC. The model with the smallest AICc is considered the best. The variable to explain is the gain in mass over the animal's foraging trip and the tested variables are: the animal mass when equipped before the post-breeding foraging trip (*MassStart*), the gain in drift rate over this trip (*DriftRateGain*), the final drift rate (*FinalDriftRate*), the percentage of intensive foraging mode in pelagic waters (*PropARS*) and the percentage of active dives displayed while the animal was in intensive foraging (*PropActiveARS*).

707 **Figure 1:** Physical oceanography in the Southern Indian Ocean and post-breeding foraging trips
708 of 9 female southern elephant seals equipped in October 2009 (solid black lines). Light grey
709 shading indicates depths less than 1,000 meters and depicts Kerguelen and Crozet plateaux. Îles
710 Kerguelen and îles Crozet coastline's contour are also indicated in white over the plateaux.
711 Dotted lines symbolized fronts (Orsi *et al.*, 1995), within the Southern Ocean: Southern
712 SubTropical Front (SSTF), Sub-Antarctic Front (SAF), Polar Front (PF) and Southern Antarctic
713 Circum-Polar Front (SACCF). In this study, we refer to the interfrontal zone as the area between
714 the STF and the PF. Locations of intensive foraging behaviour displayed by the seals are
715 indicated in dark grey dots over the tracks.

716

717 **Figure 2:** Characteristics of dive classes for all individuals: drift dives (dark green), exploratory
718 dives (light green), shallow active dives (yellow) and deep active dives (orange). (a) Variations
719 of bottom time residuals: drift dives are the longest dives while deep active present negative
720 bottom time residuals. (b) Proportion of dive classes by day and night times: all classes occur
721 by day and by night time. (c) Variations of maximum diving depth in function of bottom time:
722 depending on maximum depth distribution, time spent at the bottom of the dives varies from
723 one dive class to another. (d) Variations of sinuosity at the bottom of the dive in function of the
724 ascending speed: the higher the sinuosity, the more important the ascending speed.(e) For each
725 dive class, the density distribution of the descending speeds. The distribution similarity of
726 descending speed for the two active dive classes can be noticed meanwhile exploratory and drift
727 dives present low descending speeds. Finally, (f) distributions of the horizontal distance
728 travelled during the dives: in exploratory dives, seals tend to swim more rapidly in the
729 horizontal dimension than for the other dive classes. The dashed vertical lines indicate, for each
730 dive class, the average horizontal distance.

731

732 **Figure 3:**

733 (a) Typical Depth-Time profiles of the four dive classes. (b) Locations of the dives along the
734 seals' tracks. Orange dots correspond to deep active dives, yellow to shallow active, light green
735 to exploratory dives and finally dark green to drift dives. All dive classes occurred all along the
736 tracks, by day as well as by night.

737

738 **Figure 4:** (a) and (b) Proportions of dive classes in extensive parts (N = 15,081 dives) vs.
739 intensive foraging parts of the tracks (N = 11,463 dives). Combination of deep and shallow
740 active (hereafter referred as active classes) is more important in intensive foraging areas than in
741 extensive ones.

742

743 **Figure 5:** For all individuals, mass gain presented with (a): overall drift rate, final drift rate and
744 (b): percentage of time spent in intensive foraging and proportion of active dives realised in
745 intensive foraging. Lines correspond to the significant linear regressions between variables.

