



# Sexual segregation in juvenile Antarctic fur seals

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## Abstract

Sexual segregation, the differential space, habitat or resource use by males and females, can have profound implications for conservation, as one sex may be more vulnerable to environmental and anthropogenic stressors. The drivers of sexual segregation, such as sex differences in body size, breeding constraints, and social behaviour, have been well studied in adults but are poorly understood in immature animals. To determine whether sexual segregation occurs in juvenile Antarctic fur seals, *Arctocephalus gazella*, and investigate the underlying drivers, we deployed Global Location Sensors on 26 males and 19 females of 1–3 years of age at Bird Island, South Georgia. Sexual segregation occurred in foraging distribution, primarily in latitude, with females foraging closer to South Georgia and the Polar Front, and males foraging further south near the Antarctic Peninsula. This segregation was particularly evident in Feb–Apr and May–Nov, and males spent more time hauled out than females in May–Nov. Although juveniles have no immediate reproductive commitments, reproductive selection pressures are still likely to operate and drive sex differences in body size, risk-taking, and social roles. These factors, coupled with prey distribution, likely contributed to sexual segregation in juvenile Antarctic fur seals. Consequently, male and female juveniles may compete with different fisheries and respond differently to environmental change, highlighting the importance of considering sex and age groups in species conservation efforts.

**Keywords** Geolocation · Size dimorphism · Early life · Foraging · Pinnipeds

## Introduction

Sexual segregation, the differential space, habitat, or resource use by males and females, has been documented in a plethora of animal taxa (Ruckstuhl and Neuhaus 2005; Wearmouth and Sims 2008). The drivers of sexual segregation have been well studied in adult life stages, and include

several non-mutually exclusive hypotheses. The sexual size dimorphism hypothesis states that the sexes require different resources as one sex is larger than the other (Main et al. 1996; Stokke and Toit 2000). The predation risk hypothesis states that the sexes use different habitats owing to the costs and benefits associated with risk (Ruckstuhl and Neuhaus 2005; Croft et al. 2006). Sexual segregation may arise from sex differences in social behaviour, whereby the sexes invest in behaviours to fulfil their reproductive roles (Bon and Campan 1996; Pellegrini 2004). Sex differences in immediate breeding constraints can also drive sexual segregation, as females may be constrained by parental care and males constrained by territory-holding (Staniland 2005). However, less attention has been paid to understanding the drivers of sexual segregation prior to adulthood.

Sexual segregation in juveniles (immature individuals) has been investigated in several species, including black-handed spider monkeys, *Ateles geoffroyi*, sheep, *Ovis aries*, and New Zealand sea lions, *Phocartos hookeri*. It can occur prior to major onset of sexual size dimorphism (e.g. Rodrigues 2014; Jones et al. 2020a), indicating that additional factors may drive the phenomenon. For example, Rodrigues

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We found that reproductive selection pressures are likely to operate in juveniles, driving sex differences in body size, risk-taking, and social roles, and leading to sexual segregation.

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(2014) found that juvenile black-handed spider monkeys, which demonstrate minimal sexual size dimorphism, spend more time in same sex groups, likely to prepare for social roles in adulthood. Leung et al. (2012) found that male and female juvenile New Zealand sea lions segregate during foraging, which may act to enable resource partitioning and reduce intra-specific competition, but generate sex-specific differences in exposure to risks. Juveniles are particularly vulnerable to mortality and juvenile survival plays a key role in population demography, as low survival rates can substantially reduce recruitment and slow population growth rate (Lindström 1999; Sæther et al. 2013; Benson et al. 2018). Investigating sexual segregation in juveniles can therefore provide vital insights into the ecology, population dynamics and conservation of species.

Studying sex differences in the foraging ecology of juveniles (as opposed to adults) removes the influence of immediate breeding constraints (Salton et al. 2019), but sexual selection pressures could still drive sexual segregation. For example, sex-specific growth trajectories are geared towards fulfilling future reproductive roles. In polygynous species, males are driven to grow quickly, as larger adult males are generally more successful in competing for mates (Weckerly 1998; Isaac 2005). Males therefore tend to grow faster than females, and they also grow for longer (Payne 1979; Clutton-Brock et al. 1985; Georgiadis 1985). They must gain enough resources to attain a large body size and subsequently to maintain it (Le Boeuf et al. 2000). Males may also require more food as they have higher absolute metabolic demands, whereas females may require better quality food as they have higher mass-specific metabolic needs (Schmidt-Nielsen and Knut 1984; Stokke and Toit 2000). Thus, males have been observed foraging over larger areas than females to meet these requirements (Salton et al. 2019), as documented in white-tailed deer, *Odocoileus virginianus* (Hasapes and Comer 2016) and Eurasian lynx, *Lynx lynx* (Herfindal et al. 2005). Males may also favour foraging strategies that influence growth, whereas females may favour foraging strategies that improve their chances of survival as they have more predictable reproductive outputs (Trivers 1972; Clutton-Brock et al. 1982; Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001).

Otariids (eared seals) are ideal to study sexual segregation as they show extreme sexual size dimorphism, which develops early in life (Lindenfors et al. 2002; Payne et al. 1979). Male pups are born on average 0.5 kg heavier than females and they grow faster, weighing nearly four times more than females when they become sexually reproductive (Payne et al. 1979; Forcada and Staniland 2009). Antarctic fur seals, *Arctocephalus gazella*, are highly polygynous and males will fight to the death to gain access to mates. They are also well studied, and sexual segregation has been documented in dependent pups, weaned pups, and adults. In dependent

pups, males favour riskier habitats than females, which may benefit their ability to gain social skills (e.g. by play-fighting) and compete for mates in the future (Jones et al. 2020a). Towards the end of lactation males also travel further from their birth sites (Jones et al. 2020a), and develop a more oceanic distribution than females in their first year of life (although the sexes were tracked in different years in this study; Warren et al. 2006). The sexes have different nutritional needs, as males build greater lean tissue stores and females accumulate more fat stores (Arnould et al. 1996). Sex differences in foraging distribution may reflect the drive for males to explore the most productive foraging sites to maximise their energy intake to grow, or the physiological capabilities of males to travel further because of their larger body size. Land-based observations suggest that young adult males frequently haul out at Signy Island in the South Orkney archipelago (Waluda et al. 2010). However, the foraging distributions and existence of sexual segregation in juveniles (hereafter classed as seals aged 1–3 years) is limited.

