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DRIVERS OF ALTERNATE FORAGING BEHAVIOUR IN MARINE CENTRAL PLACE FORAGERS

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Long-nosed fur seal mum and her pup at Cape Gantheaume



Me in the field monitoring a female fur seal who I had just recovered a tag from.

DEDICATION

To my mum and dad, Toh Chui Hoon and Foo Kok Luan for raising me and supporting my decision to study in Tasmania. Especially to my mum for always looking out and checking up on me. I appreciate all the things you do for me even though I don't say thank you enough. To my brother, Derrick Foo, for being an inspiration, source of motivation and always encouraging me to pursue my interests. I am so proud to call you my bro!

STATEMENT OF ORIGINALITY

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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ABSTRACT

Understanding the drivers to foraging strategies in space and time is an important aspect of ecology that is necessary for management and conservation. Within the highly dynamic marine environment, prey availability changes spatially and temporally over seasons and years. Consequently, marine predators may have to employ different foraging strategies in response to the changing environment to ensure they acquire sufficient resources for their survival and reproductive success. This in turn ultimately affects population abundance and distribution. This study is concerned with identifying the drivers to alternate foraging strategies observed in lactating Long-nosed fur seals (LNFS) from one of the primary breeding colonies at Cape Gantheaume, Kangaroo Island, South Australia. Early in lactation (December – April), females breeding at Cape Gantheaume undertake short foraging trips (~ 5 days) to near shelf waters (70-90 km from the colony), in regions associated with localised seasonal upwelling, which occurs from the austral summer to autumn. However, around late autumn (April – May) most females switch to foraging in distant oceanic waters associated with the Subtropical Front, 700-1,000 km to the south of the breeding colony and may continue to forage in these waters up until the weaning of their pups in September/October when they are about 10 months old. These winter foraging trips can last more than two weeks. The at-sea distribution of LNFS the austral summer to winter was quantified using archival global location sensing (GLS) loggers. Whisker regrowths produced over the study period were also collected. Specifically, this thesis aims to (1) examine the spatial-temporal variability in the oceanography of the study region, (2) identify the timing of switch from shelf to oceanic foraging in relation to oceanographic changes on the shelf, (3) ascertain the degree of individual foraging site fidelity within the oceanic region and (4) examine the inter-annual spatial and temporal variability in prey trophic level of adult females.

- (1) The spatial and temporal variability in the oceanography of the study region was examined using 19 years of remote-sensed satellite data. Various environmental parameters on the shelf and oceanic waters showed seasonal and inter-annual variability. The environmental overview provided useful background information for understanding why apex predators in the region vary their foraging habitats over space and time.

- (2) Variability in the timing of the switch from predominant shelf to oceanic foraging was examined in relation to oceanographic changes on the shelf. GLS tags fitted to adult female LNFS provided continuous foraging locations from summer to winter, thus covering the anticipated transitional period from shelf to oceanic foraging. Oceanographic changes in shelf waters from summer to winter were monitored by using publicly available CTD data collected by male Australian sea lions from a nearby colony that were simultaneously fitted with satellite-linked CTD tags. The sea lions forage over the same shelf waters as the LNFS year round and sample the entire water column as they are benthic foragers. Oceanographic data for shelf waters were augmented with data collected by a national mooring off the west coast of Kangaroo Island where necessary. The switch from shelf to oceanic foraging was influenced by the cessation of the localised seasonal upwelling on the shelf. Inter-annual variability in the strength of the upwelling influenced the individual variability of the timing of the switch.
- (3) Using GLS tracking data deployed on 17 seals from Cape Gantheaume for 6 – 7 months over two years, I assessed spatial distribution patterns and reveal the environmental factors influencing individual foraging site fidelity within the oceanic realm. Core foraging areas in the oceanic region were identified and found to be located near the edges of eddies. Various environmental parameters influenced the probability of an individual returning to the same oceanic foraging area on subsequent trips. Additionally there was inter-annual variability in oceanic foraging site fidelity which may have contributed to differences in reproductive success between years.
- (4) Vibrissae re-growths were sectioned sequentially and analysed for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios. Dates at which stable isotopes were deposited into each vibrissae section were estimated using verified species-specific vibrissae growth carbon and nitrogen stable isotope ratios. This enabled the reconstruction of an isotopic data time series that could be related to concurrent at-sea locations (estimated from geolocation data) from the austral summer to winter. Female trophic position was higher on the shelf than oceanic region only in one of the two study years. There were three isotopic niches (clusters) identified by model-based clustering analysis. Two of the clusters were associated with oceanic foraging and one with shelf foraging. Multiple oceanic clusters suggest there

are two different prey types that females are targeting in oceanic waters. The results revealed that the use of vibrissae $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ has potential to identify different foraging strategies used by individuals.

This study has provided important insights into the foraging strategies used by lactating LNFS through continuous GLS tracking data that covered the period from early to late lactation. Long-term data is relatively rare in marine ecology due to logistical and species-specific challenges; hence, most studies are often cross-sectional which hinders our ability understand the dynamics of foraging strategies across seasons. Results from this study have revealed that individual foraging strategies are influenced by seasonal and inter-annual changes in the environment, which in turn affects their reproductive success through the survival of their pup. This information is not only relevant to the ecology and management of long-nosed fur seals, an important apex predator within the Great Australian Bight ecosystem, but has broader applications to the understanding of foraging decisions in relation to trade-offs that central place foragers make.

STATEMENT OF PUBLICATION AND CO-AUTHORSHIP

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

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The following publication has been produced from chapter 3 of this thesis:

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Paper 3, Environmental drivers of oceanic foraging site fidelity during the later-stages of pup-provisioning in lactating long-nosed fur seals (*Arctocephalus forsteri*):

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Paper 4, Spatial and temporal variability in the trophic level of prey of adult female long-nosed fur seal (*Arctocephalus forsteri*):

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Chapter 1 INTRODUCTION

IMPORTANCE OF FORAGING

The ability to find food is crucial for an animal's survival and reproductive success (Pistorius et al. 2011). This can be challenging for marine megafauna foraging in a highly dynamic environment as the availability and distribution of their prey can be highly variable and unpredictable. Understanding how individual marine megafauna respond to varying physical environmental conditions in terms of their foraging behaviour and movements is thus one of the key questions in movement and foraging ecology (Hays et al. 2016). Such information is fundamental to understanding a species' population viability and prey stocks (Hughes 2012, Hindell et al. 2016).

FORAGING IN A HETEROGENOUS ENVIRONMENT

The distribution (Pettex et al. 2012, Kuhn and Costa 2014) and predictability (Scott et al. 2013, Scales et al. 2014) of prey resources are strongly influenced by spatially and/or temporally variable oceanographic parameters at different scales (e.g. bathymetry, wind stress, temperature, salinity) (Benoit-Bird et al. 2013, Nordstrom et al. 2013). Water movement in response to bathymetry, wind, sea surface temperature and salinity can result in the formation of upwelling regions near shelf slopes, eddies, fronts, convergence zones and filaments, which are typically associated with elevated levels of primary production (as indicated by surface chlorophyll-a concentration) at both mesoscale (10 – 200 km) and sub-mesoscales (< 10 km) (Nordstrom et al. 2013, Scott et al. 2013, Lowther et al. 2014). Hence, these oceanographic features are relatively predictable in terms of being areas where prey tend to concentrate. Thus, foraging concentrations of marine predators are sometimes associated with these highly productive oceanographic features (Baylis et al. 2008a, Péron et al. 2010, Rodríguez et al. 2013). However, while they are predictable features, their quality as a foraging patch can still be variable (Weimerskirch 2007).

HOW MIGHT ANIMALS DEAL WITH THIS

Animals will typically alter some aspect of their foraging behaviour in response to changes in the environment (Green et al. 2005, Dragon et al. 2010). Optimal foraging theory is a framework that allows researchers to investigate individual foraging behaviour and the dynamics of predator-prey interactions (Hughes 2012). According to optimal foraging theory, animals should operate to minimise energetic cost while maximising energetic gain while foraging (Charnov 1976). In theory, there are four broad categories in which animals can optimise their foraging according to this rule: diet choice, foraging patch choice, allocation of time in different patches, and pattern and speed of movements (Pyke et al. 1977). In addition, animals also experience constraints, for example physiological or life-history related or predation risk, which can affect the range of foraging behaviours they are able to display.

CENTRAL PLACE FORAGERS

Among long-lived top marine predators, otariids (fur seals and sea lions) and diving seabirds breed on land but forage at sea. Parents provisioning a dependent offspring have to consume enough food for self-feeding and offspring provisioning. During the breeding (offspring-provisioning) season, adults alternate between periods of foraging at sea and provisioning their fasting offspring ashore (Rayner et al. 2010). They are therefore examples of central place foragers where the colony or nest is the central place. Consequently, central place foraging parents are constrained in the amount of time they can spend at sea foraging as prolonged fasting may impact offspring survival and unattended offspring risk predation (Chilvers et al. 2005, Kirkwood and Arnould 2011). This is particularly true during the offspring-provisioning period as younger offspring have more limited fasting abilities. In theory, time-constrained parents should minimise time away from the colony by maximising the rate of food delivery to their offspring under all conditions (Weimerskirch et al. 2003, Clarke et al. 2006). This means returning to the colony with a fixed amount of energy in the shortest amount of time. Thus, under central place foraging constraints, animals should forage in the closest patch that will meet the energetic requirements of self-feeding and offspring provisioning (Orians and Pearson 1979, Boyd 1999).

Later in the provisioning period however, parents may switch to become energy-constrained when their offspring gets older and energetic requirements increase and/or when their body condition declines. The reproductive success of long-lived animals can be measured by the combined survival and future reproduction of their offspring as well as the parent's future reproduction in subsequent breeding attempts (Hamel et al. 2011). Hence, parents in poor body condition may choose to prioritise allocating energy for self-feeding (Welcker et al. 2009). In this case, energy-constrained parents should maximise the rate of energy gain – this means acquiring the highest amount energy in a fixed amount of time (Clarke et al. 2006).

Foraging strategies

It is typically thought that marine central place foragers optimise their foraging at the trip level (Boyd 1999). In response to changing foraging conditions, they may alter their foraging behaviour in various ways to maintain profitability of foraging trips. Parents may change their foraging trip duration (Boyd 1999, Rayner et al. 2010), foraging location (Staniland and Boyd 2003), diet (McCafferty et al. 1998, Hume et al. 2004), foraging effort (Takahashi et al. 2003), diving behaviour (Lescroel et al. 2005, Kokubun et al. 2010), time-energy budget (Boyd et al. 1991, Boyd 1999, Biuw et al. 2009, Watanabe et al. 2012) and/or energy expenditure (Costa and Gales 2003). Changes in these foraging behaviours can affect their diet, patch choice, departure from patches and movement rules which are inextricably linked (Pyke 2003).

Patch choice and time allocation in different patches are often considered together. It is predicted that in an environment where resource depletions occur and the environment is “patchy”, animals should forage in a number of patches (Pyke 2003) and make decisions as to which patch types it will visit and when it will leave the patch (Charnov 1976). During the offspring-rearing period, it is common for otariid females (Boyd 1999, Burkanov et al. 2011, Baylis et al. 2012) and seabird parents (Clarke et al. 2006, Deagle et al. 2009, Baylis et al. 2015) to have longer foraging trips during the later stage of offspring-provisioning, typically to more distant foraging areas, as offspring fasting ability and nutritional demand increases and/or due to local prey depletions (Birt et al. 1987). It is also predicted that as transportation costs increases (i.e. foraging trip duration), central place foragers should be more selective and target more energetically dense prey (Pyke 2003). Several studies have

shown support for this. In Cook's petrels, longer foraging trip durations are associated with great range in distance, higher trophic level prey and greater chick meal mass (Rayner et al. 2010). Similarly, in years with low prey abundance, common murrens increased their maximum foraging distances from the colony delivered larger sizes of their preferred prey to their chicks (Burke and Montevecchi 2009). Consumption of more energy-dense foods on foraging trips to more distant patches is also observed in lactating Antarctic fur seals (Staniland et al. 2007).

Due to central place foraging constraints not all habitats are accessible to parents (e.g. King penguins) (Baylis et al. 2015). Therefore, in the face of foraging in a highly dynamic marine environment, individual foraging site fidelity is one strategy that individuals may use to maximise foraging success. Individuals may repeatedly return to the vicinity of a foraging area where it had previously experienced foraging success. This strategy minimises time spent searching for food and maximises time spent foraging (Call et al. 2008), assuming that the resources at the foraging area is relatively predictable. Foraging site fidelity has been hypothesised to increase longevity in southern elephant seals (Authier et al. 2012) and Antarctic fur seals (Arthur et al. 2015). Thus, knowledge of profitable and predictable foraging locations should be an advantage for individual fitness (Weimerskirch 2007).

The predictability of resources are scale and habitat dependent. Predictability is higher at larger spatial scales *i.e.* animals show greater fidelity to habitats (larger spatial scale), rather than specific foraging sites (smaller spatial scale) (Weimerskirch 2007). Foraging range is often associated with foraging trip duration (Rayner et al. 2010). The longer animals have to travel to a foraging patch, the more likely that foraging conditions at that patch has changed between visits. Additionally, shelf edges are generally more predictable features than those in oceanic waters. For example, temperate and polar seabirds showed higher foraging site fidelity to distant shelf edges as opposed to distant oceanic waters (Weimerskirch 2007). Furthermore, habitats with strong physical forcing, such as tidal fronts and shelf edges, tend to have stronger fidelity except when those same habitats are homogenous (Weimerskirch 2007).

In addition to distance, the quality of food patches to the colony also affects how long central place foragers remain in patches and how much resources it allocates for self-feeding as opposed to provisioning. In Palestine sunbirds provisioning chicks, the higher the quality of food patches, the more frequent food was delivered to their young (Markman et al. 2004). Given the variable nature of the environment, some central place foragers may continually sample different patches in order to keep updating information regarding patch quality while still retuning to previously used patches that may have more predictable but perhaps less energy-dense prey (Markman et al. 2004).

Foraging site fidelity can also be a strategy to buffer poor environmental conditions. For example, when faced with unsuccessful foraging bouts, bumblebees often quickly respond shifting foraging areas returning to known profitable areas, even if they are of lower quality (Townsend-Mehler and Dyer 2012). However, this strategy can have a negative impact on the reproductive success of individuals that continue to forage in the same area or target the same prey despite changes in the physical environment, especially in the long-term. For example, long-term foraging specialists are unable to quickly alter their diet preferences which often leads to a decline in their reproductive success and hence population viability (Casper et al. 2010).

Individuals from the same region compete with one another for resources. This can influence individuals from a colony to respond to changes in the physical environment differently, leading to high variation in individual foraging strategies. Inter-individual variability in foraging behaviour are more pronounced when environmental conditions are bad (Lynnes et al. 2002). As the rate of provisioning is determined by the meal size and frequency, under normal foraging conditions, variation foraging behaviour, e.g. trip duration, might not influence the overall rate of food delivery to offspring and hence their growth rates. This was observed in lactating Antarctic fur seals and Cory shearwaters (Arnould and Boyd 1995, Magalhaes et al. 2008). Nonetheless, when environmental conditions extremely poor, even compensation by extending foraging ranges or increasing foraging effort may not be enough to buffer reproductive success from declining (Lynnes et al. 2002, Ronconi and Burger 2008, Berlincourt and Arnould 2015).

Intrinsic factors

Additionally, intrinsic factors such as differences in experience (*i.e.* age) and size (Beauplet et al. 2004) can affect reproductive success where older and/or bigger adults will perform better reproductively, especially in years with poor foraging conditions (Lea et al. 2006). For long-lived animals, younger adults may favour investment in future offspring over the current one by prioritizing self-maintenance and survival in order to breed again in the future at the cost of their offspring. Older adults are likely to invest more in the current offspring than future offspring (Croll et al. 2006, Cresswell et al. 2012). Individual body size also limits the types of habitats accessible to animals. For example, compared to their male counterparts, female northern fur seals are physiologically less able to forage for prey at greater depths (Sterling et al. 2014). This limitation leads them to target habitats where their diving capabilities allow them to access a diverse range of prey that are predictably abundant such as eddies (Sterling et al. 2014).

STUDY ANIMAL: LONG-NOSED FUR SEAL

Study site and oceanographic features

The study site was located at Cape Gantheaume, Kangaroo Island, South Australia. The marine region around Cape Gantheaume is situated just east of a region of narrow shelf, the Bonney Coast. From the austral summer to autumn (typically November to May), classical surface upwelling plumes occur along the Bonney Coast (Robe, South Australia to Portland, Victoria). This localised seasonal coastal upwelling is known as the Bonney Upwelling and it is the most prominent upwelling area in southern Australian waters. The upwelling is driven by prevailing southeasterly winds and consequently, the area is highly productive and serves as a feeding area for seabirds, fishes, whales, fur seals and sea lions (Butler et al. 2002).

Although surface upwelling is typically only observed off the Bonney Coast, western Kangaroo Island and off the western Eyre Peninsula, subsurface upwelling that reaches well into the photic zone extends across a very large area of continental shelf in the eastern GAB, enriching coastal and shelf waters. In winter, coastal winds become westerly, driving downwelling along the Bonney Coast until spring (November) before the cycle repeats itself. The Bonney Coast region is also used by various fisheries including rock lobster and squid.

Fishing effort of trawl fishery is generally concentrated along the shelf edge of the Bonney Coast (Rogers et al. 2013).

At higher latitudes in the oceanic realm off the continental shelf, the Subtropical Front (STF) occurs at around 39 to 45°S depending on the season. There is a high incidence of eddy formation and eddy shedding in the STF region (Tomczak et al. 2004). Eddies tend to have higher marine productivity and zooplankton biomass relative to adjacent waters due to the upwelling and downwelling processes induced by eddy activity (Gaube 2012). Therefore, the STF region is highly productive (Froneman 1999, Kopczynska et al. 2001, Bender et al. 2016) and an important feeding ground for several apex predators including sharks (Rogers et al. 2015) and fur seals (Baylis et al. 2008b).

Distribution and abundance

Long-nosed fur seals (LNFS; *Arctocephalus forsteri*; also known as the New Zealand fur seal) were historically hunted to near extinction but have recovered successfully under legal protection. Currently LNFS breed in southern Australia and New Zealand. The majority of its Australian population is in South Australia, where most of the breeding population is restricted to a relatively small geographic area between Kangaroo Island and the southern tip of Eyre Peninsula (Fig. 1.1). There are five main breeding colonies within a 200 km radius of which accounts for ~82 % of the Australian population (Shaughnessy et al. 2005, 2015). The primary colonies are Cape Gantheaume and Cape du Couedic on Kangaroo Island, North and South Neptune Islands and Liguanea Island. The population size in South Australia has been increasing rapidly in the last 2 – 3 decades (Shaughnessy and Goldsworthy 2015). Therefore, due to their abundance and size, and hence potential biomass consumption, LNFS are important predators within the Great Australian Bight (Goldsworthy et al. 2003) which is a region of high ecological and commercial significance in Australia (Rogers et al. 2013).

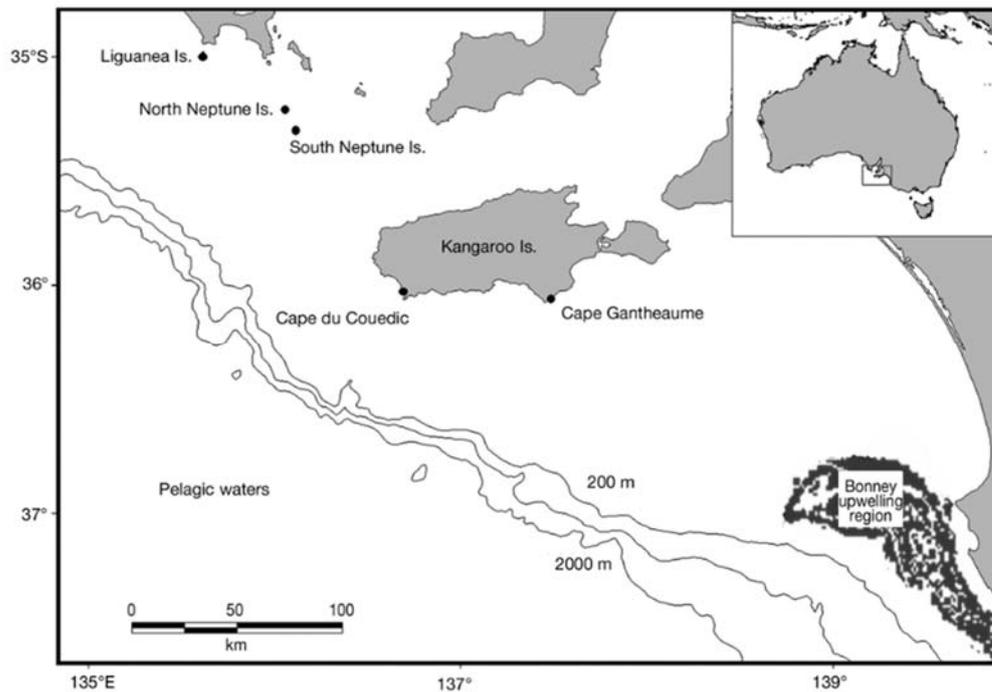


Figure 1.1 Major breeding colonies of long-nosed fur seals in South Australia. Also shown is an example of a cold-water plume that is indicative of the Bonney upwelling during austral summer months. Eyre Peninsula is the land above Liguanea Island. Reproduced from Baylis et al (2008b).

Breeding biology and foraging ecology

Long-nosed fur seal pups are born between November – February with 90% of the pups born over a 34-day period from December to January (Goldsworthy et al. 1994). The lactation period is approximately 9 months (austral summer to spring) and pups are usually weaned around October (Goldsworthy 2006). Lactating females are central place foragers where they alternate between foraging at-sea and nursing their nutritionally dependent pups onshore. Pups remain at the colony and are typically fasting while their mothers are foraging at-sea (although see Baylis et al. 2005).

A number of foraging behaviour studies of LNFS have been undertaken at Cape Gantheaume. Previous studies have investigated seasonal variability in foraging habitat, diving behaviour and diet of lactating females, adult males, juveniles and pups (Baylis et al. 2005, 2008a, 2012, Page et al. 2005, 2006). The long provisioning period of LNFS means that they experience a variety of environmental conditions during this time. This period provides a unique opportunity to study central place foraging ecology and investigate how lactating fur seals respond in terms of their foraging behaviour to changes in their prey abundance, prey

distribution and offspring demands. Similar to lactating Antarctic fur seals (Biuw et al. 2009), these factors seem to affect the foraging trip durations of long-nosed fur seals the most. Early in lactation (summer to early autumn), females undertake short foraging trips (~4 days duration) to nearby shelf waters (70-90 km from the colony), in regions associated with localised upwelling (Baylis et al. 2008a). However, between April to May (late autumn to winter), most females switch to foraging in distant oceanic waters associated with the Subtropical Front (STF), 700-1,000 km to the south of breeding colonies, where they may continue to forage at until the weaning of their pup (Baylis et al. 2008a). These winter foraging trips can last more than two weeks. However, this bimodal foraging strategy is not used by majority of the females in some years (Page et al. 2005a).

Objectives of this study

It is unclear if the major change in foraging distribution (shelf to oceanic) occurs in response to: 1) reduced prey availability as a consequence of cessation in coastal upwelling; 2) life-history/pup growth factors that enable females to switch to potentially more reliable but distant foraging grounds once their pup reaches a size and condition threshold where they can sustain longer fasts; or 3) a combination of these factors. Therefore, the overall aim of this study is to achieve better understanding of how females best utilise coastal and offshore resources and their different oceanographic features to maximise foraging success and hence fitness. Additionally, the inter-annual variability in foraging behaviour of females has not been studied in detail. In contrast to methods used by previous studies which were done by cross-sectional sampling *i.e.* different individuals in different months, I aimed to collect longitudinal observations over the majority of the lactation period for each individual sampled thus reducing biases that may result from examining behaviour over short periods of time that reflect transient conditions (Skinner et al. 2012). This information will ultimately be useful natural resource managers for understanding how population distribution matches oceanographic conditions.

Therefore, the questions addressed in this study are:

1. How do the oceanographic characteristics of the shelf and oceanic regions in which females forage in vary spatially and temporally?

2. How does seasonal upwelling on the shelf influence the bimodal nature of maternal foraging strategies?
3. What drives individual foraging site fidelity in oceanic foraging of lactating Long-nosed fur seals?
4. How does the trophic level of prey in adult female seals vary inter-annually?

THESIS OUTLINE

Each data chapter of the thesis (chapter 2 – 5) was written as an independent manuscript that has either been accepted for journal publication and is in press, submitted to a journal and is currently under review or is in preparation for submission to a scientific journal. Dahlia Foo was the primary author for each chapter and was responsible for data collection at Cape Gantheaume, data analysis, its interpretation and manuscript preparation. Co-authors helped facilitate the project, data collection and/or preparation of the manuscripts. The co-authors are listed at the start of each chapter and in the statement of publication and co-authorship.

Chapter 2: shelf-oceanic dynamics of surface environmental parameters in the Kangaroo Island–Bonney Coast region

This chapter sets the scene for the study. Remote-sensed data covering nearly two decades was extracted for the study region and analysed with the aim to compare and contrast shelf and oceanic waters' temporal and spatial variability and examine existing long-term trends in key environmental parameters.

Chapter 3: influence of shelf oceanographic variability on alternate foraging strategies in Long-nosed fur seals

This chapter aims to investigate whether the change from shelf to oceanic foraging in lactating females is driven by changes in the strength of summertime upwelling. We used a novel approach of monitoring changes in shelf oceanography by using data collected by satellite-linked loggers deployed on a sympatric species, the Australian sea lion which allowed us to identify precisely when upwelling activity on the shelf decline and relate it to continuous foraging tracks of lactating Long-nosed fur seals collected by geolocation loggers during that transition period.

Chapter 4: environmental drivers of oceanic foraging site fidelity

Continuous foraging tracks from summer to winter (6 – 7 months) collected by geolocation loggers deployed on lactating females enabled the investigation of individual foraging site fidelity for oceanic foraging trips. Due to the coarse-scale nature of geolocation estimates, shelf foraging fidelity was not investigated as the study region is characterised by narrow shelves. Nonetheless, due to greater distances from the breeding colony, there is more potential for variability in foraging behaviour during oceanic foraging trips. A measure for fidelity was calculated and then related to environmental characteristics of core foraging areas of oceanic foraging trips.

Chapter 5: spatial and temporal variability in the trophic level of prey of adult female Long-nosed fur seal

For the first time, stable isotope analysis was conducted on vibrissae collected from adult females. Regrowth vibrissae (containing data covering the duration of the study) was sectioned sequentially and each section was analysed for carbon and nitrogen stable isotope ratios. Using verified species-specific growth rates, a date for the deposition of stable isotopes was estimated for each vibrissae section. This was then related to foraging tracks collected by geolocation loggers, allowing the creation of an isoscape for the region and comparison of the trophic level of prey consumed by females in shelf and oceanic habitats between two study years.

Chapter 6: general discussion

In the final chapter, the thesis concludes with a general discussion that synthesizes how predators may respond to environmental changes at different scales. The importance of oceanic habitats in relation to central place foraging and the benefits of using stable isotope analyses to further our understanding on the foraging ecology of seals is also discussed.

Chapter 2 SHELF-OCEANIC DYNAMICS OF SURFACE ENVIRONMENTAL PARAMETERS IN THE KANGAROO ISLAND-BONNEY COAST REGION

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ABSTRACT

The shelf and oceanic waters of the Kangaroo Island-Bonney Coast region are important foraging habitats for top marine predators in the ecosystem however the dynamics between the two distinct water types has not been investigated. This study examined the spatial and temporal variability of oceanographic parameters in the southern waters of Australia (36°S – 43°S, 136°E– 141°E) associated with the Bonney Upwelling (shelf) and Subtropical Front (STF; oceanic). Using satellite data from 1997 – 2016, we found that productive oceanic waters were associated with the STF and eddy activity; they were generally furthest from the shelf break in spring-summer (during the upwelling season on the shelf) and closest to the shelf break in winter-autumn (during the nonupwelling season on the shelf). Inter-annual variabilities of chlorophyll-a, sea surface temperature, and sea surface height anomaly (SSHA) were generally higher in summer than in winter for both shelf and oceanic waters. Using break-trend analysis, the El Niño-Southern Oscillation were associated with environmental parameters in the region to a certain extent. The results in this study give a regional perspective of the spatial and temporal variability in productivity in southern Australian waters and may be useful for understanding the movements of apex predators in the ecosystem.

INTRODUCTION

The World's continental shelves, slope edges, and mesoscale oceanic features, such as eddies and fronts, are important sources of food for top marine predators (Springer et al. 1996, Bost et al. 2009, Rogers et al. 2015). As the aquatic environment is highly dynamic, the productivity of these features vary seasonally (Behrenfeld et al. 2001, Bender et al. 2016) and inter-annually (Demarcq et al. 2003, Legaard and Thomas 2006). This variability in the productivity of the local environment may influence the distribution and abundance of mid-trophic species, the foraging success of marine predators (Blanchet et al. 2015), and ultimately their fitness (Oosthuizen et al. 2016). For example, little penguins from south-eastern Australia increase their foraging effort with lower sea surface temperature in the local region (Berlincourt and Arnould 2015). Several species of seals concentrate foraging in areas with greater sea surface temperature variability, a potential proxy for long-term productivity (Bradshaw et al. 2004). Therefore, understanding how environmental conditions

change at various temporal scales is an important step in understanding how the physical and biological processes underpin the prey-base that supports marine predators.

The Bonney Upwelling is one of the most prominent and predictable upwelling centres in southeastern Australia and it is part of the eastern Great Australian Bight (GAB) ecosystem (Fig. 2.1). The Bonney Upwelling and other upwelling centres in the eastern GAB are important drivers of phytoplankton growth, feeding marine animals in the region (Butler et al. 2002). Several marine species in the region such as seabirds (Angel et al. 2015, Berlincourt and Arnould 2015), fishes (Rogers et al. 2015), whales (Butler et al. 2002), and seals (Page et al. 2006, Lowther and Goldsworthy 2011) are known to feed at or near the Bonney Upwelling area; it is also a productive fishing ground for rock lobster (Butler et al. 2002, Goldsworthy et al. 2013).

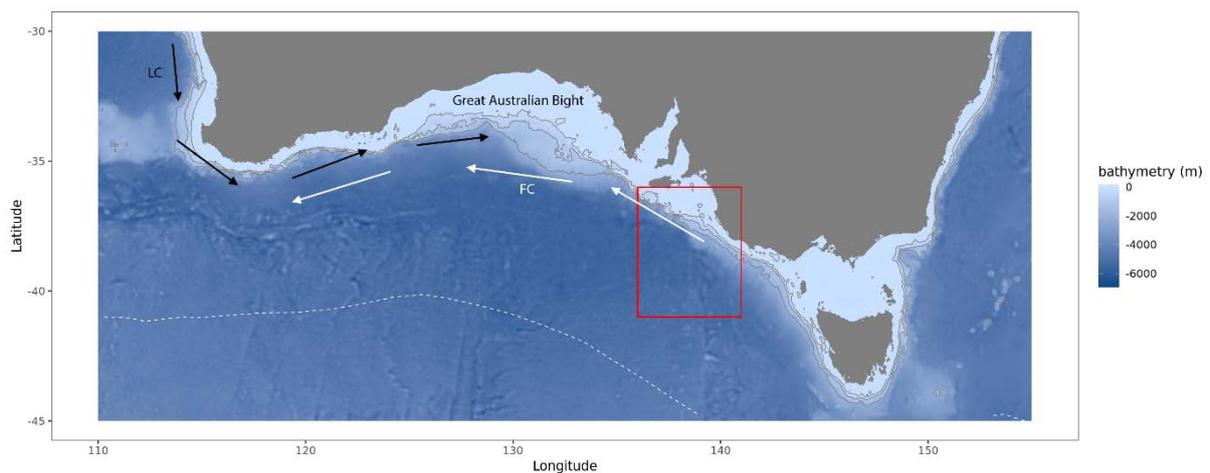


Figure 2.1 Map showing the Great Australian Bight region in southern Australia. The red box represents the study region. Kangaroo Island is just above the red box. Major coastal currents in the region during winter are shown. FC, Flinders Current; LC, Leeuwin Current. The mean position of the Subtropical Front is represented by the dashed white line.

The Bonney Upwelling occurs on the narrow shelves of the Bonney Coast where its seasonal upwelling cycle begins in the austral summer and extends to late autumn (November – April). Enhanced primary production from upwelling is greatest in March (Nieblas et al. 2009). The Bonney Upwelling is predominantly a wind-driven system (Butler et al. 2002) where the

upwelling season is characterised by westward shelf currents, and southeasterly coastal winds along the Bonney Coast (Robe, South Australia to Portland, Victoria; Fig. 2.2a) (Middleton and Bye 2007). Thus, the Bonney Upwelling plume usually extends north-west towards the local waters south of Kangaroo Island. Consequently, the distribution of zooplankton communities, consisting primarily of large copepods and dinoflagellates, are similar between on the shelf waters south of Kangaroo Island and the Bonney coast (Rogers et al. 2013). However, while evidence of surface upwelling is most prominent at the Bonney coast, extensive broad-scale subsurface upwelling also occurs in other areas in the eastern GAB (Middleton and Bye 2007).

An important current in the Bonney Upwelling system is the Leeuwin Current. It is a poleward flowing, eastern boundary current, which suppresses upwelling conditions (Waite et al. 2007b). During the upwelling season, upwelling-favourable conditions are more prevalent which results in net upwelling activity. In winter, the Leeuwin Current, which is characterised by relatively warm SST, can extend into the GAB as an upwelling-suppressing eastward flowing current; its penetration into the eastern GAB is greater in winter than in summer (Rogers et al. 2013). Additionally, the coastal winds reverse to become westerly, and together with surface cooling, lead to downwelling, which persists for the remainder of the year, lowering primary production (Nieblas et al. 2009). Thus, the nonupwelling season generally occurs from May – October, although there can still be short periods of upwelling events during this period.

At higher latitudes, the Subtropical Front (STF) is one of the major oceanic fronts which separates subtropical waters in the north from subantarctic waters in the south (Tomczak et al. 2004). The location of the STF has short-term and seasonal variability; south of Australia, the front varies in position from (38 – 44°S). The STF is typically highly productive due to prevalence of eddy activity (Kopczynska et al. 2001, Nel et al. 2001, James et al. 2002) and the phytoplankton stock at the STF is also considered relatively uniform throughout the year (Allanson et al. 1985, Weeks and Shillington 1994). For those reasons, the front is used by a

range of predators, including squid- and plankton-feeding seabirds, seals (Bost et al. 2009), and sharks (Rogers et al. 2015).

