

Influence of shelf oceanographic variability on alternate foraging strategies in long-nosed fur seals

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ABSTRACT: Central place foragers often change their foraging behaviour in response to changes in prey availability in the environment. Lactating long-nosed fur seals *Arctocephalus forsteri* (LNFS) at Cape Gantheaume in South Australia have been observed to display alternate foraging strategies, whereby they forage on the shelf in summer and switch to oceanic foraging in winter. We investigated the relationship between changes in shelf summertime upwelling and the timing and variability when females switch from predominantly shelf to oceanic foraging. Geolocation tags were deployed on females from summer to winter in 2016 and 2017, giving us longitudinal tracks over the transition period. The timing of switching from shelf to oceanic foraging was primarily driven by seasonal oceanographic changes on the shelf—specifically when the strength of the seasonal localised upwelling began to decline. The individual variability in the timing of the switch was driven by the strength of the coastal upwelling, with variability being greater in years when upwelling strength was weaker. By comparing our results to those of previous studies on the same colony, we found qualitative evidence that inter-annual environmental variability likely influences whether individuals display a single or multiple foraging strategies. This further highlights the flexibility in foraging strategies used by LNFS in response to environmental changes. The effect of inter-annual differences in foraging strategies on overall reproductive success warrants further investigation.

KEY WORDS: *Arctocephalus forsteri* · Upwelling · Continental shelf · Foraging strategies · Foraging ecology · Timing · Marine top predators · Subtropical front

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1. INTRODUCTION

The ability to acquire food in a cost-effective way is fundamental to the reproductive success of animals. All environments are dynamic at various spatial and temporal scales, resulting in changes in prey availability and distribution; predators may therefore employ flexible foraging strategies in response to these changes, to meet their energetic requirements. Other factors such as life-history stage (Clarke et al. 2006), inter-individual competition (Lynnes et al. 2002, Elliott et al. 2009), age, size and physiology also influence foraging behaviour (McDonald et al. 2009,

Zimmer et al. 2010, Hoskins et al. 2015). Predators that are provisioning offspring from a central place divide their time between foraging some distance away from this location and delivering food to their offspring (Orians & Pearson 1979). Consequently, when adopting a central place foraging strategy, predators are limited in their foraging range and have to balance between allocating food for their offspring and for their own self-maintenance (Ydenberg et al. 1994). To maximise lifetime reproductive success, central place foraging parents should aim to maximise the rate of food delivery to their offspring under any given condition (Boyd 1999).

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During the early stage of offspring-rearing, central place foragers are time-constrained due to the limited fasting abilities of their offspring (Clarke et al. 2006). As the rearing period progresses, energetic demands of offspring increase, but their fasting abilities also improve, thereby easing time constraints on parents (Clarke et al. 2006, Williams et al. 2007). Parents become energy-constrained and aim to maximise energy gain within a fixed amount of time (Boyd 1999, Staniland et al. 2007).

A common response to changing prey availability and offspring energetic demands is to alter foraging trip duration (Boyd et al. 1994) and/or range (habitat) (Lea et al. 2006). In many otariid species, foraging trip durations tend to increase as the pup-rearing period progresses, to meet increased energetic demands (Higgins et al. 1988, Boyd et al. 2002, Beauflet et al. 2004). Longer foraging trips tend to be associated with individuals travelling to more distant oceanic foraging grounds (as opposed to nearby con-

tinental shelf waters) (Nordstrom et al. 2013) where higher quality (energy-dense) prey may be found, potentially resulting in greater energetic gain (Staniland & Boyd 2003).

Long-nosed fur seals *Arctocephalus forsteri* (LNFS) were previously hunted to near-extinction levels, but after receiving protection status by the Australian government, they are currently the most abundant fur seal species in the Australian region (Shaughnessy et al. 2015). The majority of breeding colonies are concentrated within a relatively small geographical area in South Australia within the Great Australian Bight ecosystem, which has global conservation significance and supports valuable fishing, aquaculture and tourism industries (Rogers et al. 2013). One of the primary colonies is located at Cape Gantheaume, Kangaroo Island, South Australia (Fig. 1). This colony is unique because it is within close proximity to the Bonney Upwelling, the largest seasonal coastal upwelling in southern Australia (Butler et al. 2002). The

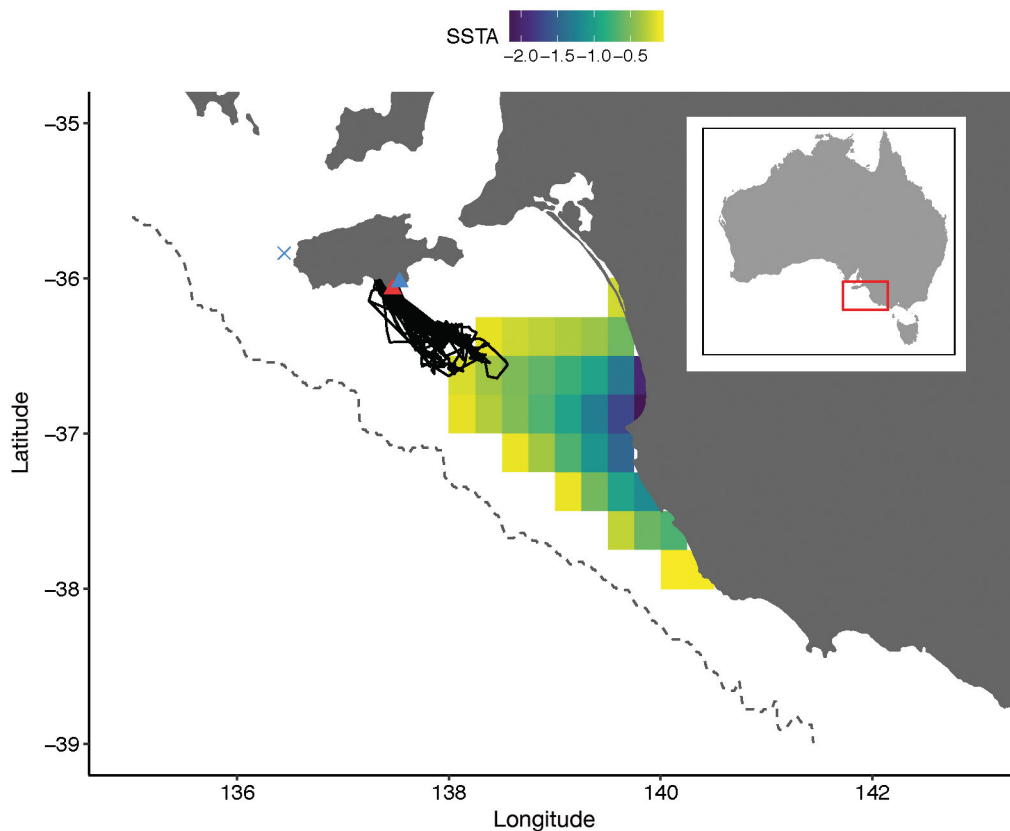


Fig. 1. Study region. The coloured squares represent the mean area of the Bonney Upwelling plume from January–April 2016 as represented by anomalously cool sea surface temperature (sea surface temperature anomaly, SSTA $\leq -1^{\circ}\text{C}$). The red triangle represents the long-nosed fur seal *Arctocephalus forsteri* colony at Cape Gantheaume, Kangaroo Island, South Australia. The blue triangle represents the Australian sea lion *Neophoca cinerea* colony at Seal Slide, from which a male sea lion was tagged with satellite-linked CTD tags as part of the Integrated Marine Observing System (IMOS). The black solid lines represent the tracks of the tagged sea lion from February to July 2016, showing that it only foraged on the shelf from summer to winter. The blue 'X' represents the Kangaroo Island National Reference Station mooring, which is also part of the IMOS. Dashed lines represent the 2000 m isobath which separates shelf from pelagic waters

