



MARINE MAMMAL SCIENCE, **(*): ***_*** (***) 2017)

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DOI: 10.1111/mms.12461

Sex-related differences in the postmolt distribution of Weddell seals (*Leptonychotes weddellii*) in the southern Weddell Sea

IZZY LANGLEY and MIKE FEDAK, Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom; KEITH NICHOLLS, British Antarctic Survey, Natural Environment Research Council, Cambridge CB3 0ET, United Kingdom; LARS BOEHME,¹ Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom.

ABSTRACT

The population of Weddell seals (*Leptonychotes weddellii*) in the southern Weddell Sea is in a unique position on the continental shelf edge, with vast shelf waters to the south, and deep Southern Ocean to the north. We describe sex-related differences in the winter distribution of this population, from data collected by 20 conductivity-temperature-depth satellite relay data loggers deployed in February 2011 at the end of the annual molt. The regional daily speed was calculated, and a state-space model was used to estimate behavioral states to positions along individuals' tracks. GLMMs estimated that males and smaller individuals, diving in shallower water, traveled less far per day of deployment (males 14.6 ± 2.26 km/d, females 18.9 ± 2.42 km/d), and males were estimated to dive in shallower water (males 604 ± 382 m, females $1,875 \pm 1,458$ m). Males and smaller individuals were also estimated to be more resident; males spent an average $83.4\% \pm 7.7\%$ of their time in a resident behavioral state, compared to females at $74.1\% \pm 7.1\%$. This evidence that male and female Weddell seals in the southern Weddell Sea are adopting different strategies has not been shown elsewhere along their circumpolar distribution.

Key words: Weddell seal, *Leptonychotes weddellii*, postmolt distribution, sex-related differences, CTD-SRDL, state-space model, resident state, Weddell Sea.

The distribution of predators within the Southern Ocean is driven by the availability of resources important for growth, reproduction and survivorship (Stephens and Krebs 1986). This relationship between resources and life-history traits can help us understand how vulnerable species are to accelerated ecosystem changes (Santora 2014). Sexual size dimorphism has been shown to increase intersexual competition, and is thought to drive sexual differences in distribution (Beck *et al.* 2003, Cullen *et al.* 2014).

¹Corresponding author (e-mail: lb284@st-andrews.ac.uk).

In the Southern Ocean, sexual differences have been described in the southern elephant seal (*Mirounga leonina*; McConnell and Fedak 1996) and the Antarctic fur seal (*Arctocephalus gazella*; Staniland and Robinson 2008). Both of these species display dramatic sexual size dimorphism, with males weighing almost three times as much as females (Ruckstuhl and Neuhaus 2002, Staniland 2005). Female southern elephant seals at Macquarie Island perform mainly pelagic dives, whereas males perform both pelagic and benthic dives (Hindell *et al.* 1991). In the Kerguelen Islands, females concentrate foraging activity in shallower shelf waters, whereas males use the shelf to benefit from the upwelling of nutrient rich water, concentrating prey (Labrousse *et al.* 2015). Antarctic fur seals show significant spatial segregation between the sexes, with males foraging in shallower shelf waters close to breeding beaches and females ranging further, foraging near the surface in deeper waters off the shelf (Staniland and Robinson 2008).

The Weddell seal (*Leptonychotes weddellii*) is not dramatically sexually dimorphic, with some studies finding no difference in size at all (Staniland 2005) and others finding females to be slightly larger (Bryden *et al.* 1984). Despite their circumpolar distribution, previous studies have focused on populations in both McMurdo Sound and towards the east of Antarctica (Kooyman 1967, Andrews-Goff *et al.* 2010, Heerah *et al.* 2013). It has been shown that the species is resident, and remains within continental shelf waters in depths of up to 500 m (Stirling 1969, fig. 1 from Lake *et al.* 2006, fig. 1 from Bestley *et al.* 2015). They forage in shallow waters associated with relatively smooth bathymetry, which is thought to facilitate prey accessibility (Heerah *et al.* 2013, 2017). However, they have also recently been recorded to dive up to 1,000 m at Davis, in East Antarctica (Heerah *et al.* 2017).

The population of Weddell seals in the southern Weddell Sea is unique in its proximity to the continental shelf edge, with water depths ranging from 500 m to >4,000 m off the continental shelf (Schenke *et al.* 1997). The seals have almost complete ice cover during winter, and are able to maintain breathing holes in the ice with their teeth (Costa and Crocker 1996). Due to the remote location and inaccessibility of the southern Weddell Sea, there is little known of how this population of Weddell seals exploits their unique environment during the austral winter.

The study of the at-sea distribution of marine predators has widened with the development of animal-attached tags (see Carter *et al.* 2016 for a critical review in pinnipeds). Satellite relay data loggers report information collected by on-board sensors, *via* the Argos satellite system, enabling us to collect data from previously inaccessible environments (Boehme *et al.* 2009). This study attached tags to adult males and females, which collected data on movement patterns, dive behavior, and environmental conditions. This positional data obtained is inherently spatial and temporally autocorrelated (Zuur *et al.* 2009). State-space modeling uses statistical inference to link the vertical and horizontal dimensions of movement through space (Breed *et al.* 2013). This results in a time series of data that uses its spatial and temporal autocorrelation to predict future behavioral states (Patterson *et al.* 2008).

