ARTICLE

Tracking the foraging migrations of Marion Island southern elephant seals (*Mirounga leonina*) during their first year of life

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Abstract

The first year of life is critical for large mammals to acquire foraging and predator avoidance skills. Southern elephant seal (*Mirounga leonina*) pups wean at approximately three weeks of age and depart on their first foraging trips in midsummer, typically remaining at sea for three to four months before returning to their natal islands. We describe the foraging trips ($n = 29$) of 16 underyearling southern elephant seals from sub-Antarctic Marion Island and compare these with trips ($n = 152$) of 94 older seals from the same population. While subadults (prebreeding age) and adult females (breeding age) displayed directional travel, underyearlings traveled in multiple directions from the island with no evidence of repeatability of travel directions within or between individuals and years. Maiden trips took longer to complete than subsequent trips during the first year of life, but we found no evidence for significant changes in other track metrics between the first three foraging trips. The comparatively inconsistent movement patterns of underyearlings suggest that foraging strategies of individuals are influenced by their learning and/or success during the first year of life

and that individual level consistency in successful foraging strategies only become apparent in subsequent years.

KEYWORDS
geolocation, habitat selection, marine mammal, ontogeny, *Phocidae*, tracking

1 | INTRODUCTION

Despite high maternal investment, juvenile large mammals tend to be sensitive to resource constraints (Eberhardt, 2002) and often have lower survival rates than adults (DeLong et al., 2017; Owen-Smith et al., 2005). The rapid acquisition of foraging skills and the ability to avoid predation are therefore crucial if juveniles are to survive and ultimately recruit into breeding populations. Developing foraging and predator-avoidance skills may have an innate component (Yoda et al., 2017), be learned from conspecifics (Takano et al., 2017; Thornton & Clutton-Brock, 2011), or be associated with specific environmental cues (Frankish et al., 2022) or other intrinsic and extrinsic factors (Carter et al., 2017).

Some phocid seal species (family Phocidae) are capital breeders and rely on solid substrates to give birth and nurse young. Female capital breeding seals fast during a relatively short lactation period (from 4 days in Hooded seals, *Cystophora cristata*; Bowen et al., 1985) to 3–4 weeks in elephant seals, *Mirounga* spp. (Fedak et al., 1994; Le Boeuf et al., 1972) before permanently leaving the weaned pups. After an initial fasting period ashore, underyearlings (defined here as individuals that had departed their natal site to forage at sea but had not yet returned to undertake their first molt haul-out; de Kock et al., 2021) undertake their first foraging trips unaccompanied by adults. Therefore, underyearling seals must rapidly learn to forage at sea while avoiding predation by apex predators such as killer whales (*Orcinus orca*).

Adult (breeding age) southern elephant seals (*M. leonina*) mostly haul out (return to land) twice annually to breed and molt (Le Boeuf & Laws, 1994). In addition to the molt, some nonbreeding seals (including underyearlings and subadults) haul out for short periods during the austral autumn and winter (Kirkman et al., 2001; Laws, 1956). The foraging migrations of southern elephant seals are well studied (e.g., Hindell et al., 2016), although there is, as for many species, a bias towards adult females with comparatively few studies addressing the at-sea behaviors of adult males and younger age classes (McIntyre, 2014). Adult and subadult southern elephant seals display high fidelity to foraging areas at sea (Bradshaw et al., 2004; McIntyre et al., 2017). The at-sea movements of recently weaned elephant seal pups were previously reported from King George Island (Bornemann et al., 2000), Macquarie Island (McConnell et al., 2002; Walters et al., 2014), and Kerguelen Island (Orgeret et al., 2019). Seals from those populations typically displayed directed movements away from their natal islands, prompting speculation that environmental cues and/or conspecifics may be responsible for the relatively consistent directions and distances travelled during their first foraging trips (McConnell et al., 2002).

The southern elephant seal population at Marion Island in the sub-Antarctic Indian Ocean has been intensively studied through a long-term mark-resight program running without interruption since 1983 (Bester et al., 2011). Adult female southern elephant seals from Marion Island generally forage west of Marion Island and south of the Sub-Antarctic Front, often pelagically in areas associated with deep bathymetric features that are prone to eddy activity (Jonker & Bester, 1998; Massie et al., 2016; McIntyre et al., 2011b, 2012; Tosh et al., 2012). While subadult seals under the age of 2 years from this population broadly seem to follow similar strategies as older cohorts (Tosh et al., 2012), the foraging behavior of underyearling southern elephant seals has not been previously described.

Here, we describe the at-sea foraging trips of underyearling elephant seals from Marion Island. The phenology of the foraging behavior of underyearling southern elephant seals differs to adults in that many younger seals interrupt the winter foraging migration with one or more short (days to weeks) midyear haul-outs for no apparent reason (Kirkman et al., 2001; Wheatley, 2001). We compare the results obtained from underyearling seals to track data available for subadult and adult seals from the same population. We distinguished between three foraging trip types,

namely postweaning (up to three trips undertaken during the first year of life), postmolt (trips undertaken at any age >0 after the first molt haul-out), and postbreeding (trips undertaken by adult seals after breeding at Marion Island). We expected to find broad similarities between these age classes in foraging trip parameters that would suggest common responses to environmental cues as a primary means of early foraging determination.

2 | METHODS

2.1 | Track data

We instrumented 79 southern elephant seal underyearlings (44 males and 35 females) at Marion Island (46°54′S, 37°45′E) with archival light-based geolocation tags (GLs; R. Hansworth, Kingston, TAS, Australia) during 2005 ($n = 19$), 2006 ($n = 35$), 2007 ($n = 20$) and 2008 ($n = 5$). The dimensions of the GLs were $60 \times 45 \times 25$ mm and tags recorded light data every 45 s. Seals were immobilized prior to instrumentation following methods detailed in Bester (1988). Instruments were glued onto the hair of the heads of seals using a quick setting epoxy resin (Field et al., 2012). Upon the return of instrumented seals to Marion Island, the adherence of GLs was carefully inspected and, if compromised, recovered by carefully shaving them off following sedation. Tags were left on instrumented seals when adherence was considered still sufficient, and these GLs were recovered when shed naturally during the subsequent annual molt. Data from recovered tags were downloaded prior to redeployment on seals that had not previously been instrumented.

