SEASONAL AND COLONY DIFFERENCES IN THE FORAGING ECOLOGY OF NEW ZEALAND FUR SEALS (*Arctocephalus forsteri*)

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ABSTRACT

The New Zealand fur seal (*Arctocephalus forsteri*) is the most abundant fur seal species in the Australian-New Zealand region. Approximately 85 % of Australia's population of New Zealand fur seals reside in the state of South Australia. As a result of their abundance and size, it has been estimated that the New Zealand fur seal population in South Australia consumes the greatest biomass of resources of all marine mammal and seabird species. However, despite the importance of New Zealand fur seals as top predators, our understanding of their foraging ecology in South Australia is limited. In order to better understand the habitat utilized and the diet of New Zealand fur seals, this study explores the foraging ecology of lactating seals from four primary colonies in South Australia, which account for ~ 78 % of the Australian population. These colonies are Cape Gantheaume (36°04'S, 137°27'E) and Cape du Couedic (36°03'S, 136°42'E) on Kangaroo Island; North Neptune Island (35°13'S, 136°03'E) and Liguanea Island (34°59'S, 135°37'E).

I start this study by assessing the seasonal variation in foraging location and dive behaviour of lactating New Zealand fur seals from Cape Gantheaume. 18 seals were fitted with satellite transmitters and time depth recorders (TDRs). The presence of thermoclines (derived from TDRs), were used as a surrogate measure of upwelling activity in continental shelf habitats. During the austral autumn 80 % of lactating fur seals foraged on the continental shelf (114 ± 44 km from the colony), in a region associated with a seasonal coastal upwelling system, the Bonney upwelling. In contrast, during winter months seals predominantly foraged in oceanic waters (62 %), in a region associated with the Subtropical Front (460 ± 138 km from the colony). Results suggested that lactating New Zealand fur seals shift their foraging location from continental shelf to oceanic habitats, in response to a seasonal decline in continental shelf productivity, attributed to the cessation of the Bonney upwelling in autumn.

To study inter-colony differences in foraging locations, 21 New Zealand fur seals were satellite tracked from four colonies within close proximity (46 km – 200km apart). Seals initiated foraging trips on a colony-specific bearing (Cape Gantheaume 141 ± 33º, Cape du Couedic 186 ± 12º, North Neptune Island 200 ± 23º and Liguanea Island 234 ± 69º), and recorded little overlap between colony-specific foraging areas. The distribution of colony-specific foraging grounds appeared to be influenced by the proximity of colonies to predictable local upwelling features, as well as a distant oceanic frontal zone, the Subtropical Front.

Foraging site fidelity and route-choice was further assessed by comparing site fidelity between continental shelf and oceanic habitats. Data from 31 lactating females, satellite tracked over 107 consecutive foraging trips indicated that females foraging on the continental shelf recorded a significantly greater overlap in foraging area between consecutive foraging routes, when compared to females that foraged in oceanic waters (55.9 ± 20.4 % and 13.4 ± 7.6 %, respectively). Findings suggest that seals learn the direction of travel to a predictable foraging region, and initiate a foraging trip on that bearing. However, actual foraging routes are likely to be influenced by a number of factors including previous foraging trip experience and prey encounter rate, which is related to prey density and the spatial scale of the patch exploited.

The final chapter integrates scat analysis with milk fatty acid (FA) analysis to investigate dietary differences between continental shelf and oceanic waters. Milk FA composition was determined for 29 satellite-tracked fur seals, that were known to forage in either shelf or oceanic habitats. Based on FA compositions, I predicted the likelihood that milk samples collected at random (*n* = 131) represented individual seals having foraged either on the continental shelf or in distant oceanic waters. FA analysis and satellite tracking results contrasted with scat analyses, from which only 6 % of scats by frequency of occurrence contained prey remains from oceanic waters. The results suggest that scats were biased toward females foraging on the continental shelf.

This study highlights the importance of two predictable ocean features utilised by New Zealand fur seals; (1) a nearby and seasonally predictable coastal upwelling system, the Bonney upwelling and; (2) a distant but permanent oceanic front, the Subtropical Front.

Statement of originality and authority of access

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Alastair M. M. Baylis

April 2008

The following peer-reviewed papers resulted from work completed during my candidature:

Baylis, A.M.M., Page, B, McKenzie, J, McIntosh, R, Goldsworthy, S (2005). The ontogeny of diving in New Zealand fur seal pups. *Canadian Journal of Zoology* 83: 1149 – 1161.

Baylis, A.M.M., Page, B., Goldsworthy, S. (2008). Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central place forager, the New Zealand fur seal. *Canadian Journal of Zoology* 86: 774-789.

Baylis, A.M.M., Page, B., Goldsworthy, S. (2008). Colony-specific foraging areas of lactating New Zealand fur seals. *Marine Ecology Progress Series* 316: 379-390.

Baylis, A.M.M. and Nichols, P.D. (in press). Milk fatty acids predict the foraging locations of a wide-ranging central place forager, the New Zealand fur seal: continental shelf vs. oceanic waters. *Marine Ecology Progress Series*.

Baylis, A.M.M., Hamer, D.J., Nichols, P.D. (in press). Assessing the use of milk fatty acids to infer the diet of the Australian sea lion (Neophoca cinerea). *Wildlife Research*.

Statement of the contribution of jointly authored papers

I offered co-authorship to people who assisted me with this project. B. Page provided general supervision, advice on the analysis of satellite tracking data and commented on manuscript drafts. P. Nichols guided me through the extraction of fatty acids from fur seal milk, provided advice on the interpretation and analysis of results and commented on manuscript drafts. D. Hamer made available the Australian sea lion satellite-tracking data, provided the opportunity to collect sea lion milk, and commented on manuscript drafts. S. Goldsworthy was involved in the initial conception of the project and facilitated this research.

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“There are known knowns. There are known unknowns. But there are also unknown unknowns. These are things we don't know we don't know.” D. Rumsfeld

CHAPTER 1

GENERAL INTRODUCTION

THESIS ORGANISATION

This thesis contains six chapters and an appendix. Chapter 1 is the general introduction, which describes the rationale behind the study and places the research within a regional context. The introduction also reviews the broader context of the study and presents the study aims. Chapter 2 explores how seasonal changes in ocean productivity influence the foraging locations of lactating New Zealand fur seals. Chapter 3 explores how lactating fur seals from four colonies within close proximity of one another, partition foraging areas. Chapter 4 assesses variability in foraging site fidelity between continental shelf and oceanic habitats. Chapter 5 integrates scat analysis with milk fatty acid analysis to investigate dietary differences between seals that foraged within continental shelf waters compared to those that foraged in oceanic waters. Chapter 6 is the general discussion. The appendix chapter further explores spatial partitioning in marine predator diets by combining satellite tracking and milk fatty acid analysis to infer Australian sea lion diet.

Excluding the introduction (chapter 1) and the general discussion (Chapter 6), all chapters are self-contained and consequently there is some repetition. Chapters are presented sequentially in terms of content. Chapters 2, 3 and the appendix chapter have been peer-reviewed and published/in press. Chapter 5 is currently in review.

BACKGROUND

Need for research

The New Zealand fur seal (*Arctocephalus forsteri*) is a temperate latitude species that is distributed from New Zealand and outlying subantarctic Islands, to southern Australia (Shaughnessy *et al.* 1994; Harcourt 2001; Goldsworthy *et al.* 2003). New Zealand fur seals are the most abundant fur seal species in the Australia-New Zealand region, with recent estimates at 100 000 individuals in New Zealand and 83 857 individuals in Australia (Taylor *et al.* 1995; Goldsworthy and Page 2007). In Australia, New Zealand fur seals are known to breed at 57 locations; one in Tasmania, three in Victoria, 17 in Western Australia and 36 in South Australia (Figure 1). The South Australian population of New Zealand fur seals represent ~ 85 % of the Australian population (Shaughnessy 2005). Of the 36 breeding colonies in South Australia, 5 colonies within a 200 km radius account for ~ 82 % of the estimated annual pup production, producing 17 600 pups annually (Shaughnessy 2005). These colonies are Cape Gantheaume and Cape du Couedic on Kangaroo Island, North and South Neptune Island and Liguanea Island and are a region of critical habitat for this species (Figure 2).

Populations of New Zealand fur seals in South Australia are currently recovering from 19th and 20th century sealing (Ling 1992). The estimated annual pup production at several New Zealand fur seal colonies indicates a high rate of population increase (although the South Neptune colony is thought to be stable) (Shaughnessy and McKeown 2002). Some authors have projected that if current estimates of population growth are sustained, the New Zealand fur seal population in South Australia may triple in the next 15-30 years (Goldsworthy *et al.* 2003).

As a result of their abundance New Zealand fur seals in South Australia are estimated to consume the greatest biomass of pelagic resources within the Great Australian Bight of all marine mammal and seabird species (Goldsworthy *et al.* 2003). The Great Australian Bight also supports five Commonwealth fisheries and six major South Australian fisheries. Fur seals interact with all major fisheries in southern Australia, including trawling, long and drop-lining, gill netting and aquaculture (Pemberton and Shaughnessy 1993; Arnould *et al.* 2003; Page *et al.* 2004; Hamer and Goldsworthy 2006; Goldsworthy and Page 2007). The extent of interactions between fisheries and New Zealand fur seals are likely to intensify with increasing and expanding populations.

Increasing populations of New Zealand fur seals, coupled with escalating and developing commercial fisheries that are within close proximity to the major New Zealand fur seal breeding colonies (for example the South Australian sardine fishery (*Sardinops sagax*) and the blue mackrel fishery (*Scomber australasicus*), respectively (Rogers and Ward 2006; Ward *et al.* 2008), has created the need to identify potential trophic and operational interactions with commercial fisheries and to better understand the role of New Zealand fur seals as top predators. In response to this need, recent studies have assessed the risk and extent of trophic and operational interactions between New Zealand fur seals and fisheries across South Australia (Goldsworthy *et al.* 2003; Goldsworthy and Page 2007). However, the accuracy of these assessments are impeded by limited knowledge of New Zealand fur seal foraging behaviour and diet in South Australia, which is currently restricted to one colony, Cape Gantheaume on Kangaroo Island.

Page *et al.* (2005a; 2005b; 2006) in their salient studies presented the first detailed information on the diet and foraging locations of New Zealand fur seals in South Australia (some dietary data is also presented in Goldsworthy *et al.* 2003). They described resource partitioning in New Zealand fur seals from Cape Gantheaume whereby juveniles exploited distant oceanic habitats and small pelagic fish, females predominantly exploited continental shelf habitats associated with the Bonney upwelling region and consumed large squid and medium sized fish, while males exploited shelf break habitats and consumed large fish, squid and seabirds. As a result New Zealand fur seal foraging behaviour has been defined as a *'marked ontogenetic shift'*, whereby nutritionally dependent pups remain within close proximity to the colony, juveniles forage in distant oceanic waters, adult females forage on the continental shelf and adult males over shelf-break waters (Goldsworthy and Page 2007).

The foraging and dietary data from Page *et al.* (2005a; 2006) has provided the basis for models which have estimated the distribution of fur seal foraging effort across South Australia and the overlap with commercial fishing effort (Goldsworthy *et al.* 2003; Goldsworthy and Page 2007). Accordingly the estimated distribution of New Zealand fur seal foraging effort across South Australia was concentrated within near-colony waters and adjacent shelf-break waters (Goldsworthy and Page 2007; Figure 3).

However, there are two factors that must be taken into consideration when interpreting the salient findings of Page *et al.* (2005a; 2005b; 2006). Firstly, the Cape Gantheaume colony is unique because it is the only New Zealand fur seal colony that is within close proximity to the seasonally predictable Bonney upwelling, the largest coastal upwelling in southern Australia (Lewis 1981; Butler *et al.* 2002) (Figure 2). Although regional extensions of the Bonney upwelling are also known to enhance productivity around the vicinity of other New Zealand fur seal colonies during summer and autumn months, these upwellings are less prominent and less predictable than the Bonney upwelling (Butler *et al.* 2002*;* Kampf *et al.* 2004; McClatchie *et al.* 2006; Ward *et al.* 2006). Therefore, the data presented for adult New Zealand fur seals from Cape Gantheaume may not be representative of the diet and foraging behaviour of adults from other colonies that are not in close proximity to the Bonney upwelling.