Hypotheses

The aim of this study was to describe the sex-related differences in the postmolt distribution of Weddell seals in the southern Weddell Sea. We expected males to travel less far, dive in shallower water, and be more resident than females. This is because males could be spatially constrained by increasing the likelihood in securing territories for the following breeding season (Bartsh *et al.* 1992). Without this spatial

constraint, and with the added energetic requirement of pregnancy, we expected female distribution to have more individual variation (Shero *et al.* 2015) and exploit the range of different habitats available to them in the southern Weddell Sea. We expected there to be a linear relationship between regional daily speed and size, with larger animals having greater metabolic requirements to meet and so traveling further than smaller animals (Staniland 2005).

MATERIALS AND METHODS

Data Collection

Conductivity-temperature-depth satellite relay data loggers (CTD-SRDs) were deployed in February 2011 on 20 Weddell seals from a population in the southern Weddell Sea (75°S, 45°W; Fig. 1a). The seals were sedated by intramuscular injection of 0.2–0.4 mg/kg tiletamine/zolazepam (Zoletil 100; Virbac, Peakhurst, NSW, Australia) (Baker *et al.* 1990) and CTD-SRDs were glued to the fur on the back of

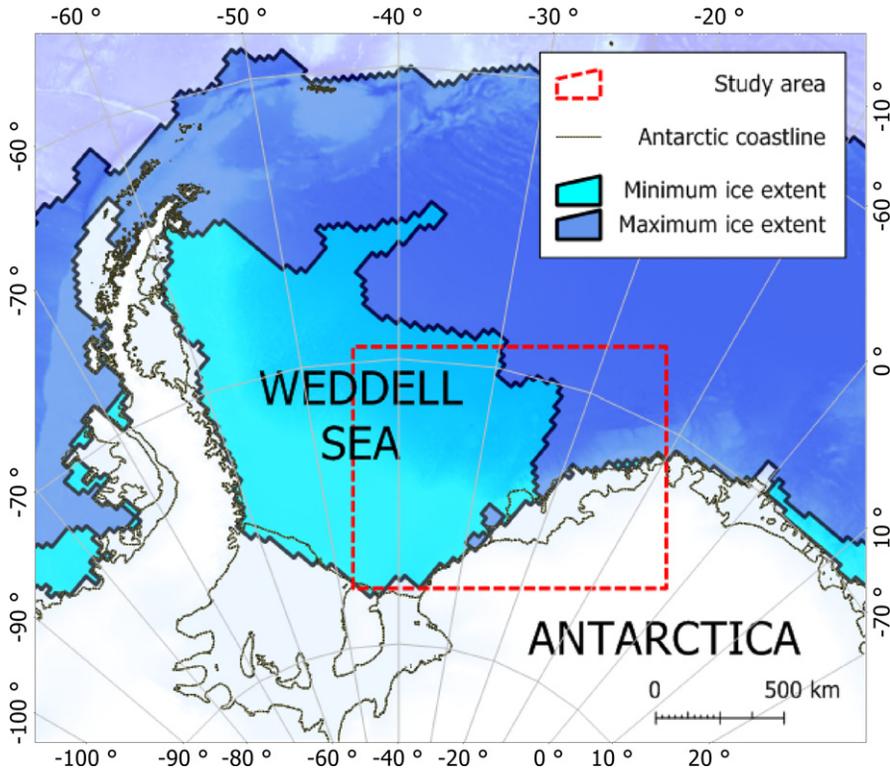


Figure 1a. Study area showing postmolt range of Weddell seals tagged with CTD-SRDs during 2011 deployment. Axes include data on both latitude and longitude. Minimum ice extent data from January 2011 and maximum ice extent data from June 2011 (Fetterer *et al.* 2002). Coastline and contours from Arnt *et al.* (2013) and bathymetry from ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009). Projection: Polar Stereographic. Datum: World Geodetic 1984 (WGS84).

