Marine habitats of juvenile southern elephant seals from Marion Island

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ABSTRACT: Marine mammals forage in dynamic environments characterized by variables that are continuously changing in relation to large-scale oceanographic processes. In the present study, behavioural states of satellite-tagged juvenile southern elephant seals (n = 16) from Marion Island were assessed for each reliable location, using variation in turning angle and speed in a state–space modelling framework. A mixed modelling approach was used to analyse the behavioural response of juvenile southern elephant seals to sea-surface temperature and proximity to frontal and bathymetric features. The findings emphasised the importance of frontal features as potentially rewarding areas for foraging juvenile southern elephant seals and provided further evidence of the importance of the area west of Marion Island for higher trophic-level predators. The importance of bathymetric features during the transit phase of juvenile southern elephant seal migrations indicates the use of these features as possible navigational cues.

KEY WORDS: Marion Island · Southern elephant seals · Juveniles · Frontal features

INTRODUCTION

The sub-Antarctic Prince Edward Islands (46° 50′ S, 37° 50′ E) form an isolated island group with a climate that is driven by prevailing regional atmospheric circulation patterns (Rouault et al. 2005). Changes in local climatic conditions that have been documented for one of the 2 islands in the group, Marion Island (Smith 2002, le Roux & McGeoch 2008), may be linked to changes in the semi-annual oscillation event in the southern hemisphere (Rouault et al. 2005) or changes in large-scale ocean dynamics (Hall & Visbeck 2002), among other factors. These changes in atmospheric circulation patterns and large-scale ocean dynamics are reflected in changing sea-surface temperature gradients at midlatitudes (Simmonds & Jones 1998, Mo 2000). Although it may be

obvious in its manifestation (le Roux & McGeoch 2008), the exact consequences of these changes in oceanographic conditions for highly mobile marine mammals are difficult to predict and require long-term studies to define and understand foraging ranges and habitats (Simmonds & Isaac 2007). Age- and sex-related responses to environmental variables also need to be considered in order to make accurate predictions about the consequences of environmental variability on a species, especially for sexually dimorphic species that may display sex-related segregation in some behaviours, such as the selection of foraging grounds and diving behaviour (McIntyre et al. 2010).

Several studies correlated foraging movements of both northern and southern elephant seals *Mirounga* spp. and variability in regional oceanographic conditions (Crocker et al. 2006, Biuw et al. 2007, 2010).

Southern elephant seals *M. leonina* make long seasonal migrations to find suitable foraging areas (McConnell et al. 1992, Campagna et al. 2000, Bradshaw et al. 2004, Bailleul et al. 2007, Tosh et al. 2009). Different populations of southern elephant seals evidently use different areas of the Southern Ocean depending on where they haul out to breed and moult (Campagna et al. 2006, Biuw et al. 2007). Recently weaned pups and 1 yr olds (i.e. yearlings) appear to forage closest to their birth sites (Bornemann et al. 2000, McConnell et al. 2002, van den Hoff et al. 2002). Sexual dimorphism is not yet apparent in young seals, but young seals are more limited in their foraging abilities than adults (Stewart 1997, van den Hoff et al. 2002). The foraging movements of weaned pups and yearlings is important because survival of these age classes is generally low (Hindell et al. 1991, Pistorius & Bester 2002, McMahon et al. 2003) and may be more sensitive to variability in oceanographic conditions, prey distribution and abundance than older age classes (Field et al. 2007). All juvenile southern elephant seals perform an initial migration after weaning; this migration is thought to be genetically programmed and occurs without any prior knowledge of the surrounding region (Bornemann et al. 2000). Juveniles at Marion Island may return to their birth sites for a subsequent winter haul-out (Kirkman et al. 2001) and will generally return to sea before returning to moult early in the following summer (Kirkman et al. 2003).

Southern elephant seals born at Marion Island must quickly learn to survive in a highly variable environment. Oceanographic conditions surrounding Marion Island are dominated by the Antarctic Circumpolar Current (ACC). The ACC is bounded in the north by the Subantarctic Front (SAF) and in the south by the Antarctic Polar Front (APF). These frontal features are characterised by strong temperature, salinity and density gradients (Belkin & Gordon 1996, Bost et al. 2009). Increased vertical mixing due to interactions between water masses and bathymetric features is often observed close to frontal features (Bost et al. 2009). The fronts of the ACC, in the vicinity of the Southwest Indian Ridge (SWIR), close to Marion Island, are considered to be variable in terms of structure and position (Durgadoo et al. 2010).

The region west of Marion Island is also characterised by higher than average kinetic energy created by the presence of eddies arising from interaction of the ACC with the regional bottom topography (Ansorge et al. 1999, Ansorge & Lutjeharms 2005). Mesoscale eddies are counter-current waterbodies within greater currents and are responsible for the transfer of the physical energy of the ocean water to trophic energy (Bakun 2006). The physical flow properties of eddies in relation to the surrounding water masses can cause enrichment, concentration and retention of resources, creating favourable foraging grounds for ocean predators (Bakun 2006), such as birds (Nel et al. 2001, Cotté et al. 2007), sea-turtles (Polovina et al. 2006), fur seals (de Bruyn et al. 2009a) and southern elephant seals (Campagna et al. 2006, Bailleul et al. 2010, Dragon et al. 2010).

Movements of juvenile elephant seals have been previously studied at Macquarie Island (Hindell et al. 1999, McConnell et al. 2002, van den Hoff et al. 2002, Field et al. 2005) and at King George Island off the Antarctic Peninsula (Bornemann et al. 2000). At Macquarie Island, young seals foraged near the APF (McConnell et al. 2002) and the Campbell Plateau (van den Hoff et al. 2002). At King George Island, weaned pups showed no individual variation, all foraging in the open sea west of the De Gerlache Seamounts that lie to the west of the Antarctic Peninsula. Our study at Marion Island covers 6 yr and assesses the variability in foraging movements of young seals in a heterogeneous and variable ocean environment.

The present study describes the movements of juvenile southern elephant seals from Marion Island. Generalised mixed effects models are used to investigate the relationship between behavioural states, namely searching or transiting, in relation to selected environmental covariates that could potentially influence feeding conditions. This research focussed on the influence of bathymetric features, frontal features and sea-surface temperatures on the behavioural state of juvenile southern elephant seals during their migrations from Marion Island.

MATERIALS AND METHODS

Telemetry data

Twenty-six satellite-linked data recorders were attached to juvenile southern elephant seals at Marion Island from 2001 through 2006 (see Table 1). The ages of seals were determined either by uniquely numbered flipper tags (n = 24; de Bruyn et al. 2008) or their body size and shape (n = 2; e.g. Campagna et al. 2006). The results in the present study do not include the first foraging trip made after weaning. All of the animals tracked had already engaged in at least 1 foraging trip. Under-yearlings in the present study are defined as animals that are 0.5 yr old, and

yearlings have already turned 1. The birth date of all elephant seals on Marion Island is 15 October, coinciding with the maximum number of females present during the elephant seal breeding season, which lasts for 3 wk.

Seals were immobilised with intramuscular injections of ketamine hydrochloride (Bester 1988, Erickson & Bester 1993), and then telemetry instruments, prepared with a base of gauze netting, were glued to the pelage on the top of their heads using quick setting epoxy resin (Araldite®, Ciba Geigy) following Fedak et al. (1983). Transmitters were either removed from sedated animals by shaving the pelage under the device to detach the device or during the moult, when devices are shed naturally with the moulting pelage.

All data were collected via the ARGOS Data Collection and Location Service and are archived and available through the data library Publishing Network for Geoscientific and Environmental Data (PANGAEA; www.pangaea.de). The list of relevant DOIs is available from the corresponding author.

Raw ARGOS location data were modelled using a state–space approach, outlined by Breed et al. (2009). This model provides location estimates from raw ARGOS location data that incorporate the inherent error associated with ARGOS location data as well as estimating either a searching (Mode 1) or travelling mode (Mode 0) at regular time intervals (Jonsen et al. 2005). A time interval of 12 h was chosen for the present study. The behaviour of satellite-tracked animals is incorporated into animal movement models based on the assumptions that when searching, animals display slower swim speeds and larger deviations in consecutive turning angles in relation to the transiting portions of the tracks. The correlated random walk model that was fit to individual tracks is explained in detail by Breed et al. (2009). The model was fit by running 2 Markov chain Monte Carlo (MCMC) chains for 10 000 iterations, with a burn-in of 7000, sampling all model parameters and each location estimate. Every fifth point of 3000 remaining samples was retained, resulting in a total of 600 MCMC samples in each chain. A mean and a variance were calculated for each location estimate and model parameter from the 600 MCMC samples.

Movement parameters and behavioural states were estimated from the modelled tracks. In cases where double migrations were recorded, each migration was analysed separately.

A series of generalised mixed effects models (*lme4* package in R) with individual as a random effect were constructed to test the influence of bathymetry

(IOC & IHO 2003), fronts and 1° gridded, weekly sea-surface temperatures (Reynolds et al. 2002) on the behavioural state of locations as predicted by the state–space models (i.e. Mode 0 = travelling and Mode 1 = searching). Bathymetry was included in the model by categorising each location based on whether or not the location fell within a 1° buffer zone of the SWIR and the ABFZ. In addition to sea-surface temperature values for each location, locations were also categorised based on whether or not the location fell within 1° of frontal features, namely the SAF and the APF. Buffers were drawn around features, incorporating the distance represented by 1° of latitude and longitude to remain consistent with the sea-surface temperature data. The models were fit using a binomial distribution with a logit link because of the binary nature of the response variable, in this case 'mode'. Models were selected using a backward model selection process (Crawley 2007, Zuur et al. 2009). Starting with a full additive model (response ~ fixed effects + random intercept), the least influential fixed effects were sequentially removed from the model. Likelihood ratio tests were used to test if there were significant differences between models with individual fixed effects retained in the final model and a NULL model. Models were run using R v. 2.12.0 (R Development Core Team 2008).

RESULTS

Model performance

Of 26 juvenile seals tracked from Marion Island (2001 to 2006), data from 16 individuals were retained and tracks shorter than 40 d were not analysed. The state–space model detected both behavioural states (0: travelling; 1: searching) in 22 of the migrations analysed in the present study (n = 16 individuals) (Fig. 1). A total of 25 migrations were analysed, and 3 tracks only showed outward movements ending before any searching behaviour was recorded. The model performed consistently across individuals, with MCMC model runs converging for all individuals. All model outputs for the state space analysis are available from the corresponding author.

Spatial behaviour and oceanographic conditions

Seven seals (GG154, OO312, BB045, BB032, BB018, BB193, BB125) (Table 1) showed outward movements of 50 d or longer (range: 50 to 144 d) without return-
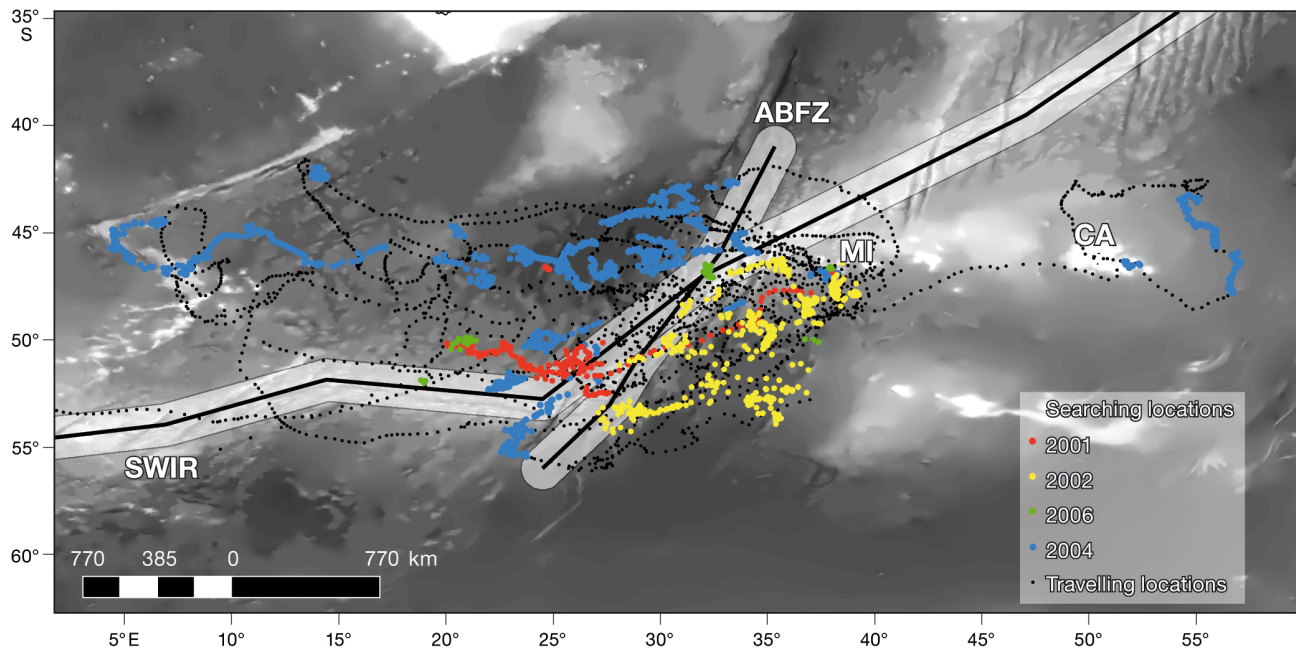
Fig. 1. State−space derived location estimates for juvenile southern elephant seals tracked from Marion Island (2001 to 2006) in relation to the bathymetry of the region. Major bathymetrical features, the Andrew Bain Fracture Zone (ABFZ) and the Southwest Indian Ridge (SWIR), are surrounded by a 1° buffer. Marion Island (MI) and the Crozet Archipelago (CA) are indicated on the map. Searching locations are indicated by different colours for each year, and travelling locations are indicated in black

ing to Marion Island. Searching behaviour was recorded for 4 of these animals; 3 animals (GG154, OO312 and BB018) showed >65% searching behaviour, starting such behaviour immediately after departure, whilst BB032 showed <10% searching behaviour. Three of the animals did not display any searching behaviour.

Nine seals were tracked for entire (double) migrations, i.e. returning to Marion Island for the winter haul-out after an initial foraging trip and completing a second foraging trip thereafter (Table 1). Postmoulting (under-yearlings and yearlings) migrations were on average longer (104 ± 12 d) than post-winter migrations (82 ± 19 d), with the exception of 2 animals (BB277 and TO340) tracked in 2004 that recorded post-moulting trips of 62 and 42 d respectively as opposed to post-winter trips of 151 and 137 d respectively. Seven of the animals displayed searching behaviour (Mode 1 locations as predicted by the state−space analysis) in discrete bouts, flanked by locations of active travelling. One animal (WW296) recorded a complex track with 90% of locations being Mode 1 locations that were scattered throughout the track. One animal (BB277) did not display any Mode 1 locations in the post-moult migration but recorded 40% Mode 1 locations in the post-winter migration. The animals that completed double mi-

grations recorded an average of 39.63% searching behaviour (range: 14 to 75%) commencing with this behaviour on average 33 d (range: 0 to 88 d) after departure.

The final model included 3 covariates, namely, the presence or absence of a location within 1° of a frontal zone, the presence or absence of a location within 1° of the SWIR and the ABFZ, and the season (Table 2). The effects of all covariates were significant (p < 0.001). The final model had a marginally better fit than the full model, which also included sea-surface temperature. Both models were improvements against the null model, which only included 'individual' as a random effect.

The probability of searching behaviour was positively influenced if a location occurred within 1° of a frontal structure. Of the 60% of searching locations found in close proximity to frontal zones, 67% were found closer to the SAF, and 33% of locations were closer to the APF. This result was not reflective of all of the years, with most of the searching locations during 2001 to 2002 and 2006 occurring in the vicinity of the APF (2001 = 95%, 2002 = 51% and 2006 = 57%; Fig. 2). The only year when the SAF was preferred, 2004 (88%), was the year with the greatest sample of individuals, which skewed the overall results (Fig. 3). The probability of searching behaviour was

Table 1. Deployment summary for juvenile southern elephant seals from Marion Island. The migration stage, migration duration, time to first search location and the percentage of searching locations for each migration are given. Search locations were identified using state-space models. Dates given as year/mm/dd. Animals recording double migrations are featured in **bold**. nd: not determined

Tag	Sex (M/F)	Age (yr)	Transmitter type	Date deployed	Migration stage	Duration (d)	Time to first search (d)	Searching locations (%)
GG154	F	1	Telonics-ST10	2001/04/16	Post-moult	50	1	100.00
GG039	**M**	**1**	**Telonics-ST10**	**2001/04/19**	**Post-moult**	**115**	**28**	**44.35**
				2001/09/06	**Post-winter**	**73**	**23**	**5.48**
OO312	F	0.5	Telonics-ST10	2002/04/09	Post-moult	95	1	94.05
WW296	**M**	**1**	**Telonics-ST10**	**2002/04/08**	**Post-moult**	**85**	**1**	**90.59**
				2002/08/12	**Post-winter**	**49**	**1**	**91.84**
YY428	F	0.5	Sirtrack Kiwisat	2004/04/13	Post-moult	120	29	44.17
			Sirtrack Kiwisat	2004/08/14	Post-winter	69	43	41.67
YY191	**F**	**0.5**	**Telonics-ST10**	**2004/04/16**	**Post-moult**	**101**	**33**	**82.46**
				2004/08/10	**Post-winter**	**105**	**5**	**75.00**
YY232	**M**	**0.5**	**SMRU/Series 9000 SRDL**	**2004/04/15**	**Post-moult**	**102**	**26**	**46.08**
				2004/08/04	**Post-winter**	**93**	**15**	**58.06**
YY302	**M**	**0.5**	**Telonics-ST10**	**2004/04/27**	**Post-moult**	**98**	**35**	**36.73**
				2004/08/19	**Post-winter**	**95**	**15**	**64.21**
BB277	**F**	**1**	**Sirtrack Kiwisat**	**2004/04/13**	**Post-moult**	**62**	**nd**	**0.00**
				2004/06/30	**Post-winter**	**151**	**27**	**39.74**
BB045	F	1	Sirtrack Kiwisat	2004/04/15	Post-moult	57	27	39.74
BB032	F	1	Sirtrack Kiwisat	2004/04/15	Post-moult	108	nd	0.00
BB018	F	1	Sirtrack Kiwisat	2004/04/16	Post-moult	122	58	10.53
BB193	F	1	Sirtrack Kiwisat	2004/04/17	Post-moult	144	32	67.01
BB125	M	1	Telonics-ST10	2004/04/18	Post-moult	88	nd	0.00
TO340	**M**	**1**	**SMRU/Series 9000 SRDL**	**2004/04/18**	**Post-moult**	**42**	**nd**	**0.00**
				2004/06/27	**Post-winter**	**137**	**16**	**14.29**
RR078	**M**	**1**	**Sirtrack/Kiwisat 101**	**2006/04/17**	**Post-moult**	**109**	**nd**	**0.00**
				2006/09/03	**Post-winter**	**89**	**39**	**3.33**

also positively influenced by season. Locations had a higher probability of being searching locations if recorded in spring and winter.

Table 2. The results of generalized linear mixed models comparing environmental variables in 2 behavioural (0: travelling, 1: searching) modes identified by state–space models. The environmental variables were (1) proximity to a bathymetric feature (0: further than 1°, 1: within 1°) (Bathy); (2) proximity to a frontal feature (0: further than 1°, 1: within 1°) (Front); (3) sea-surface temperature (SST) and (4) Season. The null and full additive models are listed first, and thereafter, the models as the least influential fixed effects are removed until a model with all significant effects is achieved. Models with individual fixed effects are listed. Akaike information criterion (AIC) and ΔAIC values are given to compare models. ±indicates the top 2 models that did not differ from each other. All models differed from the null

Fixed effects	AIC	ΔAIC	Log likelihood	df
Null	4110.8	444.6	−2051.4	4
SST + Bathy + Front + Season±	3667.5	1.3	−1825	7
Bathy + Front + Season±	3666.2	0	−1826.1	6
SST	4102	435.8	−2046	5
Bathy	4047.6	381.4	−2018.8	5
Front	3947.7	281.5	−1968.8	5

The strongest significant negative influence on the probability of foraging behaviour was whether or not a location was situated within 1° of either the SWIR or the ABFZ. Of all analysed locations, 42% were within 1° of the SWIR and the ABFZ, and of these, 75% were travelling locations (Fig. 1).

DISCUSSION

The movements of the juvenile seals tracked in the present study were strongly influenced by frontal and bathymetric features. Whilst searching behaviour tended to be associated with sea-surface temperature frontal structures, travelling behaviour tended to be associated with the ABFZ and the SWIR. Virtually all animals recorded searching behaviour along frontal zones, which

are characterised by higher abundances of secondary producers compared to the open ocean (Pakhomov & McQuaid 1996, Froneman et al. 2002, Constable et al. 2003, Bost et al. 2009). The importance of frontal structures as foraging grounds around Marion Island has been reported for subantarctic fur seals *Arctocephalus tropicalis* (de Bruyn et al. 2009a), grey-headed albatrosses *Thalassarche chrysostoma* (Nel et al. 2001) and adult female southern elephant seals (Jonker & Bester 1998), although interfrontal zones were also targeted in the latter study.

Seals tracked in 2004 ranged toward the SAF. In 2001, 2002 and 2006, seals ranged toward the APF even though the APF was further south during these years than in 2004. Ansorge et al. (1999) suggested that availability of macrozooplankton associated with the SAF would increase when the SAF is close to Marion Island. However, when the SAF lies farther north, the PFZ broadens, resulting in the dissipation of advective forces, and trapped eddies are observed over the shelf separating Prince Edward and Marion islands (Perissinotto & Duncombe Rae 1990), possibly resulting in higher chlorophyll *a* concentrations (Hunt et al. 2001). Our study shows that juvenile southern elephant seals used the SAF and did not use the shelf between Prince Edward and Marion islands when the front was situated further to the north. This may be linked to the prey species that are being targeted by juvenile southern elephant seals from Marion Island. Lanternfish (Myctophidae) and other larger prey items, such as the fish *Magnisudis prionosa* and the squid *Martialia hyadesi*, have been found in the diets of grey-headed albatross *Thalassarche chrysostoma* from Marion Island (Nel et al. 2001). Grey-headed albatross focused foraging effort along frontal zones and made conspicuous use of eddies (Nel et al. 2001). Although the use of eddies is not addressed in our study, it is likely that juvenile southern elephant seals from Marion Island also use these features, and further detailed studies are required for confirmation. Juvenile seals in 2004 may have been attracted to the SAF owing to the development of an intense area of heterogeneity known as the Subtropical Convergence Zone (STC). The STC is created by the interaction between the SAF, the Subtropical Front (STF) and the Agulhas Return Current and is a region of unpredictable, enhanced pelagic biomass (Barange et al. 1998) resulting from periodic blooms (Weeks & Shillington 1996). Increased levels of chlorophyll pigmentation (indicators of primary production) are facilitated by strong frontal gradients that are created by isotherms being in close proximity to each other (Weeks & Shillington 1996).
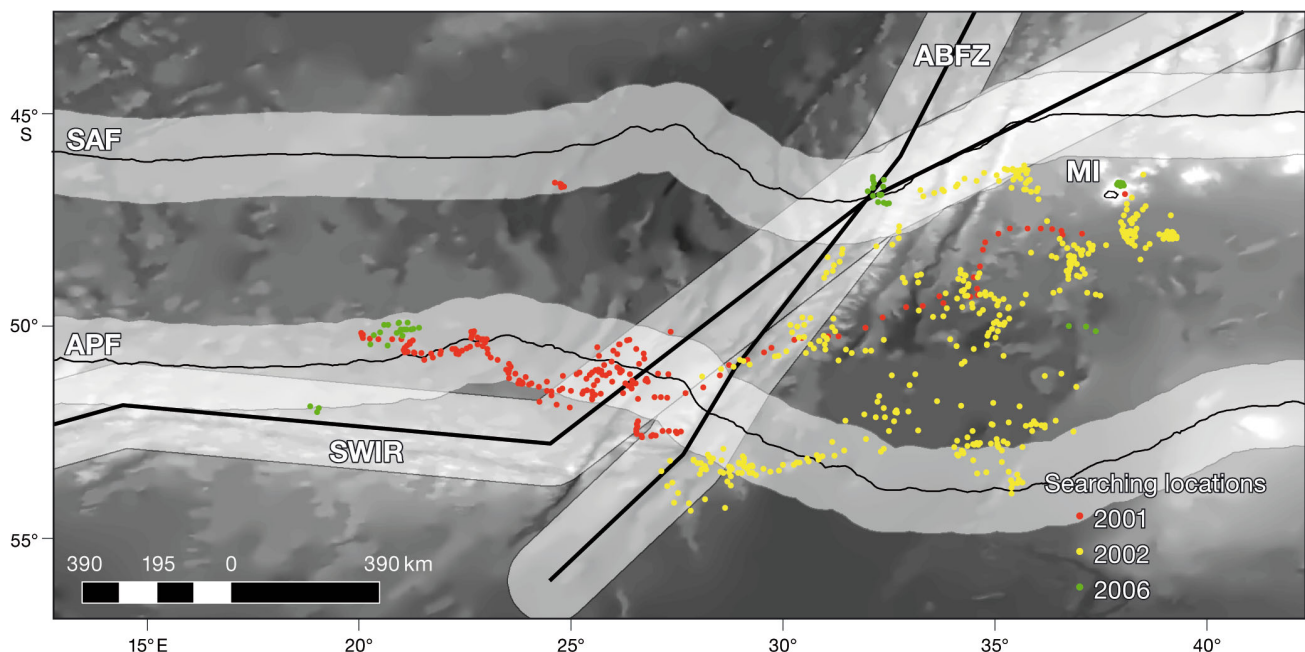

Fig. 2. State–space derived searching location estimates for juvenile seals tracked in 2001, 2002 and 2006. The Subantarctic Front (SAF) and the Antarctic Polar Front (APF), buffered by a 1° zone, are indicated. Major bathymetrical features, the Andrew Bain Fracture Zone (ABFZ) and the Southwest Indian Ridge (SWIR) are surrounded by a 1° buffer. Marion Island (MI) is indicated on the map
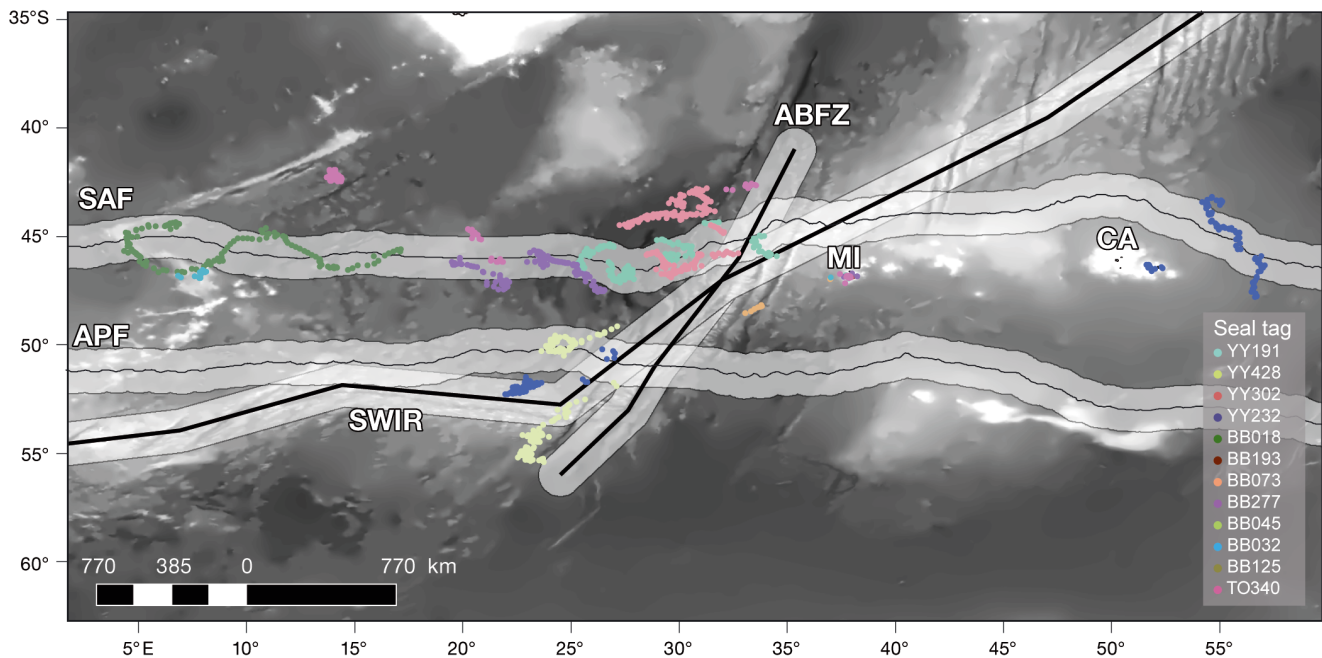
Fig. 3. State–space derived searching locations for juvenile seals tracked in 2004 (individuals are indicated in different colours). See Fig. 2 for abbreviations of major features

The strong seasonal signals evident in juvenile foraging patterns may be related to the seasonal fluctuations in frontal locations or may be an artefact of the yearly cycle that governs southern elephant seal haul-out patterns (Kirkman et al. 2001, 2003). Juvenile seals (age = 0.5 or 1 yr) are known to moult early in the season, well before older seals at Marion Island (Kirkman et al. 2003). This moulting period can last for up to a month (Condy 1979) from early December to January and would explain the lack of foraging behaviour recorded during summer. New devices were only deployed on juvenile seals at the time of Marion Island relief voyages (2001, 2002, 2004 and 2006), which take place in autumn (April/May). This precluded the collection of data during January, February and March. Transiting behaviour was predominant during autumn, representing the period when most animals were travelling to their foraging areas. Juvenile southern elephant seals from Marion Island appear to behave similarly to juvenile seals from Macquarie Island, travelling in a general direction and foraging opportunistically until a suitable prey patch is found (Field et al. 2005).

The models could explain the behavioural states of seals at only 50% of locations in the present study. This may be an indication that the effects included in the models did not take all the types of foraging patches that are available to seals from Marion Island into account. For example, while frontal zones may be the most important foraging areas for juvenile seals, seals might also rely on eddies created by the flow of the ACC over the intersection of the SWIR and the ABFZ (Froneman et al. 2002, Ansorge & Lutjeharms 2005, Bernard et al. 2007). Given that their limited foraging experience and smaller body size is likely to restrict their foraging ability (Irvine et al. 2000), juvenile seals might also use dense prey assemblages close to the sea surface and relatively close to the island. Such alternatives were not taken into account as model effects.

Of concern in tracking studies is the linkage between searching behaviour and foraging success. While we can only assume that foraging actually occurs in areas where searching behaviour has been predicted using state–space models, we cannot quantify the extent to which seals have been successful. Foraging success could be quantified using diving behaviour (e.g. Biuw et al. 2003, Thums et al. 2008), data measuring actual feeding behaviour (Liebsch et al. 2007, Naito et al. 2010) or measurement of body condition before and after foraging trips (e.g. de Bruyn et al. 2009b). Such data are vital if the links between animal movements, individual success and population dynamics (e.g. Weimerskirch et al. 2012) are to be made.

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