Secondly, the majority of lactating females were tracked in 2000 and 2001. The 2000/01 breeding season recorded the largest decline in annual pup production at Cape Gatheaume since the inception of monitoring in 1989 (a decline of ~ 25% of total estimated pup production) (Shaughnessy and Dennis 2001; McKenzie 2006). The average weight of pups born at Cape Gantheaume in the 2000/01 breeding season was also below the previous 13-year average (Shaughnessy and Dennis 2001). Variability in reproductive success and pup condition in other pinniped species has been typically related to changes in environmental variability, and large scale climatic anomalies (Croxall *et al.* 1988; McCafferty *et al.* 1998; Boyd and Murray 2001; Le Boeuf and Crocker 2005; Lea *et al.* 2006). Changes in New Zealand fur seal pup production, growth and pup condition have also been correlated with increased sea surface temperature, and by inference reduced ocean productivity (Haase 2004; Goldsworthy *et al.* 2005). This suggests that the environmental conditions experienced by breeding females prior to implantation in 2000 may have been unfavourable. Consequently, while the work of Page *et al.* (2005a; 2006) presents salient information on the diet and foraging locations of New Zealand fur seals it cannot be considered representative, as it is limited to one unique colony and aberrant years in pup production.

Most fur seal species show some degree of individual, seasonal, inter-annual and/or colony-specific variability in foraging strategies (e.g. Boyd 1999; Arnould and Hindell 2001; Lea *et al.* 2002a; Thompson *et al.* 2003; Beauplet *et al.* 2004; Robson *et al.* 2004; Staniland *et al.* 2004; Lea *et al.* 2006; Staniland *et al.* 2007). Estimating age and sex-specific foraging behaviours of New Zealand fur seals from Cape Gantheaume and extrapolating these estimates to a South Australian population-level, as presented by Goldsworthy *et al.* (2003) and Goldsworthy and Page (2007), is unlikely to yield accurate predictions without first understanding the range of possible behaviours or the range of habitats used (Sutherland 1997; Hindell *et al.* 2002). It is important to promote the significant issues associated with seal-fishery interaction. However, the broad ecological questions that the available data are currently being used to answer, the potential repercussions (e.g. McDougall 2006) and the importance of New Zealand fur seals as top predators in the South Australian ecosystem, provides the imperative to better understand their diet and habitat requirements.

The primary objective of this thesis was to assess seasonal and colony differences in the foraging locations and diet of lactating New Zealand fur seals at four major colonies in South Australia, Cape Gantheaume, Cape du Couedic, North Neptune Island and Liguanea Island (Figure 2). This study focussed on adult females as they are important in determining the dynamics of populations and consequently are particularly important to population conservation (Boyd *et al.* 2002). Documenting seasonal and colony variability in foraging ecology will assist future research to develop more accurate models. It is also hoped that additional information on the foraging habitats and prey species of New Zealand fur seals will help to further elucidate conservation issues by identifying aspects of this species ecology that may make it susceptible to environmental variability and anthropogenic impacts, and aid future management strategies.

NOTE:
This figure is included on page 9 of the print copy of
the thesis held in the University of Adelaide Library.

Fig 1: Location of New Zealand fur seal colonies in Australia. (TAS; Tasmania, VIC; Victoria, SA; South Australia, WA; Western Australia).

(Colony latitude and longitude: Shaughnessy and Goldsworthy unpublished data; Goldsworthy *et al.* 2003).

NOTE:
This figure is included on page 10 of the print copy of
the thesis held in the University of Adelaide Library.

Fig. 2: The five primary New Zealand fur seal colonies, Cape Gantheaume, Cape du Couedic, South and North Neptune Island and Liguanea Island. These colonies account for 82 % of the Australian population of New Zealand fur seals and 85 % of South Australian population of New Zealand fur seals (Shaughnessy 2005).

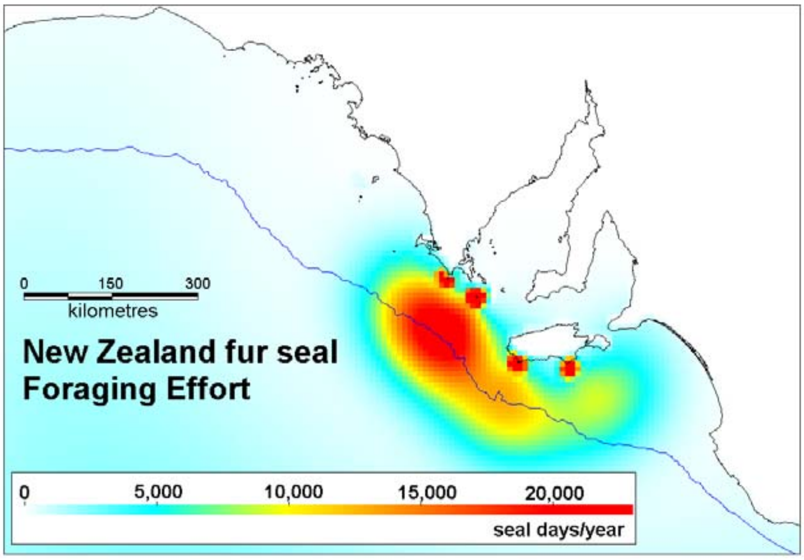

Fig. 3: Estimated distribution of New Zealand fur seal foraging effort in South Australian waters (seal days/year). Source: Goldsworthy and Page (2007).

Seasonal foraging ecology of temperate lactating fur seals

Lactation is one of the most energetically expensive life history stages in mammals (Oftedal 1984; Boness and Bowen 1996). Unlike most phocid seals, otariid (fur seals and sea lions) females cannot fast for the entire lactation period and must acquire resources to provision their nutritionally dependant young (Boness and Bowen 1996). Otariids alternate between periods of foraging at sea and periods ashore suckling their pup. They are termed ‘central place foragers’, because foraging trip distance and duration is restricted by the need to regularly provision their offspring at a fixed place. During the pup-rearing period mothers make trade-offs between the allocation of time spent foraging to meet their own energetic needs, and the allocation of resources to offspring for their growth and survival (Stearns 1992; Dall and Boyd 2002; Beauplet *et al.* 2004; Lea *et al.* 2006; Staniland *et al.* 2007). The fitness of lactating females is ultimately determined by their efficiency in locating and exploiting prey resources (Ydenberg *et al.* 1994; Boyd *et al.* 1997; Bowen *et al.* 2001). Life history patterns are subsequently influenced by environmental seasonality and resource predictability (Gentry and Kooyman 1984).

Otariid seals have evolved different life-history strategies to address seasonal variability in the predictability of prey resources. Those living in high-latitudes, such as Antarctic (*Arctocephalus gazella*) and northern fur seals (*Callorhinis ursinus*) have adapted to the highly seasonal nature of their environments by restricting their lactation to the period when resources are most abundant. Their short pup-rearing periods (~ 4 months) coincide with summer-early autumn periods characterised by elevated levels of high primary productivity (Gentry *et al.* 1986). In temperate and subtropical latitudes the levels of production and prey availability over the summer/autumn period are not sufficient to enable otariids to complete their lactation in such a short period. Therefore, temperate and subtropical otariid species have longer lactation periods of 8 months – 3.5 years.

Temperate fur seals raise their pups over ~ 10 month lactation period (Gentry *et al.* 1986; Francis *et al.* 1998; Arnould and Hindell 2001; Beauplet *et al.* 2004; Goldsworthy 2006). Because of this long lactation period, central place foraging temperate fur seals must contend with broad scale seasonal changes in ocean productivity (Gentry *et al.* 1986; Harcourt *et al.* 2002; Beauplet *et al.* 2004). Seasonal changes in resource availability can impose considerable energetic and provisioning challenges for females that are constrained in foraging distance and duration by the fasting ability of their offspring. As productivity within summer foraging grounds decline or vary spatially (i.e. temporal changes in the location of ocean fronts), and localised prey resources are depleted or disperse, temperate fur seals must maintain a suitable rate of energy delivery to their offspring while maintaining their own nutritional requirements (Georges *et al.* 2000a; Beauplet *et al.* 2004).

As such, lactating temperate fur seals are expected to adjust their at-sea behaviour to optimise the efficiency and rate of energy gain and energy delivery to nutritionally dependant offspring and energy to gestation during late lactation (Ydenberg *et al.* 1992; Georges and Guinet 2000). Recent studies on lactating subantarctic fur seals breeding at Amsterdam Island, found that foraging trip distance and duration increased from an average of 633 km and 15 days duration in summer to 1125 km and 29 days in winter (Beauplet *et al.* 2004). The increased foraging trip distance and duration was associated with seasonal declines in resource availability owing to a shift in the location of the Sub-tropical Front (Beauplet *et al.* 2004). Foraging trip distances and/or durations have also been recorded to be shortest in summer and longest in winter in most other temperate fur seal species. In these species, increased forging trip distances and (or) durations are thought to reflect increased energy demands of pups, increased fasting ability of pups and/or reduced resource availability during winter months (Francis *et al.* 1998; Georges *et al.* 2000a; 2000b; Arnould and Hindell 2001; Harcourt *et al.* 2002; Thompson *et al.* 2003; Beauplet *et al.* 2004; Page *et al.* 2006).

Similarly, seasonal changes in dive behaviour and diet have also been recorded for several temperate species (Mattlin *et al.* 1998, Georges *et al.* 2000a; 2000b; Arnould and Hindell 2001; Harcourt *et al.* 2002; Thompson *et al.* 2003; Beauplet *et al.* 2004; Page *et al.* 2005b; 2006). However, with the exception of subantarctic fur seals breeding at Amsterdam Island (Georges *et al.* 2000a; 2000b; Georges and Guinet 2000; Beauplet *et al.* 2004), our understanding of seasonal patterns in oceanographic features that influence prey distribution and consequently the foraging behaviour of temperate fur seals, remains limited. Because of the spatial separation of feeding and breeding sites, oceanographic features that influence the location and abundance of prey are likely to have profound effects on maternal foraging and provisioning behaviour (Goldsworthy 2006). The influence of seasonality on maternal behaviour is expected to vary between species and within species at different locations (e.g. subantarctic fur seals: Robinson *et al.* 2002 and Beaulplet *et al.* 2004), and according to local environmental features and phylogenetic constraints (Gentry *et al.* 1986; Francis *et al.* 1998).

New Zealand fur seals breeding in South Australia are an amenable species to examine how seasonal changes in ocean productivity influences foraging behaviour. In this species, females rear pups over an 8 - 11 month period that coincides with a coastal upwelling, the Bonney upwelling and associated down-welling periods (Lewis 1981; Butler *et al.* 2002). The Bonney upwelling is a wind-driven coastal upwelling that occurs during the austral summer and autumn (November to late April) (Lewis 1981; Gill 2002; Middleton and Platov 2003). During this period a consistent pattern of south-easterly winds combined with the Coriolis force, results in cold water from the Flinders Current being drawn onto the continental shelf where it is upwelled to near-surface waters (Butler *et al.* 2002; Middleton and Bye 2007). In contrast, during the austral winter the wind regime is typically westerly, resulting in the absence of upwelling favourable conditions (Ward *et al.* 2006; Middleton and Bye 2007). This seasonal shift in wind regime reduces primary productivity in shelf waters, which is likely to reduce secondary and tertiary productivity, and influence the abundance of prey in regions that are typically productive during summer and autumn (Ward *et al.* 2006).

Seasonal variability in New Zealand fur seal diet and foraging behaviour has been identified across their range (Mattlin *et al.* 1998; Harcourt *et al.* 2002; Page *et al.* 2005a; 2005b; 2006). However, studies describing the ocean features utilised by New Zealand fur seals and the environmental factors that drive seasonal variation in foraging behaviour are limited, partly attributed to the fact that knowledge of New Zealand fur seal diet and foraging behaviour is limited compared to other fur seal species. For example, in New Zealand dietary studies on lactating females are derived from four studies (Street 1964; Carey 1992; Fea *et al.* 1999; Harcourt *et al.* 2002). In

Australia, diet has been assessed from breeding populations in Tasmania and Kangaroo Island, South Australia (Lake 1997; Goldsworthy *et al.* 2003; Page *et al.* 2005a). Information on foraging habitats are derived from satellite telemetry based on two studies (Harcourt *et al.* 2002; Page *et al.* 2006), while dive behaviour is derived from five studies (Harcourt *et al.* 1995; Mattlin *et al.* 1998; Harcourt *et al.* 2001; 2002; Page *et al.* 2005b).

