BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH



Diving deeper into individual foraging specializations of a large marine predator, the southern sea lion

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Abstract Despite global declines in the abundance of marine predators, knowledge of foraging ecology, necessary to predict the ecological consequences of large changes in marine predator abundance, remains enigmatic for many species. Given that populations suffering severe declines are of conservation concern, we examined the foraging ecology of southern sea lions (SSL) (*Otaria flavescens*)—one of the least studied otariids (fur seal and sea lions)—which have declined by over 90 % at the Falkland Islands since the 1930s. Using a combination of biologging devices and stable isotope analysis of vibrissae, we redress major gaps in the knowledge of SSL ecology and quantify patterns of individual specialization. Specifically,

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we revealed two discrete foraging strategies, these being inshore (coastal) and offshore (outer Patagonian Shelf). The majority of adult female SSL (72 % or n = 21 of 29 SSL) foraged offshore. Adult female SSL that foraged offshore travelled further (92 \pm 20 vs. 10 \pm 4 km) and dived deeper (75 \pm 23 vs. 21 \pm 8 m) when compared to those that foraged inshore. Stable isotope analysis revealed long-term fidelity (years) to these discrete foraging habitats. In addition, we found further specialization within the offshore group, with adult female SSL separated into two clusters on the basis of benthic or mixed (benthic and pelagic) dive behavior (benthic dive proportion was 76 ± 9 vs. 51 ± 8 %, respectively). We suggest that foraging specialization in depleted populations such as SSL breeding at the Falkland Islands, are influenced by foraging site fidelity, and could be independent of intraspecific competition. Finally, the behavioral differences we describe are crucial to understanding population-level dynamics, impediments to population recovery, and threats to population persistence.

Keywords Dietary specialization \cdot Habitat selection \cdot Hidden Markov models \cdot South American sea lions \cdot Statespace models

Introduction

Changes in marine predator abundance can have profound and unexpected consequences for ecosystem structure, functioning, and resilience (Baum and Worm 2009; Estes et al. 2011). Predicting the ecological consequences of these changes underpins ecosystem management, but first requires an understanding of a species' diet and foraging behavior (Estes et al. 1998; Springer et al. 2003; Trites et al. 2007). Given that individuals within populations often differ substantially in resource use, the complexity of diet and foraging behavior (and our understanding of the ecological role of marine predators) will vary depending on whether foraging ecology can be explained at a species versus individual level (Heithaus et al. 2008; Newsome 2009; Matich et al. 2011; Araújo et al. 2011).

Recent empirical studies highlight that intraspecific competition increases individual specialization (Svanbäck and Bolnick 2007; Araújo et al. 2011). Hence, individual specialization may be expected to occur more frequently in upper trophic level marine predators that are regulated by bottom-up processes and resource competition, when compared to species of a lower trophic status regulated by top-down processes and physical disturbance (Estes et al. 2003). In particular, individual differences in diet and foraging behavior are expected to arise within central place foraging, income breeding marine predators (e.g., seabirds, fur seals and sea lions) that must compete for resources within a limited area (implying strong intraspecific competition). Accordingly, to elucidate the foraging ecology of central place foraging marine predators, an individual level approach is often necessary (Chilvers and Wilkinson 2009; Baylis and Nichols 2009; Kernaléguen et al. 2012; Ratcliffe et al. 2013). However, the cryptic nature of feeding in highly mobile marine animals means that available data often lacks the resolution required to disentangle diet and foraging behavior to the individual level. Consequently, the foraging ecology of some species that have undergone dramatic population changes, and represent key components of the marine food-web, remains enigmatic.

For example, southern sea lions (SSL) (Otaria flavescens) are one of the least studied otariids (fur seal and sea lions) and have experienced dramatic population declines in the South Atlantic (Franco-Trecu et al. 2014). One of the largest declines has occurred at the Falkland Islands, where the population plummeted from 371,500 SSL in the 1930s to just 30,000 SSL in the 1960s (reviewed in Baylis et al. 2015a). Despite the dramatic decline and failure to recover, our understanding of foraging ecology at the Falkland Islands is based on four SSL (only one of which was successfully tracked at sea), and a limited number of scats collected in 1992 (Thompson et al. 1998). Results from this seminal study indicate that SSL are principally benthic-foraging, generalist predators (Thompson et al. 1998). However, the paucity of available data are unlikely to accurately represent the foraging behavior and trophic ecology of SSL or enable impediments to population recovery to be elucidated. For instance, it is widely recognised that behavior and diet in several sea lion species, including SSL breeding in Argentina, is profoundly influenced at the individual level by sex and ontogenetic niche shifts (Drago et al. 2009; Weise et al.

2010; Jeglinski et al. 2013). In addition, individual differences in foraging behavior and diet within comparable sex and age classes can also be profound (Campagna et al. 2001; Villegas-Amtmann et al. 2008; Baylis et al. 2009; Chilvers and Wilkinson 2009; Lowther et al. 2011), but has received considerably less attention despite the potential to provide crucial insights into ecological, morphological and behavioral diversification within populations.

Here, we focus on adult female SSL because of their importance in determining population dynamics, and quantify the degree of individual specialization in foraging behavior and diet. Specifically, we combine data from biologging devices [a short-term measure of specialization (weeks to months)], with vibrissae stable isotope values, to infer temporal consistency of individual specialization over a longer period of time (years).

Materials and methods

SSL capture and device deployment

Adult female SSL observed suckling a pup were selected at random for device deployment. All adult female SSL were chemically restrained using tiletamine-zolazepam (Zoletil; Virbac, France; 3.0 mg/kg), remotely administered using 1.5 ml darts (Pneu dart) and a CO₂-powered tranquiliser gun (Dan Inject JM Standard) (Baylis et al. 2015a). Where necessary, adult female SSL were masked and anaesthesia induced or maintained using isoflurane delivered via a portable gas anaesthetic machine (VOC Rota Flush; Medical Developments International, Australia).

In 2011 (February-April), we equipped 10 adult female SSL with Platform Transmitter Terminal (PTT) tags of ARGOS location quality (Sirtrack PTT 101) at the two largest Falkland Islands sea lion breeding colonies (Fig. 1). These sites were Big Shag Island (colony size = 328 pups; 51.39°S, 58.35°W) and Kelp Island (260 pups; 58.5°S, 58.19°W) (Baylis et al. 2015b). In 2013 and 2014 (February-March), adult female SSL were equipped with an archival Fastloc® Global Positioning System (GPS) tag (Sirtrack Fastloc 1), a Time Depth Recorder tag (TDR) (Mk9 Wildlife computers) and a VHF transmitter to facilitate tag recovery. In 2013 (February-March), we deployed 10 GPS tags at Big Shag Island and one PTT tag at Turn Island (51 pups; 52.12°S, 58.92°W), while in 2014 (February-March) 10 GPS tags were deployed at Big Shag Island only (Appendix 1, Table S1). Tags were glued to adult female SSL using a two-part epoxy (Devcon 5-minute[®] epoxy). PTT tags were not recovered (fell off during moult), whereas adult female SSL with GPS tags were recaptured for data recovery after one or two foraging trips (Appendix 1, Table S1).