All tracked seals, except for one, were flipper tagged at Marion Island as weaned pups. Underyearlings were either instrumented prior to their first trip to sea or during a winter haul-out within their first year of life. The high resight effort at Marion Island (Bester et al., 2011) allowed us to identify with confidence marked seals that had only completed a single trip to sea following weaning (Pistorius et al., 2011). We assumed that if a marked seal had not been sighted at the island for 20 days or longer, that it had completed a foraging trip when it was resighted again. We estimated the age of the single nonflipper-tagged seal in our sample based on its size at deployment. This seal was instrumented as part of a training exercise and assumed to have completed one foraging trip from an unknown natal island to Marion Island preceding instrumentation, given that hauled out tagged seals of a similar size had completed single foraging trips.

2.2 | Geolocation analysis

Seal tracks were estimated from the light data using the twilight free geolocation technique (Bindoff et al., 2018). As these GLs did not concurrently record depth, light level changes at the surface could not easily be isolated for the overall time series. The twilight-free approach is well suited to these data as it was designed to deal with periodic obstruction of the light sensor (such as deep diving behavior in southern elephant seals, McIntyre et al. 2010a). The method uses the overall pattern of day and night on a particular day to calculate the likelihoods for a Hidden Markov Model, where the hidden states are geographic locations (Bindoff et al., 2018). The spatial domain is discretized to form a grid of cells and time is discretized into successive segments of 24 hr. The likelihood of a seal being in a cell is determined by a comparison between the observed light record, and the expected pattern of day and night at each cell, based on standard astronomical formulae. For our analyses we used a grid size of 1°, and a daylight threshold value calculated for each tag based on known locations while the seal was ashore.

2.3 | Comparison with older seals

Various satellite-linked tracking devices (Platform Transmitter Terminals, PTTs) were deployed on subadult and adult southern elephant seals hauled out at Marion Island between 1999 and 2016. Detailed descriptions of these data

sets are provided elsewhere (e.g., McIntyre et al., 2011b, 2012; Tosh et al., 2012, 2015). We used data from 152 complete foraging migrations undertaken by 94 individuals instrumented with PTTs. Position data from PTTs were processed using a hierarchical state space model (SSM) to obtain estimated locations at regular time intervals (24 hr) that matched the temporal resolution of location estimates obtained from the GLs. The "bsam" R package (version 0.21, Jonsen et al., 2013) was used for processing of SSMs.

2.4 | Analyses of at-sea behavior

All analyses and graphic representations of data were done in the R programming environment (R Core Team, 2022). We calculated several track metrics from location estimates, including:

- Trip durations: defined as the number of days seals were at-sea during each foraging trip;
- Maximum distance travelled from Marion Island: defined as the maximum (geodetic) distance from Marion Island recorded within a single foraging trip. Calculated using the "SoDA" package (Chambers, 2020);
- Bearing: defined as the bearing from Marion Island ($0°–360°$) of track points at weekly (7 day) intervals. Calculated using the "geosphere" package (Hijmans et al., 2021);
- Mean speed traveled: minimum speed estimates between estimated daily locations assuming seals traveled the shortest path between subsequent locations;
- Total distance traveled: defined as the sum of shortest path distances between estimated daily track locations.

The inherent differences in error structures between location estimates obtained from PTTs and GLs (e.g., Shaffer et al., 2005) precluded comparisons of travel speeds and total distances traveled, as well as the analyses of other potentially useful track metrics such as track sinuosity. However, we assumed that differences in error structures did not significantly bias estimates of trip durations, bearing of travel, and maximum distances traveled.

We used linear mixed effects models with individual seal IDs specified as random effects implemented in the "lme4" package (Bates et al., 2015) to determine whether trip number and sex influenced dependent variables during underyearling foraging trips. Similarly, we assessed the influences of sex and age class on dependent variables when including all data. Foraging trip type correlated with age class (i.e., all underyearling seals undertook postweaning trips) and we therefore did not formally include trip type into these analyses. Type II analysis of variance (Wald chi-square tests), implemented with the *car* package (Fox & Weisberg, 2019) were applied to all linear mixed effects models and Satterthwaite degrees of freedom were estimated using Kenward-Roger *F*-tests. Normality of model residuals were assessed via a series of diagnostic plots, including standard residual plots, histograms, and quantile plots.

Given the circular ($0°–360°$) nature of foraging trip bearings, we used circular mixed effects models in a Bayesian approach within the "bpnreg" package (Cremers, 2021) to estimate directional consistency (Cremers & Klugkist, 2018). Accordingly, Markov Chain Monte Carlo samplers were used to estimate parameters of candidate models with all combinations of predictor variables. The dependent variable for all models was weekly bearing in relation to Marion Island (i.e., bearing of locations extracted at weekly intervals) of all complete seal tracks. Predictor variables for intra-age group analyses (i.e., of underyearlings only) were sex and trip number (i.e., trip number 1, 2, or 3). Predictor variables for inter-age group analyses (i.e., comparing underyearlings with subadults and adults) included sex and age class. Individual animal IDs were specified as random effects in all mixed effects models. Output iterations were set to 10,000, burn-in to 100 iterations, and lags specified as 3 iterations to minimize autocorrelation between parameter estimates. Convergence was assessed using trace plots and models compared using four different model fit criteria: two versions of the deviance information criterion (DIC and DIC_{alt}) and two versions of the Watanabe-Akaike information criterion ($WAIC_1$ and $WAIC_2$; Cremers & Klugkist, 2018). Effect summaries were computed using the raw posterior samples (Cremers, 2021). We also calculated the posterior sample for the mean

resultant length of the random intercept (cRI). This variable takes a value between 0 and 1 and serves as a measure of concentration, with values closer to zero indicating a large amount of spread and values of 1 indicating all data to be concentrated at a single value (Cremers, 2021). Here, the cRI value was interpreted as an indication of similarity in bearing of completed foraging trips between individual underyearling seals, as well as broadscale similarity in bearing of completed foraging trips between all seals in our sample.

3 | RESULTS

Resighting data indicated that 59 (34 males and 25 females) of the 79 instrumented underyearling elephant seals returned to Marion Island following deployment of GLs. We successfully recovered 34 GLs from seals that returned to Marion Island (21 from males and 13 from females). Twenty-five GLs (13 from males, and 12 from females) were not recovered, even though seals were resighted at Marion Island during subsequent haul-outs. These tags were either lost at sea or on land before recovery could be accomplished. Twenty seals (10 males and 10 females) were not recorded at Marion Island again after deployment and were assumed to have died at sea or emigrated. Of the 34 successfully recovered GLs, 16 units (13 males and 3 females) recorded usable light levels, representing 29 foraging trips. These included 7 first trips to sea, 14 second trips to sea, 7 third trips to sea, and 1 fourth trip to sea—all before the first molt haul-out at age 1 (Table 1). The single fourth track was excluded from analyses of underyearling foraging trips. Summary information for the GLs and PTT instrumented seals are presented in Table 2.