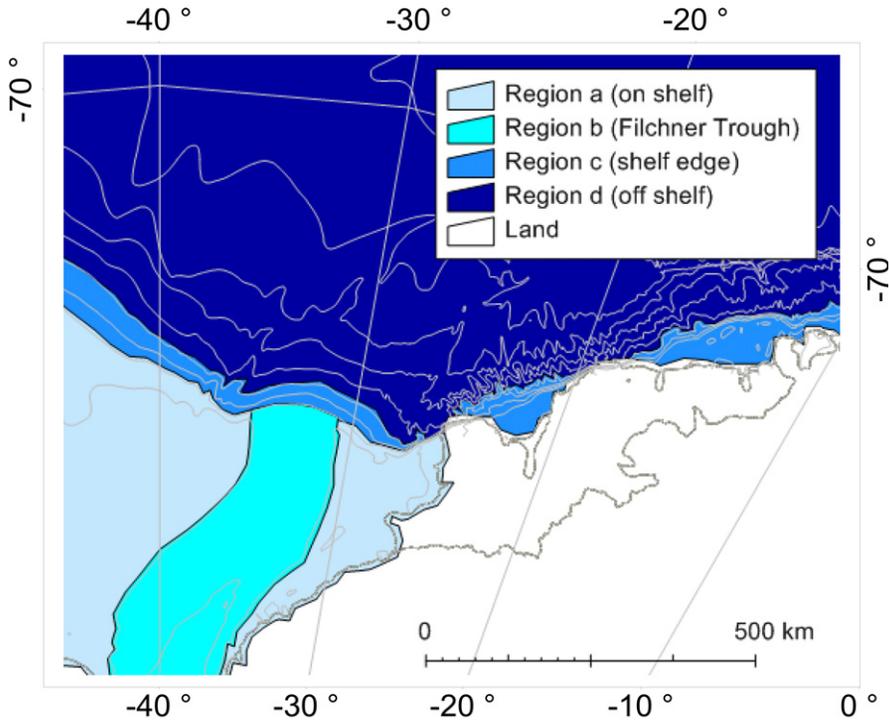


Figure 1b. Four regions categorized by chart contours and bathymetry. Region A is south of $74^{\circ}20'S$ and <600 m, region B is south of $74^{\circ}20'S$ and ≥ 600 m, region C is north of $74^{\circ}40'S$ and $<2,000$ m and region D is north of $74^{\circ}40'S$ and $\geq 2,000$ m. Coastline and contours from Arndt *et al.* (2013) and bathymetry from ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009). Projection: Polar Stereographic. Datum: World Geodetic 1984 (WGS84).

the head using fast-setting epoxy resin (Fedak *et al.* 1983). The CTD sensors were constructed by Valeport Ltd. (Totnes, Devon, U.K.) and the SRDLs were designed and manufactured at the Sea Mammal Research Unit (Boehme *et al.* 2009).

Data Format

During tag deployment, the sex of each seal was determined and for 16 individuals, straight length (nose to tip of tail), and axial girth measurements were taken. The data successfully recorded, relayed, and postprocessed by the Argos satellite system included individual seal ID, time-stamped latitude and longitude estimates, and dive parameters including duration and maximum depth. Each pair of coordinates estimated by Argos (based on the WGS84 system) was assigned a location quality based on the estimated error. The authors received the data after these estimated Argos locations were interpolated in space, a speed filter of 2 m/s was applied (McConnell *et al.* 1992) and dive positions were extracted from the corresponding timestamp.

The beginning of a dive was recorded when the tag's wet/dry sensor was wet and the CTD sensor recorded the seal at a depth below 6 m for more than 8 s (Nordøy

and Blix 2009). The end of a dive was recorded when the CTD sensor recorded the seal at a depth above this 6 m threshold.

Bathymetry data were extracted from the ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009). The bathymetry data associated with each dive position were linearly interpolated in space from the ETOPO1 data set.

Bathymetry data were used in conjunction with latitude, *via* chart contours (Schenke *et al.* 1997), to classify the position of the Antarctic continental shelf and to categorize four geographic regions (Fig. 1b). All positions south of 74°20'S were categorized as shelf water, with a water depth <600 m described as shallow shelf water (region A) and a water depth ≥600 m described as the Filchner Trough (77°S, 36°W; region B). Positions north of 74°40'S with a water depth <2,000 m were described as the edge of the continental shelf (region C), and positions with a water depth ≥2,000 m were described as deep water off the shelf (region D).

Data Filtering

Of the 20 seals tagged, data from four seals were excluded from the analysis due to tag failure after <100 d (seals 1, 9, 17, and 18 in Table 1). An additional three seals were excluded from statistical modeling due to the absence of length and axial girth data (seals 2, 4, and 5 in Table 1).

A further 4,663 dives (19%) were filtered out of the data set before analysis. These included 3,981 dives (16%) with dive duration data = 0 s, 673 dives (3%) with maximum dive depth data <6 m, 7 dives (<1%) with maximum dive depth data = 2,148.8 m, and 2 dives (<1%) with no location estimate data.

The data set also included 1,542 dives (6%) where maximum dive depth exceeded the interpolated bathymetry. Due to the remoteness of the study area, bathymetry data are low resolution and are extrapolated across a wide area (Amante and Eakins 2009). Therefore, where dive depth data exceeded the bathymetry, the bathymetry data were adjusted to meet the higher resolution dive data (Padman *et al.* 2010). Of these dives, 94% exceeded the bathymetry by <200 m.

Data Analysis

The overall distance traveled by each individual, and the maximum distance travelled from first location were calculated using the R package *sp* (R Development Core Team 2008, function *spDistsN1*). The track length was divided by the length of deployment for each individual to get the overall distance traveled per day of deployment, termed *overall daily speed*.

Individual seals' tracks were split into trips, where each trip was made up of consecutive dives within each region. For each region the distance travelled and the time between the first and last dive of each trip were summed to give regional distance traveled and regional deployment length. These were then used, as above, to calculate *regional daily speed*.

A state-space model (SSM) was fitted to the Argos estimated locations and maximum dive depth data to describe movement in three dimensions, using example code in the supplementary material from Bestley *et al.* (2015). The SSM produced an interpolated track with positions every 4 h. Two behavioral states were described based on the tortuosity of the seals' interpolated tracks and these states were assigned to the 4 h summary dive positions (Bestley *et al.* 2012). The first behavioral state was *resident*, describing a low speed and high turning rate and the second behavioral state

Table 1. Details of tag deployment, with seal ID, length, and axial girth data for those individuals where this was taken, fatness index (axial girth/length), the total length of tag deployment in days, the total distance traveled, and the maximum distance traveled from first location, both in kilometers. Mean and standard deviations are given for males, females, and overall.

Sex	No.	Seal ID	Length (cm)	Axial girth (cm)	Fatness index	Deployment length (d)	Distance traveled (km)	Maximum distance (km)
Male	1 ^a	ct70-356-11	223	162	0.73	13 ^a	376 ^a	108 ^a
	2 ^b	ct70-486-11	NA	NA	NA	146	1,978	220
	3 ^b	ct70-490-11	NA	NA	NA	144	1,726	231
	4 ^b	ct70-491-11	NA	NA	NA	140	1,633	110
	5	ct70-499-11	224	161	0.72	146	2,325	315
	6	ct70-500-11	219	158	0.72	142	2,188	343
	7	ct70-526-11	235	168	0.71	106	1,778	267
	8	ct70-633-11	197	155	0.79	142	1,901	440
	9	ct70-634-11	226	167	0.74	146	2,581	304
10 ^{a,b}	ct70-641-11	NA	NA	NA	1 ^a	NA	NA	
	Mean ± SD	221 ± 12	162 ± 5	0.74 ± 0.03	139 ± 13	2,014 ± 305	279 ± 91	
Female	11	ct70-488-11	232	178	0.77	144	2,759	236
	12	ct70-501-11	217	147	0.68	149	2,662	598
	13 ^a	ct70-502-11	245	170	0.69	41 ^a	965 ^a	202 ^a
	14	ct70-503-11	200	141	0.71	149	3,344	672
	15	ct70-637-11	181	143	0.79	137	1,922	533
	16	ct70-638-11	165	121	0.73	145	2,843	903
	17	ct70-640-11	235	174	0.74	143	2,995	394
	18 ^a	ct70-642-11	216	163	0.75	77 ^a	1,428 ^a	232 ^a
	19	ct70-643-11	211	154	0.73	137	2,557	658
	20	ct70-650-11	237	172	0.73	146	2,610	221
	Mean ± SD	214 ± 24	156 ± 17	0.73 ± 0.03	144 ± 4	2,712 ± 381	527 ± 218	
Overall mean ± SD		216 ± 22	158 ± 15	0.73 ± 0.03	141 ± 10	2,363 ± 507	403 ± 215	

^aSeal was removed from analysis due to tag failure after <100 d.

^bSeal was not included in statistical models due to the lack of morphometric data.

was *directed*, describing more linear travel at higher speeds. The proportion of dives each individual seal spent in the resident state was termed the *overall resident time* (Bestley *et al.* 2015). The proportion of dives each individual spent in a resident state in each region was termed *regional resident time*.

Length (L) and axial girth (G) were available for 13 individuals (8 females, 5 males) and were used to calculate a fatness index ($[G/L]$; Stirling 1971, Sato *et al.* 2002). All three variables together are hereafter referred to as size. Sex and size were tested for collinearity using the point-biserial correlation test within the R package *ltm* (R Development Core Team 2008, function *biserial.cor*).

Three generalized linear mixed-effects models (GLMMs) with Gaussian distributions and identity link functions used the subsetted data set ($n = 13$). We tested the effects of sex, mean bathymetry, and size on regional daily speed and regional resident time, and the effect of sex and size on bathymetry at dive positions. Individual and region were included as random effects.

Three models were built for each response variable, to test for the difference between length, girth, and fatness index (see Appendix S1 for this analysis). The minimum adequate model was chosen using second order Akaike's information criterion, AICc (with the $\Delta AICc$ threshold set to ≥ 2) and the likelihood ratio test (LRT) compared the likelihood between each pair of candidate models. Models were evaluated by plotting the residuals to check for normality and homoscedasticity. Conditional R -squared (cR^2) values were then calculated using the R package *MuMIn* (R Development Core Team 2008, function *r.squaredGLMM*) to assess how much of the variability was explained by the model.

RESULTS

Details of tag deployment are summarized in Table 1. Of the 16 tags with a deployment >100 d, the average length of deployment was 141 ± 10 d (mean \pm standard deviation) and the average distance traveled was $2,363 \pm 507$ km (Fig. 2). The seals therefore traveled an average of 16.7 km/d.

For 16 individuals, with an equal sex ratio, 18,039 dives were successfully relayed *via* the Argos satellite system. Out of 8,641 dives from males, 43.5% were made in region A, 23.0% in region B, 30.9% in region C, and 2.78% in region D. Out of 9,398 dives from females, 26.0% were in region A, 10.1% in region B, 18.0% in region C, and 45.9% in region D. The comparison of overall daily speed, bathymetry at dive positions and overall resident time between the sexes is summarized in Table 2.

The point-biserial correlation test scored length and sex 0.16, girth and sex 0.18, and fatness index and sex 0.05. As fatness index was the least correlated with sex, it was used as the size component within the GLMMs.

Regional Daily Speed

In regions A, B, and C, both male and female Weddell seals travelled an average of 20.4 ± 0.82 km/d. In region D, females travelled 21.8 ± 10.8 km/d, and the single male seal that dived off the shelf covered only 0.52 km in a single day (Fig. 3). The minimum adequate model with regional daily speed included sex, mean bathymetry, and fatness index as fixed effects, and individual and region as random effects (*m01*; Table 3, 4). This model explained 39% of the variability within the data.

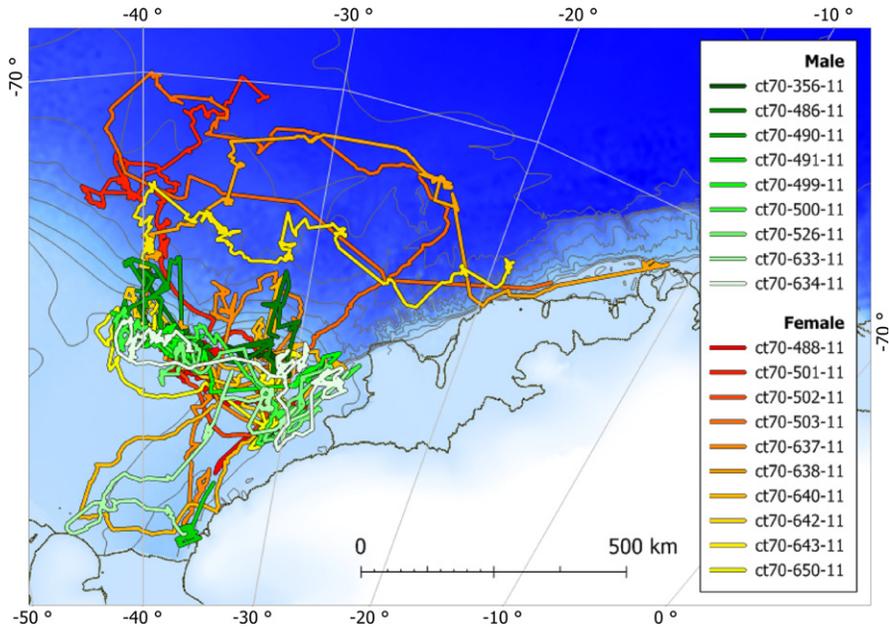


Figure 2. Weddell seal tracks created by interpolating estimated dive positions in time. Coastline and contours from Arndt *et al.* (2013) and bathymetry from ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009). Projection: Polar Stereographic. Datum: World Geodetic 1984 (WGS84).

Table 2. Male and female mean and standard deviation (SD) for overall daily speed, maximum distance from first location, bathymetry at dive positions, and overall resident time. Male and female samples had an equal sex ratio of eight individuals each.

Response	Sex	Mean	SD
Overall daily speed	Male	14.6 km/d	2.26 km/d
	Female	18.9 km/d	2.42 km/d
Bathymetry at dive positions	Male	604 m	382 m
	Female	1,875 m	1,458 m
Overall resident time	Male	83.4%	7.7%
	Female	74.1%	7.1%

The model *m01* estimated the adjustment from males to females to be -11.2 (SE = 2.98). This negative slope means that the model predicted that males had a smaller regional daily speed than females. The estimate for mean bathymetry was -0.37 (SE = 0.14) and for fatness index was -99.9 (SE = 45.9) so the model also predicted that as both bathymetry and fatness index increased, the regional daily speed decreased.

The individual variance (4.63 ± 2.15) and the region variance (0 ± 0) within the model were less than the residual variance (62.4 ± 7.9) implying there could be random variation, or variation explained by variables not included in this model.

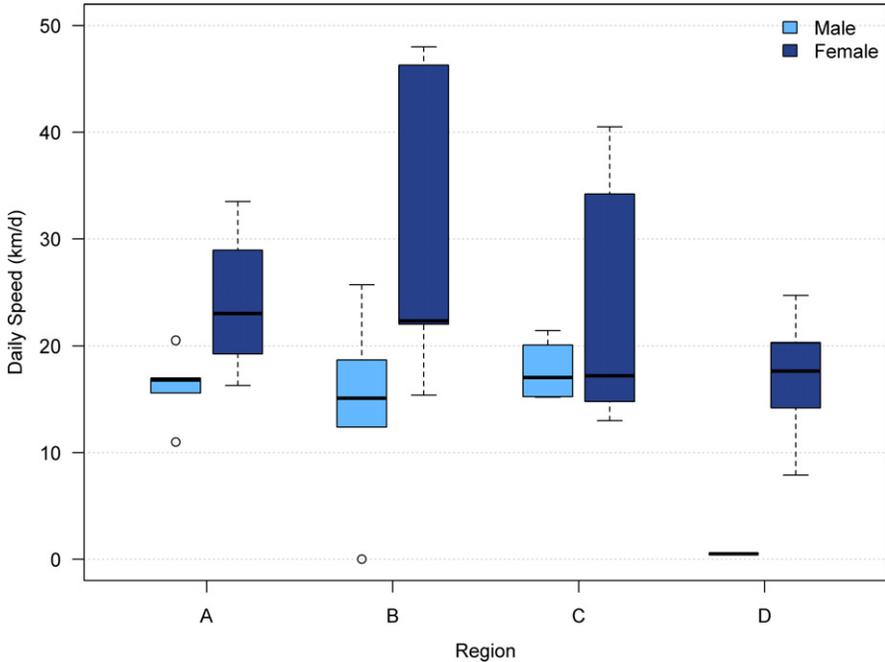


Figure 3. Daily speed (distance traveled in km/deployment length in days) for five male and eight female Weddell seals in region A (shallow water in the shelf), region B (deep water Filchner Trough), region C (continental shelf edge), and region D (deep water off the shelf).

Bathymetry at Dive Positions

The four regions categorized in this study had a depth range from 8 m in the shallow water on the shelf, to depths up to 4,426 m in the deep water off the continental shelf. The minimum adequate model with bathymetry at dive positions included sex as a fixed effect, and individual and region as random effects (*m06*; Table 3, 4). This model explained 94% of the variability within the data.

The model predicted that dive positions of male seals were associated with shallower bathymetry than those of female seals (estimate -2.28 , SE = 0.86; Fig. 4). Regional variance had a large effect (109.6 ± 10.5), and to a lesser extent, residual variance was greater than individual variance.

Regional Resident Time

Overall, the seals in this study spent an average of $78.8\% \pm 8.6\%$ of their time in a resident behavioral state. The minimum adequate model with regional resident time included sex and fatness index as fixed effects, and individual and region as random effects (*m09*; Table 3, 4). This model explained 42% of the variability within the data.

The model *m09* estimated the adjustment from males to females to be $+15.3$ (SE = 5.75), and so predicted that males spent more of their time in a resident behavioral state per region than females (Fig. 5). The residual deviance was larger than both

Table 3. Model selection for generalized linear mixed-effects models (GLMMs) with Gaussian distribution and identity link function. Second order Akaike's information criterion (AICc) and conditional R -squared (cR^2) are reported. Models are ordered by the lowest Δ AICc and the minimum adequate model is highlighted in bold.

Response variable	Model	Fixed effects	Random effects	AICc	Δ AICc	cR^2
Regional daily speed	<i>m01</i>	Sex + bathymetry + fatness index	Individual + region	305.9	0	0.39
	<i>m03</i>	Sex + bathymetry	Individual + region	307.0	1.1	0.41
	<i>m02</i>	Sex + fatness index	Individual + region	307.8	1.9	0.42
	<i>m04</i>	Bathymetry + fatness index	Individual + region	312.6	6.7	0.43
Bathymetry at dive positions	<i>m06</i>	Sex	Individual + region	225.9	0	0.94
	<i>m05</i>	Sex + fatness index	Individual + region	228.6	2.7	0.94
	<i>m07</i>	(Intercept)	Individual + region	229.4	3.5	0.94
Regional resident time	<i>m09</i>	Sex + fatness index	Individual + region	379.7	0	0.42
	<i>m08</i>	Sex + bathymetry + fatness index	Individual + region	380.3	0.6	0.36
	<i>m11</i>	Fatness index	Individual + region	382.7	3	0.23
	<i>m10</i>	Sex	Individual + region	388.5	8.8	0.08

Table 4. Likelihood Ratio Test (LRT) results for pairs of candidate models, outlined in Table 3. The Chi-squared statistic (χ^2), degrees of freedom, and P -value ($\alpha < 0.05$) are reported, along with the best model from each test.

Candidate model pair	χ^2	df	P	Best model
<i>m01</i> , <i>m02</i>	4.7536	1	0.02924	<i>m01</i>
<i>m01</i> , <i>m03</i>	9.0603	2	0.01078	
<i>m01</i> , <i>m04</i>	9.61	1	0.001935	
<i>m05</i> , <i>m06</i>	0.011	1	0.9163	<i>m06</i>
<i>m06</i> , <i>m07</i>	6.1278	1	0.01331	
<i>m08</i> , <i>m09</i>	2.2653	1	0.1323	<i>m09</i>
<i>m09</i> , <i>m10</i>	11.624	1	0.000651	
<i>m09</i> , <i>m11</i>	5.8264	1	0.01579	

individual and region variance, implying there could be random variation, or variation explained by variables not included in this model.

DISCUSSION

Our findings suggest that males and females adopt different strategies postmolt. When accounting for repeated measures in individual and region, sex differences were observed in the distance traveled per day of deployment for each region (regional daily speed), the bathymetry at dive positions, and the time spent in a resident

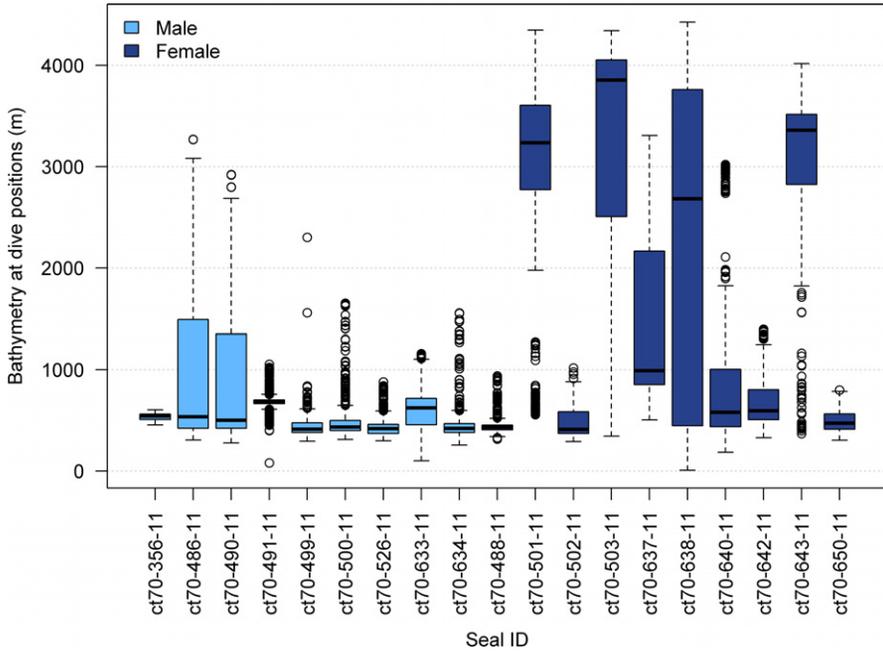


Figure 4. Bathymetry in meters associated with each estimated dive position for 9 males and 10 females. Bathymetry data were extracted from ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009).

behavioral state. We also found a negative relationship between regional daily speed and both bathymetry and individual size (fatness index) and a positive relationship between regional resident time and size.

Four tagged seals were removed from analysis due to deployment of <100 d. These short deployments were most likely due to technical faults, but tags can also fail due to seal mortality, battery exhaustion, or tag loss (Andrews-Goff *et al.* 2010). For 16 tags with a mean deployment length of 141 d, the mean track length was 2,363 m.

Regional Daily Speed

The seals overall traveled an average 16.7 km/d which was remarkably similar to the 17.6 km/d seals traveled from the population in Prydz Bay (Bestley *et al.* 2015). However, males in the Weddell Sea traveled less far per day in all regions except region C (Fig. 3). A study by McIntyre *et al.* (2013) tagged four adult Weddell seals with an equal sex ratio and found no sex effect for the maximum distance traveled from the location that they had been tagged. All adult seals tagged within Queen Maud Land remained within 15 km of the tagging location. Lake *et al.* (2006) estimated home ranges of female Weddell seals from the Vestfold Hills population in East Antarctica using kernel density analysis and calculated individuals ranged from 14 km² to 300 km². In our study, females exhibited

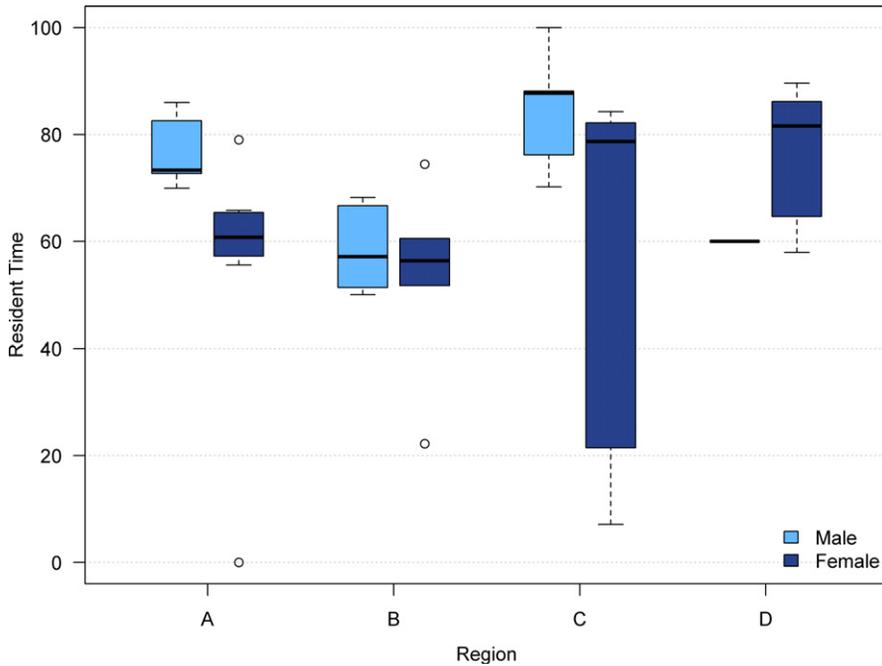


Figure 5. Resident time (the proportion of dives allocated a resident behavioral state from the state-space model taken from Bestley *et al.* 2015) for five male and eight female Weddell seals in region A (shallow water in the shelf), region B (deep water Filchner Trough), region C (continental shelf edge), and region D (deep water off the shelf).

considerable individual variation in daily speed. Nevertheless, when individual variation was accounted for in a GLMM, sex remained a significant factor related to daily speed.

Figure 2 shows that this trend could be driven by three females. There was an additional female showing a similar pattern that was not included in the model due to the unavailability of size data. We believe that regional daily speed, and the distribution of female Weddell seals, could be driven by their role in reproduction (Beck *et al.* 2013). Pregnant females have higher energetic demands post-molt than nonpregnant females (Shero *et al.* 2015). Considering that we do not have data on whether females in this study were pregnant, the variation between females could be explained by nonpregnant individuals; either younger than sexual maturity or sexually mature females taking “sabbaticals” from breeding in years of low productivity when leaving foraging areas may affect long-term fitness (Chambert *et al.* 2015).

Regional daily speed was also driven by fatness index (axial girth/length) which had a negative estimate in the model. This was unexpected as larger animals have greater metabolic requirements (Staniland 2005). However, there was very little variation around the mean for fatness index, which we suspect is a result of an over-simplified index for size. The residual error term in the minimum adequate model was larger than the variance within individuals and within regions, which implies there

are further predictors outside the scope of the model. For these reasons, we think the model would be greatly improved by collecting data on both mass and female reproductive state, to explain their effect on regional daily speed.

Mean bathymetry also had a small but significant, negative effect on regional daily speed. In deeper water, seals traveled less far per day of deployment. This seems counterintuitive but could be driven by the behavior of seals on the continental shelf, diving in deep waters over the Filchner Trough. The deepest dive recorded in the Filchner Trough in this study was made by a male seal to 704 m. Future studies could investigate this further by defining regions in oceanographic detail, using salinity data from CTD tags.

Bathymetry at Dive Positions

The southern Weddell Sea reaches depths of over 4,000 m, providing Weddell seals with a wide variety of oceanographic regimes. We found that the dive positions of males were associated with shallower bathymetry than those of females. The GLMM explained 94% of the data when individual and region were included as random effects. This sex difference has never been seen before in the bathymetry of dive positions, although no other population of Weddell seals has this unique availability of the vast continental shelf to the south, and the deep Southern Ocean to the north. The mean bathymetry recorded for diving Weddell seals in Queen Maud Land was 207 m (McIntyre *et al.* 2013), in Dumont d'Urville was 237 m (Heerah *et al.* 2013), and in the Western Ross Sea was 505 m (Goetz 2015). The deepest dives in this study were not off the shelf but over the Filchner Trough, and eight individuals (1:1 sex ratio) dived to depths >600 m.