To test for sex differences in the distribution of juvenile Antarctic fur seals and investigate possible drivers, we studied body morphology, and movements with Global Location Sensors (GLS loggers). GLS loggers record light intensity, which is used to calculate sunrise and sunset times and infer movement behaviour over several months or years (Joo et al. 2020). We hypothesize that (1) male juveniles would be larger than females; (2) the sexes would forage in different regions; (3) males would use larger areas than females; (4) the underlying drivers of these sex differences may relate to reproductive selection pressures.

## Materials and methods

### Ethics statement

Animal handling procedures were approved by the British Antarctic Survey Animal Ethics and Welfare Review Body (AWERB), and adhered to the ASAB and ARRIVE guidelines and legal requirements of the Government of South Georgia and the South Sandwich Islands.

### GLS tag deployment

During austral summers between 04-Jan-2007 and 13-Jan-2012, 26 male and 19 female juvenile Antarctic fur seals (estimated as 1–3 years of age; Table 1) were deployed with GLS loggers at Bird Island, South Georgia (54.01° S, 38.05° W). Each seal was restrained as described by Gentry and Holt (1982). Then a GLS logger developed by the British Antarctic Survey, Mk 4 (25 × 21 × 7 mm, 5 g), Mk 5 (18 × 18 × 6.5 mm, 3.6 g), Mk 9 (16 × 14 × 6 mm, 2.5 g) or Mk 15 (16 × 14 × 6 mm, 2.5 g), was secured to a Dalton

**Table 1** Details of GLS logger deployments on juvenile Antarctic fur seals at Bird Island, South Georgia. Body measurements were taken on deployment, and age at deployment was estimated from body length

Seal ID/Tag	Sex	GLS model	Deployment start	Deployment end	Deployment duration (days)	Mass (kg)	Length (cm)	Girth (cm)	Span (cm)	Estimated age (years)
W7395	M	Mk5	16-Jan-2007	25-Apr-2008	465	44.2	140	77	113	3
W7397	M	Mk5	16-Jan-2007	30-Jul-2007	195	45.5	141	91	–	3
W7398	M	Mk5	16-Jan-2007	16-Dec-2007	334	25.5	121	64	86	2
W7399	M	Mk5	16-Jan-2007	12-Nov-2007	300	43.8	145	78	115	3
W7402	F	Mk5	23-Jan-2007	29-Dec-2007	340	21.2	113	63	87	2
W7404	M	Mk5	23-Jan-2007	03-Jan-2008	345	32.9	128	71	101	2
W7410	F	Mk5	28-Jan-2007	20-Jan-2008	357	15.5	105	57	87	1
W7413	M	Mk5	26-Feb-2007	10-Dec-2007	287	24.8	111	67	100	1
W7530	M	Mk9	09-Jan-2008	18-Aug-2008	222	17.2	101	59	96	1
W7556	F	Mk9	25-Jan-2008	30-Apr-2008	96	17.7	96	61	92	1
W7587	F	Mk4	22-Feb-2008	06-Apr-2008	44	15.2	97	56	90	1
W8376	M	Mk9	12-Feb-2010	03-Jan-2011	325	27.9	109	68	111	1
W8378	F	Mk9	12-Feb-2010	09-Dec-2010	300	23.5	115	66	105	3
W8379	M	Mk9	12-Feb-2010	31-Oct-2010	261	36.8	130	80	116	2
W8381	M	Mk9	28-Feb-2010	25-Sep-2010	209	33.4	122	63	106	2
W8391	F	Mk9	04-Mar-2010	08-Dec-2010	279	23.4	110	63	113	2
W8637	F	Mk15	29-Mar-2011	30-Sep-2011	185	21.5	104	54	96	1
W8640	F	Mk15	29-Mar-2011	29-Dec-2011	275	23.7	101	59	98	1
W8645	F	Mk15	31-Mar-2011	12-Jan-2012	287	25.6	116	59	106	3
W8653	F	Mk15	06-Apr-2011	05-Oct-2011	182	21.2	116	56.5	89	3
W8667	F	Mk15	09-Apr-2011	08-Jan-2012	274	15.6	92	52.5	86	1
W8582	F	Mk15	10-Apr-2011	06-Oct-2011	179	27.8	112	63	104	2
W8678	M	Mk15	12-Apr-2011	09-Dec-2011	241	18.7	99	51	96	1
W8251	F	Mk15	17-Apr-2011	20-Dec-2011	247	28.9	119	65	109	3
W8687	F	Mk15	13-Apr-2011	08-Jan-2012	270	17	95	53	82	1
W8690	F	Mk15	13-Apr-2011	16-Feb-2012	309	16.7	99	58	87.5	1
W8695	F	Mk15	15-Apr-2011	07-Jan-2012	267	27.9	106	68	101	2
W8902	F	Mk15	17-Apr-2011	10-Nov-2011	207	22.3	99	59	93	1
W8904	M	Mk15	17-Apr-2011	24-Nov-2011	221	14.3	99	50	88	1
W8702	M	Mk15	07-Jan-2012	06-Jan-2013	365	25.2	118	59	100	2
W8706	F	Mk15	09-Jan-2012	05-Feb-2012	27	20	99	60	83	1
W8708	M	Mk15	10-Jan-2012	26-Oct-2014	1020	19.1	99	59	89	1
W8710	M	Mk15	09-Jan-2012	06-Feb-2013	394	19.9	98	56	98	1
W8712	M	Mk15	09-Jan-2012	06-Dec-2012	332	42.1	137	69	126	3
W8714	F	Mk15	09-Jan-2012	08-Jan-2013	365	22.8	101	66	90	1

Table 1 (continued)

Seal ID/Tag	Sex	GLS model	Deployment start	Deployment end	Deployment duration (days)	Mass (kg)	Length (cm)	Girth (cm)	Span (cm)	Estimated age (years)
W8716	M	Mk15	10-Jan-2012	06-Feb-2013	393	30	118	61	107	2
W8723	M	Mk15	11-Jan-2012	28-Aug-2012	230	23	108	60	101	1
W8736	M	Mk15	13-Jan-2012	03-Dec-2012	325	38	124	68	115	2
W8739	M	Mk15	13-Jan-2012	16-Nov-2012	308	28.8	110	67	104	1
W8740	M	Mk15	13-Jan-2012	06-Feb-2013	390	35.8	125	71	117	2
W8686	M	Mk15	13-Apr-2011	30-Jan-2012	292	19.6	103	57	88	1
W8715	M	Mk15	09-Jan-2012	13-Oct-2012	278	26.4	114	66	106	1
W8720	M	Mk15	10-Jan-2012	19-Feb-2012	40	15.2	96	54	87	1
W8709	M	Mk15	09-Jan-2012	03-Sep-2012	238	16.3	99	54	87	1
W8724	M	Mk15	11-Jan-2012	05-Dec-2012	329	21.9	98	62	97	1

jumbo roto tag and fixed to the trailing edge of a fore-flipper as described by Staniland et al. (2012). GLS loggers were retrieved (by cutting cable ties around the logger) when seals were resighted and recaptured. At each capture, seal mass, total body length, flipper span, and girth were recorded where possible (Committee on Marine Mammals 1967).