Underyearlings dispersed in multiple directions from Marion Island, mostly remaining within the interfrontal zone south of the Subtropical Front and north of the Polar Front (Figure 1). Within each deployment year, trip durations, maximum distances traveled from Marion Island, and total track distances were mostly correlated ($R > 0.6$; Figure S1). Mean travel speed was generally less correlated (R: 0.36–0.56) with other trip metrics.

3.1 | Trip durations

Foraging trip durations during the first year of life ranged from 27 to 189 days, depending on trip number (Table 1). Maiden foraging trips (first time to sea until first return to Marion Island; usually December to April/June) were longer on average than subsequent first year foraging trips (Table 2, Figure 2), but showed no association with sex or the year in which an animal was tracked (Table 3).

Maiden trip durations by underyearlings were typically shorter than those of subadult and adult elephant seals undertaking postmolt foraging migrations, but longer than adults undertaking postbreeding foraging migrations (Table 2, Figure S7). Second and third trips for underyearlings were similar in duration to postbreeding trip durations of adults (Table 2).

3.2 | Distances traveled from Marion Island

The mean maximum distances that underyearling seals traveled away from Marion Island did not differ significantly between trip number, sex, or year (Table 2, Figure 3). When including older age groups (subadults and adults), it became apparent that females travel further from the island than males, and that maximum distances during the longer postmolt trips exceeded distances traveled from the island during the shorter (in duration) postbreeding trips (Table 3, Figure S6). Maiden foraging trips of underyearling seals extended to similar distances away from the island as postmolt and postbreeding foraging trips of subadult and adult males but were not as distant from the island as postmolt trips by subadult and adult females (Table 2).

TABLE 1 Summary information of 29 foraging trips undertaken by underyearling southern elephant seals from Marion Island. Trip numbers refer to the trip to sea following weaning. Start age is based on an assumed birth date of October 15, the peak breeding haul-out date of female southern elephant seals at Marion Island (Bester & Wilkinson, 1994; Condy, 1978).

Individual	Trip number	Sex	Start age (days)	Start date	Trip duration (days)	Maximum distance from MI (km)	Bearing of maximum distance point from MI (degrees)	Mean speed ± SD (m/s)	Total distance traveled (km)
GW024	1	male	52	2006/12/06	158	1,544	238	0.58 ± 0.31	10,548
	2	male	229	2007/06/01	168	1,091	222	0.6 ± 0.35	12,747
GW160	1	male	59	2006/12/13	104	681	198	0.49 ± 0.3	6,196
GW185	2	female	220	2007/05/23	113	1,253	228	0.61 ± 0.36	8,698
GW305	2	male	237	2007/06/09	55	735	339	0.58 ± 0.39	4,123
LB037	1	male	62	2007/12/16	189	1,863	243	0.6 ± 0.32	13,459
LB255	1	male	57	2007/12/11	139	849	196	0.48 ± 0.28	8,371
	2	male	206	2008/05/08	67	336	27	0.38 ± 0.24	3,789
	3	male	285	2008/07/26	95	602	74	0.48 ± 0.26	6,120
PP003	1	male	47	2005/12/01	110	1,878	126	0.61 ± 0.37	7,233
	2	male	170	2006/04/03	76	1,015	241	0.63 ± 0.43	5,770
PP016	1	male	57	2005/12/11	188	1,889	98	0.58 ± 0.36	11,993
	2	male	255	2006/06/27	59	383	123	0.48 ± 0.3	3,625
PP093	1	male	53	2005/12/07	95	923	86	0.53 ± 0.39	6,303
	2	male	158	2006/03/22	81	732	153	0.51 ± 0.38	5,393
	3	male	249	2006/06/21	27	380	340	0.48 ± 0.36	1,700
PP097	2	male	214	2006/05/17	66	414	316	0.48 ± 0.31	4,082
	3	male	289	2006/07/31	105	1,556	278	0.58 ± 0.31	7,659
PP116	2	male	243	2006/06/15	169	4,141	244	0.92 ± 0.51	16,381
PP148	2	male	248	2006/06/20	118	1,273	219	0.59 ± 0.36	9,048
	3	male	375	2006/10/25	49	544	192	0.66 ± 0.39	3,387
PP163	2	male	186	2006/04/19	29	165	210	0.32 ± 0.22	1,451
	3	male	218	2006/05/21	47	302	358	0.44 ± 0.3	2,807
	4	male	275	2006/07/17	136	1,096	174	0.53 ± 0.35	8,728
PP398	2	female	190	2006/04/23	65	351	126	0.47 ± 0.31	4,153
RR306	2	female	187	2005/04/20	114	1,012	126	0.53 ± 0.32	7,793
	3	female	310	2005/08/21	96	1485	78	0.62 ± 0.5	6,540
untagged	2	male	207	2005/05/10	62	554	252	0.59 ± 0.4	4,775
	3	male	281	2005/07/23	96	1,313	232	0.62 ± 0.35	7,453

TABLE 2 Summary information of the combined first, second, and third foraging trips undertaken by underyearling southern elephant seals from Marion Island in relation to averaged data from 152 tracks undertaken by 94 subadult and adult elephant seals tracked from Marion Island between 1999 and 2016.

Cohort	Start age (days)	Trip duration (days)	Maximum distance from MI (km)	Mean speed ± SD (m/s)	Total distance traveled (km)
Underyearling trip 1 (n = 7)	47–62	140 ± 39	1,375 ± 540	0.55 ± 0.05	9,157 ± 2,878
Underyearling trip 2 (n = 14)	158–255	89 ± 42	961 ± 985	0.55 ± 0.14	6,559 ± 4,042
Underyearling trip 3 (n = 7)	218–375	74 ± 31	883 ± 545	0.55 ± 0.09	5,095 ± 2,414
Subadult ♂s PM (n = 34)		149 ± 52	1,357 ± 780	0.42 ± 0.17	5,505 ± 2,386
Subadult ♀s PM (n = 42)		172 ± 58	1,768 ± 701	0.4 ± 0.1	6,052 ± 1,844
Adult ♂s PM (n = 12)		195 ± 83	1,165 ± 1009	0.34 ± 0.21	5,722 ± 3,823
Adult ♂s PB (n = 3)		78 ± 13	1,629 ± 133	0.63 ± 0.09	3,942 ± 341
Adult ♀s PM (n = 34)		255 ± 34	2,309 ± 618	0.38 ± 0.08	8,563 ± 1,803
Adult ♀s PB (n = 27)		68 ± 12	1,171 ± 409	0.61 ± 0.31	3,474 ± 1,825