Bonney Upwelling is mainly driven by alongshore winds (south-easterly) where the upwelling and non-upwelling season occurs from November to April (austral summer to autumn) and from May to October (austral autumn to early spring), respectively (Nieblas et al. 2009). During the upwelling season, the Bonney Upwelling plume is visible from anomalously low sea surface temperature (SST) and anomalously high sea surface chlorophyll *a* (chl *a*) (Nieblas et al. 2009). During the non-upwelling season, downwelling-favourable winds (north-westerly) are stronger; however, upwelling events may still occur, although they are significantly shorter than during the upwelling period. Another important habitat for LNFS in this region is the subtropical front (STF). The STF is a strong biogeographical boundary that separates warm subtropical waters to the north of the STF from relatively cool subantarctic waters to the south (Pakhomov et al. 1994). It is usually found between 39 and 42°S in the study region and can be identified as the 14 and 12°C isotherm at the sea surface in summer and winter, respectively (Tomczak et al. 2004). The STF is also characterised by relatively high chl *a* concentrations, low SST and high biomass of myctophid fish (Pakhomov et al. 1994). Consequently, it is an important foraging habitat for several top marine predators (Georges et al. 2000, Bost et al. 2009, Rogers et al. 2015).

In some years, lactating LNFS in South Australia may employ multiple foraging strategies (Baylis et al. 2008a). During the upwelling season, individuals predominantly make short foraging trips (~5 d) to shelf and shelf break waters, associated with the Bonney Upwelling region. During the non-upwelling season, they make longer trips (~2 wk) to oceanic waters associated with the STF (Baylis et al. 2008a) until the weaning of their pups at about 9–10 mo of age (Goldsworthy 2006). It is unclear if the switch from shelf (short) to oceanic (long) foraging is driven by changes in the environment, and/or intrinsic factors such as offspring energetic demands, and age, size and experience of adults.

According to the marginal value theorem, predators foraging in a patchy environment will tend to maximise energy gain by leaving a patch once the instantaneous rate of energy intake falls to a threshold that is equal to the overall energy intake rate for the environment (Charnov 1976). Hence, longer foraging trips may result from reduced local prey availability, i.e. changes in prey availability on the shelf. In addition, if the change in foraging habitat were solely driven by environmental changes, we would expect little variability in the timing of the switch between individuals. Conversely, high variability in

the timing of the switch between individuals would suggest that other intrinsic factors might contribute to the decision to switch foraging habitats. Factors such as age/size and/or experience of reproductive success may be important during periods of poor foraging conditions (Lea et al. 2006).

Pinniped tracking studies are often cross-sectional (different individuals in each season) due to the limitations of battery life, high cost, difficulty of devices staying on the fur during moulting, and the ability to relocate and re-instrument specific individuals in consecutive periods, which is more feasible in some species as compared to others. Consequently, only a few studies have examined longitudinal at-sea behaviour (Lowther et al. 2014). However, following individuals through lactation allows us to understand dynamics of provisioning strategies across seasonal changes (i.e. how individuals cope under resource pressure during a critical period where their own survival and that of their offspring is at stake; Biuw et al. 2009, Péron et al. 2010). Geolocation (Global Location Sensor, GLS) tags record ambient light levels which can be used to derive coarse-scale locations. They are small, light, relatively inexpensive, and can be attached to the seal's fore-flipper so that they can be deployed in summer/early-autumn while LNFS are moulting. Several long-term tracking studies have used GLS tags to track specific individuals over multiple foraging trips and even years (Cleeland et al. 2014, Arthur et al. 2015). Previous tracking studies on LNFS at Kangaroo Island were done cross-sectionally, thereby making it impossible to examine the individual variability in the timing of transition between shelf and oceanic foraging.

In this study, we aimed to investigate if the transition from shelf to oceanic foraging is driven by oceanographic changes on the shelf associated with the cessation of summertime upwelling. Specifically, we aimed to investigate (1) what changes in shelf oceanographic conditions are associated with shelf and off-shelf (oceanic) foraging trips; (2) the inter-individual variability in the timing of transition; and (3) inter-annual differences in foraging strategies in relation to the strength of summertime upwelling.

2. MATERIALS AND METHODS

2.1. Study site, animal handling and instrumentation

The study was undertaken between January 2016 and September 2017 at Cape Gantheaume (36°04'S, 137°27'E), Kangaroo Island, South Australia. On

average, female LNFS give birth to pups in December and wean them around October (Goldsworthy 2006). For this study, we considered austral summer, autumn, winter and spring months to be from Dec–Feb, Mar–May, Jun–Aug and Sep–Nov, respectively. In January–February (early lactation), 45 lactating LNFS were randomly selected and captured using a hoop-net (see Table 2). Seals were anaesthetised using Isoflurane (Veterinary Companies of Australia), administered via a portable gas anaesthetic machine (Stinger™, Advanced Anaesthesia Specialists). The seals were weighed (± 0.5 kg) and their body length (nose to tail) and axial girth were measured (± 1 cm). Geolocation loggers (GLS, Intigeo-C330, $17 \times 19 \times 8$ mm, 3.3 g, Migrate Technology) were deployed on all 45 female seals. The GLS loggers were attached to the flipper tag as described by Arthur et al. (2015). The loggers were recovered between June and September (late lactation; see Table 2). For recaptures, some seals were first captured via a hoop-net and then immobilised with Zoletil (dose 2 mg kg^{-1} ; Virbac), administered by a hand injection to the rump. For other recaptures, seals were first immobilised with Zoletil, administered using 1 ml, 1.5×30 mm (diameter \times length) barbless darts (Telinject), fired from a CO₂-powered tranquilizer gun (G.U.T.50, Telinject). The lightly sedated females were then captured with a hoop-net and manually restrained.

In both study years, the GLS loggers measured ambient light every minute and recorded the maximum value every 5 min. They also recorded the time when an activity (wet or dry) state change occurred and temperature (0.125°C resolution, $\pm 0.5^\circ\text{C}$ accuracy). The 2016 loggers recorded the minimum, maximum and mean temperature for every 4 h period. The 2017 loggers sampled sea temperature after 20 min of being continuously wet and recorded the minimum, maximum and mean temperature for every 4 h period. Each logger was activated and left in an open area at the study site for approximately 5–7 d either immediately before or after deployment to obtain solar elevation estimates necessary for instrument calibration.

2.2. Pup cross-sectional weighing

In both years, pups from the same area were randomly selected and weighed using an electronic spring balance (± 0.5 kg, Kern) in summer (2016: males = 51, females = 59; 2017: males = 58, females = 52) and winter (males $n = 30$, females $n = 30$ each for 2016 and 2017). Pups weighed in summer were part

of an ongoing annual pup census conducted by the South Australia Research and Development Institute (Shaughnessy et al. 2015). Summer weighing occurred on 26 January for both years, while winter weighing occurred on 8 September 2016 and 4 August 2017.

2.3. Location estimation

All analyses were done using the R program (v.3.5.1) (R Core Team 2017). Locations were estimated from the raw light data by first using the 'BAStag' package (v.0.1-3) (Wotherspoon et al. 2016a) to estimate times of twilight (dawn and dusk). Next, the 'SGAT' package (v.0.1.3) (Wotherspoon et al. 2016b) was used to create Markov chain Monte Carlo simulations within a Bayesian framework to estimate the final posterior mean of 2 primary locations per day while incorporating temperature and land-mask constraints (Sumner et al. 2009, Lisovski et al. 2012). Additionally, seals were assumed to be back at the colony when the GLS logger was continuously dry for ≥ 4 h, which usually corresponded with noisy light curves due to the animal periodically shading the light sensor on-shore (Arthur et al. 2015). We made this assumption because lactating LNFS are not known to haul-out at other locations during a foraging trip (Page et al. 2006, Baylis et al. 2012). Hence, locations were fixed to the colony during dry logger periods and validated with ad hoc observations of seal attendance at the colony when possible. Based on validation studies of lactating LNFS carrying both GLS and GPS dataloggers simultaneously ($n = 4$), the accuracy of location estimates using this method is 45 ± 29 km (see Supplement 2 at www.int-res.com/articles/suppl/m615p189_supp.pdf for 'SGAT' validation). The durations of foraging trips were thus determined as the wet period between dry periods inferred from the GLS data.

