Foraging ecology of male

Australian fur seals

by

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B.Sc. (Hons) / B.Ed.

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University

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Abstract

Marine predators play an important role in the structure and function of the ecosystems they inhabit. Pinnipeds are large free ranging predators distributed throughout many of the world’s marine ecosystems. However, our current understanding of pinniped ecology is largely biased towards females, with many studies ignoring males. This may be problematic as variation in behaviour and in diet between sexes is often linked with differences in their body size and reproductive behaviour. Australian fur seals (*Arctocephalus pusillus doriferus*) are the largest of all fur seals, with males up to four times the mass of females. The species is endemic to the south east Australian region and, with an estimated population size of ca 120,000 individuals, it is an important resident consumer of marine resources in the area. This study investigates the spatial distribution (foraging range and habitat consistency), dive behaviour and diet of male Australian fur seals to improve our overall understanding of the species’ ecology.

The present study found that during winter, males, similarly to females, were predominantly benthic divers with a foraging range limited to the shallow continental shelf of Bass Strait (60-80 m). By remaining to forage within Bass Strait, males were able to utilise the relative abundance of haul out locations (offshore islands and rocky outcrops), that would not be available in off-shelf habitats. This allowed males to make regular short trips to nearby foraging areas (3.4 ± 0.2 d). Furthermore, most males exhibited a high degree of spatial consistency in their foraging areas (mean site fidelity index ± SE: 0.27 ± 0.03), suggesting that prior knowledge of foraging areas is important for males. The foraging behaviour observed in the present study may allow
males to minimise the metabolic costs of transiting to foraging areas and searching for prey, thereby increasing their overall net energetic gain.

In winter, males overlapped with the foraging areas of females, suggesting that males may experience a higher degree of intra-specific competition in Bass Strait than elsewhere. However, males used alternate foraging strategies (diurnal, mixed and nocturnal) to presumably target different resources, thereby reducing the degree of intra-specific competition. Furthermore, by being larger in size when compared to females, males could spend a greater time searching for prey along the sea floor enabling them access to a greater proportion of cryptic prey species. Indeed, blubber fatty acid analysis indicated that males consumed greater proportions of demersal fish and cephalopod species when compared to females.

However, the fatty acid composition of males differed between seasons (non-breeding and pre-breeding periods) and between individuals, indicating variability in diet and/or their broad-scale foraging areas. Indeed, just prior to the breeding season (in late spring/summer) some males were observed to travel away from central Bass Strait and forage in deeper waters (>200 m) along the edge of the continental shelf. These movements suggest that shelf slope waters are important habitat for males, which may be targeting alternate resources to acquire the necessary reserves for the breeding season fasting period. Overall, the present study highlights the inter-individual variation that occurs within the behaviour and diet of male Australian fur seals. Furthermore, extreme body size differences between males and females appears to contribute to resource partitioning within the species. These results have important implications for the future management of the species and the marine resources within south-eastern Australia.
Preface

All work was carried out with the approval of the Deakin University Animal Welfare Committee (Permit No. A71-2011; B12-2013) and in accordance with the regulations of Department of Environment, Land, Water and Planning (Wildlife Research Permits 1005848; 1007153). This project was supported financially from research grants provided by the Winifred Violet Scott Trust and Holsworth Wildlife Research Endowment.

The core data chapters of this thesis (Chapters 2-5) have been published or submitted for publication in peer-reviewed journals. I am the principal contributor to all chapters of this thesis and the primary author on all publications arising from this thesis. Professor John Arnould is a co-author on all publications (chapters 2 to 5) for his contribution to the study design, fieldwork and editorial advice throughout the project. Dr. Alastair Baylis is a co-author on chapters 2 to 5 due to his assistance with fieldwork, statistical advice and editorial advice throughout the project. Dr. Damian Callahan is a co-author on chapters 4 and 5 for his contribution in the lipid extraction of the blubber samples and his editorial advice. Dr. Laëtitia Kernaléguen is a co-author on chapter 5 for her contribution to fieldwork and for providing access to the 2012 summer biopsy samples.
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Chapter 1: General overview
Chapter 1: General overview

Top order predators play an important role in the structure and functioning of ecosystems and many are considered to be important sentinels of ecosystem change (Williams et al. 2004; Bossart 2006; Estes et al. 2016). Predators consume large amounts of prey biomass and, consequently, can have important effects on the overall trophic dynamics of an ecosystem (Mills et al. 1993). Predators may also move large distances and, therefore, play important roles in linking disparate ecosystems through the redistribution of nutrients over large spatial scales (Estes et al. 2016). For these reasons, knowing where, when and how predators forage is fundamental to better understanding overall ecosystem processes and has important implications for the management and conservation of predator and prey populations (Lomnicki 1978; Costa et al. 2010a).

Empirical studies often consider individuals within a predator population as ecologically equivalent and assume that the sampled individuals are representative of the whole population (Bolnick et al. 2011). However, individuals within a species or population may differ in many physical attributes, including their morphology, physiology, breeding status, experience and skills (Polis 1984; Mysterud 2000; Bolnick et al. 2003; Ruckstuhl and Neuhaus 2005). This may lead to variation in the behaviour and dietary composition within a population (i.e. resource partitioning), as different subsets utilise contrasting strategies to optimally search for and consume prey (Pyke 1984; Stephens and Krebs 1987).

In sexually dimorphic species, males and females will often differ in their spatial distribution and resource use (i.e. sexual segregation) (Gonzalez-Solis et al. 2000; Wearmouth and Sims 2008; Cleasby et al. 2015). Body size can influence an
individual’s overall metabolic requirements and its ability to access, handle and
digest prey (Charnov 1976; Pyke et al. 1977; Pyke 1984). Consequently, the larger
sex may have higher overall energetic requirements and have the ability to access a
broader range of prey resources and habitats (Shine 1989; Ruckstuhl and Neuhaus
2005). Segregation between the sexes has major implications for the overall
population structure and dynamics of a species and how it may respond to
environmental variability. As subsets of the population exploit different resources
they are not uniformly impacted by perturbations and, therefore, a population may
have a better ability to respond to environmental perturbations (Lomnicki 1978;
Clemmons and Buchholz 1997).

**Pinniped foraging ecology**

In the marine environment, pinnipeds are among the largest vertebrate
carnivores. Globally there are 33 species of pinnipeds, comprising of three major
families: the Phocidae (true seals), the Otariidae (fur seals and sea lions) and the
Odobenidae (walrus) (Berta and Chruchill 2012). The large body size of pinnipeds
mean that they consume large amounts of prey biomass and play an important role in
the redistribution of marine productivity (Bowen 1997; Morissette and Brodie 2014).
Furthermore, given that large animals typically have extensive home ranges
(McCauley et al. 2015), pinnipeds have the ability to connect oceanic ecosystems
over large spatial scales (Estes et al. 2016).

Air-breathing marine predators, such as seals, must operate within the
physiological limitations of a breath hold (Costa et al. 2001). Consequently, body
size can determine how, where and what kind of prey can be consumed. Larger animals have greater absolute energetic requirements, may consume larger sized prey and have a greater ability to store oxygen (Kooyman et al. 1983; Weise and Costa 2007; Weise et al. 2010; Andrews and Enstipp 2016). This means that larger sized individuals are able to dive deeper and longer than smaller conspecifics. Given pinnipeds exhibit some of the greatest sexual size dimorphism of any higher order group (males can be up to 10 times the mass of females) (Staniland 2005), larger sized males may be able to access prey resources that smaller sized conspecifics cannot, thereby contributing to sexual segregation in diet.

In addition, male and female pinnipeds exhibit contrasting reproductive strategies, which place different constraints on the respective foraging behaviour of each sex, potentially leading to sexual segregation in foraging areas (Gentry et al. 1986; Staniland 2005). After giving birth to a pup, females are solely responsible for the rearing of offspring. Phocid seals are generally capital breeders with relatively short lactation periods (4-60 d), where individuals utilise their energy stores acquired prior to parturition (Kovacs and Lavigne 1986). However, otariids and odobenids exhibit an income breeding strategy, where females acquire resources throughout their comparatively long lactation period (116-540 d) (Bonner 1984; Boness and Bowen 1996; Schulz and Bowen 2004). While female walruses will forage with their young along side, female otariids will balance their time between making regular short foraging trips and suckling their pup ashore at a breeding colony (Gentry et al. 1986; Kovacs and Lavigne 1992). Accordingly, female otariids are constrained to a central place foraging strategy by their pup’s ability to fast. In contrast, male
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pinnipeds do not assist with raising offspring and thus only need to return to land to rest, avoid predators, moult and breed (Costa 1991; Trillmich 1996). Hence, males may be less restricted in their foraging range, giving them access to a wider range of habitats and niches, thereby resulting in spatial segregation in foraging ranges between sexes.

Despite the high likelihood of otariid seals exhibiting substantial sexual segregation in their behaviour and diet, a significant proportion of ecological studies are heavily biased towards reproductive females (e.g. Boyd et al. 1994; Harcourt et al. 1995; Thompson et al. 1998; Boyd et al. 2002; Call et al. 2008; Auge et al. 2011; Lowther et al. 2011; Staniland et al. 2012), with many studies ignoring the male demographic. This is presumably due to their larger body size and aggressive nature making more males more difficult to capture. In addition, device recovery is often unreliable as males are not constrained to a central place. Indeed, male data only exists for seven of the 16 species of otariid (Hindell and Pemberton 1997; Boyd et al. 1998; Loughlin et al. 1999; Campagna et al. 2001; Page et al. 2005a; Kirkwood et al. 2006; Page et al. 2006; Weise et al. 2006; Staniland and Robinson 2008; Weise et al. 2010; Lowther et al. 2013; Sterling et al. 2014; Baylis et al. 2017). These studies have shown that males and females often exhibit sex-related differences in spatial distribution, dive behaviour and foraging niche, suggesting that for species where male data are lacking, we do not have a thorough understanding of the overall species’ ecology.

Furthermore, reliable dietary assessments are needed to determine how otariids (among other predators) will respond to ecological and environmental variability and
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their functional role within marine ecosystems. However, estimating the diet of marine mammals poses unique challenges due to the complex nature of trophic interactions and logistical difficulties in observing predation events that usually occur at depth (Boyd et al. 1994). Traditional methods of diet reconstruction include the identification of prey remains recovered from the stomach contents of harvested animals or from scat and regurgitate samples collected at breeding colonies. However, these methods rely on identifiable prey remains (e.g. otoliths and beaks) to be wholly consumed and to survive digestion (Pierce & Boyle 1991, Bowen & Iverson 2013). The use of biochemical techniques such as quantitative fatty acid signature analysis (QFASA) are often used to evaluate the diet of predators (e.g. (Smith et al. 1997, Herman et al. 2005, Budge et al. 2006, Thie mann et al. 2008, Bromaghin et al. 2013, Banks et al. 2014). This technique allows for the quantitative estimate of a predators’ dietary composition as predator fatty acid signatures are modelled as a mixture of prey fatty acid signatures using calibration coefficients to account for the differential metabolism of individual fatty acids (Iverson et al. 2004, Budge et al. 2006). Furthermore, QFASA allows for the integration of demographic traits into the dietary assessment and as blubber contains lipids that have been accumulated over time, it can provide a record of dietary intake over a period of weeks to months (Budge et al. 2006). Therefore, QFASA can be used to detect inter-population, spatial and temporal variation in the diet of predators (Iverson et al. 1997a, Iverson et al. 1997b, Smith et al. 1997, Best et al. 2003, Beck et al. 2005, Baylis & Nichols 2009).
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The Australian fur seal

The Australian fur seal (*Arctocephalus pusillus doriferus*) is the largest of all fur seal species with males and females weighing on average 279 kg and 76 kg, respectively (Arnould and Warneke 2002). The species is endemic to south-eastern Australia and it is known to consume a broad range of demersal fish, cephalopods and elasmobranchs (Gales et al. 1993; Page et al. 2005b; Littnan et al. 2007; Kirkwood et al. 2008; Deagle et al. 2009; Kernaléguen et al. 2015b). The Australian fur seal population is still recovering from past exploitation but is not considered threatened. Modern estimates indicate that with ca 120,000 individuals, the species is at 50% of its pre-sealing population size (Kirkwood et al. 2005; Kirkwood et al. 2010).

Like most otariids, the Australian fur seal has an annual breeding cycle, with a lactation period lasting 10-11 months. (Arnould and Hindell 2001; Hume et al. 2001). However, some females may nurse a pup throughout a second or third year (Warneke 1982). Throughout the long lactation period, females adopt a central place foraging strategy within the continental shelf of Bass Strait (marine basin between mainland Australia and Tasmania; Fig. 1.1) (Arnould and Kirkwood 2007; Kirkwood and Arnould 2011; Hoskins et al. 2015a). Female Australian fur seals utilise a benthic foraging strategy, searching for prey along the sea-floor (Arnould and Hindell 2001; Hoskins and Arnould 2013).

However, as is the case for most other otariid species, our understanding of Australian fur seal foraging ecology is derived mostly from lactating females (e.g.
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Figure 1.1: The distribution of Australian fur seal (*Arctocephalus pusillus doriferus*) breeding colonies. The majority of colonies (12 of 13) occur within Bass Strait, between mainland Australia and Tasmania. The present study was conducted at Kanowna Island (open star), located in north-central Bass Strait. The black dashed line indicates the edge of the continental shelf (200 m bathymetric contour).
Chapter 1: General overview

Arnould and Hindell 2001; Arnould and Kirkwood 2007; Littnan et al. 2007; Kirkwood and Arnould 2011; Hoskins and Arnould 2013; Hoskins and Arnould 2014; Arnould et al. 2015; Hoskins et al. 2015a). Comparatively fewer studies have investigated the ecology of Australian fur seal males, with information on male dive behaviour previously derived from only a single animal (Hindell and Pemberton 1997; Kirkwood et al. 2006; Kernaléguen et al. 2015a). This may be problematic for our overall understanding of the species’ ecology, due to the extreme sexual size dimorphism between males and females and contrasting reproductive constraints on the foraging behaviour of each sex. As males represent a considerable proportion of the species’ biomass a thorough understanding of the foraging behaviour and diet of males is integral to a comprehensive understanding of the overall ecology of the species.

Research aims and thesis overview

The overall aim of this thesis was to investigate the foraging ecology of male Australian fur seals and place this within the broader context of pinniped ecology. More specifically, the thesis aimed to investigate the fine-scale foraging behaviour (habitat use and dive behaviour) of male Australian fur seals and their dietary composition and to assess niche segregation with females of the species. To achieve these aims, behavioural data were collected using bio-logging technologies (GPS and dive recorders) and analysed in combination with the use of dietary information obtained from blubber fatty acids.
Chapter 1: General overview

This thesis is structured with the central data chapters (Chapters 2-5) reporting on specific studies that have been published or submitted for publication in peer reviewed journals. The current chapter (Chapter 1) provides an overview of pinniped ecology and our current knowledge of the Australian fur seal, while the data chapters that follow address more specific questions.

Our current understanding of male habitat use and dive behaviour suggests that male Australian fur seals are shallow divers, seemingly restricted to forage within the edge of the continental shelf (Hindell and Pemberton 1997; Kirkwood et al. 2006; Kernaléguen et al. 2015a). This challenges the hypothesis that male life history promotes dispersal (Staniland 2005) and that a larger body size leads to an increased diving capacity (Weise et al. 2010). Due to limited sampling it remains unclear if male Australian fur seals exhibit temporal or individual variability in their dive behaviour or spatial distribution (i.e. remain to forage within Bass Strait throughout the year). The year-round spatial distribution and diving behaviour of male Australian fur seals is addressed in Chapter 2. Specifically, Chapter 2 investigates the seasonal variation in movement patterns and inter- and intra-individual variation in the diving behaviour of male Australian fur seals.

Several studies have indicated that female Australian fur seals exhibit foraging ‘hotspots’ within Bass Strait (Arnould and Kirkwood 2007; Kirkwood and Arnould 2011; Hoskins et al. 2015a). In benthic habitats, site fidelity may occur if prey is associated with small-scale features, such as reefs, that may enhance localised productivity (Hixon and Beets 1993; Russell et al. 2014). Site fidelity is assumed to be beneficial to individuals because it facilitates direct travel to foraging areas and
familiarity with a foraging area may confer energetic advantages over the lifetime of an individual. Chapter 3 aims to investigate the occurrence of fidelity within male Australian fur seals. Specifically, Chapter 3 investigates spatial consistency of males within Bass Strait and examines the intrinsic parameters that might affect fidelity within males.

To date, most studies investigating the dietary composition of Australian fur seals examine it at the population level (e.g. Gales and Pemberton 1994; Hume et al. 2004; Littnan et al. 2007; Kirkwood et al. 2008; Deagle et al. 2009), without taking into consideration inter-individual variation or sex-based resource partitioning. Chapters 4 and 5 utilise blubber fatty acids to investigate the dietary composition of Australian fur seals. Given that body-size differences may lead to variation in dietary composition between males and female Australian fur seals, Chapter 4 specifically addresses sex-based niche segregation. Male resource use may also vary according to fluctuations in intrinsic (e.g. growth and reproduction) and extrinsic factors (e.g. prey availability and intra-specific competition) therefore Chapter 5 aims to investigate inter-individual and temporal differences within male diet.

The final chapter (Chapter 6) summarises the key findings of Chapters 2-5 and discusses the results of these chapters in the broader ecological context of niche segregation and individual variation in behaviour and diet. Chapter 6 also presents several key areas for future research.
Chapter 2: Habitat use and diving behaviour of male

Australian fur seals

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Abstract

Marine predators play an important role in the structure and function of ecosystems. Knowing where marine predators forage and how individual strategies vary therefore has important implications for our understanding of ecosystem processes and for species management and conservation. However, within fur seals and sea lions, knowledge of foraging ecology is typically biased towards adult females and data on other critical life history stages are often lacking. This study investigated the habitat use and dive behaviour of 16 male Australian fur seals (*Arctocephalus pusillus doriferus*) at Kanowna Island (39°10′S, 146°18′E) located in northern Bass Strait, south-eastern Australia during 2013 and 2014. Winter behaviour (inferred from location and dive data) indicates that male Australian fur seals, like females, are predominantly benthic foragers which have a restricted foraging range limited to the shallow continental shelf of Bass Strait (60-80 m). However, in late spring and summer some males travelled away from central Bass Strait and foraged in deeper waters (>200 m) along the edge of the continental shelf. These movements occurred immediately prior to the breeding season suggesting continental shelf slope waters are also important habitat for male Australian fur seals at a time of great nutritional importance. Strong inter- and intra-individual variation in diel patterns of diving were also apparent, with little spatial overlap in the core foraging range of each strategy. This variation may reflect individuals using alternate strategies to target specific prey in different areas of Bass Strait, or may be due to competitive exclusion by conspecifics.
Introduction

Marine predators have a significant influence on the structure and function of oceanic ecosystems, through the consumption of large amounts of prey biomass and the redistribution of nutrients and other resources across habitat boundaries (Estes et al. 2016). As a consequence, knowing where marine predators forage and how individual strategies vary, enables us to better understand ecosystem processes and has important implications for the management and conservation of marine predator populations (Lomnicki 1978; Costa et al. 2010a). In the marine environment, the spatial and temporal distribution of prey resources are highly variable (Harris et al. 1988; Perry et al. 2005) and predators must employ a variety of foraging strategies in order to obtain sufficient resources for survival, growth and reproduction (Boyd et al. 1994; Costa et al. 2010a). For example, in times of lower prey availability, predators may alter their foraging areas to more profitable habitats, switch their diet to more abundant prey resources, or alternatively, increase their foraging effort (Georges et al. 2000; Hall-Aspland et al. 2005; Womble and Sigler 2006; Thomas et al. 2011; Kuhn and Costa 2014; Blanchet et al. 2015; O'Toole et al. 2015; Thorne et al. 2015). However, the foraging behaviour of marine predators is often difficult to observe, largely due to their cryptic nature and with such behaviour usually occurring at depth (Boyd et al. 1994). Consequently, data on animal movements and diving behaviour provided by animal-borne data loggers allow us to infer their habitat use (Austin et al. 2004; Pinaud et al. 2005; Mattern et al. 2007; Fuller et al. 2008; Kuhn et al. 2010; Banks et al. 2014).
Otariid seals (fur seals and sea lions) are large marine predators that have been the focus of significant tracking effort using animal-borne data loggers (e.g. Campagna et al. 2001; Page et al. 2005a; Weise et al. 2010; Chilvers et al. 2013; Kuhn and Costa 2014; Arthur et al. 2015). Otariid seals display some of the most extreme sexual dimorphism of any mammal, with males weighing up to four times the mass of females (Staniland 2005). Consequently, males are important consumers of prey biomass and therefore potentially play a significant role in trophic dynamics (Estes et al. 2016). In addition, unlike lactating females that are obligate central place foragers due to the need to provision nutritionally dependent offspring, male otariids play no role in parental care (Bonner 1984; Gentry et al. 1986). Therefore, males are less restricted than lactating females in their foraging range, giving them access to a wider range of habitats and niches and potentially a greater capacity to connect ocean ecosystems over large spatial scales (Boyd et al. 1998; Estes et al. 2016). Yet, despite otariids being the subject of considerable tracking effort, our understanding of otariid foraging ecology is largely derived from ecological studies that examine lactating females (e.g. Thompson et al. 1998; Boyd et al. 2002; Harcourt et al. 2002; Call et al. 2008; Lowther et al. 2011; Baylis et al. 2015). Comparatively few studies have investigated the foraging ecology of male otariids, presumably because their larger body size makes them difficult to capture and device recovery is often unreliable because males are not constrained to a central place (Campagna et al. 2001; Page et al. 2005a; Weise et al. 2006; Lowther et al. 2013; Baylis et al. 2016).