Note: Values are reported as means ± standard deviation. PM = postmolt; PB = postbreeding.
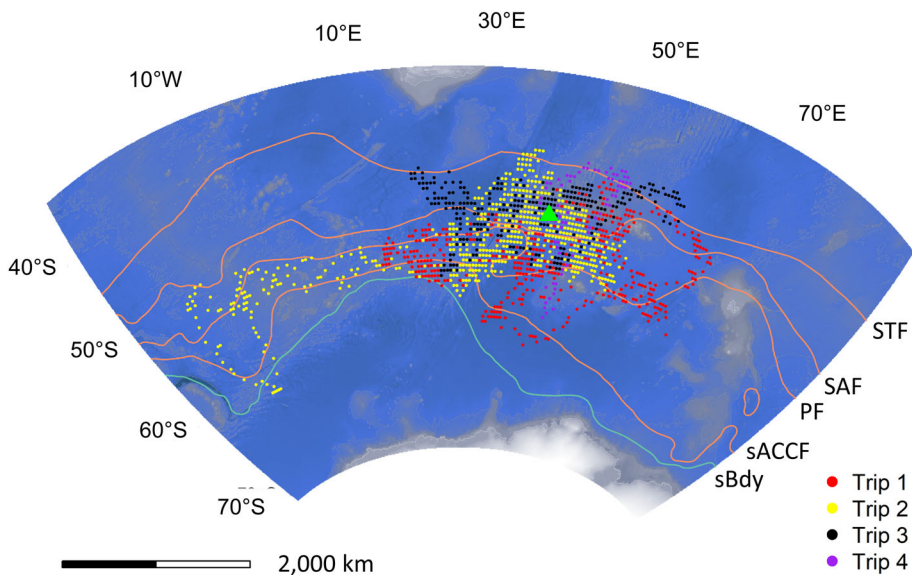

FIGURE 1 Estimated at-sea locations of 16 underyearling (<1 year old) southern elephant seals tracked from Marion Island. Frontal locations are indicated as per Chapman et al. (2020). STF = Subtropical Front, SAF = Sub-Antarctic Front; PF = Polar Front; sACCF = southern Antarctic Circumpolar Front; sBdy = Southern Boundary front.

3.3 | Travel direction

Underyearling elephant seals showed substantial variability in directions traveled from Marion Island, both within and between individuals (Figure 4). Model fit for travel direction improved with the inclusion of trip number, sex, and year (Table 4). However, posterior estimates of the circular mean of bearing from Marion Island for each predictor overlapped, providing no evidence for significant differences in bearing from Marion Island between sexes, years, or foraging trip numbers by underyearlings (Table S1). The calculated cRI for the full model was 0.77, indicating
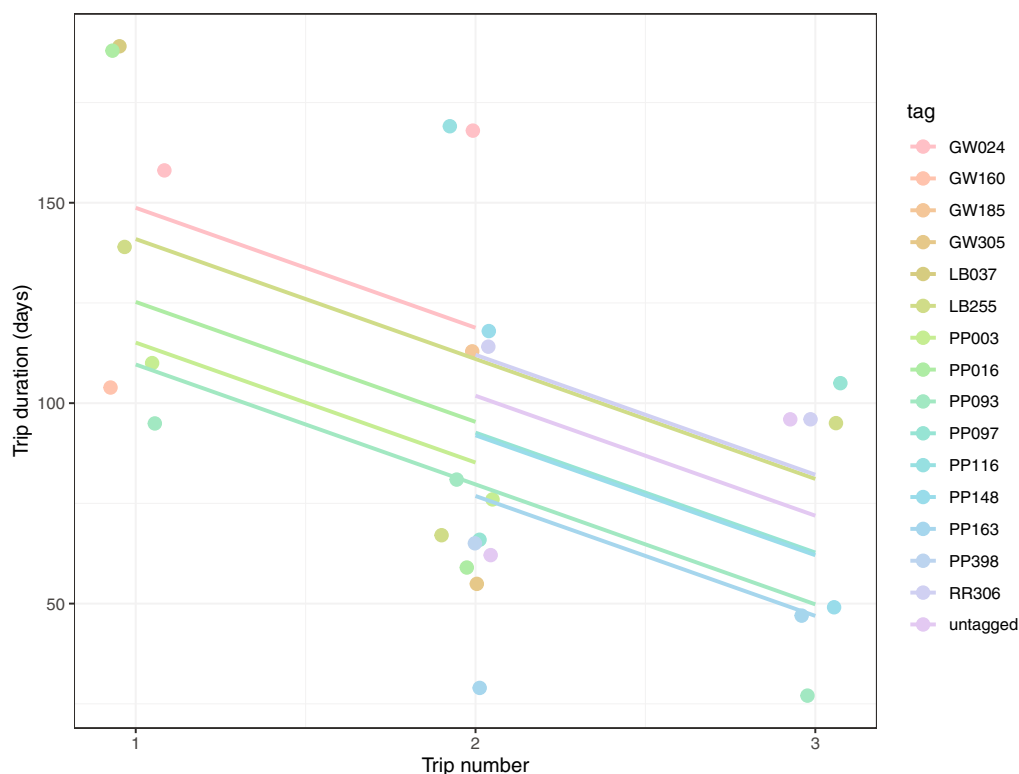
FIGURE 2 Predicted relationships between foraging trip duration and trip number of underyearling elephant seals. Colored lines represent the predicted individual intercepts and shared slope relationships from a linear mixed effect model accounting for sex and trip number. Colored dots are actual trip durations of tracked individuals.

relatively low variation in individual-level intercepts and thus, travel bearings that show some similarity between the 16 individuals when considering all possible travel directions (see Figure S8).

Older age groups, particularly subadult and adult females undertook foraging trips in more consistent directions from the island (Figure 5). When assessing travel direction from Marion Island between age classes and sexes, only the inclusion of age class consistently improved the fit of the model (Table 5). Posterior estimates of the circular mean of bearing from Marion Island for each predictor overlapped, providing no evidence for significant differences in bearing from Marion Island between sexes or age classes (Table S2). Circular random intercepts for the full model (including sex and age class predictors) of 110 seals for which 181 completed foraging trips were recorded ranged between $11°$ and $360°$. Despite the range in circular intercepts between individual seals the posterior sample for the mean resultant length of the random intercept (cRI) was 0.81, indicating less variation in individual-level intercepts when compared to the full model for travel directions of underyearlings only. This suggests that travel bearings of older seals are more concentrated (similar between individuals) than the travel bearings of underyearlings only (see Figures S8 and S9).

