

Title: Inter-population differences in diving behaviour of adult male southern elephant seals (*Mirounga leonina*).

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Abstract

This study elucidates some of the factors influencing the diving behaviour of male southern elephant seals from the King George Island (Isla 25 de Mayo) and Marion Island populations tracked between 1999 and 2002. Mixed-effects models were used to determine the influence of bathymetry, population of origin, body length (as a proxy for size) and individual variation on the diving behaviour of adult male elephant seals from the two populations. Males from King George Island and Marion Island showed differences in all dive parameters. Marion Island males dived deeper and longer (652.0 m and 34.00 min) than King George Island males (359.1 m and 25.50 min). King George Island males appeared to forage both benthically and pelagically whilst Marion Island males in this study rarely reached depths close to the seafloor and appeared to forage pelagically. Model outputs indicate that males from the two populations showed substantial differences in their dive depths when foraging in areas of similar bathymetry. Whereas dive depths were not significantly influenced by the size of the animals, size played a

significant role in dive durations, though this was also influenced by the population that elephant seals originated from. This study provides some support for inter-population differences in dive behaviour of southern elephant seals.

Keywords: Southern elephant seals; dive behaviour; adult males; inter-population variation; mixed-effects modelling, King George Island, Marion Island

Introduction

Southern elephant seals (*Mirounga leonina*) are important predators in Antarctic and sub-Antarctic food webs, mainly due to their large body size, associated high energy requirements, circumpolar distribution and large population sizes (McConnell et al. 1992). During their time spent at sea, elephant seals migrate long distances (up to 5,000 km) and dive to great depths, frequenting depths between ca. 400 and 900 m and sometimes even depths deeper than 2,000 m (Campagna et al. 1995; Malherbe 1998; Field et al. 2001; Muelbert et al. 2004; Tosh et al. 2009; McIntyre et al. 2010a).

Elephant seals from Marion and King George islands are exposed to very different environments during their foraging migrations. Seals from Marion Island tend to utilise ice-free, pelagic areas between the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF), with occasional migration tracks leading to the ice-edge of the Antarctic continent (Jonker & Bester 1998). Animals from King George Island tend to forage around the tip of and along the western side of the Antarctic Peninsula up to the Bellingshausen and Amundsen Seas, but some animals moved north-east towards South Georgia (females), as well as south-east into the Weddell Sea (adult

males) (Bornemann et al. 2000; Tosh et al. 2009). Southern elephant seals from Marion Island performed mainly pelagic dives in very deep water; with the exception of some adult males that use occasional benthic dives to exploit deeper water (McIntyre 2010a). Little information is available about the dive behaviour of elephant seals from King George Island, although Antarctic silverfish (*Pleuragramma antarcticum*) is considered to form a substantial part of their diet – suggesting pelagic diving at higher latitudes where this fish is common (Bornemann et al. 2000; Daneri & Carlini 2002).

This study attempted to elucidate some of the factors directly influencing the diving behaviour of male elephant seals from King George and Marion islands and to determine if inter-population differences exist in dive behaviour. We further aimed to test if observed differences in dive behaviour were inherent to the populations animals originate from, or if such differences were mostly a result of differences in water depth associated with diving locations.

Materials and methods

Instrumentation

Post-moult adult male elephant seals from King George Island (62°14'S; 58°40'W) and Marion Island (46°54'S; 37°45'E) (Table 1) were instrumented with Satellite-linked time-depth recorders (SLTDR) (SDR T-6 or T-10 devices Wildlife Computers, Redmond, WA, USA) in 2000 and 1999/2002 respectively. The devices were attached to the heads of immobilised seals using an epoxy resin and deployed according to the standard procedure outlined in Bornemann et al. (2000) and Ramdohr et al. (2001). Fifteen devices were deployed on animals at Stranger Point, King George Island in 2000, three of which were seals born at Stranger Point, as identified by

permanent branding marks (J11, J12 and J14). Fourteen (nine in 1999 and five in 2002) animals were instrumented at various localities on Marion Island including one seal that was tagged as a recently weaned seal (M03). This individual was later excluded from analysis due to a lack of dive related data. Detailed data related to the movements of the various animals included in this study are discussed elsewhere (Tosh et al. 2009; Tosh 2010). Only data resulting from devices that recorded most, if not all of the dive parameters for a period in excess of 30 days were analysed to ensure adequate representation of overall dive behaviour resulting in data sets of nine and four animals from King George Island and Marion Island respectively (Table 1).

Dive data were in a binned format, generating six-hourly histograms with predefined bins for depth and duration. Information obtained from all satellite-linked devices is stored in the PANGAEA data archive (www.pangaea.de).