The Australian fur seal (*Arctocephalus pusillus doriferus*) is the largest of all fur seal species with males and females weighing on average 279 and 76 kg, respectively.
Chapter 2: Habitat use and diving behaviour of male Australian fur seals

(Warneke and Shaughnessy 1985; Arnould and Warneke 2002). Its breeding
distribution is restricted almost entirely to islands within Bass Strait (Kirkwood et al.
2010), the shallow (mean depth between 50 – 70 m) continental shelf region between
mainland Australia and Tasmania (Sandery and Kämpf 2007). Despite that Bass
Strait is generally recognised as a nutrient poor region of low primary productivity, it
is influenced by numerous oceanographic features that feed it with seasonal
secondary productivity (Gibbs et al. 1986; Sandery and Kämpf 2007; Kämpf 2015).
With an estimated population of ca. 120,000 individuals (Kirkwood et al. 2010), the
Australian fur seal is an important consumer of marine resources in south-eastern
Australia.

Numerous studies on the foraging ecology of adult female Australian fur seals
reveal they feed almost exclusively on benthic/demersal prey, during foraging trips
that are typically restricted to the continental shelf of Bass Strait (Arnould and
Hindell 2001; Arnould and Kirkwood 2007; Kirkwood and Arnould 2011; Hoskins
and Arnould 2014; Hoskins et al. 2015a). To date, only a few studies have
investigated the foraging behaviour of male Australian fur seals and information on
male dive behaviour is derived from a single animal (Hindell and Pemberton 1997;
Kirkwood et al. 2006; Kernaléguen et al. 2015a). These have suggested that the
foraging range of males is also limited to the continental shelf and that male
Australian fur seals are relatively shallow divers (mean depth 20 ± 14.3m; max depth
102 m). However, information on whether diving behaviour varies between
individuals, spatially or temporally is not known.
Furthermore, with several studies having documented the presence of intra- and inter-individual variation in habitat use, diving behaviour and dietary specialisations within adult female Australian fur seals (Arnould et al. 2011; Hoskins and Arnould 2014; Kernaléguen et al. 2015b), individual differences in foraging strategies may also be apparent within males and act to reduce the pressures of intra-specific competition (Kernaléguen et al. 2012). Given that male Australian fur seals likely play a significant role in the trophic dynamics and relationships of the Bass Strait marine region, the aims of the present study were to investigate: 1) the spatial distribution and diving behaviour of male Australian fur seals; 2) how behaviour varies temporally (seasonally and diel); and 3) the inter- and intra-individual variation in male foraging behaviour.

Materials and methods

Animal handling and instrumentation

The study was conducted at the Australian fur seal colony on Kanowna Island (39°10’S, 146°18’E), in central northern Bass Strait, south-eastern Australia which has an annual pup production of ca. 3,400 (Kirkwood et al. 2010). Fieldwork was carried out in June-July of 2013 and 2014. A total of 16 males were instrumented with biologging equipment over both years of the study (2013 \( n = 6 \); 2014 \( n = 10 \)). Data from males instrumented in 2013 were used in a previous study (Kernaléguen et al. 2015a). Two males were equipped with devices in both years (Seal IDs 4/9 and 2/16). Males were chemically restrained using a 1:1 mixture of tiletamine-zolazepam (Zoletil, Virbac, France; ca 1.5 mg·kg\(^{-1}\) of estimated mass) remotely administered via
darts propelled by a CO$_2$ powered tranquilliser gun (Dan Inject JM Standard; Baylis et al. 2014). Anaesthesia was maintained during the procedure using isoflurane delivered via a portable gas vaporizer (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia).

Each seal was instrumented with a satellite-linked GPS-dive behaviour data logger (Mk10-AF Splash Tag, Wildlife Computers, Redmond, WA, USA), glued to the dorsal fur along the mid-line, just posterior to the scapula, using quick setting two-part epoxy (RS Components, Corby, UK). Devices were programmed to record depth sensor data at 5 s intervals and GPS location every 10 min. These data were transmitted to the CLS ARGOS system with transmission schedules being optimised to maximise the number of uplinks (Costa et al. 2010b). Specifically, at sea the devices were programmed to transmit GPS and dive behaviour messages every 90 s, while on land they were programmed to transmit every 30 s over six hour intervals when satellites were overhead. In addition to device instrumentation, morphometric data (standard length, axis, axillary girth and flipper length; ± 0.5 cm) and biological samples (blubber biopsy, whisker and blood) were taken for use in concurrent studies. Mass and age were estimated from previously determined allometric relationships between body mass and morphometric measurements for the species (Arnould and Warneke 2002). Upon completion of handling, individuals were monitored as they recovered from anaesthesia and left to resume normal behaviours.

After a minimum period of 2 months, individuals were recaptured opportunistically when they were present at the colony and their devices removed by cutting the fur beneath the glue. From these individuals, full archived GPS and dive
behaviour data for the duration of the deployment were downloaded. For individuals that could not be recaptured, the devices continued to transmit summary data until the battery failed or the device moulted off. To assess how representative the CLS Argos transmitted dive behaviour data were, the number and characteristics of dives from transmissions were compared to that obtained from the full archival record, for those animals that were recaptured.

Data processing and analyses

GPS location data were first filtered using a basic speed filter (max swim speed of 8 m·s\(^{-1}\)) to remove any erroneous locations (McConnell et al. 1992) and then linearly interpolated every 10 min in the R package *trip* (Sumner 2013). For each austral season (winter: Jun – Aug; spring: Sep – Nov; summer: Dec – Feb) the at-sea spatial distribution was quantified using 95% (Home Range; HR) and 50% (Core Range; CR) utilisation distribution probabilities (UD). Each seal contributed equally to the overall UD calculation for each season (i.e. the UD for each seal was standardized to a value of 1). Overlap in UD between each season was calculated using the utilisation distribution overlap index (UDOI; Fieberg and Kochanny 2005). Smoothing parameters for the UD were calculated using the *ad hoc* method (Worton 1989) and bathymetry data were used as a habitat grid to avoid unrealistic probabilities spanning across land. Spatial analyses were conducted within the R package *adehabitatHR* (Calenge 2006).
Chapter 2: Habitat use and diving behaviour of male Australian fur seals

Due to device malfunction, only the maximum depth and dive frequency were available in the satellite-transmitted dive data from animals that were not recaptured. Hence, with the exception of these two variables, analyses on diving behaviour were restricted to individuals for which the full archive was available. Data from these was corrected for any drift in depth readings and subsequently summarised for basic per dive metrics (dive duration, post-dive interval, dive depth, descent and ascent rate and bottom time) using the diveMove package in R (Luque and Fried 2011).

Consistent with prior Australian fur seal studies, a dive was defined to be > 10 m in depth (Arnould and Hindell 2001; Hoskins and Arnould 2013). In addition, as female Australian fur seals begin foraging within 2.6 ± 0.4 h of leaving the colony (Arnould and Hindell 2001), a male foraging trip was defined as any continuous at-sea period ≥ 2 h.

A common metric used to differentiate benthic and pelagic dive behaviour is the intra-depth zone (IDZ) which assumes that benthic divers will dive repeatedly to the same depth zone (i.e. sea floor) (Tremblay and Cherel 2000). Dives that occurred ± 10% of the maximum depth of the preceding dive were considered benthic, while others that fell outside of this depth zone were considered pelagic dives. Dive frequency (dives·h⁻¹), rate of vertical distance travelled (m·h⁻¹) and the proportion of time at sea spent diving (%) have all been shown to be good indicators of foraging effort in pinnipeds, including Australian fur seals (Boyd et al. 1994; Arnould and Hindell 2001; Hoskins and Arnould 2013) and were determined in the present study.

For archival individuals that were tracked over winter and spring, seasonal
differences in mean dive behaviour (dive duration, descent/ascent rates and dive rate) and trip duration were analysed using paired t-tests.

To investigate any diel preferences in diving, the daily proportion of dives for each two-hourly interval was determined for each seal and then a mean calculated for each austral season that the individual was tracked. For individuals where devices were not recovered, the daily proportion of transmitted dives were used for these calculations. Mean sunrise and sunset times were calculated using the coordinates of central Bass Strait (Geoscience Australia software, Department of Industry and Tourism and Resources, Canberra, Australia). Hierarchical clustering analysis was used to determine whether there were temporal tendencies in diving behaviour. For each individual, the mean of the proportion of dives conducted in 2 h intervals throughout the daily cycle (within each season) were used as the clustering parameter for analysis. To investigate spatio-temporal differences in foraging strategies, a second UD analysis was run on each diel group (diurnal, mixed and nocturnal) and the overlap between groups quantified using UDOI. Unless otherwise indicated all data are presented as mean ± SE

**Results**

Body length and axillary girth measurements indicated that the males were reproductively mature individuals (Warneke and Shaughnessy 1985; Stewardson et al. 1998; Table 2.1). Data were collected across three austral seasons (winter, spring and summer) for an average of 106.7 ± 12.5 d per individual (range 30-187 d), with half of the units (n = 8, from 16 individuals) being recovered to provide the raw
Table 2.1: Deployment summary and basic dive data for 16 male Australian fur seals (*Arctocephalus pusillus doriferus*) tagged at Kanowna Island in winter of 2013 and 2014. Individuals for which archival data were successfully obtained are indicated by an asterix (*). Seals ID’s 4 and 9 and ID’s 2 and 16 in each case represent the same individual tagged in consecutive years. Proportion of benthic dives were estimated based on the intra-depth zone scores for consecutive dives. Mass and age were estimated from body length following Arnould and Warneke (2002).

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Dep. date</th>
<th>Dep. dur. (d)</th>
<th>Length (cm)</th>
<th>Axillary girth (cm)</th>
<th>Est. mass (kg)</th>
<th>Est. Age (y)</th>
<th>No. of dives analysed</th>
<th>Modal max depth (m)</th>
<th>Max depth (m)</th>
<th>Benthic dives (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30/05/2013</td>
<td>76</td>
<td>162.0</td>
<td>123.0</td>
<td>130</td>
<td>4.5</td>
<td>1604</td>
<td>76.5</td>
<td>86.5</td>
<td>92.3</td>
</tr>
<tr>
<td>2*</td>
<td>30/05/2013</td>
<td>68</td>
<td>163.0</td>
<td>115.0</td>
<td>109</td>
<td>4.5</td>
<td>7766</td>
<td>77.0</td>
<td>86.0</td>
<td>75.5</td>
</tr>
<tr>
<td>3*</td>
<td>2/06/2013</td>
<td>51</td>
<td>189.0</td>
<td>126.0</td>
<td>138</td>
<td>7.5</td>
<td>4768</td>
<td>78.5</td>
<td>85.0</td>
<td>87.4</td>
</tr>
<tr>
<td>4*</td>
<td>2/06/2013</td>
<td>52</td>
<td>171.0</td>
<td>139.0</td>
<td>178</td>
<td>5.5</td>
<td>4707</td>
<td>83.5</td>
<td>86.5</td>
<td>90.2</td>
</tr>
<tr>
<td>5*</td>
<td>2/06/2013</td>
<td>149</td>
<td>173.0</td>
<td>121.0</td>
<td>125</td>
<td>5.5</td>
<td>15227</td>
<td>83.0</td>
<td>86.0</td>
<td>83.4</td>
</tr>
<tr>
<td>6</td>
<td>3/06/2013</td>
<td>86</td>
<td>194.0</td>
<td>130.0</td>
<td>150</td>
<td>8.5</td>
<td>1895</td>
<td>84.5</td>
<td>86.5</td>
<td>96.8</td>
</tr>
<tr>
<td>7</td>
<td>28/07/2014</td>
<td>140</td>
<td>167.0</td>
<td>-</td>
<td>-</td>
<td>4.7</td>
<td>4627</td>
<td>82.5</td>
<td>259.5</td>
<td>79.4</td>
</tr>
<tr>
<td>8*</td>
<td>30/07/2014</td>
<td>96</td>
<td>177.0</td>
<td>-</td>
<td>-</td>
<td>5.7</td>
<td>8152</td>
<td>82.5</td>
<td>86.5</td>
<td>92.5</td>
</tr>
<tr>
<td>9*</td>
<td>1/08/2014</td>
<td>90</td>
<td>188.0</td>
<td>134.0</td>
<td>162</td>
<td>6.7</td>
<td>6833</td>
<td>75.0</td>
<td>86.5</td>
<td>82.6</td>
</tr>
<tr>
<td>10</td>
<td>2/08/2014</td>
<td>171</td>
<td>173.0</td>
<td>143.5</td>
<td>193</td>
<td>5.7</td>
<td>2742</td>
<td>84.5</td>
<td>86.5</td>
<td>79.8</td>
</tr>
<tr>
<td>11</td>
<td>2/08/2014</td>
<td>166</td>
<td>152.0</td>
<td>130.0</td>
<td>150</td>
<td>3.7</td>
<td>3834</td>
<td>78.5</td>
<td>221.5</td>
<td>74.2</td>
</tr>
<tr>
<td>12*</td>
<td>2/08/2014</td>
<td>88</td>
<td>179.0</td>
<td>129.5</td>
<td>148</td>
<td>6.7</td>
<td>7681</td>
<td>79.5</td>
<td>83.5</td>
<td>85.6</td>
</tr>
<tr>
<td>13</td>
<td>3/08/2014</td>
<td>187</td>
<td>185.5</td>
<td>157.0</td>
<td>243</td>
<td>6.7</td>
<td>2388</td>
<td>76.5</td>
<td>86.5</td>
<td>95.4</td>
</tr>
<tr>
<td>14</td>
<td>3/08/2014</td>
<td>30</td>
<td>176.0</td>
<td>135.0</td>
<td>165</td>
<td>5.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>15</td>
<td>3/08/2014</td>
<td>172</td>
<td>207.0</td>
<td>-</td>
<td>-</td>
<td>10.7</td>
<td>2036</td>
<td>70.5</td>
<td>283.5</td>
<td>84.0</td>
</tr>
<tr>
<td>16*</td>
<td>5/08/2014</td>
<td>85</td>
<td>165.5</td>
<td>118.0</td>
<td>117</td>
<td>5.7</td>
<td>9601</td>
<td>84.0</td>
<td>86.5</td>
<td>65.5</td>
</tr>
</tbody>
</table>

| Mean ± SE | 106.7 ± 12.5 | 176.4 ± 3.5 | 130.8 ± 3.1 | 154.5 ± 9.9 | 6.1 ± 0.4 | 5590.7 ± 956.6 | 79.8 ± 1.1 | 119.8 ± 18.3 | 85.6 ± 2.4 |
archival data. Of the remaining devices, one (seal ID 14) did not transmit diving behaviour data and thus was excluded from dive related analyses. The proportion of total archived dives for which information was transmitted was $32.1 \pm 5.3\%$ (range 12.1-55.7%) and there was no temporal bias (time of day or season) in the transmitted data. No difference in mean dive depth was detected between the archival and transmitted dive data ($t_{7} = -1.20, P > 0.05$). Consequently, the transmitted data (dive depth and dive frequency) obtained from individuals that were not recaptured (i.e. no archival record) were considered representative of the dive behaviour and used in dive related analyses.

**Spatial habitat use**

A total of 26,688 GPS locations were obtained across the 16 deployments (1,668 ± 227 per individual). On average, individuals travelled a total of 3,561 ± 405 km (range 770-6,251 km) over the sampling period, covering 34.2 ± 1.9 km per day. All of the individuals returned to Kanowna Island at least once (4.2 ± 1.0 times) over the study period. While the majority of the individuals (94%) frequented other colonies and haul-out sites (2.9 ± 0.3 sites), one individual (seal ID 12) returned only to Kanowna Island from where it made 12 foraging trips to approximately the same location 50-80 km to the south-west.

The foraging trips of the eight recaptured individuals for which complete archive data records were available, lasted on average 3.1 ± 0.2 d. There was no significant difference in the mean trip duration between winter and spring ($t_{4} = 2.24, P > 0.05$, Table 2.2; archival data for summer were not available). The longest continuous at-sea period lasted 11.5 d in spring (seal ID 16: 6/Oct/14 – 18/Oct/14). The kernel UD
Table 2.2: Dive parameters for male Australian fur seals for which archived dive records were available, values are presented as mean ± SE. ‘W’ and ‘S’ refer to winter and spring, respectively.

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Trip dur (d)</th>
<th>Dive dur (min)</th>
<th>Descent rate (m·s⁻¹)</th>
<th>Ascent rate (m·s⁻¹)</th>
<th>Prop of time spent diving (%)</th>
<th>Dive freq. (no./h⁻¹)</th>
<th>Dive rate (m·h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>3.0 ± 0.4</td>
<td>2.9 ±&lt;0.1</td>
<td>1.36 ±&lt;0.01</td>
<td>1.45 ±&lt;0.01</td>
<td>35.0 ± 7.3 ± 939.4</td>
<td>- ± -</td>
<td>- ± -</td>
</tr>
<tr>
<td>3</td>
<td>5.0 ± 0.7</td>
<td>4.2 ±&lt;0.1</td>
<td>1.27 ±&lt;0.01</td>
<td>1.29 ±&lt;0.01</td>
<td>39.4 ± 7.3 ± 739.2</td>
<td>- ± -</td>
<td>- ± -</td>
</tr>
<tr>
<td>4</td>
<td>4.3 ± 0.9</td>
<td>4.3 ±&lt;0.1</td>
<td>1.54 ±&lt;0.01</td>
<td>1.55 ±&lt;0.01</td>
<td>40.6 ± 7.3 ± 876.9</td>
<td>- ± -</td>
<td>- ± -</td>
</tr>
<tr>
<td>5</td>
<td>3.3 ± 0.7</td>
<td>4.0 ±&lt;0.1</td>
<td>1.47 ±&lt;0.01</td>
<td>1.51 ±&lt;0.01</td>
<td>46.7 ± 7.3 ± 977.5</td>
<td>7.0 ± 6.8</td>
<td>931.3 ± 11.3</td>
</tr>
<tr>
<td>6</td>
<td>2.8 ± 1.4</td>
<td>4.4 ±&lt;0.1</td>
<td>1.39 ±&lt;0.01</td>
<td>1.47 ±&lt;0.01</td>
<td>31.7 ± 7.3 ± 681.0</td>
<td>4.3 ± 6.4</td>
<td>768.3 ± 11.3</td>
</tr>
<tr>
<td>9</td>
<td>4.8 ± 0.6</td>
<td>3.9 ±&lt;0.1</td>
<td>1.51 ±&lt;0.01</td>
<td>1.67 ±&lt;0.01</td>
<td>39.2 ± 7.3 ± 863.6</td>
<td>6.0 ± 7.2</td>
<td>1211.6 ± 11.6</td>
</tr>
<tr>
<td>12</td>
<td>3.1 ± 0.3</td>
<td>4.5 ±&lt;0.1</td>
<td>1.25 ±&lt;0.01</td>
<td>1.39 ±&lt;0.01</td>
<td>44.4 ± 7.3 ± 917.9</td>
<td>5.9 ± 5.9</td>
<td>893.3 ± 11.3</td>
</tr>
<tr>
<td>16</td>
<td>5.7 ± 0.7</td>
<td>3.0 ±&lt;0.1</td>
<td>1.50 ±&lt;0.01</td>
<td>1.48 ±&lt;0.01</td>
<td>34.0 ± 7.3 ± 911.0</td>
<td>6.3 ± 6.3</td>
<td>750.0 ± 11.3</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>3.7 ± 0.3</td>
<td>3.8 ±&lt;0.1</td>
<td>1.4 ±&lt;0.1</td>
<td>1.5 ±&lt;0.01</td>
<td>38.9 ± 7.3 ± 863.3</td>
<td>6.5 ± 6.2</td>
<td>910.9 ± 82.9</td>
</tr>
</tbody>
</table>
analysis revealed that the winter foraging range of all males remained within the continental shelf of Bass Strait (Fig. 2.1). This restricted foraging range was also evident for the majority of spring. However, in the period immediately prior to the breeding season (late spring), three males (seal ID’s 7, 11 and 15) dispersed from central Bass Strait and foraged along the edge of the continental shelf either side of Tasmania, where they remained until their devices stopped transmitting. During the breeding season, one individual (seal ID 13) established a breeding territory at Kanowna Island (*personal observation*). The GPS of another male (seal ID 10) revealed it spent the majority of its time hauled out at Seal Rocks (38°30’S, 145°10’E), where it is also presumed to have held a territory during the breeding period. Post-breeding movements showed that these two individuals remained to forage within Bass Strait until their devices stopped transmitting.