An important top predator species that forages in waters associated with the Bonney Upwelling and the STF is the Long-nosed fur seal (*Arctocephalus forsteri*) breeding at Cape Gantheaume, Kangaroo Island (Fig. 2.1). Typically, lactating females forage in the former region during the upwelling season and switch to the latter region during the nonupwelling season. The Long-nosed fur seals are currently the most abundant fur seal species in South Australia where the majority of the Australian population is located (Shaughnessy and Goldsworthy 2015). Additionally, the Cape Gantheaume colony is one of the major colonies for this species where about 25 % of the total pup production in South Australia are produced (Shaughnessy and Goldsworthy 2015).

As several top predators utilise both the Bonney Upwelling and the STF region for food, these are clearly important foraging habitats. Several studies have investigated and described the seasonal changes of the Bonney Upwelling, however none have explicitly put it in the broader regional context with respect to the adjacent oceanic region associated with the STF. The goal of the study is to provide a preliminary overview of the shelf-oceanic dynamics in this important region by using publicly available remotely-sensed data. We do not intend to fully characterise the oceanography of the region as an in-depth study would require robust *in situ* datasets. Hence, we specifically aimed to 1) use a long term dataset to compare the intra- and inter-annual variability of surface oceanographic parameters between the Bonney Upwelling shelf region and the adjacent STF oceanic region; 2) do a preliminary time series analysis to assess and identify abrupt changes in the long-term trends of surface oceanographic parameters for both regions and important climate indices (Southern Annular Mode and El Niño-Southern Oscillation) in the southern waters of Australia.

MATERIALS AND METHODS

Data

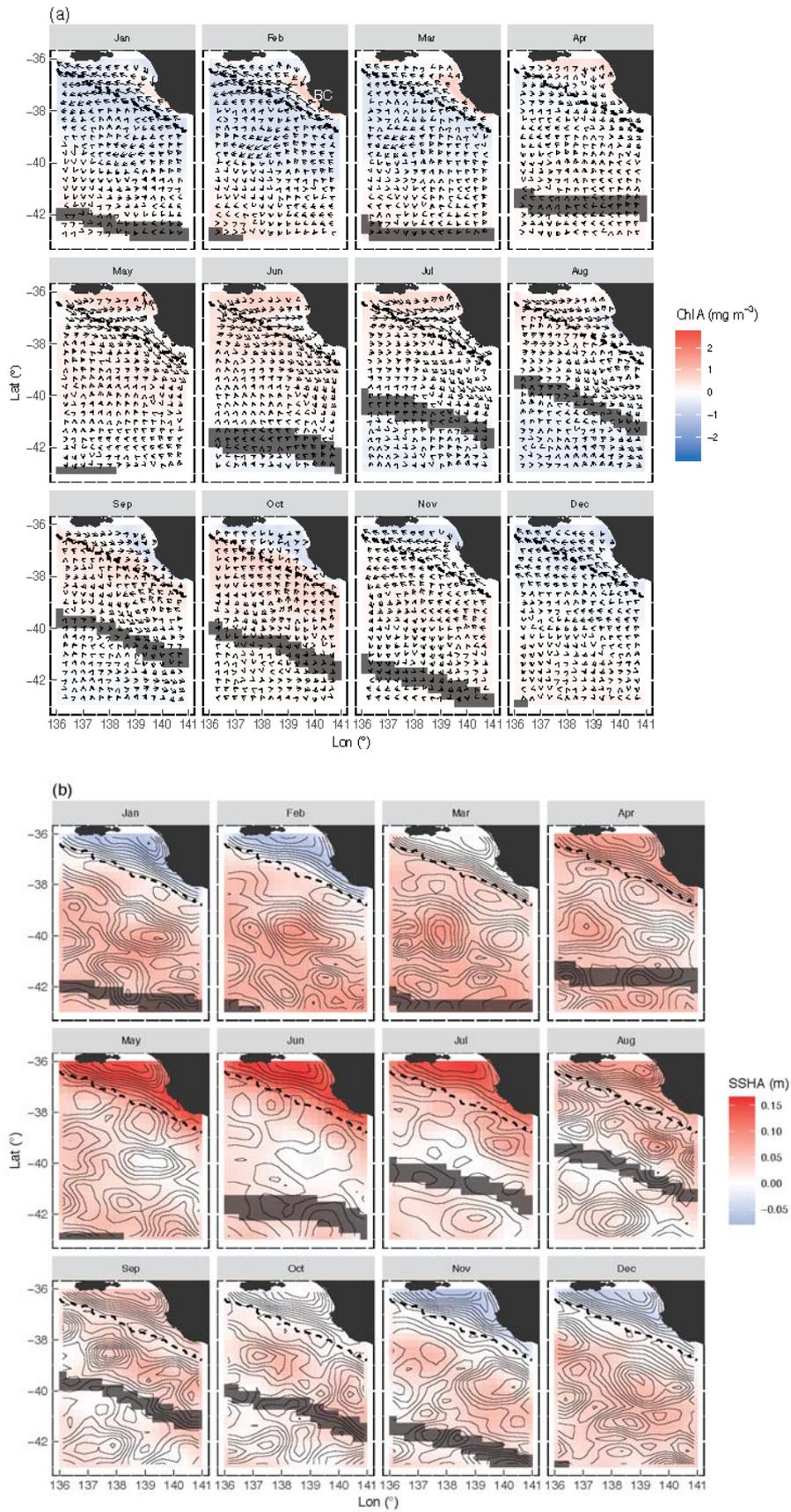
The study region was bounded by 36°S – 43°S, 136°E– 141°E (Fig. 2.2) which consisted of the southern waters of Kangaroo Island, the Bonney Upwelling plume area and the adjacent oceanic region associated with the STF (Fig. 2.2). In this study, we defined the shelf region as the continental shelf and slope up until the 2000 m isobath; beyond that, we considered it as the oceanic region. The STF is typically represented by the 14-18°C (depending on location) and 12°C sea surface temperature (SST) in summer and winter respectively (Tomczak et al. 2004). For this study, we defined the STF to be waters at 14°C SST in summer.

Table 2.1 Environmental data used in analyses. All data were summarised into a single value for the shelf region (37.5 °S – shelf boundary, 137 – 141 °E), except wind velocity which was extracted for a single point (39°S, 140.5°E). All environmental data were extracted from 1 January 1997 to 31 December 2016 except chl-a which was from 1 September 1997 to 31 December 2016.

#	Variable	Source	Frequency	Spatial resolution
1	SST - sea surface temperature (°C)	NOAA Optimum Interpolation daily Sea Surface Temperature Anomaly	Monthly	0.25 °
	SSTA - sea surface temperature (°C)	derived from SST	Monthly	0.25 °
2	SSHA – sea surface height anomaly (m)	IMOS Optimal Interpolated daily Gridded Sea Level Anomaly	Monthly	0.2 °
3	Chl-a – chlorophyll-a (mg m ⁻³)	GlobColour	Monthly	1/24 °
4	Horizontal and vertical sea surface currents (m s ⁻¹)	OSCAR	5 d	1/3 °
5	Horizontal and vertical wind velocity at 10 m (m s ⁻¹)	NCEP	6 h	2.5 °
6	Alongshore wind stress to the Bonney Coast (N m ⁻²)	derived from wind velocity	Daily	
6	Southern Oscillation Index	Bureau of Meteorology	Monthly	
7	SAM – southern annular mode	NOAA	Monthly	

URLs

1	https://www.ncei.noaa.gov/erddap/griddap/ncdc_oisst_v2_avhrr_by_time_zlev_lat_lon.html
2	https://portal.aodn.org.au/
3	http://www.globcolour.info/products_description.html
4	http://coastwatch.pfeg.noaa.gov/erddap/index.html
5	https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html
6	ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soiplaintext.html
7	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/monthly.aao.index.b79.current.ascii.table



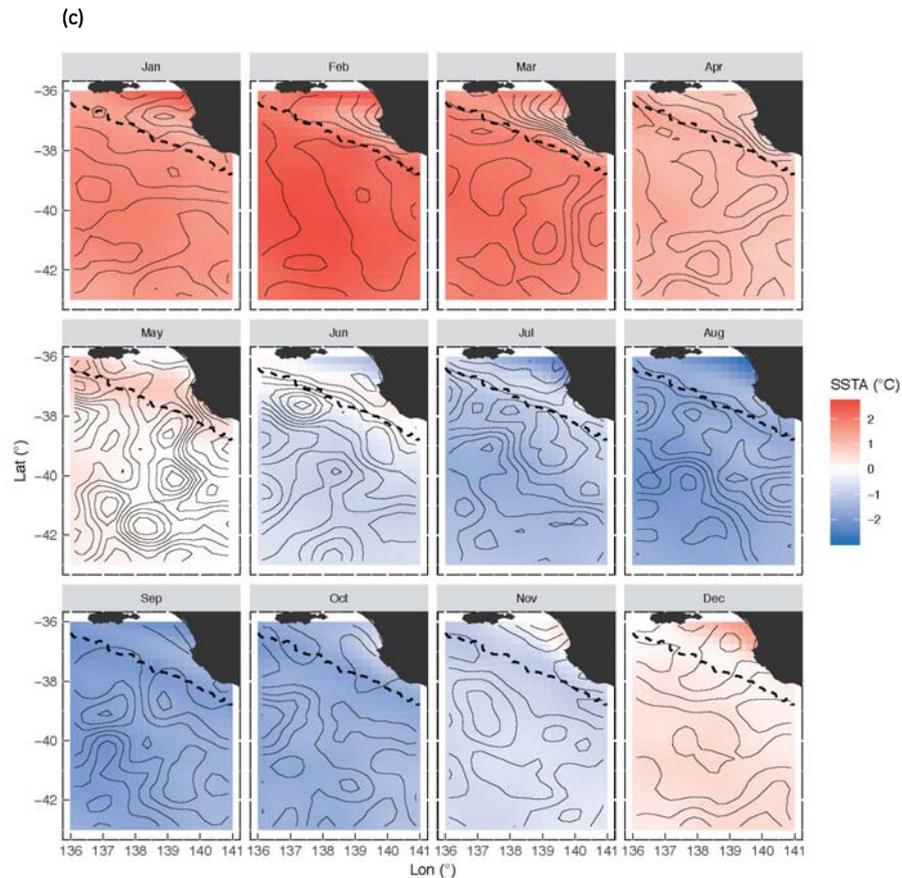


Figure 2.2 Monthly climatology plots for (a) chlorophyll-a anomaly ($\log_{10}(\text{ChlA})$, mg m^{-3}) (b) sea surface height anomaly (SSHA, m), and (c) sea surface temperature anomaly (SSTA, $^{\circ}\text{C}$). Sea surface current anomaly (represented by arrows, with length indicating magnitude) are also shown in (a). Climatology means were calculated from either monthly and 5-day (sea surface currents) time series from 1997 – 2016. The dashed line represents the 2000 m isobath. The shaded area represents the subtropical front ($14 - 14.5^{\circ}\text{C}$ SST in January to April; $12 - 12.5^{\circ}\text{C}$ SST in May to December), and the contour lines in (b) and (c) represent the standard deviation for the entire time series. BC; Bonney Coast where the Bonney Upwelling occurs.

Various remote-sensed environmental data from 1 January 1997 – 31 December 2016 were extracted whenever possible for the study region (Table 2.1). This included monthly sea surface height anomaly (SSHA), sea surface temperature (SST), and sea surface chlorophyll-a (chl-a), 6-hourly horizontal and vertical wind velocity at 10 m in height, and 5-day sea surface current velocity (sources and resolutions are detailed in Table 2.1). For wind velocity, data was extracted for a cell (39°S , 140.5°E) off the Bonney Coast which was then averaged into

daily wind speed. Wind at this location is known to directly influence upwelling along the Bonney Coast (Nieblas et al. 2009); hence, wind stress parallel to the Bonney Coast i.e. alongshore wind stress (τ'_v ; units: N m^{-2}) was used as a proxy for upwelling wind strength and 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 ($\rho_a = 1.22 \text{ kg m}^{-3}$), α is wind direction, and β is the dominant angle of the Bonney coast line ($\beta = 315^\circ$). Positive values of τ'_v correspond to upwelling-favourable alongshore wind stress. Generally, upwelling-favourable conditions in the southern hemisphere are also associated with relatively lower SST and negative SSHA while the opposite is true for downwelling conditions (Middleton et al. 2007). Cold cyclonic eddies and warm anticyclonic eddies are typically characterised by upwelling and downwelling within their core, respectively (Bakun 2008). At their edges, the opposite phenomenon may occur (i.e. downwelling at the edges of a cyclonic eddy and vice versa). Hence, eddies were identified using SSHA and surface currents (clockwise currents for cyclonic eddies and vice versa). Chl-a concentration was \log_{10} transformed before further analyses. For this study, we consider austral summer, autumn, winter and spring months to be from December – February, March – May, June – August, and September – November, respectively.

Intra-annual variability

Anomalies of SST, chl-a and sea surface velocity were calculated by subtracting the mean of the entire original time series from the raw values for each cell. Cells with missing values were removed from analysis. Next, intra-annual (seasonal) variabilities of SST anomaly, SSHA, chl-a anomaly and sea surface velocity anomaly, and alongshore wind stress were investigated by generating monthly climatologies (long-term monthly mean of the entire time series).

Inter-annual variability

To investigate inter-annual variability, we followed and adapted the methods used in (Forkel et al. 2013) and calculated the annual anomalies of chl-a, SSHA, and SST for each season (summer, autumn, winter, spring) by (1) calculating the mean of the original time series, (2)

averaging the original time series to annual values, and (3) subtracting the mean of the time series from the annual values. Inter-annual variability (*iav*) was then measured from the range and standard deviation of the annual anomalies.

Time series analysis

Time series analysis was done using the Breaks For Additive Season and Trend (*BFAST*; version 1.5.7) package in R (version 3.4.4) (Verbesselt et al. 2010a). The *BFAST* package decomposes a time series into trend, seasonal, and remainder components and detects significant ($p < 0.05$) abrupt changes (breakpoints) within the trend and seasonal components. In this study, we focused on detecting breakpoints in the trend component of SST, SSHA, and chl-a. For each oceanographic variable, the means of the shelf (36°S to the 2000 m isobath, 138° – 140°E) and oceanic (> 2000 m isobath – 42°S, 138° – 140°E) regions were calculated as input for the *BFAST* analysis. The 2000 m isobath generally marked the end of the shelf break in this region (Page et al. 2005a). In addition, the *BFAST* analysis was also done on monthly time series of Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) from 1997 – 2016. These are the two important modes of large-scale climate variability in the Australian and Southern Ocean region. The SAM describes the north-south movement in position and intensity of westerly wind. A positive SAM event indicates that the belt of strong westerly winds contracts towards Antarctica, while a negative SAM event indicates that the belt of strong westerly winds expands towards the equator. The SOI is an indicator for the El Niño-Southern Oscillation, where sustained values of the SOI below -7 indicate El Niño phases, while values above 7 indicate La Niña phases. According to the Bureau of Meteorology of the Australian Government (<http://www.bom.gov.au/climate/enso/outlook/>, date accessed: 1 October 2017), El Niño years occurred in 1997, 2002, 2006, 2009, and 2015, while La Niña years occurred in 1998 – 2000, 2007 – 2008, and 2010 – 2011 (Fig. S2.1). From 1997 – 2016, El Niño and La Niña usually began in autumn-winter, and El Niño years were often followed by 2 – 3 La Niña years (Fig. S2.1).

The minimum period between two breakpoints was 15 % of the total length of the timeseries (or three years of a 20-year time series) to support the detection of relatively longer term

changes in trend (Verbesselt et al. 2010b). For each derived trend segment, the slope of the trend was estimated by linear least-squares regression of the decomposed trend (raw time series minus the seasonal component) against time.

RESULTS

Intra-annual variation

Shelf

Favourable upwelling conditions such as increased strength of the north-west (equatorward) flowing surface currents (Fig. 2.2a), negative SSHA (Fig. 2.2b), relatively cold SST (Fig. 2.2c), and more consistent positive alongshore wind stress (Fig. 2.3) occurred on the shelf from summer to early autumn (November – March). These features were associated with positive chl-a anomaly (enhanced primary production), which began building up from the Bonney Coast in November and reached its peak (in terms of the size of the upwelling plume and magnitude of positive chl-a anomaly) in February and March (Fig. 2.2a).

In mid-autumn (April), the upwelling plume was less pronounced and began to decay as the positive chl-a anomaly dissipated to the north-west over the shelf (Fig. 2.2a). The localized area of cooler SST at the upwelling plume also weakened and SST became more homogenous over the shelf as winter cooling occurred (Fig. 2.2c). Concurrently, downwelling conditions began to take place, as SSHA became weakly positive, surface currents began to flow towards the south-east, and the median of alongshore wind stress decreased (Fig. 2.3). The intensity of these downwelling processes increased from late autumn to winter (May – August; Figs 2.2a and b). In August, the magnitude of localised negative chl-a anomaly and strength of downwelling-favourable wind stress (negative values) was greatest (Fig. 2.3).

For the remainder of the year, downwelling-favourable conditions began reversing before returning to upwelling-favourable conditions again in summer; the strength of positive shelf SSHA (Fig. 2.2b) and downwelling-favorable currents (eastward; Fig. 2.2a) reduced, and the median of alongshore wind stress began to increase. However, SST continued to cool on the shelf before warming up again in summer (Fig. 2.2c).

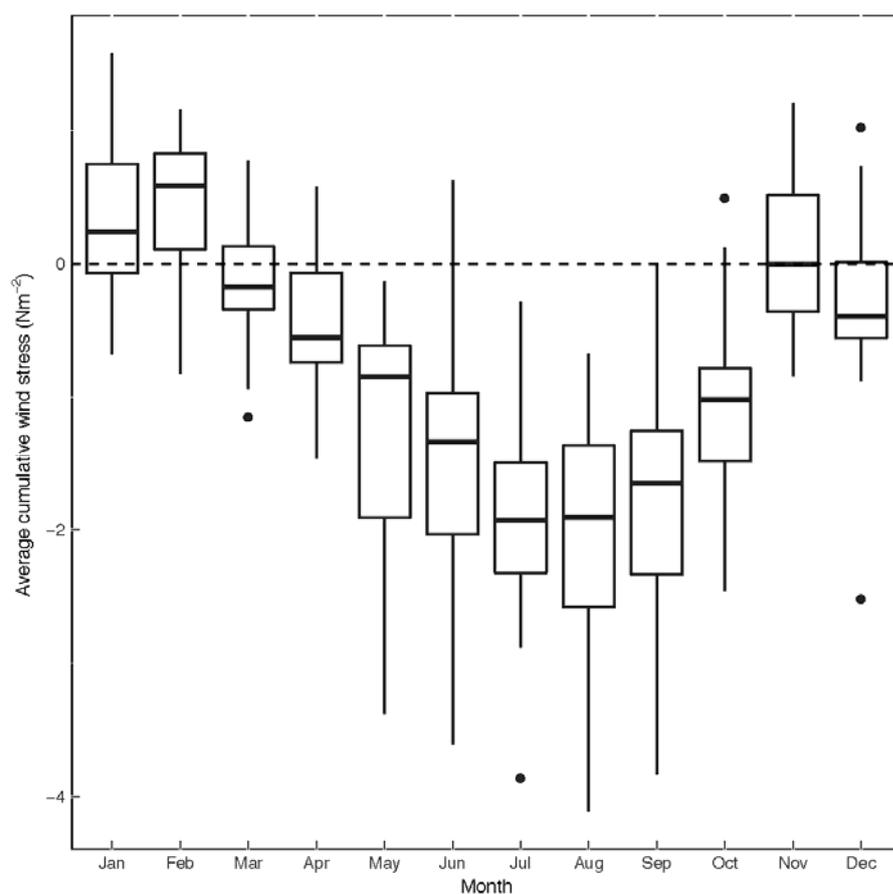


Figure 2.3 Average monthly cumulative alongshore wind stress. Positive values show the cumulative effect of long periods of upwelling-favourable winds. The whiskers of the boxplots extending from the box represent the greatest and lowest values within 1.5 times of the inter-quartile range, while black points represent values outside that range. The upper and lower boundary of the box represent the 75th and 25th percentile. The black line within the box represents the median. The dashed line represents the zero y-intercept to distinguish between upwelling favourable and non-upwelling favourable winds stress.

Oceanic

Areas of positive chl-a anomaly (Fig. 2.2a) and colder SST (Fig. 2.2c) in oceanic waters began far south from the shelf break (~41 – 43°S) in summer (November) and migrated north to the shelf break till late winter (August) before reversing and moving back south again for the remainder of the year. Additionally, the spatial extent of positive chl-a anomaly in oceanic waters was lowest in July and August. This movement corresponded to the north-south migration of the STF, where areas of positive (negative) chl-a anomaly was generally above (below) the STF (Fig. 2.2a).

From the climatology, there were no obvious localised areas of usually cold SST in oceanic waters (Fig. 2.2c) that might have represented upwelling-favourable conditions. However, the spatial variability (standard deviation over the entire time series) of SSTA in oceanic waters was relatively greater in autumn-winter compared to other seasons, with the greatest variability occurring in May (Fig. 2.2c).

Oceanic waters were usually dominated by positive SSHA throughout the year, but to a lesser extent in winter and spring (Fig. 2.2b). The climatology of surface current direction was generally variable in oceanic waters. However, in autumn-winter, strong eastward shelf currents spilled out over the shelf break into oceanic waters at the Bonney Coast where the shelf narrows, contributing to the mixing of shelf and oceanic waters (Fig. 2.2a). At the same time, localised areas of high SSHA occurred near the shelf break of the Bonney coast (Fig. 2.2b). The contours of SSHA SD (Fig. 2.2b) corresponded to mesoscale eddies in the oceanic region. This was further supported by the direction of anomalous sea surface current (Fig. 2.2a) which tends to flow in an anti-clockwise direction in anticyclonic eddies (positive SSHA).

Inter-annual variability

The inter-annual variability (*iav*; i.e. standard deviation of annual anomalies) of chl-a, SSHA, and SST for each season is shown in Fig. 2.4. The range of annual anomalies for chl-a, SSHA, and SST for each season is shown in Table 2.2. Chlorophyll-a concentration and SST *iav* was generally greatest in summer, and the lowest in winter for both shelf and oceanic waters (Fig. 2.4a and c). Sea surface height anomaly *iav* on the shelf was higher in summer-autumn than in winter-spring (Fig. 2.4b). In oceanic waters, SSHA *iav* was relatively high across all seasons but varied spatially; both SSHA and SST *iav* generally increased below the shelf break from summer to winter (Fig. 2.4b and c). For alongshore wind stress, inter-annual variability increased from summer to winter months as seen in the length of the whiskers in boxplot figures (Fig. 2.3).

Table 2.2 Range of annual anomalies (AA) for each region and season for sea surface height anomaly (SSHA), sea surface temperature (SST), and chlorophyll-a concentration (Chl-a).

	Season	Shelf			Oceanic		
		Min AA	Max AA	Range	Min AA	Max AA	Range
SSHA (m)	Summer	-0.0875	0.101	0.1885	-0.15	0.186	0.336
	Autumn	-0.102	0.0895	0.1915	-0.146	0.18	0.326
	Winter	-0.0778	0.082	0.1598	-0.151	0.167	0.318
	Spring	-0.0777	0.0735	0.1512	-0.147	0.193	0.34
SST (°C)	Summer	-1.54	1.5	3.04	-1.53	1.14	2.67
	Autumn	-1.49	2.02	3.51	-1.55	1.38	2.93
	Winter	-1.22	1.09	2.31	-1.39	1.22	2.61
	Spring	-0.921	0.845	1.766	-1.1	1.13	2.23
Chl-a (mg m ⁻³)	Summer	-3.06	2.59	5.65	-1.61	2.01	3.62
	Autumn	-3.73	2.47	6.2	-1.86	1.37	3.23
	Winter	-3.44	3.2	6.64	-1.66	2.19	3.85
	Spring	-2.86	2.23	5.09	-1.31	1.53	2.84

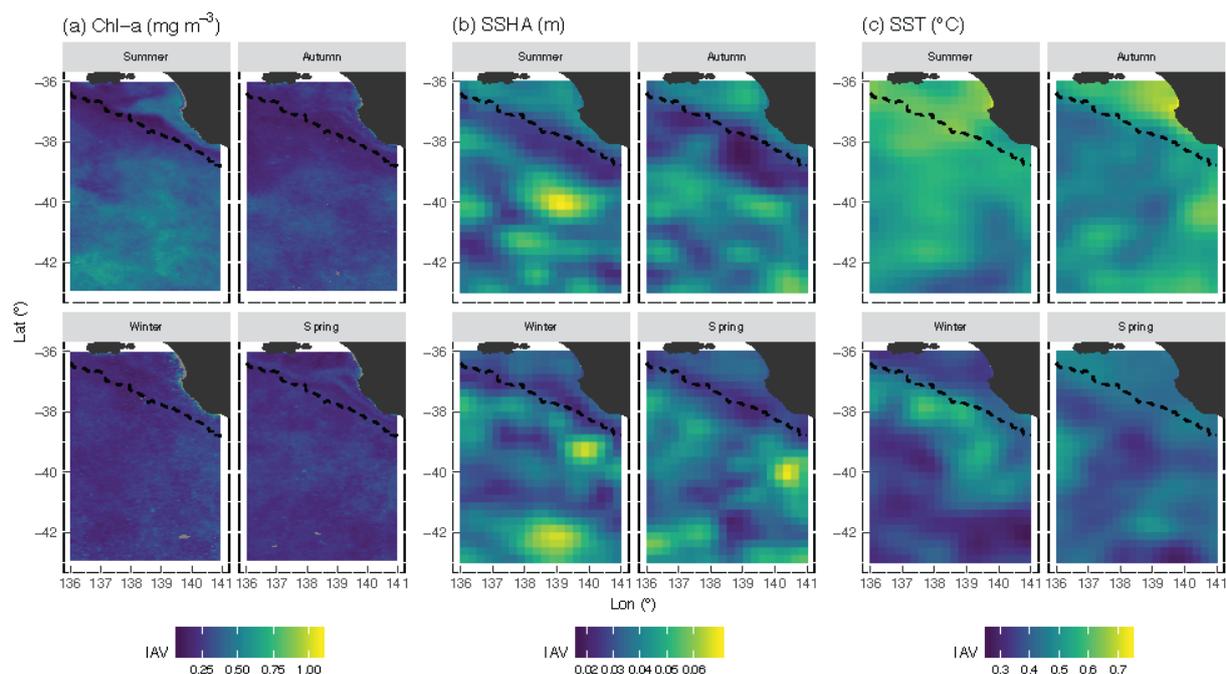


Figure 2.4 Standard deviation of the inter-annual variability (iaav, i.e. annual anomalies) for each season for (a) chl-a, (b) SSHA, and (c) SST. The black dashed line represents the 2000 m isobath separating shelf and oceanic regions.

Structural changes in long-term trends

The timing of significant trend breakpoints among the different environmental parameters were similar to a certain extent (Table 2.3). Shelf SSHA and SST and oceanic SSHA had the highest number of significant trend breakpoints (4; Fig. 2.5). The trend directions between breakpoints for shelf and oceanic SSHA were the same although there was some lag between the timing of their breakpoints. In more recent years, shelf and oceanic SSHA have been on an uptrend. There were different number of breakpoints between shelf and oceanic SST, however their trend directions between similar periods were generally the same i.e. warming periods from 1997 – 2013 and a cooling period from 2014 – 2016. Table 2.3 details the dates of breakpoints for the different environmental parameters. None of the trend segments in shelf chl-a was significant. Oceanic chl-a was usually on a downtrend but had several abrupt spikes (2003, 2006, 2011). There were two break points for SOI in 2001 and 2010 which were also identified for shelf SST. There were no trend breakpoints detected for alongshore wind stress and SAM. Several breakpoints of shelf and oceanic parameters coincided with El Niño and/or La Niña years (Table 2.3).

Table 2.3 Linear models of segments between trend breakpoints for various environmental parameters in the shelf and oceanic region, and climate indices. SST, sea surface temperature; SSHA, sea surface height anomaly; chl-a, chlorophyll-a; SAM, Southern Annular Mode; SOI, Southern Oscillation Index. Numbers within brackets represent the monthly index within a year. The ending date for each period that corresponds to an El Niño (EN) or La Niña (LN) year is also indicated. * < 0.05, ** < 0.001, *** < 0.0001. n.s. = non-significant.

Variable	Period	Slope	n	P-value	EN/LN
Shelf					
SSHA (m)	1997(1) - 2000(7)	0.0331	42	***	LN
	2000(8) - 2004(2)	-0.0163	43	***	
	2004(3) - 2009(9)	0.0108	67		EN
	2009(10) - 2013(10)	0.0207	49	***	
	2013(11) - 2016(12)	0.00313	39	n.s.	
SST (°C)	1997(1) - 2001(10)	0.152	57	***	
	2001(11) - 2006(3)	0.245	53	***	EN
	2006(4) - 2010(2)	0.289	47	***	LN
	2010(3) - 2013(10)	0.381	44	***	
Chl-a (mg m ⁻³)	2013(11) - 2016(12)	-0.133	39	*	
	1997(9) - 2002(11)	-0.00805	62	n.s.	
Alongshore wind stress	2002(12) - 2016(12)	-0.00155	170	n.s.	
	1997 (1) - 2016 (12)	0.000221	240	***	
Oceanic					
SSHA (m)	1997(1) - 1999(12)	0.0220	35	***	LN
	2000(1) - 2004(9)	-0.00860	57	***	
	2004(10) - 2009(4)	0.0101	55	***	EN
	2009(5) - 2012(8)	0.0106	40	***	
	2012(9) - 2016(12)	0.000845	53	n.s.	
SST (°C)	1997(1) - 2001(9)	0.246	56	***	
	2001(10) - 2012(12)	0.0448	135	***	
	2013(1) - 2016(12)	-0.184	49	**	
Chl-a (mg m ⁻³)	1997(9) - 2003(10)	0.00457	73	n.s.	
	2003(11) - 2006(11)	-0.0697	37	***	EN
	2006(12) - 2012(8)	-0.0229	69	**	
Climate indices	2012(9) - 2016(12)	-0.0286	53	**	
	SAM				
SOI	1997 (1) - 2016 (12)	-0.0195	240	***	
	1997(1) - 2001(3)	6.17	50	***	
	2001(4) - 2010(3)	0.848	108	**	
	2010(4) - 2016(12)	-3.93	82	***	

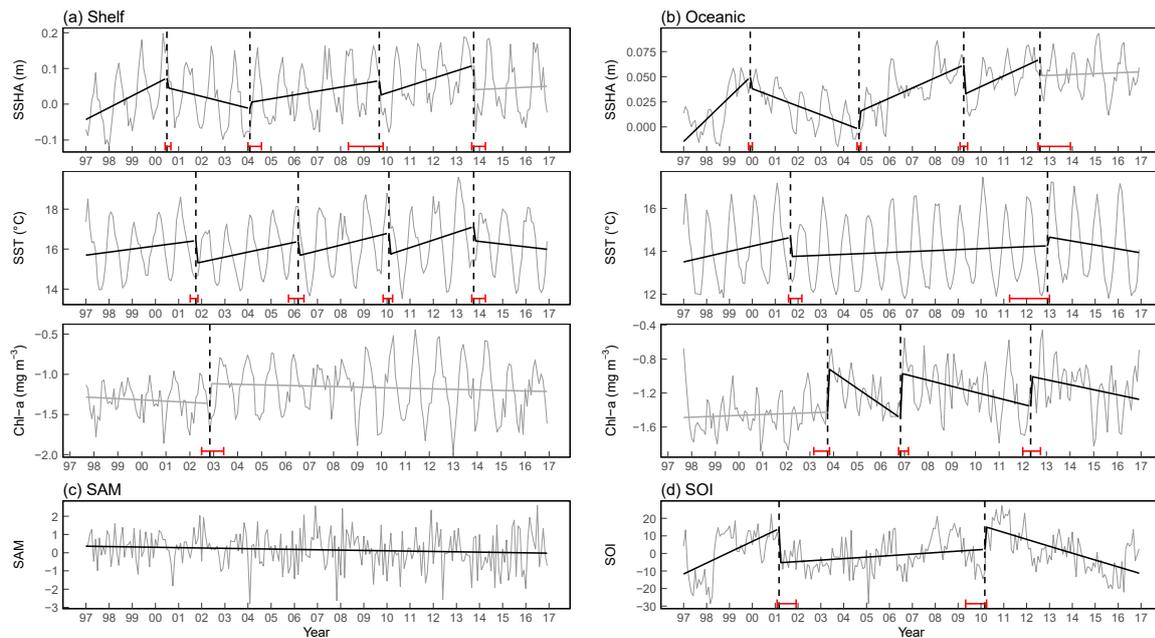


Figure 2.5 BFAST analysis on spatially averaged monthly sea surface height anomaly (SSHA, m), sea surface temperature (SST, °C), and sea surface chlorophyll concentration (Chl-a, mg m^{-3}) time series from 1997 – 2016 for the (a) shelf ($36^{\circ}\text{S} \sim 38^{\circ}$ shelf break, $138^{\circ} - 140^{\circ}\text{E}$), and (b) oceanic ($39^{\circ} - 42^{\circ}\text{S}$, $138^{\circ} - 140^{\circ}\text{E}$) regions. The BFAST analyses on the monthly values of the (c) Southern Annular Mode (SAM) and (d) Southern Oscillation Index (SOI) are also shown. The grey line graph represent the raw time series. Black and grey solid lines overlaying the raw line graph represent estimated significant (p -value > 0.05) and non-significant trend, respectively. Vertical dashed lines represent the estimated significant breakpoints in the trend and the red lines represent the 95% confidence intervals of the break dates. Black horizontal dashed lines in (d) indicate the El Niño (SOI < -7) and La Niña (SOI > 7) phases.

DISCUSSION

Several studies have been done on the seasonal changes of the Bonney Upwelling region, an important source of productivity in the Great Australian Bight ecosystem (Butler et al. 2002, Middleton and Bye 2007, Nieblas et al. 2009, Rogers et al. 2013). However, few have compared it to the adjacent oceanic waters associated with the Subtropical Front which are also an important source of productivity and food for top marine predators in the region. In this study, we described the intra- and inter-annual variability, and long-term trends of the physical oceanography of the southern waters (from shelf to oceanic) in the Kangaroo Island–Bonney Coast region. We found intra- and inter-annual variation in both shelf and oceanic

waters. Additionally, long-term trends of oceanographic parameters on the shelf and oceanic waters seemed to behave similarly to a certain extent.

Shelf vs Oceanic intra-annual variability

Our observations of seasonal changes in chl-a across the shelf waters corroborate those of Nieblas et al. (2009) where we found that the upwelling season occurred from November to April, and the nonupwelling season occurred from May to October. Within an annual cycle, upwelling-favorable conditions, such as low SSHA, localised areas of relatively low SST, and eastward alongshore wind stress and currents begin in the austral spring the year before. These conditions start off weak and peak in February and March. Downwelling-favourable conditions begin in May and tend to peak in June or August.