3.4 | Speed of travel and total distances traveled

Mean traveling speeds during the first year were consistent between foraging trips, sexes, and years (Tables 2 and 3). While mean total travel distances seemed to decrease during sequential foraging trips within the first year (Figure 2, Table 2), we found no evidence for significant differences in total distances traveled between foraging trips, sexes, or study years (Table 3).

TABLE 3 Type II Wald chi-square test outputs on full linear mixed effects models assessing relationships between trip number and sex (for underyearling seals) or age class, sex, and trip type (for all seals) for various foraging trip parameters.

Underyearlings only				All tracked seals			
	χ^2	df^a	p		χ^2	df^a	p
Trip duration							
Trip number	6.8	1,18	<.01[b]	Age class	14.9	3,120	<.01[b]
Sex	<0.1	1,14	.93	Sex	0.4	1,99	.54
Year	1.6	3,10	.67				
Distance traveled from Marion Island							
Trip number	1.2	1,13	.3	Age class	6.5	3,151	.09
Sex	0.1	1,12	.82	Sex	5.9	1,113	.02[b]
Year	0.2	3,11	.98				
Travel speed							
Trip number	0.5	1,12	.47				
Sex	0.2	1,12	.68				
Year	0.4	3,11	.95				
Total distance traveled							
Trip number	3.1	1,15	.08				
Sex	<0.1	1,13	.96				
Year	0.53	3,11	.91				

[a]Satterthwaite degrees of freedom were calculated using Kenward-Roger F tests.
[b]Significant predictors.

4 | DISCUSSION

The relative role of learning and memory in contrast to innate behaviors (including innate responses to environmental cues) in determining how movement patterns of marine megafauna develop with age is poorly understood (Hays et al., 2016) and is difficult to assess given the relative paucity of data available for juvenile animals (McIntyre, 2014). Our study is one of only a few to describe the maiden foraging trips undertaken by southern elephant seals (others include Bornemann et al., 2000; McConnell et al., 2002; Orgeret et al., 2019; Walters et al., 2014), and the first to describe the development of sequential foraging trips during the first year of life in this species. Maiden foraging trips of underyearling southern elephant seals from Marion Island ranged generally over deep water south of the Subtropical Front in multiple directions away from the island. Subsequent (second and third) foraging trips were on average shorter than maiden trips and lacked directional consistency with preceding trips undertaken during the first year. Higher variation in circular random intercepts of the underyearling only model ($n = 16$) compared to the model for all age classes ($n = 110$) further supports a lack of directional consistency of travel in the first year of life (Figures S8 and S9).

In contrast to our results, the maiden foraging migrations of underyearling southern elephant seals tracked from other islands appear to be typically directed. Seals from Macquarie Island and Kerguelen Island mostly dispersed in southeastern directions from those islands (McConnell et al., 2002; Orgeret et al., 2019), with some seals potentially being assisted by the predominantly easterly current movement tied to the Antarctic Circumpolar Current (ACC; McConnell et al., 2002). Maiden migration directions of southern elephant seals from King George Island ($n = 5$) were also directed but predominantly in a southwestern direction from their natal site (Bornemann et al., 2000).
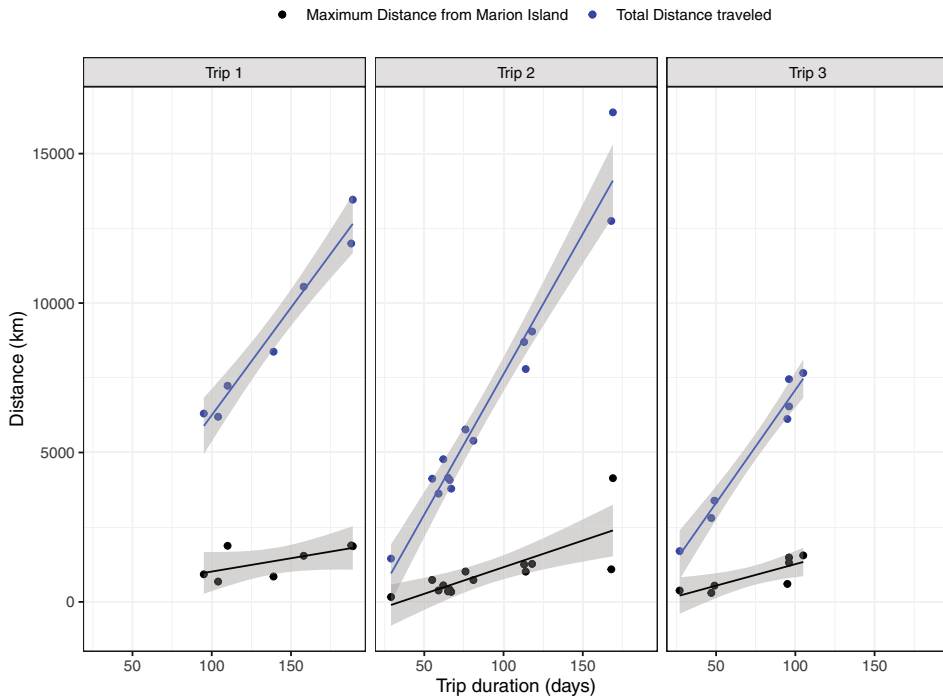
FIGURE 3 Comparative foraging trip characteristics of the first three foraging migrations of underyearling southern elephant seals.

Movements of these seals were evidently associated with avoidance of sea ice but may also indicate that they used the predominant westward current movements associated with the proximal Antarctic Slope Current (ASC; Thompson et al., 2018, 2020). Such broadly consistent foraging directions may indicate a consistent response to extrinsic cues which may play an important role in determining the foraging strategies of elephant seals in early life. Similar responses to extrinsic environmental cues have been reported for multiple taxa, including fish (Archer et al., 2019), birds (de Grissac et al., 2017; Frankish et al., 2022) and other pinnipeds such as Antarctic fur seals, *Arctocephalus gazella* (Nagel et al., 2021). In contrast, the low consistency in foraging trip directions of underyearling elephant seals from Marion Island suggest broad scale environmental cues such as large ocean currents (the ACC dominating the eastward movement of waters around Marion Island) have little effect in determining the travel directions of early foraging migrations in this population. However, given the relative proximity of Marion Island to a number of frontal features located in multiple directions from the island (e.g., Figure 1), it is feasible that the seals in our sample were actually responding to smaller scale currents and frontal structures which they would likely encounter if traveling in any given direction away from the island. Such responses to finer scale, and temporally dynamic, cues in choosing travel direction during their first foraging trips may explain the improvement of our final model fit with the inclusion of tracking year as a predictor variable.