Data Analyses

Tracks were visualised using ArcGIS 9.3.1 (ESRI 2009). Statistical analyses were done using R 2.11.1 (R Development Core Team 2010). A filtering algorithm (SDA filter) was used as outlined in Freitas et al. (2008) to eliminate data points of poor location quality and those that required unrealistic swim speeds ($\geq 3 \text{ m s}^{-1}$) and/or extreme turning angles resulting in unrealistic distances between successive localities (points creating angles smaller than 15° and 25° , with extensions in excess of 2,500 m and 5,000 m respectively). The dive data for each track was summarised to daily median values per individual track to attain the best estimate of each day's diving activity. We therefore calculated median daily dive depths (by summarising dive depth frequency data) and median daily dive durations, assuming that animals dived to the median depths specified for each depth bin, as well as for the median duration. All dive parameter values are reported as median (range) unless otherwise specified. Maps with bathymetry estimates of

the regions of interest (GEBCO Digital Atlas (GDA) (IOC et al. 2003)) were exported into ArcMap 9.3.1 (ESRI 2009) as gridded files and converted to raster format. The filtered daily track data were imported onto these maps to extract estimates of the bathymetry values for areas exploited by the animals, using the Spatial Analyst Tool.

Linear mixed-effects models were used to determine the influence of a number of variables on the selected dive parameters. Fixed effects included bathymetry (water depth), body length, and population of origin, while individual seal was included as a random effect. Dive depths of some animals from King George Island that targeted areas of shallower bathymetry (see results), would necessarily have been shallower than those recorded for other animals. We therefore restricted the model analyses to dives from both populations that were performed over regions with bathymetry estimates in excess of 2,000 m to allow for meaningful comparisons of behaviour in more similar environments. Backwards model selection, based on second order Akaike's Information Criterion (AIC) scores for small sample sizes (Burnham and Anderson 2002) was used to select final models. Various plot types were used to assess the fits of individual models (Pinheiro and Bates 2004). Autoregressive functions were incorporated into individual models to account for temporal autocorrelation inherent in the data (Pinheiro and Bates 2004; Crawley 2007). The proportion of the model variance determined by the random effect, in this case the individual animals, was determined using variance component analyses (Crawley 2007). Analysis of variance (ANOVA) was used to determine the significance of each of the fixed effects within final models.

Result and Discussion

Tracks

The movements of the various tracked animals included in this analysis are illustrated in Figs 1 and 2. Details pertaining to the spatial movements of all the King George Island animals in this study are discussed in depth elsewhere (see Tosh et al. 2009). Basic trip information is listed in table 1. Individuals J03 and J05 travelled to the Bransfield Strait, between King George Island and the Antarctic Peninsula (Tosh et al. 2009), while animals J13 and J08 both travelled towards the eastern side of Elephant Island (Fig. 1). Individuals J06 and J11 moved further afield into the region near the southern side of the Antarctic Peninsula. Individuals J09, J10 and J14, all travelled into the Weddell Sea (Fig. 1). Of the branded individuals, J11, J12 and J14, both post moult and post breeding trips were recorded for individuals J11 and J14.

The Marion Island animals migrated in various directions after departing from the island. Two individuals, M02 and M05, migrated in a westerly direction for a large proportion of their tracks, with individual M05 heading directly to the Shannon seamount but returning to Ile de l'Est in the Crozet Islands when transmissions ceased on the 17th of January 2003. M02 had also changed direction, heading eastwards, presumably to return to Marion Island when transmissions ceased on the 14th of July 2003. The remaining two individuals M06 and M04 both utilised an area north east of Marion Island in the vicinity of the Prince Edward Fracture Zone (PEFZ)

Dives

The differences observed in dive depths and durations between adult males from the two study populations (Fig 3a,b) (Table 1) are likely explained by them mostly being exposed to very different oceanographic and bathymetric environments (McIntyre et al. 2010a). Animals from King George Island often adopted benthic (though, not exclusively) foraging strategies in areas of relatively shallow bathymetry, resulting in shallower dive depths and shorter dive durations. The

males from Marion Island, however, mostly foraged in areas of very deep water and therefore displayed pelagic forage strategies. These dives were normally to deeper depths and for longer periods of time compared to those performed by the animals from King George Island (Fig 3b). Some seals from the King George Island population did, however, target areas of deep water as well, utilising pelagic foraging strategies. The differences observed in dive depths, particularly in relation to water depth, are suggestive of inter-population differences in dive behaviour which may be related to differences in diet for male southern elephant seals from different populations. Although the diet of elephant seals from Marion Island is completely unknown (Bester et al. 2011), it is unlikely to include *P. antarcticum* with its particular distribution in pelagic waters over the Antarctic continental shelf and the Antarctic Peninsula region (Gon und Heemstra 1990) where the diet of elephant seals from King George Island is reported to include this prey species (Daneri and Carlini 2002).