2.4. Timing of change in foraging location

Foraging trips were classified as either shelf (includes shelf break out to the 2000 m isobath) or oceanic (waters > 2000 m in depth) depending on the most distant point. Based on preliminary analyses of the data, the switch from predominantly shelf to oceanic foraging (hereafter referred to as switch trip) typically coincided with an abrupt change in trip length and maximum distance travelled from the colony relative to the previous trip. Subsequent trips

Table 1. Environmental variables used for analyses. All variables except MLD, SST_c, and wind velocity were used in the generalised linear mixed model. The sources, frequency and spatial resolution of the variables are also shown. IMOS: Integrated Marine Observing System; ESRL: Earth System Research Laboratory; PSD: Physical Sciences Division; SD: standard deviation. The SD column shows if SD was calculated for the variable and used in analyses. See Table S1 in Supplement 1 for more details of the sources

| Variable; abbreviation | Unit | Source | Frequency | Spatial resolution | SD? |
|--|--------------------|--|-----------|--------------------|-----|
| Sea surface temperature anomaly; SSTA ^a | °C | NOAA Optimum Interpolation daily Sea Surface Temperature Anomaly | Daily | 0.25° | Yes |
| Sea surface height anomaly; SSHA ^a | m | IMOS Optimal Interpolated daily Gridded Sea Level Anomaly | Daily | 0.2° | Yes |
| Anomalous cold SST; SST _c | °C | Subset from daily SSTA ≤ −1°C | Daily | 0.25° | |
| Subsurface temperature (uppermost 70 m) | °C | IMOS Animal Tracking Facility | Irregular | | Yes |
| Mixed layer depth; MLD | m | IMOS Animal Tracking Facility | Irregular | | |
| Subsurface salinity (uppermost 70 m) | g kg ^{−1} | IMOS Animal Tracking Facility | Irregular | | Yes |
| Southern Annular Mode; SAM | | NOAA daily Antarctic Oscillation index | Daily | | |
| Wind velocity | cm s ^{−1} | NOAA ESRL PSD | 6 hourly | 1.88 × 1.9° | |
| Alongshore wind stress ^b | N m ^{−2} | Derived from wind velocity | Daily | 1.88 × 1.9° | Yes |
| Highly collinear pairs: Subsurface temperature SD and subsurface salinity SD Subsurface salinity SD and mean SSHA SSHA SD and mean SSHA | | | | | |
| ^a Data were summarised into a single value for the shelf region (37.5° S – shelf boundary, 137–141° E) | | | | | |
| ^b For a single cell grid at 39° S, 140.5° E | | | | | |

after the abrupt change were also to oceanic waters of similar distances for all but 1 individual (see Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m615p189_supp.pdf). Hence, the trip that marked the switch was the trip that had the greatest difference in maximum distance from the previous shelf or near-shelf break trip.

2.5. Foraging habitat in relation to environmental variability on the shelf

Details of environmental data used for analyses are described in Table 1 and Table S1 in Supplement 1. Daily SST anomaly (SSTA), and sea surface height anomaly (SSHA) were extracted for each cell in the shelf foraging area (37.5° S – shelf boundary, 137–141° E). Proxies for upwelling activity are anomalously cool SST (i.e. negative SSTA) and negative SSHA which are more prevalent during the upwelling season. The opposite is true for the non-upwelling season where downwelling activity is more prevalent. Mean and standard deviation were then calculated for each parameter to create a single daily value for the entire shelf region (Table 1). Daily alongshore wind stress at a cell off the Bonney Coast (39° S, 140.5° E) was calculated from 6 h NCEP

Reanalysis wind data at 10 m height (Kalnay et al. 1996) for the study period. Alongshore wind stress τ'_v (units: N m^{−2}) was calculated as:

$$\tau'_v = \rho_a C_d W^2 \cos(\alpha - \beta) \quad (1)$$

where W is wind speed, C_d is the drag coefficient (1.2×10^{-3}), ρ_a is air density (1.22 kg m^{-3}), α is wind direction, and β is the dominant angle of the Bonney coast line (315°). Positive values of (τ'_v) indicate favourable upwelling conditions.

We monitored subsurface oceanographic changes on the shelf by using CTD data collected from satellite-linked CTD tags deployed on Australian sea lions *Neophoca cinerea* (ASL) from a nearby colony that forage on the same shelf as the LNFS year-round and a national reference station mooring located on the western end of Kangaroo Island (Table 1, Fig. 1). ASL are benthic foragers, which means that they are able to sample the entire shelf water column. Both CTD datasets are part of the Integrated Marine Observing System (IMOS), a national collaborative research infrastructure, supported by the Australian government. Subsurface temperature and salinity data obtained from ASL CTDs were used to calculate mixed layer depth (MLD) using the ‘oce’ package (v.1.0-1) (Kelly 2018) following methods detailed by Lowther et al. (2013). We were not able to accurately

calculate MLD using the mooring data, as subsurface temperature and salinity were only collected at around 40, 70 and 90 m depths. The ASL CTD data were collected at irregular time intervals and did not cover the entire study period for both years; hence daily mean and standard deviation of salinity, temperature and MLD were calculated and then interpolated to fill the date range of the dataset (Table 1). The remainder of the study period that did not have ASL CTD data was supplemented by the mooring CTD dataset for only salinity and temperature that was collected up to a depth closest to the maximum depth ASL dived to (up to 70 m in depth; Table 1).

The daily Southern Annular Mode (SAM) index was also used in the analyses (Table 1). The SAM is a large-scale climate variability index, which affects physical wind forcing in the Southern Ocean and is the most important mode at high latitudes. It describes the north–south position and intensity of westerly winds where a positive (negative) phase means that the belt of strong westerly winds contract towards (away from) higher latitudes. A positive SAM is associated with anomalously warm SST and increased stratification, leading to reduced macro-nutrient supply, and thus a decrease in chlorophyll concentration in the subtropical zone (55–50°S) (Lovenduski & Gruber 2005).

The 5 d running mean of SSTA, SSHa, subsurface temperature and subsurface salinity variables and 5 d running mean and standard deviation for wind stress were calculated and extracted for the corresponding start date of foraging trips. The running period was chosen based on the mean duration of shelf foraging trips (Baylis et al. 2008a) and to account for the environmental variability on the shelf. We used the start date of foraging trips for 2 reasons: (1) individuals only experience the shelf environmental conditions during the initial part of their outbound trip for both shelf and oceanic foraging trips and (2) there may be a lag in biological response (i.e. prey availability) to upwelling-favourable physical processes (McClatchie et al. 2006). Foraging trips that occurred outside of the date range of the combined ASL and mooring CTD dataset were excluded to avoid extrapolation.

2.6. Inter-annual variability in shelf and oceanic environmental conditions

We compared inter-annual variability in shelf and oceanic conditions during the upwelling and non-upwelling season. While the upwelling season

begins in November, for simplicity, we considered the upwelling season as January–April and the non-upwelling season as May–October. We extracted SSTA for the oceanic region (37.5–44°S, 131–141°E) using the same methods as described above. An upwelling event was defined as one or more consecutive days of positive alongshore wind stress. Unusually cold water, defined as $SSTA \leq -1^{\circ}\text{C}$ (SST_c) was used to represent the physical effect of upwelling-favourable conditions (Nieblas et al. 2009) and a proxy for productive areas (Lea et al. 2006). The spatial extent of productive areas was defined as the sum of SST_c cells ($0.25 \times 0.25^{\circ}$), and the daily intensity of SST_c for the shelf and oceanic regions was calculated from averaging across each of the respective regions.