Animals such as the wandering albatross (*Diomedea exulans*) seemingly follow oceanographic cues such as sea water color and potentially dimethyl-sulphide odor during their maiden foraging trips, and concentrate foraging activities in known productive areas after 6 or 7 months at sea (de Grissac et al., 2017). We did not assess effects of fine-scale environmental cues on the movements of underyearling elephant seals due to the relatively low resolution of location estimates obtained from GLs. However, older elephant seals do exploit mesoscale oceanographic features such as eddies (Cotté et al., 2014; Massie et al., 2016; Tosh et al., 2015), meanders (Siegelman et al., 2019), and polynyas (Arce et al., 2022; Labrousse et al., 2018), responding to variability in water masses (Guinet et al., 2014;
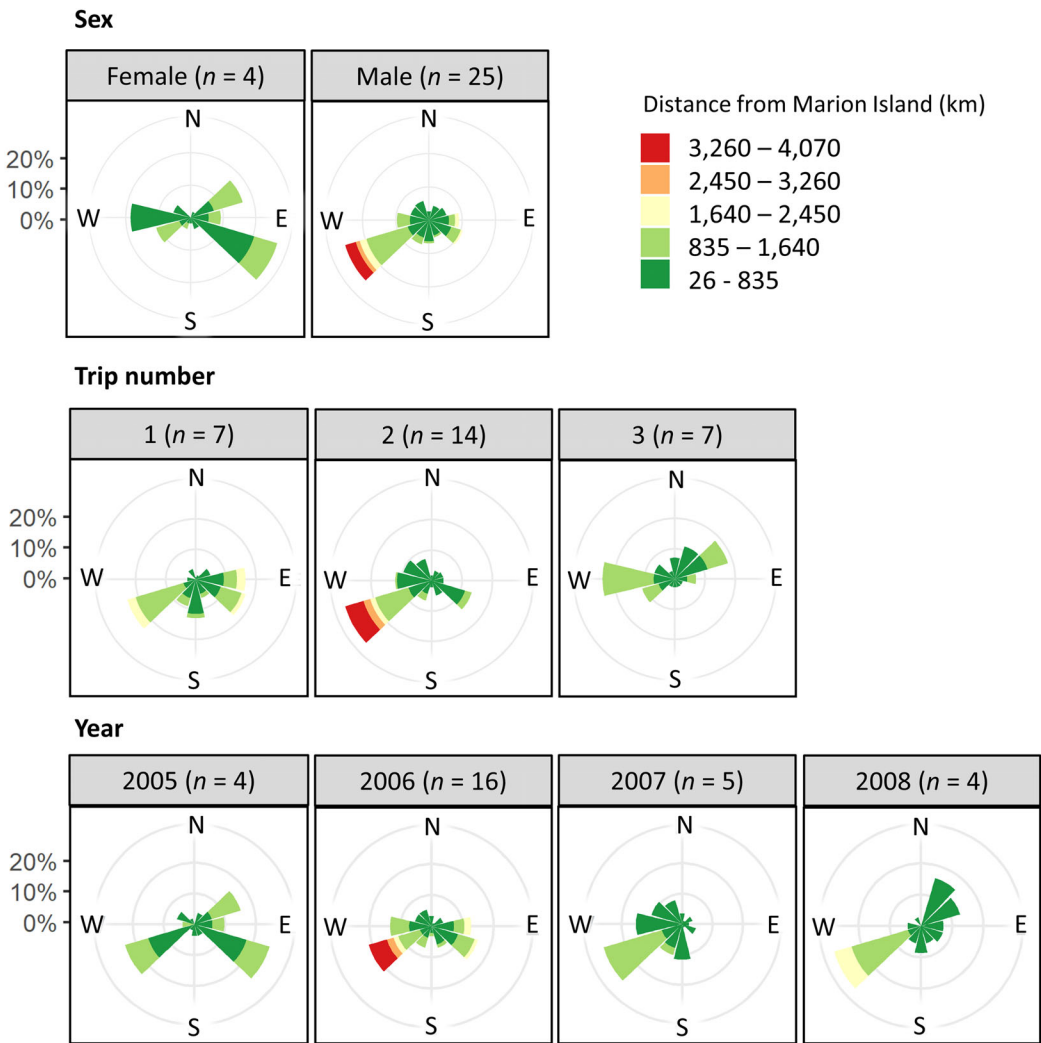
Sex

Trip number

Year

FIGURE 4 Foraging trip directions from Marion Island of underyearling southern elephant seals. All weekly track points (i.e., track locations taken every 7th day per trip) are included.

McIntyre et al., 2011a). Other factors that we were unable to account for include the potential influences of competition (Breed et al., 2013) and other underlying influences associated with fine-scale differences between natal sites within the same population (Wege et al., 2019).

Underyearling southern elephant seals tracked from Macquarie, Kerguelen, and King George Islands broadly followed similar, albeit shorter, trajectories from their natal sites when compared with older seals from their respective islands. For example, Macquarie Island maiden foraging trips were mostly in a southeastern, or southwestern direction from the island (McConnell et al., 2002), similar to older seals from the same population (Field et al., 2005; Hindell et al., 1991; Raymond et al., 2015; van den Hoff et al., 2002). Underyearlings from King George Island broadly traveled in similar directions along the western Antarctic Peninsula as adults from the same population (Bornemann et al., 2000; McIntyre et al., 2014), and underyearlings from Kerguelen Island follow broadly similar southerly (albeit less distant) trajectories to adults from this population (Bailleul et al., 2007; Orgeret et al., 2019). At Marion Island, adult and subadult southern elephant seals, including juveniles <2 years of age typically undertake

TABLE 4 Model fit criteria for circular mixed effects models applied to travel directions of underyearling elephant seals from Marion Island. Two versions of the deviance information criterion (DIC and DIC_{alt}) are reported as well as two versions of the Watanabe-Akaike information criterion ($WAIC_1$ and $WAIC_2$).