Model outputs

The final models selected for dive behaviour parameters (mean dive depth and mean dive duration) included three fixed effects, namely bathymetry, standard body length and population (Table 2). Bathymetry and the population of origin were identified as significant factors influencing the dive depths of animals, while only population of origin was identified as a significant effect on mean dive durations. The fit of all the final models chosen was improved by the inclusion of standard length as a fixed effect, even though standard length itself was not identified as a statistically significant factor. Individual variation accounted for a substantial portion of model variance for dive durations (28.5%).

Length provides an indication of body size which is thought to influence the ability of the animal to utilise deeper depths and thus a potentially unexploited prey source (Weise et al. 2010). Smaller animals have a lower capacity to dive for extended periods of time and thus body length may be an important predictor of dive duration (Hindell et al. 2000). Marion Island animals with standard lengths above that of the sample mean standard length had dive durations that were either longer or approximately equal to the sample median dive duration. The King George Island animals, however, did not show such a relationship. Large amounts of individual variation in the diving behaviour of elephant seals have been previously recorded for a number of elephant seal populations (Slip et al. 1994). Individual differences were observed for the amount of time they engage in foraging and searching behaviours, with large amounts of variation often exhibited between age classes, body sizes and sexes (Hindell et al. 1999; Field et al. 2004; Dragon et al. 2010; McIntyre et al. 2010b). The model outputs in the current study also demonstrate the effects that individual variation may have on the at-sea behaviour of elephant seals, particularly the durations of dives (Table 1).

Mixed model outputs suggest that the differences observed in dive depths and durations for pelagic dives in the two populations are largely a consequence of the population of origin, with Marion Island males diving deeper and for longer periods of time, even when in areas of similar water depths as males from King George Island. The nature of the recorded data did not allow for more behavioural inferences, though additional investigations taking oceanographic conditions into account may further clarify difference in foraging strategy between the populations. McIntyre et al. (2010a) suggested that the Marion Island elephant seal population may carry significant physiological costs associated with continual deep diving behaviour, potentially resulting in slightly shorter reproductive lifetimes in this population compared to others. This

study provides some support that Marion Island elephant seals tend to dive deeper and for longer times than males from some other populations, such inter-population differences in dive behaviour may be indicative of differing diets, as well as foraging costs, of male southern elephant seals. Detailed demographic and diet information, as well as more data on the depth use of animals from both these populations are required to further test the hypothesis that deeper diving may result in shorter reproductive life-spans.

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from Marion Island. doi:10.1594/PANGAEA.264751