2.7. Statistics

Logistic generalised linear mixed models (GLMMs) with a binomial error structure and logit-link function were used to fit the response variable, type of foraging habitat at the most distal location of a foraging trip (shelf = 1; not shelf, i.e. oceanic = 0), to various shelf environmental predictor variables (Table 1) using the 'glmer' function from the 'lme4' package (v.1.1-19) (Bates et al. 2015). Seal identity was included as a random effect. Prior to model building, collinearity among predictor variables was examined using variance inflation factors (Zuur et al. 2009). If there was high collinearity between 2 variables, the more biologically relevant variable was kept while the other was removed. The remaining predictor variables were centered and scaled. Due to convergence issues and the relatively high number of predictor variables, the full model was fitted without interaction terms. The final model was determined using Akaike's information criterion corrected for small sample sizes (AICc) and their weights of evidence (Burnham & Anderson 2004). The highest ranked model had the lowest AICc. Where the delta AICc between 2 models was <2 , the more parsimonious model was selected. Two-way interaction terms of the variables included in the highest ranked model were then included and the models were re-ranked again. The residuals of the final model were used to test for homogeneity and autocorrelation using the 'DHARMa' package (v.0.2.0) (Hartig 2018) and the 'acf' function. Due to small sample sizes, a non-parametric 2-sample Wilcoxon test was used to compare the means of 2 groups.

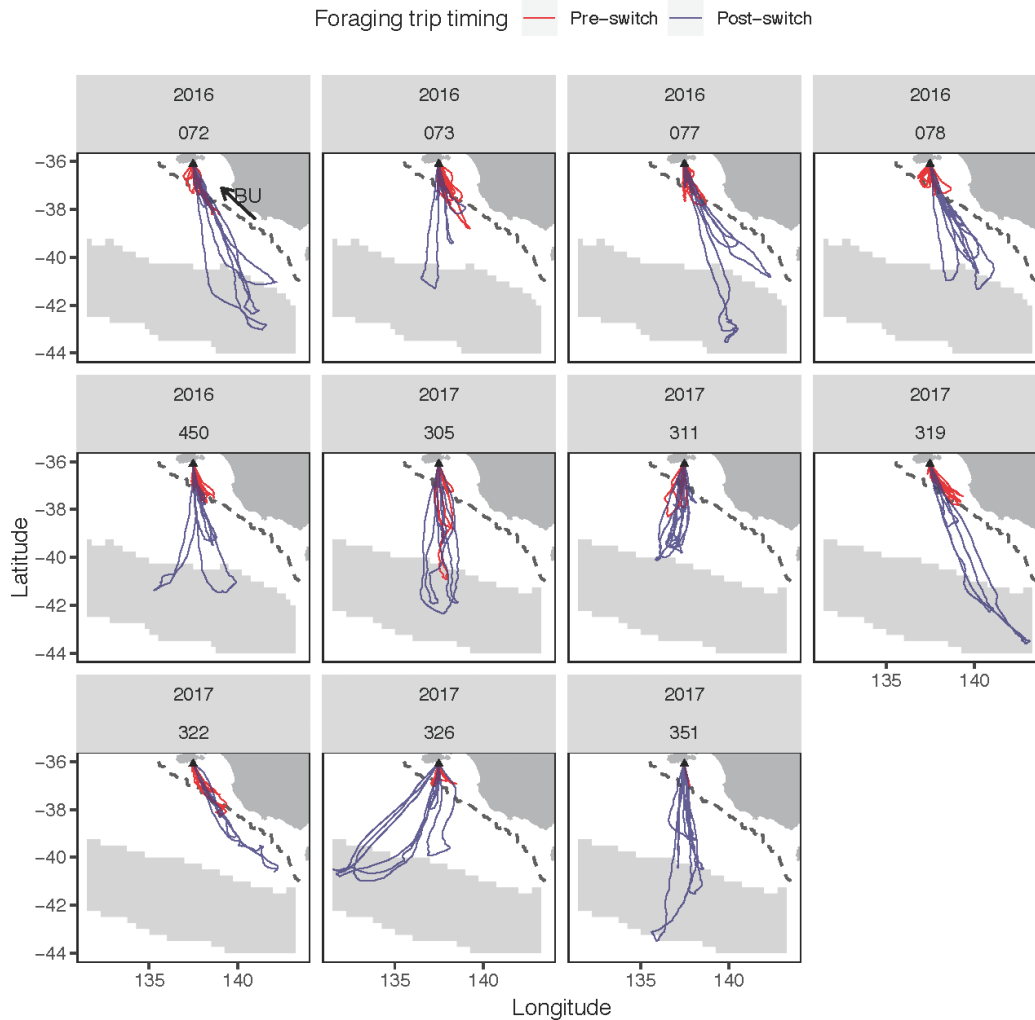


Fig. 2. Individual tracks of long-nosed fur seals provisioning pups, showing both shelf and oceanic foraging behaviour. The dashed grey line represents the shelf break (2000 m isobath). The black arrow represents the direction from where the Bonney Upwelling (BU) plume originates and flows during the upwelling season (austral summer to early autumn). Coloured tracks depict whether the foraging trip was made pre- or post-switching from predominant shelf to oceanic foraging. The shaded light-grey area represents the approximate location of the subtropical front for the entire year (annual mean sea surface temperature between 12 and 14°C)

3. RESULTS

3.1. Location statistics and track summaries

We recovered GLS loggers from 17 adult female LNFS allowing us to quantify their at-sea behaviour during lactation (Fig. 2). Unrecovered loggers were either due to them falling off individuals, time constraints in the field where individuals did not return back to the colony before the team had to leave, or possible abandonment of their pup. Based on visualisations of the tracks, seals that did not show central-place foraging behaviour (i.e. due to abandoning their pup or their pup had died; $n = 4$) or did not exhibit a switch in foraging strategies (i.e. either only foraged

on the shelf or oceanic waters; $n = 2$) were excluded from the subsequent analyses. Non-central place foraging individuals had only a few foraging trips (1–3) for the entire deployment period, and all of them made very long trips towards the southwest of Tasmania that were further than previously recorded and expected (Fig. S2 in Supplement 1). From the remaining seals, 3984 location estimates were obtained which corresponded to 167 foraging trips. Out of those trips, 9 fell outside the date range of the combined CTD dataset and were removed. A detailed summary of the number foraging trips for each individual is given in Table 2. Henceforth, all means (\pm SD) and totals reported are for the remaining 11 individuals used for analyses.

Overall, mean foraging trip duration was lower during the upwelling (7.14 ± 0.52 d; range: 1.06–26.5 d) as compared to the non-upwelling (15 ± 1.02 d; range: 3.17–34.8 d; Wilcoxon test: $W = 1126.5$, $p < 0.001$) season. Foraging trip durations during both seasons were longer in 2017 than in 2016 (Table 3). For both years combined, the mean date that females switched from shelf to oceanic foraging was 22 April \pm 8.2 d (range 23 Feb–24 May; middle of lactation period); and on average the switch date was earlier in 2017 than in 2016 by 42 d (Table 3). The mass of adult females used

in this study did not differ between the 2 years. Cross-sectional summer pup mass was greater in 2016 than in 2017 (Table 3). However, the opposite was true for the winter pup mass (Table 3).