### GLS programming

Prior to deployment, GLS loggers were calibrated for at least one month with a full view of the sky at Bird Island. GLS loggers measured light intensity every minute and recorded the maximum light intensity in each 10 min interval. They also measured salt-water immersion every three seconds and recorded the total number of immersion events in each 10 min interval: a value of 200 shows the GLS logger was immersed for the entire period, while a value of 0 shows the GLS logger was completely dry. GLS loggers additionally measured sea surface temperature when the logger was immersed for at least 20 min.

### Data processing

Data were downloaded from GLS loggers using the BAS-Trak software (British Antarctic Survey, Cambridge, UK). Light data was pre-processed following methods described by Lisovski et al. (2019) using the TwGeos package (Lisovski et al. 2016) in R v3.6.0 (R Core Team 2020). Specifically, the daily sunrise and sunset times (twilight times) were defined as the times when light intensity reached a pre-determined threshold of two. Next, the zenith angle (angle between the sun and vertical) and parameters of the error distribution of twilight times, causing uncertainties in location estimates (Lisovski et al. 2012), were determined from the calibration data. These parameters were then used to estimate the movement trajectories using the R Package SGAT (Wotherspoon et al. 2019). The applied Bayesian method makes use of Markov Chain Monte Carlo (MCMC) simulations and allows incorporation of the twilight model (calibration), a movement model, and a spatial mask to improve location estimates and estimate uncertainty (Lisovski et al. 2019). A gamma distribution was used to describe the movement model assuming a mean swimming speed of 1 m/s and variance of 0.08 m/s, suitable for relatively slow-moving species and considered an appropriate estimate for mean speed of juvenile Antarctic fur seals, as mean surface swimming speeds of adult otariids range from 0.6 to 1.6 m/s (Ponganis et al. 1990). The spatial mask, consisting of a combined land mask and sea surface temperature (SST) probability mask, was made using a land map and maps of mean daily SSTs from the NOAA OI SST V2 High Resolution Dataset. The spatial mask enabled finer accuracy of location estimates by preventing implausible movements

of seals across land and by incorporating probability of locations according to mean daily SST and GLS logger SST readings. This eliminated temperature ranges that were out of the temperature range recorded by the tag, particularly during 2–3 weeks around the equinox when latitude is inestimable from light levels alone as day length is the same globally. Mk9 tags did not record SST data, and so a land mask was used alone for these seals. The proposals for the MCMC simulations were tuned using 1000 posterior draws and a modified model with relaxed assumptions before running the model with 1000 iterations. Tracks were summarised to produce median tracks and 95% credibility intervals.

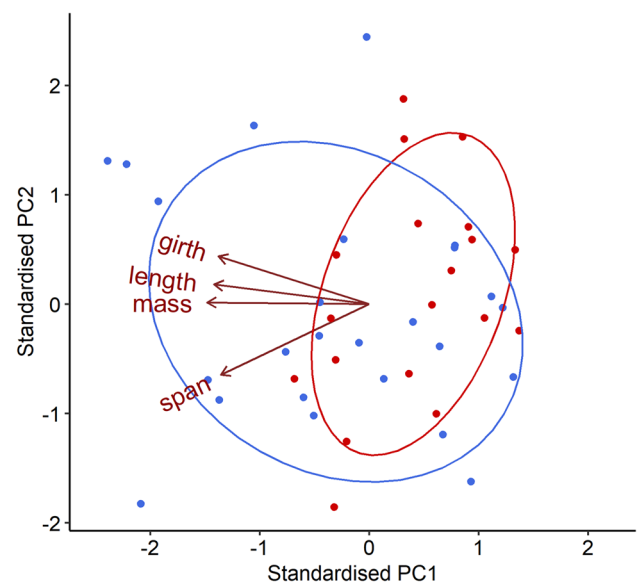
For each seal and each time period, we used all simulated tracks to calculate a Utilisation Distribution using the *adehabitatHR* package in R (Calenge 2020). We used a common bandwidth of 85,787 m, which was the mean value obtained from the sexes and time periods separately, obtained from the reference bandwidth selection method. The 95% and 50% home range was then deduced from each Utilisation Distribution, signifying the smallest area where the probability of relocating the individual was 95% and 50%.

To determine the duration of haul-out periods for each seal, we processed all immersion data according to methods by Staniland et al. (2018), using the R package *diveMove* (Luque 2007). To analyse the data, we only used dry periods for which the GLS logger was completely dry for at least one hour.

## Data analysis

To identify whether body morphology significantly differed between male and female juveniles at GLS deployment, we conducted a Principal Components Analysis (PCA) on morphology data, then used the outputs from Principal Component 1 (which explained the most variance) in a Student's *t* test. One male seal (w7397) was excluded from this analysis, as its span (length between flipper tips) was not obtained. We also estimated the age of each seal at GLS deployment, by extracting age (to the nearest year) from male and female body length curves (Fig. 1 in Payne (1979)). To determine whether estimated age at GLS deployment significantly differed between the sexes, we used a Mann Whitney *U* test.

To determine whether sexual segregation in foraging distribution occurred in juveniles during the annual cycle, we used the latitude and longitude of the median tracks as separate response variables in Generalised Additive Mixed Models using the *mgcv* package in R (Wood 2017). We included day of the year, sex, estimated age, and their interactions as predictor variables in candidate models. We specified juvenile ID as a random effect to account for variation among individuals, and we used a *corARMA* ( $p = 1$ ) autocorrelation structure to account for temporal correlation. Candidate models were ranked according to their Akaike Information



**Fig. 1** Relationship between PC1 and PC2 using morphology data from 19 female (red) and 25 male (blue) juvenile Antarctic fur seals, obtained during GLS deployment (colour figure online)

Criterion (AIC) and the model with the lowest AIC was considered the best-fit model (the simplest model was selected if AICs differed by less than two). Residual plots were checked for normality and homoscedasticity.