Figures

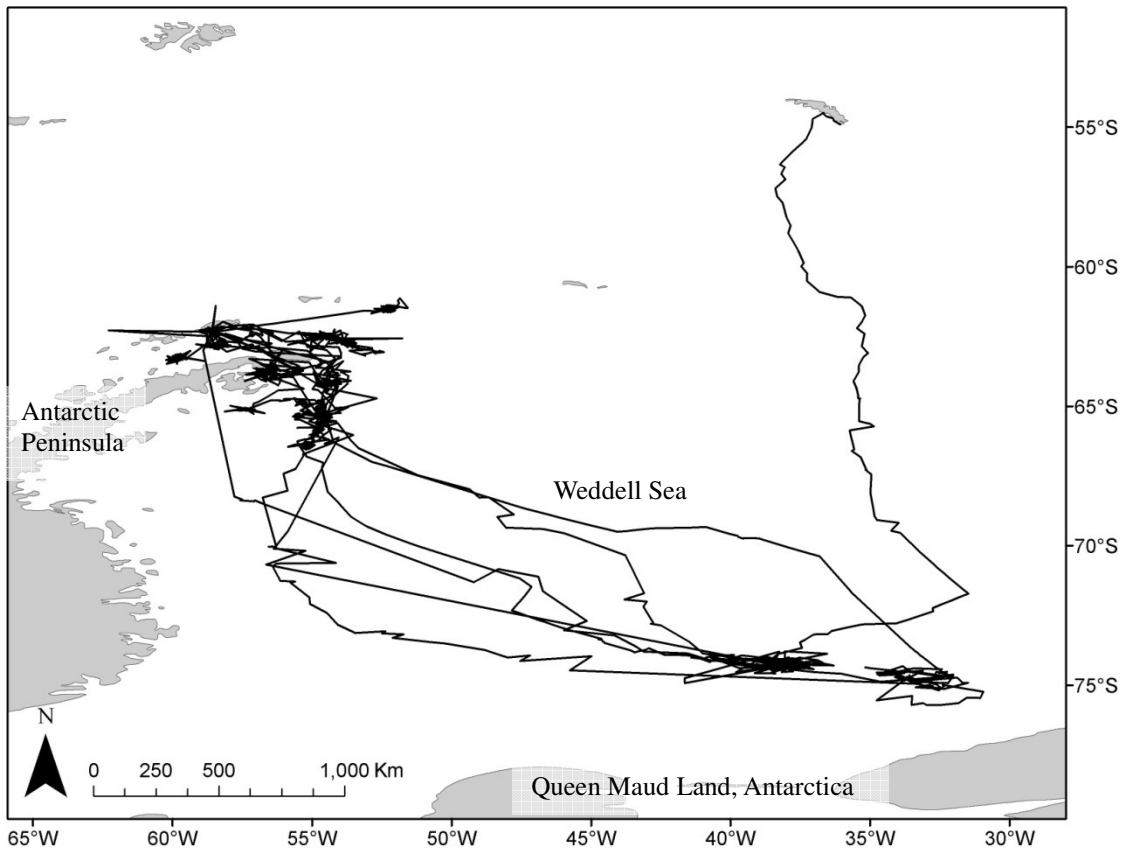


Figure 1: Map of the movements of tracked animals ($n = 9$) from King George Island.

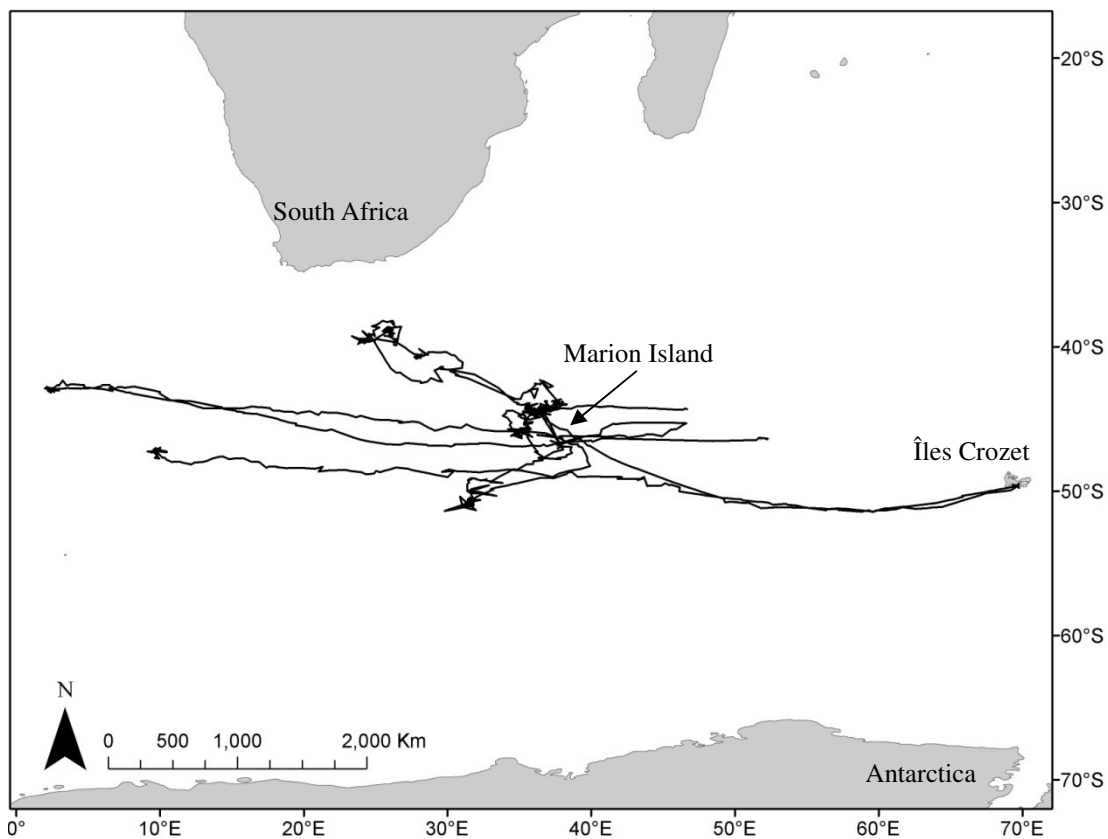


Figure 2: Map of the movements of tracked animals ($n = 5$) from Marion Island.