3.2. Foraging strategy in relation to shelf oceanographic properties

The timing of the switch from predominantly shelf to oceanic foraging was closely associated with the

Table 2. Details of the deployment of loggers on 11 lactating long-nosed fur seals from Cape Gantheaume, Kangaroo Island, in 2016 and 2017. The upwelling and non-upwelling periods spanned January–April and May–October, respectively. Columns to the right of deployment duration are seal data. ID: seal identification. The switch date is the date on which females switched from shelf to oceanic foraging. Dates are given as d/mo/yr. Where applicable, values are mean \pm SD

| ID | Deployment date | Recovery date | Deployment duration (d) | Mass (kg) | Length (cm) | No. of trips | | Total trips | Switch date |
|-----|-----------------|---------------|-------------------------|----------------|---------------|----------------|-----------------|----------------|------------------|
| | | | | | | Upwelling | Non-upwelling | | |
| 72 | 02/02/16 | 19/08/16 | 199 | 40.5 | 139 | 12 | 5 | 17 | 10/05/16 |
| 73 | 01/02/16 | 22/08/16 | 203 | 33.5 | 130 | 14 | 11 | 25 | 24/05/16 |
| 77 | 05/02/16 | 21/08/16 | 198 | 44 | 128 | 12 | 6 | 18 | 13/05/16 |
| 78 | 06/02/16 | 20/08/16 | 196 | 48.5 | 138 | 19 | 6 | 25 | 09/05/16 |
| 450 | 31/01/16 | 25/09/16 | 238 | 43.5 | 144 | 13 | 10 | 23 | 20/05/16 |
| 305 | 28/01/17 | 06/07/17 | 159 | 44 | 136 | 5 | 3 | 8 | 07/04/17 |
| 311 | 05/02/17 | 07/08/17 | 183 | 41 | 133 | 6 | 6 | 12 | 29/03/17 |
| 319 | 07/02/17 | 05/07/17 | 148 | 55 | 146 | 9 | 2 | 11 | 19/04/17 |
| 322 | 09/02/17 | 12/07/17 | 153 | 45 | 142 | 6 | 2 | 8 | 27/04/17 |
| 326 | 10/02/17 | 07/08/17 | 178 | 41 | 130 | 10 | 3 | 13 | 07/04/17 |
| 351 | 13/02/17 | 30/06/17 | 137 | 45 | 141 | 5 | 2 | 7 | 23/02/17 |
| | | | 181 ± 29.8 | 43.7 ± 5.3 | 137 ± 6.1 | 10.1 ± 4.4 | 5.09 ± 3.14 | 43.7 ± 6.8 | $22/04 \pm 27$ d |

Table 3. Comparisons of various parameters (means \pm SD) between 2016 and 2017. Upwelling and non-upwelling seasons are from January–April and May–October, respectively. The switch date is the date on which females switched from shelf to oceanic foraging. SST_c: anomalous cold sea surface temperature. Non-parametric Wilcoxon tests were used for statistical analyses. Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns: non-significant. NA: not applicable

| Variable | Sub-category | 2016 | | | 2017 | | | U | Sig-nificance |
|---|---------------|---------|---------|-------|---------|--------|------|----------|---------------|
| | | Mean | SD | n | Mean | SD | n | | |
| Switch date (d) | | 15 May | 6.53 | 5 | 3 Apr | 21.9 | 6 | 30 | ** |
| Trip duration (d) | Upwelling | 5.3 | 3.16989 | 70 | 10.3 | 6.99 | 41 | 812 | *** |
| | Non-upwelling | 13.3 | 7.48 | 38 | 18.4 | 6.85 | 18 | 195 | * |
| Adult female mass (kg) | | 42 | 5.55 | 5 | 45 | 5.15 | 6 | 9.5 | ns |
| Pup summer mass (kg) | | 6.9 | 1.41 | 110 | 6.55 | 1.46 | 110 | 7025 | * |
| Pup winter mass (kg) | | 11 | 2.11 | 60 | 12.6 | 2.25 | 60 | 1060 | *** |
| Alongshore wind stress (N m ⁻²) | Upwelling | 0.00924 | 0.0539 | 121 | 0.00262 | 0.0543 | 120 | 7886 | ns |
| | Non-upwelling | -0.0643 | 0.0836 | 184 | -0.0514 | 0.0661 | 184 | 15679 | ns |
| Sea surface height anomaly | Upwelling | -0.0118 | 0.0448 | 1815 | 0.0216 | 0.0398 | 1800 | 918760 | *** |
| | Non-upwelling | 0.0696 | 0.0696 | 2625 | 0.0578 | 0.0605 | 2760 | 3887600 | *** |
| Shelf SST _c | Upwelling | -1.74 | 0.571 | 186 | -1.22 | 0.184 | 23 | 840.5 | *** |
| | Non-upwelling | -1.23 | 0.200 | 121 | -1.02 | NA | 1 | 9.5 | ns |
| Oceanic SST _c | Upwelling | -1.35 | 0.377 | 199 | -1.21 | 0.208 | 3119 | 260350 | *** |
| | Non-upwelling | -1.22 | 0.189 | 20066 | -1.19 | 0.171 | 8402 | 79056000 | *** |
| Upwelling events | Upwelling | 13 | | | 14 | | | | |
| | Non-upwelling | 20 | | | 18 | | | | |
| Shelf area of SST _c | Upwelling | 186 | | | 23 | | | | |
| | Non-upwelling | 121 | | | 1 | | | | |
| Oceanic area of SST _c | Up-welling | 199 | | | 3119 | | | | |
| | Non-upwelling | 20066 | | | 8402 | | | | |