**Dive behaviour**

A total of 64,735 dives were obtained from devices that were recovered (*n* = 8; 8,092 ± 1177) and used for analysis. Mean dive durations per individual ranged between 2.7 ± 0.9 – 4.4 ± 0.8 min with the longest recorded dive lasting 9.8 min (seal ID 8; Table 2.1). No seasonal difference in mean dive duration was detected (*t*<sub>4</sub> = 1.0, *P* >0.05). All individuals displayed predominantly benthic diving behaviour, with 85.6 ± 2.4% (range: 65.5 – 96.8%) of dives falling within the IDZ of the preceding dive (Fig. 2.2; Table 2.2). In some cases, shorter than normal dives, followed by subsequent shallow dives near the surface were apparent (Fig. 2.2B). This behaviour
Figure 2.1: The location of Kanowna Island (Panel A; filled orange circle) and other Australian fur seal breeding colonies (A; open circles) within the south-eastern Australian region. The 95% home range (HR: light blue shading) and 50% core range (CR: dark blue) utilisation distribution probabilities for winter 2013 (B; n = 6), winter 2014 (C; n = 10), spring 2014 (D; n = 10) summer 2014 (E; n = 5). The HR and CR utilisation distribution overlap index between each season is reported in the corresponding panel. Grey lines indicate bathymetry (in 20 m intervals) to the edge of the continental shelf.
Figure 2.2: A representative dive profile of a typical foraging trip (mean = 3.1 ± 0.1 d; max = 11.5 d; Panel A) a male Australian fur seal. Dives were primarily benthic (85.3 ± 3.6%) across all individuals (modal max depth = 83.5 m), lasting on average 3.8 ± 0.1 min. In some cases, shorter than normal dives, followed by subsequent shallow dives near the surface was apparent (B; highlighted by red bar) and may be indicative of handling large prey such as squid, octopus, or stingrays at or near the surface (as seen using animal borne cameras on female Australian fur seals; Volpov et al. 2015).
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may be indicative of handling large prey at or near the surface as was previously observed using animal borne cameras on female Australian fur seals (Volpov et al. 2015). The modal maximum depth per individual ranged from 70.5 – 84.5 m (79.8 ± 1.1 m; Table 2.1). Throughout the winter tracking period of both 2013 and 2014, the maximum depth achieved was 86.5 m (86.1 ± 0.2 m and 85.2 ± 0.7 m, respectively). This depth was consistent across 70% of individuals tracked throughout spring and summer (maximum depth 85.6 m and 85.5 m, for spring and summer, respectively).

However, three of the individuals (seal ID’s 7, 11 and 15) for which transmitted data were obtained, achieved depths ≥ 220 m along the edge of the continental shelf during the same period (maximum depth 283.5 m; Table 2.1). Two of these individuals (seal ID’s 7 and 15) appeared to switch to a predominantly pelagic foraging mode, with only 44.5% and 48.7% of dives considered to be benthic, respectively.

On average, individuals spent 39.3 ± 2.1 % of their time at sea diving (mean range 28.5 – 47.9 %) and made 6.2 ± 0.2 dives per hour (Table 2.2). Vertical travel rates showed comparatively little variation between individuals, ranging from 681 – 977.5 m·h⁻¹ in winter and 750-1211.6 m·h⁻¹ in spring, with no difference detected between seasons (t₄ = -0.47, P > 0.05, Table 2.2). Mean descent (1.40 ± < 0.01 ms⁻¹) and ascent (1.46 ± < 0.01 ms⁻¹) rates were nearly identical between seasons, (t₄ = -1, P = >0.05 in both cases) and males showed relatively little individual variation with mean values for individual males ranging from 1.20 – 1.54 and 1.29 – 1.68 m·s⁻¹, for descent and ascent rates, respectively.
Hierarchical clustering of the dissimilarity matrix created from the 2 hourly mean proportion of dives produced a dendrogram of 3 well-defined groups based on their seasonal preferences of diving: nocturnal, no preference and diurnal (Fig. 2.3). Across all individuals and seasons there were 12 (40%) instances where nocturnal preferences of diving were detected, while the remaining 60% were clustered evenly across the nocturnal diving group, or the group that did not display a preference for time of day (30% each). In the winter and spring months the majority of individuals preferred to dive during the night, with nocturnal diving preferences recorded for 40% and 60% of individuals, respectively (Fig. 2.3B). In addition, diurnal diving preferences were observed to be the least prevalent strategy during these months with only 27% of individuals recorded diving during the day in winter and 20% in spring. In contrast to the behaviours observed in winter and spring, a preference for nocturnal diving was not observed at all during the summer, with 66% of the males tracked showing a preference for diurnal diving during this time (Fig. 2.3B).

The majority of males (80%) switched their foraging strategies between seasons (Figs. 2.3B and 2.4), while only one seal (seal 7) was consistent in its foraging strategy across all three seasons. The 95% HR UD analysis revealed that all three diel foraging strategies occurred throughout large areas of central Bass Strait, however, the 50% CR UD contour suggested that there was little overlap in core area use between the three strategies (Fig. 2.5).
Figure 2.3: Inter-individual variation within the diving strategies of male Australian fur seals. Representative examples (A) of the mean frequency of dives per day (% ± SE). Clustering analysis (B) revealed 3 distinct diel strategies: nocturnal (red), no preference (green) and diurnal (blue). Mean day and night hours are indicated by background shading.
Figure 2.4: *Intra-individual variation in the diving strategies of male Australian fur seals.* The mean frequency of dives (% ± SE) per day for each individual. The colour of bars represents the foraging strategy determined by the cluster analysis (blue bars represent a diurnal diel strategy, while green and red bars represent mixed and nocturnal diel strategies, respectively). Mean day and night hours for each season are indicated by grey background shading.
Figure 2.5: The 95% home range (HR) and 50% core range (CR) utilisation distribution probabilities for each diel diving strategy: diurnal (Panel A; blue) mixed (B; green) and nocturnal (C; red). The overlap between each diel strategy is presented in panels D (95% HR) and E (50% CR), with the 95% HR UDOI reported for each of the corresponding strategies (the overlap for the 50% UD was < 0.01 in all cases). Grey lines indicate bathymetry (in 20 m intervals to the edge of the continental shelf).
Discussion

Habitat use

Throughout the austral winter and most of spring, male Australian fur seals typically foraged benthically and their movements were restricted to the shallow continental shelf of Bass Strait. The findings of the present study differ from the wide ranging movements of male otariids that are characterised by a pelagic foraging mode (Page et al. 2006; Weise et al. 2010). However, these results are similar to other male otariids that have a predominantly benthic foraging mode (Lowther et al. 2013; Baylis et al. 2016). This suggests that the foraging range of male otariids are influenced by their foraging mode and available habitat. These findings provide further evidence to suggest that, despite the available continental shelf habitat adjoining Bass Strait, male Australian fur seals have a foraging range that is largely restricted to Bass Strait (Kirkwood et al. 2006; Kernaléguen et al. 2015a). There are a number of reasons why male Australian fur seals may choose to remain within the continental shelf of Bass Strait throughout the winter period. Despite the region being considered nutrient poor (Gibbs et al. 1986; Sandery and Kämpf 2007; Kämpf 2015) the benthic habitat of Bass Strait may still provide sufficient prey resources to support the Australian fur seal population during winter (Arnould and Hindell 2001; Hoskins et al. 2015a; Kernaléguen et al. 2015a). Additionally, Bass Strait has many offshore islands dispersed throughout the region and that are devoid of any land-based predators. The males of the present study visited many of these land locations in between foraging trips. By hauling out at these land sites, male Australian fur seals are able to rest in relatively close proximity to their foraging grounds within Bass
Strait, consequently, minimising their at-sea energetic costs and reducing their risk of predation (Boyd et al. 1998; Arnould and Kirkwood 2007).

The only times adult males in the present study travelled further afield and ventured outside of Bass Strait was in late spring and during summer. The spring movements of male Australian fur seals away from the foraging areas that are in close proximity to the breeding colony may reflect these areas being suboptimal for larger males at a time of great nutritional importance. Adult male otariid seals fast throughout the breeding season (up to 60 d) while they maintain a territory and, consequently, lose a significant proportion of their body mass (Stirling 1983; Warneke and Shaughnessy 1985). Hence, for territorial males, foraging conditions immediately prior to the breeding season (late spring) are critical for them to acquire the reserves necessary for territorial tenure and to replenish their body mass after the extended fasting during the breeding period (Staniland and Robinson 2008). As a consequence, prior to the breeding season, territorial Australian fur seal males may be required to search for more productive foraging areas, or seek more energetically profitable prey, located outside of central Bass Strait.

Alternatively, intra-specific competition for resources close to the breeding colony, may cause a local depletion of resources (Ashmole 1963; Boyd et al. 2002; Weise et al. 2006). Therefore, the foraging efficiency of males may be enhanced by travelling further away from foraging areas that are within close proximity to breeding colonies and likely reduce intra-specific competition with adult female Australian fur seals. Although on a much broader scale, other male otariid species, such as Californian sea lions (Zalophus californianus) and Antarctic fur seals
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(*Arctocephalus gazella*), have been shown to travel great distances (>1000 km) in order to forage in more productive waters after the breeding season, while females remain to forage in areas closer to the breeding colony (Boyd et al. 1998; Weise et al. 2006; Weise et al. 2010). Indeed, three males that did not attend a breeding colony over the breeding season, left central Bass Strait and foraged in areas along the coast of Tasmania known to support large aggregations of seabirds and other marine mammals (Brothers and Pemberton 1990; Brothers et al. 1998).

*Dive behaviour*

Throughout winter and spring, the modal dive depth of the males (72.5 – 84.5 m) was consistent with the depth of the sea floor within Bass Strait. The only previously available information on the dive behaviour of male Australian fur seals, was from a single sub-adult individual, whose data may be more typical of transient behaviour as he returned to forage at the salmon farm in southern Tasmania where he was initially captured (Hindell and Pemberton 1997). Consequently, direct comparisons with the current study are difficult. However, as previously stated, the results of the present study revealed that male Australian fur seals, like adult females, are predominantly benthic foragers (Arnould and Hindell 2001; Hoskins and Arnould 2013; Hoskins and Arnould 2014; Hoskins et al. 2015b). Such benthic diving within fur seals is rare and more typical of sea lion behaviour (Arnould and Costa 2006). The benthic foraging mode of the Australian fur seal is likely due to the relatively low productivity of Bass Strait during winter (Sandery and Kämpf 2007; Kämpf 2015), where the distribution of suitable prey resources occurs predominantly along the
benthos of the shallow continental shelf in which they forage (60-80 m; Arnould and Hindell 2001). However, during the spring and summer seasons the number of pelagic dives increased, as individuals dove to much greater depths (>200 m) along the edge of the continental shelf where they could access temporally abundant prey resources (Hume et al. 2004; Kirkwood et al. 2008; Hoskins and Arnould 2014).

Measures of dive effort within the male Australian fur seals (proportion of time diving and vertical travel rates) were similar to those reported for female Australian fur seals (ca 41% and 997-1133 m·h$^{-1}$, for mean proportion of time diving and range of vertical travel rates, respectively; Arnould and Hindell 2001; Hoskins and Arnould 2013). These results reveal that in general benthic foraging Australian fur seals, irrespective of sex, will spend substantially more time diving and have greater travel rates than pelagic fur seals (15-24 % of their time diving; Arnould and Costa 2006) and the pelagic foraging Californian sea lion (32%; Feldkamp et al. 1989). However, the dive effort of Australian fur seals is similar to other benthic foraging sea lions (44-58%; Gentry et al. 1986; Georges et al. 2000; Arnould and Costa 2006). Therefore, the increased effort displayed by Australian fur seals may reflect benthic habitats being of low prey abundance, but spatially and temporally predictable (Arnould and Hindell 2001; Arnould and Costa 2006).

Mean dive durations for male Australian fur seals were greater than reported for other smaller fur seals and more typical of larger sea lions (e.g. Boyd et al. 1991; Harcourt et al. 1995; Georges et al. 2000; Page et al. 2005a; Arnould and Costa 2006; Waite et al. 2012). In addition, male Australian fur seals have longer mean dive durations and longer foraging trip durations than female conspecifics (male 2.7 – 4.4
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min and 3.1 d, compared to 2.9 – 3.1 min and 2.9 d for females, respectively; Arnould and Hindell 2001; Hoskins and Arnould 2013). Similar sex-related differences have been observed in New Zealand fur seals (*Arctocephalus forsteri*), where males have longer dive durations than females and in southern sea lions (*Otaria flavescens*), where males will spend longer at sea than their female conspecifics (Campagna et al. 2001; Page et al. 2005a). Sex differences in dive duration are consistent with an increase in physiological capacity of larger animals due to their body mass (Costa 1991; Weise and Costa 2007; Weise et al. 2010).

Within Australian fur seals, males and females may forage in the same areas of Bass Strait and to the same depth throughout the same temporal periods. However, an increase in the foraging ability of males may enable them to search for longer, in order to pursue more cryptic prey resources and, thereby leading to sexual segregation in diet, as has been previously reported (Kernaléguen et al. 2015a).

There was strong inter-individual variation in temporal patterns of diving and some evidence to suggest that the core area use of these strategies differed in their location. Diel variation is a common feature in the diving behaviour of pelagic foraging otariids, as it is typically associated with diel movements of vertically migrating prey (Boyd and Croxall 1992; Boyd et al. 1994; Harcourt et al. 1995; Georges et al. 2000). However, it appears to be less apparent in benthic foraging otariids where cryptic prey species do not normally migrate (Costa and Gales 2003). Furthermore, few studies have examined individual or spatial variation within such diel strategies of otariids, with most examining temporal patterns in dive behaviour at the population level (Boyd et al. 1991; Lea et al. 2002). Australian fur seals are
considered opportunistic foragers that consume a broad range of fish, cephalopods and elasmobranchs (Littnan et al. 2007; Kirkwood et al. 2008; Deagle et al. 2009; Arnould et al. 2011; Kernaléguen et al. 2015b). However, the inter-individual variation in dive strategies, observed in the present study, may be indicative of individuals targeting specific resources at certain periods of the day or night. Furthermore, the intra-individual (seasonal) variation within the diel strategies may also be indicative of individuals focussing their effort on profitable prey resources that are only temporally abundant within a particular season (Kirkwood et al. 2008; Kernaléguen et al. 2015b). There was also some evidence to suggest spatial separation of foraging strategies within Bass Strait. This was surprising, given Bass Strait is considered both uniform in habitat and the distribution of prey (Gibbs et al. 1986; Gibbs 1992; Sandery and Kämpf 2007; Kämpf 2015). Spatial separation of foraging strategies may reflect male individuals targeting specific prey resources in certain areas of Bass Strait, or may be due to competitive exclusion by conspecifics (Hardin 1960; Van Valen 1965; Banks et al. 2014; Hoskins et al. 2015b). However, the spatial separation of foraging strategies could also be a result of low sample size. Consequently, additional tracking studies are ultimately required to characterise and assess any spatial separation of foraging strategies.

In summary, the present study determined that the foraging behaviour of male Australian fur seals is characterised by a primarily benthic foraging mode over the non-breeding period (winter and early spring). However, there were also strong inter- and intra-individual variation in the temporal patterns of diving, with three dive strategies (diurnal, mixed and nocturnal). Male Australian fur seals predominantly
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foraged within the relatively shallow continental shelf of Bass Strait during winter. However, during the pre-breeding period (late spring) and in summer, some males moved away from central Bass Strait and foraged in deeper waters associated with the continental shelf slope (>200 m). Over this period, the proportion of pelagic dives increased. The pre-breeding movements may be associated with increased energetic demands of males, or seasonal changes in the availability or abundance of preferred prey. The results of the present study highlight the individual and temporal variation that exists within the foraging behaviour of male Australian fur seals, which may have important implications for the future understanding of the trophic dynamics of Bass Strait and surrounding marine regions.
Chapter 3: Foraging site fidelity in male Australian fur seals

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Chapter 3: Foraging site fidelity in male Australian fur seals

Abstract

Optimal foraging theory predicts that predators will employ strategies that maximise their net energetic return. Foraging site fidelity (the re-use of a prior foraging area) is assumed to be beneficial because it facilitates direct travel to foraging areas and familiarity with a foraging area may confer energetic advantages over the lifetime of an animal. In the present study, foraging site fidelity was investigated in 16 male Australian fur seals (*Arctocephalus pusillus doriferus*) from Kanowna Island (39°10’S, 146°18’E), in northern Bass Strait, southeastern Australia, during the winters of 2013 and 2014. Male Australian fur seals used several haul-out sites and made relatively short foraging trips (3.4 ± 0.2 d) to nearby foraging areas. Males behaved liked central place foragers and foraged exclusively on the continental shelf (modal dive depth range: 70.5-85.5 m). Presumably short foraging trips enabled males to minimise the metabolic costs of transit, while maximising their net energetic intake. Site fidelity varied considerably between individuals, however, the degree of site fidelity was unrelated to individual morphology parameters (such as body length). Whereas long term fidelity could make some individuals susceptible to increased environmental variability, the inter-variability in site fidelity reported in the present study suggests that males optimise their foraging efficiency by utilising different foraging areas, ultimately maximising their fitness. Variability in male foraging site fidelity highlights behavioural flexibility within Australian fur seals, which could help to reduce intra-specific competition or be a response to environmental variability.
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**Introduction**

Optimal foraging theory predicts that when searching for prey, predators will make decisions on where, when and how to forage that maximises their foraging efficiency and, ultimately their fitness (Charnov 1976; Pyke et al. 1977; Stephens and Krebs 1987). Within a population, individuals often differ in their morphology and foraging ability, which can lead to ecologically significant variation in their resource use (Bolnick et al. 2003; Araújo et al. 2011; Bolnick et al. 2011). In addition, extrinsic factors, such as inter- and intra-specific competition and seasonal fluctuations in prey resources, can influence the profitability of foraging areas (Ashmole 1963; Birt et al. 1987; Wege et al. 2016). Therefore, prior experience may be utilised by an individual to determine when and where to forage to maximise their foraging efficiency (Orians 1969; Switzer 1993; Bolnick et al. 2003; Piper 2011).