In the oceanic realm between 38°S and 42°S, there is a clear north-south migration of positive chl-a anomaly areas intra-annually; these areas developed far south of the shelf region in summer and gradually migrated northwards reaching a peak in their northern extent in winter and then retreating back south again. This north-south migration is similar to that of the STF in the region. Furthermore, anomalously high chl-a generally occurs north of the STF in this region. This may be explained by the northward migration of the STF in summer which destabilises the vertical structure of the water column, resulting in the weakening of the thermocline below the mixed layer leading to increased vertical mixing and enhanced biological activity (Tomczak et al. 2004, Thompson et al. 2015). The STF's migration may therefore influence the spatio-temporal variability in biological production in the southern waters of Australia, which in turn allows us to predict productivity regimes.

At finer scales, biological production in oceanic waters also seem to be linked to mesoscale eddies (Waite et al. 2007b). In particular, eddy activity at the shelf break increased in late autumn-winter (Middleton and Bye 2007) as indicated from our observations of increased variability in SST and SD contours in SSHA. Spatial variability in SST is a commonly used proxy for productivity (Bradshaw et al. 2004) and such temperature gradients can induce eddy formation (Gaube et al. 2015), which increases local productivity when nutrients are

transported offshore from coastal, upwelling or frontal areas (Waite et al. 2007b). This increase in SST variability appears to be due to increased water turnover from the STF being closer to the shelf break at the end of summer (Tomczak et al. 2004). Additionally, it could also be influenced by the strong alongshore eastward surface currents on the shelf that spill over the shelf break at the eastern end near the Bonney coast (possibly due to the narrowing of the shelf) into oceanic waters, triggering the formation of eddies that entrain water from the coastal side with elevated phytoplankton concentrations relative to the background (Gaube et al. 2015). Thus elevated entrainment of phytoplankton coupled with eddy-pumping (transport of nutrients upwards from deep to shallow waters) in the core of cyclonic eddies or at the periphery of convergent anti-cyclonic eddies (Waite et al. 2007b) would result in enhanced primary production (Fig. S2.2).

Despite dominant downwelling conditions in winter, some areas of enhanced chl-a persist on the shelf. As the upwelling plume dissipates during the nonupwelling season, positive shelf chl-a anomaly becomes less localized within the upwelling plume area and more dispersed over the shelf. Furthermore, upwelling events may still occur during the nonupwelling season but less frequently and shorter in duration than during the upwelling season (Nieblas et al. 2009). Hence, there may still be some biological productivity on the shelf during the nonupwelling season but to a lesser extent than during the upwelling season. Areas of positive shelf chl-a anomaly during winter were also relatively higher than those in oceanic waters, which may be linked to high mixing rates on the shelf (van Ruth et al. 2010). Additionally, baseline chl-a on the shelf may generally be greater than in oceanic waters, as coastal chl-a may benefit from nutrient runoff from land sources (McClatchie et al. 2006).

Long-term trends and association with climate indices

In the oceanic region, positive phases of SSHA and SST usually correspond to negative phases in chl-a. This inverse relationship between SSHA/SST and chl-a is understandable given that positive SSHA is associated with downwelling within anticyclonic eddies, which in turn is associated with warm waters and low primary production (Miyamura et al. 2002). Although this relationship was also observed in the shelf region, the trends for shelf chl-a were not statistically significant at the p -value = 0.05 level.

There was some association between shelf and oceanic parameters with ENSO, however it was not consistent. For the shelf region, this result is congruent with that found in previous studies on the southern shelf waters of South Australia (Middleton and Bye 2007, Nieblas et al. 2009). Middleton and Bye (2007) found that the effects of ENSO on upwelling of the South Australia tend to have a stronger correlation during strong ENSO events (1998 – 2003). Similarly, we found that several breakpoints for environmental parameters in the shelf and oceanic region were closely associated with that period. The lack of breakpoints detected in the SAM limited our ability to find an association between it and the environmental parameters of the study region. Perhaps the monthly timeseries were too coarse to detect breakpoints. Nevertheless, as this is only a preliminary analysis, our results do not necessarily mean that the SAM does not have an effect on the environment of the study region.

The responses of SSHA and SST to ENSO was similar to that previously described on the shelf in the GAB region– there was low (high) SSHA and SST during El Niño (La Niña). El Niño (La Niña) events tended to result in enhanced (reduced) upwelling, and reduced (enhanced) downwelling (Middleton et al. 2007). Both shelf and oceanic SSHA had a negative trend from 2000 – 2004. During that period there was only one El Niño event, and it was not followed by La Niña events unlike the other El Niño events in 1997, 2006 and 2009. Hence, the negative trend in SSHA may be due to the influence of the cooler El Niño event, which was not subsequently compromised by warmer La Niña events. Similarly, the negative SST trend in both regions from 2013 – 2016 corresponded to a shift from warm La Niña to cooler El Niño years.

Implications for predators in the region

We found that surface chl-a concentration varied seasonally in the oceanic waters south of Kangaroo Island and that this was probably due to coastal upwelling (shelf), the north-south migration of the STF and high frequency eddy formation and shedding (oceanic). Mesoscale features such as eddies and fronts are important environmental features for many marine meso- and apex predators such as seals, whales, sharks, and seabirds (Bost et al. 2009). Seals breeding on Kangaroo Island may have an advantage over other seal colonies given their

proximity to the Bonney Upwelling region. For example, lactating long-nosed fur seals from the Cape Gantheaume colony have alternating foraging locations where they forage on the shelf in summer, and switch to oceanic waters close to the STF in autumn-winter (Baylis et al. 2008a); whereas lactating long-nosed fur seals from colonies further from the Bonney Upwelling region may forage primarily in oceanic waters near the STF from summer through winter (Baylis et al. 2008b). Additionally, slope waters are also commonly utilised by many marine predators as it can be highly productive (Clarke et al. 2006, Page et al. 2006, Thums et al. 2013). The oceanic waters near the slope seem to be particularly productive in winter, which may be beneficial to land-breeding marine predators provisioning offspring, as they do not have to travel too far from the colony to access productive foraging areas when summertime upwelling stops. Nevertheless, at least based on surface chl-a, the shelf may still have periods of biological productivity during the downwelling season, hence shelf waters may still be used as foraging grounds by marine predators in the region during that time (Lowther et al. 2013).

Inter-annual variability is linked to year-to-year predictability of biologically productive areas (Arthur et al. 2015). Generally, inter-annual variability of chl-a, SSHA, and SST are greater in summer than in winter, especially on the shelf. However, the opposite is true along the shelf break off the Bonney Coast for SSHA and alongshore wind stress. This inconsistency may suggest that there are other factors, for example subsurface activity and bathymetry, influencing the surface oceanographic dynamics in this region. Nevertheless, these observations show that there is a relatively high amount of inter-annual variability in the environment for this region. This variability among years can influence the foraging behaviour and hence reproductive success of marine predators that utilize it. Antarctic fur seals were found to show a high degree of interannual fidelity to foraging sites that had high long-term variation in SST (Arthur et al. 2015). Additionally, in two separate studies (one in 2000/2001 and the other in 2005) on Cape Gantheaume long-nosed fur seals, the majority of the fur seals from the earlier study foraged on the shelf in winter (Page et al. 2006), while the majority fur seals in the later study foraged in oceanic waters in winter (Baylis et al. 2008a).

CONCLUSIONS

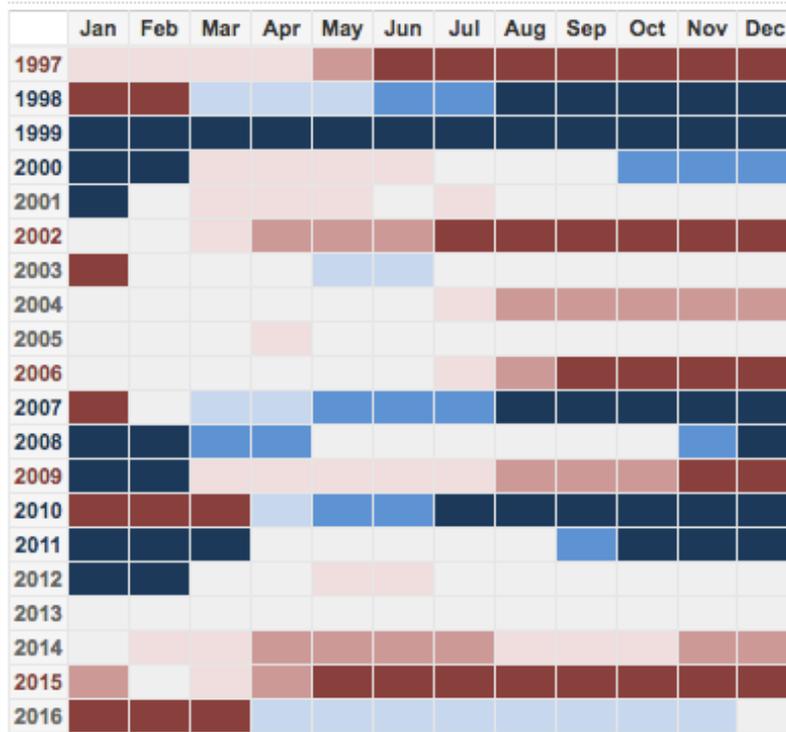
Using two decades of remote-sensed satellite data, our results agree with the current general understanding of seasonal oceanographic dynamics of the Bonney Upwelling on the shelf – shelf waters at the Bonney Upwelling are productive from late-spring to summer. In autumn-winter, the high chl-a in the summertime upwelling plume is replaced by low chl-a due to downwelling conditions. However, high chl-a can still persist on the shelf during the downwelling season, which may originate from the Bonney Upwelling plume in summer and/or smaller shelf upwelling events in winter. Productive oceanic waters are associated with the STF and eddy activity; they generally follow the north-south migration of the STF where they are furthest from the shelf break in spring-summer and closest to the shelf break in winter-autumn. Inter-annual variability of chl-a, SSHA, and SST is generally higher in summer than in winter for both shelf and oceanic waters, with some exception at the shelf break off the Bonney Coast. The results in this study gives a regional perspective of the oceanographic spatial and temporal variability which ultimately determines productivity in southern Australian waters. Such information may be useful for understanding why some apex predators in the region vary their foraging locations over space and time. Future research using more in-depth *in situ* oceanographic data and linking the temporal and spatial variability of oceanographic conditions to prey assemblages can further improve our understanding of the mechanisms driving apex predator behaviours in the region especially the triggers prompting shifts in foraging location between seasons.

ACKNOWLEDGEMENTS

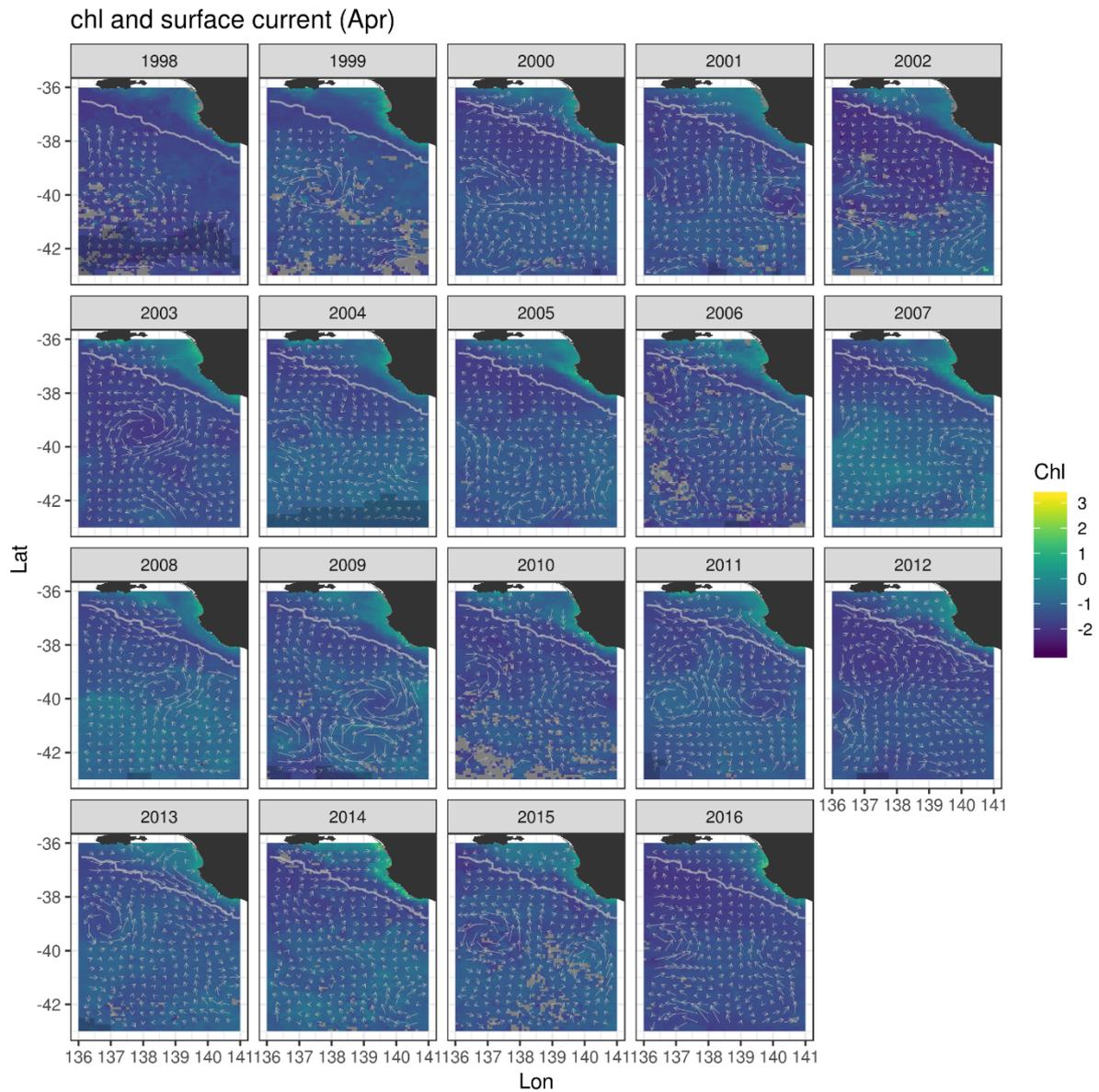
DF is supported by the University of Tasmania PhD scholarship and stipend. There are no conflicts of interests for any author. Data used in the analyses can be publicly available and can be obtained from the sources mentioned in “2. Materials and Methods”. Code used in analyses can be obtained at <https://github.com/oofd/satellite-time-series/>.

SUPPLEMENTARY INFORMATION

Monthly ENSO Outlook values



Supplementary Figure 2.1 Monthly likelihood of El Niño (red) and La Niña (blue) events based on El Niño- Southern Oscillation (ENSO) El Niño 3.4 and Southern Oscillation Index. Degree of likelihood increases from light, to medium to dark colours, with dark colours representing a confirmed El Niño or La Niña event. Red or blue coloured years indicate if the year was dominantly an El Niño or La Niña year, respectively. The figure was adapted from <http://www.bom.gov.au/climate/enso/outlook/#tabs=ENSO-Outlook-history> (date accessed: 1 October 2017).



Supplementary Figure 2.2 Annual plots during April for chlorophyll-a (Chl). Sea surface currents are represented by arrows, with length indicating magnitude). The white solid line represents the boundary between shelf and oceanic waters (2000m depth). Anti-cyclonic eddies (typically with elevated chlorophyll-a at their edges) have anti-clockwise currents and vice versa (elevated chlorophyll-a typically in the core of a cyclonic eddy).

Chapter 3 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 (LNFS; *Arctocephalus forsteri*) at Cape Gantheaume in South Australia have been observed to display alternate foraging strategies where 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 that 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.

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 and 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).

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 offspring-rearing period progresses, offspring energetic demands 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, Beuplet et al. 2004). Longer foraging trips tend to be associated with individuals traveling to more distant oceanic foraging grounds (as opposed to nearby continental shelf waters) (Nordstrom et al. 2013) where higher quality (energy-dense) prey may be found, potentially resulting in greater energetic gain (Staniland and Boyd 2003).

Long-nosed fur seals (LNFS; *Arctocephalus forsteri*) 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).

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. 3.1). 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 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 (Nieblas et al. 2009). During the nonupwelling 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 to 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 – 42° S in the study region and can be identified as the 14 °C 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 chlorophyll-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).

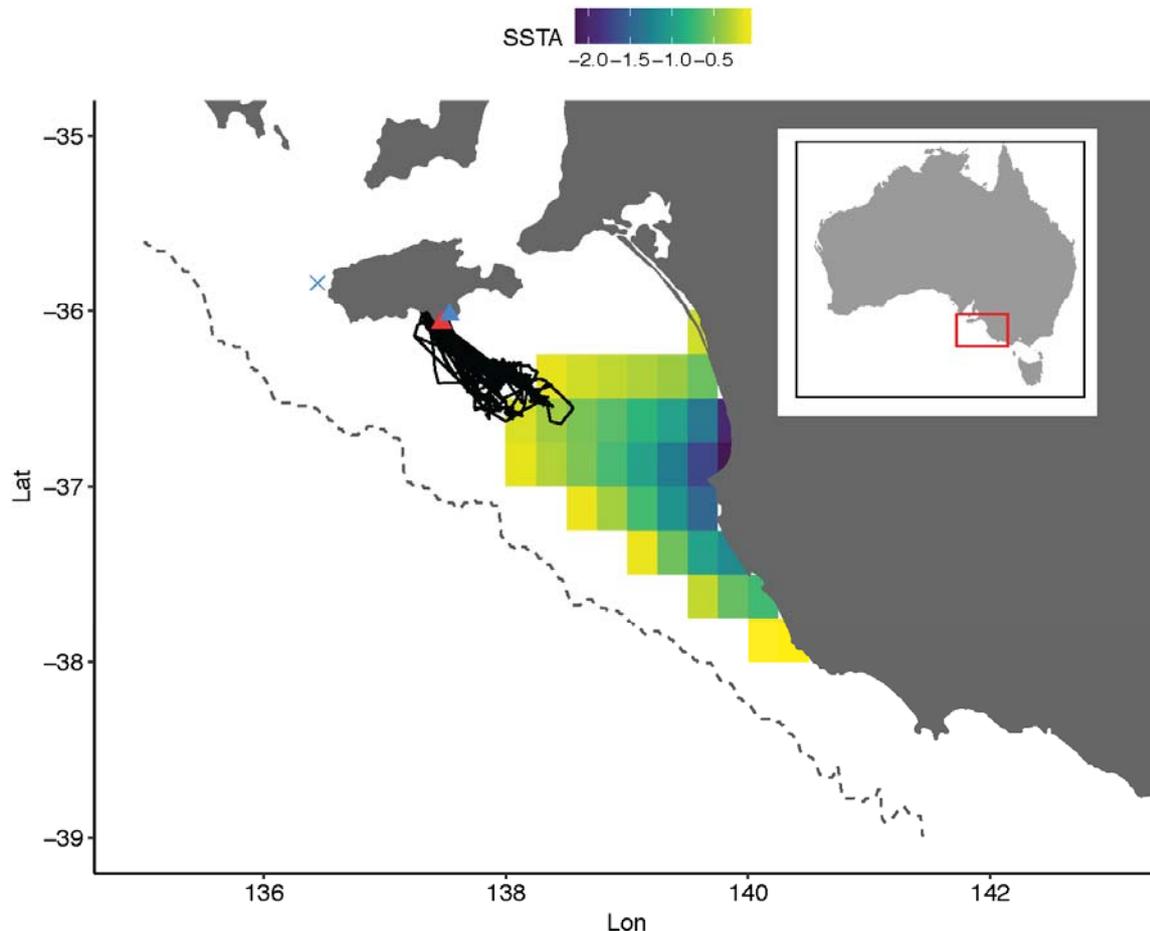


Figure 3.1 Map of the study region. The coloured squares represent the mean area of the Bonney Upwelling plume from January – April 2016 as represented by anomalously cool sea surface temperature (sea surface temperature anomaly; SSTA ≤ -1 °C). The red triangle represents the Long-nosed fur seal (*Arctocephalus 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 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.

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 days) to shelf and shelf break waters, associated with the Bonney Upwelling region. During the nonupwelling season, they make longer trips (~ 2 weeks) to

oceanic waters associated with the STF (Baylis et al. 2008a) until the weaning of their pups at about 9-10 months 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 on 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 the survival of themselves and their offspring is at stake; Biuw et al. 2009, Péron et al. 2010). Geolocation (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 aim 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.

METHODS

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 consider 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), forty five lactating LNFS were randomly selected and captured using a hoop-net (Table 3.1). Seals were anaesthetised using Isoflurane (Veterinary Companies of Australia, Artarmon, New South Wales, Australia), administered via a portable gas anaesthetic machine (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia). The seals were weighed (± 0.5 kg) and their body length (nose to tail) and axial girth were measured (± 1 cm). Geolocation (GLS, Intigeo-C330, 17 x 19 x 8 mm, 3.3 g, Migrate Technology Ltd, Cambridge, UK) loggers 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 – September (late lactation; Table 3.1). For recaptures, some seals were first captured via a hoop-net and then immobilised with Zoletil (dose 2 mg/kg; Virbac, Sydney, Australia), administered by a hand injection to the rump. For other recaptures, seals were first immobilised with Zoletil, administered using 1 ml, 1.5 x 30 mm (diameter x length) barbless darts (Telinject, Germany),

fired from a CO₂-powered tranquilizer gun (G.U.T.50, Telinject, Germany). The lightly sedated females were then captured with a hoop-net and manually restrained.

Table 3.1 The types of 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. Please see Table S3.1 for more details of the source. ^a Data was 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. Freq, frequency; res, resolution.

Variable	Unit	Source	Freq	Spatial res.	SD?
SSTA – sea surface temperature anomaly ^a	°C	NOAA Optimum Interpolation daily Sea Surface Temperature Anomaly	Daily	0.25°	Yes
SSHA – sea surface height anomaly ^a	m	IMOS Optimal Interpolated daily Gridded Sea Level Anomaly	Daily	0.2°	Yes
<u>SST_c – anomalous cold SST</u>	°C	Subset from daily SSTA ≤ -1 °C	Daily	0.25°	No
Subsurface temperature (uppermost 70 m)	°C	IMOS Animal Tracking Facility	Irregular		Yes
MLD – Mixed layer depth	m	IMOS Animal Tracking Facility	Irregular		No
Subsurface salinity (<u>uppermost 70 m</u>)	g kg ⁻¹	IMOS Animal Tracking Facility	Irregular		Yes
SAM – southern annular mode		NOAA daily Antarctic Oscillation index	Daily		No
Wind velocity	cm s ⁻¹	NOAA ESRL PSD	6 hourly	1.88 x 1.9°	No
Alongshore wind stress ^b	N m ⁻²	Derived from wind velocity	Daily	1.88 x 1.9°	Yes
Highly collinear pairs:					
subsurface temperature SD and subsurface salinity SD					
subsurface salinity SD and mean SSHA					
SSHA SD and mean SSHA					

In both study years, the GLS loggers measured ambient light every minute and recorded the maximum value every 5 minutes. 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-hour period. The 2017 loggers sampled sea temperature after 20 minutes of being continuously wet and recorded the minimum, maximum and mean temperature for every 4-hour period. Each logger was activated and left in an open area at the study site for approximately 5-7 days either immediately before or after deployment to obtain solar elevation estimates necessary for instrument calibration.

Pup cross-sectional weighing

In both years, pups from the same area were randomly selected and weighed using an electronic spring balance (Kern, Germany, ± 0.5 kg) in summer (2016: males = 51, females = 59; 2017: males = 58, females = 52) and winter (males $n = 30$, females $n = 30$). Pups weighed in summer were part of an ongoing annual pup census conducted by the South Australia Research and Development Institute (SARDI) (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.

Location estimation

All analyses were done using the R program (v3.5.1) (R Core Team 2019). Locations were estimated from the raw light data by first using the *BAStag* package (v0.1-3) (Wotherspoon et al. 2016a) to estimate times of twilight (dawn and dusk). Next, the *SGAT* package (v0.1.3) (Wotherspoon et al. 2016b) was used to create Markov Chain Monte Carlo simulations within a Bayesian framework to estimate the final posterior mean of two 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 Supplementary Information for *SGAT* validation). The durations of foraging trips were thus determined as the wet period between dry periods inferred from the GLS data.

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 after the abrupt change were also to oceanic waters of similar distances for all but one individual (Fig. S3.1). 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.

Foraging habitat in relation to environmental variability on the shelf

Details of environmental data used for analyses are described in Table 3.1 and Table S3.1. Daily sea surface temperature anomaly (SSTA), and sea surface height anomaly (SSHA) were extracted for each cell in the shelf foraging area (37.5°S – shelf boundary, $137 - 141^\circ\text{E}$). 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 nonupwelling 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 3.1). 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 in height (Kalnay et al. 1996) for the study period. Alongshore wind stress (τ'_v ; units: N m^{-2}) was calculated as:

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

Where W is wind speed (ms^{-1}), C_d is the drag coefficient (1.2×10^{-3}), ρ_a is air density ($\rho_a = 1.22 \text{ kg m}^{-3}$), α is wind direction ($^\circ$), and β is the dominant angle of the Bonney coast line ($\beta = 315^\circ$). 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 (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 3.1, Fig. 3.1). ASLs 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 (v1.0-1) (Kelley 2018) following methods detailed in 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 was 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 3.1). 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 3.1).

Daily Southern Annular Mode (SAM) index was also used in analyses (Table 3.1). 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 ($55 - 50^\circ\text{S}$) (Lovenduski and Gruber 2005).

The 5-day running mean of SSTA, SSHA, subsurface temperature and subsurface salinity variables and 5-day 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 a couple of 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.

Inter-annual variability in shelf and oceanic environmental conditions

We compared inter-annual variability in shelf and oceanic conditions during the upwelling and nonupwelling season. While the upwelling season begins in November, for simplicity, we considered the upwelling season as January – April and the nonupwelling 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 $SSTA \leq -1 \text{ } ^\circ\text{C}$ (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 ($0.25 \times 0.25 \text{ } ^\circ$) and the daily intensity of SST_c for the shelf and oceanic regions was calculated from averaging across each of the respective regions.

Statistics

Logistic generalised linear mixed models (GLMMs) with a binomial error structure 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 3.1) using the “glmer” function from the *lme4* package (v1.1-19) (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 two variables, the more biological 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 AICc for small sample sizes and their weights of evidence (Burnham and Anderson 2004). The highest ranked model had the lowest AICc. Where the delta AICc between two 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. We fitted a Gaussian generalised additive model (GAM) with identity link (*mcgv* package v1.8-23) for MLD against the smoothed interaction term between shelf salinity and season (upwelling or nonupwelling) and the season term. All final models were checked for normality, homogeneity and autocorrelation (GLMM: *DHARMA* package (v0.2.0) (Hartig 2018); GAM: “gam.check” function). If heteroscedascity or autocorrelation was present, weighted variance functions and an autoregressive term was added to the model, respectively. Due to small sample sizes, non-parametric two-sample Wilcoxon test was used to compare the means of 2 groups.

RESULTS

Location statistics and track summaries

We recovered GLS loggers from 17 adult female Long-nosed fur seals allowing us to quantify their at-sea behaviour during lactation (Fig. 3.2). 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. S3.2).

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 3.2. Henceforth, all means (\pm SD) and totals reported are for the remaining 11 individuals used for analyses.

Table 3.2 Deployment details, number of foraging trips for 11 lactating Long-nosed fur seals from Cape Gantheaume, Kangaroo Island that were tracked in 2016 and 2017. ^aJanuary – April; ^bMay – October; Uw, upwelling.

ID	Deployment date	Recovery date	Deployment duration (d)	Mass (kg)	Length (cm)	No. trips		Total trips	Switch date
						Uw ^a	NonUw ^b		
72	02/02/2016	19/08/2016	199	40.5	139	12	5	17	10/5/2016
73	01/02/2016	22/08/2016	203	33.5	130	14	11	25	24/5/2016
77	05/02/2016	21/08/2016	198	44	128	12	6	18	13/5/2016
78	06/02/2016	20/08/2016	196	48.5	138	19	6	25	9/5/2016
450	31/01/2016	25/09/2016	238	43.5	144	13	10	23	20/5/2016
305	28/01/2017	06/07/2017	159	44	136	5	3	8	7/4/2017
311	05/02/2017	07/08/2017	183	41	133	6	6	12	29/3/2017
319	07/02/2017	05/07/2017	148	55	146	9	2	11	19/4/2017
322	09/02/2017	12/07/2017	153	45	142	6	2	8	27/4/2017
326	10/02/2017	07/08/2017	178	41	130	10	3	13	7/4/2017
351	13/02/2017	30/06/2017	137	45	141	5	2	7	23/2/2017
						11.9 \pm	6.86 \pm		
						0.409	0.422		

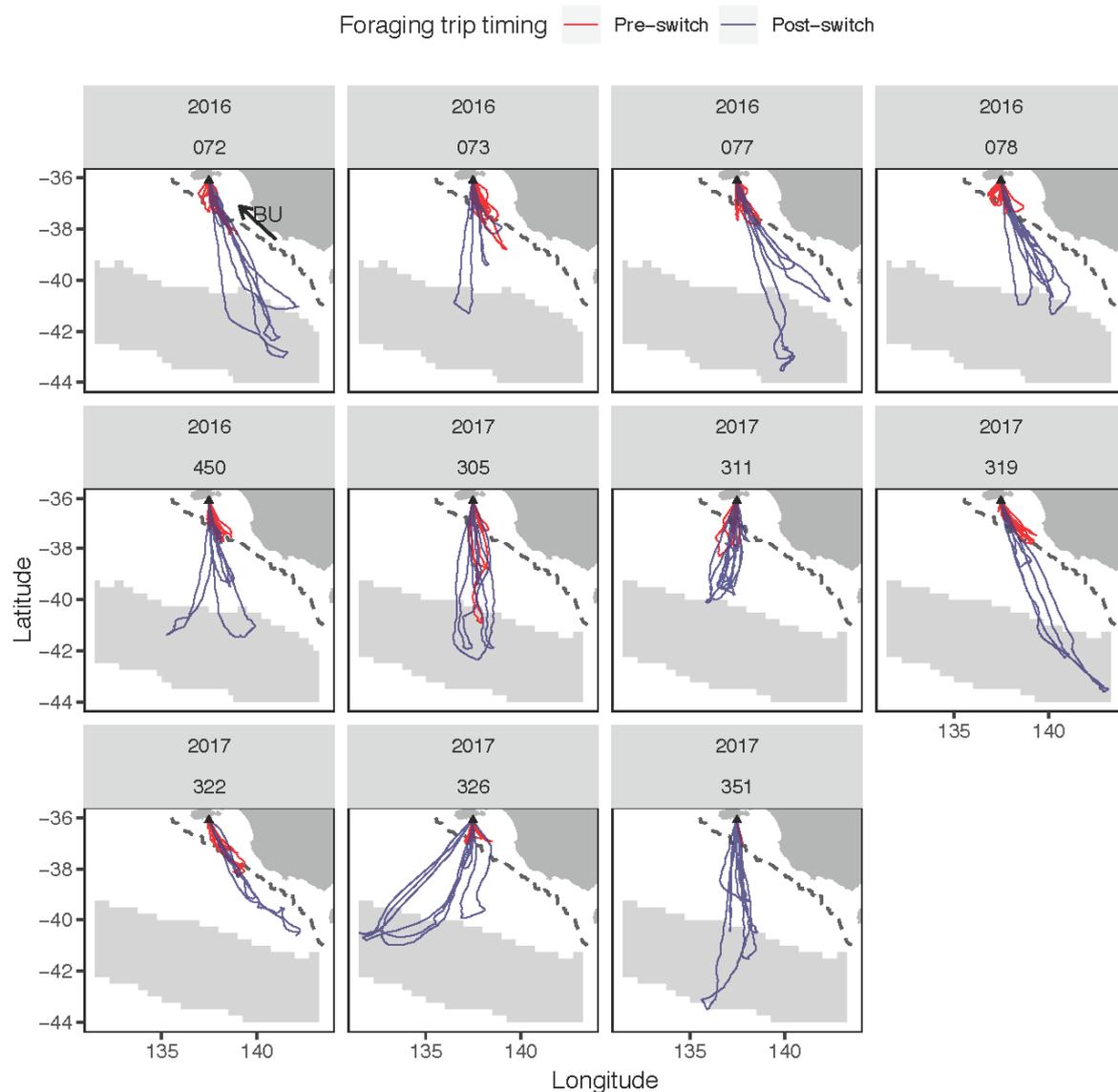


Figure 3.2 Individual tracks of long-nosed fur seals provisioning pups, which displayed both shelf and oceanic foraging behaviour. The dashed grey line represents the shelf break (2000 m isobath). The black arrow represents the direction where the Bonney Upwelling (BU) plume originates from and flows 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 grey area represents the approximate location of the subtropical front for the entire year (annual mean SST between 12 – 14°C).

Overall, mean foraging trip duration was shorter during the upwelling (7.14 ± 0.55 days; range: 1.06 – 26.5 days) as compared to the nonupwelling (15 ± 7.62 days; range: 3.17 – 34.8 days; Wilcox test: $W = 1126.5$, $p\text{-value} = < 0.001$) season. Foraging trip durations during both

seasons were longer in 2017 than in 2016 (Table 3.3). For both years combined, the mean date that females switched from shelf to oceanic foraging was 22 April \pm 8.2 days (range 23 Feb – 24 May; middle of lactation period); and on average the switch date was earlier in 2017 than in 2016 by 42 days (Table 3.3). The mass of adult females used in this study did not differ between the two years. Cross-sectional summer pup mass was greater in 2016 than in 2017 (Table 3.3). However, the opposite was true for the winter pup mass (Table 3.3, for pup growth rates by sex see Table S3.2).

Table 3.3 Comparisons of mean \pm SD of various parameters between 2016 and 2017. Upwelling and nonupwelling seasons are from Jan – Apr and May – Oct, respectively. Non-parametric Wilcoxon test were used for statistical analyses. * < 0.05; ** < 0.01; *** < 0.001; n.s. = non-significant; U, upwelling; NU, nonupwelling.

Variable	Groups	2016			2017			U	p-value
		Mean	SD	n	Mean	SD	n		
Switch date (d)		15-May	6.53	5	3-Apr	21.9	6	30	**
Trip duration (d)	U	5.3	3.16989	70	10.3	6.99	41	812	***
	NU	13.3	7.48	38	18.4	6.85	18	195	*
Adult female mass (kg)		42 \pm	5.55	5	45 \pm	5.15	6	9.5	n.s.
Pup summer mass (kg)		6.9 \pm	1.41	110	6.55 \pm	1.46	110	7025	*
Pup winter mass (kg)		11 \pm	2.11	60	12.6 \pm	2.25	60	1060	***
Alongshore wind stress (Nm ⁻²)	U	0.00924	0.0539	121	0.00262	0.0543	120	7886	n.s.
	NU	-0.0643	0.0836	184	-0.0514	0.0661	184	15679	n.s.
Sea surface height anomaly (m)	U	-0.0118	0.0448	1815	0.0216	0.0398	1800	918760	***
	NU	0.0696	0.0696	2625	0.0578	0.0605	2760	3887600	***
Shelf SSTc (°C)	U	-1.74	0.571	186	-1.22	0.184	23	840.5	***
	NU	-1.23	0.200	121	-1.02	NA	1	9.5	n.s.
Oceanic SSTc (°C)	U	-1.35	0.377	199	-1.21	0.208	3119	260350	***
	NU	-1.22	0.189	20066	-1.19	0.171	8402	79056000	***
Upwelling events	U	13			14				
	NU	20			18				
Shelf area of SSTc (n 0.25 x 0.25° cells)	U	186			23				
	NU	121			1				
Oceanic area of SSTc (n 0.25 x 0.25° cells)	U	199			3119				
	NU	20066			8402				

Table 3.4 Summary of 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 three models are presented, and the accepted model is presented in bold. For the full list of candidate models please see Table S3.3. logLik, log-likelihood; AICc, Akaike’s Information Criterion corrected; 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	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

Table 3.5 Results of the final logistic GLMM examining the effects of shelf oceanographic parameters on shelf (vs. off-shelf) foraging trips made by female Long-nosed fur seals provisioning an offspring. Model selection was done using delta AICc. sal_mean, average shelf subsurface salinity; SSHA_mean, average shelf sea surface height anomaly; N_{trips}, number of foraging trips; N_{seals}, number of individual seals.