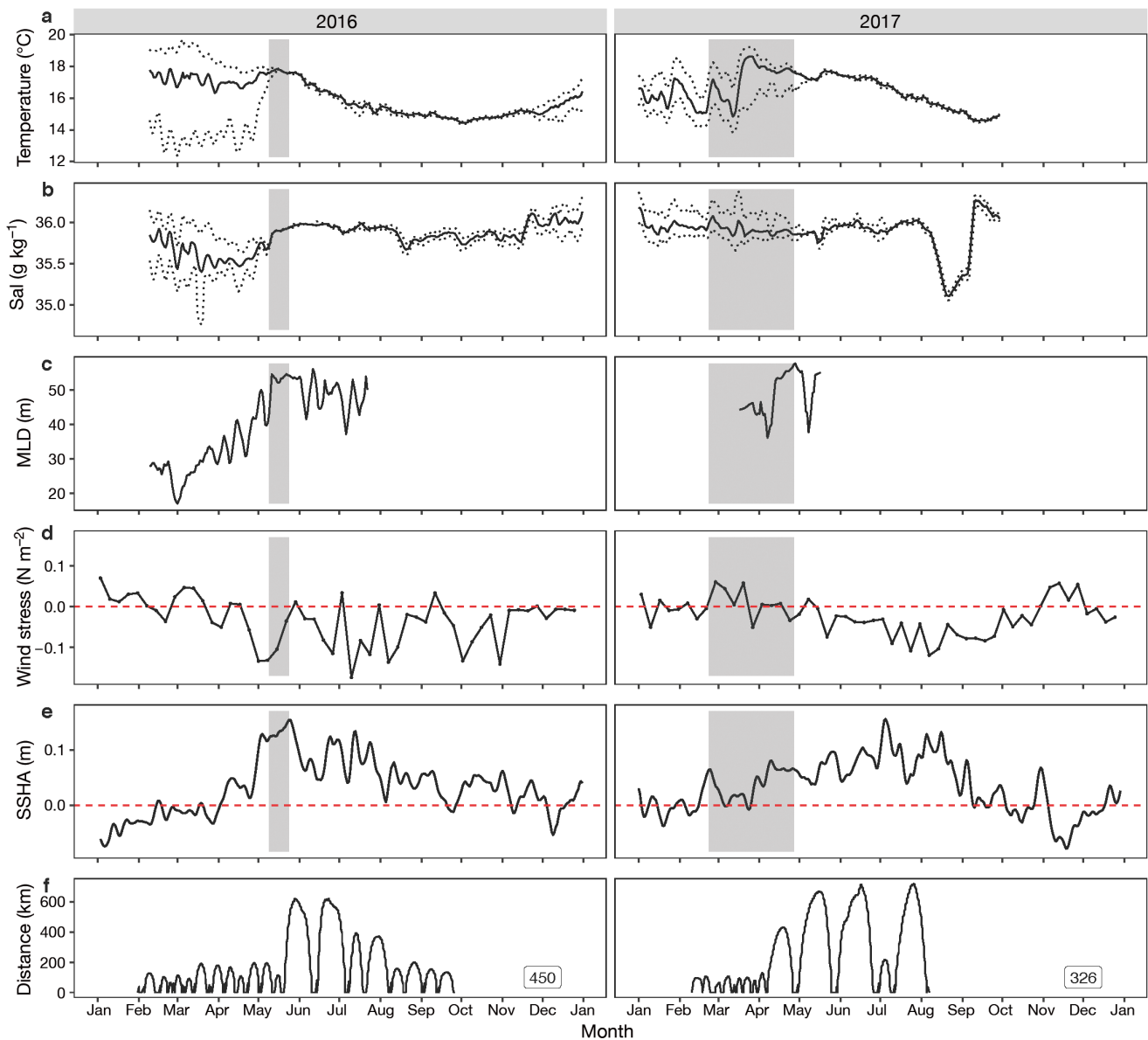


Fig. 3. Inter-annual comparison of shelf (a) 5 d running average of daily maximum, mean and minimum subsurface (up to 70 m in depth) temperature and (b) salinity (Sal); (c) shelf mixed layer depth (MLD) also obtained from the CTD tags deployed on Australian sea lions; (d) average weekly alongshore wind stress (positive wind stress is easterly and upwelling-favourable); (e) 5 d running average of sea surface height anomaly (SSHA); and (f) examples of the straight line distance travelled from the colony from 2 long-nosed fur seal (LNFS) tracks (labels represent the seals' ID). Subsurface temperature and salinity data were obtained from an Australian sea lion carrying a CTD and foraging on the same shelf as LNFS, hence the length of data is different between years. Subsurface temperature and salinity data were a combination of data obtained from a mooring station situated near Kangaroo Island (Fig. 1) and CTD tags deployed on Australian sea lions from a nearby colony. A larger temperature range in the water column is an indicator of stratification and hence upwelling-favourable conditions. The grey shaded strip represents the range of dates that lactating LNFS switched from primarily shelf to oceanic foraging. The dashed red line corresponds to the 0 value

cessation of upwelling activity on the shelf (Fig. 3). This included reduced vertical stratification in the water column as seen in subsurface temperature and salinity, an increase in the MLD and SSHA, and increased prevalence of downwelling-favourable along-

shore wind stress (Fig. 3). Variables removed as a result of high collinearity between other variables are the standard deviations of subsurface temperature, salinity and SSHA (Table 1). The most important predictors for the probability of foraging on the shelf (vs.

Table 4. Summary of logistic generalised linear mixed-effects model (GLMM) comparisons of on-shelf vs. off-shelf (i.e. oceanic) foraging trips in relation to shelf environmental covariates, including seal identity (id) as a random effect. sal: subsurface (up to 70 m in depth) salinity; SSHA: sea surface height anomaly; wind: alongshore wind stress. Only the top 3 models are presented, and the accepted model is highlighted in **bold**. For the full list of candidate models, see Table S2 in Supplement 1. logLik: log-likelihood; AICc: Akaike's information criterion corrected for small sample size; dLogLik: difference in log-likelihood; dAICc: difference in AICc from that of the best fitting model; weight: AICc weight

| Candidate models | logLik | AICc | dLogLik | dAICc | df | weight |
|---|--------------|------------|-------------|----------------|----------|----------|
| sal_mean + SSHA_mean + sal_mean:SSHA_mean + (1 id) | -82.3 | 175 | 25.5 | 0.00000 | 5 | 1 |
| sal_mean + SSHA_mean + (1 id) | -92.1 | 192 | 15.7 | 17.4 | 4 | 0 |
| sal_mean + SSHA_mean + wind_mean + (1 id) | -91.5 | 193 | 16.2 | 18.5 | 5 | 0 |

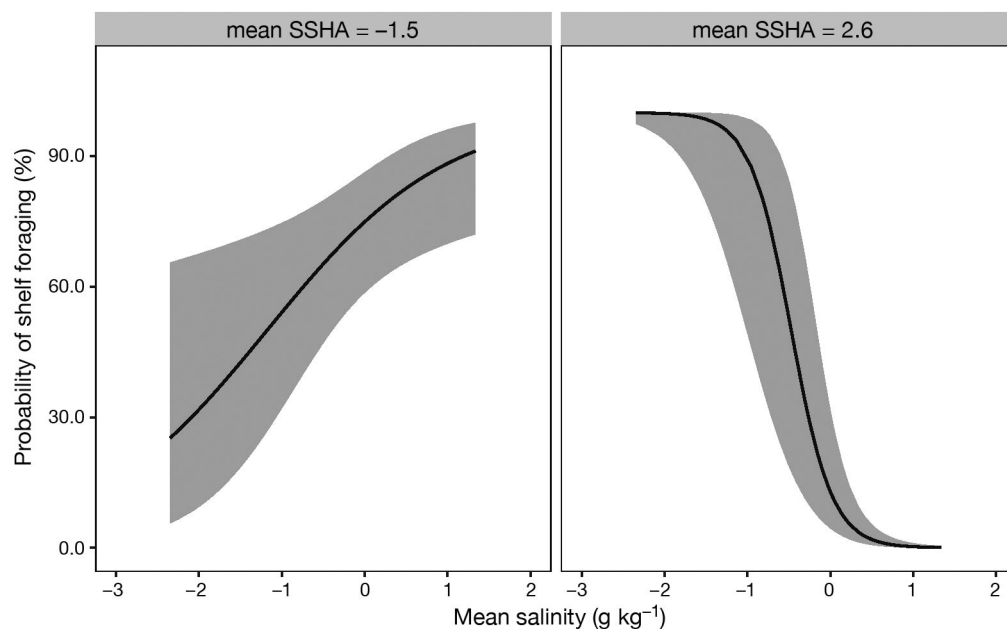


Fig. 4. Probability of foraging on the shelf (as opposed to oceanic waters) in relation to the interaction between mean shelf sea surface height anomaly (SSHA) and shelf salinity. Curves were fitted using the final logistic generalised linear mixed model as shown in Table 4. The shaded area represents the 95 % confidence intervals around the estimated effect

off-shelf) included the interaction term between mean SSHA and mean salinity (Table 4, Fig. 4). A detailed summary of the most parsimonious model is given in Table 5. When the mean shelf SSHA was strongly negative (in the lower boundaries, i.e. upwelling season), the probability of shelf foraging increased with higher shelf salinity; when the mean shelf SSHA was strongly positive (in the upper boundaries, i.e. non-upwelling season), the probability of shelf foraging increased with lower shelf salinity. From the model results, we wanted to find out the relation between shelf salinity and MLD in upwelling and non-upwelling seasons. Hence, we fitted a generalised additive model ('mcgv' package v.1.8-23) with MLD as a response and the smoothed interaction term between shelf salinity and season (upwelling or non-upwelling) and

the season term as predictors (Table 6). Results of the generalised additive model showed that MLD generally increased with shelf salinity; however, the effect was greater during the non-upwelling season (Fig. 5).

