

Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago

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ABSTRACT

Eleven satellite tags were deployed on 9 killer whales at the Prince Edwards Islands in the Southern Ocean. State-space switching models were used to generate position estimates from Argos location data, while two behavioural modes were estimated from the data.

Individuals were tracked for 5.6–53.2 days, during which time they moved 416–4,470 km (mean 82.7 km day⁻¹) but 69% of position estimates were within the 1000 m depth contour around the islands (<35 km from the tagging site). Killer whales showed restricted behaviour close to the islands, particularly inshore where they can effectively hunt seals and penguins, and at seamounts to the north of the islands.

Generalized linear mixed effect models were used to explore the relationship between environmental variables and behavioural mode. The best model included depth, sea surface temperature, latitude, sea surface height anomaly and bottom slope, but killer whales did not clearly target features such as fronts and apparent mesoscale eddies. Killer whales showed restricted behaviour in shallow water, at high latitudes and low sea surface temperature – the conditions characterising the archipelago.

Dive data from two individuals largely revealed shallow dives (7.5–50 m deep), but deeper dive bouts to around 368 m were also recorded. Dives were significantly deeper during the day and maximum dive depths were 767.5 and 499.5 m, respectively. This suggests that killer whales might also prey on vertically migrating cephalopods and perhaps Patagonian toothfish.

Three individuals made rapid and directed long-distance movements northwards of the islands, the reasons for which are speculative.

Key words: Killer whale; *Orcinus orca*; movement; diving; tracking; satellite tagging

1. INTRODUCTION

The distribution of marine predators such as marine mammals and birds is shaped by that of their prey, which in turn is dictated by physical and biological oceanographic features and processes. Among these, bathymetry, fronts and mesoscale eddies have been found to influence the distribution of marine top predators because these features may increase primary productivity, concentrate prey, or make prey more accessible (e.g., Bost et al., 2009; Bouchet et al., in press; Cotté et al., 2007; Dragon et al., 2010; Nel et al., 2001, Yen et al., 2004). Unlike seals and seabirds, cetaceans are not constrained to breed on land, and may therefore potentially move much more extensively to exploit prey (e.g., Bailey et al., 2009; Kennedy et al., 2014; Mate et al., 2011). However this fact has also made them less amenable to tracking studies (Hart and Hyrenbach, 2009; McIntyre, 2014).

Killer whales (*Orcinus orca*) have a cosmopolitan distribution, occurring in every ocean, from neritic to oceanic waters. They are the apex predators in many marine ecosystems. Overall they have been recorded feeding on more than 140 species, from cephalopods and fishes to large whales (Ford, 2008), but dietary specialisations have been described in different populations, some in sympatry (Foote et al., 2009; Ford et al., 1998, 2011). Because killer whales, like other cetaceans, spend most

of their lives under water and are wide-ranging and sparsely distributed, studying their diet, movement and distribution is challenging, even more so in oceanic environments. Accordingly, the most intensive longitudinal studies have been restricted to inshore waters (e.g., Ivkovich et al., 2010; Kuningas et al., 2014; Poncelet et al., 2010), largely in the Eastern North Pacific (e.g., Dahlheim et al., 2008; Durban et al., 2010; Ford et al., 2000; Matkin et al., 2014; review in de Bruyn et al., 2013). Movement data have arisen from photographic identification studies, which have revealed seasonal philopatry in many populations (e.g., Foote et al., 2010; Hauser et al., 2007; Ivkovich et al., 2010; Matkin et al., 2014; Olesiuk et al., 2005; Poncelet et al., 2010), sometimes combined with extensive movements over hundreds to thousands of kilometres (e.g., Dahlheim et al., 2008; Fearnbach et al., 2013; Iniguez, 2001; Matkin et al., 1997). A handful of primarily descriptive studies using satellite-linked telemetry have revealed diverse movements of killer whales, ranging from the local, restricted movements of Antarctic fish-eating (*type C*) killer whales (Andrews et al., 2008) to the extensive movements of an individual in the Canadian Arctic (Matthews et al., 2011) and a combination of behaviours among Antarctic seal-hunting (*type B*) killer whales (Durban and Pitman, 2012).

By linking distribution and movement to environmental variables the factors which determine the spatial ecology of these versatile, cosmopolitan top predators can be described. Further, killer whales may have strong influences at various trophic levels because of their catholic diet, large energy requirements and mobility (Estes et al., 1998; Reisinger et al., 2011a; Springer et al., 2003; Williams et al., 2004). However these effects are mediated by their spatial distribution and thus by describing the movements of killer whales our understanding of their role in marine ecosystems can be refined. Studying these aspects in the diverse settings in which killer whales occur will also provide insight into their foraging and movement ecology as well as their interactions with their environment.

This study therefore used satellite-linked telemetry devices, firstly, to describe the movements of killer whales at an isolated Southern Ocean archipelago – the Prince Edward Islands. Secondly, two behavioural modes ('restricted' and 'transit') were estimated from these movement data and, thirdly, the relationship between these behavioural modes and a set of environmental covariates was modelled. Lastly, a preliminary analysis of the dive behaviour of two individuals is presented.

2. METHODS

2.1 Ethics

Tagging was approved by the University of Pretoria's Animal Use and Care Committee (EC023-10) and permitted by the Prince Edward Islands Management Committee (17/12, 1/2013 and 1/2014).

2.2 The Prince Edward Islands

The Prince Edward Islands (PEIs) — comprising Marion Island and the smaller Prince Edward Island ~19 km to the north east — are situated in the Indian Ocean sector of the Southern Ocean. The nearest landfall is at the Crozet Archipelago nearly 1,000 km to the east. The PEIs are the summits of a pinnacle rising about 5,000 m from the surrounding seafloor and are separated by a shallow (<200 m deep) shelf. The islands lie between the Subantarctic Front to the north and the Antarctic Polar Front to the south; these fronts are variable and complex in this region. This mesoscale variability is further characterised by numerous eddies which form upstream of the islands as the east-flowing Antarctic Circumpolar Current flows through the Andrew Bain Fracture Zone in the Southwest Indian Ridge (Ansorge and Lutjeharms, 2003; Lutjeharms and Ansorge, 2008).

The PEIs provide breeding and moulting sites for millions of penguins and thousands of seals. Four penguin species breed at the islands: king (*Aptenodytes patagonicus*), gentoo (*Pygoscelis papua*), macaroni (*Eudyptes chrysolophus*) and southern rockhopper penguins (*E. chrysocome filholi*). Three seal species breed at the islands: southern elephant (*Mirounga leonina*), Antarctic fur – (*Arctocephalus gazella*) and Subantarctic fur seals (*A. tropicalis*) (Ryan and Bester, 2008). This aggregation of seabirds and seals attracts a population of killer whales to the inshore waters of the islands. Killer whales are most abundant inshore at Marion Island in September-December, coinciding with the breeding of seals and penguins, with a secondary peak in April-May (Condy et al., 1978; Reisinger et al., 2011c). They patrol close inshore, primarily along the east coast of Marion, where they have been documented preying on elephant seals, Subantarctic fur seals, king penguins, macaroni penguins and southern rockhopper penguins (Condy et al., 1978; Keith et al., 2001; Reisinger et al., 2011c). Carbon and nitrogen stable isotope analysis indicates that cephalopods may also be a component of their diet (Reisinger, 2015). The population comprises about 40 individuals in 9 social units, most of which return annually to Marion Island (Keith et al., 2001; Reisinger et al., 2011b; Reisinger, 2015).

Nine individuals which occur at Marion Island have also been photographed near the Crozet Archipelago (Reisinger and de Bruyn, 2014; Tixier et al., 2014) — evidence for long-range movements — but no matches have been made with killer whales off South Africa (~2000 km to the north west). At a smaller scale, Pistorius et al. (2002) described the inshore movements of groups of killer whales based on simultaneous observations at different points along the Marion Island coastline on a single day. Nothing else is known about the movement ecology of this population of killer whales; when they are not sighted inshore, their whereabouts and movements are unknown.

2.3 Satellite tagging

Wildlife Computers SPOT5 and Wildlife Computers Mk10-A (Wildlife Computers, Redmond, Washington, United States of America) satellite-linked telemetry devices (hereafter 'tags') were deployed on individually identifiable killer whales. The tags were in the 'Low Impact Minimally Percutaneous External-electronics Transmitter' (LIMPET) configuration, where the tag is externally attached to the dorsal fin of the animal by sub-dermal darts (Andrews et al., 2008). Tags were remotely deployed from shore at Rockhopper Bay, Marion Island (46.873° S 37.859° E), using a 68 kg draw weight recurve crossbow (Barnett Panzer V; Barnett Outdoors, LLC, Tarpon Springs, Florida, USA). Methods and the mid- and long-term impacts of tagging are discussed in Reisinger et al. (2014).

Both tag models allow estimation of geographic position via satellite using the Argos System (Collecte Localisation Satellites - CLS, Toulouse, France) and the Mk10-A tag additionally includes a pressure (depth) sensor and a fast-response thermistor. To extend tag battery life while maintaining biologically sensible data capture, tags were programmed with two similar transmission schedules or 'duty cycles'. SPOT5 tags were programmed to transmit 01:00 – 22:00 UTC for 30 days, thereafter 01:00 – 22:00 UTC on every second day. Mk10-A tags were programmed to transmit 01:00 – 22:00 UTC for 25 days, thereafter 01:00 – 22:00 UTC on every fourth day. Both tags were limited to 600 transmissions per day. To try and avoid biasing analyses towards short-term, inshore movements, in this paper only tags which transmitted >5 days are considered.

2.4 State space switching models

A state-space switching approach was used to model the killer whales' movements and estimate behavioural modes from the Argos position estimates, while simultaneously accounting for uncertainty in the movement dynamics and observations (Jonsen et al., 2005, 2007, 2013; Morales et al., 2004; Patterson et al., 2008). A state-space switching model (SSSM) (Jonsen et al., 2005, 2007) has two components: the process model describing the movement process of interest and the observation model relating the unobserved state (location) predictions of the process model to the observed data. The process model is a first-difference correlated random walk (DCRW) (Jonsen et al., 2005) which includes parameters for turning angle (θ) and movement persistence (i.e., the autocorrelation in both direction and speed, γ). A switching first-difference correlated random walk (DCRWS) (Jonsen et al., 2005) is obtained when the movement parameters are indexed by behavioural mode. Biologically, it is assumed that an individual will slow down and change direction more frequently when it encounters abundant prey or an otherwise favourable environment, often termed 'area-restricted search' (e.g., Kareiva and Odell, 1987) (hereafter 'restricted behaviour'), while transit behaviour will be characterised by faster, straighter movements. This can be related to turning angle (θ) and autocorrelation (γ), assuming θ will be nearer 0 and γ higher when restricted transiting (Jonsen et al., 2005, 2007).

Argos position estimates are classed by CLS based on the estimated accuracy of the position, as follows: Class A and B – no estimate; 0– >1 500 m; 1–500-1 500 m; 2–250-500 m; 3– <250 m (CLS, 2011). Position estimate errors are often dealt with by filtering data based, for example, on maximum travel speed (Austin et al., 2003; McConnell et al., 1992) or by discarding poor quality data (Class A, B and 0). However such approaches discard a great deal of expensive, hard won data and the error in the surviving data is ignored. In the SSSM, position estimate error is incorporated directly into the observation model as a *t*-distributed variable (Jonsen et al., 2005). Further, Argos positions are estimated at irregular intervals (especially for diving animals) but SSSM position estimates can be regularized. Detailed descriptions of SSSMs are provided in Breed et al. (2009), Jonsen et al. (2005, 2007, 2013), Morales et al. (2004) and Patterson et al. (2008).

Bayesian SSSMs were fitted using Markov Chain Monte Carlo (MCMC) in *rjags* (Plummer, 2014), through the *bsam* package (Jonsen, 2014) in programme R (R Core Team, 2013). Two chains were run in parallel. After a burn-in of 15,000 samples per chain, 10,000 samples were generated and

Table 1 : Details of 11 satellite-linked tags deployed on killer whales at Marion Island. Distance per day is the minimum cumulative track distance divided by the track duration. Behavioural mode proportion is the proportion of state-space switching model position estimates assigned to restricted behaviour (R), transit behaviour (T) or which were uncertain (U). Proportions may not sum to 100 due to rounding. Class: AM – adult male; AF – adult female.

Animal		Date	Tag model	Track duration (days)	Argos positions		Behavioural mode proportion (%)			Distance (km)		
ID	Class				Total	day ⁻¹	R	T	U	day ⁻¹	Cumulative	Maximum from tagging location
M001	AM	2012/04/28	SPOT5	10.7	227	21.21	85	0	15	78.9	844	59
M007	AM	2012/05/01	SPOT5	53.2	1288	24.21	90	8	1	84.0	4470	223
M017	AF	2013/01/12	SPOT5	40.0	968	24.20	82	12	6	63.8	2554	225
M035	AF	2012/12/31	SPOT5	15.9	385	24.21	47	47	7	94.7	1506	952
M005	AM	2012/12/14	SPOT5	16.0	404	25.25	98	0	2	76.8	1229	110
M059	AF	2012/12/04	SPOT5	39.4	777	19.72	77	9	14	84.1	3312	500
M026	AF	2012/11/29	SPOT5	29.7	604	20.34	35	58	6	114.8	3411	1333
M030	AM	2012/11/08	SPOT5	18.7	394	21.07	99	0	1	80.4	1503	28
M049	AF	2013/04/27	Mk-10A	12.5	302	24.16	64	0	36	89.0	1112	86
M001	AM	2013/04/28	Mk-10A	23.0	629	27.35	99	0	1	69.0	1587	35
M030	AM	2013/12/02	SPOT5	5.6	121	21.61	96	0	4	74.3	416	22

every 10th sample was retained, resulting in 1000 samples per chain. Diagnostic plots were checked following Jonsen et al. (2013). SSSM positions were estimated at 3 hour intervals, giving a mean ratio of 2.6 ± 0.3 Argos position estimates to each SSSM position estimate (Table 1). Only two behavioural modes are modelled, however the means of the MCMC samples range continuously from 1–2. Mean behaviour values <1.25 are thus considered as transiting behaviour (*T*) and values >1.75 as restricted behaviour (*R*); values 1.25–1.75 were considered uncertain (*U*) (Jonsen et al., 2007). *R*, *T* and *U* are used as subscripts where applicable.

Killer whales frequently occur very close inshore at the PEIs (Keith et al., 2001; Reisinger et al., 2011a) and even a small discrepancy between the SSSM position estimate and the true geographic location of the individual could have resulted in SSSM position estimates on land. Instead of removing positions estimates on land, which would bias subsequent analyses against positions very close inshore, on land position estimates were shifted to the nearest point 50 m offshore using Geospatial Modelling Environment (Beyer, 2012) (coastline data provided by the South African Navy Hydrographic Office). The great circle distance was calculated between SSSM position estimates, as well as the great circle distance to the tagging site for each SSSM position estimate, using the distance function in the R package *argosfilter* (Freitas, 2012). For this step, intervening land was ignored. Distance travelled and speeds between position estimates are thus regarded as minimums.

2.5 Generalized linear mixed modelling

Generalized linear mixed effect models (GLMMs) were used to explore the relationship between 7 predictor variables and SSSM behavioural mode. For each shifted SSSM position estimate, bathymetric variables – depth (DEP) and bottom slope (SLP) – and remote-sensed environmental variables – sea surface temperature (SST), chlorophyll-*a* concentration (CHL) and sea surface height anomaly (SSH) – were sampled in ArcMap 10.0 (ESRI Inc., Redlands, California, USA), using the data sources and additional tools described in Table 2. Latitude (LAT) and longitude (LON) were also included as predictors. Predictors were centred about their mean and scaled by their standard deviation (Schielzeth, 2010). Behavioural mode was treated as a binomial response (restricted or transient behaviour), and GLMMs were fitted with a logit link using the *lme4* package (Bates et al., 2014) in R. Each track was treated as a random effect. The full model was:

Behavioural mode \sim DEP + SST + LAT + SSH + LON + SLP + CHL + (1 | track)

Table 2 : Spatial data used to model the relationship between behavioural mode of killer whales satellite-tagged at Marion Island, and environmental predictors.

Abbreviation	Description	Unit	Details	Source
-	Prince Edward Islands coastline	-	-	South African Navy Hydrographic Office ¹
LON	Longitude	Decimal degrees	State-space switching model longitude estimate. On land positions shifted to nearest point 50 m offshore	-
LAT	Latitude	Decimal degrees	State-space switching model latitude estimate. On land positions shifted to nearest point 50 m offshore	-
-	Bathymetry - Prince Edward Islands inshore	m	Bathymetry raster interpolated from spot depths, using 'spline with barriers' interpolation in ArcMap 10.0. ²	Spot depths from South African Navy Hydrographic Office ¹
-	Bathymetry – large spatial scale	m	Bathymetry grid; 30 arc-seconds spatial resolution.	GEBCO_08 grid; GEBCO ³
DEP	Depth	m	Combination of inshore and large spatial scale bathymetry. Inshore bathymetry values used where large spatial scale bathymetry values were missing or positive	-
SST	Sea surface temperature	°C	Monthly daytime sea surface temperature images; 0.04 degree spatial resolution. Accessed using Marine Geospatial Ecology Tools (Roberts et al. 2010) in ArcMap ² 10.0	MODIS Aqua Level 3; NASA JPL PO.DAAC ⁴
CHL	Chlorophyll- <i>a</i> concentration	mg m ⁻³	Monthly chlorophyll- <i>a</i> concentration images; 0.04 degree spatial resolution. Accessed using Marine Geospatial Ecology Tools (Roberts et al. 2010) in ArcMap 10.0 ²	MODIS Aqua Level 3 Standard Mapped Image; NASA GSFC OceanColor Group ⁵
SSH	Sea surface height anomaly	m	Daily sea surface height anomaly grids; 0.25 degree spatial resolution. Accessed using Marine Geospatial Ecology Tools (Roberts et al. 2010) in ArcMap 10.0 ²	DUACS 2014 delayed time, all satellite mean sea level anomaly; Aviso ⁶
SLP	Bottom slope	°	Calculated from bathymetry using DEM Surface Tools (Jenness 2013) in ArcMap 10.0 ²	-

1. South African Navy Hydrographic Office (www.sanho.co.za)
2. ESRI Inc., Redlands, California, United States of America (www.esri.com)
3. General Bathymetric Chart of the Oceans (www.gebco.net)
4. NASA Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (<http://podaac.jpl.nasa.gov/>)
5. NASA Goddard Space Flight Center OceanColor Group (<http://oceancolor.gsfc.nasa.gov/>)
6. [Produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes \(www.aviso.altimetry.fr/duacs/\)](http://www.aviso.altimetry.fr/duacs/)

Autocorrelation structures cannot be fitted to GLMMs in the *lme4* package; autocorrelation may result in overestimates of model precision and the inclusion of irrelevant model variables (Aarts et al., 2008). Observations with any missing variables were removed so that all models were fitted to the same 903 observations (641 restricted position estimates and 262 transit position estimates). The *MuMIn* package (Barton, 2013) in R was used to construct a model set from the full model, and the most parsimonious models were selected using small-sample size corrected Akaike Information Criterion (AIC_c). Models with a ΔAIC_c (difference between the AIC_c of the best model and that of the model in question) < 2 , were also considered parsimonious (Burnham and Anderson, 2002). Model fit was assessed using heat map plots and heat map statistics (Esarey and Pierce, 2012a) implemented with the *heatmapFit* package (Esarey and Pierce, 2012b) in R.

2.6 Dive data

Dive data were collected by the two Mk10-A tags using the Wildlife Computers Behavior Log function and transmitted via the Argos System. Dives were defined as a submersion deeper than 7.5 m and longer than 30s, and for each dive the start and end time, maximum depth, and shape (not reported here) were recorded. The accuracy of the recorded dive depths was $\pm 2.5\%$. Hereafter the maximum depth for each dive is referred to as the 'dive depth'.

SSSM positions were estimated every 3 hours whereas dives were logged nearly continuously and thus dives were assigned to the temporally closest SSSM position estimate (with the position's associated bathymetric and environmental variables; Table 2). To investigate diurnal dive patterns solar elevation was calculated (using an Excel VBA routine¹) for each SSSM position estimate and position estimates from nautical dusk to nautical dawn (solar elevation $< -12^\circ$) were assigned as night and position estimates from nautical dawn to nautical dusk (solar elevation $\geq 12^\circ$) as day.

3. RESULTS

Eleven satellite tags were deployed on 9 individual killer whales, of which 4 were adult males and 5 were adult females (Table 1) (Supplementary Data). The mean track duration was 24.1 ± 14.8 days

¹ Translated from NOAA's calculations (<http://www.srrb.noaa.gov/highlights/sunrise/azel.html>) to Excel VBA by Greg Pelletier (Washington State Department of Ecology, Washington, United States of America). Available at <http://www.ecy.wa.gov/programs/eap/models.html>

(range 5.6–53.2 days). The mean number of Argos position estimates per day was 23.0 ± 2.4 (range 19.7–27.3) and the proportion of transit SSSM position estimates ranged from 0%–58.3%. In total, the SSSM estimated 2,130 positions (1,679 restricted; 303 transit; 148 uncertain) (Table 1). Diagnostics plots showed no obvious fitting problems.

The mean speed between SSSM position estimates was $3.44 \pm 2.43 \text{ km h}^{-1}$ and mean speeds were significantly slower for restricted behaviour ($2.95 \pm 2.01 \text{ km h}^{-1}$) compared with speeds for transit behaviour ($5.91 \pm 2.85 \text{ km h}^{-1}$; Mann-Whitney $U = 414,305$, $p < 0.001$) (Figure 1). Mean turning angle between restricted position estimates was $192.31 \pm 111.74^\circ$, while that between transit position

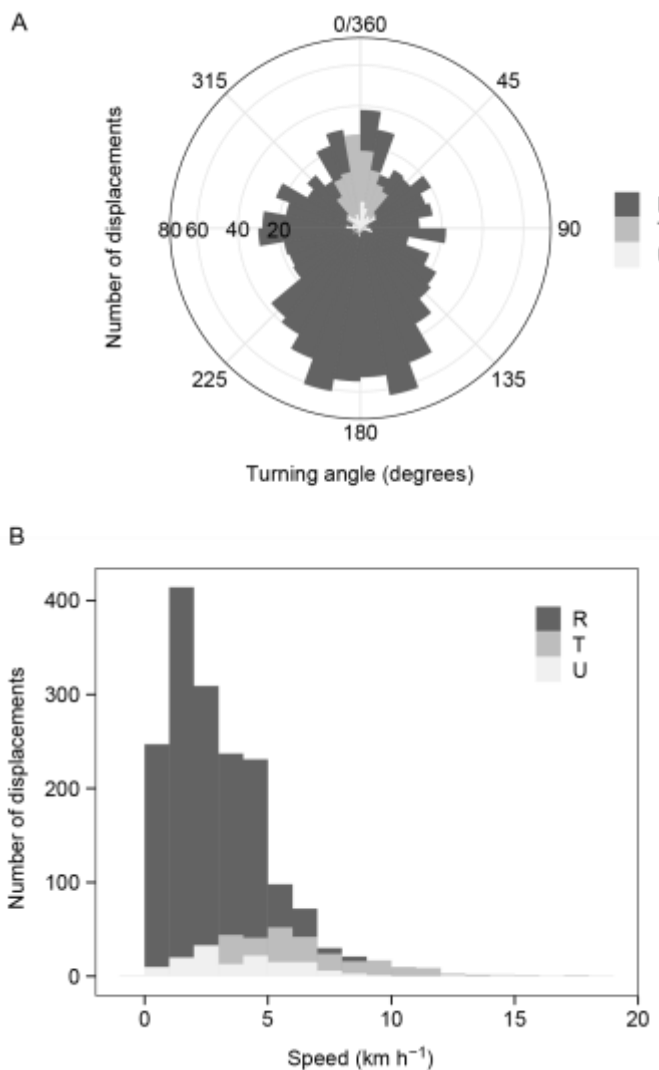


Figure 1 : Movement parameters of killer whales satellite tagged at Marion Island. A) Turning angle; B) Speed. Both turning angle and speed are calculated assuming straight line travel between two state-space switching model position estimates. R – restricted behaviour; T – transit behaviour; U – uncertain mode.

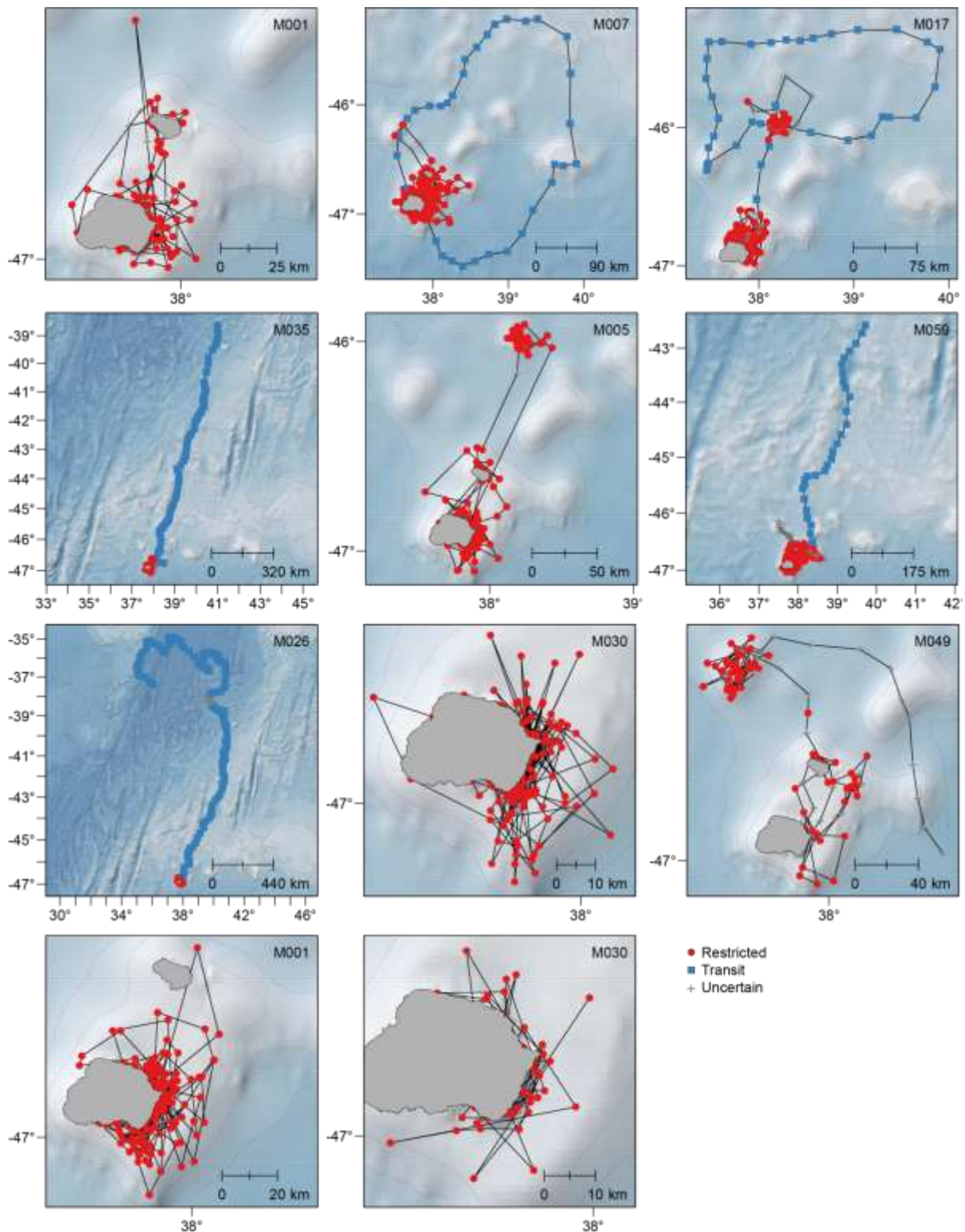


Figure 2 : Individual tracks of satellite-tagged killer whales at Marion Island. Points represent state-space switching model position estimates in three behavioural modes (restricted, transit, uncertain mode) based on ARGOS position estimates. Solid lines represent straight lines between position estimates. Individual IDs are indicated in the top right corner of each map. Depth contours are at 1000 m intervals. Spherical Mercator projection.

estimates was $359.62 \pm 39.64^\circ$; these were significantly different (Watson's $U^2 = 9.8656$, $p < 0.001$) (Figure 1). Individuals moved an average of 82.7 ± 13.7 km day⁻¹ (Table 1).

Individuals mostly remained near the islands; 1470 SSSM position estimates (69%) were within the 1000 m depth contour around the islands (<35 km from the tagging site) and 1592 positions (75%) were <50 km from the tagging site (Figure 2). The majority of the latter (1489 position estimates, 94%) were restricted behaviour. Individuals frequented inshore locations (1105 position estimates, 52% <5 km from shore), particularly along the east, north and south coasts of Marion Island. At least three individuals – M017, M005 and M049 – showed restricted behaviour on Funk Seamount to the north of the PEIs (summit depth 180 m) (Yesson et al., 2011) and an unnamed seamount to the northeast of the PEIs (summit depth 960 m) (Yesson et al., 2011). This restricted behaviour is evident as plateaus in these individuals' displacement plots (Figure 3), approximately 100 km and 70 km from the tagging site, respectively. We speculate that M017 gave birth over a seamount (see Supplementary Figure S1). One individual (M007) made a short (~6 days), mid-distance (223 km maximum distance from tagging site) round trip, including a slight deviation (but not restricted behaviour) at the Gallieni Bank. Three individuals – M035, M059 and M026 – made directed, long-distance movements to the north of the island. M026 reached 34.88°S, 1333 km from the tagging site, before turning southwards. The individual was resighted at Marion Island 203 days after its tag stopped transmitting. M035 and M059 have previously been sighted in the same group at Marion and seem to have travelled together while tagged, at least during their northward movement. M059's tag stopped transmitting 500 km from the tagging site (last position estimate at 42.57°S) and M035's tag stopped transmitting 952 km from the tagging site (last position estimate at 38.62°S). They followed a very similar northward route to M026, crossing the Southwest Indian Ridge at the Simpson Fracture Zone, approximately 1 month later. M035 was resighted at Marion Island 324 days after its tag stopped transmitting and M059 was resighted 239 days after its tag stopped transmitting. It is probable that the two whales were still associated, but this was not confirmed from photo-ID.

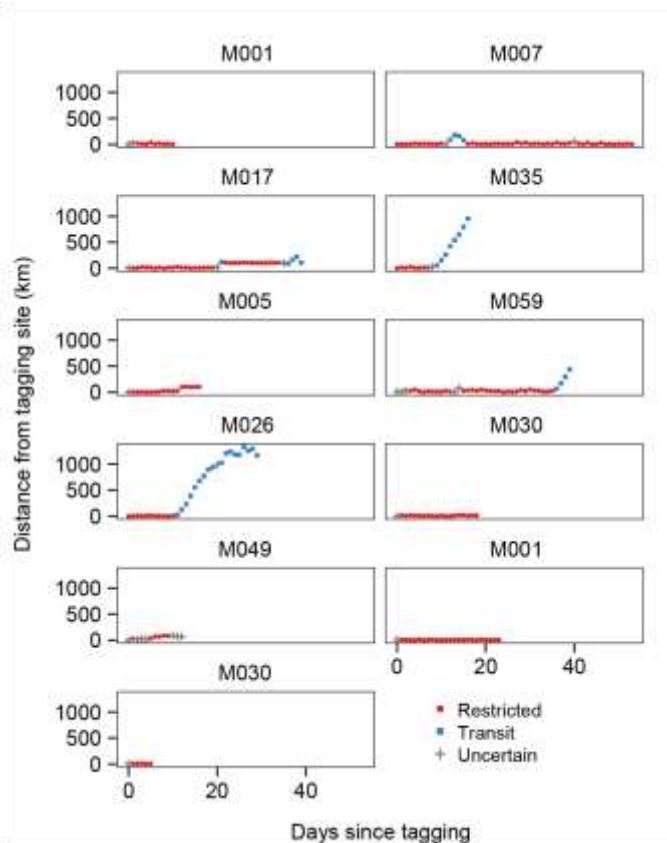


Figure 3 : Distance from the tagging site plotted against the number of days since deployment, for satellite-tagged killer whales at Marion Island. Each panel is labelled by the individual ID. Behavioural modes estimated by the state-space switching model (restricted, transit and uncertain mode) are indicated.

3.1 GLMMs

Environmental variables reflected the key features of the movements described above: restricted behaviour around the islands (particularly inshore) and at seamounts near the islands and transit behaviour further from the islands, particularly the northward movements of the three individuals mentioned above. Thus longitudes and latitude varied more for transit positions, with restricted behaviour limited to the vicinity of the islands and seamounts (mean $LON_R = 37.91 \pm 0.17^\circ$, mean $LAT_R = -46.78 \pm 0.28^\circ$) (Figure 4). Restricted behaviour occurred in much shallower waters than transit behaviour (mean $DEP_R = 569 \pm 513$ m, mean $DEP_T = 5880 \pm 1299$ m); restricted behaviour did not occur in waters deeper than 3430 m. Sea surface temperature was lower and less variable for restricted positions (mean $SST_R = 6.00 \pm 0.83^\circ$ C, mean $SST_T = 12.73 \pm 5.68^\circ$ C). Although chlorophyll- α concentration was similar at restricted and transit positions, values at restricted positions were slightly higher (mean $CHL_R = 0.34 \pm 0.18$ mg.m⁻³, mean $CHL_T = 0.27 \pm 0.2$ mg.m⁻³). Sea surface height

anomaly was similar at transit and restricted positions, but values at transit positions varied much more (mean $SSH_R = 0.044 \pm 0.037$ m, $SSH_T = 0.052 \pm 0.144$ m). Slope was greater for restricted positions (mean $SLP_R = 11.55 \pm 10.62^\circ$, mean $SLP_T = 2.90 \pm 2.85^\circ$) (Figure 4).

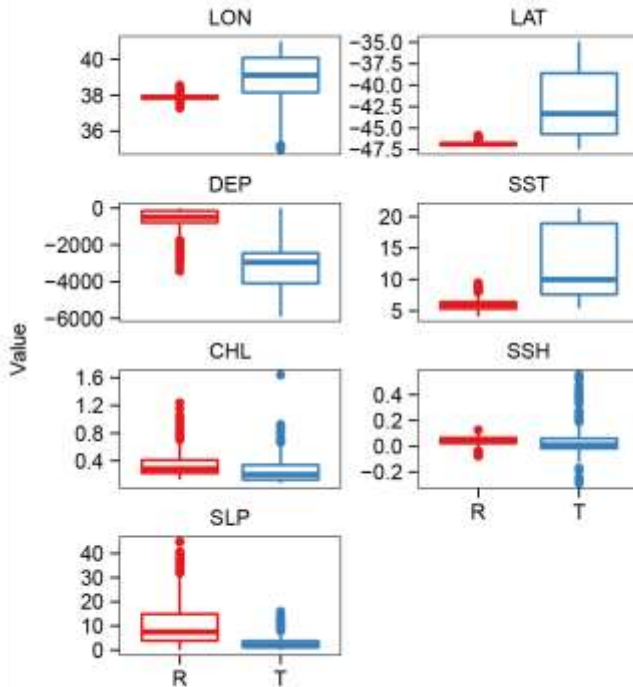


Figure 4 : Boxplots showing the values of 7 environmental variables, for different killer whale behavioural modes estimated using a state-space switching model. R – restricted behaviour; T – transit behaviour. Variable names are abbreviated following Table 2, and units of measurement may be found there.

There was some correlation among the environmental variables: latitude and sea surface temperature was correlated, as expected, (Spearman’s rank correlation coefficient, $r_s = 0.61$) as was depth and sea surface temperature ($r_s = -0.50$) (Supplementary Figure S2). Some multicollinearity was evident from variance inflation factors (VIFs) for the full model, however none of these were higher than the recommended value of 10 (Hair et al., 1995; Kennedy, 1992) (Supplementary Table S1). All variables were therefore retained in the GLMM analysis.

The first-ranked GLMM included depth, sea surface temperature, latitude, sea surface height anomaly and slope as fixed effects and the track as a random effect. Three other models had $\Delta AIC_c < 2$ (Table 3). The second-ranked model performed almost as well as the first-ranked ($\Delta AIC_c = 0.30$; weight = 0.318 vs. 0.371) (Table 3), had similar parameter estimates and had one less variable (slope

Table 3 : Model selection parameters for generalised linear mixed effects models describing the relationship between killer whale behavioural mode and environmental predictors. Abbreviations follow Table 2. All models include the track ID as random effect. Models with $\Delta AIC_c \leq 2$ are shown (with model weights calculated among them) as well as the full and null models.

Rank	Model	df	AIC _c	ΔAIC_c	Weight
1	Behaviour ~ DEP + SST + LAT + SSH + SLP	7	145.7	-	0.371
2	Behaviour ~ DEP + SST + LAT + SSH	6	146.0	0.30	0.318
3	Behaviour ~ DEP + SST + LAT + SSH + LON + SLP	8	147.3	1.67	0.169
4	Behaviour ~ DEP + SST + LAT + SSH + LON	7	147.6	1.92	0.142
Full	Behaviour ~ DEP + SST + LAT + SSH + LON + SLP + CHL	9	149.3	3.61	-
Null	Behaviour~	2	649.0	503.31	-

excluded) than the first-ranked model (Table 4). These two models are considered further, but the second-ranked model is preferred because it contains fewer variables. In both models latitude had the largest effect size (as judged by the standardised β estimates), followed by sea surface temperature and sea surface height anomaly (Table 4). Heat map plots (Figure 5) and statistics indicated that the two top-ranked models fitted well. No observations in either model had p -values ≤ 0.10 (the expected maximum for a good fit is 20% of observations) (Esarey and Pierce, 2012a).

Table 4 : Centred and standardised parameter estimates for our best generalised linear mixed effects models describing the relationship between killer whale behavioural mode and environmental predictors. Abbreviations follow Table 2. SE – standard error; z – z-score; p – p -value.

	Estimate	SE	z	p
<i>Model rank 1</i>				
Intercept	-12.07	4.42	-2.73	0.006
LAT	-33.27	7.74	-4.30	<0.001
DEP	2.16	0.56	3.85	<0.001
SST	-7.69	3.14	-2.45	0.014
SSH	-6.70	1.58	-4.25	<0.001
SLP	0.69	0.49	1.39	0.164
<i>Model rank 2</i>				
Intercept	-12.70	4.47	-2.84	0.004
LAT	-34.52	7.68	-4.49	<0.001
DEP	2.30	0.56	4.12	<0.001
SST	-8.16	3.12	-2.62	0.009
SSH	-7.02	1.57	-4.46	<0.001

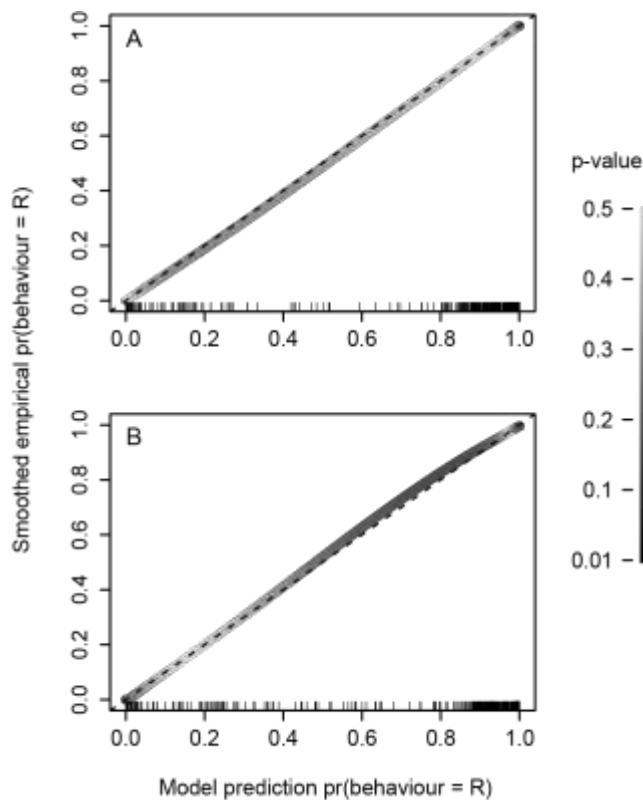


Figure 5 : Heat map plots (Esarey & Pierce 2012a) showing generalised linear mixed effects models' predicted probability of restricted behavioural mode, R, (horizontal axis) against the empirically observed frequency of that behavioural mode in the dataset (vertical axis). The dashed line indicates a perfect fit, while the solid line indicates the model fit. The line is coloured by p -values obtained through parametric bootstrapping, and indicates significantly poor fit (low p -values). A) best-ranked model; B) second-ranked model (refer to Tables 3 and 4).

The three long-distance, directed tracks (M026, M035, M059) — which were mainly transit positions — likely had a strong influence in the data, such that restricted positions are simply predicted by environmental conditions near the islands, while transit positions are predicted by conditions at lower latitudes. To see whether this was true, the models were run without these three tracks (472 position estimates). The same predictors were retained in the best models (Supplementary Table S2) but the standardised β estimates for all predictors were lower, most notably for LAT. SSH had the largest effect size (Supplementary Table S3). Goodness of fit was poorer, with heat map statistics of 25% and 19%, for the best and second best models, respectively (expected maximum = 20%).

3.2 Diving

For individual M049, 1,540 dives >7.5m for longer than 30s were recorded. Although M049's dives were typically quite shallow, they varied greatly in depth (mean = 57.5 ± 112.5 m; 80% of dives 7.5–50 m depth) (Figure 6) with a maximum dive depth of 767.5 m. Dive duration averaged 3.41 ± 2.34 min with a maximum of 13.57 min (Figure 7). For individual M001, 3,500 dives >7.5m for longer than 30s were recorded. These were also shallow on average, but less variable (mean = 43.5 ± 70.5 m; 84% of dives 7.5–50 m depth) and M001 did not dive as deep as M049 (maximum = 499.5 m) (Figure 6). Average dive duration was similar to M049's (mean = 3.65 ± 2.26 min), but the M001's maximum dive duration was longer (15.9 min) (Figure 7).

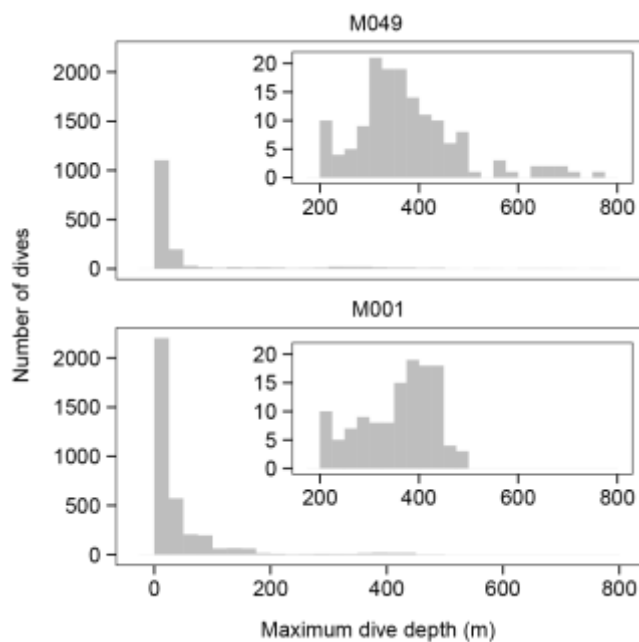


Figure 6 : Histogram showing the distribution of maximum dive depths of two killer whales around Marion Island. The bin width shown here is 25 m and the 200–800 m depth range is enlarged in the insets.

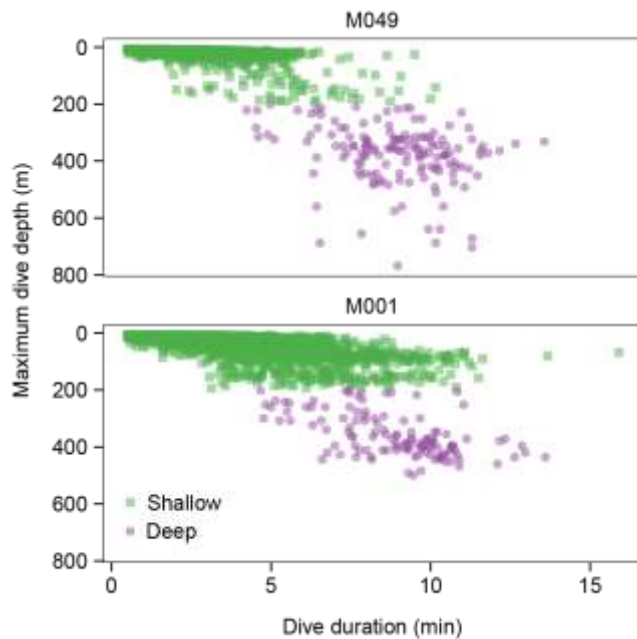


Figure 7 : Scatterplot showing maximum dive depth versus dive duration of two killer whales around Marion Island. Dives were classified into shallow and deep dives using k-means clustering.

Some clustering of the dives was evident in depth and duration (Figure 7), and *k*-means clustering (Hartigan and Wong, 1979) was therefore used to classify two dive type groups. The algorithm distinguished dives deeper than 200 m from dives shallower than this, but did not distinguish any duration classes (Figure 7). M049 made 149 dives >200 m with an average depth of 376.5 ± 107.0 m and M001 made 124 deep dives with an average depth of 357.5 ± 75.5 m. Mean number of dives per calendar day was 118 ± 47 for M049, and 146 ± 40 for M001. M049 dived deep (≥ 200 m) on average 14 ± 7 times per day, and M001 dived deep on average 9 ± 8 times per day. Examples of daily dive behaviour are shown in Supplementary Figure S3 and the position estimates for deep versus shallow dives are shown in Supplementary Figure S4.

There was a strong diel pattern in dive depths, with both individuals diving significantly deeper during the day (M049: $n_{\text{Night}} = 841$, $n_{\text{Day}} = 699$, Mann-Whitney $U = 230218.5$, $p < 0.001$; M001: $n_{\text{Night}} = 1535$, $n_{\text{Day}} = 1965$, Mann-Whitney $U = 1317344$, $p < 0.001$) (Figure 8). M049's average night-time dive depth was 30.0 ± 66.0 m compared with an average daytime dive depth of 90.5 ± 144.5 m. M001 dived to an average of 29.0 ± 28.0 m during the night, but to an average of 54.5 ± 89.5 m during the day. In M001 this diel pattern was striking: he made one night-time dive to 307.5 m, but the next deepest night-time dive was only to 137.5 m (Figure 8). For M049, the water depth at night

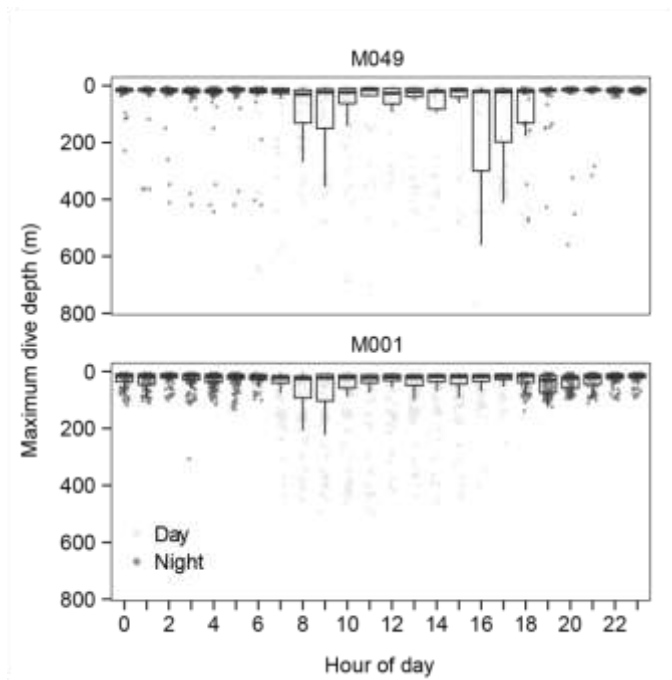


Figure 8 : Diel variation in dive depths of two killer whales tagged at Marion Island. Boxplots are shown for each hour of the day and dive depths are plotted over these. Light grey points represent day time dives and dark grey points represent night time dives.

time locations was not significantly different from day time locations (average $DEP_{Day} = 847 \pm 702$ m; average $DEP_{Night} = 880 \pm 736$ m; Mann-Whitney $U = 279870$, $p = 0.1056$). For M001, day time water depths were significantly deeper ($DEP_{Day} = 509 \pm 400$ m; $DEP_{Night} = 433 \pm 289$ m; Mann-Whitney $U = 1569936$, $p = 0.037$). However in both cases, the differences were not large.

4. DISCUSSION

Predators may be expected to maximise their foraging efficiency by hunting where prey are most dense. The results show that killer whales exploit a dense and predictable aggregation of prey inshore at the PEIs, but also that they seek out other marine habitats, presumably to exploit alternative prey when the inshore resources become less profitable. Killer whales exhibited restricted search behaviour mainly close inshore to Marion Island and Prince Edward Island. This movement pattern suggests that killer whales spend a large proportion of their time hunting seals and penguins near these land-based prey's breeding and moulting sites, and agrees with the findings of previous shore-based observational studies at Marion Island (Condy et al., 1978; Keith et al., 2001; Pistorius et al., 2002, 2012; Reisinger et al., 2011c). This contrasts with the at-sea distribution of

seals and penguins; the high density of seals and penguins near their rookeries seems to present killer whales with more favourable hunting than the dispersed distribution of seals and penguins at sea. At least three killer whales also showed restricted search behaviour at seamounts to the north of the islands, which suggests an aggregation of prey there. Dive data from two individuals revealed largely shallow dives (81% of dives were 7.5–50 m deep), but deeper dive bouts to around 368 m were also recorded. Dives were significantly deeper during the day and both individuals dived deeper (767.5 and 499.5 m) than any published dive records for killer whales (*cf.* Baird, 1994; Baird et al., 2005; Durban and Pitman, 2013; Miller et al., 2010). We therefore suggest that killer whales also prey on vertically migrating cephalopods and perhaps Patagonian toothfish (*Dissostichus eleginoides*). Some individuals made rapid and directed long-distance movements northwards of the islands, which could be ‘physiological maintenance migrations’ as proposed for killer whales tagged at the Antarctic Peninsula (Durban and Pitman, 2012).

The movement speeds and distances reported herein are similar to the handful of other studies which have satellite tagged killer whales (Andrews et al., 2008; Durban and Pitman, 2012; Matkin et al., 2012; Matthews et al., 2011; Pitman et al., 2015). *Type B* (seal-hunting) killer whales tagged at the Antarctic Peninsula moved at average speeds between 3 and 4.7 km h⁻¹ while hunting — similar to the average restricted speed in this study (2.96 km h⁻¹). When making long-distance, directed movements (discussed below), these whales travelled at 9.12–12.13 km h⁻¹ which is faster than the average transit speed in this study (5.91 km h⁻¹). Marion Island killer whales moved further per day (82.7 ± 13.7 km day⁻¹) than a *type B* killer whale (56.8 ± 32.8 km day⁻¹) and *type C* (fish-eating) killer whales (20.83 km day⁻¹) in the Ross Sea (Andrews et al., 2008). However Marion whales did not move as far daily as *transients* (mammal-eating killer whales) in the Gulf of Alaska, which moved 97 km day⁻¹ (Matkin et al., 2012) or an individual in the Canadian Arctic, which travelled between 96.1 ± 45.3 km day⁻¹ and 159.4 ± 44.8 km day⁻¹ in different areas (Matthews et al., 2011). The movements reported herein therefore appear typical for killer whales hunting prey such as seals inshore.

4.1 Long-distance, directed movements

Marion Island killer whales typically travelled >1000 km and up to 4,470 km, while tagged. Extensive movements are not unusual among killer whales. Photographic identification matches have revealed long-range movements (over months to years) of *offshore* killer whales, including minimum distances of 4,435 and 4,345 km between Alaska and California (Dahlheim et al., 2008), and of

transient killer whales (minimum distance 2,660 km between Alaska and California) (Goley and Straley, 1994). An animal satellite tagged in the Canadian Arctic travelled over 5,400 km in about a month (Matthews et al., 2011), an individual in the Gulf of Alaska travelled 3,839 km in 30 days (Matkin et al., 2012), and one tagged off Western Australia moved 1,964 km in 22 days (Pitman et al., 2015). Durban and Pitman (2012), however, documented rapid, directed movements to warm, subtropical waters (20.9–24.2°C; 30–37°S) by 6 *type B* killer whales from the Antarctic Peninsula. One of these animals made a 9,392 km round trip in 42 days. These individuals left Antarctic waters at $>9 \text{ km h}^{-1}$, but their speed decreased with latitude, and increased again on the return leg for the two individuals which made round trips. The authors discount feeding and breeding en-route, and hypothesize that these may be physiological maintenance migrations, during which killer whales repair and replace their outer skin in warmer water (Durban and Pitman, 2012). Three individuals from Marion (water temperature $\sim 5^\circ\text{C}$) made directed movements to the north; M026 reached a minimum latitude of 34.88°S and water temperatures up to 21.6°C. The other two individuals presumably continued northwards after their tags failed. Their speed increased initially after leaving Marion, and then slowed at lower latitudes, but speeds were not as high as those reported by Durban and Pitman (2012), and were variable (Supplementary Figure S5). M026 meandered eastwards at $\sim 37\text{--}35^\circ\text{S}$ in water $\sim 20\text{--}21^\circ\text{C}$, before starting to head southwards, at which time her tag failed. Feeding and breeding at lower latitudes (see, for example, speeds after the inferred birth of M017's calf; Supplementary Figure S1), cannot be ruled out, but it is possible that the movements of these three individuals are also physiological maintenance migrations.

4.2 Distribution in relation to foraging

The large proportion of restricted positions close inshore confirms the observations of previous, shore-based studies which have described how killer whales patrol close inshore along the east coast of Marion Island, hunting penguins and seals. This study shows that this is a dominant pattern in killer whale movements at the island. Positions were concentrated on the east, north and south coasts of Marion, which coincides with the distribution of seal and penguin rookeries, particularly southern elephant seals and king penguins, which are predicted to be among the most profitable prey for killer whales (Reisinger et al., 2011a). Only a single study has described killer whale behaviour at neighbouring Prince Edward Island, and this was a series of shore-based, opportunistic observations of predation on Subantarctic fur seal pups (Pistorius et al., 2012). This study shows that killer whales do use the inshore zone at Prince Edward Island, but to a far lesser extent than at

Marion, which likely reflects the substantially smaller populations of seals and penguins at Prince Edward (Ryan and Bester, 2008).

This inshore foraging behaviour, together with restricted movement on seamounts (discussed below) is underlined by the inclusion of bathymetry and slope in the best models predicting behavioural mode. Sea surface height anomaly was included in the best models and most restricted behaviour was associated with positive anomalies. A notable exception was M017's restricted behaviour over a seamount when there was a negative sea surface height anomaly, although she may have given birth over the seamount (Supplementary Figure S1), so her restricted behaviour may not have been foraging behaviour. There was not a clear association between behaviour and sea surface height anomaly, making it difficult to comment on the importance of eddies to Marion Island killer whales. The situation is further complicated by the high mesoscale oceanographic variability around the islands (Lutjeharms and Ansorge, 2008). Although sea surface temperature was included in the two best models, killer whales did not target large-scale fronts; there was no restricted behaviour around the area where these fronts usually occur (e.g., Orsi et al., 1995). Chlorophyll-*a* was not included in the best models, suggesting that primary productivity does not immediately influence killer whale behavioural mode; however links between top predators and primary productivity may be tenuous, given that top predators and primary producers are several trophic steps apart (Grémillet et al., 2008). When long distance, directed tracks (M026, M035 M059) were excluded, the same predictors were retained in the two best models, but sea surface height anomaly became the most important predictor variable. Model fit and the effect size of each predictor decreased, though, presenting a murkier description of the factors influencing behavioural mode which, again, may be tied to the high mesoscale variability around the islands.

While killer whale distribution near the islands coincided with concentrations of seal and penguin rookeries, their broader distribution was in contrast to the at-sea distribution of most land-based marine top predators from Marion Island. Seals and seabirds forage in diverse areas, often far from the PEIs, where they target frontal and bathymetric features at which their crustacean, fish and cephalopod prey are presumably concentrated (de Bruyn et al., 2009; Nel et al., 2001; Tosh et al., 2012). The shelf between the islands is somewhat enriched by topographic trapping of vertically migrating zooplankton and dense phytoplankton blooms (Perissinotto and McQuaid, 1992) but the broad distribution pattern among seals and seabirds, however, reflects that macrozooplankton

biomass over the inter-island shelf may be 3–8 times lower than in the offshore region. Also, adult mesopelagic fishes are virtually absent from the inter-island region, whereas they predominate the open waters of the Polar Frontal Zone (Mcquaid and Froneman, 2008; Pakhomov and Froneman, 1999; Pakhomov et al., 2000).

To maximise their foraging efficiency, predators should forage where prey are most dense. Given the wide and diverse foraging distribution of seals and penguins, their density at sea is probably low. In that case it would be more efficient for killer whales to hunt penguins and seals where they are most concentrated: as they arrive at and leave the terrestrial sites at which they are obliged to breed and moult. Further, seals and penguins are capable divers and hunting them in shallow water limits their escape routes. Therefore, while fronts and mesoscale eddies concentrate prey enough to make them favourable foraging areas for seals and seabirds, this may not translate into sufficiently dense prey for a higher trophic level predator, particularly compared to the prey density near the islands. Fronts and mesoscale eddies are spatio-temporally dynamic and the unpredictability of these features could also make them less attractive to killer whales.

4.3 Seamounts

Killer whales did target two seamounts less than 100 km from the PEIs, which signals an aggregation of prey. Seamounts have been linked to increased abundance of top predators such as large fishes, turtles, seabirds and marine mammals (Kaschner, 2007; Morato et al., 2008, 2010; Santos et al., 2007; Thompson, 2007). One of the seamounts targeted by killer whales – Funk Seamount – was fished for Patagonian toothfish by the demersal longline fishery which has operated around the PEIs since 1996. Killer whales steal fish off the lines of this fishery (Kock et al., 2006; Williams et al., 2009), but neither licensed vessel appeared to be in the region when we recorded restricted movement at the seamounts (Chris Heinecken, pers. comm.²). It was previously considered unlikely that killer whales could naturally prey on toothfish (e.g., Kock et al., 2006), but our data (discussed below) show that killer whales can dive deep enough to capture toothfish.

Seamounts are also important to cephalopods (Clarke, 2007) and cetaceans and seals can catch cephalopods in the comparatively shallow water over seamounts more energy cost effectively. For

² CapFish, Unit 15, Foregate Square, Table Bay Boulevard, Foreshore, Cape Town, South Africa, 8001

example, Clarke (2007) suggested that sperm whales (*Physeter macrocephalus*) use seamounts as convenient 'restaurants' as they cross the abyssal plains. Elephant seals often include a large proportion of cephalopods in their diets (e.g., Clarke and MacLeod, 1982; Daneri et al., 2004; Green and Burton, 1993; Rodhouse et al., 1992; van den Hoff, 2004) and two male elephant seals from Marion Island made heavy use of the Funk and unnamed seamount in 2008 (Bester et al., 2009a, b), emphasizing the likely aggregation of cephalopods or fishes at these sites.

Killer whales feed on cephalopods elsewhere (e.g., Aguiar dos Santos & Haimovici, 2001; Berzin and Vladimirov, 1983; Hanson and Walker, 2014; Jonsgård and Lyshoel, 1970; Nishiwaki and Handa, 1958; Rice, 1968; Yamada et al., 2007). Cephalopods represented 89.6 – 99.3% of prey by number in four killer whale specimens from across the Pacific examined by Hanson and Walker (2014); two of these individuals fed on mesopelagic squids. In the Antarctic, 1.1% of 629 'pack ice' and 7.1% of 156 'open water' killer whale stomachs contained squid (Berzin and Vladimirov, 1983). Notably, cephalopod remains have been found in killer whale stomachs containing marine mammal remains (Ford et al., 1998; Hanson and Walker, 2014; Jonsgård and Lyshoel, 1970; Rice, 1968; Yamada et al., 2007) and Hanson and Walker (2014) suggest that cephalopods represent a previously underestimated component of *transient* ('mammal-hunting') killer whales' diets.

The restricted behaviour of Marion killer whales on seamounts, in conjunction with the dive data discussed below, leads to the suggestion that cephalopods and toothfish could be a component of Marion Island killer whales' diet. Carbon and nitrogen stable isotope analysis suggests that toothfish are not significant prey for Marion Island killer whales, but that squid may be important prey in addition to seals and penguins (Reisinger, 2015).

4.4 Diving behaviour

Most of the shallow dives which characterised the dive behaviour are expected to be linked to hunting for seals and penguins inshore, local travel and socialising. These shallow-dive data are similar to those for *transient* (mammal hunting) killer whales inshore in the eastern North Pacific. Baird (1994) attached a time-depth recorder to a single individual for 3.2 hours, recording a maximum dive duration of 7.6 min and 73 m (in water <185 m). Most (82.6%) of dives were to less than 20 m. (Miller et al., 2010) attached depth recorders to 11 *transients* for up to 18.4 hours and

found that they spent 90% of their time shallower than 40 m, with maximum dive depths (per individual) of 42–254 m (average \pm SD = 107 ± 60 m) and maximum dive durations (per individual) of 5.8–11.2 min (average \pm SD = 8.4 ± 1.4 min). *Resident* (fish-eating) killer whales which were studied with the same method in the same area (water depth <330 m), for up to 30.9 hours, dived deeper (average of per deployment maximums = 141 ± 62 m, range of per deployment maximums = 24–264 m) but for shorter lengths of time (day time mean \pm SD = 2.4 ± 0.6 min, night time = 2.3 ± 0.3 min (Baird et al., 2005).

The deep dive data presented herein show that killer whale diving capability far exceeds that published to date, but the depths are by no means surprising. Preliminary data from the Ross Sea show that *type C* (fish-eating) killer whales there dive up to 700 m (Durban and Pitman, 2013) and other, smaller odontocetes are capable of very deep dives (e.g. Heide-Jørgensen and Bloch, 2002; Laidre et al., 2003; Schorr et al., 2014; Tyack et al. 2006). Based on an allometric regression among odontocetes (Schreer and Kovacs, 1997), even a 6,000 kg killer whale would be capable of diving to 885 m and dive durations up to 43 min. Thus far diving behaviour has only been described in shallow, inshore waters, and for short times, likely explaining the shallow dive depths reported.

Distinct diel variation in dive behaviour was observed, with both individuals in this study diving significantly deeper during the day. Diel variation appears common among cetaceans and pinnipeds (e.g., Aoki et al., 2007; Au et al., 2013; Baird et al., 2002, 2005; Croxall et al., 1985; Le Boeuf et al., 1988) and is generally postulated to be related to the vertical migration of prey (Benoit-Bird and Au, 2003; Benoit-Bird et al., 2004). Dense aggregations of zooplankton and associated predators have been recorded around the PEIs at 300–400 m during the day and only shallower than 100 m at night (Perissinotto and McQuaid, 1992). This seems to correspond with much of the killer whale dive data. It is thus possible that the diel variation observed results in part from killer whales targeting larger predators feeding in the deep scattering layer. Larger cephalopods which would likely also target the deep scattering layers, would represent good prey. Penguins and fur seals could target the deep scattering layer at night, but it is beyond their diving range in the day. Elephant seals can dive deep enough to feed in the deep scattering layer at any time, and indeed elephant seals from Marion Island spend most time between 300 and 400 m and dive deeper during the day (Jonker and Bester, 1994; McIntyre et al., 2010). However it would seem more efficient for killer whales to hunt air-breathing prey at or near the surface, rather than dive deep for them during the day. Killer whales

seem to rely on vision and passive listening, rather than echolocation, to hunt seals inshore (Barrett-Lennard et al., 1996; Deecke et al., 2013) and it is unknown how effective this strategy would be beyond the euphotic zone.

4.5 Summary

Killer whales make use of a dense and predictable prey aggregation in the shallow, inshore waters of the Prince Edward Islands, but seem to alternate this hunting strategy with foraging over nearby seamounts. The oceanic setting of the islands appears to make this switching profitable. This population of killer whales does not seem to utilize distant bathymetric features or fronts as penguins and seals from the Prince Edward Islands do. The restricted movements and general philopatry of individuals is interspersed with long-distance directed movements north of the islands.

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SUPPLEMENTARY TABLES

Supplementary Table S1 : Variance Inflation Factors (VIFs) for 7 predictor variables used to model behavioural mode of killer whales satellite-tagged at Marion Island. Abbreviations follow Table 2 in the main text.

Variable	VIF
LON	1.24
LAT	3.71
DEP	1.25
SST	2.25
CHL	1.12
SSH	4.75
SLP	1.03

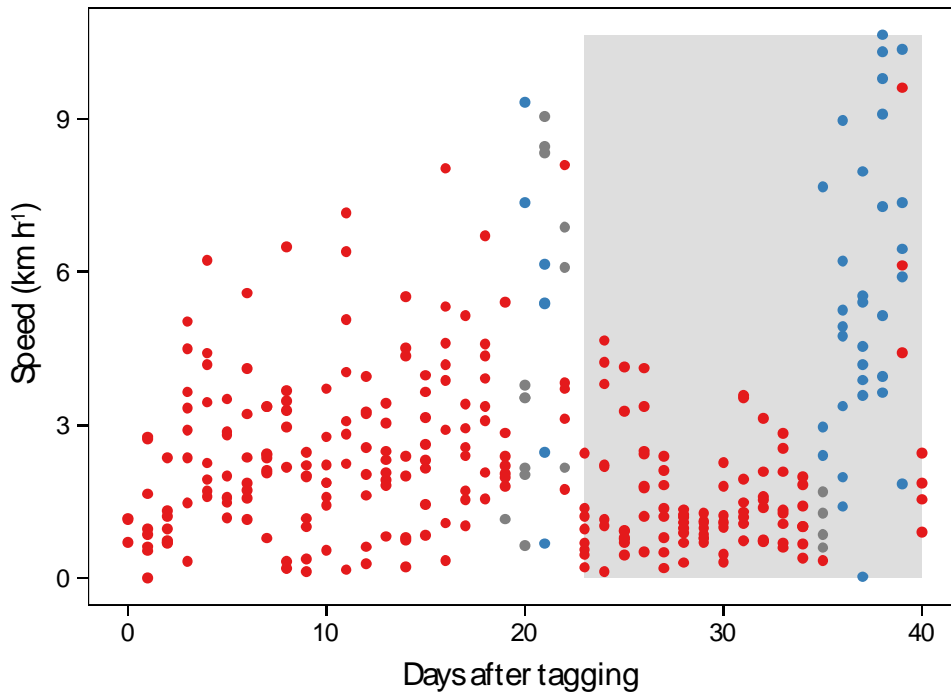
Supplementary Table S2 : Model selection parameters for generalised linear mixed effects models describing the relationship between killer whale behavioural mode and environmental predictors. Directed, long-distance tracks (M035, M059 and M026) were excluded for these models (*cf.* Table 3 in the main text). Abbreviations follow Table 2 in the main text. All models include track ID as a random effect. Models with $\Delta\text{AICc} \leq 2$ are shown (with model weights calculated among them) as well as the full and null models.

Rank	Model	df	AICc	ΔAICc	Weight
1	Behaviour ~ DEP + SST + LAT + SSH	6	96.3	-	0.266
2	Behaviour ~ DEP + SST + LAT + SSH + SLP	7	96.8	0.49	0.208
3	Behaviour ~ DEP + LAT + SSH + SLP	6	97.2	0.93	0.167
4	Behaviour ~ DEP + LAT + SSH	5	97.5	1.18	0.147
5	Behaviour ~ DEP + SST + LAT + SSH + SLP + LON	7	98.1	1.78	0.109
6	Behaviour ~ DEP + SST + LAT + SSH + SLP + CHL	7	98.2	1.91	0.102
Full	Behaviour ~ DEP + SST + LAT + SSH + LON + SLP + CHL	9	100.8	4.51	-
Null	Behaviour~	2	205.7	109.36	-

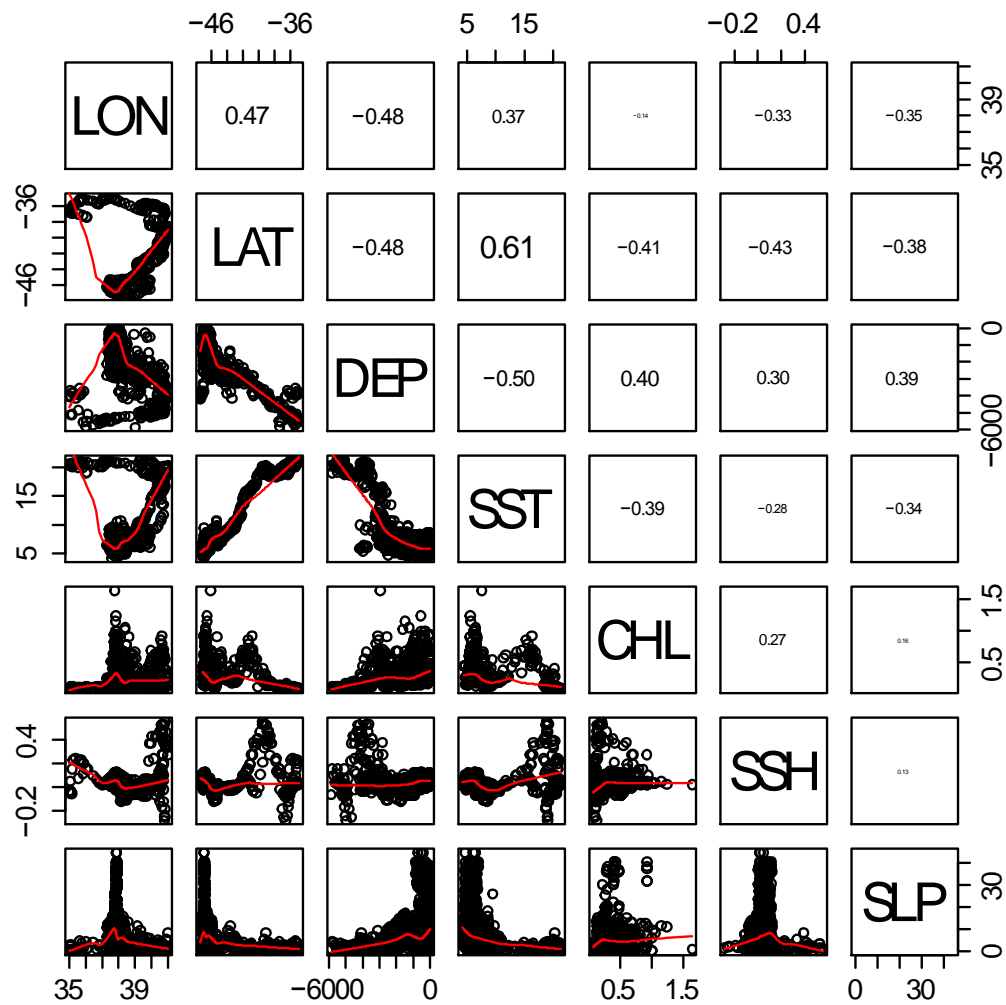
Supplementary Table S3 : Centred and standardised parameter estimates for our best generalised linear mixed effects models describing the relationship between killer whale behavioural mode and environmental predictors. Directed, long-distance tracks (M035, M059 and M026) were excluded for these models (*cf.* Table 4 in the main text). Abbreviations follow Table 2 in the main text. SE – standard error; z – z -score; p – p -value.

	Estimate	SE	z	p
<i>Model rank 1</i>				
Intercept	15.82	4.76	3.33	<0.001
LAT	-2.82	0.88	-3.22	0.001
DEP	1.13	0.34	3.38	<0.001
SST	-1.32	0.76	-1.75	0.080
SSH	-4.23	0.84	-5.06	<0.001
<i>Model rank 2</i>				
Intercept	15.61	4.72	3.31	<0.001
LAT	-2.78	0.91	-3.07	0.002
DEP	1.07	0.34	3.10	0.002
SST	-1.21	0.77	-1.57	0.117
SSH	-4.06	0.85	-4.79	<0.001
SLP	0.80	0.65	1.22	0.224

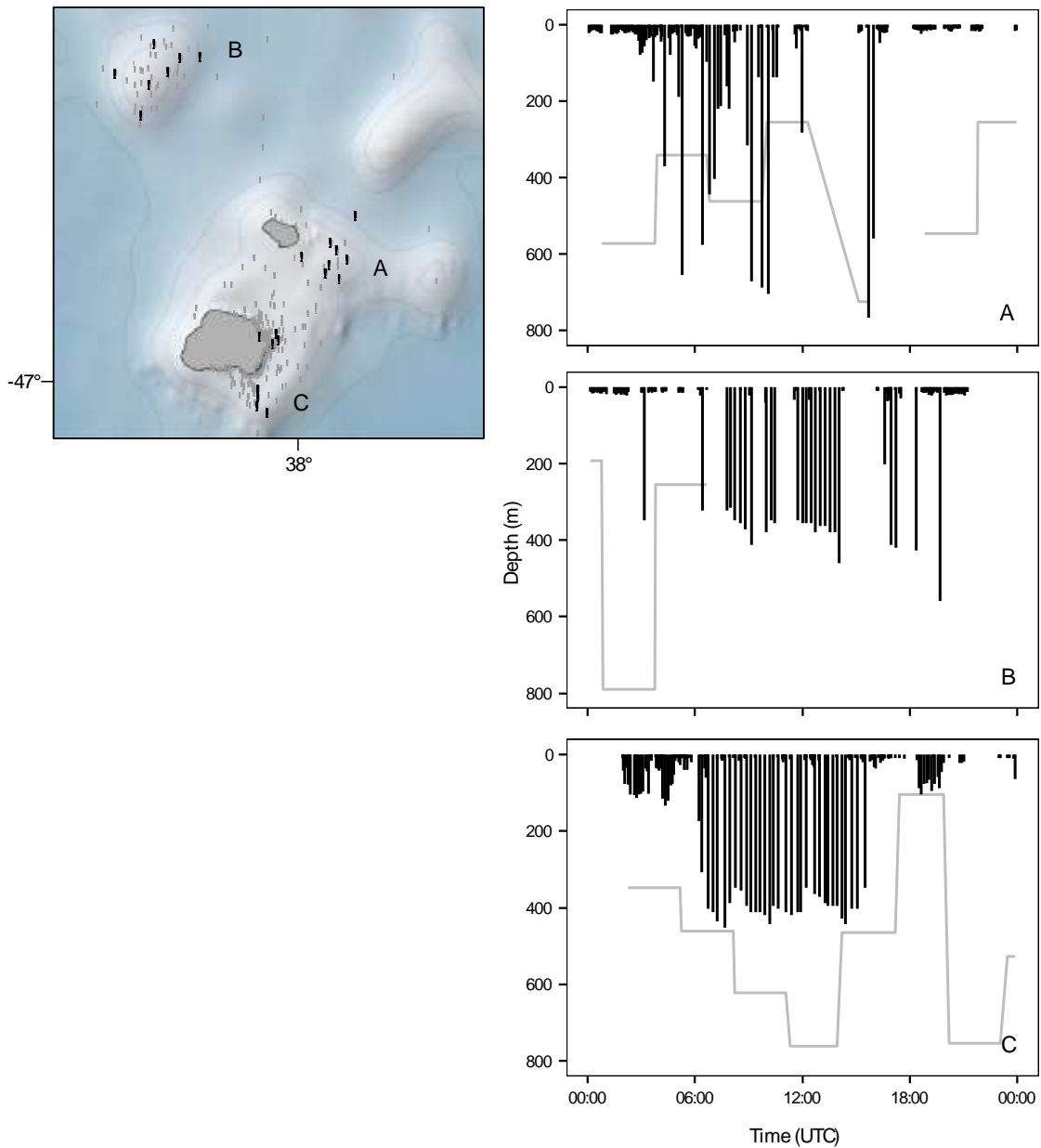
SUPPLEMENTARY FIGURES



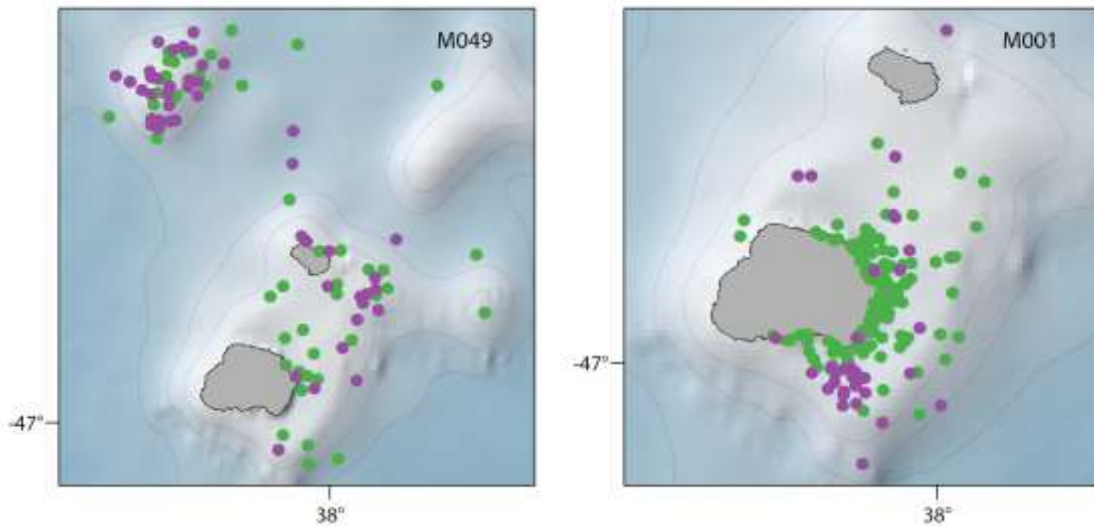
Supplementary Figure S1 : Estimated movement speed of an adult female killer whale (M017) satellite-tagged at Marion Island, plotted against time since deployment. Points are coloured by behavioural mode (restricted – red; transit – blue; uncertain – grey). The grey shaded area indicates where position estimates were in water <1000 m, over an unnamed seamount to the north of Marion Island. M017 did not have a calf when she was tagged, but was observed with a young calf 15 days after her tag stopped transmitting. Her restricted behaviour on the unnamed seamount (grey shading) coincided with reduced speeds 28–29 days after tagging, although her movement speeds were fairly high again at 35–40 days. Her calf was very likely born while she was tagged, and we speculate that she gave birth over the seamount.



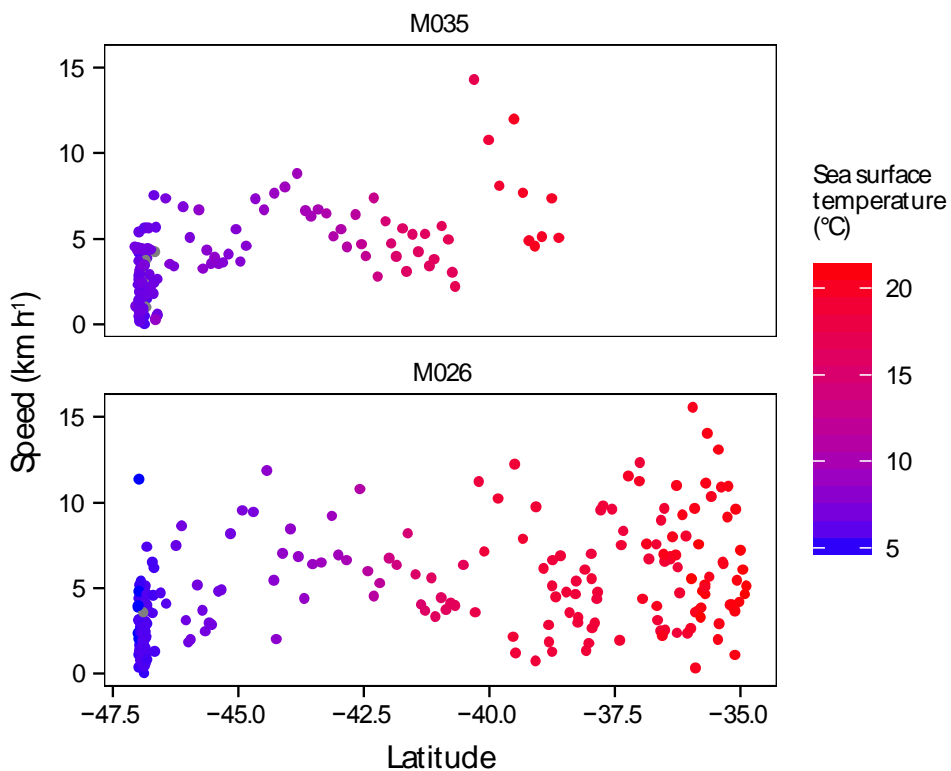
Supplementary Figure S2 : Scatterplot matrix showing the relationships among 7 explanatory variables used to model the behavioural mode of killer whales. Pairwise scatterplots with a fitted loess smoother (red line) are shown below the diagonal and Spearman's rank correlation coefficients (r_s), with text sizes proportional to the coefficient values, are shown above the diagonal. Variable names are abbreviated following Table 2 in the main text.



Supplementary Figure S3 : Daily dive behaviour examples for two killer whales from Marion Island. A) Deep diving by M049 near the inter-island shelf edge, including a dive to 767.5 m; B) Diving bout by M049 to ~400 m on a seamount; C) Diving bout by M001 to ~400 m near the shelf edge. The temporally closest position estimates to the dives shown in the plots are indicated by black points on the map (top left), all other locations are shown in grey. Depth contours on the map are at 500 m intervals. In the dive plots (right), black bars indicate maximum dive depths and grey lines indicate the approximate bottom depth at the temporally nearest position estimate. Spherical Mercator projection.



Supplementary Figure S4 : Position estimates associated with shallow (<200 m; green points) and deep (≥200 m; purple points) dives of two killer whales at Marion Island. Due to overplotting, not every dive is represented as a point on the map. Depth contours are at 1000 m intervals. Spherical Mercator projection.



Supplementary Figure S5 : Movement speed plotted against latitude for two killer whales which made long-distance, directed movements northwards from Marion Island. Points are coloured by the remote-sensed monthly average sea surface temperature measured at each position estimate.