Parameter	Variance	Estimate	SE	SD	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			0		
N _{trips} = 158						N _{seals} = 11

Table 3.6 Summary of the generalised additive model examining the effects of shelf salinity on mixed layer depth in different seasons (upwelling vs nonupwelling). ** < 0.01; *** < 0.001.

Smoothed terms	edf	F	p-value	Parametric terms	Estimate	SE	T	p-value
s(salinity):season nonupwelling	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

Foraging strategy in relation to shelf oceanographic properties

The timing of the switch from predominantly shelf to oceanic foraging was closely associated with the cessation of upwelling activity on the shelf (Fig. 3.3). 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 alongshore wind stress (Fig. 3.3). Variables removed as a result of high collinearity between other variables are the standard deviations of subsurface temperature, salinity, and SSHA (Table 3.1). The most important predictors for the probability of foraging on the shelf (vs. off-shelf) included the interaction term between mean SSHA and mean salinity (Table 3.4; Fig. 3.4). A detailed summary of the most parsimonious model is given in Table 3.5. 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. nonupwelling season), the probability of shelf foraging increased with lower shelf salinity. Results of the GAM showed that MLD generally increased with shelf salinity, however the effect was greater during the nonupwelling season (Table 3.6, Fig. 3.5).

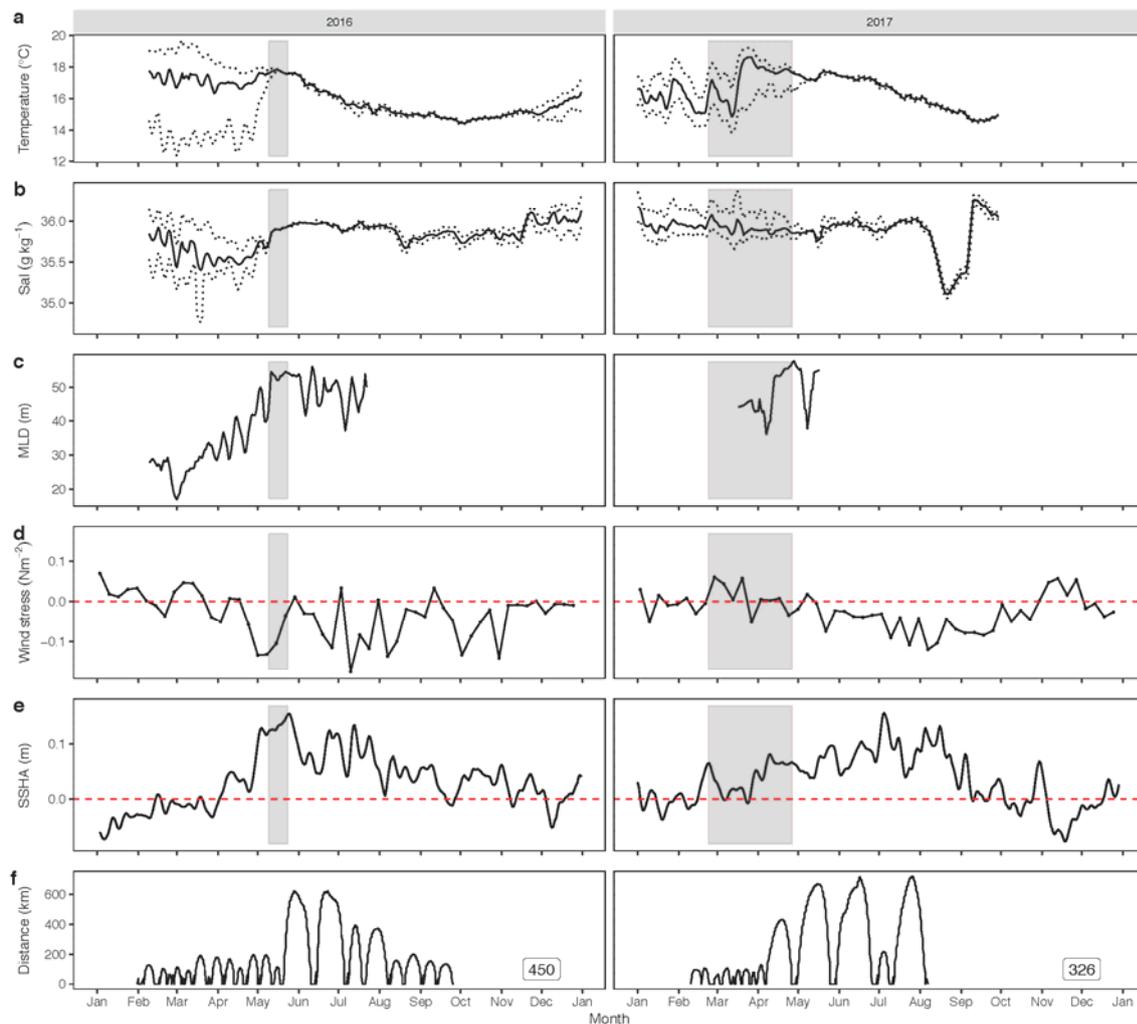


Figure 3.3 Inter-annual comparison of shelf (a) 5-day running average of daily maximum, mean, and minimum subsurface (up to 70 m in depth) temperature and (b) salinity; (c) shelf mixed layer depth also obtained from the CTD tags deployed on Australian sea lions; (d) average weekly alongshore wind stress (positive wind stress is easterly and upwelling-favourable); (e) 5-day running average of sea surface height anomaly (SSHA); and (f) examples of the straight line distance travelled from the colony from two Long-nosed fur seal tracks (labels represent the seals' ID). Subsurface temperature and salinity data was 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 was a combination of data obtained from a mooring station situated near Kangaroo Island (Fig. 3.1) and CTD tags deployed on Australian sea lions from a nearby colony. A larger temperature range in the water column is an indicator 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.

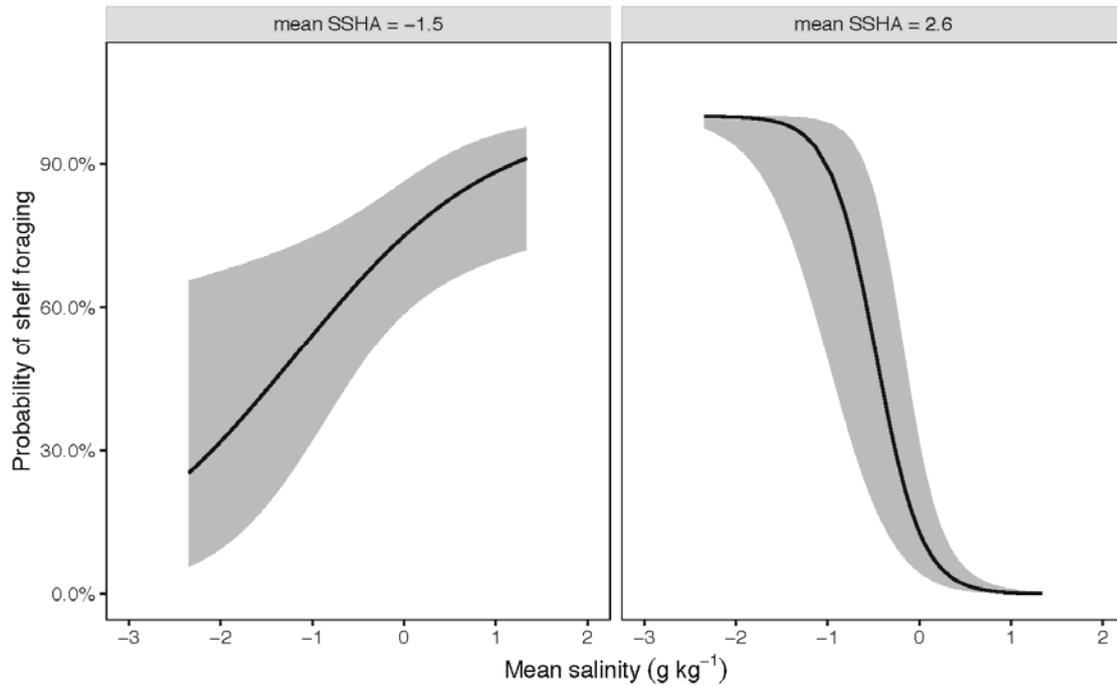


Figure 3.4 The probability of foraging on the shelf (as opposed to oceanic waters) in relation to the interaction between mean shelf sea surface height anomaly (SSHA) and shelf salinity. Curves were fitted using the final logistic GLMM as shown in Table 3.4. The shaded area represents the 95 % confidence intervals around the estimated effect.

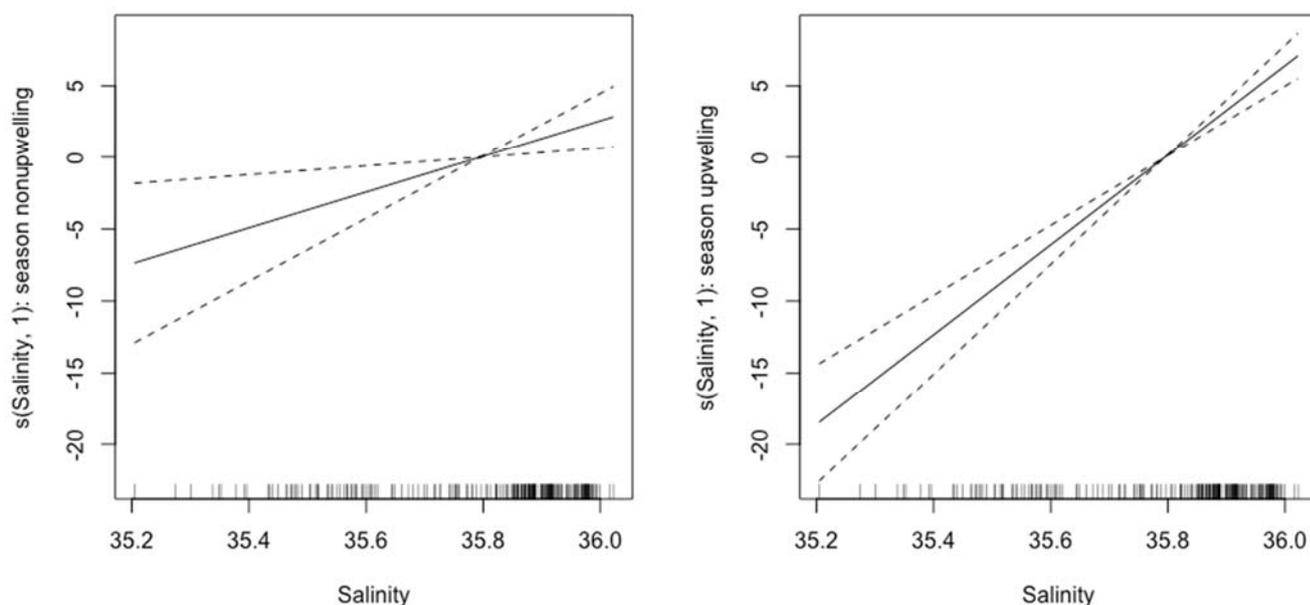


Figure 3.5 Partial residual plots of the smoothed term mean shelf salinity (g kg^{-1} ; in the uppermost 70 m of the water column; x-axis) on the mean shelf mixed layer depth (y-axis) from a fitted generalised additive model.

Inter-annual variability in shelf and oceanic oceanography between seasons

Table 3.3 contains details 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 nonupwelling season between years. There was no difference in SST_c between years only during the nonupwelling season. The intensity and area of shelf SST_c was greater in 2016 during both seasons (Table 3.3). Conversely, the area oceanic SST_c during the upwelling season was much smaller in 2016, although its intensity was greater.

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.

Our results show that lactating long-nosed fur seals 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 therefore 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 sea surface height anomaly on the shelf were the strongest predictors of whether an individual foraged on the 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.

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. 3.3). This is likely a signal for the cessation of upwelling-favourable conditions, and thus decline in shelf productivity (Nieblas et al. 2009) (and possibly 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 mixed layer depth is above the lower extent of the photic zone (Sverdrup 1953) as phytoplankton require both nutrients and light for growth. When upwelling occurs, deep cold and salty waters are upwelled to the surface (Middleton and Bye 2007), thus replenishing nutrients in the surface layer while the mixed layer depth 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 (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 Adelie 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 and Bye 2007). While deep vertical mixing during downwelling may replenish depleted surface nutrient levels, unlike in the upwelling scenario, due to deeper mixed layer depths, 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 utilise 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 nonupwelling season is associated with a shallower mixed layer

depth which in theory is more ideal for primary production in this context. A possible explanation maybe that the weakening of downwelling-favourable winds leads to a reduction in deep vertical mixing (and hence shallower MLD), allowing phytoplankton to remain and utilise 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 mixed layer depth is unclear.

Variability of 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. 3.3); 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 two 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 done on sympatric chinstrap and Adelie penguins found that in bad years, there was spatial segregation in foraging areas (i.e. higher inter-individual differences) between chinstrap and Adelie penguins, but none was observed in good years (Lynnes et al. 2002). The relatively weak shelf upwelling in 2017 may explain why 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 (Boyd 1999) and seabirds (Berlincourt and Arnould 2015).

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 of the rate of food delivery to their offspring, the distance they have to travel to access resources is an important factor to 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 is 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 pup's limited fasting ability. When foraging conditions are poor, longer foraging trips have been shown to result in greater food delivery per trip; but pups to 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 3.3, Fig. S3.3) 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 and Pistorius 2015). Kangaroo Island experienced higher than average annual rainfall, with several severe weather warnings in the winter of 2016 (Meteorology 2008).

In Steller sea lions, there is a lack of relationship between maternal attendance during the early reproductive period and population status (Burkanov et al. 2011). Hence, for females at Cape Gantheaume, the variability in trip duration during the upwelling season between 2016 and 2017 may have little impact on pup body condition. Conversely, lower pup growth rates associated with longer foraging trips by mums has been reported in Long-nosed fur seals at a different colony in Tasmania (Lea and Hindell 1997). However, 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 days on average (Baylis et al. 2008b). For the same period, 2017 foraging trips at Cape Gantheaume were comparatively shorter (~10 days, Table 3.2) despite being almost twice as long as those in 2016 (~5 days, Table 3.2). 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 nonupwelling season. Therefore, poorer shelf productivity during the upwelling season may not play a significant role in determining overall reproductive success.

Comparison with previous work

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 nonupwelling season in 2000-2001, (Fig. 3.3) (Baylis et al. 2008a). The combined observations from previous and current work done on females from the same colony indicate that there is 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 at 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 resources 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.; Fig. S3.4). 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 forage in both shelf and oceanic environments, whereas those from a declining population exclusively forage on the shelf (Paredes et al. 2012). Furthermore, deeper oceanic waters can be more productive and profitable (Staniland and Boyd 2003, Shoji et al. 2015) than weakening upwelling events that still prevail in autumn and winter. With that said, environmental conditions in spring time 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 their 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.

ACKNOWLEDGEMENTS

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Industries and Regions South Australia animal ethics committee (application 32-12), Department of Environment, Water and Natural Resources (permit A24684) and the University of Tasmania animal ethics committee (permit A0015176). We would like to thank the two reviewers who gave extensive feedback which helped improved this manuscript tremendously.

APPENDIX

Supplementary Table 3.1 Sources and their URLs of environmental data used in this study.

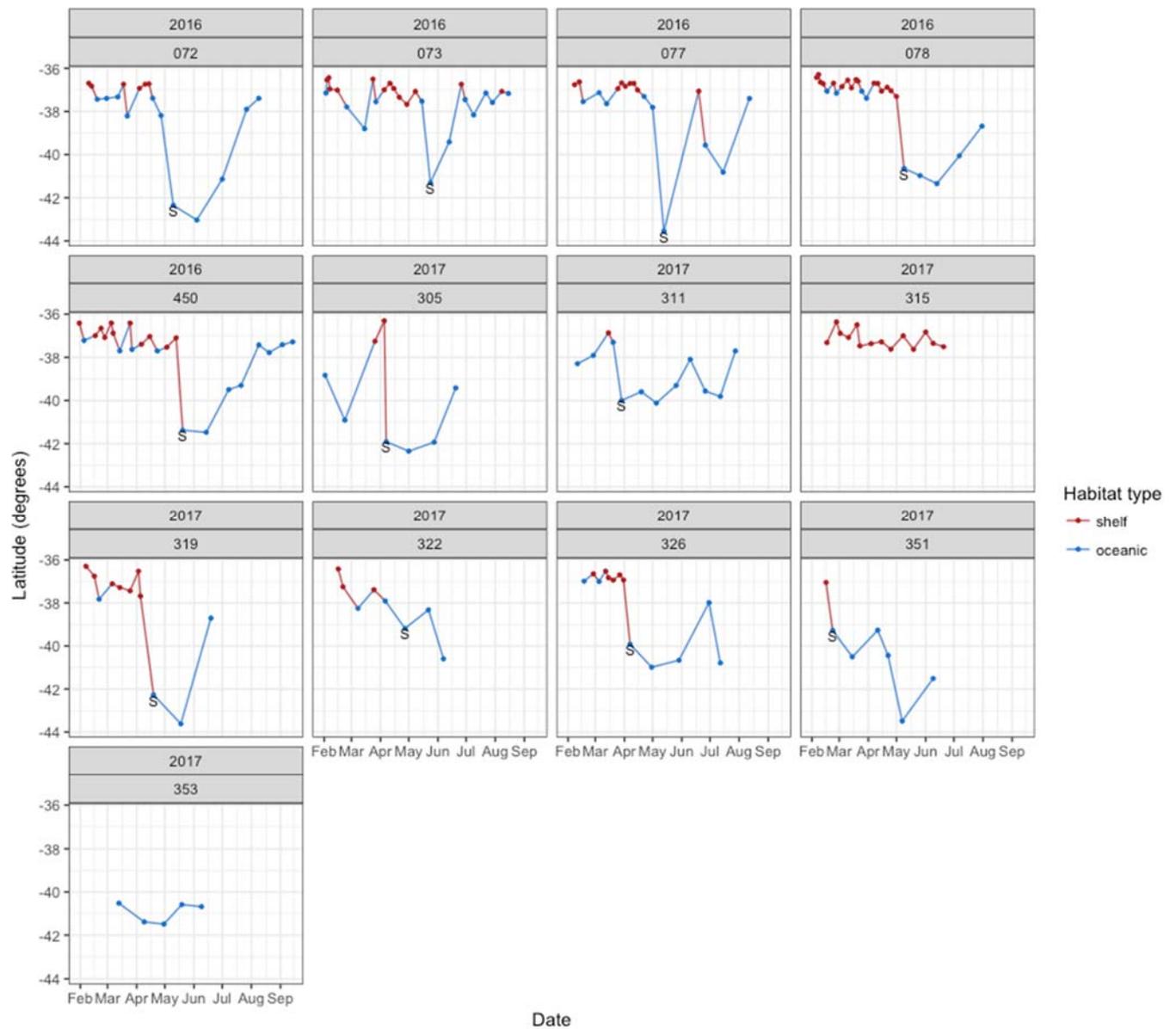
Source	URL
NOAA Optimum Interpolation daily Sea Surface Temperature Anomaly	https://www.ncei.noaa.gov/erddap/griddap/ncdc_oisst_v2_avhrr_by_time_zlev_lat_lon.html
IMOS Optimal Interpolated daily Gridded Sea Level Anomaly	https://portal.aodn.org.au/
IMOS Animal Tracking Facility	https://portal.aodn.org.au/
NOAA daily Antarctic Oscillation index	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml
NOAA ESRL PSD	https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html

Supplementary Table 3.2 Growth rates of long-nosed fur seal pups at Cape Gantheaume by sex for two study years.

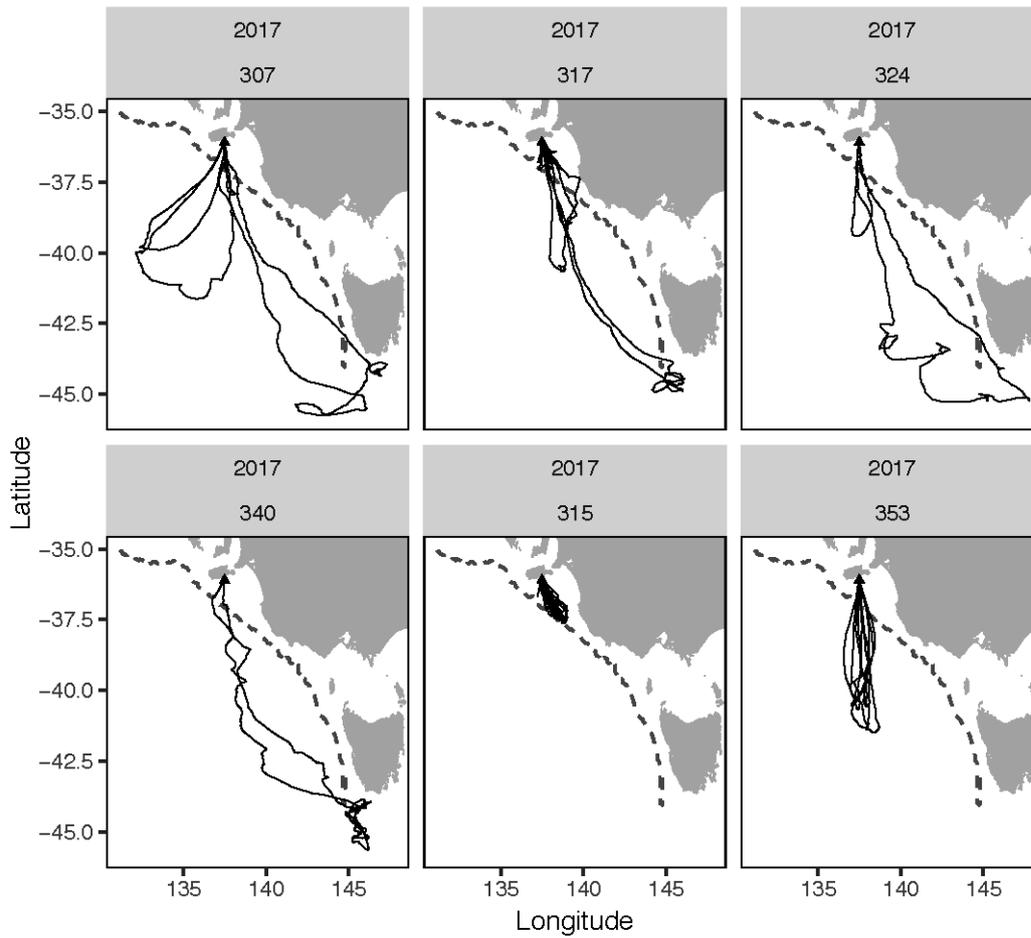
Year	Season	Sex	n	Weigh date	Mass (kg)	Days since first weigh (summer) (day)	Growth rate since first weigh (summer) (g day ⁻¹)
2016	summer	F	59	26 Jan	6.8		
	early autumn		30	16 May	10.3	111	31.2
	late autumn		30	25 Jun	9.9	151	20.6
	winter		30	8 Sep	10.3	226	15.4
	summer	M	51	26 Jan	7.0		
	early autumn		30	16 May	10.2	111	28.6
	late autumn		30	25 Jun	10.5	151	23.2
	winter		30	8 Sep	11.6	226	20.6
2017	summer	F	52	26 Jan	6.0		
	winter		30	4 Aug	11.8	190	30.6
	summer	M	58	26 Jan	7.0		
	winter		30	4 Aug	13.4	190	33.3

Supplementary Table 3.3 Candidate binomial generalised linear mixed models for investigating the effect of environmental predictors on the type of foraging trip (shelf vs non-shelf). Wind, alongshore wind stress; sal, subsurface salinity; t, subsurface temperature; SSHA, sea surface height anomaly; sam, Southern Annular Mode; SD, standard deviation.

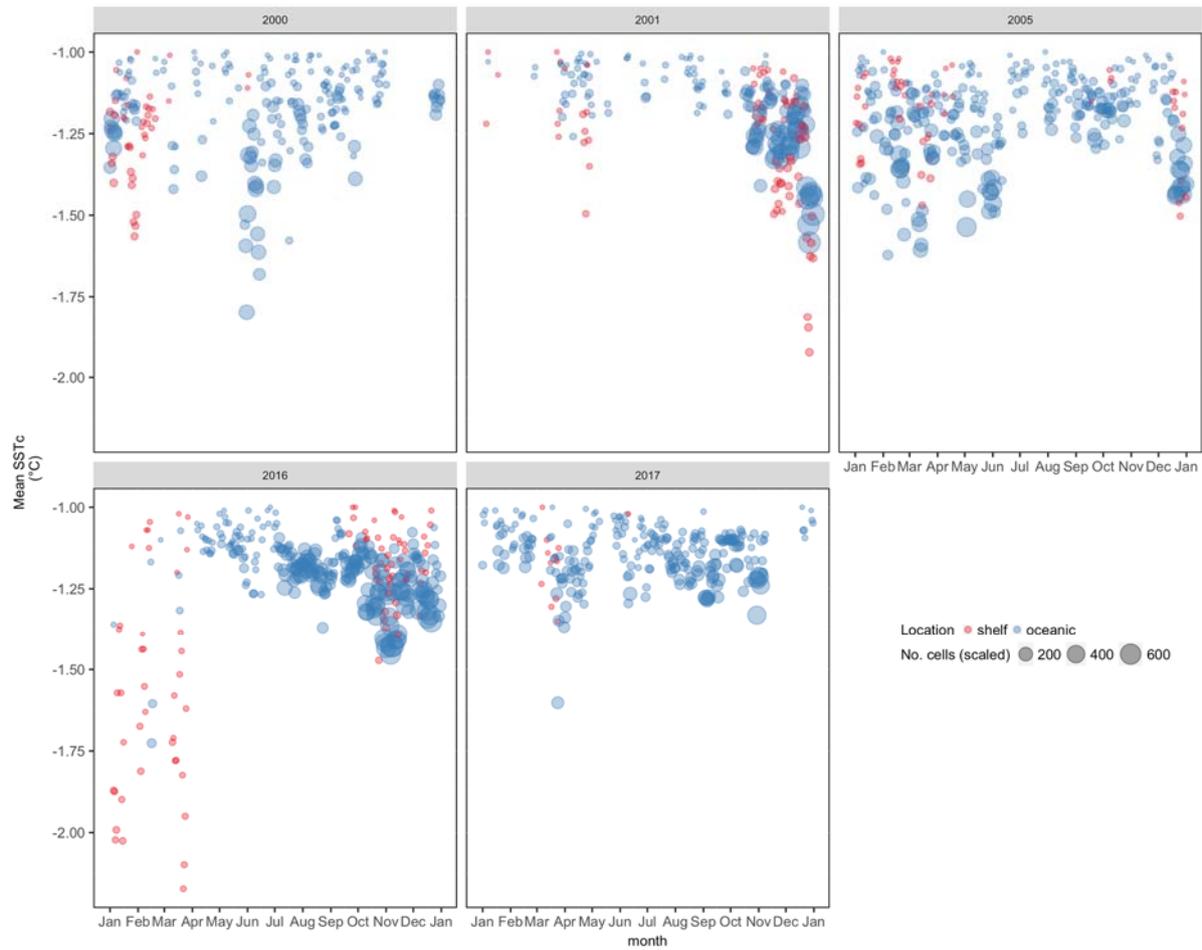
Candidate models	logLik	AICc	dLogLik	dAICc	df	weight
sal_mean + SSHA_mean + sal_mean:SSHA_mean + (1 id)	-82.3	175	25.5	0.00000	5	1
sal_mean + SSHA_mean + (1 id)	-92.1	192	15.7	17.4	4	0
sal_mean + SSHA_mean + wind_mean + (1 id)	-91.5	193	16.2	18.5	5	0
t_mean + sal_mean + SSHA_mean + wind_mean + (1 id)	-90.84	194	16.9208	19.2603	6	0
t_mean + sal_mean + SSHA_mean + wind_mean + year + (1 id)	-90.39	196	17.3659	20.5604	7	0
t_mean + sal_mean + SSTA_mean + SSHA_mean + wind_mean + year + (1 id)	-89.94	197	17.8159	21.8801	8	0
t_mean + sal_mean + sam + SSTA_mean + SSHA_mean + wind_mean + year + (1 id)	-89.67	199	18.0851	23.5916	9	0
t_mean + sal_mean + sam + SSTA_mean + SSHA_mean + wind_mean + wind_SD + year + (1 id)	-89.52	201	18.2381	25.5659	10	0
1 + (1 id)	-107.8	220	0	44.623	2	0



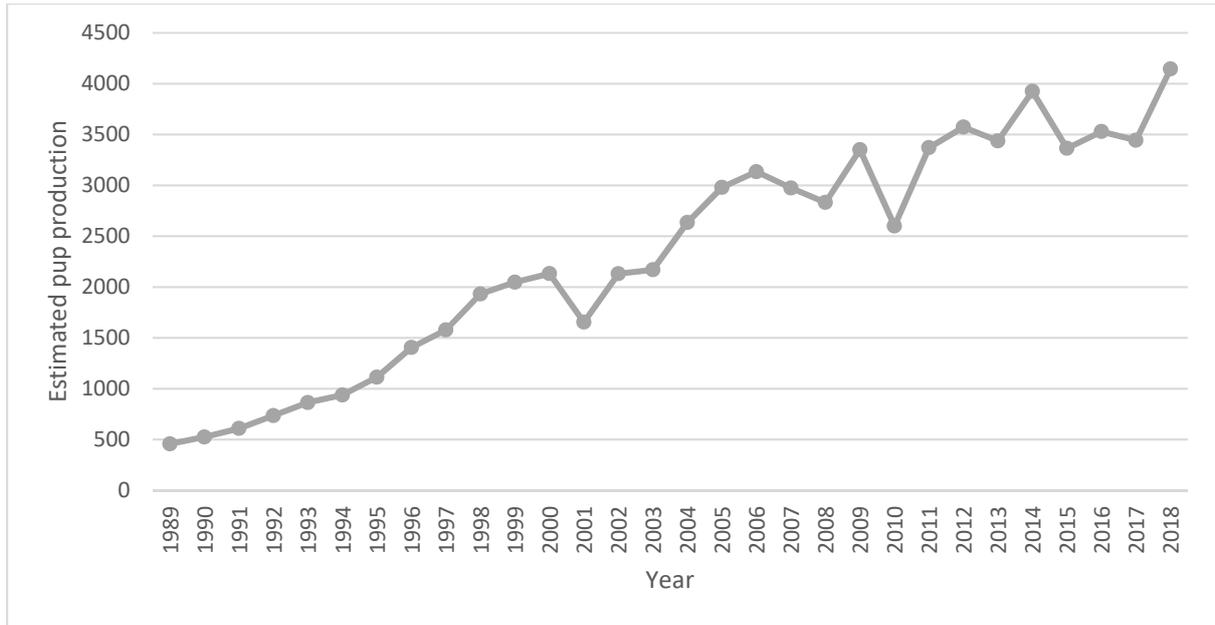
Supplementary Figure 3.1 Maximum latitude travelled for each foraging trip of each individual lactating female Long-nosed fur seal. Trips identified as the switch trip where individuals switch from predominantly shelf or near-shelf foraging to oceanic are labelled “S”. Individual #315 and #353 did not have any switch trips. Only individual #077 had a shelf foraging trip immediately after the switch trip.



Supplementary Figure 3.2 Geolocation tracks of unconstrained (non-central place foraging; #307, #317, #324, #340) and non-switching (between shelf and oceanic foraging, #315, #353) adult female Long-nosed fur seals.



Supplementary Figure 3.3 Inter-annual comparison of the strength (average SSTc) and area (no. of cells) of anomalously cool SST (SSTc, proxy of upwelling-favourable conditions) for shelf (red) and oceanic (blue) regions within the foraging range lactating LNFS. Previous study on the same LNFS colony was done in 2000-2001 and 2005.



Supplementary Figure 3.4 Time series of estimated pup production of long-nosed fur seals at Cape Gantheaume

Chapter 4 ENVIRONMENTAL DRIVERS OF OCEANIC FORAGING SITE FIDELITY DURING THE LATER-STAGES OF PUP-PROVISIONING IN LACTATING LONG-NOSED FUR SEALS (*ARCTOCEPHALUS FORSTERI*)

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ABSTRACT

Finding food is crucial to the survival and reproductive success of individuals, especially those foraging in a heterogenous marine environment. Fidelity to previous foraging sites may bring benefits to individuals as they can allocate more time foraging rather than searching for prey. We studied the degree of foraging site fidelity displayed by lactating long-nosed fur seals (*Arctocephalus forsteri*) in a variable environment within and between years and how that might affect their overall fitness. Core foraging areas of consecutive foraging trips were obtained from geolocation tracks of 12 females from summer to winter during two breeding/lactation periods (2016, 2017). All females broadly displayed foraging site fidelity behaviour with high intra- and inter-individual variability. Females appeared to focus foraging near the edges of oceanic eddies. Fidelity decreased (increased distance between core foraging areas of consecutive trips) with increasing sea surface temperature (SST) gradient in the core foraging areas of the previous foraging trip. There was also inter-annual variability in individual foraging site fidelity – the year with greater foraging fidelity was associated with lower SST gradient and sea surface height gradient variability and relatively better reproductive success. Our results show that individual foraging site fidelity may be an important foraging strategy for seals to maximise resources, especially during one of the most energetically demanding stages of the pup-provisioning period.