Model	DIC	DIC_{alt}	$WAIC_1$	$WAIC_2$
Intercept only ($\sim 1 \mid$ individual)	967.86	1,002.01	970.18	973.86
($\sim 1 \mid$ individual) + trip number	952.02	994.78	955.86	959.94
($\sim 1 \mid$ individual) + sex	962.35	1,002.55	969.65	973.46
($\sim 1 \mid$ individual) + year	944.46	983.69	953.01	957.99
($\sim 1 \mid$ individual) + trip number + sex	939.73	1,001.75	955.3	959.51
($\sim 1 \mid$ individual) + trip number + year	927.88	**983.37**	938.79	944.46
($\sim 1 \mid$ individual) + sex + year	944.1	987.19	953.21	958.5
($\sim 1 \mid$ individual) + trip number + sex + year	**885.97**	1,018.46	**938.17**	**944.06**

Note: Lowest information criteria are highlighted in bold (i.e., best models as suggested by individual information criteria).

foraging migrations into interfrontal areas to the southwest of the island where they forage pelagically (McIntyre et al., 2011b, 2012; Tosh et al., 2012). As adults, these seals display high individual fidelity to foraging strategies, traveling to the same areas in sequential foraging trips, often also foraging at similar depths (McIntyre et al., 2017). While some of the underyearlings tracked in our study did indeed follow similar trajectories to what may be considered typical for adults of this population (e.g., Trip 1 of LB037 and trip 2 of PP003; Figure S3), we found little statistical evidence for common directionality or consistency within this collection of tracks. Our results also provided no evidence for sex influencing the travel directions of underyearling elephant seals. However, the skewed sex ratio of individuals for which data were available (13 males and 3 females) limited the statistical power of this analysis and we cannot exclude the possibility that male travel directions are inherently more variable than those of females and that some level of sexual segregation already takes places immediately after weaning. Such early segregation would be surprising since sexual segregation in seals are most often associated with differences in body size and different breeding strategies that are not apparent yet during early, postweaning life (e.g., McIntyre et al., 2010b; Staniland & Robinson, 2008; but see Kernaléguen et al. (2016) for an example of early life separation of foraging niche in Antarctic fur seals).

Foraging trips during the first year were short, often lasting <100 days and some only lasting approximately 1 month. Maiden foraging trips were longer on average than the second and third trips to sea, and compared well with the duration of maiden foraging trips (averaging ~150 days) at Macquarie Island (McConnell et al., 2002; Walters et al., 2014), and the Kerguelen Islands (Orgeret et al., 2019), although some underyearlings from the Kerguelen Islands remained at sea for longer than 300 days during their maiden trips. Longer maiden foraging trips by Marion Island underyearlings generally also covered greater distances but were not strongly correlated with maximum distances that seals traveled from Marion Island or their speed of movement. This suggests that seals display more meandering trip trajectories during their maiden foraging trips when compared to subsequent ones. Unfortunately, GLs render imprecise location estimates that are not suitable for finer scale analyses of trip trajectories (i.e., sinuosity and directedness); therefore, these metrics were not tested in this study.

Foraging trip durations of other phocids such as gray seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) typically increase initially after weaning, after which they become shorter again—a pattern that may be attributed to increased foraging efficiency or a change in foraging strategy following more lengthy exploration trips (Blanchet et al., 2016; Carter et al., 2017). Trip durations of underyearling elephant seals are likely a direct result of their individual requirements to haul out during winter months. In turn, the condition of elephant seals at weaning likely influences the likelihood of seals participating in the winter haul-out and potentially the number of times that seals haul out during winter months. For example, Wheatley (2001) reported that female underyearling southern elephant seals
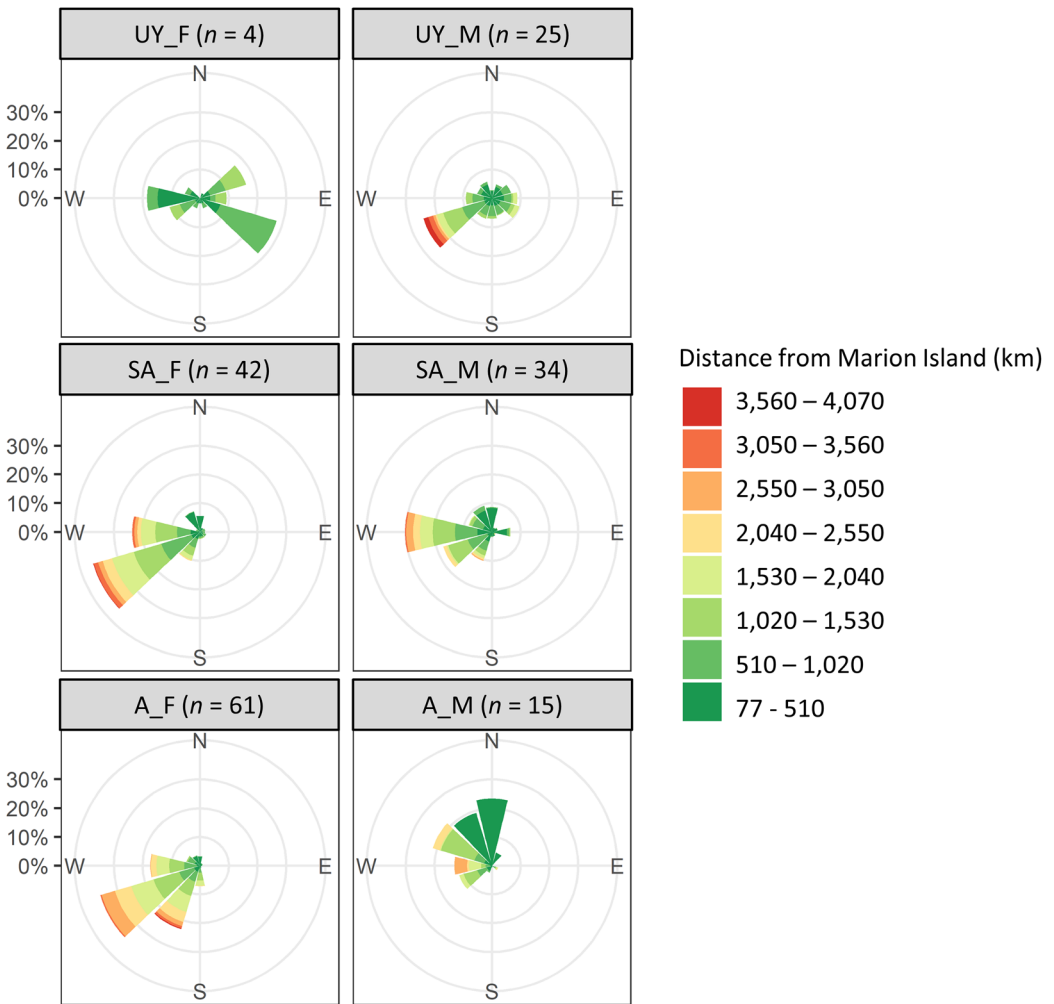
FIGURE 5 Foraging trip directions from Marion Island of different age and sex classes of southern elephants. UY_F = female underyearlings; UY_M = male underyearlings; SA_F = subadult females 1–3 years of age; SA_M = subadult males 1–6 years of age; A_F = adult females >3 years; A_M = adult males >6 years.