The proportion of dive positions were relatively similarly distributed across the four categorized regions: (1) shallow water on the shelf, (2) Filchner Trough, (3) continental shelf edge, and (4) deep water off the shelf. However, when accounting for sex, we found that only 3% of dives from males were made in the deep water off the continental shelf. We found that the males in this study were more similar to both males and females from the population in Prydz Bay, who spent 100% of their time in shelf waters (Bestley *et al.* 2015). This behavior has also been shown by both males and females from populations in Dumont D'Urville and Davis (Heerah *et al.* 2017).

Regional Resident Time

Weddell seals from this population were estimated to spend 79% of their time in a resident behavioral state. This is similar to the population tagged in Prydz Bay that had a resident time of 83% (Bestley *et al.* 2015). However we found that sex had a significant effect on regional resident time, with males being more resident than females. Males spent 83.4% ($\pm 7.7\%$) of their time in a resident state, which is more similar to both males and females together in Prydz Bay. It is possible that males in the Weddell Sea, and both males and females from the Prydz Bay population, are more resident due to their exclusive use of the Antarctic shelf habitat (Bestley *et al.* 2015). Additionally, individuals that are physically constrained in their displacements may also have a higher resident time.

We also found that larger seals (with a greater fatness index) were more resident in this study. Weddell seals are not generally sexually dimorphic (Staniland 2005), but males in this tagged sample were slightly larger (Table 1). Unlike male southern elephant seals, during the breeding season male Weddell seals have low energy

requirements due to aquatic mating reducing male-to-male aggression (Harcourt 2006, Harcourt *et al.* 2007). The selective pressure to be big is therefore greatly reduced. Additionally, Harcourt (2006) found evidence that some male Weddell seals in McMurdo Sound were foraging during the breeding season, reducing this pressure further.

The Weddell seal reproductive strategy is a variation on resource defense polygyny, where males defend underwater territories around breathing holes in the ice (Siniff *et al.* 1977). Therefore males who range less far from breeding areas could be more likely to secure territories for the following breeding season (Bartsh *et al.* 1992). We believe that this role in reproduction could be driving the distribution of male Weddell seals in the southern Weddell Sea.

During the winter, pregnant females have higher energetic requirements (Shero *et al.* 2015). It has been seen in southern elephant seals at Macquarie Island that during favorable conditions, mothers will invest more energy in their offspring than when resources are limited (McMahon *et al.* 2017). If prey availability in region A and B on the shelf is limited, the findings in this study could provide evidence for intraspecific competition. Low quality individuals, including nonbreeding females, may benefit from ranging further from these denser concentrations in years when food reserves are limited (Proffitt *et al.* 2007, Chambert *et al.* 2015). This behavior is termed temporary emigration, and is a condition-dependent strategy used by lower quality female Weddell seals in the Ross Sea, who cannot “afford” to leave foraging areas (Chambert *et al.* 2015). This could explain why we see the individual variation within females, exploiting both on shelf and off shelf habitats postmolt.

Conclusions

Despite the sample in this study being reduced to 13 individuals, due to tag failure and the lack of morphometric data for all tagged seals, our findings provide evidence for sex-related differences in the postmolt distribution of Weddell seals in the southern Weddell Sea. This is not seen elsewhere along their circumpolar distribution which remains to be explained. Future studies would benefit from describing the oceanography and prey availability of Weddell seal habitats around the Southern Ocean to better understand why we see this difference in behavior. The most abundant prey species in the Weddell Sea is the Antarctic silverfish (*Pleuragramma antarcticum*), but Weddell seals are also known to feed on *Trematomus* fish species and invertebrates (Plötz 1986, Burns *et al.* 1998). Lake *et al.* (2003) found evidence for both temporal and spatial variation in Weddell seal prey types within East Antarctica. Several ecotypes were described, including predators of benthic fish, prawns and glacial squid (*Psychroteuthis glacialis*; Lake *et al.* 2003).

Despite the lack of data on fine-scale oceanographic space, we have shown that this population of Weddell seals show sex-related differences in their postmolt distribution, which are not seen elsewhere along their circumpolar distribution. We suggest that this is driven by their unique position in the southern Weddell Sea; with a large, bathymetrically heterogeneous area of continental shelf to the south and deep, complex oceanographic regimes off the shelf to the north. There could be a selective advantage for males to remain close to breeding colonies, where they can increase their chance in securing territories for the following breeding season (Bartsh *et al.* 1992). Females do not have this spatial constraint, but could have higher energetic requirements depending on their reproductive status (Shero *et al.* 2015).

ACKNOWLEDGMENTS

This research was funded by NERC grants NE/G014833/1 and NE/G014086/1 and the research was reviewed and approved by the University Teaching and Research Ethics Committee and Animal Welfare and Ethics Committee of the University of St Andrews. Capture and deployment of satellite transmitters was carried out by experienced personnel with United Kingdom Animal (Scientific Procedures) Act 1986 personal licenses. The authors are grateful for the support of the officers and crew of RRS *Ernest Shackleton* ES054 cruise. We also thank the three anonymous reviewers for their comments on the manuscript.

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Received: 9 September 2016

Accepted: 3 October 2017

SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12461/suppinfo>.

Appendix S1. Additional model outputs and model selection information.