Fig. 1 Adult female southern sea lions (*Otaria flavescens*) breeding at the Falkland Islands foraged either inshore (coastal) or offshore (outer Patagonian Shelf), as depicted by the 90 % (*yellow*) and 50 % (*orange*) utilization distributions. A Big Shag Island [n = 19 offshore

(14 GPS and 5 PTT tags, including PTT 103751), n = 5 inshore (4 GPS tags and PTT 103751)], *B* Kelp Island (n = 1 offshore, n = 2 inshore, PTT only), *C* Turn Island (n = 1 inshore, PTT only). See also Appendix 1, Table S1 (colour figure online)

Location and dive data analysis

PTT tags were programmed to transmit every 45 s when at the surface. We removed erroneous locations from our Least Squares ARGOS locations, using the 'speedfilter' function in the R package 'trip' and a maximum speed of 3 m·s⁻¹ (Rodríguez et al. 2013). The speed-filtered data were then processed using a continuous-time correlated random walk model implemented within the R Package 'CRAWL', which incorporates ARGOS location errors for each of the six location classes (3, 2, 1, 0, A, B) (Johnson et al. 2008). Finally, we predicted locations at equally spaced points in time along the 'best-fit' track (hourly and across periods when location fixes failed).

GPS tags were programmed to acquire a position every 5 min. GPS positions were decoded using the DAP processor (Wildlife Computers, Redmond, WA, USA) and filtered for erroneous locations using a maximum speed of 3 $m \cdot s^{-1}$ (as above). We also fitted a continuous-time correlated random walk model to the GPS positions to account for measurement error and irregular, sometimes sparse location fixes that would otherwise have necessitated unrealistic

assumptions about linear movement between locations. The model integrated TDR wet/dry times to define the start and end of foraging trips and was also implemented using the R Package 'CRAWL' (Johnson et al. 2008). For adult female SSL that foraged offshore (see section "Inshore/off-shore foraging and individual specialization (location and dive data)"), both GPS and PTT tag data were used to calculate foraging trip metrics (distance and duration), based on predicted locations. In contrast, foraging trip metrics for adult female SSL that foraged inshore were based on only adult female SSL which carried GPS/TDR tags because the location error associated with PTT tags, combined with short foraging trip distances, made defining a foraging trip problematic.

TDR tags sampled depth every 1 s, had a resolution of 0.5 m and an accuracy of ± 1 %. Dives <5 m in depth and <5 s in duration were excluded when calculating diving metrics (Riet-Sapriza et al. 2013; Kuhn and Costa 2014). Dive summary statistics were calculated using the R package 'diveMove'. For each individual, we calculated the mean \pm SD of dive depth, duration, bottom time, postdive duration and whether the dive occurred during the day (between sunrise and sunset) or night (the latter calculated in the R package 'maptools'). We also calculated several indices to characterize benthic diving behavior. The first, commonly referred to as the intra-depth zone (IDZ). was calculated as the depth \pm 10 % of the maximum depth reached during the preceding dive (Tremblay and Cherel 2000). This metric assumes that benthic divers dive serially to the same depth zone (i.e., the sea floor). Finally, we extracted bathymetry (GEBCO_14 30 arc second dataset) for each dive location using ArcMap (ArcGIS, Redlands, CA, USA). The mean proximity of dives to the sea floor was calculated as the ratio of dive depth divided by bathymetric depth. To account for spatial measurement error in both location and bathymetric data, SSL were classified as benthic diving when this ratio was >0.80 (Jeglinski et al. 2013). If a bathymetry value was 0, it was treated as a missing value and not included in the classification of benthic dives. We did not calculate a benthic dive ratio for SSL that foraged inshore (see below) due to the spatial error associated with both near shore bathymetry and location data, that resulted in a mismatch between dive depth and the available bathymetry.

Inshore/offshore foraging and individual specialization (location and dive data)

Preliminary data exploration revealed that adult female SSL foraged in either inshore (coastal) or offshore waters (outer Patagonian Shelf). To characterize these distinct foraging strategies, we extracted utilization distribution probabilities (kernel analysis), where the smoothing parameters (h) for the kernel analyses were calculated using the ad hoc method (Worton 1989) within the R package 'adehabitatHR'. We used bathymetry as a habitat grid to avoid utilization distribution probabilities spanning over land, and weighted kernels based on the number of SSL within each grid cell. To assess differences in foraging trip metrics and diving metrics between adult female SSL that foraged inshore versus offshore, we ran linear mixed models (LME) (R package 'nlme') to account for multiple foraging trips recorded from some individuals, using foraging location (inshore/offshore) as a factor. There were no significant differences between dive variables and year; hence, we did not include year in the final model. Where appropriate, we log-transformed variables to fit model assumptions of constant variance and normal distribution. Model assumptions were checked by plotting residuals and via quantilequantile plots.

We were also interested in whether individual specialization could be detected within the offshore group (sample size of the inshore group limited meaningful analysis). To identify whether different foraging strategies existed within the offshore group, we initially ran a principal components

analysis (PCA) using the mean and SD of diving metrics (per individual), as a pre-processing step to reduce the number of variables, before running a Hierarchical Cluster Analysis (HCA) (Appendix 1, Table S2). Specifically, five principal components accounted for 89 % of the variance, and these were used to generate a dissimilarity matrix based on Euclidean distance (Appendix 1, Table S2). An agglomerative cluster analysis was then executed using Ward linkage in the R package 'Vegan'. The optimal number of clusters was selected using Bayesian Information Criteria (BIC) (R Package 'mclust'). We did not include stable isotope data in this analysis, because isotope data was only available for nine (out of 16) adult female SSL that foraged offshore. To evaluate the performance of our cluster analysis, we ran (1) a non-metric Multi-dimensional Scaling analysis, and overlaid the cluster and ordination results to see how they corresponded, and (2) Quadratic Discriminant Analysis using Leave One Out-Cross Validation (LOO-CV) to test the proportion of individual SSL that could correctly be re-assigned to clusters (R Package 'MASS'). To tease apart differences in foraging locations within the offshore group, we fitted a two-state (foraging/ commuting) hidden markov model to adult female SSL movement data (R package 'move.HMM'). Models were built using hourly step lengths (km) and turn angles (radians), using Weibull and wrapped Cauchy distributions, respectively (Langrock et al. 2012). Akaike's information criterion (AIC) and residual plots were used to determine the best model fit with the Viterbi algorithm used to assign states to the observations. Finally, we extracted utilization distribution probabilities based on locations identified as foraging, using the approach described above.