We then tested whether the size of foraging areas (in km<sup>2</sup>) differed between male and female juveniles in three key time periods during the year: Dec–Jan (when adult males and females are present on breeding beaches); Feb–Apr (when adult males have left breeding beaches but adult females are present when suckling their pups); May–Nov (the non-breeding period). We log-transformed the 95% home range area outputs (to improve model fit), then used the output as a response variable in Linear Models. We included time period, sex, body size at deployment (indicated by PC1), estimated age, tracking duration, and their interactions in candidate models, and we selected the best-fit model according to the lowest AIC.

To quantify spatial overlap in foraging distributions, we calculated the Utilisation Distribution Overlap Index (UDOI) for each of the three time periods using the *adehabitatHR* package. UDOI values are null (no spatial overlap) or positive, with the higher the UDOI the higher the overlap (Fieberg and Kochanny 2005). To calculate these indices, we estimated the 95% and 50% Utilisation Distributions using the median tracks and Gaussian kernels with a bandwidth of 85,787 m. To test whether the observed overlap was lower than expected by chance, we used a permutation approach. For each of the 1000 iterations, we randomised sex labels across individuals and calculated the UDOI between simulated male and female distributions. We calculated a *p* value



for the permutation test as the proportion of simulated UDOI values that were lower than the observed UDOI.

We next determined whether haul-out durations differed between the sexes and among time periods. We log-transformed haul-out durations, then used the output as a response variable in Linear Mixed Effects models using the R package nlme (Pinheiro et al. 2020). Predictor variables in candidate models included time period, sex, body size at GLS deployment (indicated by PC1), and their interactions, with juvenile ID specified as a random effect. We selected the best-fit model according to the lowest AIC. Results are reported as means  $\pm$  standard error unless stated.

## Results

### Sample sizes

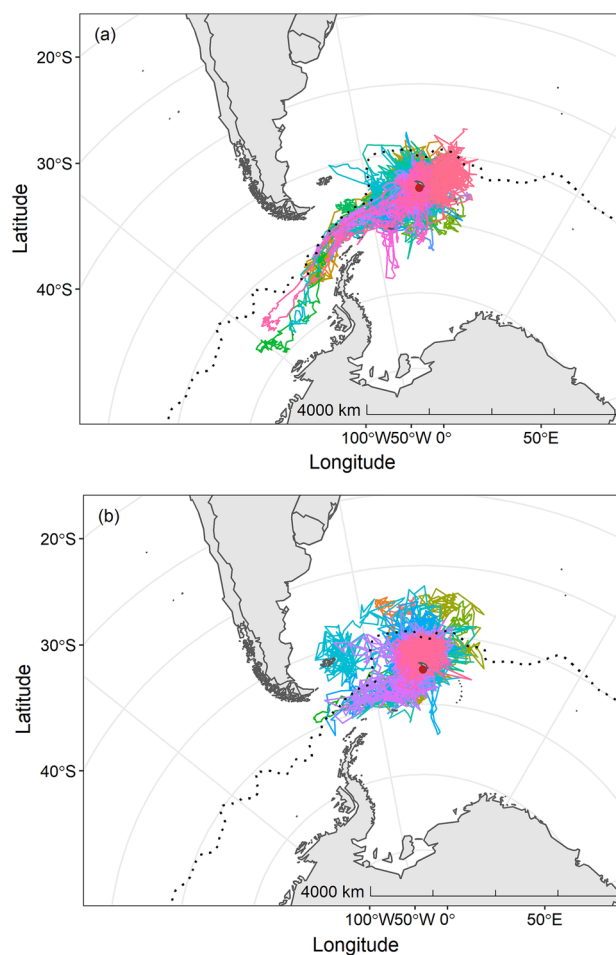
Twenty-six males and 19 females were GLS-tracked from Bird Island (Table 1). This included 23 males and 14 females tracked in Dec–Jan, 26 males and 19 females tracked in Feb–Apr, and 25 and 16 females tracked in May–Nov.

### Size dimorphism

Individual juvenile mass, body length, span, and girth measurements at GLS deployment were highly inter-correlated, with Pearson correlation coefficients ranging from 0.62 to 0.91. Males and females averaged  $27.9 \pm 1.9$  kg and  $21.4 \pm 1.0$  kg in mass respectively,  $115.1 \pm 3.0$  cm and  $105.0 \pm 1.9$  cm in length respectively,  $64.7 \pm 1.9$  cm and  $59.9 \pm 1.0$  cm in girth respectively, and  $102 \pm 2.2$  cm and  $94.7 \pm 2.1$  cm in span respectively. Combining these measurements together in the PCA indicated that male juveniles were larger than females. Loadings for PC1 were mass ( $-0.53$ ), length ( $-0.50$ ), girth ( $-0.49$ ) then span ( $-0.48$ ). PC1 explained 86.7% of the variability in morphology data, and the mean scores differed significantly between males and females by 1.32 (Student's *t* test:  $t=2.5$ ,  $p=0.02$ ) (Fig. 1). Age at GLS deployment, extrapolated from body size, averaged  $1.62 \pm 0.15$  years for males and  $1.63 \pm 0.19$  years for females, and did not significantly differ between the sexes (Mann-Whitney *U* test:  $U=245$ ,  $p=0.97$ ).

### Foraging distribution

Sexual segregation was present in juvenile foraging distribution during the annual cycle. Males generally foraged south of the Polar Front and near the Antarctic Peninsula, whereas females generally foraged closer to South Georgia and north of the Polar Front (with one seal exploring waters surrounding the Falkland Islands) (Fig. 2). This sexual segregation primarily occurred in latitude, as males

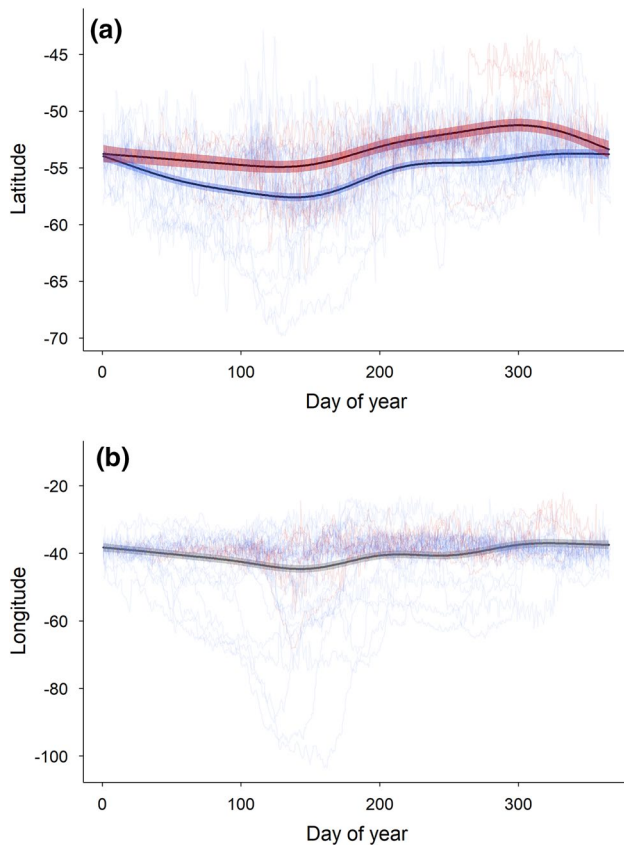


**Fig. 2** Median tracks of **a** 26 male and **b** 19 female juvenile Antarctic fur seals tracked with GLS loggers between 16-Jan-2007 and 26-Oct-2014. Grey shaded areas show South America and Antarctica, red dot shows deployment site (Bird Island, South Georgia), dotted line indicates position of the Polar Front, and colours show different individuals