While prey resources in the marine environment are often considered patchy and heterogenous (Weimerskirch 2007), many small scale-marine features, such as reefs, may lead to an increase in localised productivity and congregate prey resources (Hixon and Beets 1993; Bombace et al. 1994; Russell et al. 2014). These static features may provide temporally stable congregations of prey and may therefore be targeted repeatedly by benthically foraging predators (e.g. seals and seabirds) to increase their net energetic gain (Greenwood 1980; Switzer 1993; Piper 2011). Indeed, foraging site fidelity, or the return to a prior foraging area, is frequently reported across a broad range of benthic predators (e.g. Chilvers 2008; Auge et al. 2014; Baylis et al. 2017; Camprasse et al. 2017).
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The Australian fur seal (*Arctocephalus pusillus doriferus*) is a benthic foraging otariid species (seals and sea lions) that is endemic to the south-east Australian region (Arnould and Hindell 2001; Hoskins and Arnould 2013; Hoskins et al. 2015a; see also Chapter 2). It is the largest of all fur seals with males and females weighing on average 279 kg and 76 kg, respectively (Warneke and Shaughnessy 1985; Arnould and Warneke 2002). The species has a breeding range restricted to the continental shelf region of Bass Strait between mainland Australia and Tasmania (Kirkwood et al. 2005; Kirkwood et al. 2010) and studies have shown that males and females remain to forage within Bass Strait over winter (Hoskins et al. 2015b; Kernaléguen et al. 2015a) (Chapter 2). With an estimated population size of *ca* 120,000 individuals (Kirkwood et al. 2010), the Australian fur seal is an important resident consumer of marine resources in the region.

Throughout winter, the productivity of Bass Strait is lower than in the spring and summer months (Sandery and Kämpf 2007). Accordingly, Australian fur seals must utilise optimal foraging strategies, such as site fidelity, that maximise their net energetic intake and reduce foraging costs during this time. As obligate central place foragers over winter, females must regularly return to the same breeding colony to provision their offspring (Arnould and Hindell 2001). As a result, lactating females have shown consistency in their spatial habitat use, behaviour and diet (Arnould et al. 2011; Arnould et al. 2015; Hoskins et al. 2015a; Hoskins et al. 2015b; Kernaléguen et al. 2015b), with several studies linking differences in female behaviour to their morphology and age (Arnould et al. 2011; Arnould et al. 2015; Kernaléguen et al. 2015b).
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However, unlike lactating females, males play no role in parental care and therefore are not constrained to a central place. Consequently, males may have access to a broader range of habitats and niches (Bonner 1984; Boyd et al. 1998) and may not display the same degree of site fidelity as females. Yet despite otariids being the subject of considerable tracking effort, our understanding of otariid ecology, including Australian fur seals, is largely derived from studies that examine lactating females (Thompson et al. 1998; Boyd et al. 2002; Harcourt et al. 2002; Call et al. 2008; Lowther et al. 2011; Baylis et al. 2015). Thus it remains unclear if male Australian fur seals exhibit foraging site fidelity or whether intrinsic factors (such as morphology) contribute to individual variation in male habitat use. Given that males represent a considerable proportion of the species’ biomass (Warneke and Shaughnessy 1985), understanding individual variation in male behaviour and habitat use within the population has important implications for understanding the ecology of the species. The aims of the present study, therefore, were to investigate in male Australian fur seals: 1) individual consistency in fine-scale habitat use (dive behaviour and spatial movements) during winter; and 2) the intrinsic factors that might affect these parameters.

Materials and methods

Animal handling and instrumentation

The study was conducted at the Australian fur seal colony on Kanowna Island (39°10’S, 146°18’E), in central northern Bass Strait, south-eastern Australia (Fig 3.1). The colony has an annual pup production of ca 3,400 (Kirkwood et al. 2010).
Figure 3.1: The location of (A) the study site, Kanowna Island (filled star) in south-eastern Australia. The at-sea movements of 16 male Australian fur seals (Arctocephalus pusillus doriferus) are shown for (B) 2013 ($n = 6$) and (C) 2014 ($n = 10$). Male fur seals visited several haul-out sites / breeding colonies within the Bass Strait region (A; filled black circles). The remaining 5 haul out sites / Australian fur seal breeding colonies in Bass Strait (identified by Kirkwood et al. 2010) were not visited (indicated by open black circles). Grey lines represent bathymetry contours (in 20 m intervals) to the edge of the continental shelf (200 m).
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Fieldwork was conducted in June-July of 2013 and 2014. Adult male Australian fur seals were remotely administered a 1:1 mixture of tiletamine-zolazepam (Zoletil, Virbac, France; \( ca1.5\, \text{mg} \cdot \text{kg}^{-1} \) of estimated mass) via darts propelled by a CO\(_2\) powered tranquiliser gun (Dan Inject JM Standard; Baylis et al. 2014). Anaesthesia was maintained during the procedures using isoflurane delivered via a portable gas vaporizer (Stinger\textsuperscript{TM}, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia).

Each seal (\( n = 6 \) in 2013, \( n = 10 \) in 2014) was instrumented with a Mk10-AF Splash Tag (Wildlife Computers, Redmond, USA), glued to the dorsal fur along the mid-line, just posterior to the scapula, using quick setting two-part epoxy (Accumix 268, Huntsmen, USA). Devices were programmed to collect depth sensor data at 5 s intervals and GPS location every 10 min. These data were transmitted to the CLS ARGOS system with transmission schedules being optimised to maximise the number of uplinks when satellites were overhead. In addition to device instrumentation, morphometric data (standard length; axis length i.e. length on dorsal surface from tip of nose to fore flipper insertion point; axillary girth and length of front right flipper) were recorded using a tape measure (± 0.5 cm) and biological samples (blubber biopsy, whisker and blood) were taken for use in concurrent studies. Species- and sex-specific allometric relationships were used to estimate body mass from axillary girth (Arnould and Warneke 2002). After a minimum period of 2 months, individuals were recaptured opportunistically when they were present at the colony and their devices removed by cutting the fur beneath the glue. From these individuals, full archived GPS and dive behaviour data for the duration of the
deployment were downloaded from the recovered devices. For individuals that could not be recaptured, the devices continued to transmit summary data via CLS ARGOS until the battery failed or the device moulted off.

**Data processing and analyses**

Given male Australian fur seals alter their spatial movements and diving behaviour in late spring (Chapter 2), potentially in preparation for the extended fasting (> 60 d) associated with the breeding season (Stirling 1983; Warneke and Shaughnessy 1985; Staniland and Robinson 2008), analyses in the present study were restricted to winter and early spring (June-October). For data loggers that were recovered (n = 8), dive data were corrected for any potential drift in depth readings in the R package *diveMove* (Luque and Fried 2011) and then summarised for basic per dive metrics (dive duration, post-dive interval, dive depth, descent and ascent rate and bottom time). Due to errors with the transmitted dive data, only the maximum dive depth and dive frequency were available for individuals where the data loggers were not recovered (see Chapter 2 for further details). Hence, analyses of diving behaviour were restricted to individuals where the full dive archive was available. Furthermore, one individual did not transmit any dive data due to device malfunction and, therefore, was not included in dive related analyses. The intra-depth zone (IDZ), a common metric which assumes that benthic divers will repeatedly dive to the same depth zone (i.e. sea floor; Tremblay and Cherel 2000), was used to determine whether dives were benthic or pelagic. Dives that occurred ± 10% of the maximum depth of the preceding dive were considered benthic dives, while dives that fell
outside of this depth zone were considered pelagic. A clustering analysis was run on the mean proportion of dives for each two-hourly interval to determine the diel foraging strategy of an individual (see Chapter 2 for details). Australian fur seals have been observed to spend large periods of time at the surface for purposes other than foraging, such as thermoregulation (JPY Arnould personal communication). Therefore, given the aims of the present study were to investigate foraging behaviour, only dives when animals reached depths of >10 m were included in analyses, which is consistent with prior Australian fur seal studies (Arnould and Hindell 2001; Hoskins and Arnould 2013) (Chapter 2).

All GPS location data were filtered using a basic speed filter (maximum swim speed of 8 m·s\(^{-1}\)) to remove any potentially erroneous locations (McConnell et al. 1992) and then linearly interpolated at 10 min intervals in the R packages `diveMove` and `trip` (Luque and Fried 2011; Sumner 2013). In addition, to limit potential bias from tracks converging around haul-out sites/breeding colonies, a 2 km buffer was placed around all locations that occurred on land (Breed et al. 2011) (Chapter 2). All locations (at sea and on land) that occurred within this buffering zone were excluded from further analyses. A foraging trip was defined as any continuous at-sea period ≥ 2 h (Chapter 2). In order to quantify important foraging areas across the entire tracking period, the 95% home foraging range (HR), 50% core foraging area (CFA) and 25% intensive foraging area (IFA) utilisation distribution probabilities were calculated using the R package `adehabitatHR` (Calenge 2006). Smoothing parameters for the utilisation distribution probabilities were determined using the ad hoc method (Worton 1989) and bathymetry data were used as a habitat grid to avoid unrealistic
probabilities spanning across land. The number of kernel utilisation distributions (HR, CFA and IFA) and areas of CFAs and IFAs were then calculated for each individual.

To examine spatial consistency between foraging trips (i.e. foraging site fidelity) a 10 x 10 km grid was selected \textit{a priori} and placed over the entire foraging range of each individual in the R package \textit{raster} (Hijmans and Van Etten 2012). For each trip, the number of grid cells used that overlapped with all pairwise combinations of other trips were calculated (e.g. trip 1 vs trip 2, trip 1 vs trip 3 and trip 2 vs trip 3) and then divided by the mean number of grid cells used for each trip. The resulting metric (hereafter referred to as ‘site fidelity index’) produced a single score for each individual between 0 and 1, where a value approaching 0 indicates a low degree of spatial consistency (low site fidelity) and a value approaching 1 indicates a high degree of spatial consistency (high site fidelity). Hierarchical clustering, with Ward’s linkage criterion, was used to place seals into one of four groups according to their fidelity scores (low, moderate, high, extreme fidelity). Finally, the site fidelity index will vary depending on the grid cell size used. To investigate how grid cell size influenced site fidelity index values, the site fidelity index was calculated for grid cells of 5 km$^2$, 15 km$^2$ and 25 km$^2$.

\textit{Model specification}

To investigate the influence of intrinsic factors and foraging metrics on site fidelity, four models were applied. The first model was fitted to investigate relationships between site fidelity and individual morphology. The morphometric
variables selected were flipper length, axis length, standard length (proxy for age),
axillary girth (proxy for body condition) and the flipper length/standard length ratio
(a factor which can affect manoeuvrability in seals) (Arnould and Warneke 2002;
Fish et al. 2003). These variables correlate with different foraging behaviours in
female Australian fur seals (Arnould et al. 2011; Arnould et al. 2015; Hoskins et al.
2015b). Collinearity between candidate variables was assessed using variance
inflation factors (VIF) and two variables were removed from the model (flipper
length and axis length) so that all VIF values were < 3 (Zuur and Ieno 2016). This
left standard length, axillary girth and the flipper length/standard length ratio, for
inclusion in the first model, with year as a random effect. The second model
investigated whether site fidelity varied according to diving metrics. Mean maximum
depth was excluded from the model due to collinearity. Modal depth, IDZ score
(proportion of benthic dives) and mean trip duration were included as predictor
variables within the model, with year included as a random effect. A third model
explored whether site fidelity was influenced by dive duration, which was available
for 8 seals from which the tags were recovered. Finally, to determine if site fidelity
was influenced by diel foraging strategy, a fourth model was run, with the diel
strategy considered as a three-level factor (diurnal, mixed and nocturnal). To avoid
model over-specification for models three and four, each covariate was considered as
sole predictor variables within the model, while year was included as a random
effect. Given that only two individuals were sampled in both years (seals 4/9 and
2/16), seal ID was not included as a random effect (Bolker et al. 2009; Zuur et al.
2013).
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For all models, the response variable (site fidelity index) was a proportional score that can include 0 and 1 and, therefore, a beta GLMM model was applied (Zuur et al. 2013). Each model adopted a Bayesian analysis framework with Markov Chain Monte Carlo (MCMC) techniques using JAGS (Plummer 2003) in the R package R2jags (Su and Yajima 2015) to obtain a distribution of each parameter within the model. For each posterior distribution of the four GLMM’s, three Markov chains were applied, each of 100,000 iterations, using only every 100th value (thinning rate), while the first 30,000 values (burn in) were excluded. Diffuse normal priors were used for the regression parameters and diffuse uniform priors were used for the standard deviation parameters. Diagnostic plots were used to assess appropriate mixing of the Markov chains (Jonsen et al. 2013).

Results

Dive behaviour and habitat use

In total, 16 male Australian fur seals were successfully tracked, with two individuals instrumented in both study years (seal IDs 4/9 and 2/16). Males ranged in length from 152 – 207 cm (mean 176.4 ± 3.5 cm) and had a mean axillary girth of 130.8 ± 3.1 cm (Table 3.1). Between June – October, a total of 77,963 dives were recorded, with a mean of 4,886 ± 1,030 per individual, n = 15; Table 3.1).

Comparisons between CLS Argos transmitted and archival data from the recovered devices (n = 8) revealed that information for 25.0 ± 0.1 % of dives were obtained from the transmitted record over the investigation period. The mean dive duration ranged between 2.6 – 4.4 min (mean 3.8 ± 0.2 min), while the modal dive depth
Table 3.1: Deployment summary and dive behaviour of 16 male Australian fur seals deployed at Kanowna Island in winter of 2013 and 2014 (date is given as dd/mm/yyyy). Seal IDs 4 and 9 and 2 and 16 were the same individual tagged in consecutive years. Sampling duration represents the number of data days between the months of June to October in each year. Mass was estimated from axillary girth following Arnould and Warneke (2002). The proportion of benthic dives were determined using IDZ scores (see Tremblay and Cherel 2000 for details). Diel strategy was calculated following methods of Chapter 2. Individuals where full archival dive data were successfully obtained are indicated by (#).

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Dep date</th>
<th>Standard Length (cm)</th>
<th>Axillary Girth (cm)</th>
<th>Est. Mass (kg)</th>
<th>Sampling duration (d)</th>
<th>Dives analysed</th>
<th>Modal max. dive depth (m)</th>
<th>IDZ Score (%)</th>
<th>Diel Strategy</th>
</tr>
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<tr>
<td>1</td>
<td>30/05/2013</td>
<td>162.0</td>
<td>123.0</td>
<td>130</td>
<td>76</td>
<td>1604</td>
<td>76.5</td>
<td>92.3</td>
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</tr>
<tr>
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<td>30/05/2013</td>
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<td>115.0</td>
<td>109</td>
<td>68</td>
<td>7839</td>
<td>78.0</td>
<td>74.8</td>
<td>Diurnal</td>
</tr>
<tr>
<td>3#</td>
<td>2/06/2013</td>
<td>189.0</td>
<td>126.0</td>
<td>138</td>
<td>51</td>
<td>4876</td>
<td>79.5</td>
<td>87.0</td>
<td>Diurnal</td>
</tr>
<tr>
<td>4#</td>
<td>2/06/2013</td>
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<td>139.0</td>
<td>178</td>
<td>52</td>
<td>4714</td>
<td>84.0</td>
<td>90.0</td>
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</tr>
<tr>
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<td>2/06/2013</td>
<td>173.0</td>
<td>121.0</td>
<td>125</td>
<td>149</td>
<td>15228</td>
<td>83.0</td>
<td>83.4</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>6</td>
<td>3/06/2013</td>
<td>194.0</td>
<td>130.0</td>
<td>150</td>
<td>86</td>
<td>1895</td>
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<td>96.8</td>
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<td>7</td>
<td>28/07/2014</td>
<td>167.0</td>
<td>-</td>
<td>-</td>
<td>97</td>
<td>3239</td>
<td>82.5</td>
<td>85.0</td>
<td>Diurnal</td>
</tr>
<tr>
<td>8#</td>
<td>30/07/2014</td>
<td>177.0</td>
<td>-</td>
<td>-</td>
<td>94</td>
<td>8178</td>
<td>82.5</td>
<td>92.3</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>9#</td>
<td>1/08/2014</td>
<td>188.0</td>
<td>134.0</td>
<td>162</td>
<td>83</td>
<td>6831</td>
<td>75.0</td>
<td>92.6</td>
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<tr>
<td>10</td>
<td>2/08/2014</td>
<td>173.0</td>
<td>143.5</td>
<td>193</td>
<td>91</td>
<td>1274</td>
<td>84.5</td>
<td>77.1</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>11</td>
<td>2/08/2014</td>
<td>152.0</td>
<td>130.0</td>
<td>150</td>
<td>92</td>
<td>2010</td>
<td>78.5</td>
<td>89.1</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>12#</td>
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<td>148</td>
<td>88</td>
<td>7689</td>
<td>79.5</td>
<td>95.4</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>13</td>
<td>3/08/2014</td>
<td>185.5</td>
<td>157.0</td>
<td>243</td>
<td>91</td>
<td>1255</td>
<td>80.5</td>
<td>96.7</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>14</td>
<td>3/08/2014</td>
<td>176.0</td>
<td>135.0</td>
<td>165</td>
<td>31</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>15</td>
<td>3/08/2014</td>
<td>207.0</td>
<td>-</td>
<td>-</td>
<td>90</td>
<td>1387</td>
<td>70.5</td>
<td>94.5</td>
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</tr>
<tr>
<td>16#</td>
<td>5/08/2014</td>
<td>165.5</td>
<td>118.0</td>
<td>117</td>
<td>85</td>
<td>9944</td>
<td>85.5</td>
<td>64.0</td>
<td>Mixed</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>176.4 ± 3.5</td>
<td>130.8 ± 3.1</td>
<td>154.5 ± 9.9</td>
<td>82.8 ± 6.4</td>
<td>4886.4 ± 1030.2</td>
<td>79.8 ± 1.1</td>
<td>87.4 ± 2.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Chapter 3: Foraging site fidelity in male Australian fur seals
was consistent across all individuals (mean 79.8 ± 1.1 m). The IDZ scores (the proportion of benthic dives) confirmed a primarily benthic mode of foraging for all males (mean 87.4 ± 2.2%; Table 3.1). The hierarchical clustering analysis placed eight of the males (53%) into a nocturnal foraging group, while four (27%) and three (20%) individuals were placed into mixed and diurnal foraging groups, respectively (Table 3.1). The two seals that were sampled in both years were not consistent in their foraging strategies (seal ID 4/9 2013: mixed, 2014: nocturnal; seal ID 2/16 2013: diurnal, 2014: mixed).

Individuals were tracked for an average of 83 ± 6 d and an average of 1,495 ± 254 GPS locations per individual were obtained. After filtering and interpolation, 8,124 ± 666 GPS locations per individual were available for analysis (n = 16; total 129,983 GPS locations). A total of 248 individual foraging trips were recorded (15.5 ± 1.8 per individual), lasting on average 3.4 ± 0.2 d (Table 3.2). There was little difference in movements between years and all individuals foraged exclusively within the Bass Strait basin (Fig. 3.1). The maximum distance travelled from Kanowna Island was 214 km (mean maximum distance from Kanowna Island: 195 ± 7.9 km across all individuals). Upon leaving Kanowna Island, 81% of individuals (13 of 16) travelled on either a south-east or south-west bearing (mean bearing range 157.6° – 212.1°) towards other known Australian fur seal breeding/haul out sites located along the northern coast of Tasmania (Fig. 3.1). The remaining 19% (3) of males never travelled to the northern coast of Tasmania. Instead two individuals visited other breeding colonies/haul-out sites within northern and eastern Bass Strait (mean bearing 245.2° and 127.1°, respectively) and one foraged exclusively in an
Table 3.2: Summary of the 95% Home foraging range (HR), 50% Core foraging area (CFA) and 25% Intensive foraging area (IFA) utilisation distribution probabilities for each seal. The foraging site fidelity index was calculated for all pairwise combinations of trips (see ‘Methods: data processing and analyses’ for details). A score approaching 0 represents low fidelity, while a score approaching 1 represents high fidelity.