Dietary studies have characterised New Zealand fur seals as generalist predators because they consume a wide variety of prey. Prey species commonly identified include several species of mackerel, barracouta (*Thyrsites atun*), Gould's squid (*Nototodarus gouldi*), arrow squid (*Nototodarus sloanii*) and red bait (*Emmelichthys nitidus*). These species are typically distributed within continental shelf or shelf break waters, and corroborate satellite telemetry and dive behaviour studies from New Zealand (Otago Peninsula) and Australia (Cape Gantheaume, Kangaroo Island), that indicate females predominantly foraged over the continental shelf, where they usually dive to depths less than 60 m (Harcourt *et al.* 1995; 2001; 2002; Page *et al.* 2005b). Seasonal variability in New Zealand fur seal diet is largely attributed to changes in the abundance of squid (*Nototodarus* spp), which are prevalent in summer and autumn months, but in winter months they are thought to move offshore to deeper water becoming less abundant locally (Kailola *et al.* 1993; Harcourt *et al.* 2002; Page *et al.* 2005a). Seasonal variability in diet has been correlated with seasonal differences in dive behaviour (Harcourt *et al.* 2002). Mattlin *et al.* (1998) and Harcourt *et al.* (2002) recorded that lactating females dived progressively deeper and longer as the year progressed. These authors proposed that females were utilising more abundant vertical migrating prey during shallow diving months, and switching to benthic prey during deeper diving months.

The presence of myctophids recovered from the scats of females both in New Zealand and in Australia indicates that females also traverse the continental shelf to forage in oceanic waters (Carey 1992; Lake 1997; Fea *et al.* 1999; Harcourt *et al.* 2002; Page *et al.* 2005a). While females are known to increase foraging trip distance and duration as lactation progresses, information pertaining to oceanic foraging is limited, having been recorded in only four lactating New Zealand fur seals in New Zealand and two in Australia (Harcourt *et al.* 2002; Page *et al.* 2006).

Several temperate fur seal species are known to incorporate intrinsically long foraging trips to distant oceanic waters as part of their foraging strategy. For example, lactating subantarctic fur seals travelled distances up to 1600 km during winter foraging trips, while Juan Fernandez (*Arctocephalus phillipi*) and Galapagos fur seals (*A. galapagoensis*) travelled mean distances of 586 km and 444 km respectively (Francis *et al.* 1998; Ochoa-Acuna *et al.* 1999). The high degree of breeding synchronicity recorded in New Zealand fur seals (Goldsworthy and Shaughnessy 2004; McKenzie 2006), implies that the concentration of individuals at a central place may exert considerable pressure on local prey resources (as predicted for other colonial breeding species: Ashmole 1963; Robson *et al.* 2004). During late lactation, seasonal declines in prey resources may result in prey becoming locally depleted. Limited resources increase the potential for intra-specific competition. Competition induces animals to disperse further to forage (Hamilton *et al.* 1966). As such, distant oceanic waters may also be an important foraging location for lactating New Zealand fur seals if prey becomes locally depleted.

Colony-specific foraging areas

Central place foragers that travel to distant foraging grounds have increased time and energy costs. The time that dependent offspring fast is also extended, increasing the amount of energy that parents must deliver to offspring to maintain growth (Orians and Pearson 1979; Costa *et al.* 1989; Ochoa-Acuna *et al.* 1999; Staniland *et al.* 2007). Central place foraging theory predicts that animals that travel farther from the colony should be compensated for their increased travel costs through greater rates of energy uptake or reduced intra-specific competition (Hamilton *et al.* 1966; Diamond 1978; Orians and Pearson 1979; Boyd 1999; Robson *et al.* 2004; Staniland *et al.* 2007). In situations where multiple colonies occur within close proximity (i.e. a high density of individuals), this theory can only be true if there is inter colony partitioning of foraging areas, reducing intra-specific competition for prey resources (Cairns 1989; Robson *et al.* 2004).

Colony-specific foraging areas have been widely documented among seals and seabirds (Ainley *et al.* 2004; Brothers *et al.* 1998; Boyd *et al.* 2002; Campagna *et al.* 2001; Gremillet *et al.* 2004; Lea *et al.* 2002a; Robson *et al.* 2004). Colony-specific foraging areas require that individuals travel in colony-specific directions when commencing a foraging trip, indicating highly integrated individual behaviour at the colony level (Bernstein *et al.* 1991; Robson *et al.* 2004). Site fidelity to foraging areas is an important factor that re-enforces colony-specific foraging areas and is likely to be influenced by the availability of resources encountered during the previous foraging trip (Irons 1998; Bonadonna *et al.* 2001; Robson *et al.* 2004; Matthiopoulos *et al.* 2005). Consequently, the evolution and maintenance of colony-specific foraging areas is dependent on temporal and spatial habitat predictability, the accessibility and quality of resources and the associated predictability in reproductive outcome (Switzer 1993; Irons 1998).

The close proximity of the largest New Zealand fur seal colonies to each other in South Australia, suggests knowledge of whether colony-specific foraging exists is likely to be important in understanding and predicting the foraging habitat of lactating New Zealand fur seals.

THESIS AIMS

This thesis focuses on South Australian populations of the New Zealand fur seal, where females breed in a highly seasonal environment and are likely to experience variability in prey abundance and distribution throughout their lactation period and where several large colonies occur in close geographic proximity. Based upon these environmental and population geographic contexts, the following questions (each of which represent a chapter) were used to assess the foraging behaviour of lactating New Zealand fur seals:

- Do seasonal changes in ocean productivity associated with the Bonney upwelling influence the foraging behaviour of lactating New Zealand fur seals from Cape Gantheaume?
- Do meta populations adopt colony-specific foraging areas as shown for other colonial breeding species? What are the key regional oceanographic features that meta populations target?

These chapters identified two regions used by lactating New Zealand fur seals; (1) a nearby and seasonally productive upwelling system, and (2) a distant oceanic front. To further elucidate foraging behaviour and to determine diet, I assessed:

- Variability in foraging site fidelity between females that foraged in continental shelf waters, compared to those that foraged in oceanic waters.
- Dietary differences between seals that foraged in continental shelf waters, compared to those that foraged in oceanic waters.

CHAPTER 2

EFFECT OF SEASONAL CHANGES IN UPWELLING ACTIVITY ON THE FORAGING LOCATIONS OF A WIDE-RANGING CENTRAL PLACE FORAGER, THE NEW ZEALAND FUR SEAL

Baylis, A.M.M., Page, B. & Goldsworthy, S. (2008) Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central place forager, the New Zealand fur seal.
Canadian Journal of Zoology, v. 86 (8), pp. 774-789

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CHAPTER SUMMARY

- To assess how seasonal changes in ocean productivity influenced foraging behaviour, 18 lactating New Zealand fur seals were fitted with satellite transmitters and time depth recorders (TDRs).
- Using temperature and depth data from TDRs, I used thermoclines as a surrogate measure of upwelling activity in continental shelf waters.
- During the austral autumn 80 % of lactating fur seals foraged on the continental shelf (114 ± 44 km from the colony), in a region associated with the Bonney upwelling. In contrast, during winter months seals predominantly foraged in oceanic waters (62 %), in a region associated with the Subtropical Front (460 ± 138 km from the colony).
- Results indicate that lactating New Zealand fur seals shift their foraging location from continental shelf to oceanic waters in response to a seasonal decline in productivity over the continental shelf, attributed to the cessation of the Bonney upwelling.

CHAPTER 3

COLONY-SPECIFIC FORAGING AREAS OF LACTATING NEW ZEALAND FUR SEALS

Baylis, A.M.M., Page, B. & Goldsworthy, S. (2008) Colony-specific foraging areas of lactating New Zealand fur seals.
Marine Ecology Progress Series, v. 361, pp. 279-290

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CHAPTER SUMMARY

- 21 lactating New Zealand fur seals were tracked from 4 breeding colonies in southern Australia. The distance between colonies ranged between 46 and 207 km.
- In total, 101 foraging trips were recorded (2 to 19 trips ind.$^{-1}$). Seals initiated foraging trips on a colony-specific bearing (Cape Gantheaume 141 ± 34°, Cape du Couedic 188 ± 12°, North Neptune Island 204 ± 12° and Liguanea Island 235 ± 19°).
- During autumn, seals from Cape du Couedic, North Neptune Island and Liguanea Island predominantly targeted distant oceanic waters associated with the subtropical front (STF), while seals from Cape Gantheaume targeted shelf waters associated with a seasonal coastal upwelling, the Bonney upwelling.
- The distance of each colony from the STF (based on the preferred colony bearing) or the Bonney upwelling in the case of Cape Gantheaume was correlated with the maximum straight-line distances travelled (Cape Gantheaume 119 ± 57 km, Cape du Couedic 433 ± 99 km, North Neptune Island 564 ± 97 km and Liguanea Island 792 ± 82 km).
- The organisation of colony-specific foraging grounds appears to be influenced by the proximity of colonies to predictable local upwelling features, as well as distant oceanic frontal zones. Knowledge of whether New Zealand fur seals utilise colony-specific foraging grounds may be important in predicting and identifying critical habitats and understanding whether management requirements are likely to vary between different colonies.

CHAPTER 4

FORAGING SITE FIDLEITY IN A WIDE-RANGING CENTRAL PLACE FORAGER, THE NEW ZEALAND FUR SEAL

INTRODUCTION

Central place foragers are constrained in foraging distance and duration by the fasting abilities of their offspring (Orians and Pearson 1979). Accordingly, foraging strategies should have evolved to maximise the efficiency and rate of energy gain (Ydenberg *et al.* 1992). The tendency for an individual to repeatedly return to the same area to forage has been widely documented among marine central place foragers (e.g. Irons 1998; Bonadonna *et al.* 2001; Hedd *et al.*2001; Broderick *et al.* 2007; Chilvers 2008). From an optimal foraging perspective, foraging site-fidelity is likely to be advantageous in species that exhibit breeding site fidelity and forage in regions where resources are to some degree predictable over both spatial and temporal scales (e.g. frontal zones and coastal upwellings) (Irons 1998; Weimerskirch 2007). In such situations, familiarity with predictable resources may enhance foraging efficiency and foraging success and maximise energy gain over the lifetime of an animal (Gentry 1998; Irons 1998; Bradshaw *et al.* 2004; Gende and Sigler 2006).

Wide ranging central place foragers such as procellariiform seabirds and seals often use multiple ocean features over varying spatial scales (e.g. coastal upwellings and oceanic fronts) (Weimerskirch 2007; Beauplet *et al.* 2004). However, few studies have tested how fidelity to foraging areas varies in relation to the type of ocean features used (see Weimerskirch 2007). The New Zealand fur seal (*Arctocephalus forsteri*) is a wide-ranging central place forager that displays a high degree of breeding philopatry (McKenzie 2006). Previous studies on New Zealand fur seals have described foraging site fidelity based on directional persistence of consecutive foraging trips, within the context of colony specific foraging areas (Chapter 3). The separation of colony-specific foraging areas were thought to be influenced by the proximity of colonies to two predictable ocean features; a nearby (36 – 190 km), but seasonally productive coastal upwelling, the Bonney upwelling and a distant (380 – 1000 km), but permanent oceanic front, the Subtropical Front (STF). In general, females from the Cape Gantheaume colony (Fig. 1) exploited continental shelf waters associated with the Bonney upwelling during autumn, and shifted foraging effort to the STF during winter months (Page *et al.* 2006; Chapter 2). Over the same time period of autumn and winter, females from Cape du Couedic, North Neptune Island and Liguanea Island colonies, foraged in distant oceanic waters associated with the STF (Fig. 1; Chapter 3).