3.3. Inter-annual variability in shelf and oceanic oceanography between seasons

Table 3 contains details on the number of upwelling events on the shelf that occurred for each year. For the shelf region, there were no differences in the strength of alongshore wind stress during the upwelling and non-upwelling season between years. There was no difference in SST_c between years only during the non-upwelling season. The intensity and

Table 5. Results of the final logistic generalised linear mixed-effect model (GLMM) examining the effects of shelf oceanographic parameters on shelf (vs. off-shelf) foraging trips made by female long-nosed fur seals provisioning offspring. Model selection was done using delta AICc. sal_mean: mean shelf subsurface salinity; SSHA_mean: mean shelf sea surface height anomaly. Number of foraging trips (N_{trips}) = 158; Number of individual seals (N_{seals}) = 11

| Parameter | Variance | Estimate | SE | Lower 95 % CI | Upper 95 % CI |
|--------------------|----------|----------|-------|---------------|---------------|
| <i>Fixed</i> | | | | | |
| Intercept | | -0.019 | 0.203 | -0.416 | 0.378 |
| sal_mean | | -0.911 | 0.228 | -1.360 | -0.464 |
| SSHA_mean | | -0.736 | 0.243 | -1.210 | -0.260 |
| sal_mean:SSHA_mean | | -1.220 | 0.297 | -1.800 | -0.636 |
| <i>Random</i> | | | | | |
| Seal ID | 0.083 | | | | |

area of shelf SST_c was greater in 2016 during both seasons (Table 3). Conversely, the area oceanic SST_c during the upwelling season was much smaller in 2016, although its intensity was greater.

4. DISCUSSION

Longitudinal studies of foraging behaviour are relatively rare due to logistical and financial limitations. As a result, cross-sectional sampling is usually done in studies investigating aspects of foraging strategies; different individuals are sampled across seasons, generally for one or more foraging trips. Additionally, sample sizes for each cross-sectional period are generally small, making it difficult to extrapolate to the population level. Thus, the combined effect of these factors limits our interpretation of how and why foraging strategies change seasonally, as we cannot be entirely certain

that any change in foraging behaviour observed in individuals in different seasons is an accurate representation of the long-term foraging strategy across all individuals in the population.

Table 6. Summary of the generalised additive model examining the effects of shelf salinity on mixed layer depth in different seasons (upwelling vs. non-upwelling). Significance: **p < 0.01; ***p < 0.001

| Smoothed terms | edf | F | Significance | Parametric terms | Estimate | SE | T | Significance |
|---|-----|------|--------------|------------------|----------|------|-------|--------------|
| s(salinity):season non-upwelling | 1 | 81.1 | *** | season | -15 | 1.27 | -11.8 | *** |
| s(salinity):season upwelling | 1 | 7.07 | ** | | | | | |
| Fitted formula: mixed layer depth ~ s(salinity, by = season) + season | | | | | | | | |

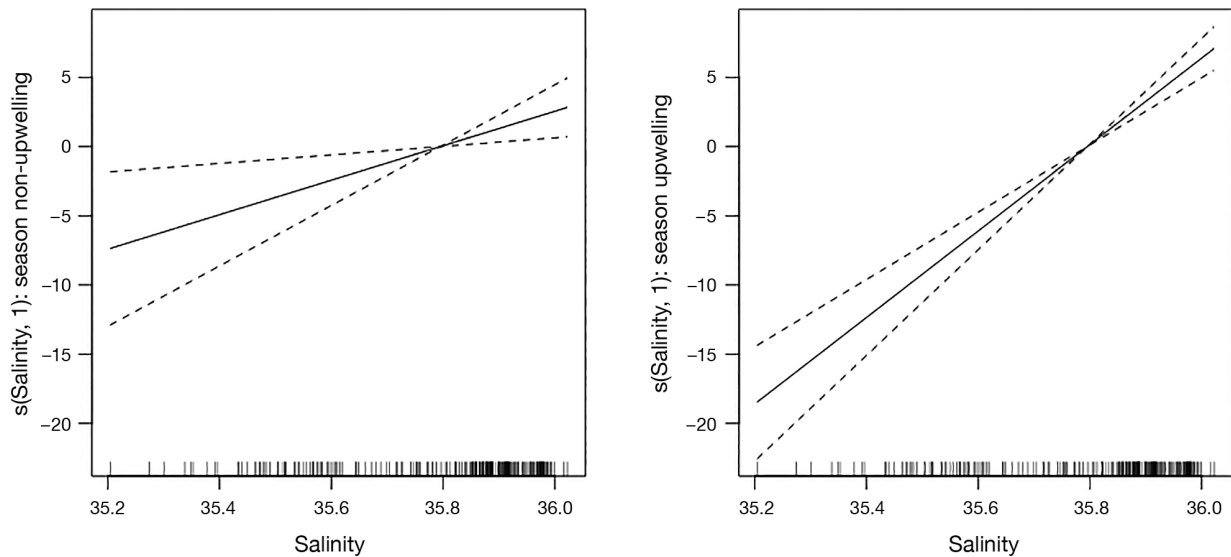


Fig. 5. Partial residual plots of the smoothed term mean shelf salinity (g kg^{-1} ; in the uppermost 70 m of the water column; x-axis) on the mean shelf mixed layer depth (y-axis) from a fitted generalised additive model. The solid line represents the fitted effect and the dashed lines are the confidence intervals. Rugplots represent the distribution of the raw data

Our results show that lactating LNFS generally switched from shelf to oceanic foraging as the pup-rearing period progressed, supporting cross-sectional evidence from previous studies (Baylis et al. 2008a). This shift is fairly abrupt rather than gradual, resulting in a bimodal pattern of trip duration and distance from the colony. While we did not model the timing of the switch in foraging strategy per se (as this would have reduced our sample size to the number of switch trips; $n = 11$), changes in subsurface salinity within 70 m of the water column and SSHA on the shelf were the strongest predictors of whether an individual foraged in shelf or oceanic waters for a given trip. The changes in these shelf properties driving the switch were associated with the weakening of the Bonney Upwelling on the shelf. Between years, the inter-individual variability of the timing of the switch depended on the strength of the local shelf upwelling.

4.1. Seasonal variation in foraging strategies

The timing of the switch from shelf to oceanic foraging strategies in lactating LNFS was driven by oceanographic changes. For both years, the earliest date for switching from shelf to oceanic foraging occurred shortly after a positive spike in mean shelf SSHA (Fig. 3). This is likely a signal for the cessation of upwelling-favourable conditions, and thus decline in shelf productivity (Nieblas et al. 2009) (and associated decline in prey availability), which prompts females to travel to more distant oceanic waters to forage. As the quality and quantity of food in the environment changes in time and space, females have to change their foraging behaviour accordingly to meet the energetic demands of self-maintenance and feeding a growing pup. According to the marginal value theorem, it makes sense for females to switch to more profitable foraging habitats if prey availability declines on the shelf and they are unable to fulfil their nutritional needs, especially later in the breeding season when pups require more food (Charnov 1976).

The probability of making a shelf foraging trip was influenced by shelf salinity, which was conditional on the degree of upwelling (as indicated by SSHA). When upwelling-favourable conditions were prevalent (i.e. low SSHA), females were more likely to forage on the shelf when shelf salinity was high. In general, high net productivity and phytoplankton blooms occur when the MLD is above the lower extent of the photic zone (Sverdrup 1953), as phytoplankton re-

quire both nutrients and light for growth. When upwelling occurs, deep cold and salty waters are upwelled to the surface (Middleton & Bye 2007), thus replenishing nutrients in the surface layer while the MLD remains relatively shallow. Consequently, this leads to enhanced primary production and thus a high-quality foraging area. High-salinity shelf waters were found to be one of the most profitable foraging habitats for southern elephant seals *Mirounga leonina* (Costa et al. 2010). Access to nearby high-quality foraging locations often leads to greater reproductive success. This is seen in cross-colony studies where a chinstrap penguin colony with access to productive local resources did better reproductively than an Adélie penguin colony which foraged much farther away (Lynnes et al. 2002). Since the upwelling season on the shelf coincides with the early stage of lactation, it is not surprising that seals would forage on the shelf during upwelling-favourable conditions.