Stable isotope analysis

The use of stable isotopes to infer pinniped diet is now well established and widely reported, with $\delta^{13}C$ values providing a proxy of foraging habitat and $\delta^{15}N$ a proxy of trophic level (Cherel et al. 2007; Newsome et al. 2010). Our analyses focussed on the isotopic signature of vibrissae because we were interested in inferring diet over an extended temporal period (Kernaléguen et al. 2015). We assumed southern sea lion vibrissae grew continuously, meaning the isotopic composition of vibrissae reflected an individual's trophic and spatial history (Hirons et al. 2001). Vibrissae were collected by cutting the largest one from each adult female SSL as close to the skin as possible (we did not collect the root of vibrissae, hence stable isotope values do not necessarily reflect the period over which SSL were tracked). A mean growth of 0.11 mm per day has previously been reported for sea lions (Hirons et al. 2001). Based on this estimate, adult female SSL vibrissae integrate diet over a period of years (vibrissae length (excluding the root) ranged from 82–192 mm (mean 134 \pm SD 38 mm), translating to 2.04-4.78 years of growth). Vibrissae were cleaned using a sponge and distilled water, placed in an ultrasonic bath of distilled water for 5 min and dried using 95 % ethanol (Kernaléguen et al. 2012). Each whisker was inspected under a microscope and, if necessary, the cleaning process repeated. Vibrissae were cut into 5 mm long consecutive segments starting from the proximal (facial) end. To produce a meaningful isotopic measurement our target mass for each whisker segment was 0.5 mg. To achieve our target mass, it was necessary to sub-sample each 5 mm long whisker section. Samples were packed in tin containers, and carbon and nitrogen isotope ratios were determined by a Carlo-Erba elemental analyser interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California Santa Cruz, Santa Cruz, CA, USA). Data were corrected for sample mass and instrument drift. Measurement precision (standard deviation), based on within-run replicate measures of the laboratory standard (pugel), was 0.06 % for carbon $(\delta^{13}C)$ and 0.08 % for nitrogen $(\delta^{15}N)$ isotope values.

Dietary specialization

To determine the sources of variance in isotope values, we also ran LME, with individual as a random effect, and colony (Big Shag Island vs. all other sites) and year included in the model as fixed effects. The residual error term (the remaining variance not explained by other terms) corresponded to within-individual variation (Newsome 2009). Variance components were calculated separately for δ^{13} C and δ^{15} N using the 'varcomp' function in the R package 'APE'. If SSL are dietary generalists, we would expect most of the variation to be within individual vibrissae. Conversely, in the case of dietary specialization, most of the variation should be between individual vibrissae (Newsome 2009).

In addition, we used isotope values to calculate a specialization index, based on dietary variation within and between individuals. The within-individual component (WIC) was calculated as the standard deviation in isotopes along vibrissae. The between-individual component (BIC) was the standard deviation in isotopic values calculated from all samples (Hückstädt et al. 2012). The specialization index (*S*) was defined as S = WIC/total niche width (TNW) where TNW = WIC + BIC. *S* values vary from 0 to 1, with 1 representing complete overlap between the individual and population, and lower values representing less inter-individual overlap and higher specialization. We defined a generalist as individuals occupying >50 % of the niche (Hückstädt et al. 2012). All values are presented as mean \pm SD.

Results

In total, 31 adult female SSL were equipped with biologging devices. PTT tags were deployed on 11 adult female SSL (Appendix 1, Table S1). Two PTT tags stopped transmitting soon after deployment (1 and 4 days, respectively; recovery of one of these tags revealed tag failure). This left PTT location data for 9 adult female SSL (n = 5 Big Shag Island 2011, n = 3 Kelp Island 2011, n = 1 Turn Island 2013). GPS and TDR tags were deployed on 20 adult female SSL at Big Shag Island (n = 10 in 2013 and 2014). Two GPS tags failed, leaving location data for 18 adult female SSL (Appendix 1, Table S1). TDR data for the two failed GPS tags were, however, included in our analysis (inshore/offshore assigned on the basis of dive depth). In total, 71 foraging trips were recorded, with repeat foraging trips from 14 adult female SSL (excluding 4 SSL that carried PTT tags and foraged inshore). Deployment period ranged between 3 and 115 days (Appendix 1, Table S1). Adult female SSL predominantly foraged on the Patagonian Shelf or at the Patagonian Shelf edge, identified as the 200 m depth contour (Fig. 1). The majority of adult female SSL foraged offshore (72 % or n = 21 of 29 SSL) (Fig. 1; Table 1).

Inshore/offshore foraging and individual specialization

Of the 9 adult female SSL that carried PTT tags (excluding the two failed PTT tags), 3 foraged inshore, 5 foraged offshore, and 1 foraged both inshore and offshore (PTT 103751 undertook one offshore foraging trip, followed by several inshore foraging trips) (Table 1; Appendix 1, Table S1). Of the 20 adult female SSL that carried GPS and TDR tags, 4 foraged inshore and 16 foraged offshore. Adult female SSL that foraged offshore travelled further (PTT: 99 ± 23 vs. 23 ± 5 km; LME: $F_{1,8} = 31.8$, P < 0.001; GPS: 92 ± 20 vs. 10 ± 4 km; LME: $F_{1.18} = 46.7$, P < 0.001), dived deeper (mean dive depth: 75 ± 23 vs. 21 ± 8 m; LME: $F_{1,18} = 22.8$, P < 0.001) and had longer inter-trip durations (59 \pm 12 vs. 16 \pm 17 h; LME: $F_{1,7} = 22.9$, P < 0.001), when compared to those that foraged inshore (Table 1). However, body length was not significantly different between adult female SSL that foraged inshore compared to those that foraged offshore (Wilcoxon's rank test, P > 0.05; Table 1). Beyond the broad inshore/offshore classification, we also detected more complex foraging patterns. Specifically, multivariate analysis of TDR data collected from 16 adult female SSL that foraged offshore revealed two clusters (which we term 'benthic' and 'mixed') (Fig. 2), supported by both Multi-dimensional Scaling analysis (Appendix 1, Fig. S1) and Quadratic Discriminant Analysis using LOO-CV that correctly

Table 1 Foraging trip statistics
 for 29 adult female southern sea lions (Otaria flavescens) breeding at the Falkland Islands. In total, 20 adult female southern sea lions carried GPS and TDR tags and 11 carried PTT tags. Two GPS tags failed, but associated TDR data were included in our analysis. Two PTT tags also failed and were excluded from our analysis. Adult females typically foraged either inshore (coastal) or offshore (outer Patagonian Shelf)