The vast difference in the distances that New Zealand fur seals travel when foraging in nearby continental shelf waters compared to distant oceanic waters and the differences in the scale of these two ocean features, suggests foraging strategies and site-fidelity also varies between these two habitats. Understanding how foraging site fidelity varies between continental shelf and oceanic habitats may further elucidate the mechanisms that influence the foraging locations of marine predators that can ultimately modulate the spatial distributions of populations. Additionally, the degree of foraging site-fidelity exhibited has potentially important implications for species management and conservation because foraging site-fidelity may affect an individuals ability to respond to changes in the distribution of prey or to broad scale environmental changes (Chilvers 2008). The current study compares foraging site fidelity of lactating New Zealand fur seals that foraged in continental shelf waters, to those that foraged in distant oceanic waters.

MATERIALS AND METHODS

Study site and animal handling

This study was conducted at four sites: Cape Gantheaume (36°04'S, 137°27'E) and Cape du Couedic (36°03'S, 136°42'E) on Kangaroo Island; North Neptune Island (35°13'S, 136°03'E) and Liguanea Island (34°59'S, 135°37'E) (Fig. 1). The foraging locations and directional movement of females were monitored using KiwiSat 101 satellite transmitters (Sirtrack, Havelock North, New Zealand) during 2005 and 2006. Lactating adult females were captured using a hoop net and manually restrained. Upon capture, anaesthesia was induced and maintained using Isoflurane® (Veterinary Companies of Australia, Artarmon, New South Wales), administered via a portable gas anaesthetic machine (Komesaroff Small Animal Anaesthetic Machine, Medical Developments Australia, Melbourne). Satellite transmitters were attached to guard hairs on the mid-dorsal line using a flexible araldite epoxy (Araldite 2017, Vantico, Basel, Switzerland). Devices were removed by cutting guard hairs attached to the unit using a scalpel blade. For certain re-captures, females were first immobilised with Zoletil® (dose 2 mg/kg; Virbac, Sydney, Australia), administered using 0.5cc barb less darts (Darts: Pneu-Dart®, Pennsylvania, USA), fired from a CO_2-powered tranquilliser gun (Taipan 2000, Tranquil Arms Company, Melbourne, Australia). The lightly anaesthetised females were then captured using a hoop-net and manually restrained.

Satellite transmitter data treatment

The duration of a foraging trip was defined as the period of time between a seal's departure from the breeding site and its return to land. Satellite location data was obtained through the Argos satellite system. The location-class B and Z positions were omitted due to the magnitude of their error (Robson *et al.* 2004). To further improve the accuracy of satellite tracks, the R statistical software (version 2.0.1, R Development Core Team, R Foundation for Statistical Computing, Vienna) and timeTrack package (version1.0-9, M.D. Sumner, University of Tasmania, Hobart) were used to apply the filter described by McConnell *et al.* (1992), based on a maximum horizontal speed of 2 m/s (Page *et al.* 2006). Each foraging trip was summarised as a proportion of the total time spent in 5 x 5 km grid cells. To determine the number of different 5 x 5 km grid cells entered on each foraging trip and the proportion of time they spent in different cells, I assumed a constant horizontal speed between the filtered locations and interpolated a new position for each hour of time along the satellite track using the R statistical software and the timeTrack package. The number of original and interpolated positions, which were located within 5 x 5 km cells of a predetermined grid, were then summed and assigned to a central node. Values were then converted to a proportion to avoid bias toward longer foraging trips.

Along with time spent in 5 x 5 km grid cells, several additional foraging trip parameters were calculated to summarise foraging behaviour on each foraging trip. These were: (1) maximum straight-line distance from the colony to the distal point reached; (2) cumulative distance travelled (sum of distances between locations); (3) mean bearing; (4) horizontal travel speed (the distance between consecutive locations, divided by duration (60 min)); (5) linearity index (LI) values for outbound and inbound portions of each foraging trip (maximum straight line distance / cumulative total distance) (Robson *et al.* 2004). These parameters were extracted at 60 min time intervals along each interpolated satellite track (excluding parameters describing minimums, maximums and totals).

Site fidelity

Site fidelity was assessed by:

(i) Directional persistence between consecutive foraging trips. Analysed by calculating the mean destination bearing from interpolated positions for each foraging trip for each individual. The *V*-test was used to determine whether the bearings of consecutive foraging trips differed among foraging trips for each individual (Zar 1996).

(ii) Consistency of the maximum straight-line distance travelled on consecutive foraging trips (Hamer *et al.* 2001). Quantified as the coefficient of variation (CV = SD x 100/mean).

(iii) Overlap in foraging area and time spent in area between consecutive foraging trips. Measured by comparing the overlap in 5 x 5 km grid cells entered and the overlap in time spent in area within 5 x 5 km grid cells between consecutive foraging trips.

All statistical tests were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, USA) and Oriana (V d.02c, Kovach Computing Service, Pentreath, Wales, UK). I used linear mixed models (LMM) to analyze arcsine-transformed area-overlap and overlap in time spent in area, recorded from consecutive foraging trips using seal identity as a random factor. Akaike's Information Criterion (AIC) values were used to determine the covariance structure that best suited the model. The linear mixed model does not assume homogeneity of variances and only assumes a moderately normal distribution of the residuals from the entire model. For all other tests, transformations to meet assumptions of normality and homogeneity of variances were performed as necessary. If normality could not be achieved, then equivalent non-parametric tests were used. All values are given as mean ± SD and considered significant at the $P < 0.05$ level.

RESULTS

A total of 31 lactating females were satellite tracked over 106 consecutive foraging trips (range 2 – 8 foraging trips per female) (Table 1). Consecutive foraging trips were recorded from 17 females from Cape Gantheaume, 7 from Cape du Couedic, 3 from North Neptune Island and 4 from Liguanea Island. Of the 106 foraging trips, 39 were recorded from 11 females that foraged on the continental shelf, in a region associated with the Bonney upwelling, while 67 foraging trips were recorded from 20 females that foraged in oceanic waters. Examples of consecutive foraging trips to continental shelf and oceanic waters are presented in Fig. 1.

Excluding class B and Z, I received 5186 locations from service Argos. Filtering removed 280 locations, leaving 4906 locations for analysis (Cape Gantheaume 2041; Cape du Couedic 1408; North Neptune 552; and Liguanea Island 905 locations). Typically, females travelled directly to and from foraging grounds. On average, the linearity index (LI) for both the outbound and inbound portion of foraging trips was 0.9 ± 0.1. Individual LI are presented in Table 1. The outbound and inbound portion of foraging trips were also characterised by relatively high swimming speeds (3.2 ± 0.9 and 3.4 ± 0.8 km/h respectively).

Differences between the mean bearing of consecutive foraging trips ranged from 1.2 – 65° (mean 17.7° ± 14.2°). There were no significant differences in the mean bearings of individuals' consecutive foraging trips, suggesting directional fidelity (*V*-test: $P = < 0.001$ in all cases). Maximum trip distances and durations were variable between consecutive foraging trips, as reflected by CV values (range 6 – 70.5 %; Table 1; Table 2). Cape du Couedic and Liguanea Island recorded the greatest variability in maximum distances between foraging trips, as indicated by high CV values. This reflects seasonal variation in foraging trip distances which ranged from 385 ± 135 km in autumn to 263 ± 102 km in winter for Cape du Coeudic and 727 ± 102 km in autumn for Liguanea Island, compared to 343 ± 120 km in winter (LMM: $F_{1,23.4} = 5.5$, $P = 0.027$ and LMM: $F_{1,4.7} = 12.1$, $P = 0.019$ respectively).

While persistence in foraging direction was evident, foraging route overlap varied between consecutive foraging trips, ranging between 1.1 – 93.1 % in area overlap and 0.7 - 77.5 % overlap in time spent in area (Table 3). Foraging route overlap varied in relation to the habitat utilised. Cape Gantheaume females that foraged on the continental shelf had a significantly greater overlap in foraging area and time spent in area, compared to females that foraged in oceanic waters (area: 55.9 ± 20.4 % and 13.4 ± 7.6 % respectively; LMM on transformed values: $F_{1,25.8} = 32.1$, $P < 0.001$) and time spent in area (43.7 ± 16.8 % and 9.0 ± 5.7 % respectively; LMM on transformed values: $F_{1,28.0} = 30.6$, $P < 0.001$) (Table 3).

Maximum distance from the colony was correlated with the cumulative total distance travelled ($R^2 = 0.97$, $P < 0.001$) and foraging trip duration ($R^2 = 0.81$, $P < 0.001$) (Fig. 2). Continental shelf foraging trips were shorter in both distance (124 ± 50 km and

458 ± 134 km respectively) and duration (7.5 ± 2.8 days and 18.3 ± 6.9 days respectively) than oceanic foraging trips (LMM: $F_{1,22.9} = 60.8$, $P < 0.001$ and $F_{1,21.9} = 8.9$, $P = 0.007$ respectively). Continental shelf foragers spent significantly more time in the same grid cell than oceanic foragers (maximum time spent in 5 x 5 grid cell: 14 ± 5 % and 4 ± 2 % respectively; LMM: $F_{1,54.5} = 23.8$, $P < 0.001$).

For females that foraged in oceanic waters, the maximum distance of foraging trips (LMM: $F_{3,55} = 6.5$, $P = 0.001$) and duration of foraging trips (LMM: $F_{3,18.0} = 4.8$, $P = 0.012$) differed significantly between colonies (Table 2). Despite differences in distance and duration between seals foraging in oceanic waters, the mean speed travelled was not statistically different between colonies (LMM: $F_{3,25.6} = 0.26$, $P = 0.8$) (Table 1).

Differences in colony distances and duration of foraging trips were reflected in differences in foraging route overlap. There was a significant negative correlation between mean foraging trip distance and the mean proportion of overlap in successive foraging routes for oceanic females ($R^2 = -0.59$, $P = 0.\ 006$) (Fig. 3). The mean foraging route overlap between consecutive foraging trips to oceanic waters varied significantly between colonies (LMM: $F_{3,45} = 4.2$, $P = 0.010$). The mean overlap recorded from Cape Gantheaume and Cape du Couedic was 18 ± 11 % and 16 ± 12 % respectively, which were greater than the 9 ± 2 % and 4.7 ± 1.4 % recorded from North Neptune Island and Liguanea Island, respectively.

DISCUSSION

Several species of pinnipeds are known to utilise large-scale oceanographic features and show directional persistence towards them over consecutive foraging trips (Boyd *et al.* 2002; Beauplet *et al.* 2004; Bradshaw *et al.* 2004; Robson *et al.* 2004; Campagna *et al.* 2006). The high density of New Zealand fur seals in South Australia relative to other regions along the southern Australian coastline has been proposed to reflect the accessibility and predictability of large-scale ocean features (the Bonney upwelling and STF) to breeding colonies (Chapter 3). The high degree of similarity in consecutive foraging trip bearings recorded in the current study, and the tendency for lactating females to swim directly to foraging areas, confirms the Bonney upwelling and oceanic regions associated with the STF, are predictable foraging habitats.

However, actual foraging route overlap varied considerably. The degree of spatial overlap between consecutive foraging routes (and therefore the degree of foraging site fidelity) was influenced by the type of habitat exploited and the distance travelled to foraging sites. New Zealand fur seals that used continental shelf habitats associated with the Bonney upwelling recorded a higher spatial overlap between consecutive foraging trips and comparatively shorter foraging trip distances and durations. Conversely, females that foraged in oceanic waters recorded little spatial overlap between consecutive foraging trips, with the degree of spatial overlap varying according to foraging trip distance and duration. This is consistent with Bonadonna *et al.* (2001) who reported a higher ‘fidelity-index’ (based on foraging trip bearing) for lactating Antarctic fur seals on short foraging trips, when compared to females on longer foraging trips. Additionally, Wiemerskirch (2007), reviewed site fidelity for 10 species of seabirds that foraged over continental shelf waters and found high (although variable) foraging site fidelity (50.4 %), while for 12 species that foraged in oceanic waters foraging site fidelity was comparatively low (4.6 %) because individuals rarely returned to the same patch.