INTRODUCTION

The marine environment is highly dynamic with physical parameters determining the spatial and temporal distribution of primary productivity, resulting in patchily distributed food resources. Marine predators therefore face the challenge of locating the prey which their survival and reproductive success depends on in this heterogenous environment (Oosthuizen et al. 2015). From an optimal foraging perspective, there may be long-term breeding and survival benefits (Bradshaw et al. 2004) for animals which use prior knowledge about where food is (*i.e.* predictable) and return to the same foraging area rather than randomly searching for food (Call et al. 2008). Indeed, many marine species such as sea birds (Weimerskirch 2007), sharks (Espinoza et al. 2011), whales (Yates et al. 2007), turtles (Tucker et al. 2014) and seals (Oksanen et al. 2014, Arthur et al. 2015) display individual foraging site fidelity. However, repeated use of the same foraging patch may lead to prey depletion and/or the

prey distribution and density may have changed over time, resulting in site fidelity being a sub-optimal foraging strategy (Pichegru et al. 2010). Thus, this illustrates a trade-off between a relatively low risk strategy of sticking to what one already knows and a higher risk strategy of switching and searching for new and potentially more profitable foraging patches.

Land-breeding marine predators that are provisioning offspring, such as fur seals (Staniland and Boyd 2003), sea lions (Womble et al. 2009), and seabirds (Croll et al. 2006, Rayner et al. 2010), can be considered as central place foragers because they alternate between foraging at-sea and returning to the colony to feed their nutritionally-dependent offspring. When the offspring are young, they have a limited ability to fast, restricting the foraging trip duration of parents. As the offspring gets older and their nutritional demand increases, parents may have to increase foraging effort by making longer trips to more distant oceanic foraging areas, which may be more energetically profitable than remaining in coastal foraging areas (Boyd 1999, Kowalczyk et al. 2015). Individual foraging site fidelity may be an important foraging strategy particularly during the later-stages of the pup-provisioning period where energetic demands for self-maintenance and parental investment increases. This crucial period may be important in determining pup weaning mass which is a significant factor influencing juvenile survival (McMahon et al. 2005, Burkanov et al. 2011). Therefore, understanding the factors influencing foraging site fidelity in the oceanic realm may provide insights into the foraging ecology of these marine central place foragers.

Lactating long-nosed fur seals (LNFS; *Arctocephalus forsteri*) provide a unique opportunity to investigate individual foraging site fidelity in oceanic environments due to the plasticity of their foraging behaviour over a long 10 month pup-rearing period, and the ability to track seals over consecutive foraging trips. In a typical breeding cycle, adult female LNFS give birth to pups in December (austral summer) and mating takes place shortly after. Mothers nurse their pups for 8 – 11 months while in gestation (Goldsworthy 2006). During the austral summer, the majority of the lactating females from Kangaroo Island (South Australia) forage on the Australian continental shelf and shelf break associated with seasonal upwelling (Foo et al, 2019); whereas during the austral winter, the majority of the lactating females forage in oceanic waters associated with the Subtropical Front (Baylis et al. 2008a). The marked

change from coastal to oceanic foraging as lactation progresses is referred to as an alternate or bimodal foraging strategy (Foo et al, 2019). There is nonetheless variability in their oceanic foraging trip distances and not all females travel as far as the Subtropical Front. In oceanic regions, several marine predator species (e.g. Cleeland et al., 2014; Miller et al., 2015; Simmons et al., 2007) preferentially target mesoscale features such as eddies and frontal systems which are relatively productive as they provide intermittent pulses of nutrients to the photic layer for phytoplankton growth which would attract prey (Williams et al. 2011). Indeed, the oceanic waters north of the Subtropical Front are known to have high incidences of eddies (Foo et al. In review; Tomczak et al. 2004). Furthermore, it is possible there may be marked inter-annual variability in the extent to which alternate foraging strategies are adopted by fur seal populations. In some years the majority of females appear to remain foraging on the continental shelf even in winter (Page et al. 2006).

By comparing intra- and inter-annual differences in foraging fidelity behaviour, we can test whether females pursue a “conservative” strategy *i.e.* do they return back to the same foraging sites despite changes in productivity between and within years; or do they use a “risky” strategy by switching sites where there may be higher uncertainty with high gains or great loss. Hence, our aims are to: 1) determine if female’s target mesoscale features such as eddies when undertaking oceanic foraging trips; 2) identify the extent to which environmental factors are used to mediate the degree of foraging site fidelity expressed; and 3) compare individual foraging site fidelity within and between years.

METHODS

Study site, animal handling and instrumentation

The study was undertaken between February and August/September in 2016 and 2017 at Cape Gantheaume (36°04’S, 137°27’E), Kangaroo Island, South Australia. Forty-five lactating female long-nosed fur seals were randomly selected and captured using a hoop-net. Upon capture, anaesthesia was induced and maintained using Isoflurane (Veterinary Companies of Australia, Artarmon, New South Wales, Australia), administered via a portable gas anaesthetic machine (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW,

Australia). Anaesthetised seals were weighed (± 0.5 kg) and their body length (nose to tail) and axial girth were measured (± 1 cm). Geolocation (GLS, Intigeo-C330, 17x19x8mm, 3.3 g, Migrate Technology Ltd, Cambridge, UK) loggers 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 August. Females were recaptured with similar methods as their initial capture. For recaptures, some seals were first captured via a hoop-net and then immobilised with Zoletil (dose 2 mg/kg; Virbac, Sydney, Australia), administered by a hand injection to the rump. For other recaptures, seals were first immobilised with Zoletil, administered using 1 ml, 1.5 x 30 mm (diameter x length) barbless darts (Telinject, Germany), fired from a CO₂-powered tranquilizer gun (G.U.T.50, Telinject, Germany). The lightly anaesthetised females were then captured with a hoop-net and manually restrained.

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

Location estimation

All data analyses were done using the R program (R Core Team, 2017). Locations were estimated from the raw light data by first using the *BAStag* (v0.1-3) (Sumner et al. 2009, Wotherspoon et al. 2016a) package to estimate times of twilight (dawn and dusk). Next, the *SGAT* (v0.1.3) (Wotherspoon et al. 2016b) package was used to create Markov Chain Monte Carlo simulations within a Bayesian framework to estimate the final posterior mean of two primary locations per day while incorporating temperature and land-mask constraints (Sumner et al. 2009, Lisovski et al. 2012). The accuracy of location estimates using this method was 45 ± 29 km (mean \pm SD) for a lactating LNFS carrying GLS and GPS tags

simultaneously (Foo et al. 2019). Females usually begin to move from shelf to oceanic foraging as upwelling activity on the shelf declines in April, hence we classified locations into early autumn (February – March), late autumn – winter (April – August) or spring (September). However, because of the relatively small number of locations obtained in spring, those were excluded from further analyses.

Raw light and activity state data were used to estimate the times when the seal was ashore to identify the start and end of foraging trips. This was determined from obviously messy light curves due to the animal periodically shading the light sensor while on-shore (Arthur et al. 2015), and the GLS logger being continuously dry for a relatively long time (≥ 4 h). We assumed that lactating LNFS were at the colony when they were ashore as they are not known to haul-out at other locations during a foraging trip (Page et al. 2006, Baylis et al. 2012). This means that the duration of a foraging trip is the wet period between the relatively long dry periods inferred from the GLS data.

Oceanic foraging site fidelity

We calculated the time spent (h) *per* 30 x 30 km grid cell, as a proxy for foraging effort like others (Pistorius et al. 2017), for each foraging trip using the *trip* package (v1.5.0)(Sumner 2016a). The size of the grid cell was chosen to account for the error associated with GLS tags while still providing realistic representation of true locations. Trips with less than 3 locations and locations within a 10 km buffer around the colony were removed. Foraging trips were classified as shelf, which included the continental shelf and shelf break (bathymetry ≥ 2000 m), or oceanic (bathymetry < 2000 m) depending on where the ultimate foraging location was. The 2000 m isobath generally marked the end of the shelf break in this region (Page et al. 2005a). As we were interested cells where females were actually foraging and not simply transiting, we identified core foraging areas as cells (1) within the 90th percentile of the range of time spent values and (2) within two degrees in latitude north from the southernmost core foraging cell identified (this was done to exclude outlier cells in the 90th percentile near the shelf region) for each trip.

Table 4.1 Deployment, trip and oceanic foraging site fidelity summaries of 12 lactating long-nosed fur seals from Cape Gantheaume, Kangaroo Island, tracked in 2016 and 2017.

ID	Start Date	End Date	Length	Girth	Mass	Foraging trips				Distance between consecutive core foraging areas (km)				Maximum distance from colony		Proportion of overlap (%)	Proportion of overlap in core foraging areas (%)
						Single oceanic	Continuous oceanic	Shelf	Total	Mean	Median	SD	n	Mean	SD		
72	2/2/2016	19/8/2016	139	80	40.5	1	9	7	16	198	125	175	9	337	269	43.3	9.3
73	1/2/2016	22/8/2016	130	71	33.5	3	7	12	19	221	186	138	7	273	139	32.4	7.7
77	5/2/2016	21/8/2016	128	89	44	1	4	13	17	429	429	247	4	509	265	30.8	0
78	6/2/2016	20/8/2016	138	91.5	48.5	0	7	16	23	125	139	38	7	365	200	51.4	10.3
450	31/1/2016	25/9/2016	144	78.5	43.5	3	9	7	16	175	202	168	9	285	191	34.2	12.1
305	28/1/2017	6/7/2017	136	74.5	44	0	6	1	7	137	131	106	6	488	146	69.6	11.1
311	5/2/2017	7/8/2017	133	85.5	41	0	11	1	12	130	107	89	11	287	114	75.3	44.1
319	7/2/2017	5/7/2017	146	91	55	0	3	7	10	420	420	255	3	618	302	56.8	0
322	9/2/2017	12/7/2017	142	84	45	1	4	2	6	170	118	110	4	363	140	39.4	5
326	10/2/2017	7/8/2017	130	81	41	1	5	6	11	320	375	186	5	489	187	58.3	17.5
351	13/2/2017	30/6/2017	141	84.5	45	0	6	1	7	196	140	96	6	494	173	50.6	6.8
353	13/3/2017	29/6/2017	141	80	41.5	0	5	0	5	70	65	33	5	497	54	71.4	22.6
Overall																	
Mean			137.3	82.5	43.5	6.3	6.08	12.4		189				387		50.2	12.2
Median			138.5	82.5	43.8	6	6.5	11.5		131				369		50.3	9.8
SD			5.9	6.3	5.1	2.4	5.4	5.8		149				200		16.3	22.9
SE			1.64	1.75	1.42	0.69	1.48	1.6		17.1				22.9		4.7	3.45
Total						76	73	149									

Site fidelity is often measured via grid cell overlap, however the results can be influenced by the spatial resolution of grid cells used (Arthur et al. 2015), hence we decided to use the proximity between core foraging areas of consecutive trips as a measure of foraging site fidelity. This was done by first calculating the mean location of all core foraging cells for each trip; hence the core foraging area of each trip is represented by a single point (hereafter core foraging point). Next, the great circle distance between the core foraging point of a foraging trip (trip_j) to that of the subsequent foraging trip ($\text{trip}_j + 1$) was calculated. Then we filtered out shelf foraging trips and oceanic trips that were followed by a shelf foraging trip leaving only data from continuous oceanic foraging trips for the remainder of the analyses (Table 4.1). To characterise the at-sea environment encountered by the seals in core oceanic foraging areas, we compiled 10 environmental variables (Table 4.2) using the *raster* (v2.6-7) (Hijmans et al. 2017), *raadtools* (v0.5.1) (Sumner 2016b) and *xtractomatic* (v3.4.2) (Mendelssohn et al. 2018) packages. The means and standard deviation of all dynamic environmental variables were calculated from intra-day to daily values over the period of each foraging trip. Missing values were removed from calculations. Values of each environmental covariate were then extracted for each core foraging cell and the mean of all core foraging cells was calculated for each trip. Year was also included as a factor covariate to investigate possible inter-annual differences oceanic foraging site fidelity.

Table 4.2 Environmental variables and whether their variability were also used to characterise lactating long-nosed fur seal core oceanic foraging habitat, All environmental variables are dynamic except BATHY. Further details are in Table S4.1. Abbr, abbreviation.

Abbr	Environmental variable	Unit	Spatial resolution	Temporal resolution	Source	Variance (standard deviation)
BATHY	Bathymetry	m	0.02 °	–	General Bathymetric Chart of the Oceans	
SST	Sea surface temperature	°C	0.25 °	Daily	NOAA/OAR/ESRL	Yes
SSHA	Sea surface height anomaly	m	0.12 °	Daily	SSALTO/DUACS – AVISO	Yes
CURRU	Zonal current	cm s-1	0.25 °	Weekly	SSALTO/DUACS – AVISO	Yes
CURRV	Meridional current	cm s-1	0.25 °	Weekly	SSALTO/DUACS – AVISO	Yes
WINDU	Horizontal wind	m s-1	1.9 °	Daily	NOAA/OAR/ESRL PSD	Yes
WINDV	Vertical wind	m s-1	1.9 °	Daily	NOAA/OAR/ESRL PSD	Yes
SSTgrad	SST gradient	°	0.25 °	Daily	Derived from SST	Yes
SSHgrad	SSH gradient	°	0.12 °	Daily	Derived from SSH	Yes
CHL	Chlorophyll-a	mg m-3	0.04 °	8 day	NASA – MODIS	Yes

Inter-annual oceanic fidelity

For completeness, we also investigated inter-annual variability in oceanic foraging site fidelity by comparing the proportion of 30 x 30 km grid cell overlap among 1) only core foraging cells and 2) all cells in all oceanic foraging trips. For example, the calculation for the former statistic is number of unique 30 x 30 km core foraging cells in the oceanic region entered more than once among foraging trips divided by the total number of unique core foraging cells in the oceanic region entered from all oceanic foraging trips. By measuring overlap using all cells entered during a foraging trip instead of just core foraging cells, we account somewhat for directional persistence or similarity in foraging paths, which is also a measure of fidelity (Pettex et al. 2012). We also compared the overall average variance of SST, SSHA, SSTgrad, SSHgrad, CHL, CURRU, and CURRV (acronyms defined in Table 4.2) of oceanic cells entered during a trip for each year since stability of an environment is relevant to fidelity.

Statistical analyses

We fitted generalised additive mixed models (GAMMs; *mgcv* package v1.8-23) with a Gaussian error distribution and identity link for proximity between consecutive core foraging locations against all environmental variables of the earlier foraging trip as smoothed fixed terms and seal identity as a random effect. Full models fitted with the restricted maximum likelihood (REML) method were first compared with and without the random effect using Akaike's information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2004). Non-significant fixed terms were sequentially removed from the full model until only significant ($P < 0.05$) ones remained. These models were fitted with the maximum likelihood method. The optimal model selected had the lowest AICc. If delta AICc of two models is < 2 , the more parsimonious model was selected. The final model was presented using the REML method. Normality and homogeneity of residuals were checked graphically using the "gam.check" function. To address heteroscedasticity, the response variable was transformed and/or a weighted variance function was added to the model. To address autocorrelation, an autoregressive structure was included in the model. All t-tests are two-tailed and if values do not fulfil normality assumptions, then the non-parametric Wilcoxon t-test was used. Results are reported as mean \pm SE unless otherwise stated.

RESULTS

Location statistics and track summaries

We recovered GLS loggers from 17 adult female seals. However, based on estimated tracks derived from light data, four seals did not show central-place foraging behaviour (possibly due to pup death or abandonment) and one seal only made shelf foraging trips. These were excluded from subsequent analyses. From the remaining 12 seals, a total of 3585 at-sea locations were obtained from 159 foraging trips from summer to spring in two years (2016 = 99 trips, 2017 = 60 trips; Table 4.1). Of the total number of foraging trips, 86 were oceanic trips, 73 were continental shelf trips (Table 4.1).

Table 4.3 Fitted generalised additive mixed models used to assess how the proximity of core foraging areas between consecutive trips is influenced by environmental parameters of the previous trip's core oceanic foraging areas. Only the top five fitted models are presented here. LogLik, log likelihood; AICc, corrected Akaike Information Criterion; dAICc; delta AICc; df, degrees of freedom. The significance of the smooth terms in the optimal model is also presented. All fixed effects were fitted as smoothed terms.

Model selection						Significance of smoothed terms			
Models	logLik	AICc	dLogLik	dAICc	df	Term	edf	F	p-value
SSTgrad	-168.78	344.02	2.92	0	3	SSTgrad	1.18	1.12	< 0.01
SSTgrad + SSHgrad	-168.78	346.34	2.92	2.32	4	N = 56			
SSTgrad + SSTgrad_sd + SSHgrad	-168.54	348.29	3.15	4.27	5				
SSTgrad + SSTgrad_sd + SSHgrad + topo	-167.69	349.09	4.01	5.07	6				
SSTgrad + SSTgrad_sd	-171.7	349.86	0	5.84	3				

Table 4.4 Average variance of environmental parameters in the oceanic region between years. Wilcox (W) t-test was used. *** < 0.005; n.s., non-significant.

Variable	2016		2017		W	P-value
	Mean	SE	Mean	SE		
SSTgrad_SD	2.90E-06	3.53E-08	2.52E-06	2.02E-08	500,000	***
SSHgrad_SD	3.30E-07	4.65E-09	2.77E-07	2.59E-09	400,000	***
SST_SD	0.292	0.00314	0.3123	0.00252	400,000	***
CURRV_SD	0.0246	0.000486	0.026	0.000343	300,000	***
SSHA_SD	0.0242	0.000324	0.0222	0.000212	400,000	n.s.
CURRU_SD	0.0241	0.000467	0.0224	0.000312	400,000	n.s.

Oceanic foraging site features and fidelity

The distribution of oceanic core foraging areas tended to occur near the periphery of eddies (as indicated by SSHgrad; Fig. 4.1), and consecutive trips tended to return to the approximate location of the previously visited eddy. Due to the high number of missing chlorophyll-a data, it was excluded as an environmental covariate. SST and WINDV were also dropped as environmental covariates due to their high variance inflation factors. The inclusion of seal identity as a random effect did not improve model fit (compared with REML method; with random effect AICc = 205; without random effect AICc = 202). The final GAM included SSTgrad of the previous trip as covariates (Table 4.3) where the distance between core foraging areas of consecutive trips increased with increasing SSTgrad (Fig. 4.2).

The overall mean distance between consecutive core foraging areas was 189 ± 17.1 km (range = 12.5 – 603 km) and the median was 131 km. The mean maximum distance from colony of oceanic foraging trips was 362 ± 21.6 km (range = 84.5 – 890 km). Oceanic individual foraging fidelity was not influenced by day of the year. The overall proportion of spatial overlap in the oceanic region between consecutive foraging routes is $51.1 (\pm 4.3)$ % (Table 4.1; Fig. 4.3a). When only core foraging cells were considered, the overall proportion of spatial overlap was $12.2 (\pm 3.45)$ % (Table 4.1; Fig. 4.3b). Although year did not influence proximity of consecutive core foraging areas in the GAMM, on average there was greater oceanic spatial overlap for the entire foraging route in 2017 ($59.5 \% \pm 5.2$) than in 2016 ($37.1 \% \pm 4.05$; Two sample t-test: $t = -3.15$, $df = 10$, $p\text{-value} = 0.01$). The same was true for only core foraging areas however it was not statistically significant (2017: 15.3 ± 5.6 %; 2016: 7.87 ± 2.1 %; Welch two-tailed t-test: $t = -1.24$, $df = 7.57$, $p\text{-value} = 0.25$). The mean variance of SSTgrad and SSHgrad was lower in 2017 than in 2016 while it was opposite for that of SST and CURRV (Table 4.4). There was no difference in the mean variance of SSHA and CURRU between both years (Table 4.4). Additionally, female length (proxy for age) did not influence proportion of spatial overlap in the oceanic region (linear model: slope = 0.225, t-value = 0.27, $p\text{-value} = 0.79$).

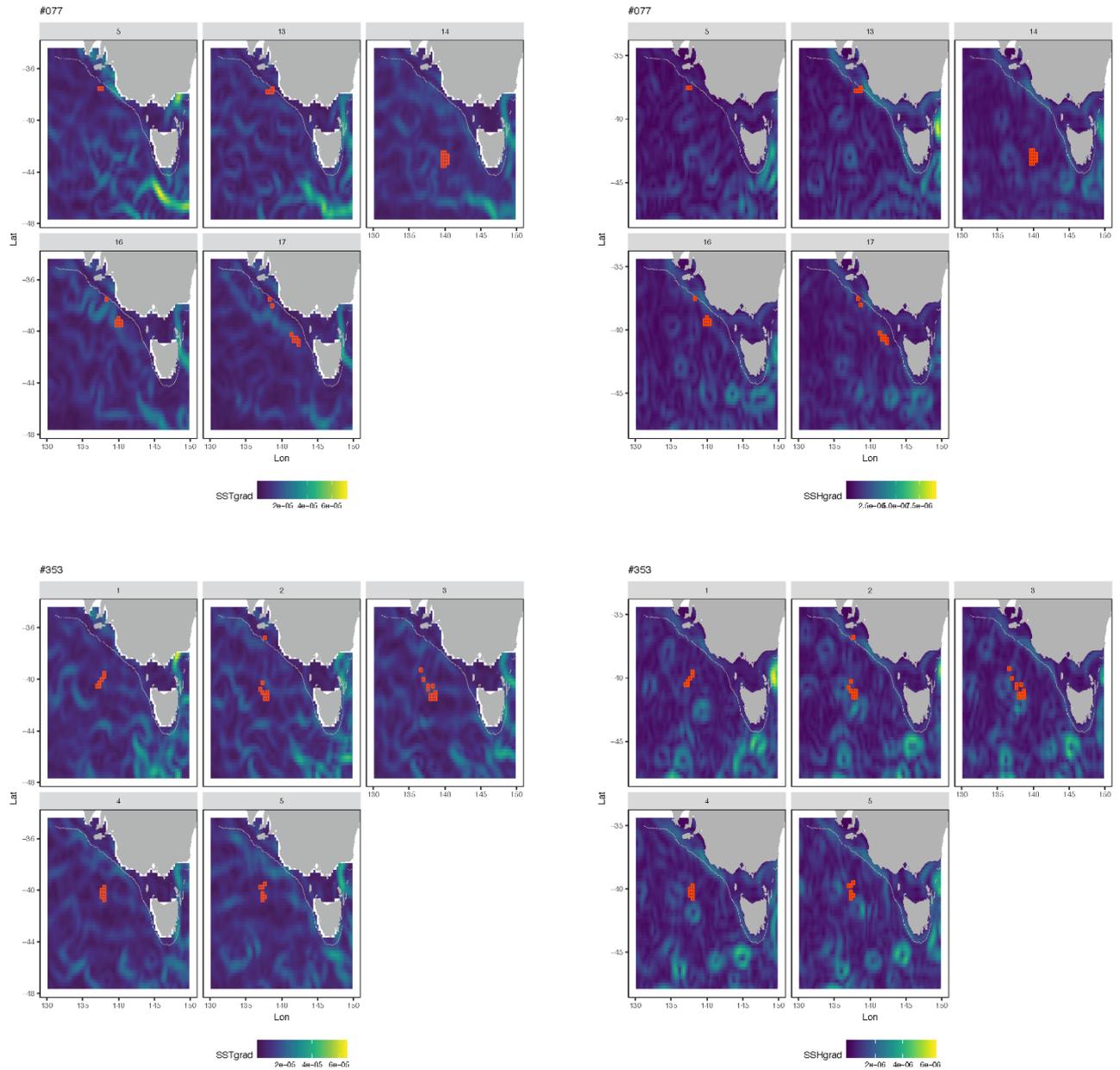


Figure 4.1 Examples of core foraging locations (90th percentile of time spent in cell of each trip; red) for sequential oceanic foraging trips (missing consecutive foraging trips are shelf foraging trips which are not shown) overlaid onto either the mean sea surface temperature gradient (SSTgrad) or sea surface height gradient (SSHgrad) over the period of each foraging trip for a female in 2016 (female ID #077, top) and 2017 (female ID #353, bottom). The solid grey line represents the 2000 m isobath. See Fig. S4.1 for additional examples.

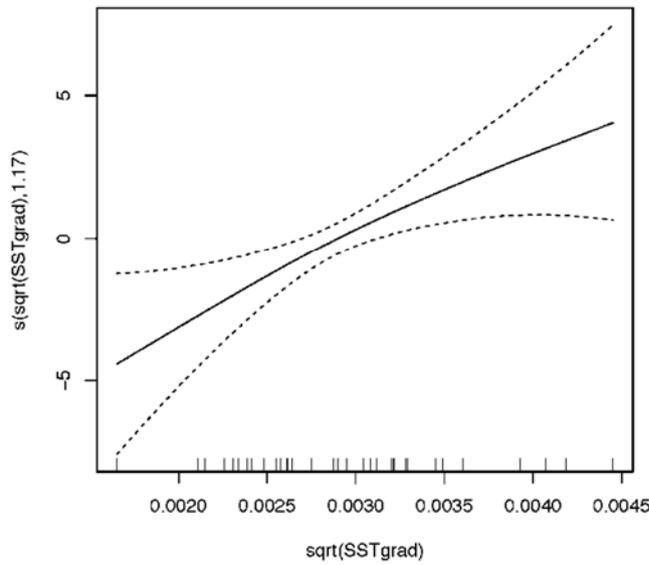


Figure 4.2 Functional forms for the smoothed covariate in the final generalised additive model. Dashed lines indicate the approximate 95% confidence intervals. SSTgrad, sea surface temperature gradient. Units are °C.

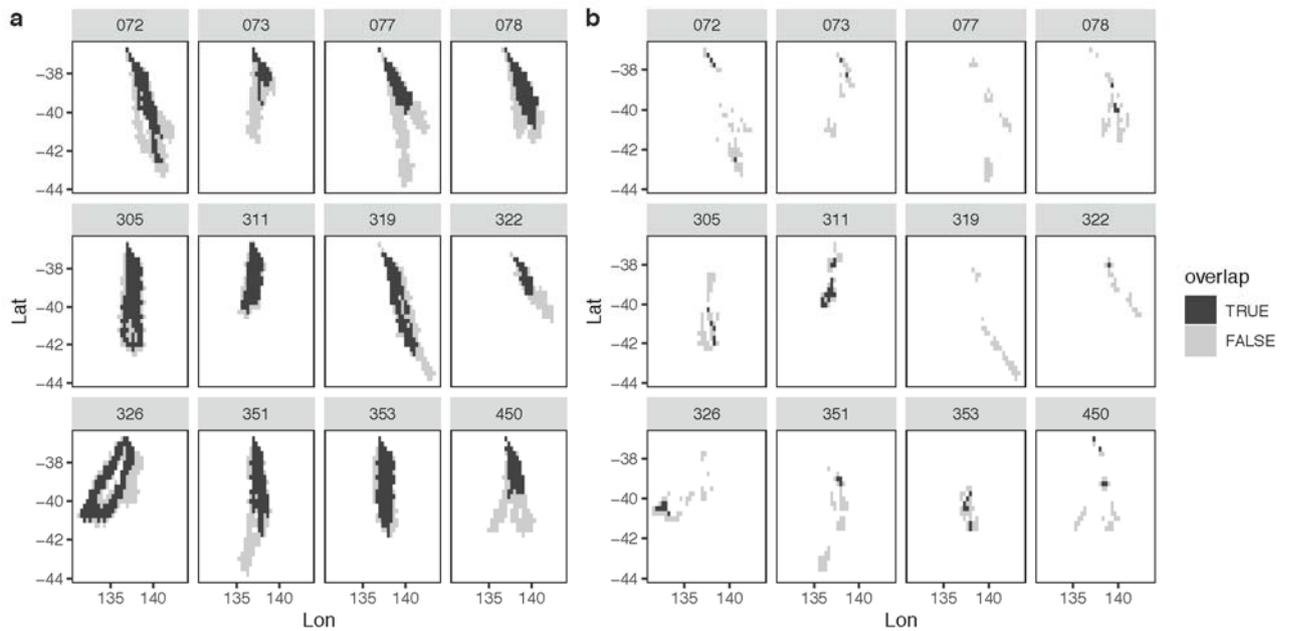


Figure 4.3 Amount of cell overlap for entire foraging tracks (a) and only core foraging cells (b) of oceanic foraging trips of individual female long-nosed fur seals. Seal IDs are located above each plot. Seal IDs beginning with “3” were tagged in 2017.

DISCUSSION

Previous studies on this species have reported differences in individual foraging site fidelity between shelf and oceanic habitats (Baylis et al. 2012) but none have compared inter-annual differences or related it to environmental parameters to uncover potential environmental drivers to fidelity. Here, we address those questions with a focus on foraging in the oceanic region which typically occurs at the later stage of lactation when energetic demands are highest. During this time, females are likely to be operating at their limits so there is pressure for them to forage as optimally as possible since a huge amount of energy has already been invested in their pup. Using continuous foraging tracks of individuals from summer to winter of two breeding seasons, we found that females display both conservative and risky foraging strategies which varies intra- and inter-annually. This is seen in the variability of the degree of oceanic foraging site fidelity where intra-annual individual foraging site fidelity is driven by variability in sea surface properties associated with eddy and frontal activity.

Foraging Strategies

Within a year, females broadly show individual foraging site fidelity. Relative to the maximum distances (84.5 – 890 km) from the colony of oceanic foraging trips, individual foraging site fidelity was highly variable between and within individual seals (12.5 – 603 km). Generally, there were periods where there was high fidelity for several consecutive foraging trips. These were interspersed with sporadic spikes of low fidelity (Fig. S4.2). This makes sense as females are likely to change foraging patches after extended periods of foraging in the current one due to prey depletion or temporal and spatial variability in prey distribution (Charnov 1976). Females also occasionally made a shelf foraging trip after a particularly long oceanic foraging trip (Fig. S4.2), presumably indicating that they experienced relatively low foraging success during the oceanic foraging trip. They are unlikely to return to a foraging patch if their experience there was unproductive and hence would keep changing foraging patches until a profitable one is found. Nevertheless, all females showed periods of high oceanic foraging site fidelity indicating that this is a foraging strategy that may be used by them.

Lactating female long-nosed fur seals generally showed greater foraging route fidelity during the transit phase (direction) of a foraging trip than fidelity to specific foraging sites (overlap

of whole foraging routes vs only core foraging areas; Table 4.1). Our results concur with those previously reported in females from the same colony (Baylis et al. 2012) and similar behaviours have also been observed in Antarctic fur seals (Bonadonna et al. 2001) and Northern gannets (Pettex et al. 2012). These foraging behaviours suggest memory-based foraging tactics (Bonadonna et al. 2001, Patrick et al. 2014) where individuals learn the broad direction of travel to a profitable area experienced in the previous trip and therefore show directional fidelity during the outbound phase of subsequent trips (Baylis et al. 2012). However, during a trip they may forage opportunistically whenever good patches are encountered which would ultimately decay overtime in the short-term (Wakefield et al. 2015). Furthermore, prey patches tend to be widespread in oceanic waters where small, high-density patches are nested within larger, lower density aggregations (Fauchald and Tveraa 2006). The high degree of flexibility in foraging sites may reflect the generalist diet of female Long-nosed fur seals. This characteristic combined with directional fidelity to the general vicinity of profitable foraging areas allows females to leverage on the benefits of foraging fidelity which may include increased fitness (Call et al. 2008) and longevity in the long-term (Authier et al. 2012) while still being adaptable to changes in prey availability.

Nevertheless, if females are truly using a memory-based strategy, it begs the question of how they knew where to go in the first instance. The diet profile of juveniles from this colony are similar to those of adult females (Page et al. 2005a), hence successful foraging routes may have been self-learned when adults were juveniles (McConnell et al. 2002). It would be interesting to find out if females use the same foraging routes over multiple years which would provide some evidence to long-term learning. To investigate this, longitudinal data of foraging tracks of the same individuals ideally from weaning into adulthood would be required or a stable isotope approach may be used (Lowther et al. 2011, Authier et al. 2012).

Environmental drivers of oceanic foraging site fidelity

Sea surface temperature and SSH gradients are often used as a proxy for frontal regions and eddy activity, respectively (Reisinger et al. 2018). Sea surface temperature gradient may also be associated with eddy activity, as eddies can induce spatial variability in the surrounding SST field particularly at the margins of eddies (Gaube 2012). Even though SSH gradient was

not an environmental predictor for foraging site fidelity, core oceanic foraging sites appeared to be located primarily near the edges of eddies (indicated by high SSHgrad) and frontal regions, and occasionally within the core of eddies. Similarly, Southern elephant seals (Campagna et al. 2006, Della Penna et al. 2015), loggerhead sea turtles (Polovina et al. 2004) and Antarctic fur seals (Guinet et al. 2001) have all been observed to forage in the proximity of the eddy edges where prey tend to aggregate. It would not be surprising if females were selectively foraging in areas associated with eddy activity as the eddy field in the oceanic region tends to become more intense in winter (Foo et al. in review; Tomczak et al. 2004) when females are also likely to have moved from shelf to oceanic foraging.

The use of eddy edges as opposed to eddy cores may explain why foraging site fidelity decreases (*i.e.* increasing distance between consecutive foraging trips) with increasing SST gradient. This is because areas outside the edges of eddies may have lower SST gradient. Indeed, weak temperature gradients can exist between eddies, which has been observed during winter in the Polar Front region (Bailleul et al. 2010). Another possible explanation is that areas of high SST gradient are generally associated with high surface current velocity (Campagna et al. 2006) and actively swimming in strong surface currents may be energetically costly for a relatively small seal species such as the long-nosed fur seals. The preference of oceanic regions with lower SST gradient is also seen in seabirds in the Gulf of Alaska where they have a higher probability of avoiding areas with steep SST gradients in oceanic than shelf regions (O'Hara et al. 2006). Alternatively, geolocation data may simply be too coarse-scale to accurately tease out the foraging behaviour around eddy and frontal features.

Inter-annual variability in foraging site fidelity

There were inter-annual differences in individual oceanic foraging site fidelity. We observed that fidelity was greater in 2017 than 2016 and this had some profound effects on the condition of pups. The strategy of oceanic foraging site fidelity may have contributed to heavier winter pup mass in 2017 (12.6 ± 2.25 kg; mean \pm SD) than in 2016 (11 ± 2.11 kg) (Foo et al. 2019). Not only were winter masses great in 2017 but long-nosed fur seal pup production at Cape Gantheaume in the 2017/18 breeding season was the largest ever

recorded and the average summer (2 month old) pup mass was greater in the 2017/18 than in 2016/17 breeding season (S. Goldsworthy, pers. comm.). Together these observations suggest that 2017 was a good year for pup growth rates (higher winter mass) and pup production in the following year probably driven by higher implantation rates, which occurs around 4 months post-partum, and carrying pups to term. Environmental conditions in the oceanic region may have been better in 2017 which encouraged females to return to the same profitable foraging site repeatedly, thus maximising time spent foraging and minimising time spent searching for prey. Prior knowledge of profitable areas is particularly beneficial for long foraging trips as the result of increased changing of foraging routes and foraging habitat may lead to mass loss for adults (Call et al. 2008).

In oceanic waters, good foraging patches may be spatially and temporally stable (*i.e.* predictable) (Staniland et al. 2004). The average variability of oceanic SSTgrad and SSHgrad was lower in 2017, indicating that the environment was more stable and thus may be contributed to greater individual foraging site fidelity. That variability of environmental parameters (e.g. SSTgrad_SD) at the foraging trip level was not in the final model for fidelity suggests that perhaps foraging site fidelity is associated more with variability at the annual level instead. Indeed, Antarctic fur seals show higher fidelity to foraging sites with lower annual SST variance (Arthur et al. 2015). We are unable to confirm this for our study animals as we do not have multi-year data for the same individuals. Nevertheless, the concentration of foraging activity in 2017 may have led to greater energy transfer to their fasting pups ashore and better self-maintenance during gestation (Georges and Guinet 2000).