foraged further south than females on average throughout the year (Fig. 3a; Table 2a). Patterns in longitude were best explained by day of year, although the effect size was low at 0.07 (Fig. 3b; Table 2b). Three males foraged further west than  $75^\circ$  from April, and moved rapidly further east in May and June (Fig. 3b). Two of these individuals (w8379 and w8740) were larger in body size than the male average at deployment, and one (w8708) was tracked for longer than any other individual (1020 days). These individuals did not drive the results, as variables in the best-fit models were the same when these males were removed from the analyses.

### Extent of foraging areas

The extent of foraging areas, calculated using all simulated tracks, did not significantly differ between male and female juveniles. However, extent of foraging areas significantly



**Fig. 3** **a** Latitude and **b** longitude of GLS-tracked juvenile Antarctic fur seals throughout the year. Black lines indicate fitted values from Generalised Additive Mixed Models, shading around black lines represent standard error of fitted values (red=females, blue=males), and points show raw data values from median tracks from 19 females and 26 males

differed among all three time periods (Table 3), including between Feb–Apr and May–Nov (Tukey post-hoc test;  $p=0.022$ ). Larger individuals (with lower PC1 values at deployment) also had significantly larger home ranges than smaller individuals, and juveniles tracked for longer time periods had larger foraging areas (Table 3). In Dec–Jan (when both adult males and females were present on breeding sites), both sexes remained in proximity to Bird Island and the average home range area was  $1,444,028 \pm 48,188 \text{ km}^2$ . In Feb–Apr (when adult males have departed from breeding beaches), some males foraged south in maritime Antarctica and most females remained around South Georgia; the average home range area was  $1,885,408 \pm 18,776 \text{ km}^2$ . In May–Nov (the non-breeding season), the average home range area increased to  $2,294,062 \pm 133,003 \text{ km}^2$ .

### Spatial overlap

The overlap between the 95% home ranges indicated that sexual segregation in space was particularly evident in

Feb–Apr (UDOI = 0.749) and May–Nov (UDOI = 1.56), as the UDOIs were significantly lower than expected by chance (Permutations tests,  $p < 0.0001$  and  $p = 0.002$  respectively) (Fig. 4). Sexual segregation in space was less apparent in Dec–Jan (UDOI = 1.41), as the UDOI was not significantly lower than expected by chance (Permutations test,  $p = 0.103$ ) (Fig. 4). The overlap between the 50% home ranges indicated similar findings (UDOIs in Feb–Apr, May–Nov and Dec–Jan were 0.116, 0.192, and 0.228 respectively, and Permutation test  $p$  values were 0.001, 0.003, and 0.095 respectively).

### Haul-out duration

GLS logger immersion readings indicated that male and female juveniles spent an average of 24.5% and 15.0% of their time hauled out respectively. The duration of haul outs was best explained by sex and time period. Specifically, both males and females spent more time hauled out in Dec–Jan and Feb–Apr, than in May–Nov (Table 4; Fig. 5). Additionally, males had significantly longer haul-out bouts, on average, than females in May–Nov ( $18.0 \pm 1.1 \text{ h}$  for males;  $8.32 \pm 1.2 \text{ h}$  for females) (Table 4; Fig. 5). The second best-fit model was within two AIC of the simpler best-fit model, and included body size as an additional predictor variable (Table 4).

### Discussion

We found clear sex differences in body size and foraging distribution in a highly polygynous species during the juvenile life stage. Male juvenile Antarctic fur seals were significantly larger than females (Fig. 1) and males generally foraged further south near the Antarctic Peninsula, whereas females foraged closer to South Georgia and the Polar Front (Fig. 2; Fig. 3). Contrary to our prediction, the extent of foraging areas did not significantly differ between the sexes (Fig. 4). However, males spent more time hauled out than females during the non-breeding season (Fig. 5). These findings enable us to investigate the underlying drivers shaping sexual segregation in juveniles.

### Sexual size dimorphism

Sexual size dimorphism in pinnipeds is thought to be driven by both natural selection and sexual selection (Krüger et al. 2014). Initially, sexual size dimorphism may have evolved to enable niche partitioning, with larger males exploiting deeper waters than smaller females (Krüger et al. 2014). Sexual size dimorphism is also driven by sex differences in reproductive success, which is more variable among males than females (Darwin 1871). This sexual selection pressure was reflected in the higher mass and body length

**Table 2** Generalised Additive Mixed Model selection to study the effect of sex, estimated age and day of year on latitude and longitude of GLS-tracked juvenile Antarctic fur seals

Model terms	AIC	$\Delta$ AIC	$R^2$	$n$
<b>Latitude</b>				
Sex + s(day of year, by Sex)	53,418.91	0	0.29	26,104
Sex + age + sex:age + s(day of year, by Sex)	53,420.99	2.08	0.30	26,104
Sex + age + sex:age + s(day of year, by Age)	53,427.78	8.87	0.33	26,104
s(day of year)	53,422.25	3.34	0.19	26,104
Sex	53,535.29	116.38	0.14	26,104
Parametric coefficients	Value	SE	$t$ value	$p$ value
Intercept	– 53.34	0.40	– 133.92	< 0.0001
Sex (male)	– 2.29	0.50	– 4.64	< 0.0001
Approximate significance of smooth terms	edf	Ref. df	$F$	$p$ value
s(day of year, by female)	4.85	4.85	7.77	< 0.0001
s(day of year, by male)	6.71	6.71	24.10	< 0.0001
Model terms	AIC	$\Delta$ AIC	$R^2$	$n$
<b>Longitude</b>				
s(day of year)	88,865.64	0	0.07	26,104
s(day of year, by Sex)	88,865.60	– 0.04	0.07	26,104
Sex + s(day of year, by Sex)	88,865.93	0.029	0.07	26,104
Age + s(day of year, by Sex)	88,867.69	2.05	0.09	26,104
Sex + age + sex:age + s(day of year, by Sex)	88,870.58	4.94	0.1	26,104
Parametric coefficients	Value	SE	$t$ value	$p$ value
Intercept	– 40.80	0.88	– 46.52	< 0.0001
Approximate significance of smooth terms	edf	Ref.df	$F$	$p$ value
s(day of year)	7.13	7.13	6.47	< 0.0001