High site fidelity in sea bird species typically occurs in regions where there is strong physical forcing, such as shelf edges and tidal fronts (Irons 1988; Weimerskirch 2007). Therefore, differences in foraging route overlap between continental shelf and oceanic habitats in the current study are likely to reflect differences in both the spatial scale of the habitats and the physical processes that operate within these habitats. In terms of spatial scale, the Bonney upwelling region to the southeast of Cape Gantheaume is confined to a relatively small, highly productive area (Butler *et al.* 2001). Conversely the STF is a major ocean boundary that separates warm, saline, nutrient poor subtropical waters to the north of the STF, from relatively cool, less-saline, nutrient rich subantarctic waters to the south (Bradford-Grieve *et al.* 1999). The STF is also a continuous east-west oceanographic feature south of Australia (Tomczak *et al.* 2004).

While both of these features are predictable over larger spatial scales, at finer-scales resources are likely to be distributed heterogeneously (i.e. hierarchical patch system) (Fauchald *et al.* 2000; Weimerskirch *et al.* 2005). Foraging routes (and therefore foraging route overlap) are likely to be affected by the distributions, densities and renewal rates of resources encountered on a foraging trip (Bernstein 1975; Irons 1998; Bradshaw *et al.* 2004). The concentration of primary, secondary and tertiary productivity within the Bonney upwelling region, implies a well-structured high density/small-scale patch (Ward *et al.* 2006; Fauchald 1999). The high proportion of overlap between consecutive continental shelf foraging trips as measured by time spent within the same area, suggests a rapid turnover rate (consumption and renewal) of resources.

Conversely, seals that foraged in oceanic waters did not focus their foraging effort within a particular area, but tended to cover more area, presumably searching for prey. A similar finding was also reported for Antarctic fur seals on ‘long’ foraging trips (Bonadonna *et al.* 2000). The oceanic foraging habitats used by New Zealand fur seals may be lower-density/larger-scale patches, where prey are more dispersed or less predictable on fine-scales. The longer foraging trip durations and distances travelled to reach oceanic habitats increases the probability that resources have been depleted or have moved actively or passively before seals return to the same region (Fauchald 1999; Weimerskirch 2007). Therefore the reduced overlap in both area and time spent in area recorded from oceanic foragers is to be expected. The reasons for a seasonal shift in oceanic foraging trip distance recorded from the Cape du Couedic and Liguanea Island females remains unclear, although we can suppose that it reflects productive foraging regions becoming available closer to continental Australia during winter months.

Temporal and spatial resource predictability is an important concept within central-place foraging theory. Resource predictability over broad spatial scales, may allow New Zealand fur seals to conduct long foraging trips to distant oceanic waters, while still maintaining a regular rate of milk delivery to dependent offspring and meeting their own energetic requirements. The current study suggests that seals learn the direction of travel to predictable foraging regions and initiate a foraging trip on that bearing, as has been previously described for other pinnipeds (Bonadonna *et al.* 2001; Bradshaw *et al.* 2004; Robson *et al.* 2004). This type of memory-based knowledge is valuable from an optimal foraging perspective because it allows individuals to travel directly to foraging regions. Actual foraging routes are however, likely to be influenced by a number of factors including previous foraging trip success and prey encounter rates, which are related to prey densities and the spatial scale of the ocean feature exploited (Boyd 1999; Bonadonna *et al.* 2001, Boyd *et al.* 2002, Robson *et al.* 2004, Weimerskirch 2007).

Table 1: Foraging trip bearing, mean linearity index (LI) from the outbound and inbound portions of foraging trips respectively, and cumulative variance (CV) in maximum distances travelled recorded from 31 lactating New Zealand fur seals from CG; Cape Gantheaume, DC; Cape du Couedic, NN; North Neptune Island and LIG; Liguanea Island. All values are mean ± SD.

Colony	ID	Season	Foraging location	FT	Mean Bearing (^{o})	LI Out bound	LI In bound	CV
CG	68	Winter	Shelf	3	144 ± 13	0.8 ± 0.1	0.9 ± 0.1	21.9
CG	691	Autumn	Shelf	2	132 ± 2	0.9 ± 0.09	0.9 ± 0.1	15.0
CG	692	Autumn	Shelf	4	192 ± 1	0.8 ± 0.08	0.8 ± 0.2	15.9
CG	693	Winter	Shelf	5	116 ± 3	0.9 ± 0.1	1.0 ± 0.1	10.8
CG	702	Autumn	Shelf	5	125 ± 5	0.8 ± 0.1	0.9 ± 0.2	26.5
CG	711	Autumn	Shelf	4	122 ± 4	0.9 ± 0.1	0.9 ± 0.1	8.0
CG	712	Autumn	Shelf	2	121 ± 2	0.9 ± 0.1	0.8 ± 0.2	9.2
CG	721	Autumn	Shelf	4	192 ± 3	0.9 ± 0.2	1.0 ± 0.1	33.2
CG	723	Winter	Shelf	4	112 ± 7	0.7 ± 0.1	0.8 ± 0.1	34.8
CG	731	Autumn	Shelf	3	133 ± 7	0.8 ± 0.1	0.9 ± 0.1	32.8
CG	732	Autumn	Shelf	3	117 ± 9	0.9 ± 0.1	0.9 ± 0.01	37.5
	Mean		**CG**		**137 ± 29**	**0.8 ± 0.1**	**0.9 ± 0.1**	**22.3 ± 11.1**
CG	74	Autumn/winter	Oceanic	3	191 ± 9	0.9 ± 0.03	1.0 ± 0.01	18.5
CG	76	Autumn/winter	Oceanic	3	152 ± 12	0.9 ± 0.05	0.9 ± 0.1	29.3
CG	703	Autumn/winter	Oceanic	2	150 ± 3	0.8 ± 0.01	0.7 ± 0.02	6.0
CG	713	Autumn/winter	Oceanic	3	152 ± 4	0.9 ± 0.05	0.9 ± 0.03	41.7
CG	722	Autumn/winter	Oceanic	3	150 ± 10	0.9 ± 0.02	0.9 ± 0.1	12.8
CG	733	Autumn/winter	Oceanic	2	167 ± 1	0.8 ± 0.1	0.9 ± 0.09	10.9
	Mean		**CG**		**160 ± 16**	**0.9 ± 0.1**	**0.9 ± 0.1**	**19.9 ± 13.3**

DC	69	Autumn/winter	Oceanic	4	189 ± 9	0.9 ± 0.02	0.8 ± 0.2	25.4
DC	7	Autumn/winter	Oceanic	4	195 ± 11	0.8 ± 0.1	0.9 ± 0.08	38.1
DC	74	Autumn/winter	Oceanic	5	180 ± 8	0.9 ± 0.05	0.9 ± 0.05	32.7
DC	75	Autumn/winter	Oceanic	8	173 ± 8	0.8 ± 0.07	0.9 ± 0.1	67.2
DC	76	Autumn/winter	Oceanic	3	161 ± 11	0.9 ± 0.06	0.8 ± 0.07	53.6
DC	77	Autumn/winter	Oceanic	2	188 ± 7	1.0 ± 0.1	0.8 ± 0.7	46.6
DC	36	Autumn/winter	Oceanic	4	186 ± 16	0.8 ± 0.04	0.8 ± 0.2	14.3
	Mean		**DC**		**182 ± 12**	**0.9 ± 0.1**	**0.8 ± 0.05**	**39.7 ± 17.7**
NN	73	Autumn	Oceanic	3	216 ± 7	0.8 ± 0.1	0.9 ± 0.09	9.2
NN	75	Autumn	Oceanic	2	187 ± 9	0.8 ± 0.1	0.9 ± 0.07	25.9
NN	53	Autumn	Oceanic	3	208 ± 3	0.9 ± 0.1	0.9 ± 0.05	19.5
	Mean		**NN**		**204 ± 15**	**0.8 ± 0.06**	**0.9**	**18.2 ± 8.4**
LIG	68	Autumn/winter	Oceanic	2	233 ± 28	0.7 ± 0.1	0.7 ± 0.2	35.8
LIG	72	Autumn/winter	Oceanic	3	232 ± 17	0.9 ± 0.06	0.9 ± 0.05	70.5
LIG	56	Autumn/winter	Oceanic	4	211 ± 19	0.9 ± 0.09	0.8 ± 0.09	42.6
LIG	61	Autumn/winter	Oceanic	4	222 ± 20	0.9 ± 0.05	0.9 ± 0.07	44.4
	Mean		**LIG**		**224 ± 10**	**0.8 ± 0.1**	**0.8 ± 0.1**	**48.3 ± 15.2**
	Mean		**Shelf**		**137 ± 29**	**0.8 ± 0.1**	**0.9 ± 0.1**	**22.3 ± 11.1**
	Mean		**Oceanic**		**187 ± 27**	**0.9 ± 0.1**	**0.9 ± 0.1**	**32.2 ± 18.5**

Table 2: Maximum distance travelled from the colony, cumulative total distance, foraging trip duration and mean foraging trip speed (km/h) recorded from 31 lactating New Zealand fur seals from CG; Cape Gantheaume, DC; Cape du Couedic, NN; North Neptune Island and LIG; Liguanea Island. All values are mean ± SD.

Colony	ID	FT	Season	Foraging location	Mean max distance (km)	Range of max distance (km)	Cumulative total distance travelled (km)	Mean duration (days)	Mean speed (km/h)
CG	68	3	Winter	Shelf	181 ± 40	143 – 222	529 ± 60	13.4 ± 1.9	1.7 ± 0.1
CG	691	2	Autumn	Shelf	118 ± 18	105 –130	328 ± 107	7.3 ± 0.4	1.9 ± 0.5
CG	692	4	Autumn	Shelf	61 ± 10	51 – 71	194 ± 57	4.8 ± 0.3	2.1 ± 0.2
CG	693	5	Winter	Shelf	143 ± 15	128 – 164	325 ± 48	7.9 ± 2.0	1.9 ± 0.5
CG	702	5	Autumn	Shelf	151 ± 40	109 – 197	410 ± 100	5.9 ± 2.3	3.1 ± 0.8
CG	711	4	Autumn	Shelf	88 ± 7	78 – 94	226 ± 30	5.7 ± 0.6	1.8 ± 0.5
CG	712	2	Autumn	Shelf	203 ±19	190 – 211	560 ± 48	10.3 ± 2.4	2.3 ± 0.7
CG	721	4	Autumn	Shelf	58 ± 19	36 – 82	197 ± 95	4.4 ± 2.3	1.8 ± 0.2
CG	723	4	Winter	Shelf	149 ± 52	89 – 181	483 ± 155	10.4 ± 4.0	2.1 ± 0.7
CG	731	3	Autumn	Shelf	110 ± 36	72 – 144	310 ± 110	5.3 ± 1.5	2.5 ± 0.5
CG	732	3	Autumn	Shelf	131 ± 49	48 – 187	342 ± 126	6.8 ± 1.3	2.1 ± 0.4
	Mean			**CG**	**127 ± 46**		**355 ± 128**	**7.5 ± 2.8**	**2.1 ± 0.4**
CG	74	3	Autumn/winter	Oceanic	285 ± 53	226 – 329	686 ± 142	12.0 ± 2.3	2.4 ± 0.3
CG	76	3	Autumn/winter	Oceanic	346 ± 102	256 – 456	810 ± 249	11.5 ± 3.8	2.9 ± 0.2
CG	703	2	Autumn/winter	Oceanic	474 ± 28	454 – 494	1269 ± 115	23.8 ± 7.6	2.2 ± 0.5
CG	713	3	Autumn/winter	Oceanic	448 ± 187	271 – 643	1213 ± 549	16.5 ± 6.2	3.0 ± 0.4
CG	722	3	Autumn/winter	Oceanic	526 ± 67	448 – 569	1236 ± 134	18.4 ± 2.6	2.8 ± 0.6
CG	733	2	Autumn/winter	Oceanic	509 ± 55	470 – 548	1391 ± 216	20.6 ± 2.9	2.8 ± 0.0
	Mean			**CG**	**431 ± 96**		**1101 ± 283**	**17.1 ± 4.8**	**2.7 ± 0.3**