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>95% HR (km²)</th>
<th>50% CFA (km²)</th>
<th>25% IFA (km²)</th>
<th>No. of foraging trips</th>
<th>Mean trip duration (d)</th>
<th>Foraging site fidelity index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total n</td>
<td>Total Mean</td>
<td>n Total Mean</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>6578 1</td>
<td>744 -</td>
<td>251 -</td>
<td>10</td>
<td>4.3 ± 0.6</td>
<td>0.34</td>
</tr>
<tr>
<td>2</td>
<td>10769 2</td>
<td>2213 1106 ± 858</td>
<td>790 -</td>
<td>17</td>
<td>4.7 ± 0.8</td>
<td>0.22</td>
</tr>
<tr>
<td>3</td>
<td>10632 1</td>
<td>1170 -</td>
<td>389 -</td>
<td>15</td>
<td>2.5 ± 0.2</td>
<td>0.20</td>
</tr>
<tr>
<td>4</td>
<td>6798 1</td>
<td>1155 -</td>
<td>431 215 ± 85</td>
<td>8</td>
<td>2.2 ± 0.4</td>
<td>0.37</td>
</tr>
<tr>
<td>5</td>
<td>8356 4</td>
<td>1739 435 ± 200</td>
<td>505 253 ± 186</td>
<td>26</td>
<td>4.3 ± 0.9</td>
<td>0.37</td>
</tr>
<tr>
<td>6</td>
<td>9921 2</td>
<td>1973 987 ± 963</td>
<td>702 -</td>
<td>29</td>
<td>4.6 ± 0.4</td>
<td>0.10</td>
</tr>
<tr>
<td>7</td>
<td>9145 1</td>
<td>1741 -</td>
<td>553 -</td>
<td>16</td>
<td>3.5 ± 0.4</td>
<td>0.29</td>
</tr>
<tr>
<td>8</td>
<td>24075 3</td>
<td>5309 1770 ± 654</td>
<td>2064 1032 ± 21</td>
<td>19</td>
<td>1.4 ± 0.3</td>
<td>0.12</td>
</tr>
<tr>
<td>9</td>
<td>7071 1</td>
<td>1245 -</td>
<td>424 -</td>
<td>10</td>
<td>4.2 ± 0.5</td>
<td>0.34</td>
</tr>
<tr>
<td>10</td>
<td>18656 2</td>
<td>3278 1639 ± 1538</td>
<td>1102 -</td>
<td>12</td>
<td>5.6 ± 1.8</td>
<td>0.15</td>
</tr>
<tr>
<td>11</td>
<td>12127 3</td>
<td>3101 1034 ± 916</td>
<td>1181 590 ± 490</td>
<td>27</td>
<td>2.1 ± 0.4</td>
<td>0.16</td>
</tr>
<tr>
<td>12</td>
<td>1704 2</td>
<td>329 165 ± 144</td>
<td>117 -</td>
<td>19</td>
<td>2.8 ± 0.3</td>
<td>0.60</td>
</tr>
<tr>
<td>13</td>
<td>10024 1</td>
<td>1578 -</td>
<td>607 304 ± 232</td>
<td>11</td>
<td>7.0 ± 1.7</td>
<td>0.39</td>
</tr>
<tr>
<td>14</td>
<td>5087 2</td>
<td>812 406 ± 185</td>
<td>266 -</td>
<td>6</td>
<td>3.7 ± 0.7</td>
<td>0.27</td>
</tr>
<tr>
<td>15</td>
<td>6033 1</td>
<td>776 -</td>
<td>276 -</td>
<td>9</td>
<td>6.9 ± 1.7</td>
<td>0.33</td>
</tr>
<tr>
<td>16</td>
<td>23172 2</td>
<td>5098 2549 ± 758</td>
<td>1849 925 ± 615</td>
<td>14</td>
<td>2.8 ± 0.6</td>
<td>0.10</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>10634 ± 1566</td>
<td>2016 ± 371</td>
<td>1156 ± 151</td>
<td>719 ± 141</td>
<td>512 ± 78</td>
<td>15.5 ± 1.8</td>
</tr>
</tbody>
</table>
area approximately 50-75 km WSW from Kanowna Island (mean bearing 294°). Over the tracking period, the males in the present study visited a total of 16 separate land sites (haul-out locations/breeding colonies) that were dispersed throughout the entire Bass Strait region (Fig 3.1), spending on average 1.5 ± 0.1 d hauled out (maximum 12 d).

**Spatial consistency in habitat use**

The area covered by the 95% HR UD contour varied considerably between individuals and ranged from 1,704 – 24,075 km² (mean 10,634 ± 1,566 km²; Table 3.2 and Fig 3.2). The majority of males occupied a relatively narrow HR as they made direct foraging trips between haul-out sites and breeding colonies located in northern and southern Bass Strait (e.g. seals 1, 3, 4 and 5). Other males (e.g. seals 2, 6 and 13) travelled to southern Tasmania where they alternated between two haul-out sites/breeding colonies located along the northern coast of Tasmania. Although all of these individuals spent considerable periods regularly transiting between these locations, the 50% CFA and 25% IFA UD distributions for these individuals were primarily located in the southern areas of Bass Strait and in close proximity to rest sites (haul-out sites/breeding colonies) along the northern coast of Tasmania (Fig 3.2). Conversely, a smaller proportion of individuals had a large HR UD that encompassed large portions of Bass Strait (e.g. seals 8, 10, 11 and 16). These males would typically roam Bass Strait in looping trajectories, where they visited many different haul-out sites/breeding colonies distributed throughout the region. The CFA and IFA for these individuals were also larger and located further away from
Figure 3.2: The 95% home foraging range (blue), 50% core foraging areas (yellow) and 25% intensive foraging areas (orange) calculated from individual utilisation distribution probabilities for each of the 16 Australian fur seals tracked June – October of 2013 (n = 6, males 1-6) and 2014 (n = 10, males 7-16). Males 4 and 9, and 2 and 16 were the same individual tagged in consecutive years.
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Peripheral haul-out sites/breeding colonies (i.e. closer to central Bass Strait) than those with a narrower HR. In addition, these individuals had multiple IFA and CFA areas, whereas those with a narrow HR would typically display a single CFA or IFA area.

The calculated foraging site fidelity index (for a 10km$^2$ grid cell size) varied considerably between individuals (range: 0.10 – 0.60; Table 3.2). Irrespective of grid cell size used (5km$^2$, 10km$^2$, 15km$^2$ and 25km$^2$) site fidelity index values for each seal were highly correlated (Pearson’s $r$ range: 0.91 – 0.98, $P < 0.001$ in all cases; Fig. S3.1 and Table S3.1). Hence, while the site fidelity index varied depending on the grid cell size used, the general trend in fidelity across individuals (and therefore, the interpretation of results) did not. Clustering analysis categorized four seals as having ‘low’ fidelity scores (mean SFI: 0.12 ± 0.01; Fig 3.3a), reflecting their broad movements around Bass Strait. Five seals were classified as having a ‘moderate’ degree of fidelity (mean SFI: 0.23 ± 0.02; Fig 3.3b) and six seals displayed a ‘high’ degree of fidelity (mean SFI: 0.36 ± 0.01; Fig 3.3c). Upon inspection of cumulative cell use plots (Figs 3.3f and 3.3g) these individuals displayed fidelity to multiple sites (i.e. exploited a single site over multiple consecutive trips and then commuted to another site to exploit repeatedly). When compared to other males, one seal (seal 12) had a substantially higher site fidelity score (0.60), reflecting faithfulness to a single foraging site located ca 75 km WSW of Kanowna Island (Fig 3.3d). This individual made 19 consecutive foraging trips back and forth to this foraging site from Kanowna Island and was the only male to be placed into the ‘extreme’ fidelity cluster. The two seals that were deployed over both years exhibited slightly lower fidelity scores in
Figure 3.3: The foraging tracks of 16 male Australian fur seals separated by their respective site fidelity index. Each male was placed into the corresponding group using hierarchical clustering analysis: (A) individuals with low fidelity ($n = 4$; mean site fidelity index $\pm$ SE $0.12 \pm 0.01$); (B) moderate fidelity ($n = 5$; $0.23 \pm 0.02$); (C) high fidelity ($n = 6$; $0.36 \pm 0.01$) and (D) extreme fidelity ($n = 1$; $0.60$). The number of 10 x 10 km grid cells entered in each trip were used to calculate the site fidelity index for each male (mean $\pm$ SE: $15.2 \pm 1.8$ trips per individual). The corresponding cumulative grid cell use for each seal are presented by the same colour in panels E-H, respectively.
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2014 when compared to 2013 (seal 2/16: 0.22 and 0.10; seal 4/9: 0.37 and 0.34, in 2013 and 2014, respectively). While seal ID 4/9 remained in the same ‘high’ cluster over both years, seal ID 2/16 was placed in the ‘moderate’ fidelity cluster in 2013 and then into the ‘low’ fidelity cluster in 2014. However, their UD’s indicated that they used similar areas of Bass Strait during both years (Fig 3.2). Inspection of the posterior distributions from the MCMC beta GLMM outputs determined that none of the variables assessed within each of the four models (model one: axillary girth, standard length and the flipper length/standard length ratio; model two: modal depth, IDZ and mean trip duration; model three: mean dive duration; and model four: diel strategy) significantly influenced site fidelity (Table 3.3).

Discussion

Dive behaviour and habitat use

Male Australian fur seal dive depth showed little variation within and between individuals, which is consistent with the dive behaviour of female Australian fur seals (Arnould and Hindell 2001; Hoskins and Arnould 2014). Most dives were characterised as benthic, which reflects the shallow depths associated with Bass Strait (60-80 m). While a benthic foraging strategy is inconsistent with the pelagic strategies of many other fur seals (Arnould and Costa 2006), it has frequently been reported in studies examining the foraging behaviour of Australian fur seals (Arnould and Hindell 2001; Hoskins and Arnould 2014) (Chapter 2). This benthic behavior may reflect the relatively low productivity of the continental shelf habitat (Gibbs et al. 1986; Sandery and Kämpf 2007) and the distribution of preferred prey resources.
Table 3.3: Results of the Bayesian beta generalised linear mixed effects models assessing the response of the site fidelity index (see Table 3.2) to variations in body shape (model 1), foraging metrics (model 2), dive duration (model 3) and diel foraging strategy (model 4).

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Terms</th>
<th>Posterior Mean</th>
<th>2.5% Credible Interval</th>
<th>97.5% Credible Interval</th>
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</thead>
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<tr>
<td>Model 1</td>
<td>Intercept</td>
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<td>-1.61</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td>(n = 13)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Standard length</td>
<td>0.00</td>
<td>-0.41</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Axillary girth</td>
<td>0.14</td>
<td>-0.32</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>FL/STL</td>
<td>-0.08</td>
<td>-0.59</td>
<td>0.41</td>
</tr>
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<td>Model 2</td>
<td>Intercept</td>
<td>-0.62</td>
<td>-1.62</td>
<td>1.08</td>
</tr>
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<td></td>
<td>(n = 15)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>IDZ</td>
<td>0.25</td>
<td>-0.10</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Modal depth</td>
<td>-0.13</td>
<td>-0.50</td>
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<td></td>
<td>Mean trip duration</td>
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<td>-0.19</td>
<td>0.48</td>
</tr>
<tr>
<td>Model 3</td>
<td>Intercept</td>
<td>-0.50</td>
<td>-1.54</td>
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<td>(n = 8)</td>
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</tr>
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<td></td>
<td>Dive duration</td>
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<td>-0.07</td>
<td>0.96</td>
</tr>
<tr>
<td>Model 4</td>
<td>Diurnal strategy</td>
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<td>-1.60</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td>(n = 15)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mixed strategy</td>
<td>-0.42</td>
<td>-1.21</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>Nocturnal strategy</td>
<td>-0.31</td>
<td>-1.17</td>
<td>0.54</td>
</tr>
</tbody>
</table>
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along the sea floor of Bass Strait (Arnould and Hindell 2001).

In the present study, male Australian fur seals foraged exclusively within the continental shelf of Bass Strait over winter. This finding is consistent with prior studies that have examined the spatial distribution of male and female Australian fur seals, indicating a high degree of spatial overlap between the sexes during winter (Arnould and Hindell 2001; Arnould and Kirkwood 2007; Kirkwood and Arnould 2011; Hoskins et al. 2015a; Kernaléguen et al. 2015a) (Chapter 2). Given a high degree of intra-specific competition surrounding breeding colonies, local prey resources may become depleted (Ashmole 1963; Birt et al. 1987). While nursing females must continue to return to the same breeding colony in between foraging trips (Arnould and Hindell 2001), males have the option to utilise other rest sites (haul-out locations) that are in closer proximity to profitable foraging areas, or areas that contain preferred prey not available in other areas, thereby leading to sexual segregation in diet (Chapter 2).

Indeed, males in the present study visited many of the islands that are dispersed throughout Bass Strait, which is consistent with previous reports on the locations of male Australian fur seal haul-out sites during winter (Warneke and Shaughnessy 1985; Kirkwood et al. 2006). Males utilised these sites in a similar manner to a central place forager, by making regular short commutes to nearby foraging areas. Similar central place foraging behaviour has also been observed in other male otariids, such as southern sea lions (Otaria flavescens) (Baylis et al. 2017), which highlights that the degree of post-breeding dispersal in male otariids varies depending on life history and habitat availability (Boyd et al. 1998; Sterling et al. 2014).
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Utilising haul out sites that are located nearby foraging areas may reduce the metabolic costs of transiting to foraging areas and provide access to higher quality prey patches (Staniland et al. 2012). This could be an optimal foraging strategy for male otariids as it may maximise their net energetic intake (Pyke 1984; Stephens and Krebs 1987).

Spatial consistency and individual variation in habitat use

Some study animals exhibited a high degree of foraging site fidelity and one male (seal ID 12) exhibited an 'extreme’ degree of fidelity to a single foraging site, south west of Kanowna Island. These results are consistent with the behaviour of other benthic foraging otariid species (e.g. Chilvers 2008; Auge et al. 2014). Furthermore, the results are consistent with a prior study investigating spatial consistency within female Australian fur seals (Hoskins et al. 2015a). This suggests that prior knowledge of foraging areas is important for Australian fur seals and other benthic foraging otariids, when deciding where to forage. Fidelity to foraging areas may enable individuals of these species to minimise the metabolic costs associated with searching for prey thereby increasing their net energetic gain (Greenwood 1980; Switzer 1993; Piper 2011). Sea floor characteristics or bathymetric features could provide visual cues for benthic foragers, such as Australian fur seals, to memorize the location and quality of specific foraging habitats (Cook et al. 2006; Mattern et al. 2007; Woo et al. 2008). Consequently, given that prey resources within Bass Strait are likely to be associated with spatially predictable static features (e.g. reefs), site fidelity is likely to be an advantageous foraging strategy for Australian fur seals.
Chapter 3: Foraging site fidelity in male Australian fur seals

However, the foraging success of individuals which exhibit extreme fidelity may be affected by environmental variability and associated fluctuations in prey resources within the area. In ‘poor’ years, individuals that continue to exhibit a high degree of faithfulness over the longer term, may be more susceptible to environmental variability (Switzer 1993; Bolnick et al. 2003; Wakefield et al. 2015). Within the present study, fidelity was not consistent between males, with some individuals exhibiting a higher fidelity index score when compared to others. There are several hypotheses that may help explain the findings of the present study. Firstly, if prey resources are spatiotemporally predictable and a predator was previously successful in a specific foraging area, individuals may employ a ‘win-stay, lose-shift’ approach to optimise their foraging efficiency (Battin 2004; Wakefield et al. 2015). Hence, site fidelity may only occur over a relatively short temporal period. In the present study, most individuals exhibited some degree of fidelity to several sites over the tracking period. Although, the present study was limited to winter (ca 3 months), temporal fluctuations in prey resources and fluctuations in intra-specific competition will impact the profitability of foraging patches over time (Ashmole 1963; Charnov et al. 1976; Birt et al. 1987; Ropert-Coudert et al. 2009; Garthe et al. 2011; Wege et al. 2016). By moving between several foraging sites, most male Australian fur seals could maximise their fitness by optimising the time spent in different foraging areas (Piper 2011; Merkle et al. 2015; Patrick and Weimerskirch 2017). Furthermore, the two males that were studied during both years (seal ID’s 2/16 and 4/9) exhibited lower fidelity scores in 2014 when compared to 2013 (0.22 and 0.10 in 2013 and 0.37 and 0.34, respectively) and neither male displayed the same diel strategy. This
suggests that the variability in foraging site fidelity between years may be a response to environmental variability and associated fluctuations in prey resources, thereby implying behavioural flexibility within male Australian fur seals.

Given that male Australian fur seals have a winter foraging range that is restricted to the continental shelf waters of Bass Strait, the individual differences in site fidelity reported in the present study, may also be important in reducing the niche overlap between individuals (Bolnick et al. 2003; Araújo et al. 2011). Indeed, individual differences in foraging behaviour and diet is commonly reported with Australian fur seals (Hoskins et al. 2015b) (Chapter 2), with age, body size and body shape shown to influence the prey selection and foraging areas of females (Arnould et al. 2011; Arnould et al. 2015; Hoskins et al. 2015b). While the morphometrics used in the present study may be good body size and/or shape proxies for females, no relationship between the degree of foraging site fidelity and morphometrics of males were found. This may be due to the foraging ability of males showing stronger relationships with other morphometric variables that were not measured, or given that site fidelity was only examined over winter (ca 3 months), it is possible that any intrinsic factor signal would not be strong enough to be detected. Alternatively, the males in the present study may be operating within their physiological limits (Weise et al. 2010) and body size or shape may not influence the foraging behaviour of male Australian fur seals.

In summary, male Australian fur seals displayed a high degree of individual consistency in their fine-scale habitat use over winter. Most males utilised known Australian fur seal breeding colonies and haul-out sites and typically behaved like a
central place forager. However, in contrast to adult females that must regularly return to the same breeding colony to provision offspring, males are able to utilise other sites (haul-out locations) that are adjacent to foraging areas. By using haul out sites as a central place, males minimise the metabolic costs of transit, presumably maximising their net energetic intake. While some individuals exhibited a higher degree of fidelity than others, intra-individual variation indicates that male Australian fur seals have the flexibility to respond to environmental variability and associated fluctuations in prey resources. Furthermore, variation in site fidelity between males may also be important in reducing niche overlap between individuals.
Figure S3.1: Correlation of the site fidelity index for each seal at different grid cell resolutions (5, 10, 15 and 25 km²). The numerical output of the SFI index increased with larger grid cell size.
Table S3.1: *Pearson’s correlation of the site fidelity index*. Irrespective of grid size, all cell resolutions were highly correlated ($P < 0.001$ in all cases).

<table>
<thead>
<tr>
<th></th>
<th>SFI 5 km</th>
<th>SFI 10 km</th>
<th>SFI 15 km</th>
<th>SFI 25 km</th>
</tr>
</thead>
<tbody>
<tr>
<td>SFI 5 km</td>
<td>1</td>
<td>0.97</td>
<td>0.97</td>
<td>0.91</td>
</tr>
<tr>
<td>SFI 10 km</td>
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<td>0.98</td>
<td>0.96</td>
<td></td>
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<td>1</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>SFI 25 km</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
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Chapter 4: Sex-specific and temporal variation in the foraging behaviour and diet of Australian fur seals

A version of this chapter has been submitted for publication as:

Chapter 4: Variation in behaviour and diet of Australian fur seals

Abstract

Top order consumers play an important role in determining the structure and functioning of marine ecosystems. Accordingly, understanding how groups (e.g. sexes) may segregate in their behaviour and diet, and how this may vary temporally is an important component in understanding the foraging ecology of a species. The present study investigated the behaviour and diet of 16 male and 14 female Australian fur seals (*Arctocephalus pusillus doriferus*) during winter of 2013 and 2014 at Kanowna Island (39°10’S, 146°18’E) in northern Bass Strait, south-eastern Australia. Both sexes exhibited a high degree of spatial overlap and foraged benthically within the continental shelf of Bass Strait. Quantitative fatty acid signature analysis (QFASA) of blubber samples indicated that there was substantial variation in the diet of seals between years ($P = 0.0001$), suggesting that Australian fur seals, irrespective of sex, have the ability to respond to fluctuations in prey abundance, availability, and distribution. Estimates of diet revealed no significant difference in dietary composition between sexes ($P = 0.0893$). However, when taking year into account, the difference trended towards significance ($P = 0.052$). Variability in dive behaviour between sexes may promote biologically significant variation in diet between males and females. Specifically, the larger body size of males enabled them to spend longer than females searching for prey along the sea-floor and presumably, enables males to handle larger prey resources. Small-scale resource partitioning within Australian fur seals may aid to resource the high degree of intra-specific competition for resources that occurs within the Bass Strait basin.
Chapter 4: Variation in behaviour and diet of Australian fur seals

Introduction

Top order consumers play an important role in determining the structure and functioning of marine ecosystems (Ripple et al. 2014, Estes et al. 2016). Understanding how individuals or groups may segregate in behaviour and diet, and how this may vary temporally is, therefore, an important component in understanding the foraging ecology of a species. Resource partitioning is observed within a wide range of taxa and is commonly related to variation in an individual’s social status (e.g. age and/or sex), physiology (e.g. foraging ability), and/or life-history constraints (e.g. reproduction) (Polis 1984, Shine 1989, Ruckstuhl & Neuhaus 2005, Field et al. 2007, Wearmouth & Sims 2008). In addition, morphology (e.g. body size and/or shape) has an influence on the foraging capabilities of an individual and, in sexually dimorphic species, it may lead to sexual segregation in behaviour and diet (Gonzalez-Solis et al. 2000, Mysterud 2000). For example, the larger sex may have higher overall energetic needs, or may access a larger variety of prey, than smaller conspecifics and, consequently, each sex may not have the same dietary composition (Clutton-Brock et al. 1987, Kamilar & Pokempner 2008, Call & Ream 2012). This leads to a broadening in the niche breadth of the species (Polis 1984) and, therefore, it must be examined when determining the functional role of a species within an ecosystem.