That females in 2017 performed better reproductively than females in 2016 despite a weaker seasonal upwelling on the shelf (a common food resource during the earlier stages of the pup-provisioning period) in 2017 (Foo et al. 2019) suggests that foraging efficiency during the later stage of lactation is important for reproductive success. Variation in offspring-provisioning rate is one of the factors that can affect pup weaning mass (Goldsworthy 2006), which influences first year survival (Georges and Guinet 2000). Foraging site fidelity is generally high in continental shelf habitats (Baylis et al. 2012, Sommerfeld et al. 2015) and the continental shelf in our study region is narrow, concentrating productivity into a small

area. Conversely, prey in larger scale oceanic habitats are likely more dispersed and ephemeral (Kotliar and Wiens 1990) reducing the advantages of foraging site fidelity (Baylis et al. 2012). Therefore, oceanic habitats allow for more inter-individual provisioning variability to influence the performance of different foraging strategies likely making the effects of inter-individual variability in winter to be more pronounced.

Central place foraging parents should be time-minimisers earlier in the lactation period (Boyd 1999, Clarke et al. 2006). This means that parents should aim to maximise the rate of food delivery to their offspring instead of maximising the rate of energy gain. This is because early in the lactation period, the transfer of energy from mother to pup is limited by their pup's fasting ability and milk ingestion which is linked to their smaller body size when they are younger (Stearns 1976, Georges et al. 2001, Goldsworthy 2006). Later in the lactation period, mothers should be energy-maximisers as the energy requirement of pups increases and the rate of food delivery is primarily determined by pup suckling behaviour while their mums are ashore (Goldsworthy 2006). Hence, when females switch to oceanic foraging in late autumn to winter, the influence of environmental conditions on foraging success can affect milk volume and quality available for pups (Arnould and Boyd 1995) which in turn may have a greater effect on pup mass and body condition than shelf foraging (Bradshaw et al. 2004, Goldsworthy 2006).

In summary, foraging route behaviours displayed by lactating long-nosed fur seals concur with those previously reported in the species and also other central place foraging marine predators that forage in oceanic waters. Inter-annual differences in individual foraging site fidelity exemplify the high degree of flexibility in this species, where they are able to adapt to both intra- and inter-annual changes in environmental conditions. This trait is possibly a key factor for the success of the population's recovery (Cotte et al. 2015) from near extinction due to historical hunting. Future research on the persistence of individual foraging fidelity over multiple years would give us insight to the limits of their flexibility which would affect their ability to cope with possible severe environmental changes.

ACKNOWLEDGEMENTS

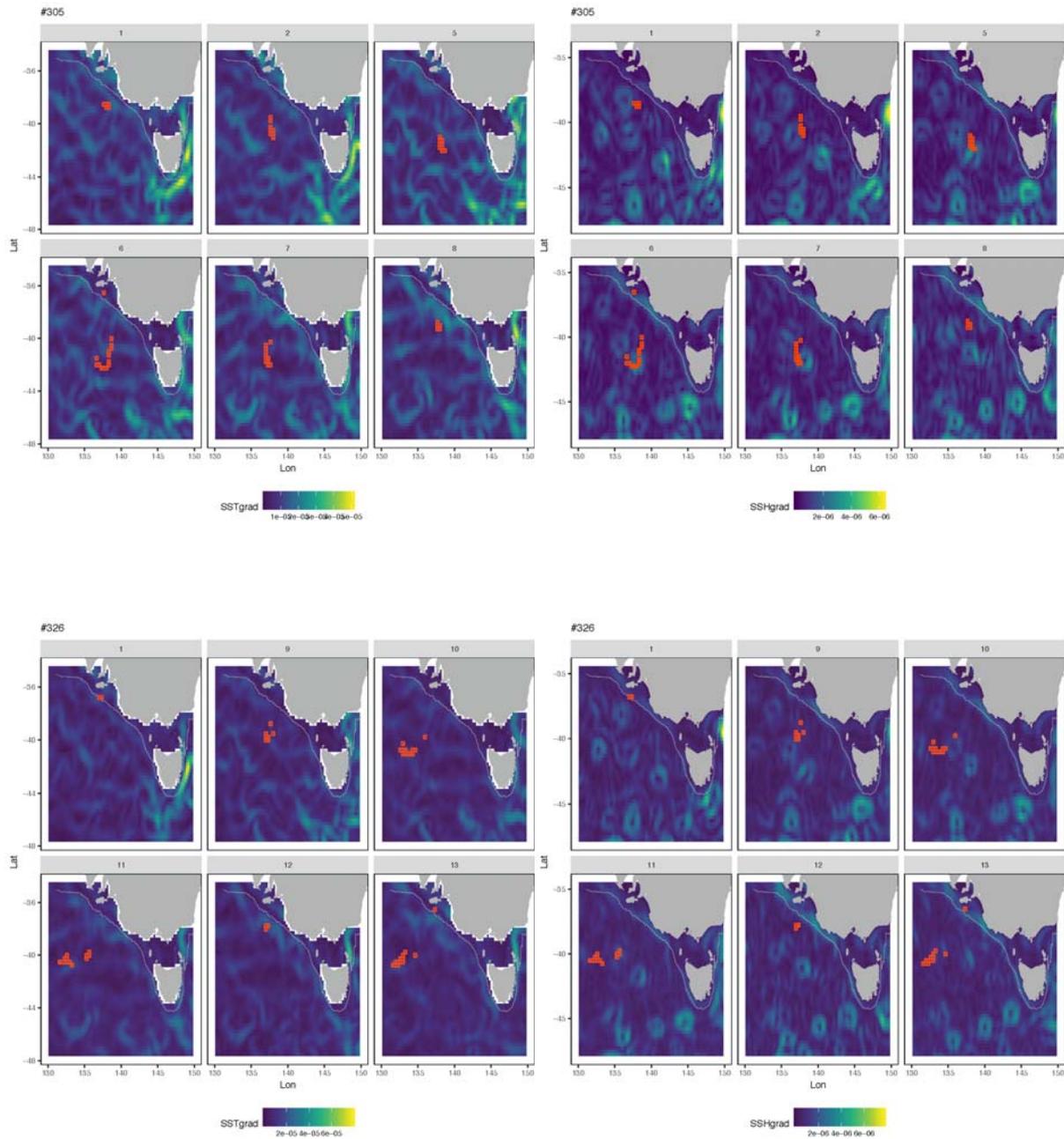
This study was supported through grants from the Sea World Research and Rescue Foundation, the Holsworth Wildlife and Research Endowment, and the Lirabenda Endowment Fund (issued by the Field Naturalists Society of South Australia). We thank the Department of Environment, Water and Natural Resources, in particular A. Maguire for logistical support. We also thank the many people who assisted in fieldwork, especially the guides at Seal Slide, R. Boeren, A. Proctor, A. Doole, L. Stephens, and K. Gilbert. All animal handling and experimentation were undertaken with the approval from the Primary Industries and Regions South Australia animal ethics committee (application 32-12), Department of Environment, Water and Natural Resources (permit A24684) and the University of Tasmania animal ethics committee (permit A0015176).

APPENDIX

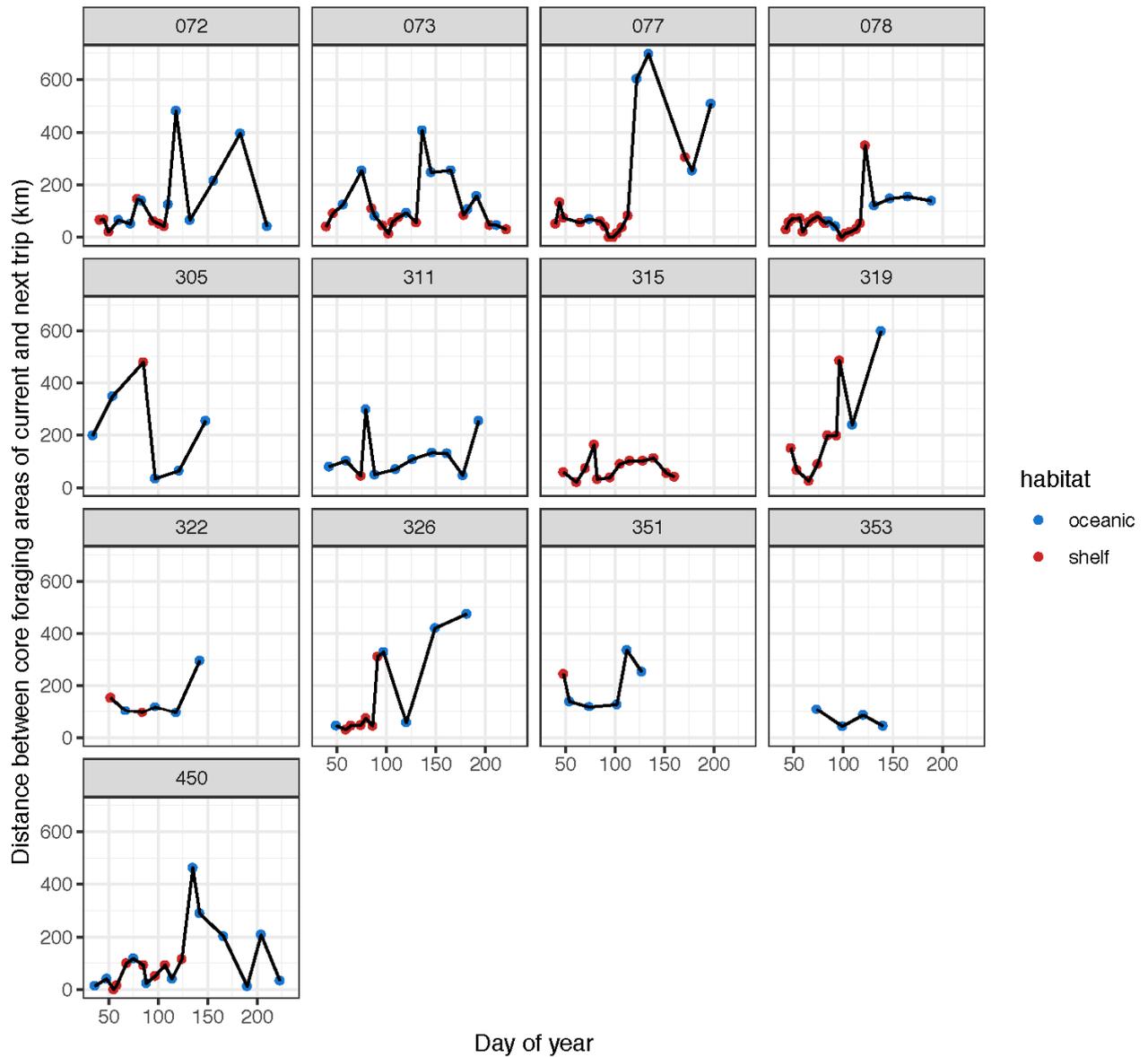
Supplementary Table 4.1 Source and URL of environmental variables listed in Table 4.1.

Source	URL
General Bathymetric Chart of the Oceans	https://www.gebco.net/data_and_products/gridded_bathymetry_data/
NOAA/OAR/ESRL	https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html
SSALTO/DUACS – AVISO	https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/index.html
NOAA/OAR/ESRL PSD	https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.pressure.html
NASA – MODIS	http://oceancolor.gsfc.nasa.gov/cms/doi/10.5067/AQUA/MODIS/L3B/CHL/2014

Additional examples of seal foraging locations near eddy features:



Supplementary Figure 4.1 More examples of core foraging locations of seals (#305, #326) in 2017 in relation to either the mean sea surface temperature gradient (SSTgrad) or sea surface height gradient (SSHgrad) over the period of each foraging trip (trip number, which is in sequence, indicated in the header of each panel).



Supplementary Figure 4.2 Distance between the mean location of core foraging areas of consecutive foraging trips across time (day of the year) for individual lactating Long-nosed fur seals. Foraging trips are classified into shelf (bathymetry ≥ 2000 m) or oceanic foraging trips based on the ultimate foraging location.

Chapter 5 IDENTIFYING FORAGING HABITATS OF ADULT FEMALE LONG-NOSED FUR SEAL (*arctocephalus forsteri*) BASED ON VIBRISSA STABLE ISOTOPES

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ABSTRACT

We investigated how foraging ecotypes of female long-nosed fur seals (*Arctocephalus forsteri*) could be identified from vibrissa stable isotopes. We collected regrowths of vibrissae from adult females ($n = 18$) from Cape Gantheaume, Kangaroo Island, South Australia from two breeding seasons (2016, 2017). The period represented by the regrowth was known and 8 individuals were administered with ^{15}N -enriched glycine as a biomarker to mark the start date of the regrowth. Non-glycine marked and glycine marked vibrissae were used to estimate the rate of the individual vibrissa regrowth. Using individual growth rates ($0.18 \pm 0.04 \text{ mm d}^{-1}$), we reconstructed a stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) time series for each regrowth and allocated them to corresponding at-sea locations either based on geolocation tracks ($n = 14$) or foraging habitat type (shelf or oceanic) based on diving data ($n = 2$) of the sampled seals. Mean $\delta^{15}\text{N}$ from vibrissa segments was higher when females foraged on the continental shelf region (16.1 ± 0.7 , $n = 29$) compared to oceanic waters (15.1 ± 0.7 , $n = 106$) in 2017, whereas it was similar in both regions in 2016 (shelf: 15.3 ± 0.4 , $n = 13$; oceanic: 15.4 ± 0.4 , $n = 15$). Based on the stable isotope signatures of vibrissa segments, model-based clustering analysis correctly classified 79.8% of them into shelf or oceanic foraging habitats. This demonstrates the potential of using vibrissa stable isotopes for studying the foraging ecology of an important top marine predator.

INTRODUCTION

Marine predators, including pinnipeds, whales, sharks and seabirds, play an important role in ecosystem structure and function (Camphuysen 2006, Estes et al. 2011). The spatial and temporal variability of their foraging behaviour can influence prey species populations and fisheries interactions; and can be used to monitor the state of marine ecosystems (Boyd and Murray 2001, Reid and Croxall 2001). An important aspect for foraging ecology is understanding how individuals adapt their foraging strategies (such as feeding location and prey type) in response to intra- and inter-annual changes in prey availability and quality. This is especially relevant for animals foraging in the highly dynamic marine environment.

Naturally occurring stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$; $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$; $\delta^{15}\text{N}$) in marine environments are good indicators of habitat source and consumer trophic level within

food webs, respectively (Zeppelin and Orr 2010, Ramos and González-Solís 2012). Ratios of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) can indicate a consumer's trophic position as ^{15}N is enriched along the food chain (Crawford et al. 2008). In the southern hemisphere, $\delta^{13}\text{C}$ values of marine plankton show broad-scale geographical gradients which increases from the equator with latitude up to the subtropics before decreasing with latitude in the Southern Ocean (Francois et al. 1993, Trull and Armand 2001, Cherel et al. 2007). Similarly, $\delta^{13}\text{C}$ also varies from inshore benthic to offshore/pelagic food sources, where $\delta^{13}\text{C}$ generally decreases from coastal to the offshore (Hobson et al. 1994). As $\delta^{13}\text{C}$ values vary little along the food chain, it can be used to indicate a consumer's habitat (Crawford et al. 2008). However, habitat information obtained from $\delta^{13}\text{C}$ are broadscale at most and oftentimes need to be validated with location data (Newsome et al. 2010). By combining tracking information with stable isotopes, it allows a more thorough investigation of foraging ecology (Lowther et al. 2013, Walters et al. 2014, Jeanniard-Du-Dot et al. 2017). As diet is the primary contributor of an animal's isotopic composition (Peterson and Fry 1987), stable isotopes are increasingly being used to investigate foraging ecology, including individual variability in foraging strategies (Kernaléguen et al. 2012, Baylis et al. 2016), ontogeny (Chaigne et al. 2013, Vales et al. 2015), and migration patterns (Best and Schell 1996, Walters et al. 2014, Dannecker 2016), and diet (Cherel et al. 2008, Jeanniard-Du-Dot et al. 2017).

Various animal tissues have different isotopic turnover rates which influences the inferential timescale of isotopic data. Keratinous tissues such as vibrissae (whiskers) of pinnipeds have a turnover rate which integrates isotopic information over days to weeks (Cherel et al. 2009). This means that for otariids that do not shed their vibrissae periodically (as opposed to phocids that do) (Hirons et al. 2001, Newland et al. 2011), their vibrissae provide a time series of historical information that can date back on average 4 to 5 (up to 8) years (Kernaléguen et al. 2015, Rea et al. 2015). Additionally, sampling vibrissae is logistically easier and less costly than using biologgers for studying certain aspects of their foraging ecology, thus allowing for greater sample sizes.

To accurately obtain a time series of isotopic information from vibrissae, two pieces of information are required: vibrissa growth rates and the length of the vibrissa segment

analysed. One method of “time stamping” stable isotope signatures in vibrissae is to administer a ^{15}N -enriched glycine, which is incorporated into vibrissa keratin providing a temporal marker. Glycine is found in vibrissa keratin. Therefore, the administration date of ^{15}N -enriched glycine would appear as a spike in the $\delta^{15}\text{N}$ results of sequentially sampled segments along a vibrissa which would enable growth rate calculations (Hirons et al. 2001, Tyrrell et al. 2013).

The goal of this study was to validate if vibrissae isotope values can be used to infer foraging ecotypes of female long-nosed fur seals (*Arctocephalus forsteri*; LNFS). Long-nosed fur seals are common in southern Australia where they are important top predators within the Great Australian Bight ecosystem. The Great Australian Bight is important for fishing, aquaculture and ecotourism industries (Rogers et al. 2013). One of the major breeding colonies of LNFS colonies is located at Cape Gantheaume, Kangaroo Island. During the breeding season and subsequent lactation period, adult females provision a single pup onshore. These females forage from this central place, typically feeding on the continental shelf during the austral summer time coastal upwelling period (January – April), and then switching to feeding in oceanic waters in late autumn to winter (mid-April – September) when the upwelling activity ceases (Baylis et al. 2008a, Foo et al. 2019). While the seasonal changes in foraging habitat of lactating LNFS are fairly well documented (Foo et al. 2019), our understanding of individual inter-annual variability in their foraging behaviour is still limited. Tracking and measuring the foraging behaviours of the same individuals over multiple years using biologgers can be challenging, however the use of vibrissa stable isotopes may be able to solve this problem. Specifically, we aim to 1) quantify individual vibrissa growth rates, 2) quantify temporal and spatial variability of carbon and nitrogen stable isotope ratios from vibrissae, and 3) identify stable isotopic niches and evaluate the extent they reflect the observed switch between shelf and oceanic foraging.

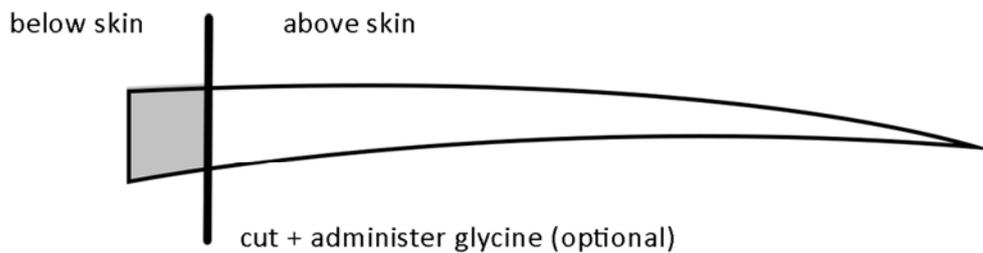
METHODS

Study site, animal handling and instrumentation

The study was undertaken between February 2016 and September 2017 at Cape Gantheaume (36°04'S, 137°27'E), Kangaroo Island, South Australia (Foo et al. 2019). In late summer (February – March), 18 lactating female fur seals ($n(2016) = 5$, $n(2017) = 13$) were randomly selected and captured using a hooped-net. Upon capture, anaesthesia was induced and maintained using Isoflurane (Veterinary Companies of Australia, Artarmon, New South Wales, Australia), administered via a portable gas anaesthetic machine (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia). Anaesthetised seals were weighed (± 0.5 kg) and their body length (nose to tail) and axillary girth were measured (± 1 cm). Miniature time-depth recorders (TDR, 2016: LAT1800L 36x11x17 mm, 10 g; 2017: LAT1800SFP, 36x11x8 mm, 5.4 g, Lotek, Ontario, Canada) and geolocation (GLS, Intigeo-C330, 17x19x8mm, 3.3 g, Migrate Technology Ltd, Cambridge, UK) loggers were deployed on all female seals via attachment on the flipper tag following Arthur et al. (2015). The time-depth recorders recorded depth every second. Geolocation loggers recorded ambient light and temperature from which twice-daily locations were estimated. A vibrissa was also cut as close to the seal's cheek as possible. In 2017, 12 of the tagged females were also administered with glycine enriched in ^{15}N isotope (98%; Novachem Pty Ltd, Victoria, Australia). This was done by subcutaneous injection into the fat layer of the belly as a solution of 100 mg/mL in sterile physiological saline at a dosage of approximately 5 mg glycine/kg of body mass (Hirons et al. 2001). Glycine was used to timestamp the vibrissa due to the high mole percentage of glycine found in vibrissa keratin (Hirons et al. 2001). In winter, tagged females were recaptured and the GLS loggers were recovered and the regrowth vibrissa were collected by (i) again cutting as close to the cheek as possible in 2016 and (ii) plucked to include the root in 2017 (Fig. 5.1). In addition to the regrowth vibrissa, a new vibrissa was plucked at the same time in both years, however these were not used in this study.

Initial capture

* Not drawn to scale



Recapture (after 6 -7 months)

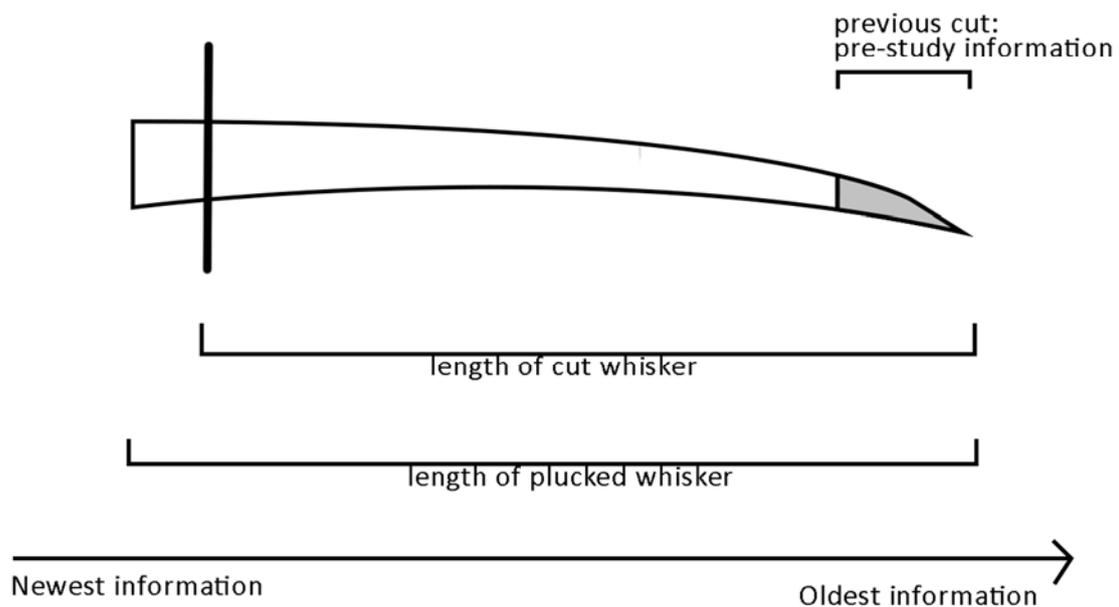


Figure 5.1 Schematic of how vibrissa regrowths from individuals were obtained at recapture. A portion from the tip of the vibrissa at recapture contained pre-study information. The unshaded portion of the vibrissa at recapture represents the actual regrowth with information from the study period. The length of the pre-study portion of the vibrissa was assumed to be the same length as the subcutaneous length of the vibrissa sample. At recapture, regrowths from individuals in 2016 and 2017 were cut and plucked, respectively. Most recent information is located at the base.

Sample preparation and stable isotope analyses

The vibrissae were washed in deionised water cleaned with successive rinses in a 2:1 chloroform:methanol solution, and then dried in an oven at 60°C for 48 hours. The vibrissae were then weighed and sectioned into approximately 2 mm segments. Starting from the base, the segments from each vibrissa were numbered sequentially. Vibrissa segments were packed in tin containers, and the relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass, UK) continuous-flow isotope-ratio mass spectrometer. Stable isotope concentrations were expressed in standard δ notation: $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio, *i.e.* $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. R_{standard} is the Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 (Air) for $\delta^{15}\text{N}$. The units are expressed in parts per thousand (‰). Stable isotope analysis was performed by the Central Science Lab, University of Tasmania, Hobart, Australia. Precision of measurements are ± 0.1 ‰ standard deviation for both carbon and nitrogen stable isotopes. A total of 47 standards were used for carbon and nitrogen where a new standard was used typically after every 10th sample. Nitrogen standards used included ammonium sulphate and L-glutamic acid. Carbon standards included limestone, graphite, and L-glutamic acid.

The re-grown vibrissa consists of the subcutaneous section of the vibrissa at the date of the first cut (pre-study information) and the actual regrowth which reflects information generated during the study period (Fig. 5.1). We assumed that the length of the subcutaneous section of the vibrissa was constant at both vibrissa sampling occasions. Because the regrowth vibrissae was sampled differently in both years (cut in 2016 but plucked in 2017), the length of the regrowth section for 2016 equalled the length from base to tip of vibrissa; while the vibrissae lengths plucked in 2017 equalled the length from base to tip of vibrissa minus the length of subcutaneous section (Fig. 5.1).

Individual vibrissa growth rates were expressed as millimetres per day and were calculated by the equation:

$$\text{length of regrowth} \div \text{duration between } t_1 \text{ and } t_2 \quad (1)$$

where t_1 is the date of the first cut and t_2 is the date when the regrowth was re-sampled. The glycine marker causes a sharp increase in $\delta^{15}\text{N}$ values indicating its injection date. Thus, the vibrissa growth rate for glycine-injected seals was also calculated by the equation:

$$\text{base to spike length} \div \text{days since injection} \quad (2)$$

Using individual vibrissa growth rates, corresponding dates were estimated for each vibrissa segment starting from the final sampling date (*i.e.* base). For the cut vibrissa regrowths, we accounted for the missing subcutaneous section (newest information) by measuring that of the plucked vibrissae which were sampled at the same time. For glycine-injected seals, the vibrissa growth rate calculated using the glycine spike was used for estimating dates since it was more accurate than the alternative. If the glycine spike covered more than one vibrissa segment, the earliest segment was assigned to the injection date (*i.e.* initial capture date).

We used data from the glycine-injected seals to estimate the potential error in date estimation using individual vibrissa growth rates calculated from the regrowth length (equation 1). To do this, we calculated the difference between the actual injection date (as indicated by the glycine spike) and the estimated injection date (t_1) obtained from equation 1. To ensure consistency, subsequent analyses were done using the vibrissa growth rates obtained from equation 1 for all seals.

Statistical analyses

All data analyses were done using the R program (v. 3.5.1) (R Core Team 2019). Raw light data from the GLS loggers allowed us to obtain two locations estimates per day during the deployment which were divided into individual foraging trips (details in Foo et al. (2019)). The accuracy of the geolocation estimates is 45 ± 29 km (Foo et al. 2019). In areas with higher prey density, we would expect longer residence time associated with periods of area-restricted search and hence a proxy for foraging effort (Dragon et al. 2010, Pistorius et al. 2017). Thus, the cell residence time in each 30-km grid cell was calculated for each foraging trip using the ‘Trip’ package (v1.5.0) (Sumner 2016a). The size of the grid cell was chosen to account for the error associated with GLS tags while still providing a realistic representation of true locations. Trips with < 3 locations and locations within a 10 km buffer around the colony were removed. Core foraging areas were determined as those in the 90th percentile of the cell residence time for each foraging trip. Each foraging trip was then classified as “shelf” (includes continental shelf and shelf break; bathymetry ≥ -2000 m) or “oceanic” (bathymetry < -2000 m), depending on the furthest point of that foraging trip from the colony. If the

corresponding location data was not available for a seal's vibrissa stable isotope data, we inferred if the seal foraged exclusively on the shelf or oceanic waters, or both from associated unpublished diving data if they were available. Typically, the maximum depths of dives are distinct between shelf (~100 m) and oceanic foraging (~ 200 m). We matched vibrissa segments to the core foraging cells of the nearest foraging trip for each individual by comparing the estimated date of each vibrissa segment and the median date of foraging trips. By restricting vibrissa segments to the trip-level we avoided matching them to a date that happens to correspond to a location during the transit phase of a foraging trip. While this means that the isotopic data of individual vibrissae segments may represent periods of transit and feeding in a given foraging trip, stable isotopes assimilated into an animal's tissue occur mainly from foraging.

Since all the vibrissa regrowths contained pre-study period information, segments with estimated dates prior to the first capture date of the seal were removed from further analyses. Additionally, $\delta^{15}\text{N}$ values that were influenced by glycine were also excluded from further analyses but their corresponding $\delta^{13}\text{C}$ values were still included. To compare stable isotopes between shelf and oceanic habitats, we used a model-based clustering approach (based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) using the package 'Mclust' (v. 5.4.4) (Fraley and Raftery 2007). In this approach, a clustering model that allows for overlapping clusters with varying geometric properties and quantifies the uncertainty of observations belonging to clusters is estimated for the data. Model selection was made using Bayesian information criteria because this method commonly penalises overly complicated models.

To investigate the relationship between latitude and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values, we fitted Gaussian error distribution with identity link generalised additive mixed models for each stable isotope with trip nested within individuals as random effects and the two-way interaction between year and latitude as smoothed terms. Autocorrelation and heterogeneity issues were addressed by specifying a first order autocorrelation structure and/or power variance function, respectively. Linear mixed models were fitted separately for each stable isotope against the interaction between region and year and the interaction between region and breeding state (provisioning vs unconstrained, see section 3.3), with trip

nested within individual as a random effect. All model selections were done using a backward selection process where Akaike's Information Criterion (AIC) was used to assess model performance where appropriate. Models with a better fit have lower AIC values. All t-tests are two-tailed and if values do not fulfil normality assumptions, then the non-parametric Wilcoxon t-test was used. We assessed significance of statistical tests at the 0.05 level. Mean values are given \pm standard deviation (SD).

Table 5.1 Details of 18 adult female LNFS whose vibrissa regrowths were sampled and if they had simultaneous data from geolocation (GLS) or time-depth recorder (TDR) tags. Four individuals were not provisioning a pup and hence were considered unconstrained to central place foraging. Some individuals were also administered ^{15}N -enriched glycine on the capture date to biologically mark the date. Individual vibrissa growth rates were calculated using two methods – with or without using the spike in ^{15}N from the glycine biomarker (see methods for details). Foraging habitats were determined from biologger data. (more details of vibrissa lengths in Table S5.1).

ID	Capture date (A)	Recapture date	Provisioning a pup?	Glycine	Growth rate (mm d ⁻¹)		Estimated injection date (B)	B – A (days)	GLS	TDR	Foraging habitats
					Without glycine	Glycine					
2016											
69	26-Feb	19-Sep	Y		0.23						
71	5-Feb	27-Aug	Y		0.23						
73	1-Feb	22-Aug	Y		0.13			Yes			Shelf/Oceanic
77	5-Feb	21-Aug	Y		0.14			Yes			Shelf/Oceanic
450	16-Feb	25-Sep	Y		0.12			Yes			Shelf/Oceanic
2017											
307	29-Jan	4-Aug	N		0.16			Yes			Oceanic
311	5-Feb	7-Aug	Y		0.17			Yes			Shelf/Oceanic
329	12-Feb	25-Jun	Y		0.17				Yes		Oceanic
340	14-Feb	18-Jul	N		0.17			Yes			Oceanic
353	13-Mar	29-Jun	Y		0.21			Yes			Oceanic
315	6-Feb	6-Jul	Y	Yes	0.16	0.19	29/01/2017	-8	Yes		Shelf
317	7-Feb	7-Aug	N	Yes	0.25	0.27	4/02/2017	-3	Yes		Oceanic
318	7-Feb	29-Jun	Y	Yes	0.13	0.14	15/02/2017	8		Yes	Shelf
319	7-Feb	5-Jul	Y	Yes	0.22	0.25	2/02/2017	-5	Yes		Shelf/Oceanic
322	9-Feb	12-Jul	Y	Yes	0.18	0.19			Yes		Shelf/Oceanic
324	10-Feb	11-Jul	N	Yes	0.18	0.15			Yes		Oceanic
326	10-Feb	7-Aug	Y	Yes	0.18	0.16	19/03/2017	37	Yes		Shelf/Oceanic
351	13-Feb	30-Jun	Y	Yes	0.18	0.17	2/03/2017	17	Yes		Oceanic
Overall mean					0.18 \pm	0.19 \pm		7.7 \pm			
					0.04	0.05		17.1			

RESULTS

Stable isotope and foraging habitat data

We recaptured and obtained regrowth vibrissae from 18 females across both study years. Three of the recaptured individuals had lost their GLS loggers and the GLS data from one individual was corrupted leaving the remaining 14 with corresponding GLS tracks. Two of the individuals without GLS data had dive data up to May (unpublished; Fig. S5.1). A summary of the vibrissa sampling process and the types of data obtained from individuals is shown in Table 5.1. Across all individuals, a total of 306 vibrissa segments were obtained with an average of $17.3 (\pm 4)$ per individual. The average length of the subcutaneous section for plucked vibrissae was $8.7 (\pm 1.1)$ mm (Table 1). The average length of cut and plucked vibrissa regrowths were $34.8 (\pm 11.2)$ mm and $36.7 (\pm 7.3)$ mm, respectively. Out of those possible segments, 18 of those vibrissa segments were lost during the process of sectioning and $n = 13$ subcutaneous segments of plucked vibrissae were excluded because their isotope values have been shown to be affected by anomalous values (Huckstadt et al. 2012). Pre-study whisker segments were also excluded from further analyses, leaving a final total of 222 segments. Out of that final total, 18 segments were influenced by glycine hence their $\delta^{15}\text{N}$ information were also removed from further analyses. Overall, 204 vibrissa segments had complete $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ information. Out of those segments, 151 corresponded with GLS-derived core foraging areas and 12 corresponded with foraging habitat information derived from dive data during the study period.