DC	69	4	Autumn/winter	Oceanic	440 ± 112	331 – 572	1006 ± 172	18.0 ± 6.7	2.5 ± 0.7
DC	7	4	Autumn/winter	Oceanic	330 ± 126	219 – 467	860 ± 285	17.0 ± 7.5	2.3 ± 0.7
DC	74	5	Autumn/winter	Oceanic	308 ± 101	197 – 430	707 ± 229	13.0 ± 2.2	2.3 ± 0.5
DC	75	8	Autumn/winter	Oceanic	259 ± 174	111 – 414	893 ± 709	8.8 ± 2.7	1.7 ± 1.3
DC	76	3	Autumn/winter	Oceanic	360 ± 193	350 – 459	920 ± 387	14.4 ± 4.6	2.6 ± 0.7
DC	77	2	Autumn/winter	Oceanic	253 ± 118	136 – 383	622 ± 292	7.3 ± 2.5	3.5 ± 0.8
DC	36	4	Autumn/winter	Oceanic	420 ± 60	186 – 636	1006 ± 187	13.8 ± 3.6	3.1 ± 0.3
	Mean			**DC**	**339 ± 73**		**859 ± 146**	**13.2 ± 3.9**	**2.6 ± 0.6**
NN	73	3	Autumn	Oceanic	684 ± 63	639 – 728	1750 ± 293	25.7 ± 7.8	2.7 ± 0.4
NN	75	2	Autumn	Oceanic	556 ± 144	455 – 658	1452 ± 345	19.3 ± 7.7	3.2 ± 0.7
NN	53	3	Autumn	Oceanic	594 ± 116	475 – 707	1354 ± 307	19.8 ± 3.6	2.9 ± 0.6
	Mean			**NN**	**611 ± 65**		**1518 ± 206**	**21.6 ± 3.6**	**2.9 ± 0.3**
LIG	68	2	Autumn	Oceanic	647 ± 232	136 – 811	2591 ± 63	36.6 ± 6.0	2.3 ± 0.3
LIG	72	3	Autumn/winter	Oceanic	539 ± 380	227 – 1023	1287 ± 887	17.7 ± 10.0	2.9 ± 0.6
LIG	56	4	Autumn/winter	Oceanic	630 ± 268	320 – 798	1744 ± 368	23.5 ± 1.9	3.0 ± 0.5
LIG	61	4	Autumn/winter	Oceanic	554 ± 246	355 – 887	1298 ± 547	27.1 ± 11.1	2.7 ± 0.4
	Mean			**LIG**	**592 ± 54**		**1605 ± 388**	**26.2 ± 8.0**	**2.7 ± 0.2**
	Mean			**Shelf**	**127 ± 46**		**355 ± 128**	**7.5 ± 2.8**	**2.1 ± 0.4**
	Mean			**Oceanic**	**458 ± 134**		**1180 ± 390**	**18.3 ± 6.9**	**2.7 ± 0.4**

Table 3: The overlap in area and time spent in area between consecutive foraging trips. Also presented in the maximum time spent in 5 x 5 km area as recorded from 31 lactating New Zealand fur seals from CG; Cape Gantheaume, DC; Cape du Couedic, NN; North Neptune Island and LIG; Liguanea Island. All values are mean ± SD.

Colony	**ID**	**FT**	**Foraging location**	**Overlap in area (%)**	**Overlap in time spent in area (%)**	**Max time spent in area (% total time)**
CG	68	3	Shelf	24.5 ± 4.2	24.3 ± 14.8	9.9 ± 5.9
CG	691	2	Shelf	78.7	42.7	19.1 ± 4.8
CG	692	4	Shelf	68.9 ± 10.2	55.9 ± 16.3	16.1 ± 1.1
CG	693	5	Shelf	62.9 ± 4.8	58.3 ± 16.5	13.0 ± 4.2
CG	702	5	Shelf	53.6 ± 16.7	48.8 ± 19.5	8.2 ± 2.8
CG	711	4	Shelf	76.7 ± 14.2	66.8 ± 17.8	18.3 ± 11.0
CG	712	2	Shelf	58.6	42.5	13.4 ± 8.9
CG	721	4	Shelf	54.4 ± 34.5	45.7 ± 33.7	25.2 ± 7.3
CG	723	4	Shelf	58.9 ± 2.7	43.3 ± 13.7	14.7 ± 12.2
CG	731	3	Shelf	65.6 ± 13.3	47.6 ± 12.2	9.0 ± 6.9
CG	732	3	Shelf	12.5 ± 7.3	5.1 ± 2.6	11.8 ± 5.4
			CG	**55.9 ± 20.4**	**43.7 ± 16.8**	**14.4 ± 5**
CG	74	3	Oceanic	12.3 ± 6.1	8.3 ± 5.9	8.1 ± 2.1
CG	76	3	Oceanic	19.0 ± 4.6	18.0 ± 10.2	2.8 ± 0.2
CG	703	2	Oceanic	25.0	23.4	2.5 ± 0.5
CG	713	3	Oceanic	10.9 ± 2.2	6.0 ± 2.5	3.4 ± 2.2
CG	722	3	Oceanic	9.0 ± 10	4.5 ± 3.3	2.6 ± 1.7
CG	733	2	Oceanic	34.5	15.7	3.0 ± 1.9
			CG	**18.5 ± 10.8**	**12.7 ± 7.8**	**3.7 ± 2.2**
DC	69	4	Oceanic	21.2 ± 30.3	15.8 ± 19.9	2.5 ± 0.7
DC	70	4	Oceanic	13.3 ± 2.2	8.1 ± 3.2	5.0 ± 2.3
DC	74	5	Oceanic	14.4 ± 8.2	10.9 ± 4.8	3.0 ± 0.5
DC	75	8	Oceanic	17.3 ± 9.1	12.7 ± 6.1	6.8 ± 5.9
DC	76	3	Oceanic	16.1 ± 20.6	12.0 ± 16.0	4.9 ± 4.0
DC	77	2	Oceanic	16.6	7.9	6.5 ± 3.8
DC	36	4	Oceanic	12.9 ± 1	6.0 ± 2.7	4.5 ± 0.4
			DC	**16.0 ± 11.9**	**10.5 ± 8.5**	**4.7 ± 1.6**
NN	73	3	Oceanic	7.5 ± 0.1	4.0 ± 0.1	2.9 ± 0.4
NN	75	2	Oceanic	11.4	5.0	4.3 ± 1.1
NN	53	3	Oceanic	8.0 ± 0.6	7.8 ± 6.6	5.5 ± 1.9
			NN	**9.0 ± 1.7**	**5.6 ± 3.8**	**4.2 ± 1.3**
LIG	68	2	Oceanic	2.9	2.8	3.3 ± 0.2
LIG	72	3	Oceanic	4.5 ± 3.0	2.9 ± 0.8	2.3 ± 0.3
LIG	56	4	Oceanic	5.6 ± 3.7	4.6 ± 3.3	5.1 ± 2.6

LIG	61	4	Oceanic	5.8 ± 3.7	4.9 ± 3.7	2.4 ± 0.4
			LIG	**4.7 ± 1.4**	**3.6 ± 1.3**	**2.7 ± 1.0**
			Shelf	**55.9 ± 20.4**	**43.7 ± 16.8**	**14.4 ± 5**
			Oceanic	**13.4 ± 7.6**	**9.0 ± 5.7**	**4.0 ± 1.7**

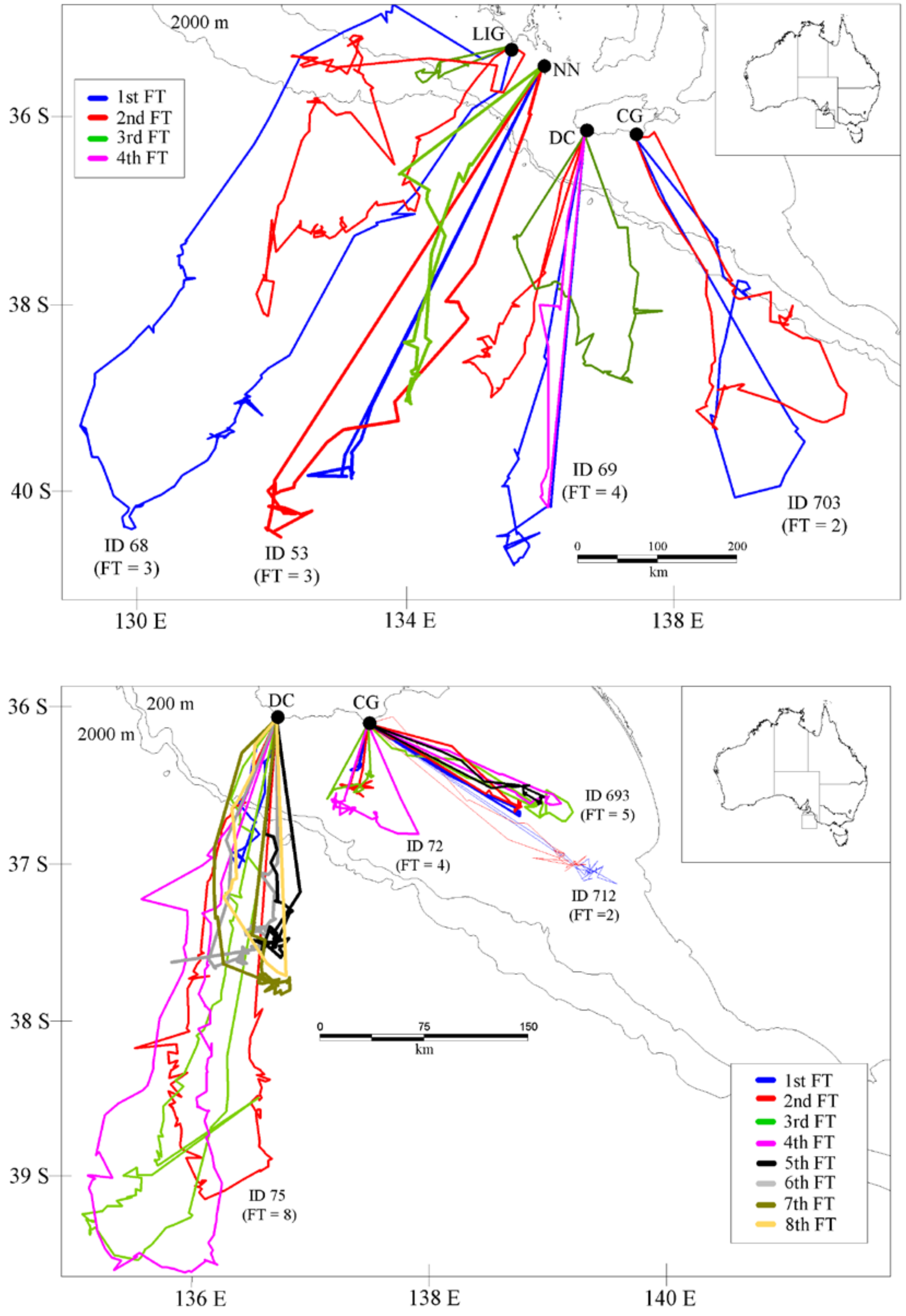

Fig. 1: The four study sites: CG; Cape Gantheaume, DC; Cape du Couedic, NN; North Neptune Island and LIG; Liguanea Island and examples of consecutive foraging trips (FT) recorded from lactating New Zealand fur seals that foraged in oceanic and continental shelf waters.