AIC Akaike's Information Criterion,  $\Delta$ AIC difference in AIC between candidate model and best-fit model,  $R^2$  proportion of variance explained by predictors,  $n$  number of observations of the response variable. Results are shown for the top five best-fit models, and parameters are shown for the best-fit models

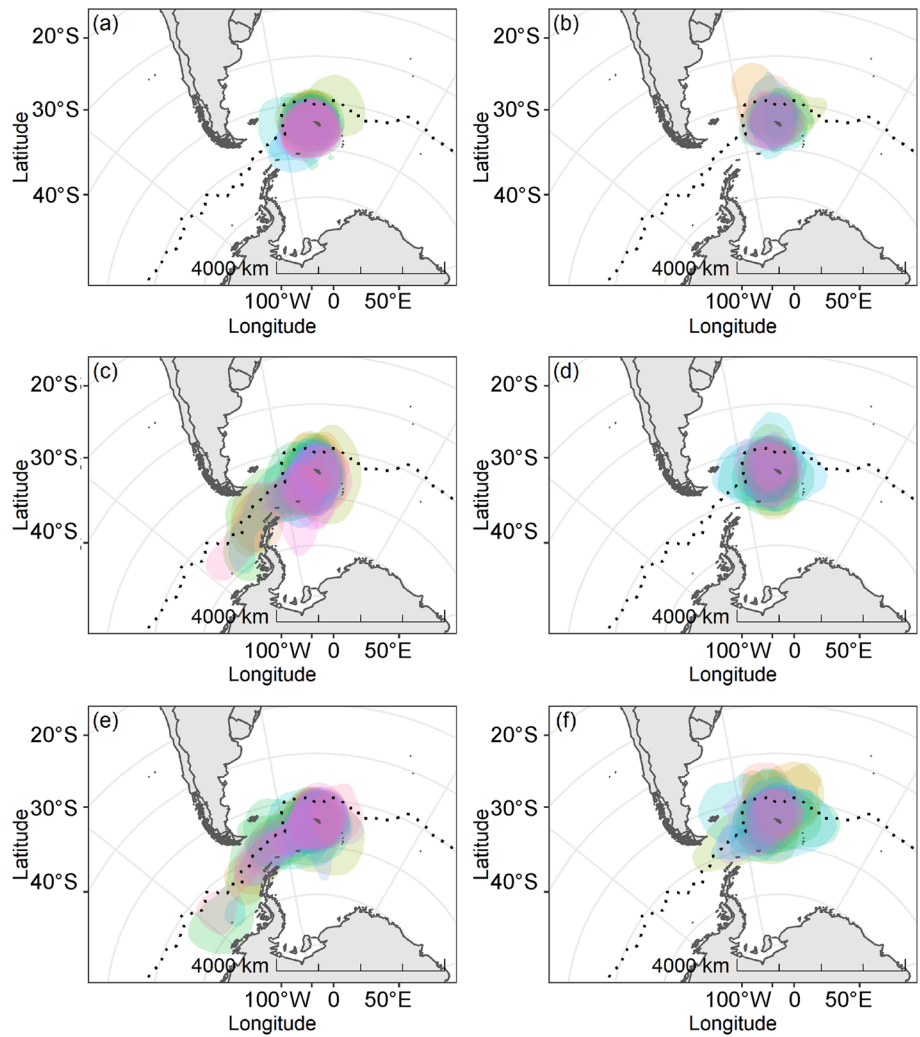
**Table 3** Linear Model selection to study the effect of sex, body size (indicated by PC1, with larger individuals having lower values), estimated age, and time period on home range size of juvenile Antarctic fur seals

Model terms	AIC	$\Delta$ AIC	$R^2$	$n$
Body size + time period + tracking duration	72.9	0	0.27	120
Body size + time period + tracking duration + body size:time period	73.9	1	0.28	120
Sex + body size + time period + tracking duration	74.0	1.1	0.27	120
Sex + body size + time period + tracking duration + body size:time period	74.9	2	0.28	120
Sex + body size + time period + tracking duration + sex:time period	75.6	2.7	0.28	120
	Value	SE	$t$ value	$p$ value
Intercept	27.8	0.08	334.75	< 0.001
Months (Feb–Apr)	0.22	0.07	3.01	0.003
Months (May–Nov)	0.40	0.07	5.48	< 0.001
Body size	– 0.04	0.02	– 2.67	0.009
Tracking duration	0.0006	0.0002	2.72	0.007

AIC Akaike's Information Criterion,  $\Delta$ AIC difference in AIC between candidate model and best-fit model,  $R^2$  proportion of variance explained by predictors,  $n$  number of observations of the response variable. Results are shown for the top five best-fit models, and parameters are shown for the best-fit model



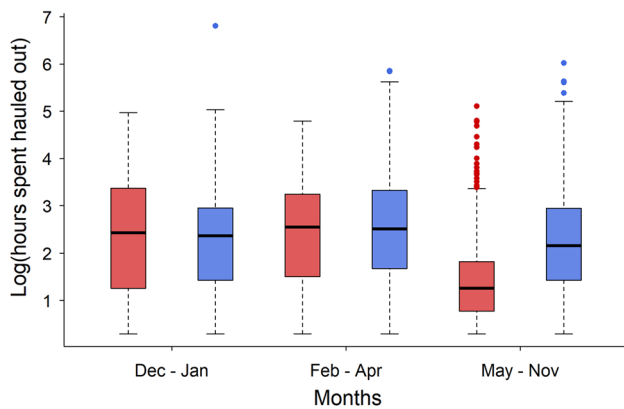
**Fig. 4** Home ranges (where probability of relocating each individual is 95%) of **a** 23 males and **b** 14 females in Dec–Jan; **c** 26 males and **d** 19 females in Feb–Apr, and **e** 25 males and **f** 16 females in May–Nov. Colours indicate different individuals



**Table 4** Linear Mixed Effects model selection to study the effect of sex, body size at GLS deployment (indicated by PCI, with larger individuals having lower values) and time period on the duration of time that juvenile Antarctic fur seals spend hauled out in between foraging trips