Pinnipeds (seals, sea lions and walruses) exhibit some of the most extreme sexual dimorphism of any mammal, with males up to four times the mass of females (Staniland 2005). Correspondingly, sex-based resource partitioning is a common feature within the foraging ecology of this group (e.g. Lewis et al. 2006, Staniland &
Chapter 4: Variation in behaviour and diet of Australian fur seals

Robinson 2008, Leung et al. 2012). The larger body size of males may allow them to handle larger sized prey with more efficiency than smaller conspecifics (Beck et al. 2003). Furthermore, an increased physiological capacity is often associated with a larger body size (Weise et al. 2010) and, as such, it may allow males to dive for longer and/or access deeper waters where prey may not be accessible to females (Boyd et al. 1998, Page et al. 2005a, Staniland 2005, Weise & Costa 2007). In addition, adult males play no role in parental care and, therefore, are less restricted in their foraging range and/or duration than nursing females (Bonner 1984, Gentry et al. 1986). Given that increased intra-specific competition near breeding colonies may deplete nearby food resources (Ashmole 1963, Birt et al. 1987), adult males may be expected to travel further than nursing females to forage in a broader range of habitats and, potentially access a broader range of resources (Boyd et al. 1998, Campagna et al. 2001, Staniland 2005, Page et al. 2006, Wearmouth & Sims 2008).

The Australian fur seal (Arctocephalus pusillus doriferus) has a breeding distribution largely restricted to Bass Strait in south-eastern Australia (Warneke & Shaughnessy 1985, Kirkwood et al. 2010). It is the largest fur seal species, with males and females weighing on average 279 kg and 75 kg, respectively (Arnould & Warneke 2002). Correspondingly, given the extreme dimorphism and different reproductive constraints between the sexes, it would be expected that sexual segregation in foraging behaviour and diet might exist in this species. However, recent studies of the winter at-sea movements of Australian fur seals have shown that males and females greatly overlap in their foraging areas within the shallow (max. depth 80 m) continental shelf of Bass Strait (Kirkwood et al. 2006, Hoskins et al.
Chapter 4: Variation in behaviour and diet of Australian fur seals

2015a, Kernaléguen et al. 2015a) (Chapters 2 and 3). Yet to date, studies have not examined dive behaviour in male and female Australian fur seals concurrently and, therefore, it is not clear if differences in their behaviour may contribute to sexual segregation in foraging niche within the species.

Previous stable isotope studies suggest there is little segregation in trophic niche between sexes in Australian fur seals (Kernaléguen et al. 2015a). However, prey of the same trophic level may exhibit similar isotopic signatures such that stable isotope analysis lacks the sensitivity to distinguish the precise composition of predator diets (Tieszen et al. 1983, Hobson et al. 1994, Hobson 1999, Post 2002, Michener & Kaufman 2007). This is especially so when predators consume a broad array of prey species from a narrow trophic range. The Australian fur seal is known to consume > 100 prey species (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004, Page et al. 2005b, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Kliska 2015, Hoskins et al. 2017), many of which are from a relatively narrow isotopic niche (Arnould et al. 2011, Knox et al. 2014, Kernaléguen et al. 2015b). Consequently, the ability to infer the degree of dietary segregation and/or overlap between males and females of the species from stable isotope data is limited.

Quantitative fatty acid signature analysis (QFASA) has been used to estimate the diets of many marine mammal species (Herman et al. 2005, Thiemann et al. 2008, Grahl-Nielsen et al. 2010, Bromaghin et al. 2013, Banks et al. 2014). This technique allows for the quantitative estimate of a predators’ dietary composition. Predator fatty acid signatures are modelled as a mixture of prey fatty acid signatures after using calibration coefficients to account for the differential metabolism of individual fatty
acids (Iverson et al. 2004, Iverson 2009). As blubber contains lipids that have accumulated over time, it can provide a record of dietary intake over a period of weeks to months (Budge et al. 2006). This information can provide insights into the variation in diet among individuals and/or groups of predators, particularly when combined with behavioural data, such as movement and diving data (Beck et al. 2005, Beck et al. 2007, Meynier et al. 2008).

The aims of the present study, therefore, were to investigate in male and female Australian fur seals, concurrently: (1) variation in dive behaviour that may contribute to dietary differences between sexes; (2) differences in the fatty acid composition of blubber samples, as a proxy for diet; and (3) determine potential prey species from the fatty acid profiles of seals to assess sexual segregation in the foraging niche of the species.

**Materials and methods**

*Animal handling and instrumentation*

The study was conducted at the Australian fur seal breeding colony on Kanowna Island (39o10’S, 146o18’E), in central northern Bass Strait, south-eastern Australia. Kanowna Island is the third largest Australian fur seal colony with an annual pup production of ca 3,400 pups (Kirkwood et al. 2010). Field seasons were conducted in the austral winter (June – August) of 2013 and 2014. Following methods outlined by Baylis et al. (2014), individual males were chemically immobilised using a 1:1 mixture of tiletamine-zolazepam (Zoletil, Virbac, Milperra,
Chapter 4: Variation in behaviour and diet of Australian fur seals

N.S.W., Australia, ca 1 mg kg\(^{-1}\) of estimated mass), remotely administered via darts propelled by a CO\(_2\) powered tranquiliser gun (Dan Inject JM Standard, Harcourt, Vic., Australia). Anaesthesia was maintained during the handling procedure using isoflurane delivered via a portable gas vaporizer (Stinger TM, Advanced Anaesthesia Specialists, Gladesville, N.S.W., Australia). Due to their smaller size, adult females were captured using a modified hoop net (Fuhrman Diversified, Seabrook, TX., U.S.A) and manually restrained until fully anaesthetised using isoflurane as described above.

Given male pinnipeds are free from central place foraging constraints, they were not expected to return regularly to the breeding colony (Gentry et al. 1986). In view of this, males were instrumented with a satellite-linked GPS and dive behaviour data logger (Mk10AF; Wildlife Computers, Redmond, WA, U.S.A.), which were programmed to collected and transmit data via the CLS ARGOS system (refer to Chapter 2 for detailed information on transmission of data). Unlike males, females are obligate central place foragers and, therefore, were expected to return regularly to the breeding colony (Gentry et al. 1986), thereby enabling device recovery. Females were instrumented with an archival Fastloc GPS device (Fastloc 1; Sirtrack, Havelock North, New Zealand), dive logger (Mk9 TDR; Wildlife Computers) and a small VHF transmitter (Sirtrack) to facilitate recapture. All loggers were glued in series to the dorsal mid-line fur just posterior to the scapula using quick setting two-part epoxy (Accumix 268, Huntsmen; RS Components, Deer Park, Vic, Australia). All GPS loggers were programmed to collect location data every 10 min, while dive loggers collected dive data every 5 s. After a minimum period of 2 months,
Chapter 4: Variation in behaviour and diet of Australian fur seals

individuals were recaptured opportunistically, and devices retrieved by cutting the fur beneath the device. Some males were opportunistically recaptured, which enabled complete dive and location data to be recovered. However, where males were not able to be recaptured, devices continued to transmit summary behaviour data until they fell off due to moult or their battery stopped working.

**Fatty acid analyses**

A blubber biopsy sample was taken from the posterior flank of each animal. Briefly, a small incision using a scalpel blade was made through the skin and then a 6 mm biopsy punch inserted into incision and a blubber core taken to the depth of the muscle layer. Blubber samples were stored frozen at -20°C until lipid extraction in the laboratory. In the laboratory, thawed samples were extended to their full length and any muscle or skin left attached to the adipose tissue was removed. Prior studies have documented vertical stratification within several marine mammal species, such as cetaceans and phocids, which can affect dietary interpretation (Koopman et al. 1996, Best et al. 2003, Guerrero & Rogers 2017). However, in comparison, vertical stratification of otariid blubber is limited, that is, inner and outer layers are similar in fatty acid composition (Budge et al. 2006, Lambert et al. 2013). Therefore, blubber samples were homogenized prior to lipid extraction.

Lipids were quantitatively extracted from accurately weighed diced blubber samples (30-40 mg) using a modified overnight Bligh and Dyer (1959) method. Methanol washed 10 mL glass tubes with Teflon lids (Kimble) were used throughout
to minimise fatty acid contamination. To each sample, 0.750 mL of 2:1 chloroform:methanol was added and then the samples were homogenised using an IKA Ultra-turrax stick tissue disruptor. Samples were shaken overnight at room temperature followed by the addition of 0.380 mL of water. Tubes were then shaken for 30 min and centrifuged at 2000 rpm for 5 min. The bottom lipid layer was transferred to pre-weighed glass tubes and dried under vacuum (Christ speed vac) before being re-weighed. The lipid extract was re-constituted in 45 µL chloroform:methanol containing 100 µM d27 myristic acid as an internal standard then derivatized with 5 µL Methprep II (Grace) to produce fatty acid methyl esters (FAMES).

The FAMES were then analysed using a Trace DSQ gas chromatography mass spectrometer (GC-MS; Thermofisher) with a 100 m x 0.25 mm 0.2 µm film TR-FAME column (Thermofisher). The following temperature gradient and instrument settings were used: the GC columns initial temperature was 140°C, this was held for 5 min then ramped at 4°C/min to 240°C, then a 15 min hold giving a total runtime of 45 min. An 11 min solvent delay was used on the MS which scanned from 40-400 m/z at 1.5 scans per second. For quantitation a standard curve from 1 – 100 µm of free fatty acids (Nuchekprep mix 463) were converted to FAMES as above. Peak areas were determined using Xcalibur quantitative analysis software (Thermo). Peak area ratios using the internal standard were used for quantitation. Concentrations of individual fatty acids were converted into a proportion of total fatty acids by mass (%). To improve normality, fatty acids were transformed using a log transformation designed for proportional data: $x_{trans} = \ln(x_i/c_r)$; where $x_i$ is a
Chapter 4: Variation in behaviour and diet of Australian fur seals

given fatty acid and $c_r$, a reference fatty acid, in this case C18:0 was used (Budge et al. 2006).

Statistical analyses

Location data (GPS) were filtered using a speed filter (8 ms$^{-1}$) to remove obviously erroneous locations (McConnell et al. 1992) and then linearly interpolated every 10 min in the R package trip (Sumner 2013). In addition, to limit the influence of foraging tracks converging around haul-out sites / breeding colonies, a 2-km buffer was placed around these land sites (Breed et al. 2011) (Chapters 2 and 3). All GPS relocations that occurred within this buffer zone (on land or at sea) were subsequently excluded from further analyses. In order to quantify the foraging areas of each sex and for each year, the 95% home range (HR) and the 50% core range (CR) utilisation distribution probabilities (UD) was calculated in the R package adehabitatHR (Calenge 2006). Smoothing parameters for the UD probabilities were determined using the ad hoc method (Worton 1989) and bathymetry data were used as a habitat grid to avoid unrealistic probabilities spanning across land. Overlap between each sex, year, and the pairwise interaction of sex and year, were calculated using Bhattacharyya’s affinity index (BA) which is a general measure of similarity between UD estimates, ranging from 0 (no overlap) to 1 (identical UD’s) (Fieberg and Kochanny 2005).

Due to device malfunction, only maximum dive depth and dive frequency were available in the male satellite-transmitted dive summary data. Therefore, except
for these two variables, analyses on diving behaviour were restricted to individuals for which the full dive archive was available. Archival data obtained from the recovered male and female tags were subsequently summarised for basic per dive metrics (dive duration, post-dive interval, dive depth, descent and ascent rates, and bottom time) using the *diveMove* package in R (Luque & Fried 2011). The intra-depth zone (IDZ) was used to calculate the proportion of benthic dives (%). The IDZ assumes that benthic divers will dive repeatedly to the same depth zone (i.e. sea floor) and is a common metric used to differentiate between benthic and pelagic dive behaviour (Tremblay & Cherel 2000). Dives that occurred within ±10% of the depth of the preceding dive were considered benthic, while others that fell out of this depth zone were considered pelagic. The proportion of time spent diving (%), the rate of vertical distance travelled (m·s⁻¹) and dive frequency (dives·h⁻¹), as measures of foraging effort were also calculated. Consistent with prior Australian fur seals studies, a foraging dive was defined as any dive > 10 m in depth ensuring that non-foraging surface behaviour (such as resting and thermoregulation) was excluded from analyses (Arnould & Hindell 2001) (*Chapter 2*).

To investigate sex differences in foraging behaviour, generalised linear models (GLMs) were used. For each GLM, sex and year were included as predictor terms against each response variable: dive duration (s), descent rate (m·s⁻¹), ascent rate (m·s⁻¹), mean max dive depth (m), modal dive depth (m), bottom time (s), proportion of dive time spent on bottom (%), proportion of benthic dives (%), dive frequency (dives·h⁻¹) dive rate (m·h⁻¹), and proportion of time spent diving (%). Seal ID was not included as a random effect within the models as repeat sampling was
limited to two male individuals only (Bolker et al. 2009, Zuur et al. 2013). For all models, assumptions were checked using the methods of Zuur et al. (2009).

To investigate if the fatty acid composition of seals differed between years and/or sexes, a permutational multivariate ANOVA (PERMANOVA) was run in the R package vegan (Oksanen et al. 2018). Year and sex were included within the PERMANOVA, as was their interaction, against the fatty acid profile of seals. Statistical significance was determined using 9999 unrestricted permutations of the proportional (%) fatty acid data. Fatty acids within individuals were homogenously dispersed by year (PERMDISP, $F_{1,24} = 1.49, P = 0.22$) and sex ($F_{1,24} = 0.41, P = 0.53$) thus the assumption of homogeneity for PERMANOVA analysis was met (Anderson 2001).

The dietary composition of seals was then estimated using QFASA (Iverson et al. 2004) in the R package qfasar (Bromaghin 2017). First, known Australian fur seal prey species were determined from the literature (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004, Page et al. 2005b, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Arnould et al. 2011, Hoskins et al. 2017), with a fatty acid profile obtained from a database of marine species collected in the south-east Australian region (Nichols et al. 1998, Mooney et al. 2002). Fatty acid profiles of prey are assumed to be representative of respective prey species consumed by Australian fur seals in the present study. However, as seal blubber samples were obtained during device instrumentation procedures, fatty acid profiles do not necessarily reflect the period of which the seals were tracked. Calibration coefficients do not exist for Australian fur seals, therefore, to account for predator metabolism of
fatty acids, calibration coefficients obtained for Steller sea lions (Eumetopias jubatus; (Rosen & Tollit 2012) were used in the QFASA model, with the assumption that Steller sea lion calibration coefficients are appropriate for inferring the diet of Australian fur seals. Only fatty acids that were present in the three data sets (predator, prey, and calibration coefficients) were included in the QFASA model. The resulting QFASA model determined the most likely prey composition of seals for each year, sex, and their interaction based on the combination of available prey (Table S1).

Unless otherwise indicated, all data are presented as mean ± SE and statistical significance was considered when \( P < 0.05 \).

**Results**

*Habitat use and behaviour*

A total of 30 Australian fur seals (n=16 male, 14 female; Table 4.1) were instrumented with GPS and dive logger recording devices over the winter of 2013 (n=6 male, 7 female) and 2014 (n=10 male, 7 female). Male seals were longer than females (177.5 ± 3.5 cm compared to 144.8 ± 1.8 cm), larger in girth (129.8 ± 3.1 compared to 98.8 ± 1.4 cm) and had a larger right flipper length (54.9 ± 1.4 cm compared to 40.3 ± 0.5 cm) (Table 4.1). Due to equipment failure or device loss, GPS data were available for 16 males (100%) and 12 females (86%), while dive data were available for 8 males (50%) and 12 females (86%).

All seals sampled in the present study foraged exclusively within the continental shelf of Bass Strait (Figs. 4.1 and 4.2). There was little difference in the
Chapter 4: Variation in behaviour and diet of Australian fur seals

Table 4.1: Deployment summary and morphometric measures of male and female Australian fur seals deployed at Kanowna Island in winter of 2013 and 2014. Males 4 and 9, and 2 and 16 were the same individuals sampled in both years.

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Deployment Date</th>
<th>Sampling duration (d)</th>
<th>Dives analysed (n)</th>
<th>Biopsy sampled</th>
<th>Standard length (cm)</th>
<th>Axillary girth (cm)</th>
<th>Right flipper length (cm)</th>
</tr>
</thead>
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<tr>
<td>Female 1</td>
<td>23/5/2013</td>
<td>52</td>
<td>7395</td>
<td>Y</td>
<td>148.0</td>
<td>98.0</td>
<td>42.5</td>
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<tr>
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<td>24/5/2013</td>
<td>45</td>
<td>10167</td>
<td>Y</td>
<td>146.0</td>
<td>104.0</td>
<td>42.0</td>
</tr>
<tr>
<td>Female 3</td>
<td>24/5/2013</td>
<td>45</td>
<td>6446</td>
<td>Y</td>
<td>136.0</td>
<td>102.0</td>
<td>39.0</td>
</tr>
<tr>
<td>Female 4</td>
<td>25/5/2013</td>
<td>38</td>
<td>7292</td>
<td>Y</td>
<td>143.0</td>
<td>97.5</td>
<td>41.0</td>
</tr>
<tr>
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<td>6939</td>
<td>Y</td>
<td>146.0</td>
<td>92.0</td>
<td>42.0</td>
</tr>
<tr>
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<td>8717</td>
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<td>98.0</td>
<td>37.0</td>
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<tr>
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<td>26/5/2013</td>
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<td>150.0</td>
<td>105.5</td>
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<td>22/5/2014</td>
<td>-</td>
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<td>104.5</td>
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<td>95.0</td>
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<td>100.0</td>
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<td>Female 14</td>
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<td>-</td>
<td>-</td>
<td>Y</td>
<td>151.5</td>
<td>97.5</td>
<td>39.0</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td></td>
<td>42 ± 2</td>
<td>7642 ± 336</td>
<td></td>
<td>145 ± 2</td>
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<td>40 ± 1</td>
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Chapter 4: Variation in behaviour and diet of Australian fur seals

Table 4.1 continued

<table>
<thead>
<tr>
<th>Male</th>
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<th>Length</th>
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<td>-</td>
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<td>162.0</td>
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<td>8403</td>
<td>-</td>
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<td>5052</td>
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<td>189.0</td>
<td>126.0</td>
<td>61.0</td>
</tr>
<tr>
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<td>4714</td>
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<td>134.0</td>
<td>56.0</td>
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<td>-</td>
<td>Y</td>
<td>173.0</td>
<td>143.5</td>
<td>51.0</td>
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<tr>
<td>Male 11</td>
<td>2/8/2014</td>
<td>26</td>
<td>-</td>
<td>Y</td>
<td>152.0</td>
<td>130.0</td>
<td>49.0</td>
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<tr>
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<td>2588</td>
<td>Y</td>
<td>179.0</td>
<td>129.5</td>
<td>52.0</td>
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<tr>
<td>Male 13</td>
<td>3/8/2014</td>
<td>27</td>
<td>-</td>
<td>Y</td>
<td>185.5</td>
<td>157.0</td>
<td>56.5</td>
</tr>
<tr>
<td>Male 14</td>
<td>3/8/2014</td>
<td>25</td>
<td>-</td>
<td>-</td>
<td>176.0</td>
<td>135.0</td>
<td>47.0</td>
</tr>
<tr>
<td>Male 15</td>
<td>3/8/2014</td>
<td>23</td>
<td>-</td>
<td>Y</td>
<td>207.0</td>
<td>-</td>
<td>67.0</td>
</tr>
<tr>
<td>Male 16</td>
<td>5/8/2014</td>
<td>20</td>
<td>2836</td>
<td>Y</td>
<td>165.5</td>
<td>118.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>39 ± 5</td>
<td>4789 ± 918</td>
<td>178 ± 4</td>
<td>130 ± 3</td>
<td>55 ± 1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 4: Variation in behaviour and diet of Australian fur seals

Figure 4.1: The overall 95% home range (HR) and 50% core range (CR) utilisation distribution (UD) probabilities of male (blue, n=16) and female (ref, n=14) Australian fur seals and the overall HR and CR UD distribution probabilities in 2013 (green, n=13) and 2014 (black, n=17). All seals were instrumented at Kanowna Island (represented by star), located in northern Bass Strait, south-eastern Australia (inset). Grey lines represent bathymetric contours (in 20 m intervals) to the edge of the continental shelf.
Figure 4.2: The 95% home range and 50% core range utilisation distribution probabilities of male and female Australian fur seals in each year (2013 and 2014). All seals were instrumented at Kanowna Island (represented by star) located in northern Bass Strait. Grey lines represent bathymetric contours (in 20m intervals) to the edge of the continental shelf.
foraging range between males and females over both years of the study (95% HR BA overlap = 0.70 between sexes; Table 4.2), or between sampling years irrespective of sex (95% HR BA overlap = 0.73). Within years, males and females exhibited a high degree of overlap (95% HR BA overlap = 0.60 for 2013; 0.53 in 2014). However, the majority of female and male core foraging areas (50% UD) occurred in different areas of northern and southern Bass Strait, respectively (Figs. 4.1 and 4.2). This was reflected within the 50% CR BA overlap scores of the inter-sex overlap of each year (2013: 0.10; 2014: 0.09; Fig. 4.2) being lower than the intra-sex overlap between years (Female: 0.17; Male: 0.14; Table 4.2).