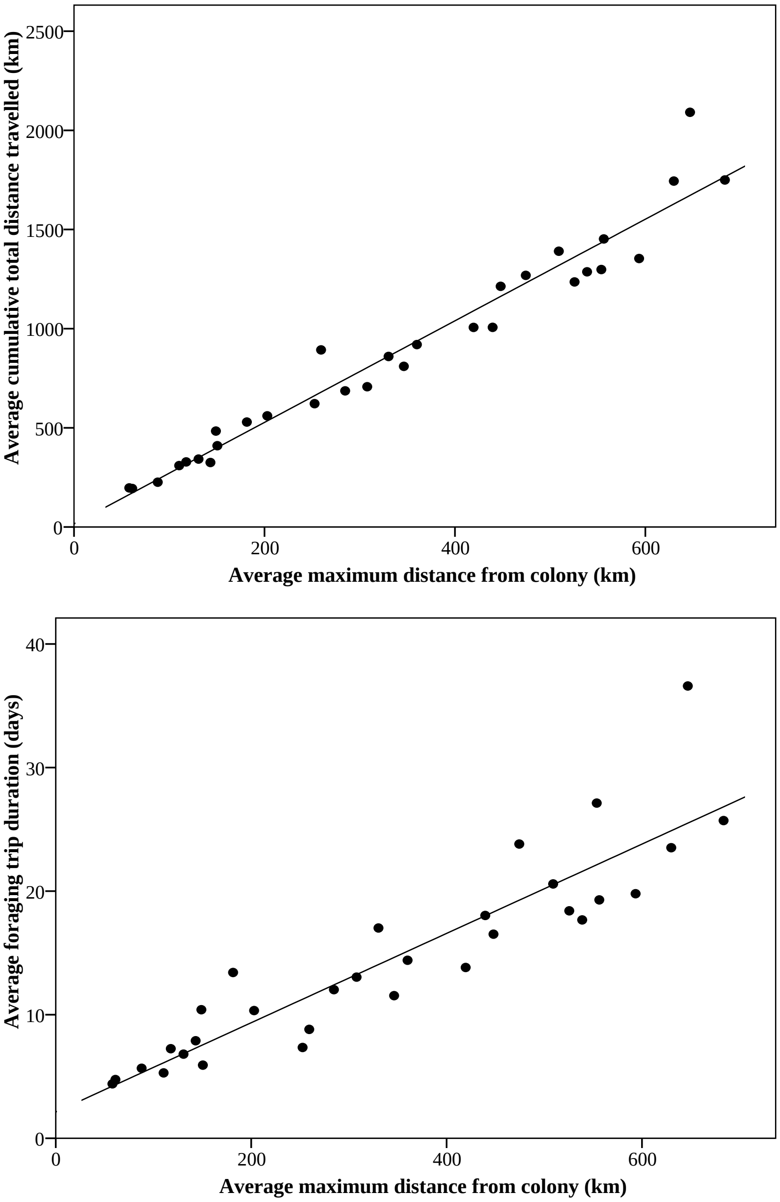

Fig. 2: The relationship between the mean maximum distance traveled and the mean cumulative total distance (R^2 = 0.97, P <0.001) and the mean foraging trip duration (R^2 = 0.81, P <0.001), as recorded by 31 lactating New Zealand fur seals.

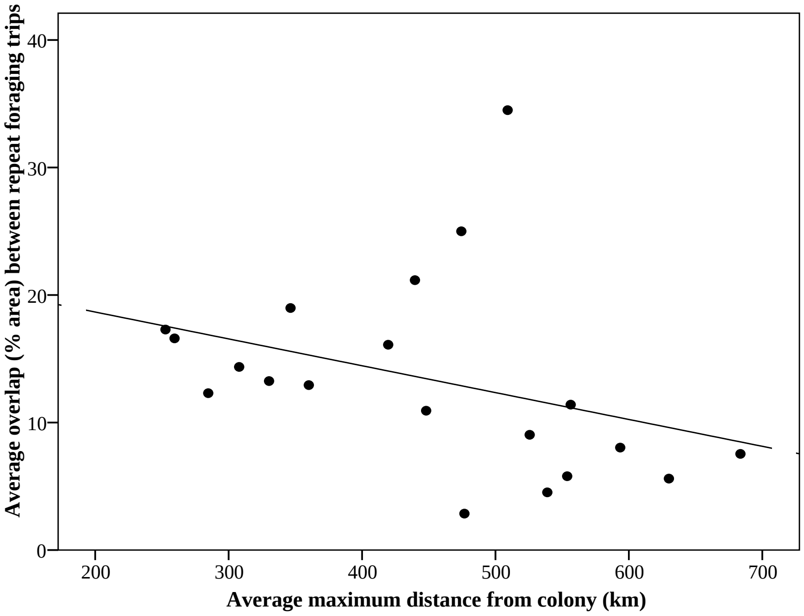

Fig. 3: The relationship between the mean maximum distance traveled and the mean overlap in consecutive foraging trips (R^2 = -0.59, P = 0.006), recorded by 20 lactating New Zealand fur seals that foraged in oceanic waters.

CHAPTER SUMMARY

- In order to determine how foraging site fidelity varied between continental shelf and oceanic foraging habitats, 31 lactating females were satellite tracked over 106 consecutive foraging trips.
- 39 foraging trips were recorded from 11 females that foraged on the continental shelf, in a region associated with the Bonney upwelling, while 67 foraging trips were recorded from 20 females that foraged in oceanic waters.
- There were no significant differences in the mean bearings of individual's consecutive foraging trips, suggesting directional fidelity. However, actual foraging route overlap varied considerably between continental shelf and oceanic foragers. Females foraging on the continental shelf recorded a significantly greater overlap in foraging area between consecutive foraging routes, when compared to females that foraged in oceanic waters (55.9 ± 20.4 % and 13.4 ± 7.6 %, respectively).
- Females foraging on the continental shelf spent significantly more time within the same grid cell than oceanic foragers (maximum time spent in 5 x 5 grid cell: 14 ± 5 % and 4 ± 2 %, respectively).
- Results suggest that seals learn the direction of travel to a predictable foraging region, and initiate a foraging trip on that bearing. However, actual foraging routes are likely to be influenced by a number of factors including previous foraging trip experience and prey encounter rate, which is related to prey density and the spatial scale of the patch exploited.

CHAPTER 5

MILK FATTY ACIDS PREDICT THE FORAGING LOCATIONS OF A WIDE-RANGING CENTRAL PLACE FORAGER, THE NEW ZEALAND FUR SEAL: CONTINENTAL SHELF VS OCEANIC WATERS

Baylis, A.M.M., & Nichols, P.D. (2009) Milk fatty acids predict the foraging locations of a wide-ranging central place forager, the New Zealand fur seal: continental shelf vs. oceanic waters.
Marine Ecology Progress Series, v. 380, pp. 271-286

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CHAPTER SUMMARY

- Using milk FA obtained from 29 satellite-tracked fur seals, I characterise the FA composition of seals that foraged on the continental shelf, and those that foraged in oceanic waters.
- Seals foraging within continental shelf waters were high in polyunsaturated fatty acids (PUFA) (36.1 ± 5.9 %), and lower in monounsaturated fatty acids (MUFA; 32.1 ± 5.3 %) compared to seals that foraged in oceanic waters (MUFA: 46 ± 5.3 % and PUFA: 24.9 ± 4.5 %).
- Based on FA compositions, I predicted the likelihood that milk samples collected at random (*n* = 131) represented individual seals having foraged either on the continental shelf or in distant oceanic waters. Results indicated that 74 % (*n* = 97) of seals were likely to have foraged in oceanic waters, with 26 % (*n* = 34) likely to have foraged within continental shelf waters. These results were supported by the small sub-sample of 29 satellite-tracked seals, which indicated that 62 % of seals had foraged in oceanic waters.
- FA analysis and satellite tracking results contrasted with scat analyses, from which only 6 % of scats by frequency of occurrence contained prey remains from oceanic waters. The results suggests that scats were biased toward females foraging on the continental shelf, and/or the last foraging bout, if seals travelling from distant waters consumed prey on the continental shelf during the return trip.

CHAPTER 6

GENERAL DISCUSSION

GENERAL DISCUSSION

The primary aim of this thesis was to determine whether seasonal or inter-colony differences were evident in the foraging behaviour and diet of lactating New Zealand fur seals. The proximity of colonies to predictable ocean features, seasonal differences in ocean productivity and colony-specific foraging areas played an important role in determining the foraging behaviour of New Zealand fur seals in South Australia. This species appears to be well adapted to exploiting both locally abundant and distant resources.

Lactating females used two spatially distinct but predictable habitats: the Bonney upwelling and the Subtropical Front (STF). The Bonney upwelling was an important resource for females from the Cape Gantheaume colony during summer (Page *et al.* 2006), and autumn. During winter months lactating females from Cape Gantheaume predominantly used oceanic waters associated with the STF (Chapter 2). Lactating females from Cape du Couedic, North Neptune Island and Liguanea Island predominantly foraged in association with the STF (Chapter 3). The extended distances travelled by seals from Cape du Couedic, North Neptune and Liguanea Island colonies in early autumn, suggests the STF is likely to be less variable and more predictable than continental shelf or shelf-slope habitats near these colonies. The importance of the STF as critical foraging habitat is further supported by the post-weaning movement of New Zealand fur seal pups, which travelled 800 km south of Cape Gantheaume, to forage at the southern extent of the STF (A. Baylis unpublished data).

Resource predictability emerged as an important concept when comparing inter-seasonal and inter-colony variability in the foraging ecology of New Zealand fur seals. Lactating females tended to swim directly to foraging areas and displayed remarkable tendencies to forage along similar bearings both at the individual level (as measured over consecutive foraging trips) and at the colony level (Chapters 3 and 4). As has been suggested for other marine central place foragers, New Zealand fur seals target predictable large-scale oceanographic features, where they search for patchily distributed prey (i.e. prey distribution ultimately determines foraging behaviour) (Bonadonna *et al.* 2001; Pinaud and Weimerskirch 2005; Weimerskirch 2007). Resource predictability may allow New Zealand fur seals to alter their foraging location from nearby continental shelf waters to distant oceanic waters, while still maintaining a regular rate of milk delivery to dependent offspring, and meeting their own energetic requirements.

The existence of colony-specific foraging areas (and the high density of New Zealand fur seals in South Australia relative to other regions along the southern Australian coastline) also reflects the accessibility and predictability of resources to suitable breeding areas. The colony-specific foraging areas reported for lactating female New Zealand fur seals and in other studies on seals and seabirds, provide a fascinating insight as to how central place foragers distribute their foraging effort to optimize foraging success. It is important to recognise that with a larger sample size, the foraging area and overlap in colony-specific foraging areas may have been greater. Nonetheless, the partitioning of foraging areas may have significant implications for the dynamics and distribution of populations on a larger scale (Fretwell and Lucas 1970; Pereira *et al.* 2003).

From an optimal foraging perspective, foraging site fidelity and colony specific foraging areas are likely to be advantageous in species that exhibit breeding site fidelity and forage in regions where suitable resources are to some degree predictable over both spatial and temporal scales (Irons 1998; Weimerskirch 2007). In such situations, familiarity with predictable resources may enhance foraging efficiency and foraging success and maximise energy gain over the lifetime of an animal (Gentry 1998; Irons 1998; Hamer *et al.* 2001; Bradshaw *et al.* 2004; Gende and Sigler 2006).

The intrinsically long foraging trips among temperate fur seal species during autumn/winter months, suggests these are a response to seasonal variability in ocean productivity and allow seals to exploit distant oceanic habitats when prey resources become depleted closer to the colony (Francis *et al.* 1998; Beauplet *et al.* 2004). The ability to conduct long foraging trips are facilitated by pups having extended fasting capabilities, and mothers having the capability to efficiently store and then transfer energy to pups (Georges and Guinet 2000; Beauplet *et al.* 2004). Differences in foraging trip distance and durations between: (i) continental shelf and oceanic habitats (maximum distance 222 km and duration 15 days and 1000 km and 42 days, respectively); (ii) between colonies and; (iii) between seals that foraged in oceanic waters from the same colony, highlights the remarkable plasticity in both foraging and provisioning strategies in this species (Chapters 2 and 3).

According to central place foraging theory maternal provisioning tactics are expected to maximize the rate of energy acquisition to the offspring (growth rate). Georges and Guinet (2000) reported that for subantarctic females breeding at Amsterdam Island, different foraging trip durations (10 days verses 16 days during winter) enabled the same growth rates for pups. Outside of this foraging trip duration ‘window’, pup growth declined with increasing foraging trip duration (despite the absolute amount of mass transferred to the pup increased with foraging trip duration), as reported for other otariid species including New Zealand fur seals (Lea and Hindell 1997; Haase 2004). The variability in foraging trip durations observed in New Zealand fur seals, suggests that a range of maternal attendance patterns are used to maximise fitness as hypothesised by Georges and Guinet (2000), but the extremes of foraging trip distance and duration may not favour increased pup growth. Females performing longer foraging trips may compensate offspring by increasing the quality or mass of milk provided, or females/pups may extend weaning age (Trillmich and Lechner 1986; Arnould and Boyd 1995; Georges and Guinet 2000; Robinson 2002; Beauplet *et al.* 2004; Haase 2004).

The high milk lipid content presented in Chapter 4 (mean of 47 %) was comparable to other temperate fur seal species that incorporate long trips to distant oceanic waters as part of their foraging strategy (e.g. Juan Fernandez fur seal 41.4% and subantarctic fur seal 45 %; Ochoa-Acuna *et al.* 1999; Georges *et al.* 2001). High milk lipid content is likely to be important in compensating dependant offspring for the extended periods of fasting they must endure (Ochoa-Acuna *et al.* 1999; Georges *et al.* 2001; Beauplet *et al.* 2003). While untested, New Zealand fur seal pups may also combine larger lipid stores with lower daily mass loss rates and/or high early growth rates (Lea and Hindell 1997) to compensate for extended periods of fasting as reported by Beauplet *et al.* (2003) for subantarctic fur seals.

During very early lactation (December – January) when pups are young and have limited ingestion abilities, limited lipid stores and limited fasting capabilities, it is unlikely that lactating females would conduct long foraging trips to forage in distant oceanic waters (Harcourt *et al.* 2002; Page *et al.* 2006). Maternal foraging during early lactation is likely to be primarily driven by pup fasting and ingestion abilities, which would require lactating females to preferentially conduct short distance and duration foraging trips, possibly at the expense of maternal condition (Georges and Guinet 2000; Beauplet *et al.* 2004). Near colony foraging at all colonies during December - January may be facilitated by conditions favouring upwelling being more prevalent.

Identifying foraging habitats and understanding trophic relationships between predator-prey populations is important for management, because knowledge of diet provides information on habitat preference, behaviour, physiology, survival, and reproductive success as well as providing some measure of the potential for trophic interactions with commercial fisheries (Arnould *et al.* 2005). Traditional methods provided valuable taxonomic information for New Zealand fur seals that foraged on the continental shelf and have been previously used to re-construct the diet of fur seals on short oceanic foraging trips (such as those recorded for Antarctic fur seals and northern fur seals; 267 km and 8.2 days and 263 km and 8.8 days respectively) (Staniland and Boyd 2003; Robson *et al.* 2004; Chapter 5). However, oceanic foraging trips performed by lactating New Zealand fur seals in the current study were considerably longer (458 km, lasting 18.2 days) (Chapter 4). Scat analysis indicated that New Zealand fur seal prey identified from scats were biased toward continental shelf habitats and implies that our present knowledge of New Zealand fur seal diet in

South Australia is limited because scat samples were not representative of females that foraged in distant ocean waters.

I employed fatty acid (FA) analysis to elucidate the spatial separation of foraging habitats within and between populations and to make inferences regarding prey composition. I was able to distinguish between seals that foraged in continental shelf and oceanic waters based on their FA profiles. Results corroborated with satellite tracking data and indicated that from a sub-sample of 160 seals sampled between March - October, 73 % foraged in oceanic habitats. However, there were considerable limitations using FA analysis to interpret diet. These limitations were largely attributed to inadequate knowledge of the FA composition of potential prey and knowledge regarding how FA are passed from prey to predator and the elongation/desaturation of particular FA that may occur during deposition or mobilization to the mammary gland.

Without this understanding, it is difficult to validate how ratios or levels of individual FA are attributed to the prey type likely consumed, and results must therefore be interpreted with caution. Additionally, the interpretation of diet from milk FA is also complicated by the fact that milk FA can originate from recent dietary intake and/or from the mobilization of stored body fat, depending on when the seal last fed and the period of time a seal has been ashore suckling its pup (Georges *et al.* 2001; Staniland and Pond 2005). This is likely to be an important factor to account for when interpreting prey composition from milk FA of oceanic foragers because of the extended distance and duration of oceanic foraging trips.

Management implications and future research

The management requirements of New Zealand fur seals vary according to colony location (and therefore the colony-specific foraging area) and the related ocean features used. Within continental shelf waters, the higher degree of foraging route overlap reflects that foraging effort is concentrated within a relatively small area when compared to oceanic regions (Chapter 4). Interactions with commercial fishing activity and fur seals are most likely to take place in continental shelf regions where commercial fishing effort and fur seal foraging effort overlap. Based on the spatial distribution of foraging effort described in this study, seals from Cape Gantheaume and seals from North Neptune that forage in continental shelf regions, are likely to be the most vulnerable to interactions with fisheries as they spend proportionally more time foraging on the continental shelf, within marine fishery areas. Accounting for seasonal and colony differences in foraging location will improve the accuracy of models which aim to estimate the spatial and trophic overlap between New Zealand fur seals and commercial fisheries.

The data presented in this thesis do not support the study of Goldsworthy and Page (2007) that suggests lactating females predominantly utilise continental shelf waters and described a '*marked ontogentic shift*' in New Zealand fur seal foraging behaviour. This study indicates that the foraging behaviour and foraging location of lactating females is governed by the proximity of colonies to predictable ocean features that are located in both continental shelf and distant oceanic waters. This is an important point to emphasize because managers must be aware that factors influencing New Zealand fur seal populations extend far beyond the continental shelf region. While this thesis presents only a snapshot of New Zealand fur seal foraging behaviour, satellite tracking and dietary data derived from milk FA indicated that the STF is more important to New Zealand fur seals during mid-late lactation, than continental shelf waters.

Understanding the processes that influence the productivity and location of the STF south of Australia is imperative to the future management of this wide-ranging central place forager. Factors that influence the productivity or location of the STF are likely to effect foraging trip length and duration, which inturn influences maternal provisioning, pup growth and ultimately offspring survival and reproductive success (Beauplet *et al.* 2004; Haase 2004; Lea *et al.* 2006). Currently little information exists on physical and biological oceanography of the STF south of Australia, or spatial and temporal scales of change (James *et al.* 2002). The paucity of data available limits our ability to interpret and predict how individuals and populations respond to seasonal, inter-annual and longer-term environmental variability. For example, the reasons for a seasonal shift in foraging trip distance recorded from Cape du Couedic and Liguanea Island females remain unclear, although we can suppose that it reflects productive regions becoming available closer to continental Australia during winter months. Belkin and Gordon (1996) described a northern STF between 60º – 110º E that was likely to shift seasonally by 5º latitude. Whether a migrating component of the STF south of Australia accounts for the observed seasonal shift in the foraging locations of seals from Cape du Couedic and Liguanea Island is unknown.

Alternatively, the foraging trip distances and durations of lactating New Zealand fur seals foraging in association with the STF are among the longest reported for any temperate otariid species, with only lactating subantarctic fur seals recording longer foraging trips (Beauplet *et al.* 2004). It is unclear whether these intrinsically long foraging trips are close to the limit of a central place foraging fur seal. However, it does imply that lactating New Zealand fur seals may be vulnerable to climactic anomalies or anthropogenic impacts such as climate change that may influence the location (i.e. increase the distance travelled to reach foraging grounds) or the productivity of the STF south of Australia, as projected for baleen whales migrating to forage in Antarctic ocean fronts (Tynan and Russell 2008).

Maternal mass gain relative to foraging trip characteristics, and maternal input (e.g. pup mass, condition and weaning mass) was not measured in the current study. Bradshaw *et al.* (2002) and Boren *et al.* (2006) reasoned that differences in New Zealand fur seal pup condition between closely related colonies in New Zealand, reflected proximity of breeding sites to foraging grounds. Considering colonies recorded significantly different foraging trip distances and durations, it is likely that pup growth, condition, weaning mass, timing of weaning (see Haase 2004), or reproductive rates (Dabin *et al.* 2004) may vary between colonies (in particular between Cape Gantheaume and all other colonies). Pup growth rates and weaning masses in seals are good indicators of parental foraging success and may be informative when interpreting inter-annual environmental variability because environmental conditions influence maternal provisioning tactics which in turn affects pup growth rates (Arnould and Boyd 1995; Georges and Guinet 2000; Beauplet *et al.* 2004; Lea *et al.* 2006).

To elucidate the diet of New Zealand fur seals future studies must account for the spatial variation in foraging areas. Without accounting for the fact that individuals within the same population forage in discrete habitats, dietary studies are unlikely to accurately represent the diet of New Zealand fur seals in South Australia. This study highlighted the value of scat analysis in providing taxonomic information, but also its limitations. Scat analysis was unable to characterise the diet of female fur seals that foraged in distant oceanic habitats. Future dietary studies should augment scat analysis with alternative methods to improve the understanding of New Zealand fur seal diet.

Despite significant limitations and challenges, FA analysis is one of the few techniques that provide dietary information at time scales relevant to understanding the diet of females foraging in oceanic waters. Stable isotope analysis is also a valid technique, although its application is also likely to be limited to qualitative descriptions. If future studies pursue FA analysis, carefully controlled feeding experiments should first be conducted to better understand how dietary fatty acids are deposited and mobilized from predator lipid stores and to develop ‘calibration coefficients’ that may account for metabolism, deposition and biosynthesis of individual FA (Iverson *et al.* 2004; Budge *et al.* 2006). Additionally little information is available on prey assemblages associated with the STF region, and how these species vary temporally. An understanding of the above and a FA database that includes a broad range of potential prey species sampled from both the STF and continental shelf are key requirements to the successful application of this method.

In conclusion, New Zealand fur seals from Cape Gantheaume foraged in association with the Bonney Upwelling region during autumn, and shift foraging effort to distant oceanic waters associated with the STF during winter months. When considering the findings of Page *et al.* (2006), it would appear that the shift to oceanic foraging is dependent on the strength and duration on the Bonney upwelling during summer/autumn months. In contrast, females from other colonies in South Australia tended to target the STF during autumn and winter, rather than continental shelf waters. Females from all colonies foraged within colony-specific foraging areas and recorded a high degree of foraging site-fidelity. The great distances females travel to forage in distant oceanic waters suggests the current understanding of diet is incomplete because scat analysis alone cannot provide reliable dietary information for females foraging in distant oceanic waters. Finally, this new information suggests New Zealand fur seals that forage in distant oceanic waters and show high foraging site fidelity may be vulnerable to anthropogenic impacts such as climate change, or climactic anomalies that influence the location and productivity of the STF south of Australia.

APPENDIX

ASSESSING THE USE OF MILK FATTY ACIDS TO INFER THE DIET OF THE AUSTRALIAN SEA LION (*Neophoca cinerea*): A PRELIMINARY INVESTIGATION FROM OLIVE ISLAND, SOUTH AUSTRALIA

”Things will not be necessarily continuous. The fact that they are something other than perfectly continuous ought not to be characterized as a pause.” D. Rumsfeld

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ABSTRACT

Information on the diet of threatened species is important in devising appropriate management plans. The Australian Sea lion (*Neophoca cinerea*) is Australia's only endemic and globally one of the least numerous pinniped species. However, dietary information is currently limited because of the difficulty in using traditional methods (identification of prey hard parts from scats, regurgitates and stomach samples) to reliably provide dietary information. We assessed the use of fatty acid (FA) analysis to infer diet using milk samples collected from 11 satellite tracked Australian sea lions from Olive Island, South Australia. Satellite tracking revealed that females foraged in two distinct regions; 'inshore' regions characterised by shallow bathymetry (10.7 ± 14.8 m) and 'offshore' regions characterised by comparatively deep bathymetry (60.5 ± 13.3 m). Milk FA analysis indicated significant differences in the FA composition between females that foraged inshore compared to those that foraged offshore. The greatest differences in relative levels of individual FA between the inshore and offshore groups were for 22:6n-3 (6.5 ± 1.2 % compared to 16.5 ± 1.9 %, respectively), 20:4n-6 (6.1 ± 0.7 compared to 2.5 ± 0.7, respectively) and 22:4n-6 (2.4 ± 0.2 % compared to 0.8 ± 0.2 %, respectively). Using discriminant scores, we differentiated crustacean, cephalopod, fish and shark-dominated diets. The discriminant scores from Australian sea lions that foraged inshore indicated a mixed fish and shark diet, whereas discriminant scores from Australian sea lions that foraged offshore indicated a fish-dominated diet, although results must be interpreted with caution. FA analysis in combination with satellite tracking proved to be a powerful tool for assessing broad-scale spatial dietary patterns.

Baylis, A.M.M., Hamer, D.J. & Nichols, P.D. (2009) Assessing the use of milk fatty acids to infer the diet of the Australian sea lion (*Neophoca cinerea*).
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