| GPS and TDR | Inshore $(n = 4)$ | | Offshore $(n = 16)$ | |
|---|---------------------|-----|----------------------|-----|
| | Mean | SD | Mean | SD |
| Dive | | | | |
| Mean diving depth (m) | 21 | 8 | 75 | 23 |
| Mean max diving depth (m) | 47 | 15 | 158 | 32 |
| Max dive depth (m) | 62 | | 256 | |
| Mean depth at night (m) | 19 | 8 | 53 | 19 |
| Mean depth at day (m) | 24 | 10 | 87 | 26 |
| Mean duration (s) | 124 | 28 | 154 | 28 |
| Mean bottom time (s) | 110 | 22 | 99 | 23 |
| Post-dive duration (min) | 2.0 | 0.6 | 5.2 | 1.8 |
| Day dives (%) | 51 | 14 | 67 | 13 |
| Intra-depth zone (IDZ) | 46 | 16 | 53 | 14 |
| Mean dive frequency/h | 12 | 2 | 9 | 2 |
| Total number of dives | 795 | 260 | 813 | 367 |
| Foraging trip duration (days) | 1.1 | 0.6 | 2.9 | 0.8 |
| Location | | | | |
| Max distance from coast (km) ^a | 10 | 4 | 92 | 20 |
| Mean bathymetric depth (m) ^a | _ | _ | 114 | 20 |
| Deployment period (days) | 2.7 | 0.7 | 3.7 | 1.2 |
| Inter-trip duration (h) | 16 | 17 | 59 | 12 |
| Total number of trips | 12 | | 21 | |
| Length (cm) | 175 | 11 | 175 | 12 |
| PTT | Inshore $(n = 3)^c$ | | Offshore $(n = 5)^c$ | |
| | Mean | SD | Mean | SD |
| Location only | | | | |
| Max distance from coast (km) ^b | 23 | 5 | 99 | 23 |
| Deployment period (days) | 30 | 19 | 44 | 40 |
| Total number of trips ^b | _ | | 38 | |
| Length (cm) ^c | 178 | 14 | 191 | 10 |

^a Excludes two failed GPS tags

^b Includes inshore/offshore foraging trip/s for PTT 103751

^c Excludes PTT 103751

re-assigned 88 % individuals to their respective clusters. Of the five principal components used in the cluster analysis, principal component 1 was associated with dive depth, while the remaining principal components were associated with different combinations of dive depth and duration indices (Appendix 1, Table S2). The 'benthic' cluster comprised adult female SSL that dove to comparatively deeper depths (mean max depth: 99 ± 13 vs. 60 ± 11 m; Wilcoxon's rank test, P < 0.001) and were more accurately described as benthic foragers (76 ± 9 vs. 51 ± 8 % of dives benthic) when compared to the 'mixed' diving cluster, that was characterized by adult female SSL that performed both benthic and pelagic dives (Table 2). Overall, adult female SSL dove both day and night, but typically performed deeper dives during the day (Tables 1, 2).

Dietary specialization

A total of 22 adult female SSL vibrissae (n = 585 segments) were analysed (2011 = 8 [includes the two failed PTT tags, that were assigned to the offshore group on the basis of their vibrissae stable isotope values (Appendix 1, Table S1)], 2013 = 8, 2014 = 6 vibrissae). Intra-individual variations in vibrissae δ^{13} C and δ^{15} N values were evident, particularly within the inshore group (Appendix 1, Fig. S2). Nevertheless, there was a clear distinction in mean isotope values between adult female SSL that foraged inshore compared to those that foraged offshore, with the inshore group having significantly higher δ^{13} C values (-12.6 ± 0.2 vs. -14.1 ± 0.4 %, respectively) and δ^{15} N values (18.0 ± 0.2 vs. 16.2 ± 0.2 %, respectively) (Fig. 3; Wilcoxon's rank test, P < 0.001 for both δ^{13} C and δ^{15} N). There were two



Fig. 2 A hierarchical-cluster analysis using Ward Linkage and Euclidean distance revealed adult female southern sea lions (*Otaria flavescens*) that foraged offshore (outer Patagonian Shelf) could be separated into two clusters based on benthic (*Cluster 1*) or mixed benthic and pelagic (*Cluster 2*) diving behavior. The analysis was based on 16 adult female southern sea lions breeding at Big Shag Island (that carried GPS and TDR tags) and five principal components derived from their diving metrics (Appendix 1, Table S2). Also presented are the 90 % (*yellow*) and 50 % (*orange*) utilization distributions, based on the locations identified as 'foraging' calculated using a hidden markov model on adult female southern sea lions movement metrics (colour figure online)

exceptions. Based on sequential vibrissae segments, the δ^{13} C values of female GPS1_2013 indicated that this individual switched from inshore to offshore habitats (Fig. 3; Appendix 1, Fig. S3). Secondly, PTT 103751, which undertook both inshore and offshore foraging trips, had δ^{13} C values that resembled the offshore group, but intermediate δ^{15} N values (Fig. 3; Appendix 1, Fig. S3). The dietary history of this individual implies that offshore foraging trips were more frequent than inshore foraging trips, which was contrary to the PTT data.

Our variance component analysis of δ^{13} C and δ^{15} N values indicated that neither year nor breeding site was significant (Table 3). Between-individual differences explained a larger proportion of the variation in isotopic values when compared to within-individual isotopic differences (Table 3). Hence, there was more support for adult female SSL being dietary specialists than dietary generalists. This finding was supported by our specialization index (*S*) (mean *S* = 0.35 ± 0.09 based on δ^{13} C and 0.33 ± 0.06 based on δ^{15} N values) (Fig. 4). As expected, GPS1_2013 was the only generalist adult female SSL based on δ^{13} C values (*S* = 0.54; Fig. 4). When **Table 2** Foraging trip statistics and mean vibrissae stable isotope values for adult female southern sea lions (*Otaria flavescens*) that foraged offshore and were separated into two clusters [termed 'benthic' and 'mixed' (benthic and pelagic dive behaviour)] on the basis of a hierarchical-cluster analysis (see also Fig. 2)

| | Cluster 1 Benthic $(n = 6)$ | | Cluster 2 Mixed (n = 10) | |
|---|--------------------------------|-----|--------------------------------|-----|
| | Mean | SD | Mean | SD |
| Dive | | | | |
| Mean diving depth (m) | 99 | 13 | 60 | 11 |
| Mean max diving depth (m) | 157 | 28 | 159 | 36 |
| Mean depth at night (m) | 71 | 7 | 42 | 16 |
| Mean depth at day (m) | 108 | 18 | 74 | 23 |
| Mean duration (s) | 182 | 15 | 137 | 15 |
| Mean bottom time (s) | 111 | 20 | 92 | 22 |
| Post-dive duration (min) | 5.5 | 1.5 | 5.0 | 2.0 |
| Day dives (%) | 78 | 6 | 61 | 12 |
| Intra-depth zone (IDZ) | 68 | 6 | 44 | 7 |
| Mean dive frequency/h | 7 | 1 | 10 | 2 |
| Foraging trip duration (days) | 3.2 | 0.9 | 2.8 | 0.7 |
| Benthic dives (%) | 76 | 9 | 51 | 8 |
| Location | | | | |
| Max distance from coast (km) ^a | 100 | 22 | 88 | 18 |
| Mean bathymetric depth (m) | 122 | 31 | 110 | 11 |
| Deployment period (days) | 3.7 | 1.4 | 3.8 | 1.1 |
| Total number of trips | 7 | | 14 | |
| Diet | | | | |
| δ ¹³ C (‰) | -14.0 | 0.9 | -14.1 | 0.4 |
| δ^{15} N (%) | 16.5 | 0.4 | 16.3 | 0.6 |

Stable isotope analysis is based on vibrissae from n = 3 adult female southern sea lions from Cluster 1, and n = 7 from Cluster 2 (see also Fig. 2)

^a Excludes one failed GPS tag

we considered these foraging groups separately (i.e., TNW is based on SD in the vibrissae of either adult female SSL that foraged inshore or offshore, including GPS1_2013), we found a similar degree of specialization based on δ^{13} C ($S = 0.48 \pm 0.06$ vs. 0.41 ± 0.09 , respectively; Wilcoxon's rank test, P > 0.05), but adult female SSL that foraged inshore appeared to be less specialized based on δ^{15} N values ($S = 0.52 \pm 0.06$ vs. 0.41 ± 0.05 , respectively; Wilcoxon's rank test, P = 0.006).