Within Bass Strait, both sexes utilised the same mode of foraging with 85.8 ± 3.4 % of male and 84.3 ± 3.6 % of female dives considered benthic (GLM: F_{1,18} = 0.06; P = 0.804; Table 4.3). The predominantly benthic behaviour was evident within the mean modal dive depth of each sex (males: 80.8 ± 1.1 m; females: 78.4 ± 3.5 m), which was similar to their maximum dive depth (males: 86.0 ± 0.6 m; females: 84.5 ± 2.1 m), indicating that Australian fur seals, irrespective of sex, regularly dive to the sea floor. Male dive duration was significantly longer than that of females (231.9 ± 14.1 s compared to 154.3 ± 9.6 s, respectively; GLM F_{1,18} = 22.23, P < 0.0001). While a longer dive duration presumably enabled males to spend a greater periods of absolute time at the bottom phase of the dive (152.6 ± 10.9 s compared to 91.4 ± 6.5 s for males and females, respectively; GLM: F_{1,18} = 26.48, P < 0.0001), they allocated a greater proportion of their dive time to the bottom phase (61.9 ± 1.5 % and 54.5 ± 1.5 % for males and females, respectively; GLM: F_{1,18} = 10.94, P = 0.004). Measures of foraging effort also differed between the sexes, with females
Table 4.2: Bhattacharyya’s affinity (BA) scores for the 95% home range (HR) and 50% core range (CR) utilisation distribution probabilities estimated for each year (2013 and 2014) and sex (male and female) presented in Figure 4.1. The lower panel represents the BA scores for each sex in their respective year (presented in Figure 2). **Bold typeface** represents the BA overlap score for the corresponding 95% HR utilisation distribution. **Italicised typeface** represents the BA overlap score for the corresponding 50% CR utilisation distribution.

<table>
<thead>
<tr>
<th></th>
<th>95% HR</th>
<th>50% CR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male:Female</td>
<td>0.70</td>
<td>0.08</td>
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<tr>
<td>2013:2014</td>
<td>0.73</td>
<td>0.12</td>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>Male 2013</th>
<th>Female 2013</th>
<th>Male 2014</th>
<th>Female 2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male 2013</td>
<td>-</td>
<td>0.60</td>
<td>0.58</td>
<td>0.56</td>
</tr>
<tr>
<td>Female 2013</td>
<td>0.10</td>
<td>-</td>
<td>0.61</td>
<td>0.62</td>
</tr>
<tr>
<td>Male 2014</td>
<td>0.14</td>
<td>0.14</td>
<td>-</td>
<td>0.53</td>
</tr>
<tr>
<td>Female 2014</td>
<td>0.06</td>
<td>0.17</td>
<td>0.09</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 4.3: Variation in dive behaviour between male and female Australian fur seals. All values are presented as mean ± SE. Sex and year differences were assessed using generalised linear models (GLMs) and statistical significance was considered as $P < 0.05$. Year was not significant in any model ($P > 0.05$ in all cases) and, therefore, results reported are for the final model containing only sex as a predictor variable. Significant sex differences in dive behaviour are denoted by **bold typeface** and an asterix (*).

<table>
<thead>
<tr>
<th>Dive behaviour</th>
<th>Male (n=8)</th>
<th>Female (n=12)</th>
<th>GLM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dive duration (s)</td>
<td>231.9 ± 14.1</td>
<td>154.3 ± 9.6</td>
<td>$F_{1,18} = 22.23; P = &lt; 0.0001^*$</td>
</tr>
<tr>
<td>Descent rate (m·s$^{-1}$)</td>
<td>1.7 ± 0.1</td>
<td>1.9 ± 0.1</td>
<td>$F_{1,18} = 14.43; P = 0.001^*$</td>
</tr>
<tr>
<td>Ascent rate (m·s$^{-1}$)</td>
<td>1.8 ± 0.1</td>
<td>1.9 ± 0.1</td>
<td>$F_{1,18} = 5.68; P = 0.028^*$</td>
</tr>
<tr>
<td>Max depth (m)</td>
<td>86.0 ± 0.6</td>
<td>84.5 ± 2.1</td>
<td>$F_{1,18} = 0.55; P = 0.469$</td>
</tr>
<tr>
<td>Modal dive depth (m)</td>
<td>80.8 ± 1.1</td>
<td>78.4 ± 3.5</td>
<td>$F_{1,18} = 0.94; P = 0.346$</td>
</tr>
<tr>
<td>Bottom time (s)</td>
<td>152.6 ± 10.9</td>
<td>91.4 ± 6.5</td>
<td>$F_{1,18} = 26.48; P = &lt; 0.0001^*$</td>
</tr>
<tr>
<td>Prop. of dive time on bottom (%)</td>
<td>61.9 ± 1.5</td>
<td>54.5 ± 1.5</td>
<td>$F_{1,18} = 10.94; P = 0.004^*$</td>
</tr>
<tr>
<td>Prop. Benthic dives (IDZ; %)</td>
<td>85.8 ± 3.4</td>
<td>84.3 ± 3.6</td>
<td>$F_{1,18} = 0.06; P = 0.804$</td>
</tr>
<tr>
<td>Dive frequency (dives·h$^{-1}$)</td>
<td>6.4 ± 0.3</td>
<td>8.4 ± 0.5</td>
<td>$F_{1,18} = 10.75; P = 0.004^*$</td>
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<tr>
<td>Dive rate (m·h$^{-1}$)</td>
<td>905.8 ± 24.8</td>
<td>1072.2 ± 46.3</td>
<td>$F_{1,18} = 7.55; P = 0.013^*$</td>
</tr>
<tr>
<td>Prop. time spent diving (%)</td>
<td>40.6 ± 1.6</td>
<td>35.8 ± 0.02</td>
<td>$F_{1,18} = 2.53; P = 0.130$</td>
</tr>
</tbody>
</table>
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having a higher dive rate than males (1072.2 ± 46.3 m·h⁻¹ compared to 905.8 ± 24.8 m·h⁻¹; GLM: F₁,₁₈ = 7.55, P = 0.013) and making more dives per hour than males (8.4 ± 0.5 dives h⁻¹ compared to 6.4 ± 0.2 dives h⁻¹; GLM: F₁,₁₈ = 10.75, P = 0.004). For all models investigating dive behaviour, no significant difference between years were detected for either sex (P > 0.05 in all cases; Table 4.3).

Dietary analyses

A total of 37 individual fatty acids were identified within the blubber samples of the Australian fur seals. On average, the most abundant fatty acids present within the blubber samples were 16:0 (25.55 ± 1.27%), 18:1n-6 (12.64 ± 2.42%), 22:6n-3 (11.03 ± 1.76%), 18:1n-9 (8.31 ± 0.56%), 18:1n-7 (8.16 ± 1.53%) (Fig. 4.3). On average, saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), and polyunsaturated fatty acids (PUFAs) each contributed 43.98 ± 2.42%, 33.88 ± 3.87% and 22.14 ± 3.15% to the overall fatty acid composition of individuals, respectively. The fatty acid composition differed significantly by year (PERMANOVA, F₁,₁₂₅ = 12.78, P = 0.0001), but not by sex (F₁,₁₂₅ = 2.00, P = 0.0893; Fig. 4.4). However, when taking year into account (i.e. interaction between year and sex), the relationship trended towards significance (F₁,₁₂₅ = 2.44, P = 0.052).

The results of the QFASA model determined that a total of 17 prey species (out of 75 potential prey; Table S4.1) were consumed by seals in the present study (Fig. 4.5). Individuals in 2013 consumed a greater variety of prey, with 13 species identified compared to 11 in 2014. Seven prey species were consumed by seals in
Figure 4.3: Mean proportion (± SE, %) of the individual fatty acids identified in male and female Australian fur seals. Each sex and year was characterised by differences in their saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA).
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Figure 4.4: Fatty acid composition of Australian fur seals differed significantly by year (PERMANOVA, $F_{1,25} = 12.78$, $P = 0.0001$) but not by sex ($F_{1,25} = 2.00$, $P = 0.0893$). The interaction between year and sex was not statistically significant ($F_{1,25} = 2.44$, $P = 0.052$). The 95% CI ellipses represent the inter-year and inter-sex differences in fatty acid composition of Australian fur seals.
Figure 4.5: The estimated dietary composition (mean ± SE) of Australian fur seals in 2013 (n=10) and 2014 (n=16) determined using quantitative fatty acid signature analysis (QFASA) of blubber samples. The fatty acid composition of Australian fur seals, as a proxy for their dietary composition, differed significantly by year (PERMANOVA, F_{1,25} = 12.78, P = 0.0001).
both years: arrow squid (*Nototodarus gouldi*; 8.6 ± 2.4 % and 59.7 ± 12.2 %, respectively), Australian angel shark (*Squatina australis*; 5.3 ± 2.5 % and 2.2 ± 10.5 %), blue mackerel (*Scomber australasicus*; 20.5 ± 4.1 % and 1.0 ± 4.0 %), broadnose shark (*Notorynchus cepedianus*; 2.1 ± 4.4 %), dark banded whiptail (*Caelorinchus maurofasciatus*; 7.1 ± 3.9 % and 3.2 ± 5.6 %), greenback flounder (*Rhombolecoa tapirina*; 8.2 ± 5.1 % and 27.4 ± 5.8 %), and southern calamari (*Sepioteuthis australis*; 5.8 ± 4.6 % and 0.5 ± 3.6 %). In 2013, seven prey species accounted for a total of 83.5% of the dietary composition, with blue mackerel and dusky shark considered the predominant prey items (20.5 ± 4.1 % and 27.9 ± 5.9 %, respectively). However, only two species: arrow squid and green black flounder; contributed greater than 87% of the total dietary composition in 2014 (59.7 ± 12.2 % and 27.4 ± 5.8%, respectively). While not statistically significant (*P* = 0.052), within each year males and females showed some variation in the species of prey consumed which could have biological implications (Fig. 4.6).

**Discussion**

*Temporal variability in behaviour and diet*

Irrespective of sex, Australian fur seals foraged within Bass Strait. There was little variation in their foraging range or dive behaviour between years, with both males and females being characterized by a benthic foraging mode. This is consistent with prior studies investigating the spatial distribution and dive behaviour of...
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Figure 4.6: The estimated dietary composition of male and female Australian fur seals in 2013 (n=3 male and 7 female, respectively) and 2014 (n=10 male and 7 female, respectively) determined using quantitative fatty acid signature analysis (QFASA) of blubber). Variation of fatty acid profiles of male and female Australian fur seals in 2013 and 2014, as a proxy for their dietary composition, did not differ statistically (PERMANOVA $F_{1,25} = 2.44$, $P = 0.052$).
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Australian fur seals (Arnould & Hindell 2001, Hoskins et al. 2015a, Kernaléguen et al. 2015a) **(Chapters 2 and 3)**. Given their limited foraging range, Australian fur seals are expected to be heavily influenced by local environmental conditions that influence the distribution and abundance of prey resources within Bass Strait. Indeed, several studies have documented Australian fur seal responses to seasonal and inter-annual fluctuations in environmental conditions (e.g. Gibbens et al. 2010, Arnould et al. 2011, Hoskins & Arnould 2014, Knox et al. 2014). Consistent with these studies, the diet of Australian fur seals varied considerably between study years.

Given that the Australian fur seal are considered a generalist predator that forages upon a range fish, cephalopods and elasmobranchs (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004, Page et al. 2005b, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Kliska 2015, Hoskins et al. 2017), it was not surprising that the QFASA models determined that a large number (n=13) of prey species were consumed by seals in 2013. However, in 2014 QFASA models revealed that arrow squid was by far the most important prey biomass consumed by seals in 2014, constituting 59.7% of their total dietary composition. Reported by multiple studies, arrow squid has previously been shown to be important prey within the diet of Australian fur seals (Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Kliska 2015). However, variability in the size and quantity of arrow squid consumed by Australian fur seals has been shown to fluctuate with local environmental conditions (Kirkwood et al. 2008, Kliska 2015). Warmer ocean temperatures provide favourable conditions for the growth of cephalopods and may lead to a greater biomass of arrow squid becoming available to Australian fur seals (Jackson &
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Domeier 2003). Indeed, mean annual sea-surface temperatures in central Bass Strait (38.5-40.2°S, 144.1-146.8°E) were higher in 2013 and 2014 when compared to the previous three years (2010-2012; AVHRR, 4km resolution, CSIRO Oceans and Atmospheric Remote Sensing; Fig. S4.1). Therefore, an increase in arrow squid biomass during the time of sampling may explain the prevalence of this prey species in the diet of Australian fur seals during 2014.

While these results are compelling, the present study is limited by its ability to detect new prey species and, therefore, the study animals may have consumed additional prey species. The interpretation of the fatty acid profiles of seals and resulting QFASA models were limited by the potential prey species that have previously been reported within the diet of Australian fur seals and also by the availability of prey fatty acid profile data. Consequently, diet could only be inferred from 75 potential prey species and the present study was not able to report any previously unreported prey species. Nonetheless, this study provides interesting results regarding the temporal variability of prey species consumed by Australian fur seals and it would be useful to undertake further investigations as new data becomes available.

Niche segregation

Variation in the fatty acid composition of seals, as a proxy for their dietary composition, did not differ statistically between male and female Australian fur seals. Both sexes remained to forage within the confines of the continental shelf and so it
was not surprising that QFASA models revealed that males and females exhibited considerable niche overlap and consumed similar prey. The limited dietary variation between sexes observed in the present study contrasts many other pinniped species, as males and females of these species usually forage in discrete areas or exhibit variation in behaviour that promotes sex-specific diets (e.g. Beck et al. 2005, Page et al. 2005a, Beck et al. 2007, Trites & Calkins 2008, Kernaléguen et al. 2012). As male and female Australian fur seals exhibit a high degree of spatial overlap within the benthic habitats of Bass Strait they presumably foraging upon similar prey resources and encounter a higher degree of intraspecific competition.

Australian fur seals appear to exhibit a lower degree of sex-specific resource partitioning when compared to other pinnipeds (e.g. Page et al. 2005b, Cherel et al. 2007, Kernaléguen et al. 2012, Kernaléguen et al. 2015a). However, the strong presence of arrow squid and greenback flounder in the diet of seals during 2014 may have influenced the findings of the present study, as sex differences in dietary composition trended towards significance when taking year into account. Predators will balance a trade-off between the cost of searching for preferred, nutrient rich prey and targeting lower quality but abundant resources (Womble & Sigler 2006). In 2014, both sexes may have responded similarly to a substantial increase in the availability and abundance of arrow squid and greenback flounder within Bass Strait. In contrast, there appeared to be some difference in the dietary composition of males and females in 2013, with females and males consuming a broader range of resources. During periods where there lacks a dominant resource type, differences in morphology may influence the foraging ability and prey selection of each sex,
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thereby leading to subtle sex differences in diet that was not able to be detected in the present study.

Being larger in size than females, males have greater absolute energetic requirements when compared to females (Mysterud 2000). However, a larger body size also enables males to handle larger prey more efficiently, and provides them with a greater physiological capacity (Weise et al. 2010). These advantages likely translate into males being better adept at searching for large cryptic prey, which is likely to be particularly beneficial for a benthic foraging species (Beck et al. 2003). While the present study was unable to determine the size class of prey consumed by seals, males were able to dive for longer than females and spent longer in the foraging zone of the dive (bottom time). In contrast, the smaller body size limits the diving ability of a female and they are required to surface more regularly than males. However, optimum dive models suggest that benthic divers, such as Australian fur seals, will aim to maximise their time spent foraging along the sea-floor (Houston & Carbone 1992). Indeed, females exhibited higher measures of foraging effort (dive rate, dive frequency, descent/ascent rates), appearing to compensate for the reduced time they have to search for benthic prey resources. Similar sex-related differences in dive behaviour have been observed in other pinniped species (e.g. Hindell et al. 1991, Le Boeuf et al. 1993, Campagna et al. 2001, Beck et al. 2003, Page et al. 2005a, Staniland & Robinson 2008, Weise et al. 2010). When operating within the limitations of their aerobic capacity, males may be able to access a greater range of resources when compared to females. Hence, while we did not detect sexual
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Segregation in diet, presumably there is potential for resource partitioning in the diet of Australian fur seals.

In summary, Australian fur seal diet, irrespective of sex, is mediated by annual fluctuations in prey availability, abundance and distribution within Bass Strait. As both male and female Australian fur seals remained to forage within the confines of the marine basin, they rely heavily on the resources within the region which may fluctuate on a seasonal or annual basis. Although resource partitioning between sexes was not detected in the present study, sexual segregation may still occur due to the contrasting constraints on the foraging ability of each sex. For example, the larger body size of males presumably enables them to consume larger prey and consume prey resources that may be more difficult to capture or handle, which cannot be detected using fatty acid analysis. However, given substantial spatial overlap between males and females, it would be expected that the degree of niche segregation would be lower when compared to other species that exhibit extreme sexual-size dimorphism and where each sex forages within discrete foraging zones. Accordingly, temporal trends and consideration for sex-specific diets should be taken into account for future studies investigating the role of Australian fur seals within Bass Strait.
### Table S4.1: List of 75 Australian fur seal prey species included as potential prey in the QFASA model.

Fatty acid data for each species were obtained from the literature (Nichols et al. 1998, Mooney et al. 2002).