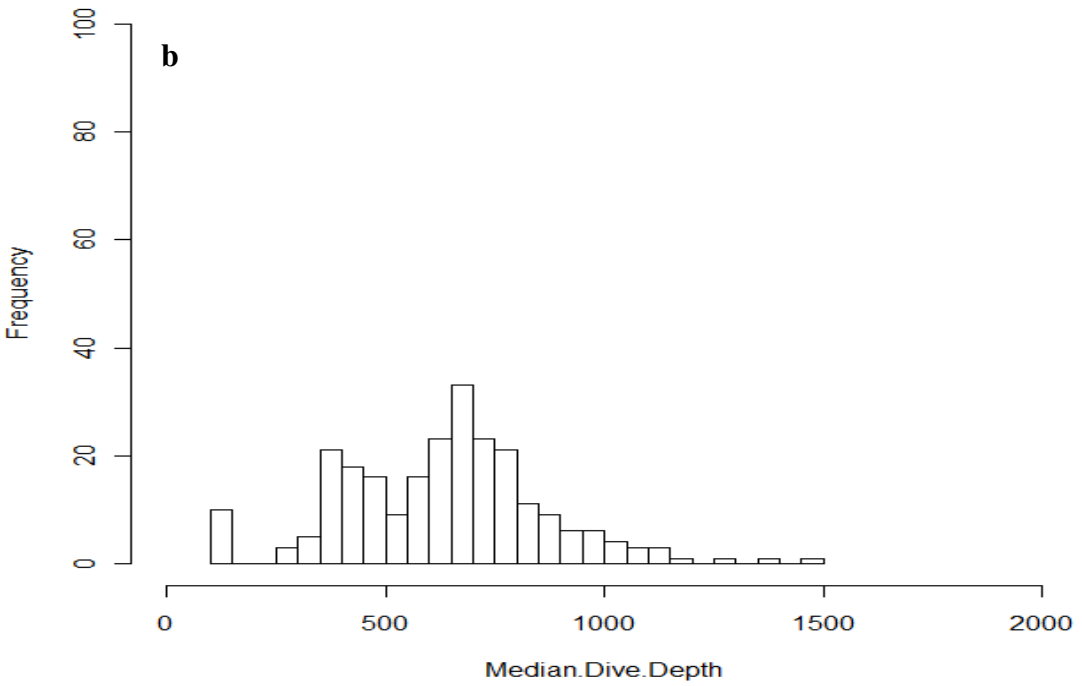
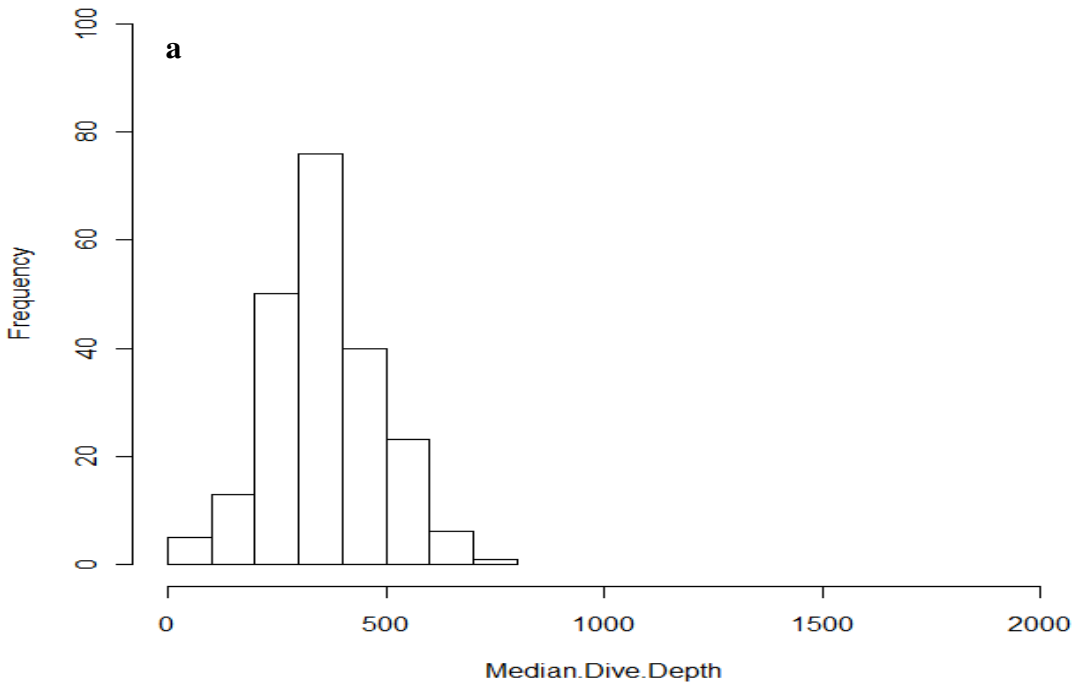