Of the 16 adult female SSL that carried TDRs and foraged offshore (Fig. 2), we analysed 9 vibrissae, with n = 3from cluster one (benthic diving) and n = 6 from cluster two (mixed benthic and pelagic diving). Values of δ^{13} C and δ^{15} N were similar between clusters (Table 2). However, the benthic cluster consisted of individuals that were, on average, more specialized than adult female SSL belonging to



Fig. 3 The δ^{13} C and δ^{15} N values of vibrissae from 22 adult female southern sea lions (*Otaria flavescens*). A offshore (outer Patagonian Shelf, n = 14). B inshore (coastal, n = 6). C one adult female (PTT 103751) that undertook both inshore and offshore foraging trips. D one adult female (GPS1_2013) that appeared to switch from inshore to offshore habitat based on δ^{13} C values (see also Appendix 1, Fig. S3). The *error bars* for A and B (*solid circles*) represent total variability in isotope values for adult females that foraged inshore or offshore, respectively (i.e., means are estimated from all vibrissae segments). Error bars for C and D (*solid triangles*) correspond to variability in isotope values for one individual. Values are mean \pm standard deviation

Table 3 Percentage of variance in adult female southern sea lion

 (Otaria flavescens) vibrissae isotopes explained by within-individual variation and between-individual variation

| Effect | Variance explained (%) | | |
|------------------------------|------------------------|----------------|--|
| | $\delta^{13}C$ | $\delta^{15}N$ | |
| Between individual variation | 0.62 | 0.75 | |
| Within individual variation | 0.38 | 0.25 | |
| Breeding colony | NS | NS | |
| Year | NS | NS | |

Year and breeding colony (Big Shag Island vs. all other sites) were non-significant (NS) fixed effects

the mixed cluster, when considering δ^{13} C ($S = 0.43 \pm 0.13 \pm 0.33 \pm 0.05$, respectively). This implies individuals that comprised the benthic cluster had a greater degree of separation in foraging habitat. However, sample size limits a meaningful comparison.

Discussion

Using biologging devices and stable isotope analysis of vibrissae, we show that adult female SSL foraging ecology is more complex than previously described. Not only did adult female SSL display long-term fidelity to inshore or offshore regions (months to years), but we also found evidence of further specialization within the group of SSL



Fig. 4 Specialization index (*S*) calculated for individual adult female southern sea lions (*Otaria flavescens*). The frequency distribution reveals 22 adult female southern sea lions show a high degree of dietary specialization, with only 1 (GPS1_2013) classed as a generalist

that foraged offshore. Although characterized as benthic foraging, generalist predators, we revealed both benthic and pelagic diving behavior at the Falkland Islands, and a population comprised of specialists. However, our study is not without caveats. In particular, we were unable to determine the age of pups and, therefore, cannot exclude that the behavior we observed was correlated with pup age (females with older pups, undertaking longer foraging trips) (Rodríguez et al. 2013). Nevertheless, the data presented overwhelming support fidelity to discrete foraging habitats. In other wide-ranging marine taxa, including fish, sea turtles and seabirds, recent studies have also revealed marked individual specialization in foraging ecology related to discrete habitats (e.g., Masello et al. 2013; Vander Zanden et al. 2013; Cleasby et al. 2015). Our findings form part of this emerging picture of individual specialization in foraging ecology, and are significant because the individual differences we describe may affect a population's ecological and evolutionary dynamics through energetic income, pathogen exposure, vulnerability to anthropogenic hazards, response to environmental change, and life-history traits, such as rates of female reproduction (Bolnick et al. 2003).

In the present study, adult female SSL predominantly foraged on the Patagonian Shelf or at the Patagonian Shelf edge, (identified by the 200 m depth contour). Adult female SSL that foraged inshore (coastal), performed shallow, presumably benthic dives, that showed no obvious diurnal pattern. These findings corroborate earlier studies at the Falkland Islands (mean dive depth 25 ± 17 m) and studies from other breeding sites in the South Atlantic, specifically Uruguay (mean dive depth 21 ± 8 m), and northern Patagonia (Thompson et al. 1998; Campagna et al. 2001; Riet-Sapriza et al. 2013). In contrast, adult female SSL that foraged offshore undertook extended foraging trips and displayed either benthic (99 \pm 13 m) or mixed (benthic and pelagic) diving behavior (60 \pm 11 m). Although in most sea lion species adult females are typically considered to be benthic foragers (the exception being California sea lions, *Zalophus californianus*; Weise et al. 2010; Kuhn and Costa 2014), pelagic diving is also described for adult female SSL breeding in northern Patagonia (Werner and Campagna 1995) and more recently, in New Zealand (*Phocarctos hookeri*) (Chilvers and Wilkinson 2009) and Galapagos sea lions (*Zalophus wollebaeki*) (Villegas-Amtmann et al. 2008). This implies that pelagic diving behavior is not uncommon among adult female sea lions and could be a more important mode of foraging than previously thought.

In addition to benthic and pelagic diving behavior, the inshore and offshore foraging behaviors we describe have also been reported for adult female SSL breeding in northern Patagonia (referred to as 'coastal and pelagic') (Campagna et al. 2001). However, offshore foraging trips in northern Patagonia are restricted to shallow Patagonian Shelf waters, typically <80 m (the exception being deep shelf areas associated with the San Matias Gulf) (Campagna et al. 2001). In contrast, the majority of adult female SSL in our study (72 %) foraged offshore in deeper waters associated with the outer Patagonian Shelf (mean bathymetry 114 ± 20 m), and, on average, dived deeper than their conspecifics at other South Atlantic breeding locations (Campagna et al. 2001; Riet-Sapriza et al. 2013). Differences in SSL foraging ecology between South Atlantic breeding locations, therefore, may ultimately reflect available bathymetry, oceanography and the proximity of breeding colonies to the Patagonian Shelf edge.

For example, the breeding colonies we studied are within 100 km of the Patagonian Shelf edge, a region of enhanced productivity where the shelf waters meet the cooler, more saline waters associated with the Falkland Current, a highly productive northward flowing current originating from the Antarctic Circumpolar Current (Acha et al. 2004; Arkhipkin et al. 2012). In contrast, SSL breeding in Uruguay and northern Patagonia are further from the Patagonian Shelf Edge (ca. 150 and ca. 400 km, respectively) and their foraging areas tend to be associated with regions of enhanced productivity in bays and estuaries (e.g., tidal fronts) (Campagna et al. 2001; Rodríguez et al. 2013). Given that adult female SSL foraging trips are typically short in distance and duration (e.g., Uruguay, 99 \pm 31 km and 1.5 \pm 0.9 days, northern Patagonia, 104 ± 60 km and 3.4 ± 1.3 days) the deeper water associated with the highly productive Patagonian Shelf edge is apparently beyond the optimal foraging range of adult female SSL breeding in northern Patagonia and Uruguay (at least during the early lactation period) (Campagna et al. 2001; Riet-Sapriza et al. 2013).

The short term (weeks to months) specialization observed in the tracking data were also reflected in the stable isotope data, indicating that these foraging strategies (foraging site fidelity to inshore or offshore habitats) typically persisted over several years. Specifically, adult female SSL that foraged inshore had characteristically higher δ^{13} C values when compared to adult female SSL that foraged offshore (Hobson et al. 1994). In addition, coastal benthic SSL prey on the Patagonian Shelf have higher δ^{13} C and δ^{15} N values relative to pelagic prey (Drago et al. 2010a; Franco-Trecu et al. 2012). Hence, the differences in stable isotope values between adult female SSL that foraged inshore versus offshore presumably signify differences in diet and the trophic level at which adult female SSL fed. SSL diet includes crustaceans, cephalopods and fish (Thompson et al. 1998). Differences in stable isotope values may, therefore, reflect different proportions of these prey items, with more benthic fish and octopus species being consumed by adult female SSL that foraged inshore and more squid and pelagic fish consumed by adult female SSL that foraged offshore.

However, the intra-individual variation we observed along vibrissae suggests that the link between isotopes and SSL diet is complex. In particular, variation along the vibrissae of adult female SSL that foraged inshore may reflect seasonal variation in the isotopic values of SSL prey (e.g., SSL could switch prey, or prey isotope values themselves could vary seasonally) (Quillfeldt et al. 2015), or be evidence of seasonal changes in foraging habitat (Drago et al. 2010b; Franco-Trecu et al. 2012). The latter would imply that adult female SSL which foraged inshore exploited a greater variety of foraging habitats when compared to adult female SSL which foraged offshore, perhaps in response to contrasting periods of competition and resource availability or related to winter movements, when females may disperse from breeding colonies (Hamilton 1939). Yet, we found only two clear exceptions to the inshore/offshore dichotomy. These were PTT 103751 which undertook one offshore foraging trip, followed by several inshore foraging trips over a 19-day deployment, while GPS1_2013 switched from inshore to offshore habitats on the basis of δ^{13} C values. Hence, during our study, it was uncommon for adult female SSL to alternate between inshore and offshore habitats or to undertake a persistent switch from one foraging habitat to the other.

Whilst a growing number of studies report individual specialization within apparently generalist species, the proximate and ultimate causes of behavioral diversification in foraging decisions remain poorly understood, particularly in species that have experienced large population declines (Svanbäck and Persson 2004; Merkle et al. 2015). Commonly invoked predictions of individual specialization are intuitively appealing when considering the very large

population size of SSL at the Falkland Islands in the 1930s (i.e., strong intraspecific competition, with the degree of individual specialization positively related to population density) (Estes et al. 2003: Svanbäck and Persson 2004: Baylis et al. 2015b). However, if strong intraspecific competition promotes individual specialization, then the degree of specialization should decline when intraspecific competition is relaxed (Estes et al. 2003; Tinker et al. 2008). Contrary to these expectations, recent studies on bison (Bison bison) suggest that individuals in a declining population face a trade-off between two optimal behaviors (Merkle et al. 2015). These are to forage in the most profitable patches as intraspecific competition is relaxed, or to continue to choose resource patches that are familiar (Merkle et al. 2015). Hence, the foraging specialization we report (in a population that has declined by >90 %) could reflect foraging decisions influenced by the benefits associated with foraging site fidelity rather than intraspecific competition. However, if the dramatic decline in the number of SSL breeding at the Falkland Islands was associated with changes in resource availability rather than sealing (as proposed by Baylis et al. 2015b), then maintaining specialization (or diversification into multiple foraging specialists and the expansion of the population dietary niche breadth) would, presumably, be beneficial (Estes et al. 2003). Either notion could help explain why northern fur seals (Callorhinus ursinus) have maintained foraging specialization and fidelity to foraging habitats, despite a 40 % population decline (Kuhn et al. 2014).

Regardless of the ultimate causes of specialization, an individual may use only a subset of the available resources if differences exist in prey handling or search efficiency (Wolf et al. 2008; Tinker et al. 2008). For example, body size in sea lions is an important determinant of diving capacity and, therefore, foraging ability (Richmond et al. 2006; Villegas-Amtmann et al. 2008; Weise et al. 2010; Jeglinski et al. 2012; Leung et al. 2013). Unfortunately, our estimates of body size were limited to a crude proxy (body length) that indicated that size was unrelated to the foraging behaviors we report. Other factors that could influence an individual's resource use include age/experience, matrilineal transmission of foraging preferences (Estes et al. 2003; Svanbäck and Bolnick 2007) or individual differences in the ability to use different foraging skills (Beauchamp et al. 1997). Assuming individuals act to maximize their net rate of energy intake and that individual differences in prey capture efficiency exist, then optimal foraging theory suggests that individuals should ignore certain types of prey which are less profitable and invest time searching for more valuable prey (Stephens and Krebs 1986; Svanbäck and Bolnick 2007; Tinker et al. 2008). For example, offshore pelagic prey may have higher energy density and lipid content than coastal benthic prey, as proposed for SSL breeding in northern Patagonia (Drago et al. 2010a). Such efficiency trade-offs may help to explain why some adult female SSL undertook extended foraging trips to the outer Patagonian Shelf, whilst other individuals reduced travel costs but fed in presumably less productive areas (Acha et al. 2004). In addition, for-aging site fidelity (as already noted) is an important adaptive force shaping animal behavior and distribution (Piper 2011; Baylis et al. 2012, 2015c; Merkle et al. 2015). Hence, the long-term fidelity of SSL to inshore or offshore foraging habitats implies foraging decisions are not only influenced by an energy-maximizing foraging strategy but also by foraging site fidelity.

Presumably, the energetic costs of foraging (and how these costs are balanced) varies depending on foraging habitat (e.g., differences between inshore vs. offshore in distance travelled, dive depth) and the energy density of prey. This, in turn, is likely to influence adult female SSL reproductive performance and success (but see Chilvers and Wilkinson 2009). For example, in Antarctic fur seals (Arctocephalus gazella), adult female foraging trip durations are negatively correlated with pup birth mass, while time spent ashore is positively correlated with pup weaning mass (Doidge and Croxall 1989; Lunn et al. 1994). Similarly, the use of different foraging areas by adult females influences weaning mass in southern elephant seals (Mirounga leonina) (Authier et al. 2012), the reproductive output of loggerhead sea turtles (Caretta caretta) (Vander Zanden et al. 2013), and the breeding performance of kittiwakes (Rissa tridactyla) (Paredes et al. 2012). Finally, and perhaps most compelling, adult female SSL in northern Patagonia with a dietary signature consistent with 'offshore' pelagic prey have higher pup growth rates when compared with adult females that have a dietary signature which is consistent with 'inshore' benthic prey (Drago et al. 2010a). This implies that a particular foraging behavior may be associated with higher reproductive success, meaning that some individuals could contribute disproportionally to the population in a given year. However, the coexistence of multiple foraging strategies is counterintuitive if these strategies do not provide equivalent benefits. The different foraging strategies we describe may be adaptive if other costs and benefits exist.