Vibrissa growth rates

The threshold for identifying the glycine spike was $\delta^{15}\text{N} > 17.6$ ‰, which generally consisted of 1 – 4 vibrissa segments (Fig. S5.2). Using growth rates of glycine marked vibrissae, on average the estimated glycine injection date was $7.6 (\pm 17.1)$ d later than the actual glycine injection date (Table 1). This calculation was done excluding two of the glycine marked seals which had missing data covering the entire duration of the glycine spike. The average vibrissa growth rate calculated with and without using the glycine spike as a reference was 0.18 ± 0.04 and 0.19 ± 0.05 mm d⁻¹ (Wilcox test: $W = 64$, p -value = 0.68), respectively.

Spatial and temporal variability in vibrissae isotope ratios

The number of foraging trips per individual ranged from 5 to 22 (mean = 11.4 ± 5.5). The average duration of each foraging trip was 10.6 ± 8.8 d. The cell residence time in a core foraging 30 x 30 km cell ranged from 8 to 136.3 h (mean = 27 ± 14.2 h). Core foraging areas primarily occurred on the distal portion of the track (Fig. S5.3). Four individuals did not display central place foraging behaviour which might have been due to either pup abandonment or their pup dying; hence we considered these females unconstrained (Table 5.1).

Table 5.2 Approximate significance of smooth terms from generalised additive models. Statistically significant terms are in bold.

Term	edf	ref.df	Statistic	P-value
<i>$\delta^{15}N \sim s(\text{latitude}, \text{by} = \text{year})$</i>				
s(latitude):year2016	1	1	1.44	0.23
s(latitude):year2017	4.21	4.21	17.13	0.00
<i>$\delta^{13}C \sim s(\text{latitude}, \text{by} = \text{year})$</i>				
s(latitude):year2016	1.05	1.05	3.82	0.05
s(latitude):year2017	1.39	1.39	5.54	0.02

Generalised additive mixed models revealed that $\delta^{13}C$ increased while $\delta^{15}N$ decreased with increasing latitude. These relationships were only significant for 2017 (Fig. 5.2 and Fig. S5.4; Table 5.2). 66.4% of individual trips (obtained from GLS data) had one vibrissa segment assigned to it (range = 1 – 4). Because sample sizes per individual trip group were small, trip was not used as a nested random effect within individual seals in mixed models. From the 16 seals that had all or some corresponding foraging habitat information (from GLS or TDR data; Table 5.1), a total of 42 and 121 vibrissa segments were assigned to shelf and oceanic habitats, respectively. $\Delta^{13}C$ was influenced by habitat (shelf vs oceanic) where $\delta^{13}C$ was lower on the shelf (Fig. 5.3a; Table 5.3). The final model for $\delta^{15}N$ included the breeding state of females and the interaction between year and habitat (Table 5.3). $\delta^{15}N$ of provisioning females were greater than unconstrained females (Fig 5.3b). The effect of habitat on $\delta^{15}N$ differed between years where $\delta^{15}N_{\text{shelf}}$ was slightly lower than $\delta^{15}N_{\text{oceanic}}$ in 2016 whereas the $\delta^{15}N_{\text{shelf}}$ was greater than $\delta^{15}N_{\text{oceanic}}$ in 2017 (Fig. 5.3c; Table 5.3). Unconstrained females

were generally smaller in length (128 ± 5.6 cm) than females provisioning pups (136 ± 6.6 cm; Welch two-sample t-test: $t = 2.55$, $df = 5.69$, $p = 0.0457$).

Table 5.3. Statistical summaries of the final models. $\Delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were fitted as linear mixed models. The oceanic cluster model was a logistic mixed model. For the results of the model selection process please see Table S2.

Term	Effect	Estimate	SE	Statistic
$\delta^{15}\text{N}$				
(Intercept)	fixed	15.36	0.29	52.8
regionshelf	fixed	-0.05	0.19	-0.27
year2017	fixed	0.03	0.34	0.1
stateunconstrained	fixed	-0.66	0.29	-2.28
regionshelf:year2017	fixed	0.64	0.24	2.7
seal (intercept) SD	random	0.45		
residual SD	random	0.49		
$\delta^{13}\text{C}$				
(Intercept)	fixed	-15.9	0.04	-369
regionshelf	fixed	-0.1	0.04	-2.37
seal (intercept) SD	random	0.15		
residual SD	random	0.18		
Oceanic cluster				
(Intercept)	fixed	-6.68	2.8	-2.38
yday	fixed	0.12	0.04	2.7
year2017	fixed	6.32	3.14	2.01
yday:year2017	fixed	-0.1	0.04	-2.23
seal (intercept) SD	random	1.75		

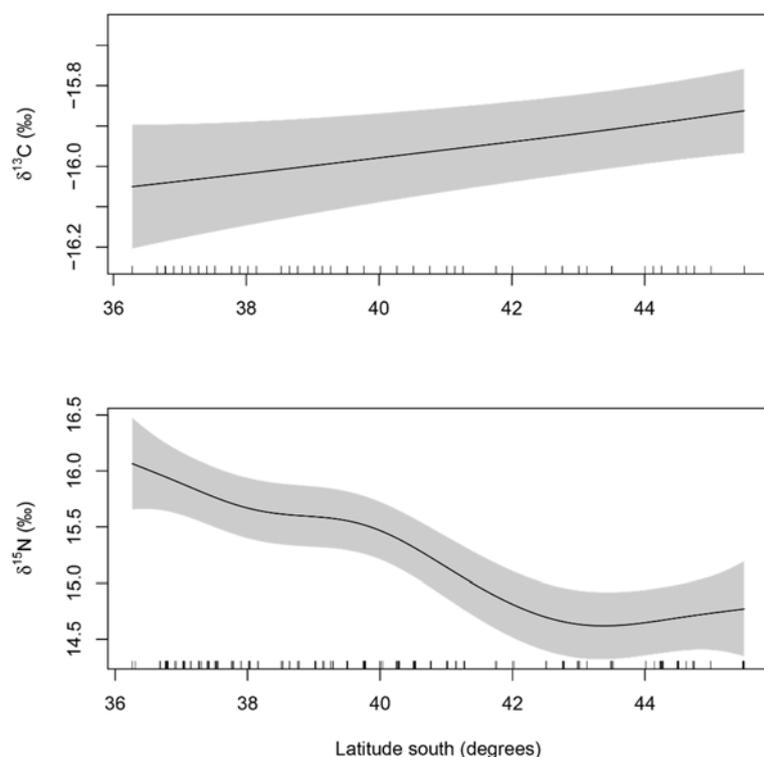


Figure 5.2 Smoothed effects of latitude on (a) carbon and (b) nitrogen stable isotopes for 2017 as determined by generalised additive models. The shaded area indicates a 2 standard error uncertainty about the overall mean of the model.

Variability of isotopic niches among individuals

Model-based clustering revealed that segments of individual adult female vibrissa regrowths during the lactation period could be separated into three clusters represented by ellipses that encompassed distinct isotopic niches (Fig. 5.4). The uncertainty in the classification ranged from 0.005 to 49.6% where 75% ($n = 153$) of our samples had an uncertainty of 14.5% or less. One of the clusters was primarily associated with shelf foraging (cluster 2) while the other two were primarily associated with oceanic foraging (cluster 1 and 3; Fig. 5.4). Out of 163 vibrissae samples, 79.8% of them were correctly classified into an oceanic or shelf cluster based on their stable isotope signature. Misclassified samples were primarily located in between cluster ellipses, had high uncertainty and corresponded to the shelf break region where points from different clusters overlap (Fig. 5.4b). There were no 2016 stable isotope samples that were allocated to cluster 2 (Table S5.2). Between the oceanic clusters (1 and 3), cluster 3 had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and their spatial range was similar (Fig. 5.4b).

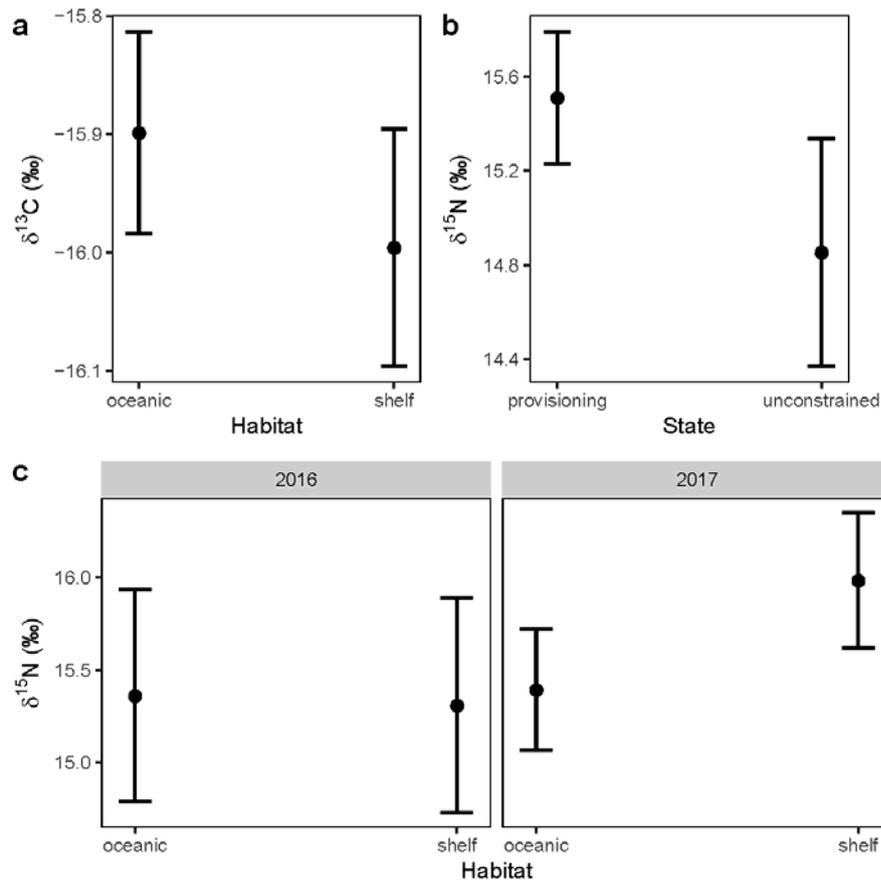


Figure 5.3 Effect of (a) habitat on $\delta^{13}\text{C}$, (b) breeding state on $\delta^{15}\text{N}$ and (c) conditional effect of habitat on $\delta^{15}\text{N}$ depending on year. Error bars represent the confidence intervals.

After obtaining the cluster groups, we were interested to investigate the relationship between oceanic clusters (1 or 3) and the interaction between year and the day of the year (based on the estimated date for each vibrissae segment). Cluster 2 (shelf) was not considered since it had a relatively small sample size ($n = 20$). Using a logistic mixed model, with the same model selection process as described in the Methods, we found that the probability of being in cluster 3 increased with later in the year for both years but the rate of change in probability was greater in 2016 (Fig. 5.5; Table 5.3). A summary of individual and cluster stable isotope values is shown in Table S5.4.

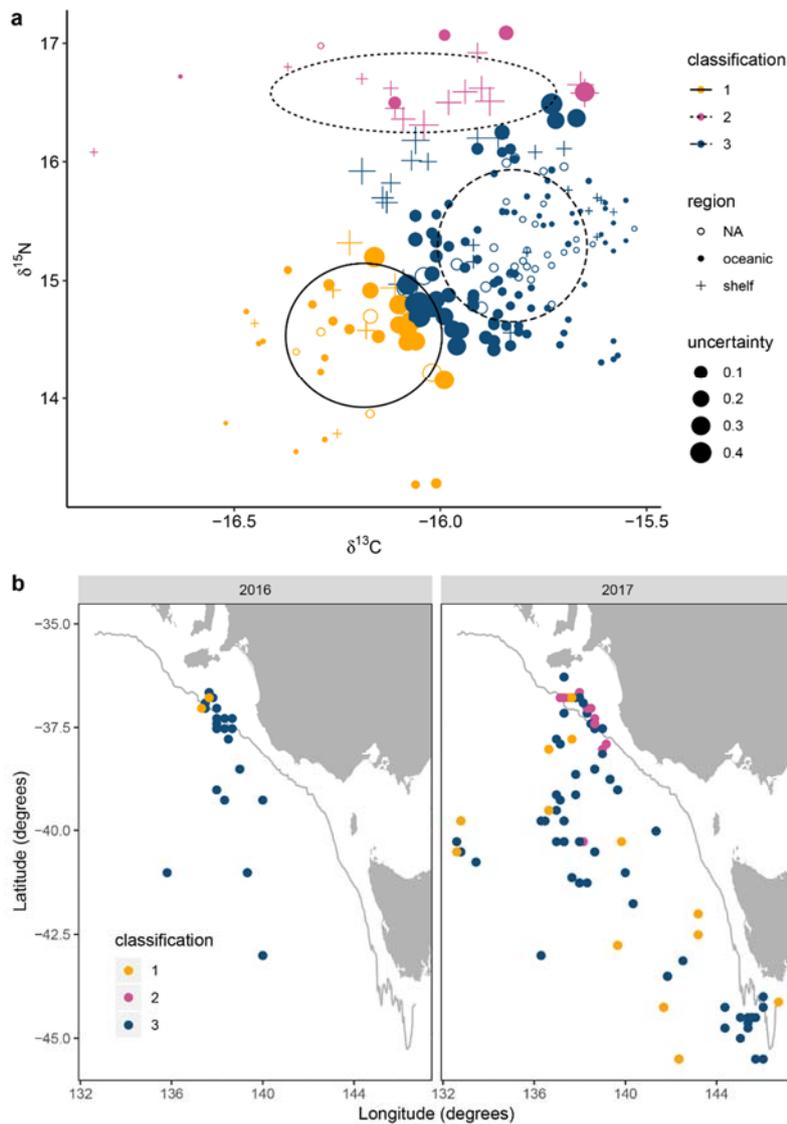


Figure 5.4. Isotope biplots (a) of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) values for lactating long-nosed fur seal 133ibrissae sampled from Cape Gantheaume. Each data point represents the stable isotopic composition of a segment that was sampled sequentially along each 133ibrissae. Using individual estimated 133ibrissae growth rates, we reconstructed a stable isotope time series from each 133ibrissae and matched them to corresponding foraging locations (shelf vs. oceanic) obtained from GLS tags or TDRs. Vibrissa segments without corresponding foraging region information are “NA” and do not appear as data points in (b). Ellipses surrounding data points depicted significant clusters derived from model-based cluster analysis, with data points from the same cluster represented by the same colour. The size of data points represented relative classification uncertainty by the cluster analysis where larger symbols indicate less certain observations. (b) Spatial map of core foraging areas (each point is the median core foraging location of a trip) distinguished by their classification group

and by year. The grey line represents the 2000 m isobath separating the continental shelf and shelf break from oceanic waters.

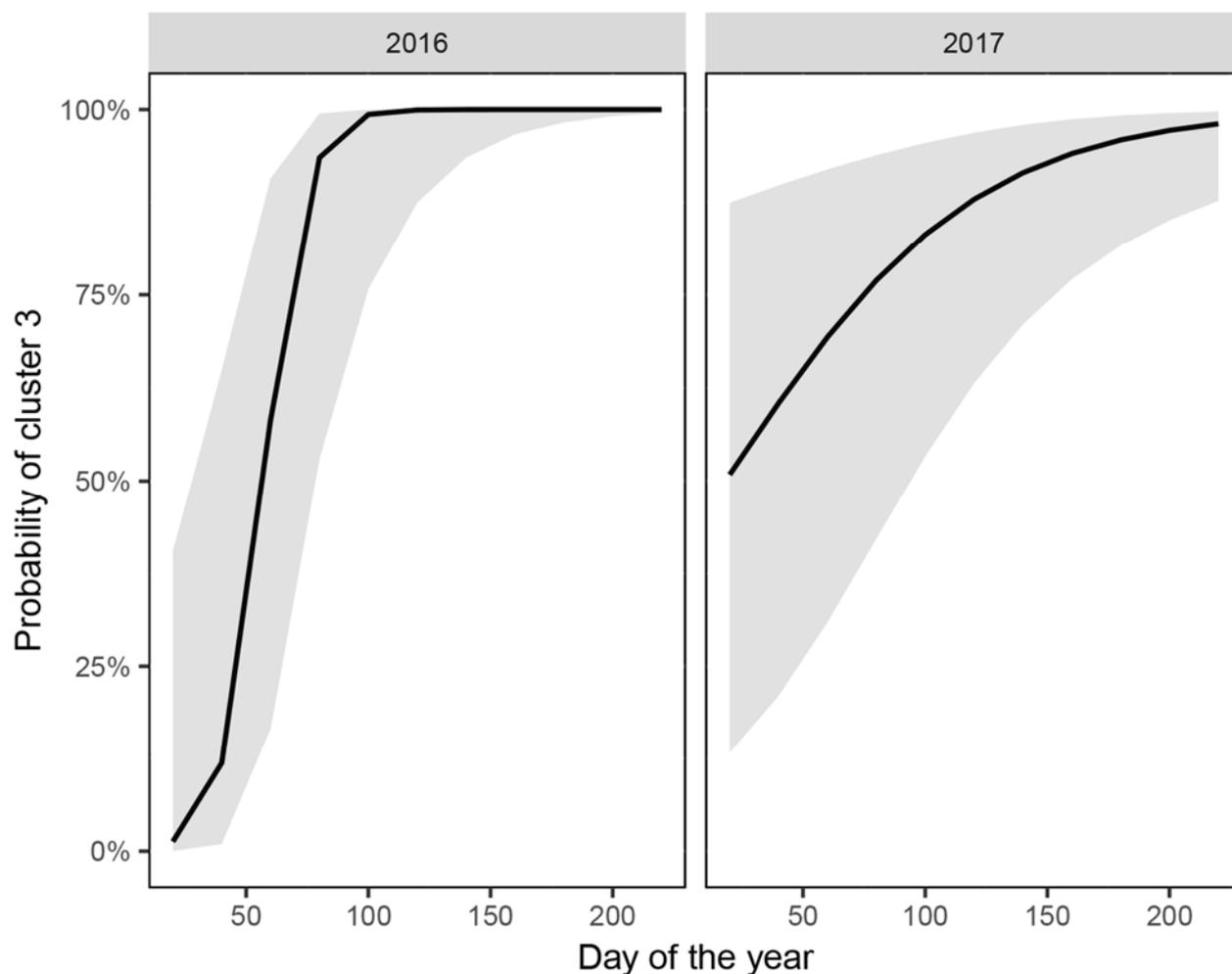


Figure 5.5 Interaction effect between day of the year and year on the probability of a vibrissae stable isotope sample being in cluster 3 (as opposed to cluster 1). Both cluster groupings were obtained from model-based clustering analysis and are primarily associated oceanic foraging. The shaded area represents the confidence intervals of the model.

DISCUSSION

Our study contributes to the literature of vibrissa growth rates in pinnipeds (Hirons et al. 2001, Kernaleguen et al. 2012, McHuron et al. 2016, Chilvers 2018). Few other studies have used $\delta^{15}\text{N}$ -enriched glycine to estimate the growth rates of otariid vibrissae (Hirons et al. 2001, de Lima et al. 2019). By combining the vibrissae stable isotopic and geolocation data, we showed the broad scale foraging habitats (*i.e.* shelf vs. oceanic clusters) of females can be

identified based on bulk nitrogen and carbon stable isotopes. Thus, vibrissae stable isotope signatures show potential for distinguishing different foraging strategies of adult females (*i.e.* oceanic or shelf only or both, or unconstrained; Fig. S5.5) and fidelity to foraging sites (*i.e.* diversity of isotopic niches) (Zeppelin and Orr 2010) which can affect their reproductive performance in different years (Bradshaw et al. 2004).

Vibrissae growth rates

The vibrissae growth rates obtained without the use of the glycine marker would be minimum estimates as we did not take into account potential wear at the tip of vibrissae (Rea et al. 2015, McHuron et al. 2019). Nevertheless, the mean vibrissae growth rate calculated with (0.19 mm d^{-1}) and without (0.18 mm d^{-1}) glycine were similar thus providing support for the accuracy of our results. Furthermore, stable isotope information at the tip of the regrowth vibrissa would have corresponded to pre-study information which was not used in this study. This study's vibrissae growth rates were comparable to those of other otariids such as wild subadult and adult Stellar sea lions (*Eumetopias jubatus*, $0.1 - 0.17 \text{ mm d}^{-1}$, glycine method) (Hirons et al. 2001) and adult male Antarctic (*Arctocephalus gazelle*) and subantarctic fur seals (*Arctocephalus tropicalis*; 0.14 mm d^{-1}) but were more than twice that of female Antarctic (0.08 mm d^{-1}) and subantarctic (0.09 mm d^{-1}) fur seals (Kernaleguen et al. 2012). The differences in vibrissae growth rates among species and animal sizes indicates that caution should be taken when referencing vibrissae growth rates of other species in analyses.

Spatial variability of stable isotope ratios

Variation in carbon ratios is generally influenced by SST with lower $\delta^{13}\text{C}$ in cooler waters; producing a broad latitudinal gradient where $\delta^{13}\text{C}$ decreases towards the poles (Trueman et al. 2012). However, in the southern hemisphere, this negative relationship between $\delta^{13}\text{C}$ and latitude is more prominent south of the subtropical convergence zone ($\sim 42^\circ\text{S}$). North of this zone the correlation between $\delta^{13}\text{C}$ and latitude is positive (Best and Schell 1996, Bax et al. 2001, Trull and Armand 2001). This is likely due to other factors that can influence particulate organic matter $\delta^{13}\text{C}$ such as plankton growth rates, cell geometry and taxonomy (Trueman et al. 2012). This is consistent with our results which showed a positive correlation between

$\delta^{13}\text{C}$ and latitude. Additionally, the mixing of shelf waters with carbon-depleted waters from the subtropical front that spill onto the shelf in association with upwelling events in summer and carbon-depleted east-ward flowing Leeuwin Current off Western Australia at the start of winter may lead to lower $\delta^{13}\text{C}$ on the shelf (Lowther et al. 2013). Furthermore, Australia has an extensive northern boundary ocean system where cross-shelf exchange of water (Middleton and Bye 2007) may transport relatively carbon-enriched coastal waters off the shelf via more mobile mid-trophic level animals thus in turn enriching the $\delta^{13}\text{C}$ values of the adjacent oceanic waters.

The mixing of different water masses due to the unique geographical characteristics of our study region may also explain our relatively low range of $\delta^{13}\text{C}$ values (1.2‰). In comparison, Bax et al. (2001) reported that the range of $\delta^{13}\text{C}$ from 37°S to 45°S for their study was ~4‰. The $\delta^{13}\text{C}$ POM values obtained by Bax et al. (2001) were taken from oceanic waters within the Indian Ocean; whereas the relatively small spatial range in this study may be influenced by the inshore/offshore $\delta^{13}\text{C}$ gradient (where $\delta^{13}\text{C}$ generally decreases offshore) as well as the broader $\delta^{13}\text{C}$ latitudinal gradient. The small $\delta^{13}\text{C}$ range likely also contributed to the misclassification of some data points between the shelf and oceanic clusters. There may not always be a clear difference in $\delta^{13}\text{C}$ between inshore and offshore habitats due to the combined effects of biological and physical properties of the local area including currents and food web structure (Hansen et al. 2012). It is also possible for stable isotope signatures of zooplankton communities within different water types (*i.e.* shelf versus oceanic warm and cold core eddies) to be similar which would contribute towards overlapping shelf and oceanic stable isotope signatures (Henschke et al. 2015). Compound specific stable isotope analysis (Crawford et al. 2008, Lorrain et al. 2009) would be useful in finding out the baseline values of carbon and nitrogen stable isotopes in different water types and hence their origin for accurate comparison.

The range of $\delta^{13}\text{C}_{\text{shelf}}$ (-16.8 – -15.6 ‰) and $\delta^{15}\text{N}_{\text{shelf}}$ (13.7 – 16.9 ‰) overlapped with those obtained from the vibrissa of a sympatric male Australian sea lion (*Neophoca cinerea*; $\delta^{13}\text{C}$: mean = -17.6, range = -18.7 – -16.2 ‰; $\delta^{15}\text{N}$: mean = 15.5, range = 15.2 – 16 ‰) which forages on the continental shelf year-round in the same region (Lowther et al. 2013). The

range of $\delta^{15}\text{N}_{\text{shelf}}$ is greater for female LNFS than the male Australian sea lion which may suggest the former group is consuming a wider range of prey than the latter. However, a direct comparison of stable isotope values between different species and sex may not be entirely accurate since their trophic discrimination factors may differ slightly (Jenkins et al. 2001). Nonetheless, Australian sea lions are benthic foragers (Lowther et al. 2013) whereas LNFS are pelagic foragers (Page et al. 2005b); the lower range of $\delta^{13}\text{C}_{\text{shelf}}$ of the Australian sea lion may reflect benthic foraging since $\delta^{13}\text{C}$ tends to be lower in cooler waters and with increasing depth (Kroopnick 1985).

Prey consumed in the different habitats may have been different between years. In 2017, prey consumed during shelf foraging trips had a higher $\delta^{15}\text{N}$ than prey consumed during oceanic foraging trips. This likely explains why unconstrained females which forage more frequently in oceanic waters generally had lower $\delta^{15}\text{N}$ than provisioning females. Conversely, in 2016 $\delta^{15}\text{N}$ was very similar between both habitats suggesting that the diet composition of females, particularly on the shelf, can vary inter-annually (*i.e.* proportion of each prey type) or that there was a shift in $\delta^{15}\text{N}$ at the base of the food web between years (Ruiz-Cooley et al. 2014). The primary diet of female LNFS on the shelf includes red bait, jack mackerel and Gould's squid; whereas in oceanic waters it is primary myctophids (e.g. lantern fish) (Baylis et al. 2009). If the former reason was true, the higher $\delta^{15}\text{N}$ on the shelf in 2017 may have been due to females consuming more shelf prey with higher $\delta^{15}\text{N}$ such as Gould's squid (Fig. S5.6). The increased consumption of relatively low-energy benthic fish and cephalopods (higher $\delta^{15}\text{N}$) may have been driven by relatively weaker upwelling on the shelf in 2017 (Foo et al. 2019). If variability in $\delta^{15}\text{N}$ in our study was due to baseline $\delta^{15}\text{N}$ variability between years instead, it would mean that the mean trophic level of prey that females are consuming in their respective habitats may actually be the same in different years after accounting for baseline $\delta^{15}\text{N}$ shifts.

Identifying foraging strategies based on clusters

There was a relatively strong isotope signature for the shelf (Fig. S5.5) as represented by cluster 2. This may be useful as a baseline reference for foraging strategies used by lactating LNFS, *i.e.* shelf-only foraging during the pup-rearing period is represented by minimum

threshold of -16.8 ‰ and 16.1 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Interestingly, cluster 2 was only found in 2017 which suggests that the trophic landscape in 2016 somehow led to more similar foraging behaviour and that cluster 1 and/or 3 also include shelf foraging isotope signatures. This may explain the lack of distinction between shelf and oceanic stable isotope signatures (especially $\delta^{15}\text{N}$) in 2016 which may have been due to oceanic prey also occurring on the continental shelf slope and outer shelf water and/or the extent of females foraging on the shelf during the transit phase of oceanic foraging trips.

Nevertheless, clusters 1 and 3 also occurred in the oceanic region far away from the continental shelf which suggests that there were different groups of oceanic prey. One possible explanation is that females may encounter various frontal and eddy features which may have different stable isotopic signatures that can also change over time (Henschke et al. 2015). Indeed, oceanic cluster 3, which generally has higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than oceanic cluster 1, was associated with foraging later in the year and when females spent more time foraging. There is high eddy activity within the oceanic region especially in winter (Foo et al. In review) and the subtropical front region has a high incidence of eddy formation and eddy shedding (Tomczak et al. 2004). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of a warm core (anticyclonic) eddy can increase significantly after a phytoplankton bloom induced by upwelling (Henschke et al. 2015). Warm core eddies may also have higher $\delta^{13}\text{C}$ than cold core (cyclonic) eddies. The different stable isotopic signatures between eddy types is a reflection of the type of zooplankton community (Waite et al. 2007a) which may attract different types of prey.

Conclusion

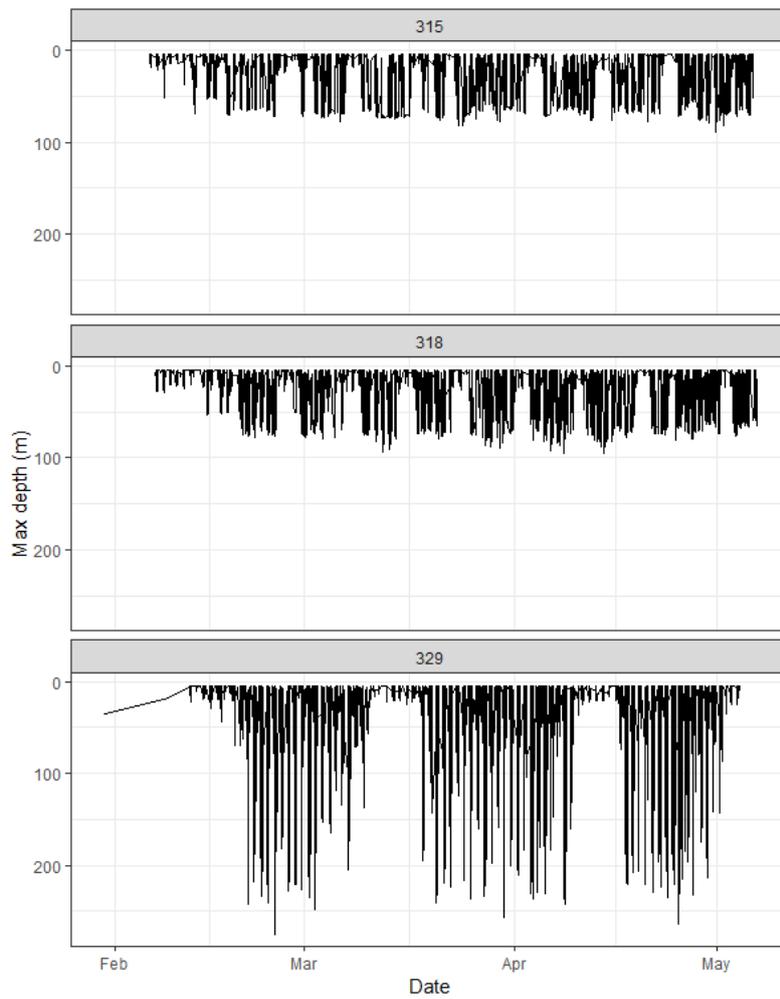
The isoscape generated from vibrissae stable isotopes shows relatively high spatial variability which may be characteristic of this region with complex biophysical process on the shelf and oceanic waters. However, using biogeomarkers from vibrissae regrowths may still allow us to broadly distinguish between the shelf and oceanic foraging locations and hence the type of individual foraging strategy (shelf or oceanic only foraging, or both). Future studies may consider analysing complete vibrissae to identify annual cycles in stable isotopes to further verify vibrissae growth rates (Kernaleguen et al. 2012). Additionally, vibrissae of pups may also be used to assess within and between population variability in maternal alternate

foraging strategies (Scherer et al. 2015, Baylis et al. 2016), including individual foraging fidelity to foraging locations between years.