Model terms	AIC	$\Delta$ AIC	$R^2$	$n$
Time period+sex+time period: sex	7222.7	0.8	0.07	2416
Time period+sex+body size+time period: Sex	7221.9	0	0.08	2416
Time period+sex+body size+time period: sex+body size: sex	7226.8	4.9	0.08	2416
Time period+sex+body size+time period: sex+time period: body size	7234.2	12.3	0.08	2416
	Value	SE	$t$ value	$p$ value
Intercept	2.40	0.11	21.26	<0.001
Sex (male)	-0.18	0.14	-1.23	0.22
Months (Feb–Apr)	0.08	0.12	0.69	0.49
Months (May–Nov)	-0.87	0.12	-7.43	<0.001
Sex (male): months (Feb–Apr)	0.17	0.14	1.20	0.23
Sex (male): months (May–Nov)	0.83	0.14	5.83	<0.001

AIC Akaike’s Information Criterion,  $\Delta$ AIC difference in AIC between candidate model and best-fit model,  $R^2$  proportion of variance explained by predictors,  $n$  number of observations of the response variable. Results are shown for the top five best-fit models, and parameters are shown for the best-fit model



**Fig. 5** Log of the average number of hours spent hauled out in between foraging trips by 14 females (red) and 23 males (blue) in Dec–Jan, 19 females and 26 males in Feb–Apr, and 16 females and 25 males in May–Nov (colour figure online)

of juvenile males at GLS deployment compared to females (indicated by PC1), as these metrics increase more rapidly in males from birth to 5 years of age (Payne 1979). Males also invest more energy into lean tissue growth (Arnould et al. 1996), as future reproductive success will depend on fighting and fasting abilities (Arnould and Duck 1997). In contrast, females grow more conservatively (Payne 1979) and accumulate greater fat stores (Arnould et al. 1996). This strategy decreases risk of starvation and enables females to invest resources in reproduction earlier than males to maximise lifetime reproductive output at the expense of reduced growth (Mueller et al. 2011).

### Foraging distribution

Juveniles must develop a range of skills to forage independently, including successfully finding, competing for and handling food, as well as escaping predation (Sullivan, 1989; Votier et al. 2017; Carter et al. 2017). In the South Atlantic Ocean, Antarctic fur seals predominantly feed on krill, *Euphausia superba*, but also consume squid and fish (e.g. mackerel icefish, *Champsocephalus gunnari*, which are associated with krill aggregations; Doidge and Croxall 1985; Reid 1995; Reid and Arnould 1996). Since juveniles have no immediate reproductive requirements, they have time to explore and discover the most productive foraging areas (Salton et al. 2019), as matching their distribution to that of their preferred prey can maximise foraging efficiency (Stephens and Krebs 1986). Juvenile Antarctic fur seals dispersed further at sea than weaned pups tracked with Platform Terminal Transmitters from the same colony in their first year of life (Fig. 2 in Warren et al. 2006), as they developed the experience and physiological abilities to travel further. Sexual segregation was more apparent in juveniles than weaned pups, in line with greater sex differences in body

size, suggesting that sexual size dimorphism contributes to the development of sexual segregation in Antarctic fur seals.

Juvenile males mainly foraged around South Georgia, the Polar Front and the Antarctic Peninsula. Their foraging distribution overlapped with an Area of Ecological Significance AES (Hindell et al. 2020), and regions of high krill density west of the Antarctic Peninsula (Atkinson et al. 2019). Since adult females and other predators can cause local depletion of prey near South Georgia, males may forage more successfully in maritime Antarctica (Boyd et al. 1998), where prey availability is likely greater. Males are generally more risk-prone than females (e.g. Pellegrini 2004), and the benefits of food availability around Antarctica may outweigh the higher costs of travel, thermoregulation and predation risk (e.g. from orcas, *Orcinus orca*, and leopard seals, *Hydrurga leptonyx*). This more risk-prone foraging strategy can enable males to spend more time seeking the most productive foraging areas to maximise food intake and obtain a larger body size to improve ability to compete for mates in the future (e.g. Carter et al. 2019).

Females mainly foraged around South Georgia, and some individuals foraged north of the Polar Front. Their foraging distributions coincided with an AES spanning the Scotia Sea and surrounding waters, where prey available to marine predators is high in biodiversity and biomass (Hindell et al. 2020). Adult females and an abundance of marine predators also forage in this region (Boyd et al. 2002; Staniland et al. 2012; Arthur et al. 2015; Hindell et al. 2020), and intense competition for shared prey resources could lead to divergent foraging strategies (Schoener 1974; Navarro et al. 2013). Stable isotopes analysed along adult whiskers indicated that ~30% of adult females may consistently forage north of the Polar Front and consume different prey to the ~70% of adult females that consistently forage to the south of it (Jones et al. 2020b). Our findings indicate that divergent foraging strategies potentially develop in juvenile females (Fig. 3), which could be a mechanism to maximise foraging efficiency. Young female seals may adopt a more risk-averse strategy than young males, targeting more predictable environments and spending less time searching for prey—as documented in weaned grey seal pups, *Halichoerus grypus* (Carter et al. 2019). Indeed, females must prioritise survival to fulfil their reproductive potential (Trivers 1972; Clutton-Brock et al. 1982; Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001; Carter et al. 2019).

These sex-specific foraging strategies may become more pronounced as juveniles grow and develop. As seals grow, they can increase their travel speed, aerobic limits (i.e. by increasing mass-specific oxygen stores; Fowler et al. 2006) and thermoregulation abilities (Staniland and Robinson 2008). Since males grow for a longer time than females (Payne 1979), these factors could enable males to travel further and spend more time foraging in maritime Antarctica

as they develop (Jones et al. 2020b). Indeed, tracked adult males mostly foraged within 50° and 80° West around Antarctic Peninsula between the end of January and May (Lowther et al. 2020), whereas most juveniles remained further east throughout the year. The three males that foraged further west than 75° abruptly foraged further east in May and June in a similar pattern to the adult males (Lowther et al. 2020).