For example, given that SSL are a long-lived, slow reproducing species, with a long lactation period (Hamilton 1939), parental care is also important to reproductive success, the quality of which may differ between foraging strategies. Specifically, if the shorter inshore foraging trips that we report (Table 1) translate to adult female SSL spending a greater period of time ashore over the lactation period, parental care may be enhanced and, presumably, this would benefit pup survival (Campagna et al. 1992). Alternatively, resources within inshore habitats could be more predictable when compared to offshore habitats. Hence, while the less preferred or less optimal strategy may have fewer individuals in the population, we speculate that different foraging strategies could result in equally successful reproductive outputs over the lifetime of an adult female SSL.

Finally, the individual specialization we describe raises intriguing questions about SSL population-level dynamics and community ecology. For example, our results indicate that adult female SSL will be differentially affected by changes in prey abundance and anthropogenic hazards (e.g., hydrocarbon activities, fisheries) depending on where they forage. At the Falkland Islands, this will provide a framework to better understand impediments to population recovery and threats to population persistence. The inshore/ offshore foraging we describe also implies that SSL play a larger role in community ecology than previously thought, through, for example, linking disparate food webs via the transport of nutrients across habitat boundaries. In addition, our findings highlight that the accuracy of conventional beliefs about SSL foraging ecology (benthic foraging mode and dietary generalists) implicitly depends on breeding location (e.g., Argentina, Falkland Islands, Uruguay). Hence, an integrated, collaborative approach is ultimately required to understand the ecology of the species, and to evaluate the vulnerability of SSL breeding in the South Atlantic to anthropogenically driven habitat modifications.

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Author contribution statement AMMB and IJS conceived the study and analysed the data. AMMB and RAO led the field work, with contributions from all authors. AMMB wrote the paper, with contributions from all authors.

References

- Acha EM, Mianzan HW, Guerrero RA et al (2004) Marine fronts at the continental shelves of austral South America. J Mar Syst 44:83–105. doi:10.1016/j.jmarsys.2003.09.005
- Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. Ecol Lett 14:948–958. doi:10.1111/j.1461-0248.2011.01662.x
- Arkhipkin AI, Brickle P, Laptikhovsky V, Winter A (2012) Dining hall at sea: feeding migrations of nektonic

predators to the eastern Patagonian Shelf. J Fish Biol 81:882–902. doi:10.1111/j.1095-8649.2012.03359.x

- Authier M, Dragon A-C, Richard P et al (2012) O' mother where wert thou? Maternal strategies in the southern elephant seal: a stable isotope investigation. Proc R Soc Lond B 279:2681–2690. doi:10.1098/rspb.2012.0199
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78:699–714. doi:10.1111/j.1365-2656.2009.01531.x
- Baylis AMM, Nichols PD (2009) Milk fatty acids predict the foraging locations of the New Zealand fur seal: continental shelf versus oceanic waters. Mar Ecol Prog Ser 380:271–286. doi:10.3354/ meps07919
- Baylis AMM, Hamer DJ, Nichols PD (2009) Assessing the use of milk fatty acids to infer the diet of the Australian sea lion (*Neophoca cinerea*). Wildl Res 36:169–176. doi:10.1071/WR08046
- Baylis AMM, Page B, McKenzie J, Goldsworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: continental shelf vs. oceanic habitats. Mar Mammal Sci 28:276–294. doi:10.1111/j.1748-7692.2011.00487.x
- Baylis AMM, Page B, Staniland I et al (2015a) Taking the sting out of darting: risks, restraint drugs and procedures for the chemical restraint of Southern Hemisphere otariids. Mar Mammal Sci 31:322–344. doi:10.1111/mms.12148
- Baylis AMM, Orben RA, Arnould JPY et al (2015b) Disentangling the cause of a catastrophic population decline in a large marine mammal. Ecology. doi:10.1890/14-1948.1
- Baylis AMM, Orben RA, Pistorius P et al (2015c) Winter foraging site fidelity of king penguins breeding at the Falkland Islands. Mar Biol 162:99–110. doi:10.1007/s00227-014-2561-0
- Beauchamp G, Giraldeau L, Ennis N (1997) Experimental evidence for the maintenance of foraging specializations by frequency-dependent choice in flocks of spice finches. Ethol Ecol Evol 9:105–117
- Bolnick DI, Svanbäck R, Fordyce JA et al (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28. doi:10.1086/343878
- Campagna C, Bisioli C, Quintana F et al (1992) Group breeding in sea lions: pups survive better in colonies. Anim Behav 43:541– 548. doi:10.1016/S0003-3472(05)81014-0
- Campagna C, Werner R, Karesh W et al (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). J Zool 255:205–220. doi:10.1017/S0952836901001285
- Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. J Anim Ecol 76:826–836. doi:10.1111/j.1365-2656.2007.01238.x
- Chilvers BL, Wilkinson IS (2009) Diverse foraging strategies in lactating New Zealand sea lions. Mar Ecol Prog Ser 378:299–308. doi:10.3354/meps07846
- Cleasby I, Wakefield E, Bodey T et al (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. Mar Ecol Prog Ser 518:1–12. doi:10.3354/meps11112
- Doidge DW, Croxall JP (1989) Factors affecting weaning weight in Antarctic fur seals Arctocephalus gazella at South Georgia. Polar Biol 9:155–160. doi:10.1007/BF00297170
- Drago M, Cardona L, Crespo EA, Aguilar A (2009) Ontogenic dietary changes in South American sea lions. J Zool 279:251–261. doi:10.1111/j.1469-7998.2009.00613.x
- Drago M, Cardona L, Aguilar A et al (2010a) Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. Mar Mammal Sci 26:309–323. doi:10.1111/j.1748-7692.2009.00321.x
- Drago M, Cardona L, Crespo EA et al (2010b) Change in the foraging strategy of female South American sea lions (Carnivora: Pinnipedia) after parturition. Sci Mar 74:589–598. doi:10.3989/ scimar.2010.74n3589

- Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on Sea Otters linking oceanic and nearshore ecosystems. Science 282(80):473–476. doi:10.1126/science.282.5388.473
- Estes JA, Riedman ML, Staedler MM et al (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72:144–155. doi:10.1046/j.1365-2656.2003.00690.x
- Estes JA, Terborgh J, Brashares JS et al (2011) Trophic downgrading of planet Earth. Science 333(80):301–307
- Franco-Trecu V, Aurioles-Gamboa D, Arim M, Lima M (2012) Prepartum and postpartum trophic segregation between sympatrically breeding female Arctocephalus australis and Otaria flavescens. J Mammal 93:514–521. doi:10.1644/11-MAMM-A-174.1
- Franco-Trecu V, Drago M, Inchausti P et al (2014) Postharvesting population dynamics of the South American sea lion (*Otaria byronia*) in the southwestern Atlantic. Mar Mammal Sci. doi: 10.1111/mms.12197
- Hamilton JE (1939) A second report on the southern sea lion (*Otaria byronia*) (de Blainville). Discovery Reports 19
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210. doi:10.1016/j.tree.2008.01.003
- Hirons AC, Schell DM, St Aubin DJ (2001) Growth rates of vibrissae of harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*). Can J Zool 79:1053–1061. doi:10.1139/ cjz-79-6-1053
- Hobson KA, Piatt JFJ, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786– 798. doi:10.2307/5256
- Hückstädt LA, Koch PL, McDonald BI et al (2012) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. Oecologia 169:395–406. doi:10.1007/s00442-011-2202-y
- Jeglinski J, Werner C, Robinson P et al (2012) Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. Mar Ecol Prog Ser 453:279–296. doi:10.3354/ meps09649
- Jeglinski JWE, Goetz KT, Werner C et al (2013) Same size same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. J Anim Ecol. doi:10.1111/1365-2656.12019
- Johnson D, London J, Lea M, Durban J (2008) Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215
- Kernaléguen L, Cazelles B, Arnould JPY et al (2012) Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. PLoS ONE 7:e32916. doi:10.1371/journal.pone.0032916
- Kernaléguen L, Dorville N, Ierodiaconou D et al (2015) From video recordings to whisker stable isotopes: a critical evaluation of time-scale in assessing individual foraging specialisation in Australian fur seals. Oecologia. doi:10.1007/s00442-015-3407-2
- Kuhn CE, Costa DP (2014) Interannual variation in the at-sea behavior of California sea lions (*Zalophus californianus*). Mar Mammal Sci 30:1297–1319. doi: 10.1111/mms.12110
- Kuhn CE, Ream RR, Sterling JT et al (2014) Spatial segregation and the influence of habitat on the foraging behavior of northern fur seals (*Callorhinus ursinus*). Can J Zool 92:861–873
- Langrock R, King R, Matthiopoulos J et al (2012) Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93:2336–2342. doi:10.1890/11-2241.1
- Leung ES, Chilvers BL, Nakagawa S, Robertson BC (2013) Size and experience matter: diving behavior of juvenile New Zealand sea lions (*Phocarctos hookeri*). Polar Biol 37:15–26. doi:10.1007/ s00300-013-1405-6
- Lowther AD, Harcourt R, Hamer D, Goldsworthy SD (2011) Creatures of habit: foraging habitat fidelity of adult female Australian

sea lions. Mar Ecol Prog Ser 443:249-263. doi:10.3354/ meps09392

- Lunn NJ, Boyd IL, Croxall JP (1994) Reproductive performance of female Antarctic fur seals : the influence of age, breeding experience, environmental variation and individual quality. J Anim Ecol 63:827–840
- Masello JF, Wikelski M, Voigt CC, Quillfeldt P (2013) Distribution patterns predict individual specialization in the diet of dolphin gulls. PLoS ONE 8:e67714. doi:10.1371/journal.pone.0067714
- Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J Anim Ecol 80:294–305. doi:10.1111/j.1365-2656.2010.01753.x
- Merkle J, Cherry S, Fortin D (2015) Bison distribution under conflicting foraging strategies: site fidelity versus energy maximization. Ecology 96:1793–1801. doi:10.1890/14-0805.1
- Newsome SD (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mammal Sci 26:509–572. doi:10.1111/j.1748-7692.2009.00354.x
- Paredes R, Harding AM, Iron DB et al (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. Mar Ecol Prog Ser 471:253–269. doi:10.3354/ meps10034
- Piper WH (2011) Making habitat selection more "familiar": a review. Behav Ecol Sociobiol 65:1329–1351. doi:10.1007/ s00265-011-1195-1
- Quillfeldt P, Ekschmitt K, Brickle P et al (2015) Variability of higher trophic level stable isotope data in space and time - a case study in a marine ecosystem. Rapid Commun Mass Spectrom 29:667– 674. doi:10.1002/rcm.7145
- Ratcliffe N, Takahashi A, O'Sullivan C et al (2013) The roles of sex, mass and individual specialisation in partitioning foragingdepth niches of a pursuit-diving predator. PLoS ONE 8:e79107. doi:10.1371/journal.pone.0079107
- Richmond JP, Burns JM, Rea LD (2006) Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eume-topias jubatus*). J Comp Physiol B 176:535–545. doi:10.1007/ s00360-006-0076-9
- Riet-Sapriza FG, Costa DP, Franco-Trecu V et al (2013) Foraging behavior of lactating South American sea lions (*Otaria flavescens*) and spatial-temporal resource overlap with the Uruguayan fisheries. Deep Sea Res Part II 88–89:106–119. doi:10.1016/j.dsr2.2012.09.005
- Rodríguez DH, Dassis M, Ponce de León A et al (2013) Foraging strategies of Southern sea lion females in the La Plata River Estuary (Argentina–Uruguay). Deep Sea Res Part II 88–89:120– 130. doi:10.1016/j.dsr2.2012.07.012
- Springer AM, Estes JA, van Vliet GB et al (2003) Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proc Natl Acad Sci USA 100:12223–12228. doi:10.1073/pnas.1635156100
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton
- Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. Proc R Soc Lond B 274:839–844. doi:10.1098/rspb.2006.0198
- Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. J Anim Ecol 73:973–982. doi:10.1111/j.0021-8790.2004.00868.x
- Thompson D, Duck CD, McConnell BJ, Garrett J (1998) Foraging behavior and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. J Zool 246:135–146. doi:10.1017/S0952836998010024

- Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc Natl Acad Sci USA 105:560–565. doi:10.1073/pnas.0709263105
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behavior in rockhopper penguins. Mar Ecol Prog Ser 204:257–267. doi:10.3354/meps204257
- Trites AW, Miller AJ, Maschner HDG et al (2007) Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: assessing the ocean climate hypothesis. Fish Oceanogr 16:46–67. doi:10.1111/j.1365-2419.2006.00408.x
- Vander Zanden HB, Pfaller JB, Reich KJ et al (2013) Foraging areas differentially affect reproductive output and interpretation of trends in abundance of loggerhead turtles. Mar Biol 161:585– 598. doi:10.1007/s00227-013-2361-y
- Villegas-Amtmann S, Costa D, Tremblay Y et al (2008) Multiple foraging strategies in a marine apex predator, the Galapagos

sea lion Zalophus wollebaeki. Mar Ecol Prog Ser 363:299–309. doi:10.3354/meps07457

- Weise MJ, Harvey JT, Costa DP (2010) The role of body size in individual-based foraging strategies of a top marine predator. Ecology 91:1004–1015
- Werner R, Campagna C (1995) Diving behavior of lactating southern sea lions (*Otaria flavescens*) in Patagonia. Can J Zool 73:1975– 1982. doi:10.1139/z95-232
- Wolf JBW, Harrod C, Brunner S et al (2008) Tracing early stages of species differentiation: ecological, morphological and genetic divergence of Galápagos sea lion populations. BMC Evol Biol 8:1–14. doi:10.1186/1471-2148-8-150
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168