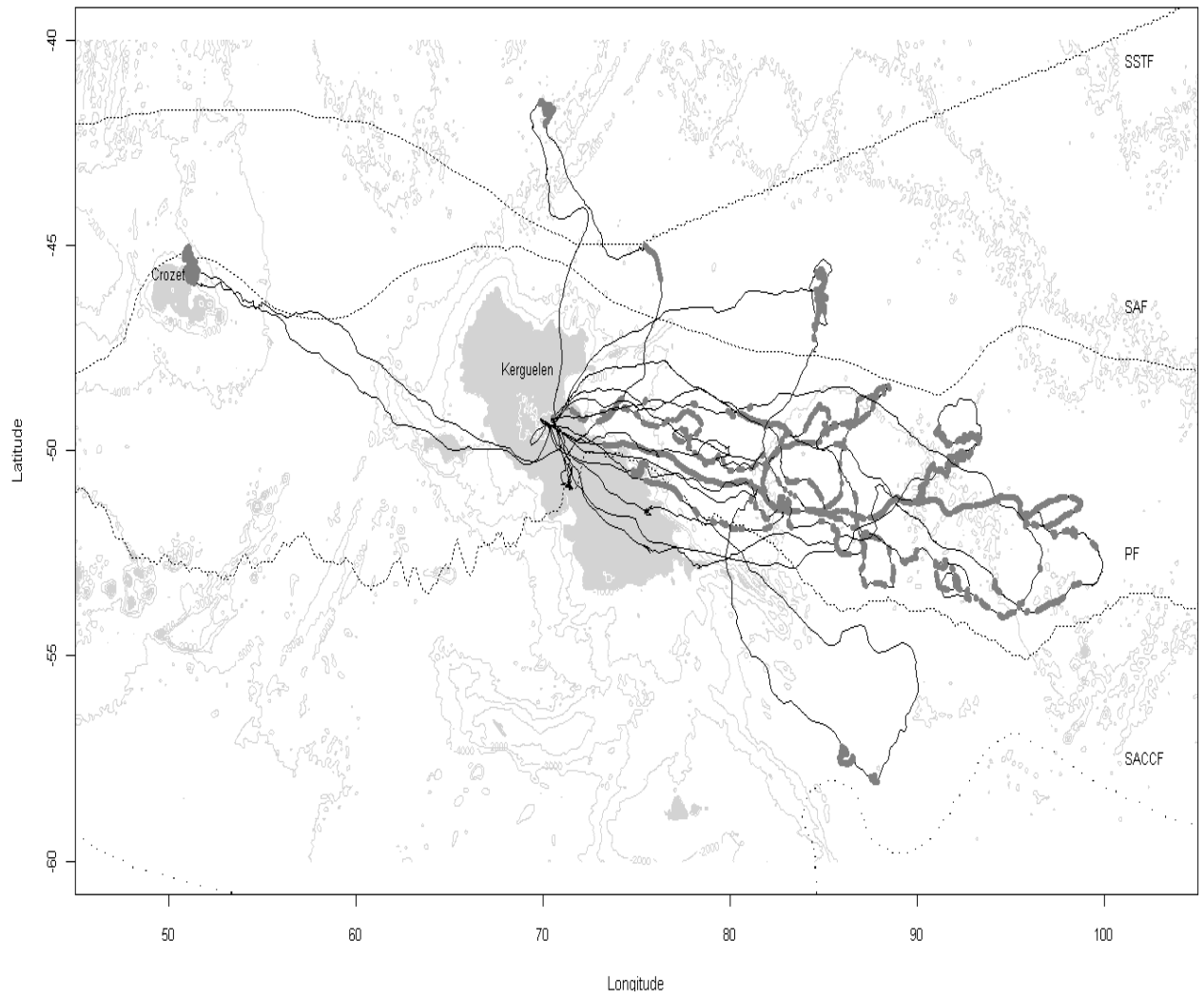


Figure 1:

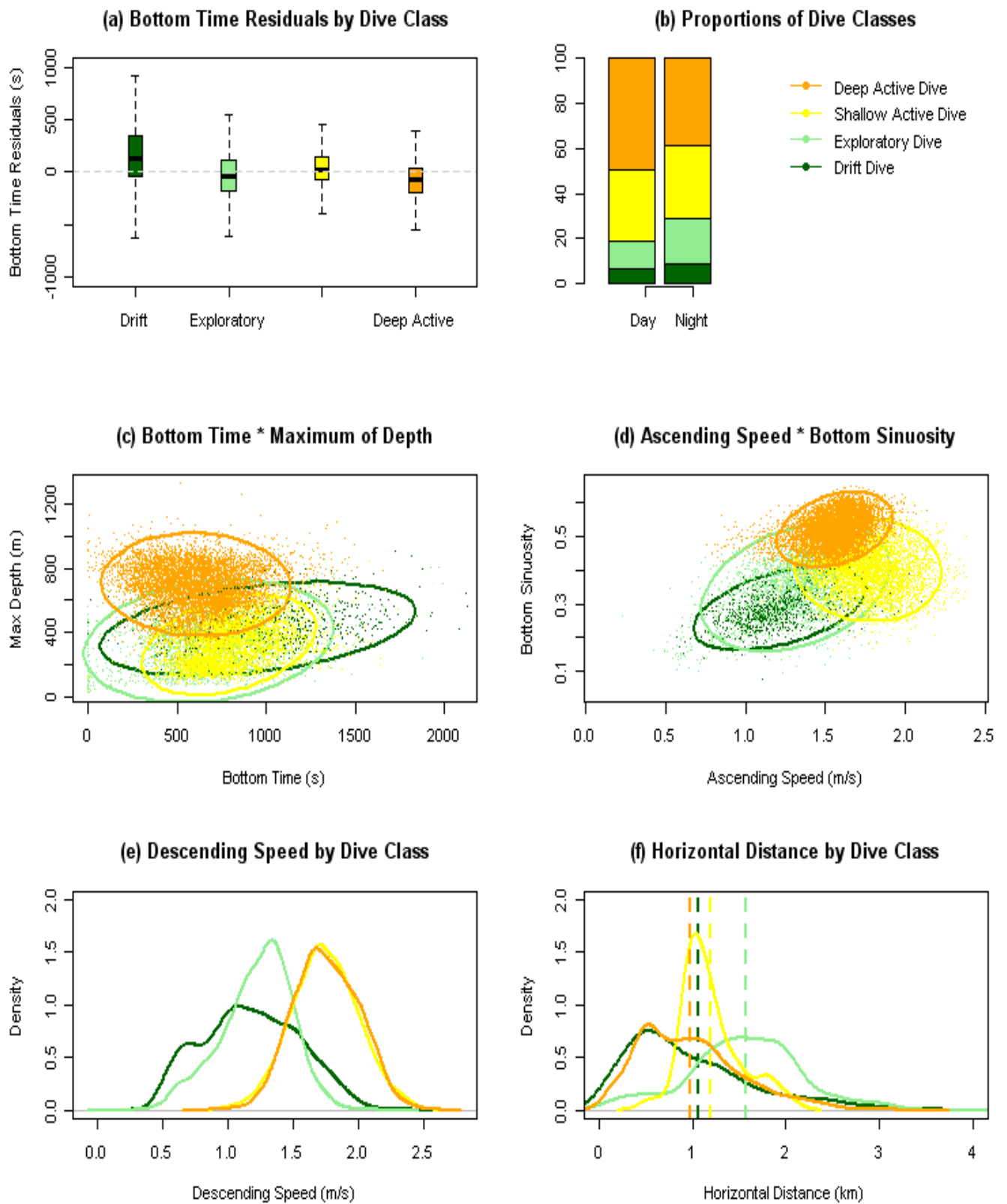


Figure 2:

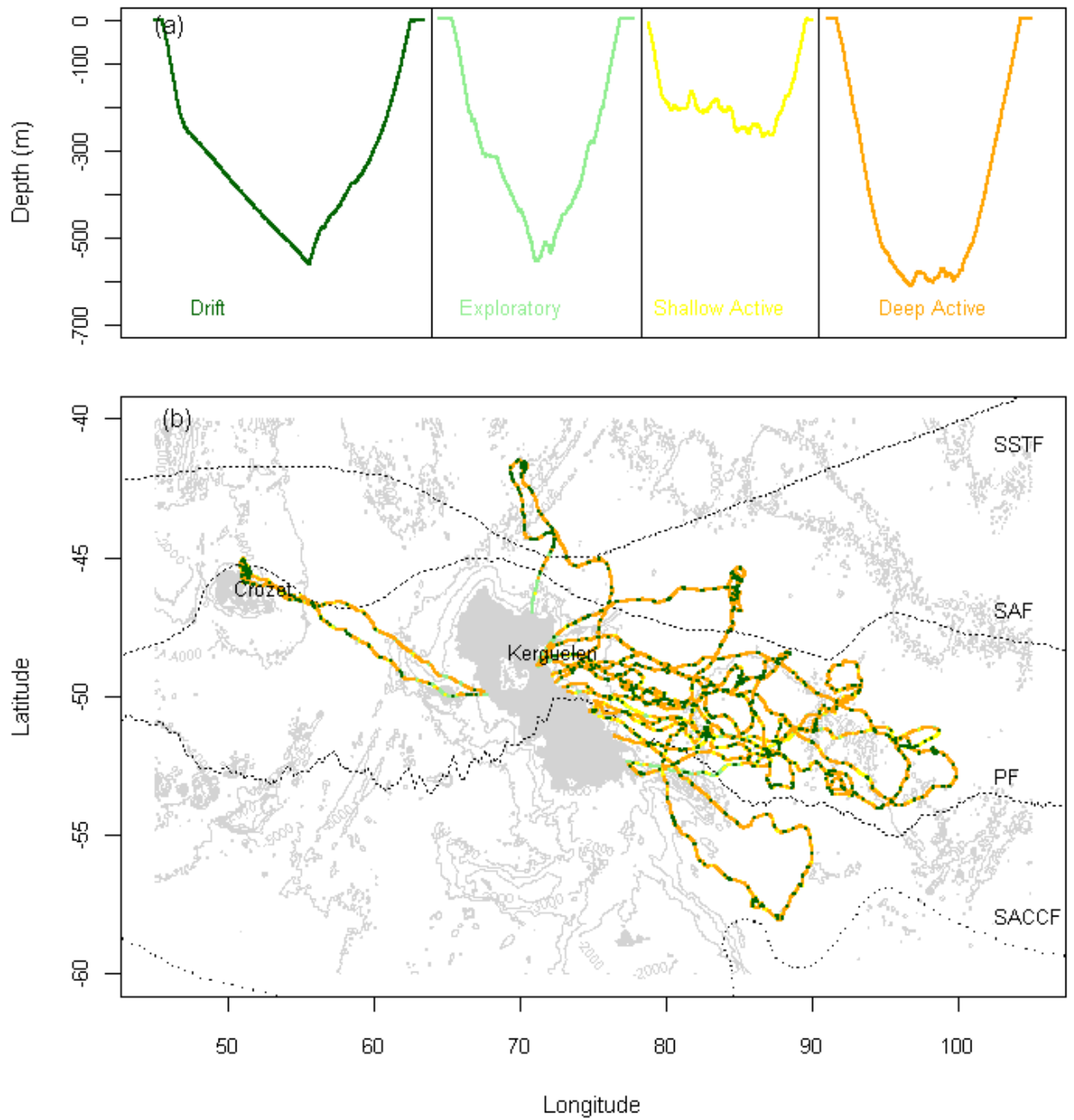


Figure 3:

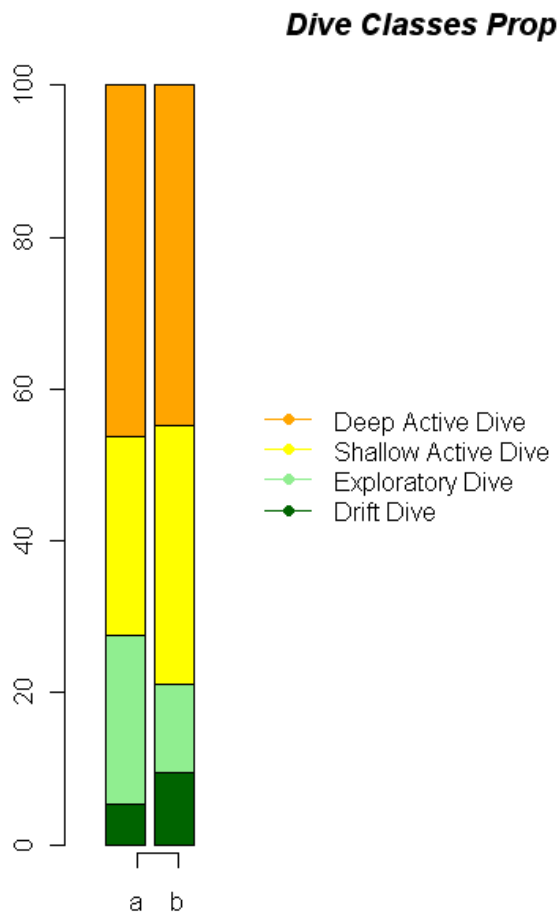


Figure 4:

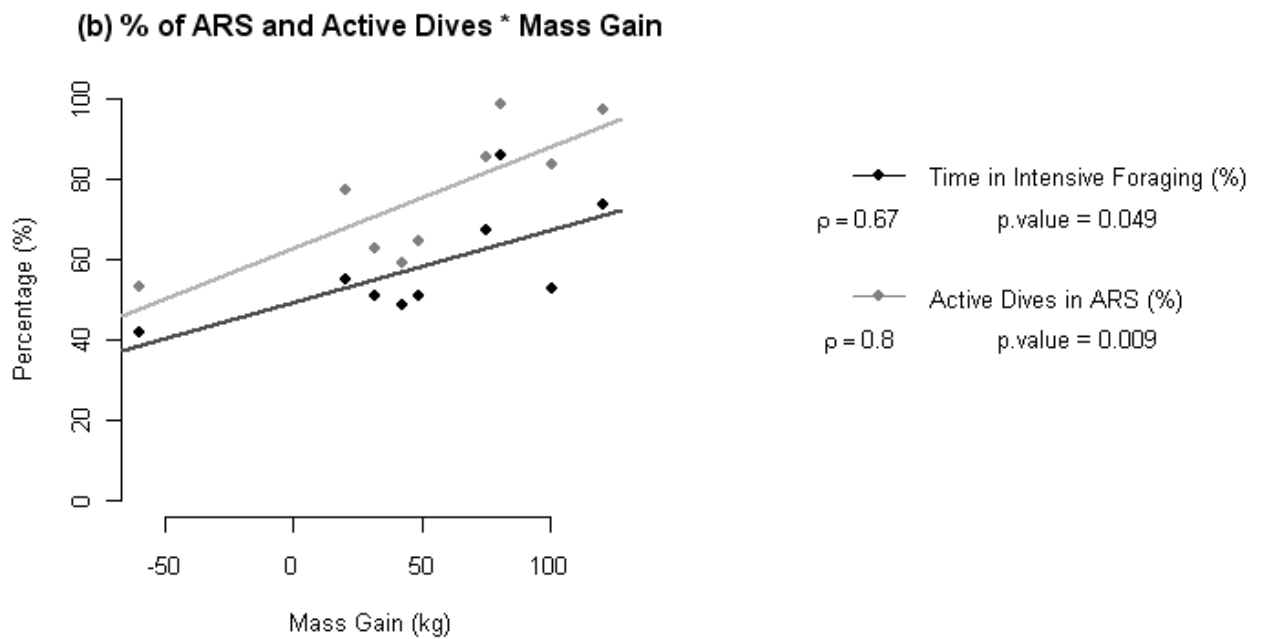
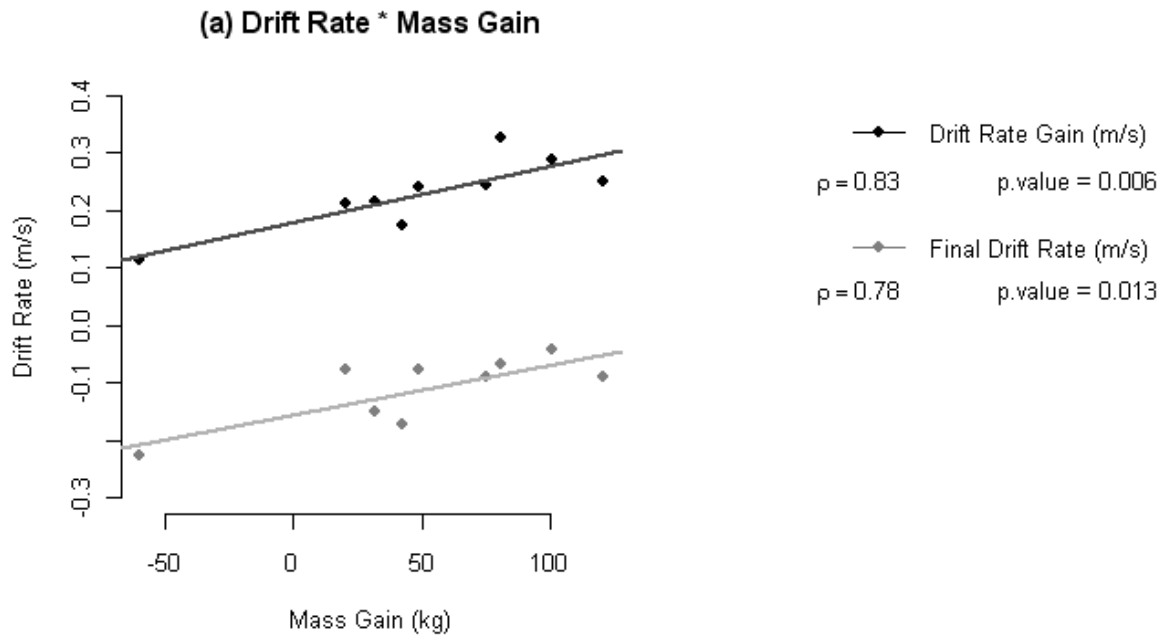


Figure 5: