Vol. 521: 265–275, 2015
doi: 10.3354/meps11120

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 17

Spatial patterns in activity of leopard seals *Hydrurga leptonyx* in relation to sea ice

J. Meade[1,2,*], M. B. Ciaglia[1], D. J. Slip[2], J. Negrete[3], M. E. I. Márquez[3], J. Mennucci[3], T. L. Rogers[1]

[1]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
[2]Taronga Conservation Society Australia, Sydney, NSW 2088, Australia
[3]Instituto Antártico Argentino, Cerrito 1248 (C1010 AAZ), Buenos Aires, Argentina

ABSTRACT: Rapid changes to climate in the western Antarctic Peninsula region over the last 50 yr, which have led to decreases in the extent and duration of sea ice, are likely to have significant impacts upon the Antarctic ecosystem as a whole. Understanding the behaviour of higher trophic level animals occupying these regions is important, as they may be indicators of changes in prey availability and food-web structure. Leopard seals *Hydrurga leptonyx* are important components of the Antarctic ecosystem, because they are widespread and adapted to consuming prey at a range of trophic levels. They rely on sea ice for breeding, moulting and as a resting platform. Using tracks of 12 leopard seals, we calculated first-passage times (indicative of the intensity of area-restricted behaviour) and quantified relative habitat use, including both foraging and resting areas, using Cox proportional hazard models, in relation to coastline, bathymetry and sea ice. We also correlated monthly home range size with monthly sea-ice extent. We found that when sea-ice extent was low, leopard seals were restricted to coastal habitat, but that this effect was lost when sea-ice extent was greater. This was supported by the finding that leopard seal home range size decreased as the sea-ice extent decreased. Since leopard seals and other animals that consume krill are likely to be increasingly limited by sea-ice cover if the warming trend continues, we suggest that the krill fishery be restricted to offshore areas to avoid conflict with krill predators.

KEY WORDS: Antarctica · Area-restricted behaviour · First-passage time · Krill · Pack ice · Cox proportional hazard model

INTRODUCTION

Over the last 50 yr, the climate of the western Antarctic Peninsula (WAP) region has changed rapidly, with annual mean temperatures increasing by 3°C and winter mean temperatures by 6°C (Meredith & King 2005, Stammerjohn et al. 2008). Sea ice has decreased in duration by 100 d in the last 35 yr (Ducklow et al. 2013), and sea-ice cover has reduced by 47% (Forcada et al. 2012). Sea ice is a key driver of the Antarctic ecosystem, and changes in the timing of sea-ice expansion and contraction, as well as sea-ice coverage, are likely to have profound effects on marine mammals (Massom & Stammerjohn 2010). A reduction in the duration of sea-ice coverage also allows greater opportunity for the Antarctic ecosystem to be exploited by humans; for example, the extended periods of ice-free water have allowed a temporal and spatial expansion of the krill fishery, leading to increased krill catch (CCAMLR 2011, Nicol et al. 2012). Animals at higher trophic levels are likely to be key indicators of changes in food availability, distribution and food-web structure (Croxall et al. 2002); it is therefore important to understand the behaviour of large predators in areas affected by climate change and human exploitation.

*Corresponding author: j.meade@unsw.edu.au

Leopard seals *Hydrurga leptonyx* are apex predators adapted to consuming prey at a range of trophic levels, including seals, penguins, fish, cephalopods and Antarctic krill (Hofman et al. 1977, Øritsland 1977, Siniff & Stone 1985, Rogers & Bryden 1995, Hall-Aspland & Rogers 2004, Hall-Aspland et al. 2005). Leopard seals have a circumpolar distribution, and the main population occurs within the circumpolar pack ice, with higher densities close to the pack-ice edge (Bester et al. 1995, 2002, Rogers 2009). Leopard seals are pagophilic and use sea ice as a haul-out platform (Rogers & Bryden 1997), for pupping (late spring and early summer; Southwell et al. 2003), moulting (mid- to late summer) and as a resting platform throughout the year (Rogers et al. 2013). Unlike other ice seals, leopard seals are known to disperse beyond the sea-ice edge as the sea-ice extent expands, and return towards the Antarctic continent as the sea ice contracts (Southwell et al. 2008, Nordøy & Blix 2009, Aguayo-Lobo et al. 2011), and are commonly observed hauling out on sub-Antarctic islands in winter (e.g. Gwynn 1953, Rounsevell & Eberhard 1980, Bester & Roux 1986). These dispersal events may be related to sea-ice conditions, with more leopard seals hauling out on Bird Island, South Georgia, in years of greater sea-ice extent (Jessopp et al. 2004). Despite sightings of individuals beyond the pack-ice extent, previous tracking studies have suggested that most of the population is likely to spend most, if not all, of the year within the pack ice (Rogers et al. 2005, Kuhn et al. 2006). Leopard seal habitat is likely to decrease as sea-ice coverage decreases, and leopard seals have been observed at greater densities when sea-ice coverage is low (Bester et al. 1995), but this hypothesis has never been tested directly. Three previous studies have used satellite devices to track leopard seals (Rogers et al. 2005, Kuhn et al. 2006, Nordøy & Blix 2009), but because no quantitative assessment of leopard seal habitat selection has been made, our understanding remains limited (Southwell et al. 2008, 2012, Rogers et al. 2013).

Habitat selection analysis typically involves the assumption that the study area, or an individual's home range, is available at all times (Manly et al. 1992, Hjermann 2000). An alternative approach is to infer habitat selection from the intensity of habitat use along an animal's track, thus only habitat directly experienced by an animal is included in the analysis. First-passage time (FPT; Fauchald & Tveraa 2003) can be used to quantify the intensity of habitat use along an animal's path. A recent novel analytical method that has been used to quantify habitat use for several species of marine animals (e.g. Suryan et al. 2006, Freitas et al. 2008a,b, 2009, Einoder et al. 2011) utilises FPT as the response variable in Cox proportional hazard models (CPH: Freitas et al. 2008a). This allows relative habitat preference to be quantified, with a low hazard ratio (low risk of leaving an area) interpreted as a preference for a particular type of habitat.

In this study, we investigated adult leopard seal spatial behaviour in relation to sea ice in the WAP during the austral autumn and winter. First we used CPH models to quantify habitat selection. We predicted a preference for habitat within the sea-ice extent, given that leopard seals use sea ice as a haul-out platform; alternatively, we could expect to find a preference for habitat close to the sea-ice edge, as high densities of leopard seals have been observed there (Siniff 1991, Bester et al. 2002), and the ice edge consistently produces areas of high productivity which attract many top predators (Ainley & DeMaster 1990). We also expected to find a significant negative interaction between sea-ice extent and distance to coastline, because when sea-ice extent is reduced, most available ice will be found close to the coastline (e.g. having calved from glaciers, or been blown against the coast), and seals hauling out on sea ice have no option but to inhabit areas close to the coast. To test the assumption that leopard seal habitat is limited by sea-ice extent (Bester et al. 2002), we examined the relationship between monthly home range size and monthly sea-ice extent, and we predicted that monthly home range size will increase as the sea-ice coverage increases, as sea ice required for haul-out will be available over a wider area.

MATERIALS AND METHODS

Seal capture and study site

Field work was conducted at the Argentine Antarctic Station Primavera, on the Danco Coast, WAP (64° 09′ S, 60° 57′ W), in February of 2008, 2009 and 2012. Twelve Advanced Research and Global Observation Satellite (ARGOS) platform transmitter terminals (PTTs) were deployed on leopard seals judged to be adults based on standard length (nose to tail; Table 1) and tooth condition: 2 in 2008, 6 in 2009 and 4 in 2012. One tracker (20769, Table 1) was an ST-18 PTT (Telonics, packaged by Sirtrack NZ) and weighed 350 g; the remaining 11 tags were KiwiSat 101 Argos PTTs (Sirtrack) and weighed 500 g.

Table 1. Details of sex, mass (kg), date and location of capture, number of days each platform transmitter terminal (PTT) transmitted locations and satellite fixes per day before and after filtering for leopard seals *Hydrurga leptonyx* tracked in this study. All animals were equipped with KiwiSat tags except LS07-16, which received a Telonics tag

Seal ID	Sex	Mass (kg)	Capture date (d/mo/yr)	Total no. days transmitting	Capture location	Average no. fixes d^{-1} pre-filter	Average no. fixes d^{-1} post-filter
LS07-16	F	423[a]	27/02/2008	137	64.19° S, 60.96° W	34.23	29.88
LS07-19	M	303[a]	28/02/2008	347	64.15° S, 60.93° W	30.69	28.07
LS08-03	F	270[a]	11/02/2009	258	64.15° S, 60.94° W	28.79	25.02
LS08-08	M	240[a]	16/02/2009	145	64.26° S, 60.98° W	21.88	20.44
LS08-12	M	288[a]	20/02/2009	243	64.16° S, 60.93° W	13.42	12.65
LS08-16	F	413[a]	26/02/2009	116	64.26° S, 60.99° W	22.35	18.34
LS08-17	F	363[a]	26/02/2009	311	64.15° S, 60.95° W	21.71	19.76
LS08-19	F	360[a]	27/02/2009	303	64.22° S, 60.98° W	33.00	30.27
LS07-06	M	314	21/02/2012	313	64.16° S, 60.93° W	51.42	28.04
LS11-18	M	283	23/02/2012	131	64.20° S, 60.93° W	30.90	30.17
LS11-01	F	304	25/02/2012	272	64.19° S, 60.05° W	35.19	21.14
LS11-23	F	335	26/02/2012	160	64.20° S, 60.95° W	29.75	28.98

[a] Mass estimated from morphometrics (van den Hoff et al. 2005)

Seals were immobilised using a Tele-inject air gun darting system when hauled out on ice. Animals were darted and sedated using tiletamine/zolazepam (Higgins et al. 2002). Following immobilisation, sex was determined and seals were either weighed or mass was estimated from standard length and pectoral girth (van den Hoff et al. 2005; Table 1). PTTs were attached to the fur on the seals' backs using epoxy resin. Attachment ensured the antenna would break the surface when the seal was swimming at the surface. These trackers transmit positional information estimated by Doppler shift.

Data handling

Seals were caught in February at the end of the moult, and the trackers transmitted for varying periods, from 116 to 347 d (Table 1). Analysis was restricted to day of year (DOY) 60 (1 March, 29 February in leap years) to DOY 304 (31 October, 30 October in leap years), as all trackers were transmitting from 1 March and only 4 trackers continued to transmit after 30 October.

ARGOS locations are associated with a location class (3, 2, 1, 0, A and B, in descending order of accuracy), which correspond to estimated errors of 0.49, 1.01, 1.20, 4.18, 6.19 and 10.28 km, respectively (Costa et al. 2010). We used a filter based on swimming speed and turning angle to remove low-quality locations (Freitas et al. 2008c). The mean (± SE) distance between points of filtered paths was 1.59 ± 0.01 km, and the mean time between fixes was 0.91 ± 0.01 h. Post filtering, the mean number of locations per day recorded by the Telonics tracker (29.9) was within the range of the KiwiSat devices (range 12.7 to 30.3, mean = 24.4), so we assumed that there was no difference in the number or accuracy of fixes between the 2 tracker types.

FPT and area-restricted behaviour

To investigate area-restricted behaviour along the length of the seals' tracks, we performed FPT analysis (Fauchald & Tveraa 2003). Because FPT is designed to identify area-restricted behaviour along the entire path, each part of the path must have an equal probability of being sampled. Since satellites take positional fixes at relatively regular intervals in time, areas through which animals move slowly are sampled more frequently than areas through which animals move quickly. For this reason, we used linear interpolation to create new points uniformly distributed along the track, retaining the original shape (Freitas et al. 2009). We used a 5 km interval, as this was greater than the mean distance between filtered points and also greater than the mean error in the ARGOS system (Vincent et al. 2002, Costa et al. 2010).

FPTs were calculated for linearly interpolated points along complete tracks of individual seals for radii ranging from 5 to 50 km (at 5 km increments). To facilitate inter-individual comparisons, we calculated the mean scale of maximum variance of FPT (Calenge 2006) and found the peak to be at 15 km

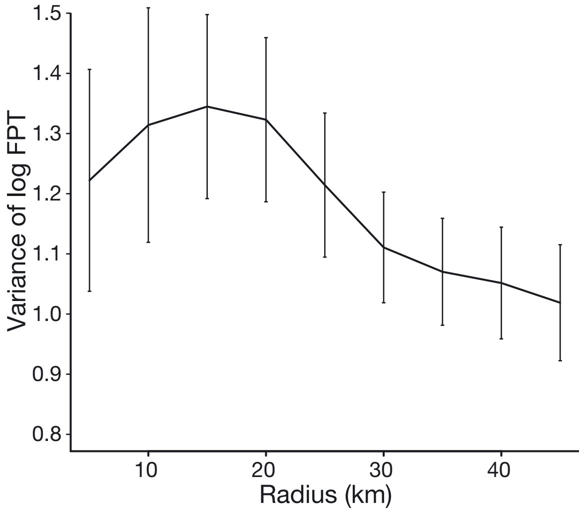

Fig. 1. Mean (± SE) of the variance in log-transformed first-passage time (h) plotted against radius (km) for 11 adult leopard seals *Hydrurga leptonyx* that exhibited area-restricted behaviour. The peak of mean variance occurred at a radius of 15 km

(Fig. 1). FPTs calculated at this common scale (Fauchald & Tveraa 2006) were used to compare area-restricted behaviour between individuals. One seal (LS11-23; Table 1, also see Fig. S1h in the Supplement at www.int-res.com/articles/suppl/m521p265_supp.pdf) did not exhibit a peak in variance for FPT, indicating that the animal did not concentrate its time in any particular area along its path, so it was excluded from further analysis (see 'Discussion').

Mixed effects CPH models were fitted in the R package 'coxme'. We fitted both fixed effects and mixed effects (incorporating a random effects term for each individual) CPH models (Therneau & Grambsch 2000). We used FPT (h) at the common scale (15 km) as the response variable. Depth, distance to coastline, distance to ice edge and sea-ice extent were included as linear explanatory variables. A binary factor was included to indicate whether the seals' position was within the sea-ice extent (1) or in open water (0). An interaction between 'ice extent' and 'distance to coastline' was included, because when sea-ice extent is low, ice would be expected to be found close to the coastline (e.g. having calved from glaciers, or been blown against the coast). Therefore, leopard seals may be restricted to areas close to the coastline when ice extent is low, but not when it is high.

Environmental variables were obtained for the positions at which FPTs were calculated. Sea bottom depths were extracted from a 30 arc second grid (ca. 0.93 km; the GEBCO_08 Grid, www.gebco.net). Shortest distance to the nearest coastline was calculated from a vector map of the WAP (Baddeley & Turner 2005). Daily sea-ice polygon shape files were obtained from the US National Ice Center (www.natice.noaa.gov). The shortest straight-line distance to sea-ice edge was calculated from these files in the same way as for coastline. To quantify sea-ice extent, the smallest rectangle encompassing positions of all seals from March to October (1 018 045 km^2) was drawn, and the percentage of the sea in this area covered by ice per day was calculated.

FPTs at a 15 km radius were often long (mean ± SE: 6.3 ± 0.16 d), and there is potential for spatial autocorrelation when the FPT radius is larger than the distance between points. To avoid spatial autocorrelation in FPTs, we used a Mantel test (Mantel 1967) within the R package ade4 (Calenge 2006) to determine the minimum distance between points along each seal track for which spatial autocorrelation is absent. Using the sub-sampled data, we then tested whether the models satisfied the assumption of proportionality required for CPH models (Therneau & Grambsch 2000, Collett 2003) we tested whether the scaled Schoenfeld residuals were equal to 0. This was verified from fixed effects CPH models as there is currently no method of testing for mixed effects CPH models (Freitas et al. 2008a). All variables used in the models satisfied the assumptions of proportionality.

We computed models including all additive combinations of the variables plus the interaction term. Once the candidate models were generated, we used Akaike information criterion corrected to effective sample size (AICc) values to select the best fitting model. We did this for both mixed effects and fixed effects models, and found the results to be very similar. We then went on to investigate the interaction between sea-ice extent and distance to coastline by dividing sea-ice coverage into 4 levels (0–40 %, >40–60 %, >60–80 %, >80 %). The area used to calculate sea-ice extent included an area to the east of the WAP that was always ice covered, and therefore the percentage coverage was never below 20 %. Using the averaged fixed effects model, we were able to predict hazard functions for seals at a set distance to the coastline under different sea-ice extents (this method is not yet available for mixed effects CPH models).

Home range

To investigate whether home range size varied in relation to sea-ice extent, we calculated 90 % kernel

Table 2. Candidate models ranked based on Akaike information criterion corrected to effective sample size (AICc) values calculated using the R package 'MuMIn'. Models up to 2 ΔAICc from the top model are shown in order of best fit for the mixed effects models. The top 6 best fitting fixed effects models are shown for comparison. Change in AICc, relative model weight, integrated log likelihood (log (*L*)) and degrees of freedom are also included. Sample size (number of positions) is 434. Coast: shortest distance to coastline (km), depth: sea bottom depth, ice extent: percentage sea-ice coverage, edge: shortest distance to ice edge (km), ice: a binary variable where 0 indicates that the seal is in open water and 1 indicates the sea is within the sea-ice extent

Model	AICc	ΔAICc	Weight	log(*L*)	df
Random effects included					
Coast + ice extent + coast × ice extent	4300.1	0.00	0.212	–2138.1	9
Coast + ice extent + coast × ice extent + depth	4300.4	0.24	0.188	–2137.2	10
Coast + ice extent + coast × ice extent + ice	4300.8	0.69	0.151	–2137.5	10
Coast + ice extent + coast × ice extent + depth + ice	4301.3	1.12	0.121	–2136.7	11
Coast + ice extent + coast × ice extent + edge	4301.9	1.80	0.086	–2137.9	11
Coast + ice extent + coast × ice extent + edge + depth	4302.0	1.86	0.084	–2137.0	11
Fixed effects only					
Coast + ice extent + coast × ice extent + depth + ice	4339.8	0.00	0.324	–2164.8	5
Coast + ice extent + coast × ice extent + depth	4340.1	0.32	0.277	–2165.9	4
Coast + ice extent + coast × ice extent + depth + edge + ice	4341.4	1.63	0.143	–2164.5	6
Coast + ice extent + coast × ice extent + depth + edge	4342.0	2.27	0.104	–2165.9	5
Coast + ice extent + coast × ice extent + ice	4343.2	3.49	0.057	–2167.5	4
Coast + ice extent + coast × ice extent	4343.5	3.74	0.050	–2168.7	3

utilisation distributions (Börger et al. 2006, Calenge 2006) for each month in which an individual was tracked for a minimum of 10 d (Fieberg & Börger 2012). Daily sea-ice extent was calculated as stated above, and the mean sea-ice extent was calculated to give a monthly estimate of sea-ice extent for each year that seals were tracked.

We used a linear mixed effects model with a Gaussian error structure and an identity link function. Individual identity was included as a random effect, and $\log_{10}$ monthly home range size (km^2) was the response variable. Monthly sea-ice extent was the explanatory variable. Marginal (fixed effect only) and conditional (entire model) R^2 values were calculated (Nakagawa & Schielzeth 2013).

RESULTS

FPT and area-restricted behaviour

In our models of habitat selection, the parameter most strongly affecting FPTs was the interaction between distance to coastline and sea-ice extent. The model-averaged results were very similar for both mixed effects and fixed effects CPH models (Table 2). As predicted, the coefficient was negative, indicating that proximity to the coastline has a greater effect on habitat selection when sea-ice extent is low (Table 3, Fig. 2). To investigate this result further, we estimated hazard ratios (e^{β}) at a fixed distance from the coastline (5 km), under low (<40%) and high

Table 3. Estimated coefficients (β), hazard ratios (e^{β}), 95% confidence intervals (CI(β)) and the relative variable importance for mixed effects and fixed effects Cox proportional hazard models. Sample size (number of positions) is 434. Confidence intervals which do not cross 0 (indicating significance) are shown in **bold**. Coast: shortest distance to coastline (km), ice extent: proportion of sea-ice coverage

Parameter	Random effects included				No random effects			
	β	e^{β}	CI (β)	Relative variable importance	β	e^{β}	CI (β)	Relative variable importance
Coast	0.074	1.076	**(0.04, 0.11)**	1.00	0.071	1.074	**(0.04, 0.10)**	1.00
Ice extent	2.060	7.871	**(1.43, 2.69)**	1.00	1.679	5.358	**(1.07, 2.29)**	1.00
Coast × ice extent	–0.079	0.924	**(–0.11, –0.03)**	1.00	–0.079	0.924	**(–0.12, –0.04)**	1.00
Depth	–0.000	1.000	(–0.00, 0.00)	0.47	–0.001	0.999	(–0.00, 0.00)	1.00
Ice	–0.256	0.774	(–0.65, 0.14)	0.32	–0.281	0.755	(–0.62, 0.06)	0.63
Edge	–0.000	1.000	(–0.00, 0.00)	0.00	–0.000	1.000	(–0.00, 0.00)	0.19

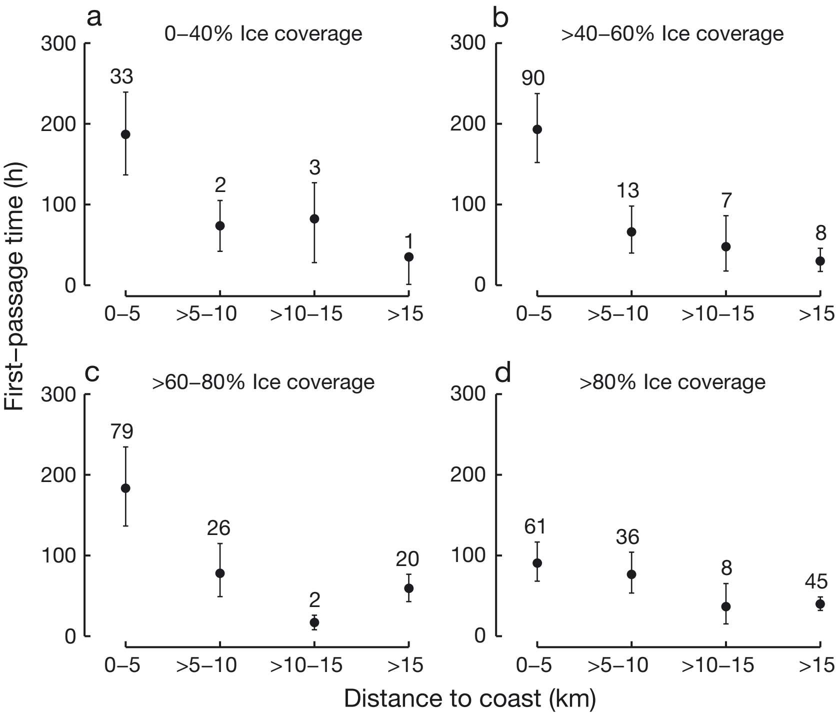

Fig. 2. Mean (± 95% confidence intervals) first-passage time (FPT; h) of adult leopard seals *Hydrurga leptonyx* for a 15 km radius, showing the relationship between distance to coastline (km) and FPT for 4 levels of sea-ice cover. Mean FPT was calculated using the percentile method of bootstrapping. Sample sizes are shown

(>80%) sea-ice cover. Hazard ratios were estimated from the fixed effects model only, as this method is not available for the mixed effects model; however, the results are likely to be similar since the estimates and hazard ratios from the mixed and fixed effects models are very similar. We found that when ice coverage was low (<40%) the hazard ratio at 5 km from the coastline was 0.75, indicating that seals were 25% less likely to leave an area than average, whereas at high levels of ice coverage (>80%), the hazard ratio was 1.39, indicating that seals were 39% more likely to leave a given area than average. This indicates that seals are likely to spend longer periods of time in a given area close to the coastline when the sea-ice extent is low, whereas they are relatively less likely to spend long periods close to the coastline when the sea-ice extent is greater.

Although depth, distance to ice edge and 'ice' (the binary variable indicating whether the seal was within the sea-ice extent or in open water) were included in the model-averaged results for both mixed effects and fixed effects CPH models, none of these factors had a significant effect on FPTs. In all 3 cases, the confidence intervals cross 0 for both mixed effects and fixed effects models (Table 3).

To investigate the relationship between sea-ice coverage and distance to coastline, we fitted a linear mixed effects model with a Gaussian error structure and an identity link function. We used mean daily straight-line distance to nearest coastline (km^2) as the response variable, and daily sea-ice extent as the explanatory variable. Seal identity was included as a random effect. We found a significant positive relationship between distance to coastline and proportion of sea-ice coverage (estimate = 20.64, SE = 4.34, df = 1, $p < 0.001$; Fig. 3). The marginal R^2 of the model was 0.21, and the conditional R^2, when taking into account individual variation, was 0.26.

Tracks plotted for each month with the corresponding position of the ice edge on Day 15 of each month showed no strong association between the position of the seal and the ice edge (Fig. 4; Fig. S1 in the Supplement). The ice edge extended up to 298 km beyond the position of the seals.

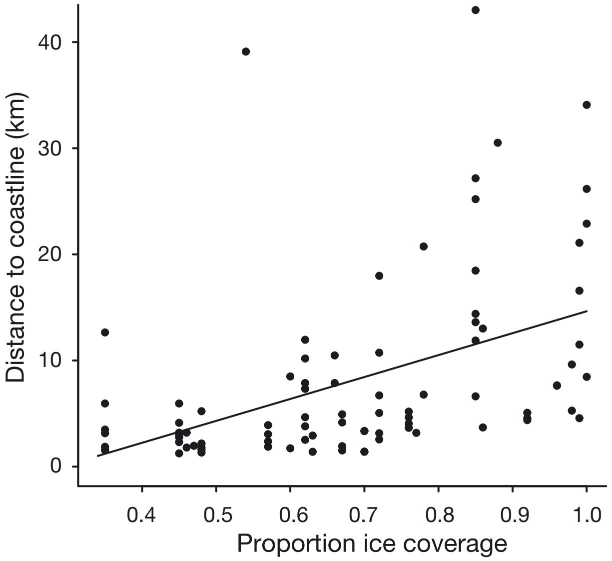

Fig. 3. Relationship between mean daily straight-line distance (km) to the nearest coastline and daily proportion of sea-ice coverage, used as a proxy for sea-ice extent. Points represent raw data for individual leopard seals *Hydrurga leptonyx*, and the line is the predicted slope (estimate = 20.64, $p < 0.001$). The conditional R^2 of the model was 0.26

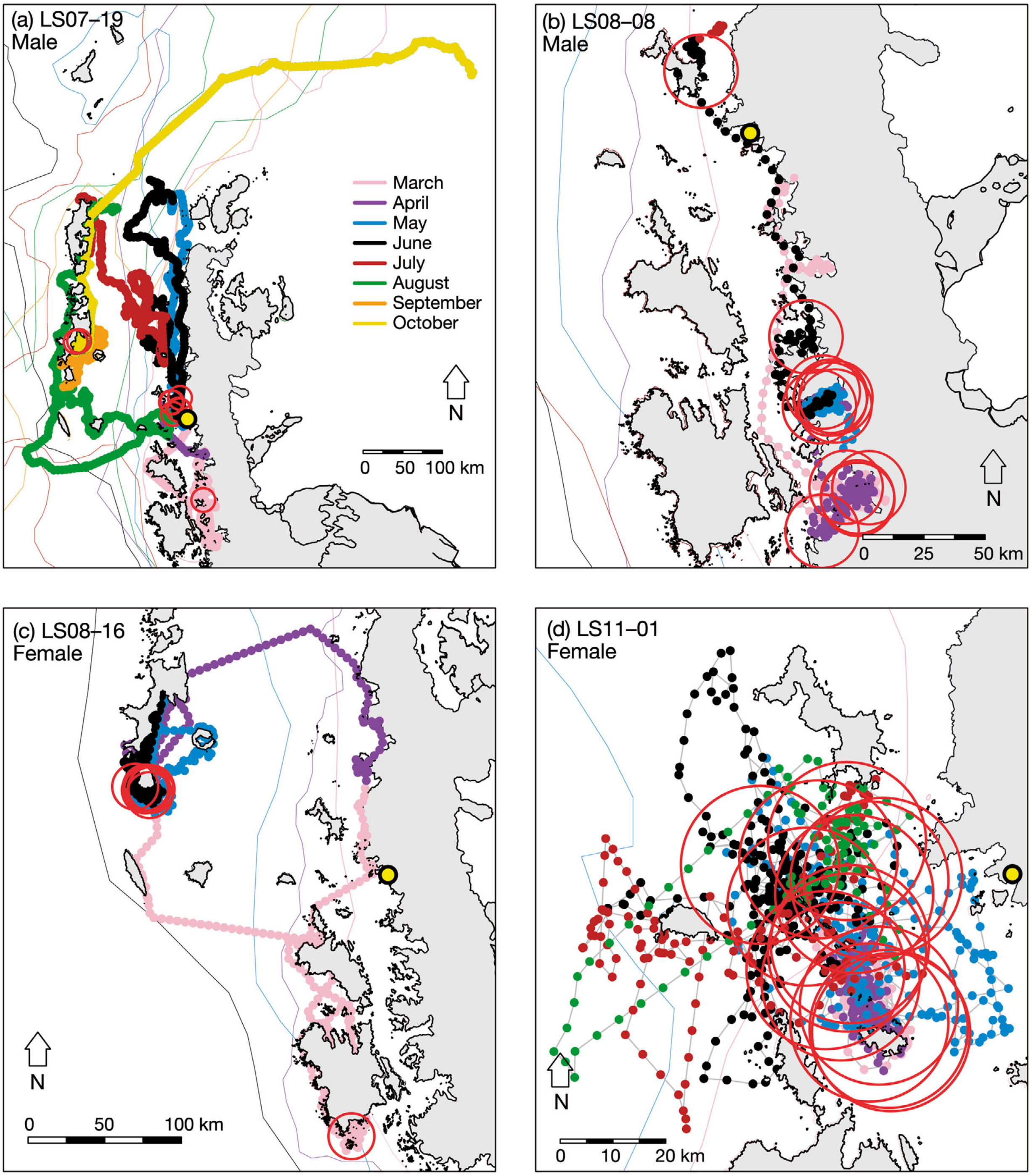

Fig. 4. Tracks of 4 adult leopard seals *Hydrurga leptonyx* recorded using ARGOS satellite tags. Filtered tracks with interpolated points at 5 km intervals are shown in different colours for the month that they were recorded (colour key in panel a). The position of the ice edge on the 15th day of each month is shown by a thinner line of the corresponding colour. A yellow dot indicates the capture location for each seal. Red circles indicate the position of long (>5 d) first-passage times (FPTs), and are scaled to a 15 km radius for each map. Labels include seal identification and sex. (a) Track from March to October of an adult male that moved from the Antarctic continent to the South Shetland Islands before travelling north in October. There were 9 areas of long FPT, 1 to the south of the capture locations, 2 overlapping areas close to the coast of the South Shetland Islands, and 6 overlapping radii close to the coast of the Antarctic continent and near the capture location. (b) Track from March to July of an adult male that gradually moved north up the western Antarctic Peninsula (WAP). There were 13 areas of long FPT, with considerable overlap between them, all close to the coast of the Antarctic continent. (c) Track from March to June of an adult female that moved between the coast of the WAP and the coast of the South Shetland Islands. FPTs >5 d occurred 9 times in 2 areas. (d) Track from March to August of an adult female that remained within a small area close to the WAP coast and several small islands. FPTs >5 d were recorded 13 times, and the radii overlapped each other

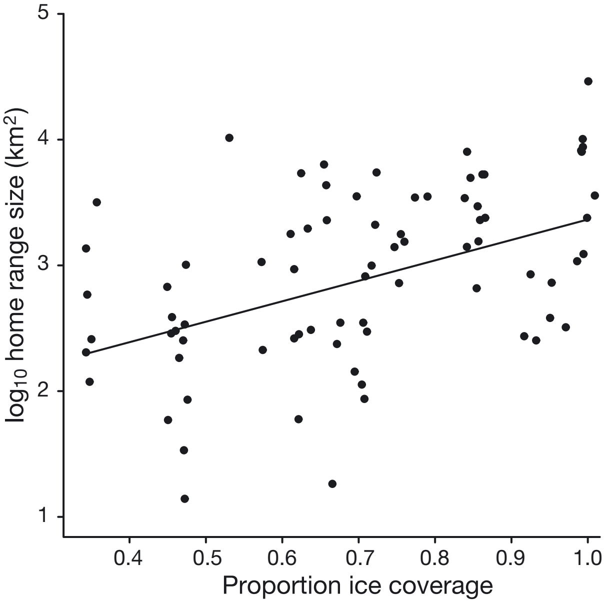

Fig. 5. Relationship between log$_{10}$ monthly home range (km^2) and mean monthly percentage ice cover, calculated as the percentage of the smallest rectangle containing all leopard seal *Hydrurga leptonyx* positions from March to October covered by ice, and used as a proxy for sea-ice extent. Each point represents monthly home range for an individual seal. The line is the predicted slope (estimate = 1.63, $p < 0.001$) from a linear mixed effects model with individual seal included as a random variable. The conditional R^2 of the model was 0.39

Home range

We found a significant positive relationship between log$_{10}$ monthly home range (km^2) and monthly percentage ice cover (Fig. 5; estimate = 1.63, SE = 0.36, df = 1, $p < 0.001$). The marginal R^2 of the model was 0.17, and when individual variation was taken into account, the conditional R^2 was 0.39.

DISCUSSION

We tracked adult leopard seals during the austral autumn/winter (March to October) in the WAP using ARGOS satellite transmitters to model habitat selection in relation to sea ice, and investigated monthly home range in relation to sea-ice extent. We expected that FPTs would be longer when seals were located within the sea-ice extent, since leopard seals are pagophilic and rely on sea ice as a resting platform. Contrary to our prediction, there was no significant difference in the length of FPTs of leopard seals within the sea-ice extent when compared to FPTs in open water. However, 88% of positions where FPTs were estimated were within the sea-ice edge, so this result of a lack of preference for sea-ice habitat is likely to be a limitation of the fact that our study was based on the relative intensity of habitat use along an animals' path and therefore included only habitat actually visited, rather than the relative proportion of habitat 'available'. Interestingly, positions of all long (>2 d) FPTs outside the sea-ice extent occurred within 3.6 km of island coastline. It is possible that sea-ice suitable for hauling out may get caught in bays and protected areas close to islands, leading to an apparent lack of preference for habitat within the sea-ice extent. Alternatively, seals may have been attracted to a food source on the islands, although this is perhaps more likely in late January and early February when young penguins are fledging (Siniff 1991, Rogers & Bryden 1995), which is outside of the time that we were tracking the animals.

We found a significant negative interaction between distance to coastline and sea-ice extent. When sea-ice extent was low (<40%), leopard seals spent relatively longer periods of time within a given area close to the coastline compared to when there was greater sea-ice extent. This suggests that despite observations of leopard seals dispersing beyond the sea-ice extent (e.g. Gwynn 1953, Brown 1957, Bester & Roux 1986, Borsa 1990, Jessopp et al. 2004), leopard seals are limited in their habitat selection by sea-ice coverage, and when the sea-ice extent is low, leopard seals spend more time close to the coastline. To further examine this idea, we investigated the relationship between monthly home range size and monthly sea-ice extent. We found that home range size increased significantly as sea-ice area increased, and that sea-ice extent explained 38% of the variation in the data when repeated observations for individuals were taken into account. This is an important result, as the sea-ice area in the WAP region has significantly decreased over the last 50 yr (Ducklow et al. 2013); moreover, leopard seal habitat is predicted to decrease by 1.1% yr^{-1} (Forcada et al. 2012), so leopard seals will be further restricted to areas close to the coastline in the future.

Leopard seal densities are thought to be greatest at the sea-ice edge (Bester et al. 1995, 2002), but we found no association between preferred leopard seal habitat and the sea-ice edge. In fact, the ice edge often extended far beyond (298 km) the area inhabited by the seals. It is possible that previous associations between leopard seals and the sea-ice edge made during the summer months were due to an increase in density of leopard seals when sea-ice coverage is low, leading to an increase in the probability of observing seals close to the ice edge.

All animals tracked in this study were captured on irregular bits of sea ice or weathered bergs within 20 km of each other in a bay that had fairly dynamic summer sea ice (capture locations of each individual are marked on maps in Figs. 4 & S1). All seals were caught when hauled out on ice and not within sight of ice-free open water, although the distance to ice-free open water was variable. Seven of the 11 seals for which FPT was calculated (Fig. 4a & S1b–g) spent long periods of time (>5 d) within a 15 km radius close to or including the capture location. It is possible that capturing seals within this small area may have biased our sample towards animals with particular habitat preferences, e.g. a preference for areas close to the coastline during periods of low sea-ice extent, but it is difficult to say whether this was the case. Seal LS11-23 (Fig. S1h) was the only seal for which a peak in variance for FPT was not observed, indicating that it did not concentrate its time in a particular area along its path, and it was excluded from the FPT analysis. We feel that the exclusion of this individual from the FPT analysis was unlikely to have influenced our results, since this animal covered an area similar to that of seals LS08-08 (Fig. 4b) and LS11-18 (Fig. S1g). In addition, it is unlikely that there were any significant impacts on behaviour as a result of carrying either type of tag. Both tag types represented less than 0.2 % of seal mass, and hence were unlikely to affect behaviour, as loggers of up to 1 % body mass have been shown to have no long- or short-term effects on phocid seals (McMahon et al. 2008)

The δ^{15}N values of the tissues of the seals in this study suggest that most (11/12) individuals had been consuming krill the year prior to being tracked (T. L. Rogers unpubl. data). Although krill stocks in the WAP are reported to have declined (Atkinson et al. 2004), our study site remains a krill hotspot, with densities reaching >128 m^{-2}. The WAP has been the site of a commercial krill fishery since the 1970s (Jones & Ramm 2004), and one of the most heavily fished areas includes the study area (CCAMLR 2011, Nicol et al. 2012). The loss of winter sea ice in recent years has reduced pack-ice habitat (Forcada et al. 2012) and has allowed a temporal and spatial expansion of the krill fishery, leading to increased krill catch (CCAMLR 2011, Nicol et al. 2012). Currently much of the commercial krill fishing takes place in nearshore areas (Warren & Demer 2010), and this local depletion of krill resources in summer months may affect krillivores such as Adélie penguins *Pygoscelis adeliae*, crabeater seals (Friedlaender et al. 2011) and leopard seals. Commercial fishing limits have been set by CCAMLR (Hewitt et al. 2004), with small-scale management units (SSMUs; Hewitt et al. 2004) designated to avoid localised depletion of krill. SSMUs remain large (the smallest comprises 10 800 km^2), and CCAMLR has yet to reach a consensus as to how krill catch will be divided between these areas (Nicol et al. 2012), and there are no regulations regarding distance to coastline. We propose that proximity to coastline should be considered when setting catch limits for the krill fishery.

There has been speculation that climate-change driven changes in the pack-ice ecosystem may have a relatively minor effect on leopard seals, due to their diverse diet and ability to haul out on a variety of ice floe types and sizes (Siniff et al. 2008). However, as the sea ice in continental slope regions becomes less extensive or less persistent, Antarctic krill abundance will probably diminish (Atkinson et al. 2004). Cascading effects may also occur, where some dominant physical change could cause major shifts at several ecosystem levels (Siniff et al. 2008). Evidence of this is that the declining sea-ice presence off the WAP has not only affected the physical environment, but also the distribution and abundance of prey for higher trophic level species as well (Atkinson et al. 2008, Ducklow et al. 2013). Under this scenario, the potential impact of increased commercial krill fishing may have profound impacts on top-order predators (Ainley et al. 2007), including leopard seals.

Acknowledgements. We dedicate this publication to our dear colleague and friend Dr. Alejandro R. Carlini, with whom we shared many years of fruitful collaboration and friendship. This work is part of a collaboration between seal biologists from the Instituto Antártico Argentino, Taronga Conservation Society Australia and the University of New South Wales. The immobilisation and deployment of satellite transmitters on leopard seals within the Antarctic Specially Protected Area No. 134 were approved by the Dirección Nacional del Antártico, Buenos Aires, Argentina, and were carried out pursuant to the SCAR Code of Conduct for Animal Experiments under UNSW Animal Care and Ethics Committee Protocols 08/103B and 11/112A. We thank the support staff at Base Primavera for hospitality and excellent support during our stay there. We also thank Jorge Gomez, Sebastian Poljak, Federico Beaudoin, Miguel Gasco, Nigel Edwards, Larry Vogelnest, Tiffanie Nelson, Nadine Constantinou, Marie Attard, Marlee Tucker and Birgit Buhleier for assistance in the field. We thank 4 anonymous referees for helpful comments on the manuscript. This research was conducted under the ARC Linkage Program, grant no. LP0989933 to T.L.R. and D.J.S.

LITERATURE CITED

Aguayo-Lobo A, Acevedo J, Brito JL, Acuna P, Bassoi M, Secchi ER, Dalla Rosa L (2011) Presence of the leopard seal, *Hydrurga leptonyx* (de Blainville, 1820), on the coast of Chile: an example of the Antarctica — South America connection in the marine environment. Oecol Aust 15:69–85

Ainley DG, DeMaster DP (1990) The upper trophic levels in polar marine ecosystems. In: Smith WO (ed) Polar oceanography, Part B: chemistry, biology and geology. Academic Press, San Diego, CA, p 599–630

Ainley D, Ballard G, Ackley S, Blight LK and others (2007) Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? Antarct Sci 19: 283–290

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103

Atkinson A, Siegel V, Pakhomov EA, Rothery P and others (2008) Oceanic circumpolar habitats of Antarctic krill. Mar Ecol Prog Ser 362:1–23

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Bester MN, Roux JP (1986) Summer presence of leopard seals *Hydrurga leptonyx* at the Courbet Peninsula, Iles Kerguelen. S Afr J Antarct Res 16:29–32

Bester MN, Erickson AW, Ferguson JWH (1995) Seasonal change in the distribution and density of seals in the pack ice off Princess Martha Coast, Antarctica. Antarct Sci 7:357–364

Bester MN, Ferguson JWH, Jonker FC (2002) Population densities of pack ice seals in the Lasarev Sea, Antarctica. Antarct Sci 14:123–127

Börger L, Franconi N, De Michele G, Gantz A and others (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75: 1393–1405

Borsa P (1990) Seasonal occurrence of the leopard seal, *Hydrurga leptonyx*, in the Kerguelen Islands. Can J Zool 68:405–408

Brown KG (1957) The leopard seal at Heard Island, 1951–54. Australian National Antarctic Research Expeditions, Interim Report 16. Antarctic Division, Department of External Affairs, Commonwealth of Australia, Melbourne

Calenge C (2006) The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) (2011) Krill fishery report: 2011 update. Document WGEMM-11/5. CCAMLR, Hobart. Available at www.ccamlr.org/

Collett D (2003) Modelling survival data in medical research. Chapman & Hall/CRC, London

Costa DP, Robinson PW, Arnould JP, Harrison AL and others (2010) Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. PLoS ONE 5:e8677

Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. Science 297: 1510–1514

Ducklow HW, Fraser WR, Meredith M, Stammerjohn SE and others (2013) West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. Oceanography 26:190–203

Einoder LD, Page B, Goldsworthy SD, de Little SC, Bradshaw CJA (2011) Exploitation of distant Antarctic waters and close neritic waters by short tailed shearwaters breeding in South Australia. Austral Ecol 36:461–475

Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282–288

Fauchald P, Tveraa T (2006) Hierarchical patch dynamics and animal movement pattern. Oecologia 149:383–395

Fieberg J, Börger L (2012) Could you please phrase ‘home range’ as a question? J Mammal 93:890–902

Forcada J, Trathan PN, Boveng PL, Boyd IL and others (2012) Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. Biol Conserv 149:40–50

Freitas C, Kovacs KM, Lydersen C, Ims RA (2008a) A novel method for quantifying habitat selection and predicting habitat use. J Appl Ecol 45:1213–1220

Freitas C, Kovacs KM, Ims RA, Fedak MA, Lydersen C (2008b) Ringed seal post-moulting movement tactics and habitat selection. Oecologia 155:193–204

Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008c) A simple new algorithm to filter marine mammal Argos locations. Mar Mamm Sci 24:315–325

Freitas C, Kovacs KM, Ims RA, Fedak MA, Lydersen C (2009) Deep into the ice: over-wintering and habitat selection in male Atlantic walruses. Mar Ecol Prog Ser 375:247–261

Friedlaender AS, Johnston DW, Fraser WR, Burns J, Patrick NH, Costa DP (2011) Ecological niche modeling of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula. Deep-Sea Res II 58:1729–1740

Gwynn AM (1953) The status of leopard seals at Heard Island and Macquarie Island, 1948–1950. Australian National Antarctic Research Expeditions, Interim Report 3. Antarctic Division, Department of External Affairs, Commonwealth of Australia, Melbourne

Hall-Aspland SA, Rogers TL (2004) Summer diet of leopard seals, *Hydrurga leptonyx*, in Prydz Bay, Eastern Antarctica. Polar Biol 27:729–734

Hall-Aspland SA, Rogers TL, Canfield RB (2005) Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Mar Ecol Prog Ser 305:249–259

Hewitt RP, Watters G, Trathan PN, Croxall JP and others (2004) Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. CCAMLR Sci 11:81–97

Higgins DP, Rogers TL, Irvine AD, Hall Aspland SA (2002) Use of midazolam/pethidine and tiletamine/zolazepam combinations for the chemical restraint of leopard seals (*Hydrurga leptonyx*). Mar Mamm Sci 18:483–499

Hjermann DØ (2000) Analyzing habitat selection in animals without well-defined home ranges. Ecology 81:1462–1468

Hofman RJ, Reichle RA, Siniff DB, Müller-Schwarze D (1977) The leopard seal (*Hydrurga leptonyx*) at Palmer Station, Antarctica. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, p 769–782

Jessopp MJ, Forcada J, Reid K, Trathan PN, Murphy EJ (2004) Winter dispersal of leopard seals (*Hydrurga leptonyx*): environmental factors influencing demographics and seasonal abundance. J Zool (Lond) 263:251–258

Jones CD, Ramm DC (2004) The commercial harvest of krill in the southwest Atlantic before and during the

CCAMLR 2000 Survey. Deep-Sea Res II 51:1421–1434

Kuhn CE, McDonald BI, Shaffer SA, Barnes J, Crocker DE, Burns J, Costa DP (2006) Diving physiology and winter foraging behavior of a juvenile leopard seal (*Hydrurga leptonyx*). Polar Biol 29:303–307

Manly BB, McDonald L, Thomas DL (1992) Resource selection by animals: statistical design and analysis for field studies. Springer, Berlin

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27: 209–220

Massom RA, Stammerjohn SE (2010) Antarctic sea ice change and variability–physical and ecological implications. Polar Sci 4:149–186

McMahon CR, Field IC, Bradshaw CJA, White GC, Hindell MA (2008) Tracking and data-logging devices attached to elephant seals do not affect individual mass gain or survival. J Exp Mar Biol Ecol 360:71–77

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604, doi:10.1029/2005GL024042

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed effects models. Methods Ecol Evol 4:133–142

Nicol S, Foster J, Kawaguchi S (2012) The fishery for Antarctic krill–recent developments. Fish Fish 13:30–40

Nordøy ES, Blix AS (2009) Movements and dive behaviour of two leopard seals (*Hydrurga leptonyx*) off Queen Maud Land, Antarctica. Polar Biol 32:263–270

Øritsland T (1977) Food consumption of seals in the Antarctic pack ice. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, p 749–768

Rogers TL (2009) The leopard seal, *Hydrurga leptonyx*. In: Perrin WF, Wursig B, Thewissen JGM (eds) Encyclopedia of marine mammals, 2nd edn. Academic Press, San Diego, CA, p 673–674

Rogers TL, Bryden MM (1995) Predation of Adélie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay. Can J Zool 73:1001–1004

Rogers TL, Bryden MM (1997) Density and haul-out behaviour of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. Mar Mamm Sci 13:293–302

Rogers TL, Hogg CJ, Irvine A (2005) Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. Polar Biol 28:456–463

Rogers TL, Ciaglia MB, Klinck H, Southwell C (2013) Density can be misleading for low-density species: benefits of passive acoustic monitoring. PLoS ONE 8:e52542

Rounsevell D, Eberhard I (1980) Leopard seals, *Hydrurga leptonyx* (Pinnipedia), at Macquarie Island from 1949 to 1979. Wildl Res 7:403–415

Siniff DB (1991) An overview of the ecology of Antarctic seals. Am Zool 31:143–149

Siniff DB, Stone S (1985) The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, New York, NY, p 555–560

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425–435

Southwell C, Kerry K, Ensor P, Woehler EJ, Rogers T (2003) The timing of pupping by pack-ice seals in East Antarctica. Polar Biol 26:648–652

Southwell C, Paxton C, Borchers D, Boveng P, Rogers T, de la Mare W (2008) Uncommon or cryptic? Challenges in estimating leopard seal abundance using conventional but state-of-the-art methods. Deep-Sea Res I 55:519–531

Southwell C, Bengtson J, Bester MN, Schytte-Blix A and others (2012) A review of data on abundance, trends in abundance, habitat utilisation and diet for Southern Ocean ice-breeding seals. CCAMLR Sci 19:1–49

Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to ENSO and Southern Annular Mode variability. J Geophys Res 113:C03S90, doi: 10.1029/2007JC004269

Suryan RM, Sato F, Balogh GR, Hyrenbach D, Sievert PR, Ozaki K (2006) Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. Deep-Sea Res II 53: 370–386

Therneau TM, Grambsch PM (2000) Modeling survival data: extending the Cox model. Springer, Berlin

van den Hoff J, Fraccaro R, Mitchell P, Field I and others (2005) Estimating body mass and condition of leopard seals by allometrics. J Wildl Manag 69:1015–1023

Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Mar Mamm Sci 18: 156–166

Warren JD, Demer DA (2010) Abundance and distribution of Antarctic krill (*Euphausia superba*) nearshore of Cape Shirreff, Livingston Island, Antarctica, during six austral summers between 2000 and 2007. Can J Fish Aquat Sci 67:1159–1170

Editorial responsibility: Per Palsbøll,
Groningen, The Netherlands

Submitted: August 12, 2013; Accepted: November 12, 2014
Proofs received from author(s): January 13, 2015