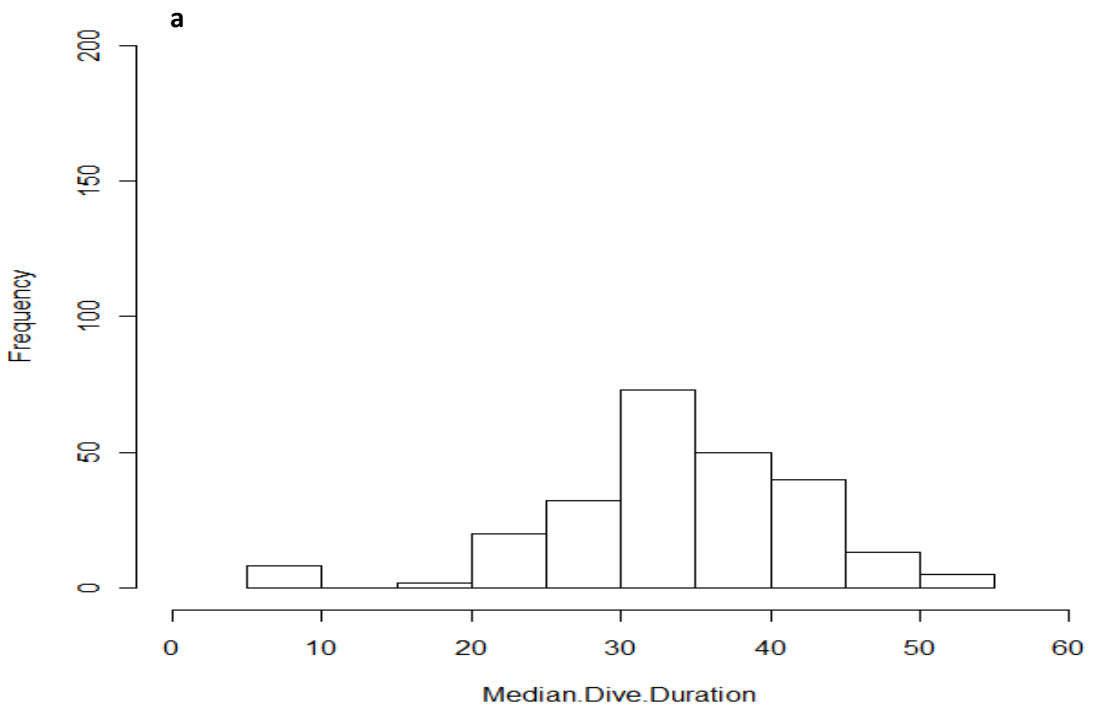
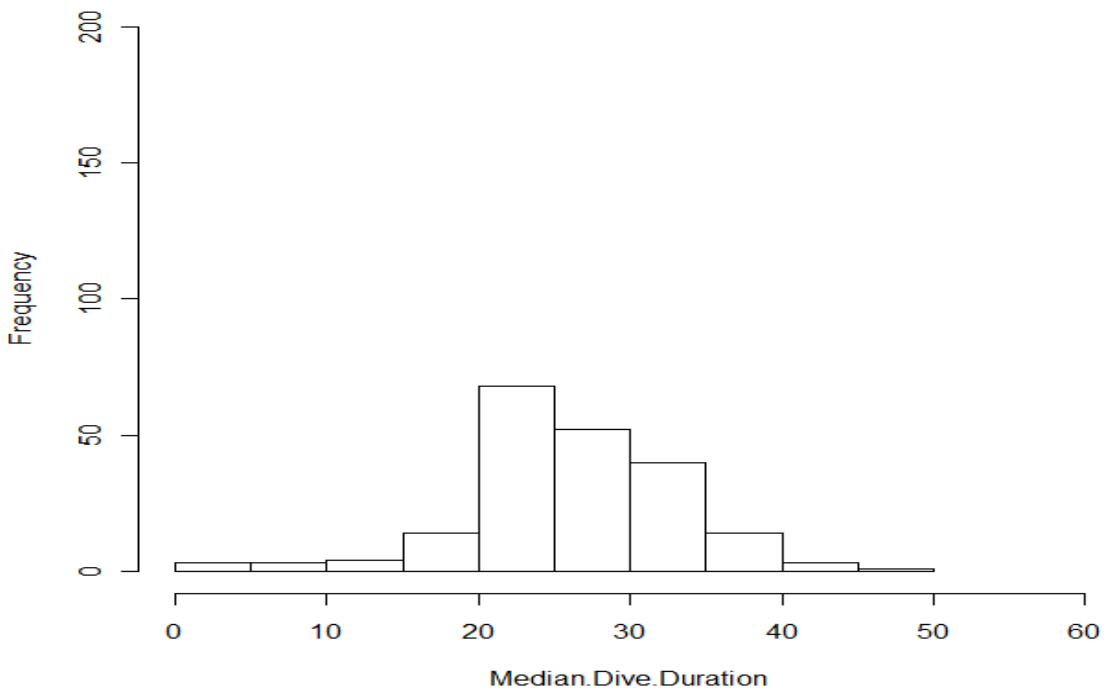


Figure 3: Histograms of the median dive depth values, in metres, across the sampled populations for dives occurring over depths greater than 2000 m. **a:** King George Island (n=9). **b:** Marion Island (n=4).



b

Figure 4: Histograms of the median dive duration values, in minutes, across the sampled populations for dives occurring over depths greater than 2000 m. **a:** King George Island (n=9). **b:** Marion Island (n=4).

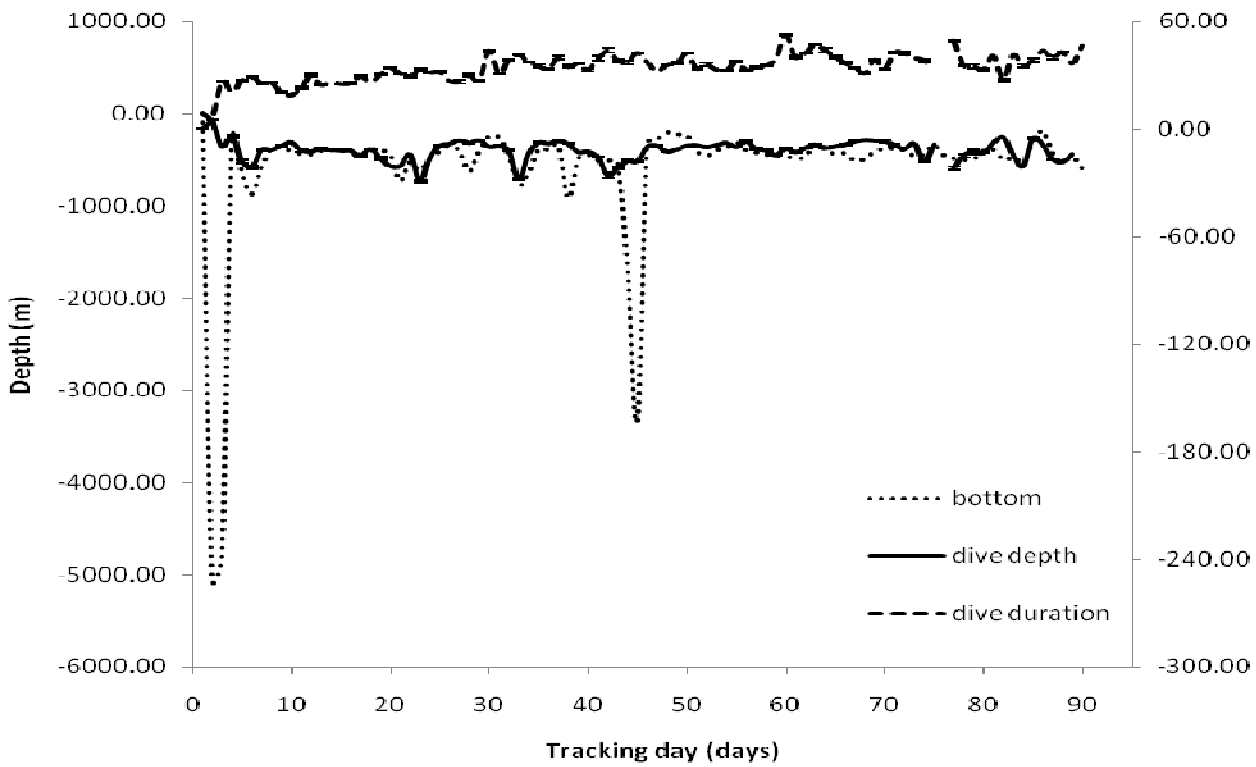


Figure 5: Dive durations (min) and mean depths (m), in relation to bottom depth (m) values encountered by J13 over the number of days the animal was tracked after departing from King George Island. The proximity of mean dive depths with estimates of the seafloor depth indicates a likely benthic forage strategy.

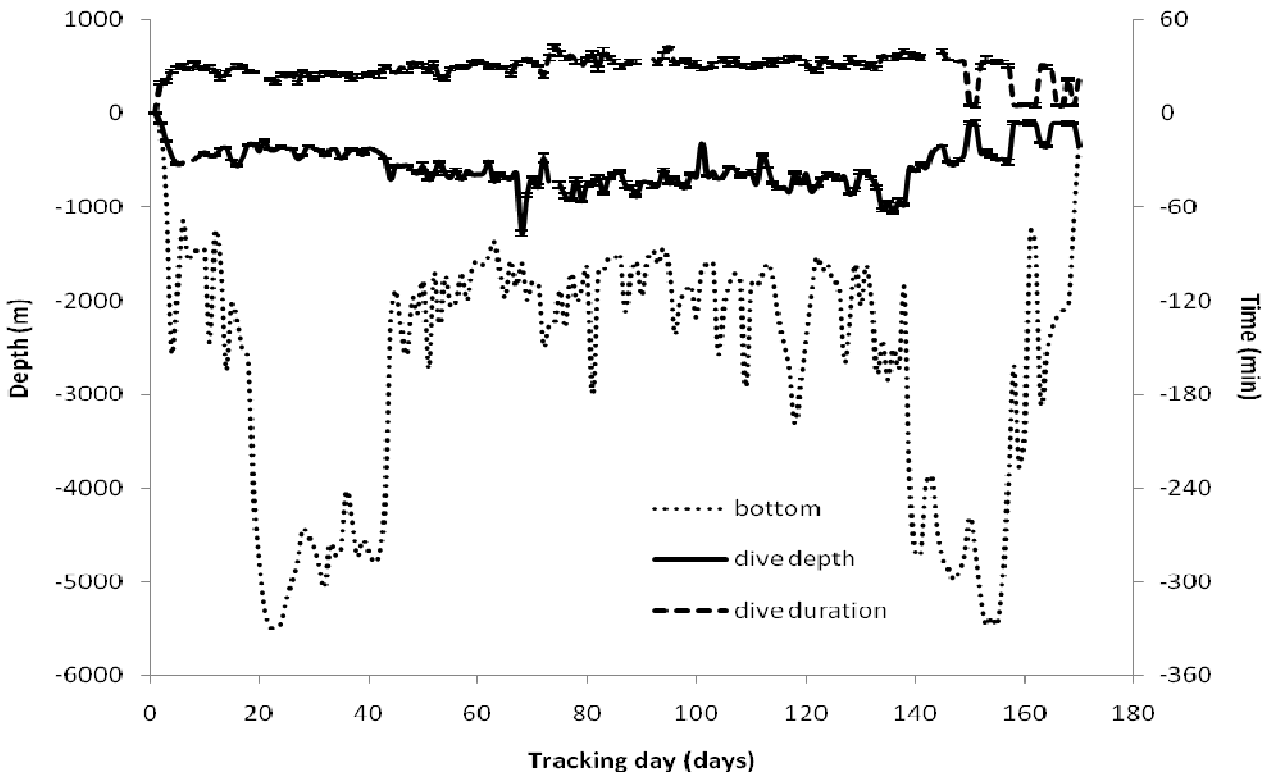


Figure 6: Dive durations (min) and mean depths (m), in relation to bottom depth (m) values encountered by individual M05, over the number of days the animal was tracked after departing from Marion Island, illustrating an evident pelagic forage strategy.

Tables

Table 1: Summary of dive results obtained from adult male southern elephant seals from King George Island and Marion Island.

Animal	Deployment date	# Days tracked	Length (cm)	Median daily dive depth (m)		Dive duration (min)	
				Median (range)	Max	Median (range)	Max
King George Island							
Median			414.5	359.1 (57.0-710.1)	1960	25.50 (2.5-45.36)	45.36
J03	2000-03-09	146	390	252.0 (130.7- 802.0)	1000	35.39 (14.23-54.17)	54.17
J05	2000-03-13	31	378	512.4 (60.0- 725.3)	1960	24.50 (7.5-32.98)	32.984
J06	2000-03-18	100	378	310.1 (57.0-546.2)	1002	30.29 (2.5-41.25)	41.25
J08	2000-03-31	136	432	487.3 (280.7-634.4)	1960	33.68 (23.0-54.17)	54.17
J09	2000-04-07	197	460	532.6 (60.0-981.4)	1960	28.41 (2.5-40.0)	40.00
J10	2000-04-12	48	430	277.11 (76.79-568.0)	1960	25.878 (3.71-36.94)	36.944
J11	2000-04-12	294	420	420.5 (166.7- 706.8)	1960	25.28 (12.83-45.36)	45.36
J13	2000-04-21	92	405	381.0 (76.94-732.6)	1458	34.858 (5.19-52.5)	52.5
J14	2000-04-21	338	438	511.1 (57.0-807.3)	1494	27.80 (7.5-42.5)	42.5
Marion Island							
Median			409.3	652.0 (106.0-1468.7)	1960	34.00 (5.0-53.5)	53.50
M02	2002-04-09	96	430	743.0(60.0-1141.5)	1960	37.82 (5.49-49.17)	49.17
M04	2002-04-10	77	403	652.0 (513.9-786.4)	1960	35.39 (25.92- 44.11)	44.11
M05	2002-04-17	275	364	592.6 (106.0-1282.0)	1960	29.58 (5.0-42.5)	42.5
M06	2002-04-19	132	440	979.5 (424.7-1632.0)	1960	40.78 (31.5-53.5)	53.50

Table 2: Summary of final model outputs with the best fit to the data. AICc is a second order Akaike's Information Criterion (AIC) statistic, significant effect based on F-test values, and RE = the random effect due to individual variation.

Parameter	Final Model	AIC _c	Significant effects	RE (%)
Mean dive depth	Bathymetry + Length + Population	5662.6	Bathymetry + Population	0.04
Mean dive duration	Bathymetry + Length + Population	2662.7	Population	28.5