TABLE 5 Model fit criteria for circular mixed effects models applied to travel directions of all elephant seals tracked from Marion Island. Two versions of the deviance information criterion (*DIC* and *DIC*$_{alt}$) are reported as well as two versions of the Watanabe-Akaike information criterion (*WAIC*$_1$ and *WAIC*$_2$).

Model	DIC	DIC$_{alt}$	WAIC$_1$	WAIC$_2$
Intercept only ($\sim$1 | individual)	6,831.54	**7,037.48**	6,899	6,945.99
($\sim$1 | individual) + age class	6,763.92	7,089.16	**6,851.83**	**6,897.21**
($\sim$1 | individual) + sex	6,826.02	7,059.71	6,902.47	6,949.37
($\sim$1 | individual) + age class + sex	**6,761.6**	7,101.3	6,854.08	6,899.36

Note: Best model fit per information criterion is indicated in bold.

from Macquarie Island that participate in the winter haul-out are lighter on average at weaning than females that do not, while all seals that return for a second haul out during their first year weighed less on average at weaning than those who did not return a second time. We did not assess the condition at weaning of underyearling seals tracked

in our study and report only on a small number of underyearling individuals ($n = 16$, all of which returned for at least one winter haul-out) and can therefore only speculate on potential reasons for shorter second and third foraging trips when compared to maiden foraging trips.

Seals from the Kerguelen Islands seemingly traveled similar distances during their maiden trips (500–2,600 m from the Kerguelen Islands; Orgeret et al., 2019) to those traveled by seals from Marion Island. Maiden foraging trip lengths from other populations were also similar—underyearlings from King George Island and Macquarie Island traveled distances of up to 2,300 km and 1,900 km from their respective natal islands (Bornemann et al., 2000; McConnell et al., 2002). Interestingly, the farthest that any of the seals in our sample, including subadults and adults, traveled from Marion Island is the 4,140 km trip by a male seal that was 8 months old at the start of his recorded foraging trip (PP116), culminating in an estimated total travel distance of more than 16,000 km. This foraging trip was assumed to be the individual's second foraging trip, as he was not observed at Marion Island during regular beach surveys between weaning at the end of 2005 and June the following year when a GL was deployed.

Taken together, our results suggest that underyearling southern elephant seals from Marion Island rely minimally on innate behaviors or responses to large external cues in guiding the direction and distance of travel during maiden and subsequent foraging trips during their first year of life. Rather, foraging trips from the island show little evidence for common travel directions or distances between individuals or subsequent trips by the same individuals. Possibly the simplest interpretation of our results would be that underyearling elephant seals largely explore potential foraging ranges during their first year of life in a relatively undirected way, learning about beneficial foraging trip strategies and potentially extrinsic cues associated with profitable foraging patches. Therefore, learning through experience likely plays a critical role in determining future foraging strategies. Older southern elephant seals typically display substantial interindividual variation in at-sea movements and dive behavior, but remarkable intraindividual consistency seemingly once they survived the first year or two of life (McIntyre et al., 2017). Such subsequent consistency is likely best explained by a reliance on memory, rather than common responses to environmental cues which may be expected to lead to less interindividual variation. Indeed, evidence suggesting that other large mammals rely to a large extent on memory to inform foraging decisions is increasing (Abrahms et al., 2019; Bracis & Mueller, 2017; Ranc et al., 2021).

Elephant seal survival is low during the first year of life (McMahon et al., 2003; Pistorius et al., 1999) and underyearlings face severe pressure to find suitable foraging resources and simultaneously avoid predation (Reisinger et al., 2011). Orgeret et al. (2019) illustrated that underyearling elephant seals lose condition over the first 30–50 days at sea, before starting to regain condition, with survivors ultimately returning to their natal island only once they have regained all condition lost during the first phase of their maiden foraging trips. Juvenile (including underyearling) southern elephant seals are predominantly low trophic foragers, feeding especially on crustaceans (Lübcker et al., 2017; Walters et al., 2014) and finding adequate prey aggregations during the first year of life is crucial to survival and ultimate recruitment into the breeding population. This becomes especially challenging in environments where the distribution of prey items is likely to be unpredictable — e.g., the swarming nature of many krill species (Tarling & Fielding, 2016) and other micronekton's spatially and temporally patchy distributions (Béhagle et al., 2017; Bestley et al., 2018; Tarling et al., 2009) add to the challenge of locating them over large spatial scales. The archival nature of the GLs used in our study means we are unable to speculate on any correlations between foraging trip strategies and mortality; we do not have data for animals that did not survive. However, at a broader level the high variability of track directions of underyearlings in our study, together with the temporal and spatial heterogenous nature of prey aggregations suggests that in any given annual elephant seal cohort some animals are likely to find suitable forage resources by chance and some not. Such comparatively random and naïve foraging trip characteristics may concurrently result in an overall higher mortality rate during the first year of life when compared to populations where underyearlings seemingly perform earlier, similarly directed foraging trips (e.g., McMahon et al., 2003). However, increased individual level variation in early life foraging strategies may also provide population-level advantages in the temporally fluctuating environment of the broader Southern Ocean as a means of bet-hedging (Wolf & Weissing, 2010). Our limited sample number of underyearling tracks did not allow for further

exploration of such hypotheses and further longitudinal studies combining data about early life at-sea behavior and survival are required to better understand the population level impacts of variation in juvenile phenotypes and associated behaviors in southern elephant seals.

AUTHOR CONTRIBUTIONS

Trevor McIntyre: Conceptualization; formal analysis; methodology; writing – original draft. **W. Chris Oosthuizen:** Methodology; writing – review and editing. **Marthán Bester:** Funding acquisition; project administration; resources. **Mark Hindell:** Formal analysis; writing – review and editing. **Ryan R. Reisinger:** Investigation; writing – review and editing. **Cheryl Tosh:** Writing – review and editing. **John Van den Hoff:** Resources; writing – review and editing. **P. J. Nico de Bruyn:** Investigation; writing – review and editing.

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