### Extent of foraging areas

Juvenile Antarctic fur seals extended their foraging areas between the breeding and non-breeding seasons. In Dec–Jan adult males compete for mates and may forage in the vicinity of South Georgia (Staniland and Robinson 2008). At this time, some juvenile females may approach breeding beaches to seek their first mating opportunities, as the average age of primiparity is 4.6 years (Forcada and Hoffman 2014). Juvenile female northern fur seals, *Callorhinus ursinus*, also show greater homing behaviour and fidelity to their natal sites than males, likely due to their earlier sexual maturity (Kenyon and Wilke 1953; Zeppelin et al. 2019). In Feb–Apr dominant adult males are absent from breeding beaches, so juvenile males can come ashore to socialise and gain fighting skills with less likelihood of harassment by elders. In May–Nov juveniles extended their foraging areas, similarly to adults. At this time, adult males migrate south and forage in maritime Antarctica (Boyd et al. 1998; Jones et al. 2020b; Lowther et al. 2020), whereas adult females forage near to South Georgia, north of the Polar Front, or south to the northern edge of the Antarctic pack ice (Boyd et al. 2002; Staniland et al. 2012). Since juveniles have no immediate breeding constraints, this change in foraging extent may relate to seasonal changes in preferred prey. Antarctic krill transports to South Georgia via currents when the Antarctic sea ice retreats in spring (Murphy et al. 2004). In winter, Antarctic krill around South Georgia is smaller in size and less lipid-rich (Reid 1995), so juvenile and adult Antarctic fur seals may forage further afield to exploit krill or alternative prey elsewhere. Juveniles potentially follow adults to gain experience of the most productive foraging areas to exploit in future years.

Contrary to our prediction, there was no sex difference in foraging extent. Bishop et al. (2018), found that male juvenile Steller's sea lions, *Eumetopias jubatus*, tended to have larger home ranges (which also encompassed more haul outs) than females, potentially attributed to their sexual size dimorphism and higher energetic requirements. The absence of sex differences in juvenile Antarctic fur seal foraging extent could result from the nature of the prey landscape, or because body size alone (indicated by PC1) was a better indicator of foraging extent than sex and age—with larger individuals physically capable of exploring larger areas.

However, since body size and sex are confounded, we cannot rule out that sex does not contribute to foraging extent.

### Spatial overlap

Sexual segregation in space, indicated by the UDOI, was less evident in Dec–Jan than other time periods—a time when adults are present on breeding beaches. In Dec–Jan, juveniles foraged near South Georgia, which may be an innate or a learned behaviour (i.e. from following adult seals), which could enable them to gain experience of foraging grounds and of central place foraging constraints before they start reproducing, as found in immature wandering albatrosses, *Diomedea exulans* (Riotte-Lambert and Weimerskirch 2013). Male and female juvenile foraging distributions at this time could be limited by the distribution of prey, and the proximity of foraging grounds to South Georgia. Although the sexes overlap horizontally, it is possible that they still segregate by dive depth or diet, as males—with a larger body size and greater oxygen stores—can dive deeper and handle prey more efficiently than smaller females (Staniland 2005; Staniland and Robinson 2008).

### Haul-out

Juvenile Antarctic fur seals spent more time hauled out during the breeding season (Dec–Apr) than the non-breeding season (May–Nov), even though most individuals were not yet breeding. During the breeding season, juveniles may come ashore to rest, and females may seek mating opportunities while males play-fight on the breeding beaches. During the non-breeding season, males spent more time hauled out between foraging trips than females, concurring with observations of more subadult and adult males ashore at this time (e.g. Reid 1995; Waluda et al. 2010). Male juveniles may haul out more than females to gain long-term benefits from social interactions. In winter, food is more limited and females may need to increase foraging time to meet daily food requirements, presumably resting in the water for extended time periods as found in adult females (Staniland et al. 2012). As juveniles grow and age, predation risk decreases and thermal costs of immersion decrease (Liwanag et al. 2009), potentially enabling seals to spend longer offshore. Indeed, GLS-tracked adult females spent 95.6% of time in the water in winter (Staniland et al. 2012).

### Consequences of sexual segregation

Sexual segregation may expose the sexes to different localised sources of mortality. For example, female juvenile New Zealand sea lions overlap with trawl fisheries to a greater extent than males, exposing females to higher resource competition and risk of by-catch (Leung et al. 2012). In summer,

the krill fishery operates around the Antarctic Peninsula (and is seasonally closed at South Georgia; Government of South Georgia and the South Sandwich Islands 2020), so fishing effort is more likely to overlap with juvenile males. In winter, the krill fishery operates around South Georgia (outside of the 12 nm no-take zone; Government of South Georgia and the South Sandwich Islands 2020), so fishing could overlap with both males and females. Krill fishing nets are equipped with mandatory Seal Exclusion Devices to reduce risk of by-catch (CCAMLR 2015). However, competition may occur, and will likely increase as fishing pressure in the Southern Ocean is expected to intensify (Nicol et al. 2012; Chown and Brooks 2019).

Environmental change is altering sub-Antarctic and Antarctic ecosystems. It has been suggested that Antarctic krill distribution contracted towards Antarctica between 1926 and 2016 (Atkinson et al. 2019), and Antarctic krill density is projected to decline in coastal waters around the Western Antarctic Peninsula (Hückstädt et al. 2020). Sub-Antarctic AESs are also projected to expand in area and move southward (Hindell et al. 2020). Given their reliance on krill, juvenile Antarctic fur seals may alter their foraging distributions to match new regions of prey availability. Such changes could alter the degree of segregation between males and females observed in this study. Sex differences in mortality could have important consequences for demography since female survival has a particularly high influence on population dynamics (Boyd et al. 1995).

## Conclusion

We found that sexual segregation in foraging distribution develops in the juvenile life stage of a highly polygynous species, the Antarctic fur seal. Although juveniles have no immediate breeding constraints, they are subject to pressures that anticipate the sex-specific requirements of later reproduction. The inter-linking drivers of sexual size dimorphism, sex differences in risk, and sex-specific social roles, coupled with prey distribution, likely contributed to sexual segregation. As a result of this segregation, juvenile males may compete with krill fisheries for a greater proportion of the year and over a greater geographic area than females, and the sexes may thus respond to global change in different ways. Further research should focus on testing for potential sex differences in dive behaviour and diet, as well as combining approaches to quantify the impacts of climate change and fisheries on male and female juvenile Antarctic fur seals. Since juvenile survival has a high impact on population demography, understanding the nature of sexual segregation in juveniles of additional species is critical to improve

understanding of species' ecology and to develop effective conservation measures.

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**Author contribution statement** IJS conceived the study. All co-authors advised on analyses. IJS, NR and SL provided extracts of code to process GLS data, and ASBL provided code to calculate the Utilisation Distribution Overlap Index. KAJ analysed the data and wrote the manuscript. All co-authors edited and provided feedback on the manuscript.

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**Data Availability** The datasets for the current study are available from the British Antarctic Survey Polar Data Centre.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

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