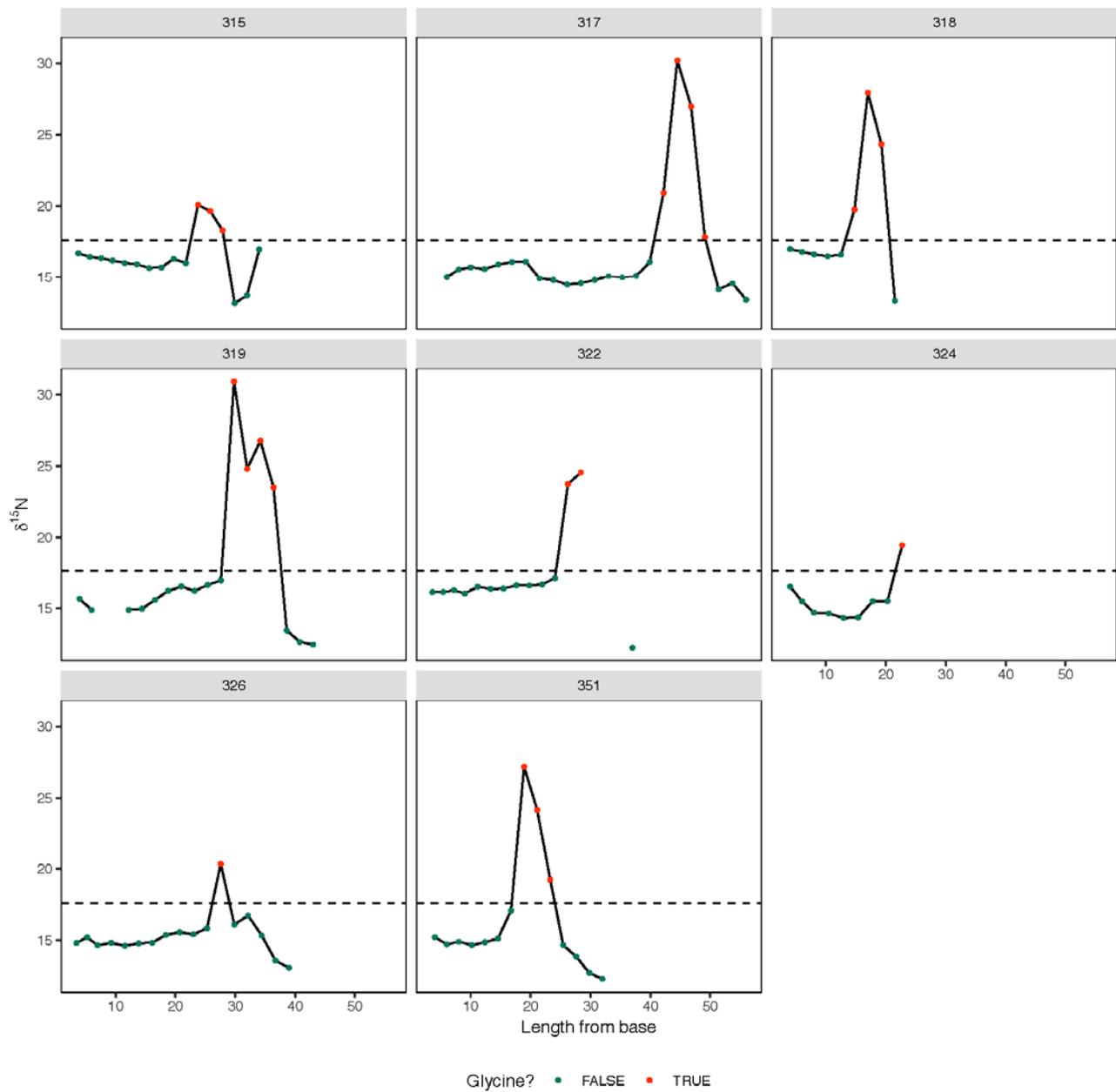
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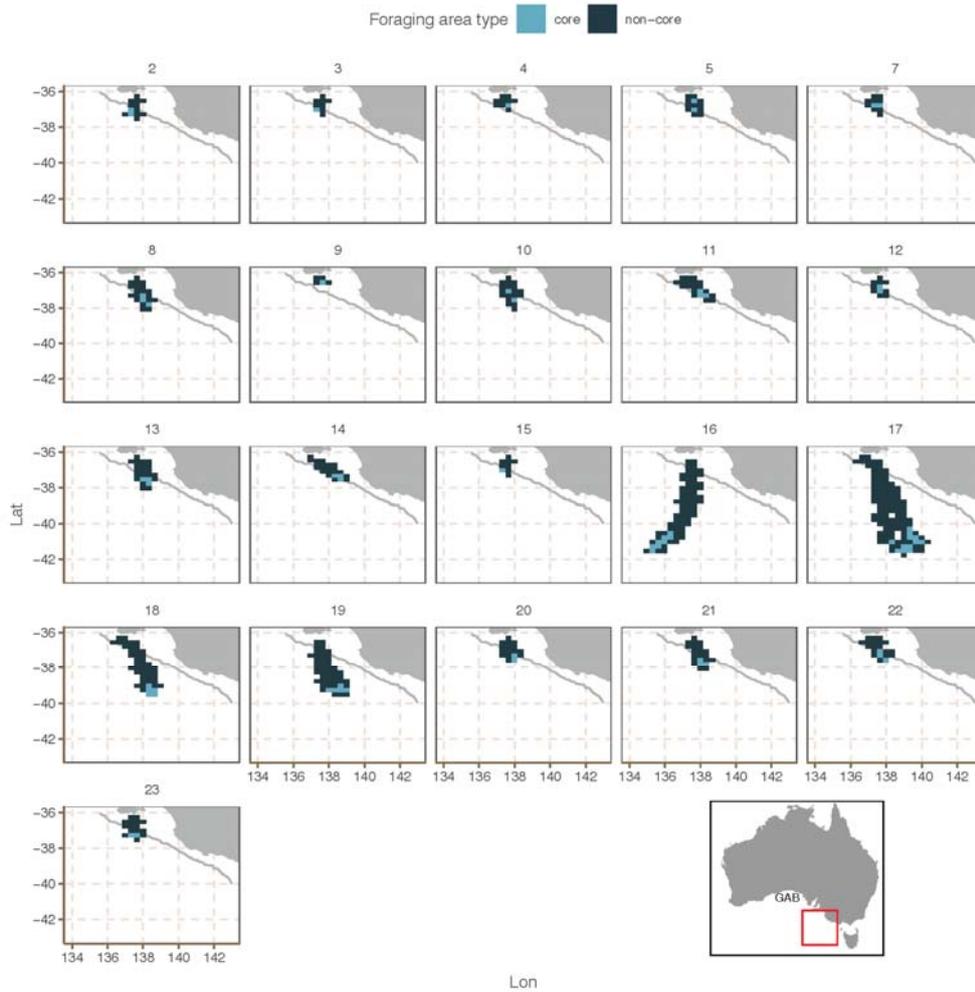
APPENDIX



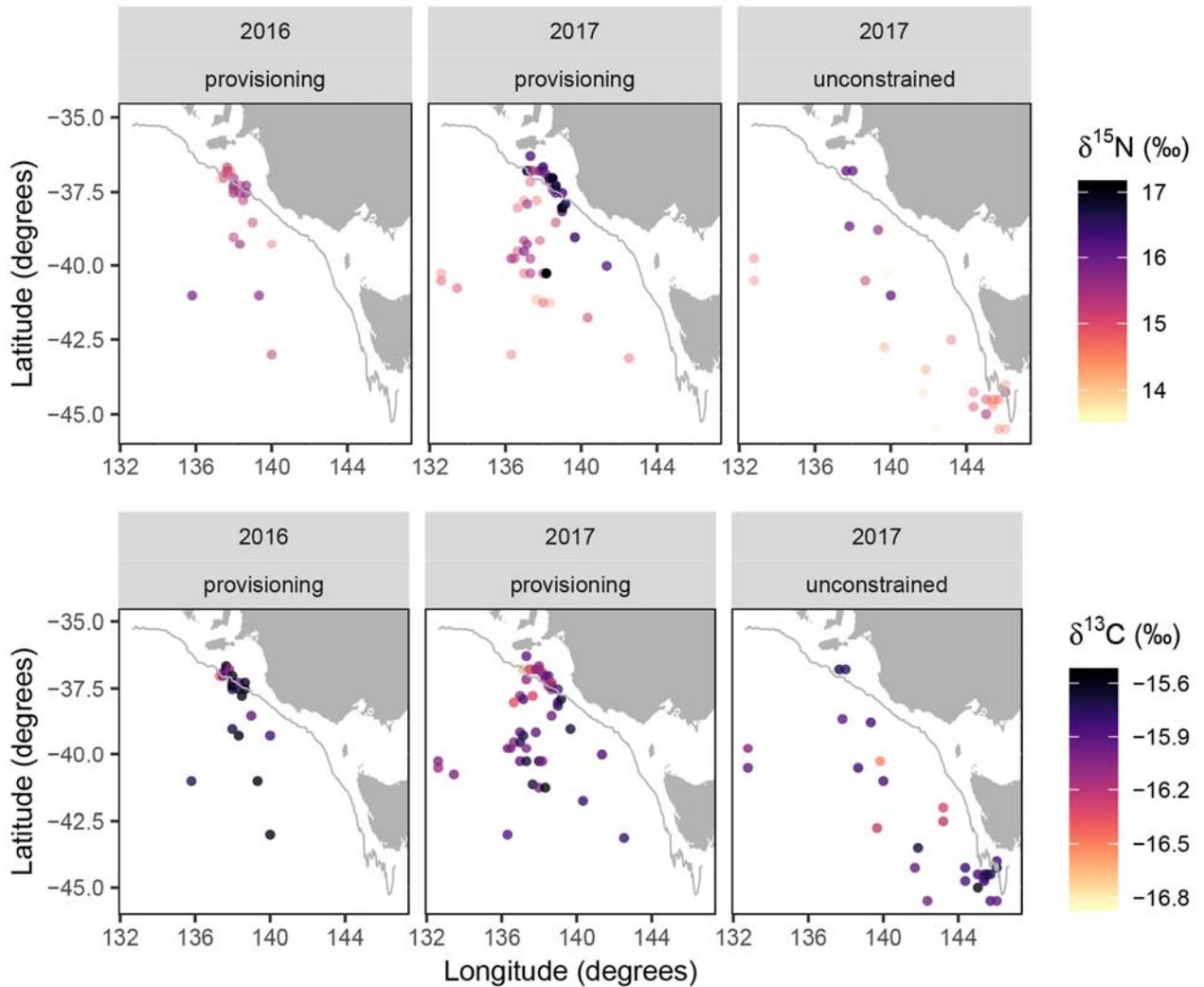
Supplementary Figure 5.1 Dives made by seals #315, #318, and #329. Seal #315 is a reference of what shelf foraging trip dives look like as validated by location data. #318 only made shelf foraging trips whereas #329 made only oceanic foraging trips.



Supplementary Figure 5.2 Sequence of $\delta^{15}\text{N}$ from adult female long-nosed fur seals administered with a ^{15}N -enriched glycine biomarker at initial capture. The threshold for segments influenced by the glycine was visually determined to be 17.6 ‰. Units: length from base (mm); $\delta^{15}\text{N}$ (‰).



Supplementary Figure 5.3 Example of core foraging areas of consecutive trips (number above each plot) from adult female Long-nosed fur seal #450. Core foraging areas are defined as cells in the 90th percentile of the time spent (h) in 30 x 30 km cells for each trip. Inset: the study region relative to Australia. Great Australian Bight, GAB.

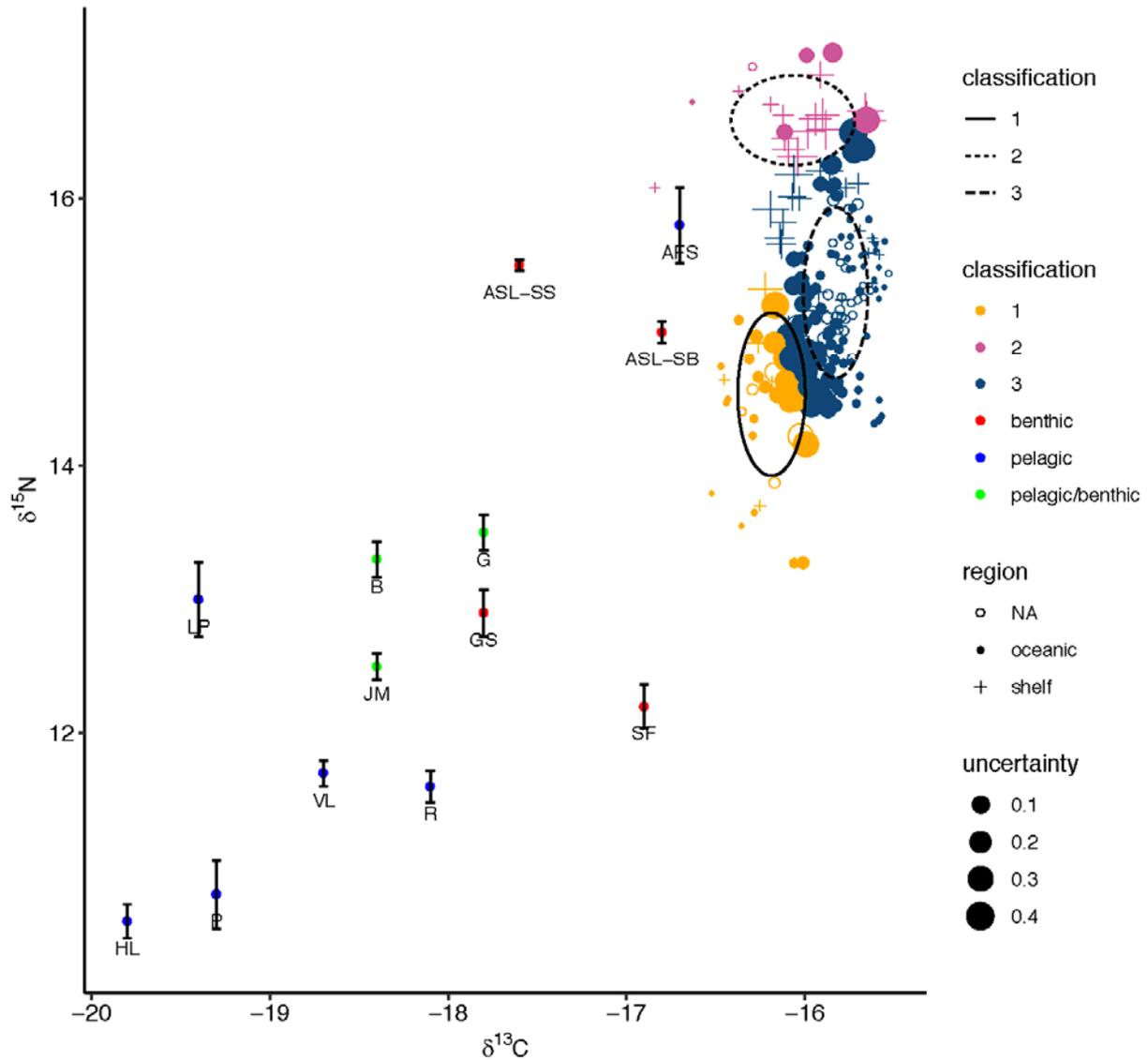


Supplementary Figure 5.4 The annual mean stable isotope values at the median core foraging location of individual trips. Lower isotope values are lighter in colour and more transparent. Provisioning represents females that were provisioning a pup whereas unconstrained females were not. The grey solid line represents the 2000 m isobath which separates the continental shelf and shelf break from oceanic waters.



Supplementary Figure 5.5 Combined carbon (diamond shape, dashed line) and nitrogen (circle shape, solid line) stable isotope plot of individual adult females. Clusters and uncertainty groupings were obtained from model-based clustering analysis. Clusters 1 and 3 are associated with oceanic foraging while cluster 2 is associated with shelf foraging. Provisioning females are rearing a pup and are considered central place foragers whereas unconstrained females are not. Provisioning females tend to display a bimodal foraging strategy where they switch from predominantly shelf to predominantly oceanic foraging in the middle of lactation. However, some provisioning females may only forage on

the shelf or oceanic habitat for most of the lactation period. Unconstrained females are less limited in the foraging range and tend to travel further south than provisioning females.



Supplementary Figure 5.6 The same isotope biplot as in Fig. 5.5 with isotope signatures (mean \pm SE) of common female Long-nosed fur seal prey (Page et al. 2005b) (sampled from southeastern Australia, Davenport & Bax, 2002) and nearby marine mammals – AFS, Australian fur seal (Davenport and Bax 2002) and ASL, Australian sea lion from Seal Bay (SB) and Seal Slide (SS) (Lowther et al. 2013). G, gemfish, B, barracouta, LP, Little penguin, GS, Gould’s squid; JM, Jack mackerel; VL, Velvet leatherjacket; R, rebait; SF, sand flathead, P, pilchard, HL, Hector’s lanternfish. Y- and X-axes units in ‰.

Supplementary Table 5.1 Regrowth vibrissa lengths of 18 adult female long-nosed fur seals. Vibrissae were cut and plucked in 2016 and 2017, respectively. Each vibrissa was sectioned and sampled sequentially into ~ 2 mm segments. ^a the subcutaneous length of a different vibrissa that was plucked on the recapture date.

ID	Whisker length (mm)	Sub. length (mm)	No. sections
2016			
69	48	10 ^a	24
71	46	10 ^a	24
73	26	9 ^a	12
77	28	7 ^a	15
450	26	8 ^a	14
Sub mean	34.8 \pm 11.2		
2017			
307	39	10	20
311	39	8	18
329	31	8	14
340	33.5	8	16
353	33	10	14
315	34	9.5	17
317	56	10	25
318	26	8	12
319	43	10	20
322	37	9	18
324	35	8	15
326	39	7	18
351	32	8	15
Sub mean	36.2 \pm 8.2	8.7 \pm 1.1	
Overall mean			17.3 \pm 4

Supplementary Table 5.2 Results of the model selection process to obtain the final models. Models were selected using backwards selection and evaluated using Akaike's Information Criterion (AIC). d, delta; df, degrees of freedom.

Model	AIC	dAIC	df
$\delta^{15}\text{N}$			
state + region*year + (1 seal)	283.0	0.0	7
region*year + region*state + (1 seal)	284.1	1.0	8
region*year + region*state	320.6	37.5	7
$\delta^{13}\text{C}$			
region + (1 seal)	-44.6	0.0	4
region + year + (1 seal)	-43.4	1.2	5
region + year + state + (1 seal)	-38.7	5.9	6
state + region*state + (1 seal)	-36.9	7.8	7
region*year + region*state + (1 seal)	-31.9	12.7	8
region*year + region*state	-15.9	28.7	7
Oceanic cluster			
yday*year	138.5	0.0	5
yday + year	148.7	10.2	4

Supplementary Table 5.3 Number of vibrissae stable isotope samples allocated to each cluster group for each study year.

Cluster	Year	
	2016	2017
1	8	29
2	0	20
3	58	89
Total	66	138

Supplementary Table 5.4 Stable isotope values of each individual female long-nosed fur seal (glycine-biased $\delta^{15}\text{N}$ values were excluded from calculation) and clusters from model-based cluster analysis.

Seal/cluster	$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
069	15.1	0.2	14.4	15.3	-15.9	0.2	-16.4	-15.7
071	15.4	0.4	14.6	16	-15.8	0.2	-16.3	-15.5
073	15.3	0.3	14.9	15.7	-15.8	0.3	-16.3	-15.6
077	15.3	0.3	14.8	15.7	-15.8	0.2	-16.1	-15.6
307	14.1	0.6	13.3	14.8	-16.1	0.2	-16.5	-15.8
311	15.3	0.4	14.7	15.8	-16.1	0.2	-16.5	-15.7
315	16.1	0.3	15.7	16.7	-16.1	0.1	-16.2	-16
317	15.3	0.6	14.5	16.1	-15.8	0.1	-15.9	-15.7
318	16.7	0.2	16.5	17	-16.1	0.2	-16.4	-15.9
319	15.8	0.8	14.9	16.9	-15.9	0.1	-16	-15.8
322	16.4	0.3	16	17.1	-15.8	0.1	-15.9	-15.7
324	15.1	0.8	14.3	16.5	-15.7	0.2	-16.1	-15.6
326	15.3	0.6	14.6	16.7	-16.2	0.3	-16.8	-16
329	14.5	0.4	13.9	15.3	-16.1	0.1	-16.3	-15.9
340	14.6	0.2	14.2	15.1	-16	0.2	-16.4	-15.8
351	15.1	0.8	14.6	17.1	-16	0.2	-16.4	-15.9
353	15	0.5	14.4	15.5	-15.7	0.1	-15.8	-15.6
450	15.5	0.5	14.5	15.9	-15.8	0.3	-16.4	-15.6
Overall	15.3	0.7	13.3	17.1	-15.9	0.2	-16.8	-15.5
Cluster 1	14.5	0.5	13.3	15.3	-16.2	0.1	-16.5	-16
Cluster 2	16.6	0.3	16.1	17.1	-16.1	0.3	-16.8	-15.7
Cluster 3	15.3	0.5	14.3	16.5	-15.8	0.1	-16.2	-15.5

Chapter 6 GENERAL DISCUSSION

PREFACE

The objective of this thesis was to examine predator responses to spatial and temporal variation in the environment in order to understand how an apex predator specie, long-nosed fur seals, optimise their foraging strategies in relation to intra - and inter-annual variability in environmental conditions. Through the use of miniature geolocation light (GLS) loggers, this study has provided insights into the foraging ecology of pup-provisioning long-nosed fur seals. The GLS loggers were able to remain on the seal over long periods of time allowing behavioural responses during transitional periods, such as when significant changes in the environment occurred, to be collected. Additionally, vibrissae stable isotopes combined with movement data, were able to provide additional insights into the temporal and spatial variability in individual trophic position and allowed for the identification of the broad foraging strategies used by females during the pup-provisioning period.

This study has three major findings. Firstly, that the timing of changing from predominantly shelf (short) foraging trips to oceanic (long) foraging trips was dependent on the strength of summertime shelf upwelling. Secondly, that individual foraging site fidelity in oceanic waters is linked to the characteristics of eddies and frontal structures. Thirdly, that the dietary composition of females can vary inter-annually even if they are foraging in the same habitat, suggesting that the foraging strategies used by individuals in the population can vary in different years. In combination, these findings have provided insights to the extent of the adaptability of foraging strategies used by marine central place foragers intra- and inter-annually to maximise their reproductive success.

Prior to this study, tracking studies on females from the same colony were cross-sectional, limiting our ability to confirm that the foraging habitat switching behaviour was indeed occurring at the individual level. Furthermore, while it was hypothesised that the switching behaviour was driven by changes in shelf upwelling, there was no data from the transition period. By using GLS loggers attached to flipper tags (Fig. 6.1), we obtained 6 -7 months of

data with low risk of the battery running out and loggers falling off due to moulting. The locations from GLS data are coarse scale (Phillips et al. 2004), but double-tagging experiments from this study, demonstrated that the precision was sufficient to answer these questions (RMSELon = 0.23°, RMSELat = 0.5°, 45 km). The accuracy of geolocation estimates for other species have been reported to be between 0.5 – 3.9 ° (SD) and 0.8 – 3.6 ° (SD) for longitude and latitude, respectively (Winship et al. 2012). It was also reported that the accuracy was 180 km for albatrosses (Phillips et al. 2004) and 114 km for penguins (Thiebot and Pinaud 2010). The relatively high accuracy for GLS locations in this study was predicated on our understanding that lactating females from this population do not usually haul out at other places besides the breeding colony (Baylis et al. 2012) which allowed me to limit the range if possible locations when estimating locations during analyses.



Figure 6.1 Adult female Long-nosed fur seal showing GLS logger attachment on the left fore flipper tag.

ALTERNATE FORAGING STRATEGIES (DUE TO CHANGES IN LOCAL FORAGING CONDITIONS)

Within an annual cycle, changes in environmental conditions and different life-history stages can influence the foraging strategy used by marine predators (Thums et al. 2011). Central

place foragers provisioning offspring tend to have restricted foraging ranges (in comparison to non-breeding individuals) and are predicted to forage in the closest suitable foraging area to the colony (Orians and Pearson 1979). In order to maximise the probability of offspring survival, it is thought that they should maximise the rate of food delivery to their offspring as opposed to rate of energy consumption. Hence, having productive nearby foraging areas that can meet the energetic requirements of self-maintenance for parents and the provisioning of their offspring is crucial, especially in the early stages of the offspring-provisioning period when offspring are small and have limited fasting ability. This also means that time constrained central place foragers are likely to be more sensitive to variations in the availability of local resources (Costa 2007; Chapter 3).

How should parents respond when the productivity of local waters changes? Switching to more distant foraging locations is a common way to compensate for reduced prey availability in the local area. Lactating long-nosed fur seals shifted their foraging location from predominantly near-by shelf waters to distant oceanic waters (Chapter 3). Similarly, macaroni penguins rearing a chick shifted from inshore foraging early in the breeding period to offshore foraging later in the breeding period, presumably due to depletion in local resources (Deagle et al. 2008). The same has been observed in king penguins which shifted from waters located ~400 km from the colony to waters located 1600 km from the colony (Charrassin and Bost 2001). In blue petrels long foraging trips are associated with greater travel cost and foraging efficiency while the opposite was true for short foraging trips (Weimerskirch et al. 2003). In many seabird species, parents adopt a dual foraging strategy where short foraging trips are mainly for chick provisioning and long trips are mainly for self-feeding (Cherel et al. 2005, Welcker et al. 2012), where the decision to make a long or short foraging trip is determined by the parent's body condition. This suggests that long foraging trips to distant foraging sites lead to greater energetic gains for adults. Observations from unconstrained female long-nosed fur seals in this study support this as they foraged in distant oceanic sites even during the shelf upwelling season (Chapter 3).

Alternatively, if local prey patches are sufficiently productive, parents may not need to alternate between short and long feeding trips (Welcker et al. 2009, Ford et al. 2015). For

example, king penguins at the Falkland Islands tend to make shorter winter foraging trips than conspecifics from other breeding colonies. It was hypothesised that these penguins are maximising the rate of provisioning relative to their conspecifics due to the geographical advantage of being located close to the Patagonian shelf slope (Baylis et al. 2015). However, in one year with poor foraging conditions, little penguins at Port Phillip Bay made shorter foraging trips in distance which led to poorer reproductive success. Conversely, in other years when the penguins expanded their foraging range and made longer foraging trips, their fledgling success was significantly higher (Kowalczyk et al. 2015). Similarly, cape gannets from a declining population continued to forage in local waters when productivity in the foraging site declined, but compensated by spending more time searching for prey in the local area and switched to a less energy dense prey (Pichegru et al. 2007, 2010). Hence, short foraging trips do not necessarily lead to greater reproductive success particularly when foraging conditions are poor. Nonetheless, under normal feeding conditions, different foraging strategies of adaptive species may be equally successful and have similar breeding success regardless of how close different breeding colonies are situated to productive regions (Harding et al. 2013).

IMPORTANCE OF PRODUCTIVE OCEANIC REGIONS

The oceanic region is characterised by mesoscale eddies and surface frontal structures which have distinct physical and biological patterns of distribution (Bakun 2008). These structures are areas of high productivity where many fish tend to aggregate and are thus relatively predictable foraging areas (Bakun 2008, Nieblas et al. 2014, Sequeira et al. 2018). Indeed, oceanic foraging of marine predators, such as lactating long-nosed fur seals and juvenile mako sharks (Rogers et al. 2015), in the Great Australian Bight region tend to be associated with these oceanographic features. Due to increased competition from individuals in waters closer to breeding colonies, prey density should increase with increasing distance from large and dense colonies, this phenomenon is also known as “Ashmole’s halo” (Ashmole 1963, Birt et al. 1987). The marginal value theorem hypothesises that in order to maximise the rate of energy intake, a predator foraging in a heterogenous environment should leave its current foraging patch when the rate of intake from that patch falls to the overall mean rate of intake from the environment (Charnov 1976) (Fig. 6.2). The combination of all these factors suggest

that longer foraging trips to usually more distant foraging patches (typically to oceanic waters) should result in greater energy gain (Shoji et al. 2015). Furthermore, in central place foragers, foraging trip duration tends to increase with offspring age as energetic demands increases (Clarke et al. 2006, Williams et al. 2007). Longer foraging trips can result in higher milk energy delivered to pups as seen in long-nosed fur seals (Goldsworthy 2006) and Antarctic fur seals (Arnould and Boyd 1995) and mass gain in parents of many seabird species (Weimerskirch and Cherel 1998, Welcker et al. 2012). Hence, if not for the time restrictions of offspring provisioning, predators may actually do better to forage in more distant waters, as seen from the behaviour of unconstrained female long-nosed fur seals in this study, if their goal was solely to maximise energy gain. That being said, there is likely a limit to how far central place foragers have to travel to access productive foraging areas before it starts having an overall negative impact on their reproductive success (Zurbuchen et al. 2010). For example, in central place foraging bees the offspring production declined with increasing foraging distances from the colony (Zurbuchen et al. 2010). Oceanic oceanographic features can also be spatially and temporally variable. For example the lifespan of an eddy may last for a day or a full year and move kilometres a day (Elliott 2002, Dufois et al. 2017). Hence, longer foraging trips do not necessarily lead to maximum profitability or reproductive success for central place foragers, particularly in years where overall foraging conditions are poor (Georges and Guinet 2000). This may be characterised by reduced prey availability and/or predictability of productive oceanographic features (Chapter 4).

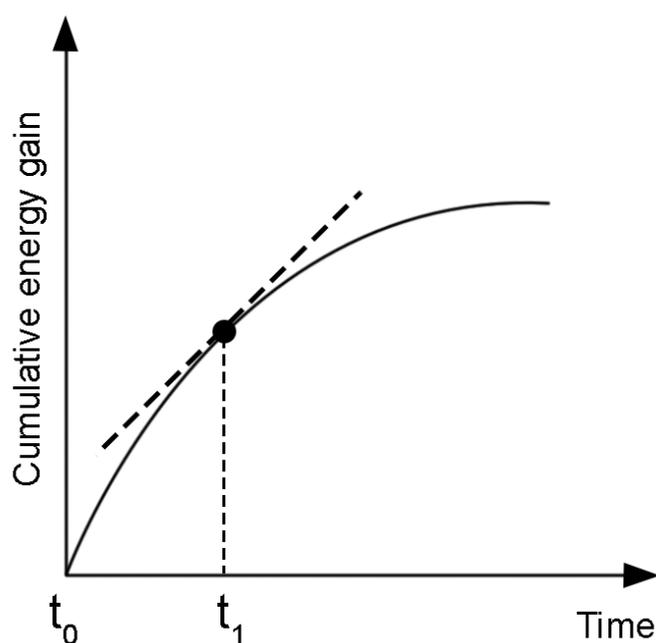


Figure 6.2 According to the marginal value theorem, an animal should forage in a prey patch until the instantaneous rate (solid line) of energy intake reaches the average overall rate of energy gain (diagonal dashed line) for the long-term habitat. t_0 = time when animal first arrives at the patch; t_1 = time when animal is predicted to leave the patch.

INTER-INDIVIDUAL VARIATION

Greater inter-individual variation in foraging behaviour may be a sign of good overall foraging conditions since that implies reduced inter-individual competition which in turn means enhanced quality of foraging patches (Bonadonna et al. 2001). In my study, despite weaker summertime shelf upwelling in 2017, it contributed to greater inter-individual variability in the timing in which females switched from predominantly shelf to oceanic foraging and was associated with seemingly higher reproductive success than 2016 (Chapter 3 and 5). The benefits of greater inter-individual variation in the timing of the switch may have led to reduction in inter-individual competition for seals that remained foraging on the shelf and those that chose to switch to oceanic foraging earlier; thus possibly leading to greater foraging success for the overall population. Similarly, in Antarctic fur seals, a decline in inter-individual variability in diving strategies was associated with conditions of lower food availability in their foraging zone and majority of individuals foraging closer to the colony (Lea

et al. 2006). In Australian fur seals breeding in the Bass Strait, Australia, females from colonies closer to the highly productive continental shelf edge had smaller ranges and less diversity in foraging trip strategies than females from colonies further away from the continental shelf edge (Kirkwood and Arnould 2011). Coincidentally the rates of population decline of colonies closer with lower inter-individual variability in foraging strategies were greater in magnitude than their counterparts (McIntosh et al. 2018). It may be individuals that have learnt to adapt to more challenging foraging conditions such as low abundance and/or unpredictable prey distributions are better off in the long-term especially in the context of climate change which can greatly affect the physical environment from year to year (Constable et al. 2014).

Additionally, the timing of foraging decisions can play an important role in the reproductive success of individuals. For example, the breeding success of the pallid harrier in north-central Kazakhstan is influenced by the timing of their breeding attempts which in turn may be dependent on the predictability of spatial and temporal variation of their prey abundance (Terraube et al. 2012). Pallid harriers that are late breeders tend to have small clutch sizes and lower hatching rates than earlier breeders. I was not able to evaluate the individual foraging strategies in relation to the timing of their switch due to the lack of a performance parameter such as corresponding pup growth rates or weaning mass. The inclusion of this data in future research on this species would be highly beneficial for understanding this aspect of their foraging ecology.

INDIVIDUAL FORAGING SITE FIDELITY (INTRA-INDIVIDUAL VARIATION)

In a complex system with many interacting components, the difficulty of predicting the outcome of an action or event increases (Zimmerman 2009). Thus, the decisions that marine predators are making in their complex environment are essentially bets, where the ideal bet is one with asymmetrical rewards *i.e.* low risk/cost but high gain/reward. Individuals can respond and learn from the feedback of decisions to develop strategies that give them an edge for attaining the most benefit in their environment. One such foraging strategy is individual foraging site fidelity. Animals in unfamiliar environments tend to spend more time travelling and searching rather than foraging which results in lower foraging success

(Provenza et al. 2005). Therefore, as explained in Chapter 4, returning to previous foraging sites where individuals experienced foraging success can be a profitable strategy since it minimises time spent searching and maximises time spent foraging so as long as there is a degree of predictability within the observed time scale in question (Weimerskirch et al. 2005). Hence, at the individual level, increased variability in individual foraging behaviour may not lead to greater foraging and reproductive success. For example, in our study, a comparison between 2016 and 2017 data showed that greater within-year intra-individual foraging fidelity (*i.e.* decreased individual variability) and diversity of foraging strategies among individuals (*i.e.* increased inter-individual variability) were associated with greater reproductive success in lactating long-nosed fur seals. Similarly, Lea et al. (2006) found lower variability in foraging trip duration of Antarctic fur seal mothers was associated with increased pup mass and individual pup growth during the later stage of pup-provisioning. Patrick and Weimerskirch (2017) also found that while black-browed albatrosses were faithful to their foraging habitat, it is individual fidelity to specific foraging sites that was associated with greater reproductive success. Indeed, my findings in Chapter 4 also show support for this.

However, this is assuming that individuals are flexible and adaptive. Some species are considered specialists where they do not change their foraging strategies despite changes in foraging conditions. In this context, the lack of intra-individual variability can be costly (Wakefield et al. 2015). Indeed, specialists are often more threatened than generalists (Terraube et al. 2012). For example, specialist foragers such as Australian sea lions (Lowther et al. 2011) and New Zealand sea lions (Chilvers 2008) show high long-term fidelity to foraging sites and coincidentally have low population numbers that are considered vulnerable for the species. Similarly diet-specialist diving sea birds also have declining populations that are possibly associated with changes in their prey availability (Vilchis et al. 2015). Sympatric chinstrap and Gentoo penguin species have specialist (dominated by a single prey species with little variation) and generalist (broader diet with high degree of variation) diets, which coincides with population trends that are declining and increasing, respectively (Polito et al. 2015). Specialists are vulnerable to single-prey fluctuations whereas generalists can access a wider prey spectrum. The inability to adapt foraging behaviour

according to changes in prey distribution and availability may lead to less foraging success and consequently reduced fitness for the species. However, stable isotope analyses of southern elephant seal tooth have shown positive correlation between long-term individual foraging site fidelity and longevity in that species (Bradshaw et al. 2004). Also, in a long-lived seabird, Brünnich's guillemot, generalist and specialist foraging strategies are equivalent in terms of evolutionary fitness (Woo et al. 2008). This disparity may be due to different spatial scales which are an important consideration in understanding foraging ecology (Arthur 2016) and also geographical differences in environmental variability (Ceia and Ramos 2015). Logically, it is easier to detect foraging site fidelity at coarser spatial scales which stable isotope habitats probably are. Nonetheless, our understanding of long-term individual foraging site fidelity is relatively limited due to the challenges in obtaining individual long-term datasets.

FUTURE STUDIES

The diet of marine predators can change inter-annually in response to changes in prey distribution and availability. In this study, the trophic position of seals varied between years (Chapter 5). While the diversity of prey type consumed may be the same in different years, the composition of each prey type may differ. For example, chick-rearing northern gannets displayed different foraging strategies in years with contrasting oceanographic and prey conditions. It was hypothesised that the different strategies reflected when gannets were pursuing small fishes or large pelagic fishes (Garthe et al. 2011). Similarly, a decline in blood plasma $\delta^{15}\text{N}$ of female Australian fur seals was associated with the decline of one of their primary prey, Gould's squid, and female body condition (Arnould et al. 2011).

The inter-annual differences in foraging behaviour in relation to environmental variability observed in this study requires further investigation. While the focus of this study was primarily on the foraging habitat switching behaviour of lactating females, the small number of individuals that deviated from that in 2017, *i.e.* only shelf or oceanic foraging, brings up interesting questions. It would be informative to investigate if females who remained as shelf-only foragers retain this strategy long-term, or does it change accordingly in response to environmental changes. For example, does the strength of summertime upwelling influence the proportion of the females that remain on the shelf versus those that display the switching

strategy. Long-term data of individuals over multiple years will be required to investigate this. Previously, Page et al (2005a) found that majority of the females studied that year were foraging on the shelf in autumn and winter. However, that was a cross-sectional study and cannot prove that individuals have been foraging on the shelf for most or all of the pup-rearing period. Our study confirms that that is one type of foraging strategy. In addition, we have also potentially identified a third foraging strategy and that is oceanic-only foraging. Understanding how the proportion individuals using each type of foraging strategy changes inter-annually will help with understanding the temporal variability of the importance of shelf and oceanic habitats. Such information may be useful for making management decisions especially with regards to fisheries overlap.

Studying individual animals is an important aspect of foraging ecology since natural selection acts at the individual level and this information is important for understanding population dynamics. The use of vibrissae stable isotopes has potential answer these questions related to inter-annual variability in foraging behaviour. Additionally, it may also allow for greater sample sizes and thus the study of inter-individual variation is more detail. This is also important because not all individuals are affected to the same extent by environmental changes (Cherel et al. 2007) and intrinsic factors such as age and experience of long-lived species can also influence foraging strategies (Chapter 5).

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