Conversely, when downwelling-favourable conditions were prevalent, females were more likely to forage on the shelf when shelf salinity was low. Seals may also forage on the shelf in winter in between oceanic foraging trips. In winter, surface cooling in combination with downwelling-favourable winds lead to very deep surface mixed layers (up to 200 m in depth) associated with cold (dense) and salty waters (Middleton & Bye 2007). While deep vertical mixing during downwelling may replenish depleted surface nutrient levels, unlike in the upwelling scenario, due to deeper MLDs, phytoplankton are pushed further away from the photic zone, thus potentially resulting in diminished surface phytoplankton concentrations (van Ruth et al. 2010). For primary production to occur, there needs to be local phytoplankton concentrations in the euphotic zone (uppermost 80 m of the water column that has sufficient light for photosynthesis) to use nutrients for phytoplankton growth (Gaube et al. 2013). Indeed, a decline in shelf salinity in the uppermost 50 m of the water column during the non-upwelling season is associated with a shallower MLD which in theory is better for primary production in this context. A possible explanation may be that the weakening of downwelling-favourable winds leads to a reduction in deep vertical mixing (and hence shallower MLD), allowing phytoplankton to remain and use nutrients in the euphotic layer. The result of primary production is a decline in salinity in the upper layer of the water column. Alternatively, a reduction in salinity in the upper layer of the water column (for reasons we are not sure of) may counter deep vertical mixing caused by downwelling-favourable winds, thus leading to a

shallower MLD. Whether the decrease in salinity is a cause or effect of a shallower MLD is unclear.

4.2. Variability in timing of the switch

The timing of the switch from shelf to oceanic foraging was more variable in 2017 than in 2016. There was a clear environmental signal in 2016 that could possibly indicate a decline in prey availability on the shelf, while no such clear signal was present in 2017. The clear environmental signal in 2016 consisted of a breakdown in vertical temperature stratification, substantial decline in upwelling-favourable wind and dramatic increase in mean SSHA on the shelf (Fig. 3); there was no similar environmental signal in 2017. Based on shelf SST_c and SSHA, the strength of upwelling-favourable conditions was greater in 2016 than in 2017. Furthermore, the prevalence of upwelling-favourable conditions appeared later in the upwelling season in 2017, suggesting that these 2 years represent a marked contrast in environmental conditions, which may have contributed to the associated responses observed in the foraging decisions by LNFS females. A study on sympatric chinstrap and Adélie penguins found that in bad years, there was spatial segregation in foraging areas (i.e. higher inter-individual differences) between the 2 species, but none was observed in good years (Lynnes et al. 2002). The relatively weak shelf upwelling in 2017 may explain why LNFS females switched earlier and foraged in more distant oceanic waters to buffer for the shortage of food on the shelf as also seen in the behaviour of Antarctic fur seals *Arctocephalus gazella* (Boyd 1999) and seabirds (Berlincourt & Arnould 2015).

4.3. Inter-annual variability in winter pup mass

Since upwelling is directly linked to an increase in primary productivity, it should affect prey availability up the food chain. As reproductive success of central place foraging parents is dependent on the rate of food delivery to their offspring, the distance they have to travel to access resources is an important factor in their overall fitness (Boyd 1999). Hence, stronger upwelling on the shelf is expected to be beneficial for the reproductive success of LNFS. Indeed, pup abundance estimates for Cape Gantheaume are correlated with colder shelf SST (i.e. proxy for upwelling-favourable conditions) in the springtime (Shaughnessy et al. 2015). Despite relatively poorer

conditions for shelf productivity in 2017 than in 2016, pups were heavier in 2017 than in 2016 during the winter season. It is important to note that as pups were not weighed on the same days in both years, interpretation of results should be done with care. Nevertheless, pups were weighed earlier in winter in 2017, and we would expect younger pups to be lighter. During periods of reduced prey availability, central place foragers may respond by increasing foraging effort or extend their foraging range to meet the nutritional needs of their offspring and their own maintenance (Boyd 1999, Angel et al. 2015). Indeed, females in 2017 made longer foraging trips than females in 2016 during the upwelling season. During the early stage of breeding, females are expected to be time minimisers because they are constrained by their young pups' limited fasting ability. When foraging conditions are poor, longer foraging trips have been shown to result in greater food delivery per trip, but pups of mothers making shorter trips still display faster growth rates over longer periods of consecutive foraging trips (Lunn et al. 1993, Guinet et al. 2000). Hence, we would expect pups in 2016 to have better body condition than in 2017. It is possible that the greater diversity in foraging strategies made by 2017 females due to poorer shelf productivity may have worked in their favour by reducing inter-individual competition on the shelf. Furthermore, females that foraged in oceanic waters in summer may have been rewarded with greater summer oceanic productivity in 2017 (Table 3; Fig. S3 in Supplement 1) which may have offset the poor shelf conditions and even resulted in greater foraging success, and hence healthier pups.

Factors other than maternal investment, such as exposure to harsh weather (McDonald et al. 2009), can also affect pup growth, especially while their mothers are at sea. In years with adverse weather conditions, seabirds have lower reproductive success (Rishworth & Pistorius 2015). Kangaroo Island experienced higher than average annual rainfall, with several severe weather warnings in the winter of 2016 (Bureau of Meteorology 2008).

In Steller sea lions *Eumetopias jubatus*, there is a lack of relationship between maternal attendance during the early reproductive period and population status (Burkanov et al. 2011). Hence, for female LNFS at Cape Gantheaume, the variability in trip duration during the upwelling season between 2016 and 2017 may have little impact on pup body condition. Long foraging trip durations are not unusual for lactating LNFS, who display among the longest foraging trips recorded for any fur seal (Baylis et al. 2008b). The

foraging trip duration of females from neighbouring colonies in autumn is ~15–25 d on average (Baylis et al. 2008b). For the same period, 2017 foraging trips at Cape Gantheaume were comparatively shorter (~10 d, Table 2) despite being almost twice as long as those in 2016 (~5 d, Table 2). Furthermore, in this study, oceanic foraging trips earlier in the year were still relatively close to the shelf break compared to those later during the non-upwelling season. Therefore, poorer shelf productivity during the upwelling season may not play a significant role in determining overall reproductive success.

4.4. Comparison with previous work

The majority of the females studied from the same colony in 2000–2001 foraged on the shelf in both autumn and winter (Page et al. 2006), but in 2005, most females switched from shelf to oceanic foraging in the winter (Baylis et al. 2008a). This may be explained by the fact that relatively more upwelling events and areas of SST_c were still prevalent during the non-upwelling season in 2000–2001, (Fig. S3) (Baylis et al. 2008a). The combined observations from previous and current work on females from the same colony indicate inter-annual variability in foraging strategies which is primarily influenced by environmental conditions on the shelf, particularly during the upwelling season. The adoption of a single or dual foraging strategy in seabirds is fundamentally driven by annual or geographic environmental variation (Welcker et al. 2009). Similarly, king penguins in the Falkland Islands shifted foraging habitat between early and late winter in one year and not in another, which may have been the result of inter-annual variability in resource availability and distribution (Baylis et al. 2015).

Interestingly, pup production numbers dropped from 2000 to 2001, but increased from 2017 to 2018 (S. Goldsworthy pers. comm.). This suggests that the year where females made longer foraging trips to oceanic waters had better conditions for gestation than in the year where females made shorter trips and remained on the shelf. Although this seems to counter the idea that overall shorter foraging trips should lead to higher reproductive success, it is not uncommon. Little penguins with longer foraging trips had higher reproductive success when they foraged further from the colony to maximise resource acquisition, presumably due to local prey depletion (Kowalczyk et al. 2015). Central place foraging black-legged kittiwakes from a stable population

foraged in both shelf and oceanic environments, whereas those from a declining population exclusively foraged on the shelf (Paredes et al. 2012). Furthermore, deeper oceanic waters can be more productive and profitable (Staniland & Boyd 2003, Shoji et al. 2015) than weakening upwelling events that still prevail in autumn and winter. Environmental conditions in springtime may play an important role in pup production as well (Shaughnessy et al. 2015). Unfortunately, there has been very little study done during this period, and how lactating long-nosed fur seals foraging strategy changes in spring is not understood. The effect of inter-annual differences in foraging strategies and foraging ecology during springtime on overall reproductive success warrants further investigation.

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