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alfonsino</td>
<td>Beryx splendens</td>
</tr>
<tr>
<td>Arrow squid</td>
<td>Nototodaros gouldi</td>
</tr>
<tr>
<td>Australian angel shark</td>
<td>Squatina australis</td>
</tr>
<tr>
<td>Australian bonito</td>
<td>Sarda australis</td>
</tr>
<tr>
<td>Baby octopus</td>
<td>Octopus australis</td>
</tr>
<tr>
<td>Banded morwong</td>
<td>Cheilodactylus spectabilis</td>
</tr>
<tr>
<td>Barracouta</td>
<td>Thrysites atun</td>
</tr>
<tr>
<td>Bay flounder</td>
<td>Ammotretis rostratus</td>
</tr>
<tr>
<td>Black bream</td>
<td>Acanthopagrus butcheri</td>
</tr>
<tr>
<td>Blue grenadier</td>
<td>Macruconus novaezelandiaeae</td>
</tr>
<tr>
<td>Blue mackerel</td>
<td>Scomber australasicus</td>
</tr>
<tr>
<td>Blue morwong</td>
<td>Nemadactylus valenciennesi</td>
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<tr>
<td>Blue warehou</td>
<td>Seriolella brama</td>
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<tr>
<td>Blue-throated Wrasse</td>
<td>Notolabrus tetricus</td>
</tr>
<tr>
<td>Broadnose shark</td>
<td>Notorynchus cepedianus</td>
</tr>
<tr>
<td>Butterfly gurnard</td>
<td>Lepidotrigla vanessa</td>
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<td>Calamari spp.</td>
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<td>Maori rockcod</td>
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Chapter 4: Variation in behaviour and diet of Australian fur seals

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<td>Yellowfin bream</td>
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Figure S4.1: Mean (±SE) annual sea-surface temperature data for central Bass Strait (38°30’-40°12’S, 144°5’-146°48’E) between 2010 and 2014. Data were extracted from the Advanced Very High Resolution Radiometer (AVHRR) at a 4 km resolution courtesy of CSIRO Oceans and Atmospheric Remote Sensing.
Chapter 5: Blubber fatty acids reveals variation in the diet of male Australian fur seals

A version of this chapter has been submitted for publication as:

Chapter 5: Variation in the diet of male Australian fur seals

Abstract

Top order predators play an important role in the structure and function of marine ecosystems. Optimal foraging theory predicts that predators will utilise foraging strategies that maximise their net energetic intake and, consequently, individuals within a population may utilise different strategies to target different prey resources. The present study investigated variation within the diet of 41 male Australian fur seals (*Arctocephalus pusillus doriferus*) using quantitative fatty acid signature analysis (QFASA) of blubber. The study was conducted during the pre-breeding seasons of 2012 and 2013 and the non-breeding seasons of 2013 and 2014 at a colony on Kanowna Island (39°10’S, 146°18’E) in northern Bass Strait, southeastern Australia. QFASA models revealed that while males consumed prey commonly reported within the diet of Australian fur seals, elasmobranchs appear to be consumed in greater proportion to the rest of the species. These results suggest that sole examination of female diet is not representative for Australian fur seals. Prey composition also varied between males which may reflect individuals using different strategies to target different resources, serving to broaden the trophic niche of a species and reduce intraspecific competition. Furthermore, substantial temporal variation in male diet was apparent presumably reflecting variation in the distribution, availability and abundance of prey resources within Bass Strait at the time of sampling. Given that the energetic content of prey is expected to differ between species, temporal variation in dietary composition presumably has important implications for the growth and reproductive success of males.
Chapter 5: Variation in the diet of male Australian fur seals

Introduction

Top order predators play an important role in the structure and function of ecosystems and many are considered to be sentinels of ecosystem change (Williams et al. 2004, Bossart 2006, Estes et al. 2016). Predators consume large amounts of prey biomass and, can have important effects on the overall trophic dynamics of an ecosystem (Mills et al. 1993). Predators may also move large distances and play an important role in linking disparate ecosystems through the redistribution of nutrients over large spatial scales (Estes et al. 2016). Knowledge of how predators interact with prey populations is fundamental to better understanding of overall ecosystem process and has important implications for the management and conservation of predator and prey populations (Lomnicki 1978, Costa et al. 2010). However, empirical studies often consider individuals within predator populations as ecologically equivalent and assume that sampled individuals are representative of the whole population (Bolnick et al. 2011). This may be problematic as individuals within predator populations can vary substantially in their resource use.

Optimal foraging theory suggests that predators will utilise foraging strategies that maximises their net energetic intake (Stephens & Krebs 1987). Given that several intrinsic factors can vary substantially within a population (e.g. morphology, physiology, breeding status and experiences), individuals may utilise different optimal foraging strategies to target different prey resources (Polis 1984, Pyke 1984, Mysterud 2000, Bolnick et al. 2003, Ruckstuhl & Neuhaus 2005). Furthermore, extrinsic factors, such as inter-and intra-specific competition and temporal fluctuations in prey resources may influence the long-term profitability of foraging
Chapter 5: Variation in the diet of male Australian fur seals

strategies (Ashmole 1963, Birt et al. 1987, Svanbäck & Bolnick 2007, Wege et al. 2016). Individuals may alter their behaviour or dietary composition to maximise their net energetic intake while foraging (Paltridge 2002, Eide et al. 2005). Such inter- and intra- individual variation in behaviour can lead to ecologically significant variation in resource use (Bolnick et al. 2003, Bolnick et al. 2011). Furthermore, species that exhibit intra- and inter- individual variation in foraging behaviour and diet may have a better ability to respond to environmental perturbations as individuals would not be affected equally (Svanbäck & Bolnick 2007, Bolnick et al. 2011).

In marine ecosystems, determining the dietary composition of predators can be challenging due to the complex nature of trophic dynamics and the logistical difficulties of observing predator-prey interactions that usually occur at depth (Boyd et al. 1994). Consequently, indirect techniques such as quantitative fatty acid signature analysis (QFASA) have been used to infer the diet of marine predators (e.g. Smith et al. 1997, Herman et al. 2005, Budge et al. 2006, Thiemann et al. 2008, Bromaghin et al. 2013, Banks et al. 2014). This technique allows for the quantitative estimate of a predators’ dietary composition. Predator fatty acid signatures are modelled as a mixture of prey fatty acid signatures after using calibration coefficients to account for the differential metabolism of individual fatty acids (Iverson et al. 2004, Iverson 2009). As blubber contains lipids that have been accumulated over time, it can provide a record of dietary intake over a period of weeks to months (Budge et al. 2006). QFASA of blubber can be used to detect inter-population, spatial and temporal variation in the diet of predators (Iverson et al. 1997a, Iverson et al. 1997b, Smith et al. 1997, Best et al. 2003, Beck et al. 2005, Baylis & Nichols 2009).
Chapter 5: Variation in the diet of male Australian fur seals

The Australian fur seal (*Arctocephalus pusillus doriferus*) is a large marine predator endemic to the south-eastern Australia region (Warneke & Shaughnessy 1985) It is the largest of all fur seal species, with males and females weighing on average 279 kg and 76 kg, respectively (Arnould & Warneke 2002). The species has a breeding range that is restricted to the continental shelf between mainland Australia and Tasmania and an estimated population size of *ca* 120,000 individuals (Kirkwood et al. 2010). Consequently, the species represents an important resident consumer of marine resources within south-eastern Australia.

The Australian fur seal is an opportunistic predator, known to forage on > 100 prey species (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004, Page et al. 2005b, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Arnould et al. 2011, Kliska 2015, Hoskins et al. 2017). However, studies have shown that Australian fur seals exhibit temporal, spatial and individual variation in their foraging strategies and dietary composition (Littnan et al. 2007, Kirkwood et al. 2008, Arnould et al. 2011, Hoskins et al. 2015b, Kernaléguen et al. 2015b, Kliska 2015). Most of the studies investigating the diet of Australian fur seals have obtained data from lactating females, or from samples collected opportunistically at breeding colonies where there is a large female presence (e.g. (Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Arnould et al. 2011, Kliska 2015). In contrast, comparatively fewer studies have investigated the diet of male Australian fur seals (Knox et al. 2014) *(Chapter 4)* and, consequently, it remains unclear if they exhibit the same dietary variation that has been previously reported in females. Given that males represent an important component of the species' biomass, the aims of the
present study were to use fatty acid analysis of blubber samples to investigate: (1) the dietary composition of male Australian fur seals; (2) whether diet varies between males; and (3) seasonal variation in dietary composition.

**Materials and methods**

*Biopsy extraction and fatty acid analyses*

The study was conducted at the Australian fur seal colony on Kanowna Island (39°10’S, 146°18’E) in central northern Bass Strait, south-eastern Australia. Kanowna Island is the third largest Australian fur seal colony with an annual pup production of ca 3,400 pups (Kirkwood et al. 2010). Sample collection was conducted immediately prior to the breeding season in late spring/summer (October – December; hereafter referred to as ‘pre-breeding’) of 2012 and 2013 and during the winter non-breeding seasons (June – August; hereafter ‘non-breeding’) of 2013 and 2014.

In the pre-breeding season of 2012, biopsy samples were collected from the posterior flank of males using an 8 mm biopsy head attached to an arrow launched by a crossbow (Sanlida Chase Wind 90 lbs) Kernaléguen et al. (2016b). For both non-breeding seasons and the pre-breeding season of 2013, individual males were chemically immobilised using a 1:1 mixture of tiletamine zolazepam (Zoletil, Virbac, Milperra, N.S.W., Australia; ca 1 mg kg$^{-1}$ of estimated mass), remotely administered via darts propelled by a CO$_2$ powered tranquiliser gun (Dan Inject JM Standard, Harcourt, Vic., Australia). Anaesthesia was maintained during the handling procedure using isoflurane delivered via a portable gas vaporizer (Stinger TM,
Chapter 5: Variation in the diet of male Australian fur seals

Advanced Anaesthesia Specialists, Gladesville, N.S.W., Australia). A small incision (ca 1 cm) was made using a scalpel blade through the skin along the posterior flank of each seal. A 6 mm biopsy punch was then inserted into the incision and a whole-blubber core was taken from the skin layer to the muscle layer. Morphometric data (standard length, axillary length and the length of right flipper; ± 0.5 cm) were also recorded.

Blubber samples were stored frozen at -20°C until lipid extraction. In the laboratory, thawed samples were extended to their full length and any muscle, skin or hair left attached to the adipose tissue was removed. Several prior studies have documented vertical stratification within the blubber samples of marine mammal species, including the conspecific Cape fur seal (A. p. pusillus), which may affect dietary interpretation (Best et al. 2003, Arnould et al. 2005, Guerrero & Rogers 2017). Therefore, blubber samples were homogenized prior to lipid extraction (Lambert et al. 2013).

Lipids were quantitatively extracted from weighed homogenized blubber samples (30-40 mg) using a modified overnight Bligh and Dyer (1959) method. Methanol washed 10 mL glass tubes with Teflon lids (Kimble) were used throughout to minimise fatty acid contamination. To each sample, 0.750 mL of 2:1 chloroform:methanol was added and then samples homogenized using an IKA Ultra-turrex stick tissue disruptor. Samples were agitated overnight at room temperature followed by the addition of 0.38 mL of water. Tubes were then shaken for 30 min and centrifuged at 2000 rpm for 5 min. The bottom lipid layer was transferred to pre-weighed glass tubes and dried under vacuum (Christ speed vac) before being re-
Chapter 5: Variation in the diet of male Australian fur seals

weighed. The lipid extract was re-constituted in 45 µL chloroform:methanol containing 100 µM d27 myristic acid as an internal standard then derivatized with 5 µL Methprep II (Grace) to produce fatty acid methyl esters (FAMES).

The FAMES were then analyzed using a Trace DSQ gas chromatography mass spectrometer (GC-MS; Thermofisher) with a 100 m x 0.25 mm 0.2 µm film TR-FAME column (Thermofisher). The following temperature gradient and instrument settings were used: the GC columns initial temperature was 140°C; this was held for 5 min then ramped at 4°C/min to 240°C; and then a 15 min hold giving a total runtime of 45 min. An 11 min solvent delay was used on the MS which scanned from 40-400 m/z at 1.5 scans per second. For quantitation, a standard curve from 1-100 µm of free fatty acids (Nuchekprep mix 463) were converted to FAMES as above. Peak areas were determined using Xcalibur quantitative analysis software (Thermo). Peak area ratios using the internal standard were used for quantitation. Concentrations of individual fatty acids were converted into a proportion of total fatty acids by mass (%). To improve normality, fatty acids were transformed using a log transformation designed for proportional data: x_{trans} = \ln(x_i/c_r); where x_i is a given fatty acid and c_r a reference fatty acid, in this case C18:0 was used (Budge et al. 2006).

Statistical analyses

To investigate variation in fatty acid composition of individuals between seasons a permutational multivariate ANOVA (PERMANOVA) was run in the R package vegan (Oksanen et al. 2018). Within the PERMANOVA, season was
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included as a four-level factor (interaction of field season and year), as was morphometric variables (standard length, axial length, flipper length, and the ratio of flipper length and standard length) against the fatty acid data (%). Statistical significance was determined using 9999 unrestricted permutations of the proportional (%) fatty acid data. Predictor variables were dropped using backwards stepwise-selection until all terms in the PERMANOVA were significant.

Examination of non-metric multidimensional scaling (nMDS) plots obtained in the PERMANOVA analysis suggested that some seals within each season exhibited large differences in their fatty acid profiles. To place seals into cluster groups according to similarities in their fatty acid composition, a principal component analysis (PCA) was first conducted on the proportional fatty acid data to reduce its dimensionality. Only principal components (PC’s) with eigenvalues > 1 were retained. Then, an agglomerative hierarchical clustering analysis with Euclidean distance and Ward’s linkage criterion was conducted on the retained PC’s. The optimal number of clusters was then selected using a model-based clustering technique (Fraley & Raftery 2002) and Bayesian Information Criteria (BIC) in the R package mclust (Fraley et al. 2012).

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Australian region (Nichols et al. 1998, Mooney et al. 2002). Fatty acid profiles of prey are assumed to be representative of respective prey species consumed by Australian fur seals in the present study. Calibration coefficients do not exist for Australian fur seals, therefore, to account for predator metabolism of fatty acids, calibration coefficients obtained for Steller sea lions (*Eumetopias jubatus*; Rosen & Tollit 2012) were used in the QFASA model, with the assumption that Steller sea lion calibration coefficients are appropriate for inferring the diet of Australian fur seals. Only fatty acids that were present in the three data sets (predator, prey, and calibration coefficients) were included in the QFASA model. The resulting QFASA model determined the most likely prey composition of seals for each season, and for each cluster based on the combination of available prey (Table S5.1). All data are presented as mean ± SE and statistical significance was considered when $P < 0.05$.

**Results**

A total of 41 biopsies were obtained from male Australian fur seals, with 12 in the pre-breeding season of 2012, three in the non-breeding season of 2013, 17 in the pre-breeding season of 2013 and nine in the non-breeding season of 2014 (Table 5.1). A total of 37 individual fatty acids were identified within the seal data set. On average, the most abundant fatty acids that were present within the blubber samples were 16.0 (23.5 ± 1.2%), 18.1p (14.2 ± 2.6%), 18.1w7 (11.0 ± 2.0%), 18.1w9 (10.1 ± 0.6%), 18.0 (7.8 ± 0.7%). Saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) each contributed 40.7 ± 2.2%,
Chapter 5: Variation in the diet of male Australian fur seals

Table 5.1: Summary data from 41 male Australian fur seals sampled at Kanowna Island in south eastern Australia between 2012 and 2014. Pre-breeding field seasons were conducted in the months of Oct-Dec of 2012 and 2013, while non-breeding field seasons were conducted between May-Jun of 2013 and 2014. As biopsies for 2012 males were retrieved remotely (see text for details) morphometric measurements were not available. Some morphometrics were not available for all seals and, therefore, sample sizes are given for each variable. The ratio of flipper length and standard length of individuals is represented as ‘FL/STL’. All results are presented as mean ± SE.

<table>
<thead>
<tr>
<th>Season</th>
<th>Biopsy (n)</th>
<th>Standard length (cm; n = 27)</th>
<th>Axis (cm; n = 24)</th>
<th>Axillary girth (cm; n = 18)</th>
<th>Flipper length (cm; n = 29)</th>
<th>FL / STL (n = 27)</th>
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<td>12</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>(Oct – Dec)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Non-breeding 2013</td>
<td>3</td>
<td>168.7 ± 3.4</td>
<td>75.3 ± 3.5</td>
<td>127.7 ± 5.7</td>
<td>54.8 ± 3.4</td>
<td>0.32 ± 0.02</td>
</tr>
<tr>
<td>(May – Jun)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-breeding 2013</td>
<td>17</td>
<td>194.3 ± 2.2</td>
<td>78.5 ± 1.6</td>
<td>171.6 ± 5.8</td>
<td>53.6 ± 0.4</td>
<td>0.27 ± &lt;0.01</td>
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<tr>
<td>(Oct – Dec)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-breeding 2014</td>
<td>9</td>
<td>177.1 ± 5.2</td>
<td>79.0 ± 2.5</td>
<td>135.3 ± 5.5</td>
<td>54.2 ± 1.8</td>
<td>0.31 ± 0.01</td>
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<tr>
<td>(May – Jun)</td>
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<tr>
<td>Mean ± SE</td>
<td>10.3 ± 2.9</td>
<td>185.7 ± 2.8</td>
<td>78.3 ± 1.2</td>
<td>152.2 ± 5.8</td>
<td>53.9 ± 0.7</td>
<td>0.29 ± &lt;0.01</td>
</tr>
</tbody>
</table>
Chapter 5: Variation in the diet of male Australian fur seals

45.8 ± 3.2% and 12.9 ± 1.9% to the overall fatty acid composition of individuals, respectively.

PERMANOVA analysis revealed that the fatty acid composition, as a proxy for dietary composition, of seals differed significantly over the duration of the study (PERMANOVA F_{1,40} = 3.508, \( P = 0.0248 \); Fig. 5.1). Seals sampled in both pre-breeding periods were highest in saturated fatty acids (44.3 ± 5.0% and 43.0 ± 3.8% for 2012 and 2013, respectively; Fig. 5.2), and exhibited moderate levels of monounsaturated fatty acids (46.0 ± 5.7% and 50.1 ± 4.5%, respectively), and polyunsaturated fatty acids (18.3 ± 3.2% and 17.4% and 3.2%, respectively). The fatty acid profiles of these males presumably reflect their broad variation in dietary composition. Males in 2012 consumed 18 of 20 total prey species detected by QFASA analysis, and 2013 males consumed 14 prey species (Fig. 5.3). While there was no dominant prey species in 2012, a large proportion of the 2013 pre-breeding diet was comprised of alfonsino (\textit{Beryx splendens}; 40.2 ± 6.1%). Males in the 2013 non-breeding period were the highest in monounsaturated fatty acids (69.1 ± 1.3%) but lowest in polyunsaturated fatty acids (5.2 ± 1.3%), reflecting an increase in the consumption of dusky shark (\textit{Carcharhinus obscurus}; 41.1 ± 1.2%) and blue mackerel (\textit{Scomber australasicus}; 37.1 ± 4.5%). In contrast, 2014 non-breeding males were highest in polyunsaturated fatty acids (58.1 ± 4.9%), consuming the greatest proportion of arrow squid (\textit{Notodarus gouldi}; 50.2 ± 9.1%) and greenback flounder (\textit{Rhombosolea tapirina}; 30.2 ± 7.8%).
Figure 5.1: A permutational multivariate ANOVA (PERMANOVA) revealed that the fatty acid composition of Australian fur seals differed over the duration of the study ($F_{1,40} = 3.508, P = 0.0248$). Ellipsoid hulls represent the differences in fatty acid composition of seals between the pre-breeding season (Oct-Dec) of 2012 (n=12; red square), non-breeding (May-Jun) season of 2013 (n=3; green triangle), pre-breeding season of 2013 (n=17; blue circle), and non-breeding season of 2014 (n=9; black diamond).
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Figure 5.2: Mean proportion (SE; %) of individual fatty acids identified in male Australian fur seal blubber samples. Each season was characterised by variation in the saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA) indicating dietary variation.
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Figure 5.3: The estimated dietary composition (mean ± SE) of male Australian fur for each season determined using quantitative fatty acid signature analysis (QFASA). The fatty acid composition of Australian fur seals, as a proxy for their dietary composition, differed significantly over the duration of the study (PERMANOVA, $F_{1,40} = 3.508$, $P = 0.0248$).
Chapter 5: Variation in the diet of male Australian fur seals

Hierarchical clustering of the dissimilarity matrix created from the five retained PC’s (accounting for 82.6% of the total variation within the dataset) produced a dendrogram that largely reflected seasonal variation in fatty acid composition. A Gaussian finite mixture model determined that the optimal cluster model contained three distinct clusters (Fig. 5.4). Clusters one, two and three each contained 21, 5 and 15 seals, respectively. Although most seals sampled in the same season were closely related (i.e. occurred within the same branch of the dendrogram), individual variation in diet within each season was apparent as seals from the same season were dispersed among the clusters. Seals in cluster one were highest in saturated fatty acids (39.2 ± 3.8%) and monounsaturated fatty acids (56.2 ± 4.1%), while being lowest in polyunsaturated fatty acids (9.6 ± 0.9%; Fig. 5.5). Clusters two and three exhibited similar levels of saturated fatty acids (47.3 ± 4.6% and 42.2 ± 2.8%, respectively) but were differentiated by cluster two being lower in monounsaturated fatty acids (25.8 ± 3.4% and 38.0 ± 4.3% for clusters two and three, respectively) and higher in polyunsaturated fatty acids (52.8 ± 12.4% compared to 39.1 ± 3.9, respectively). This variation in fatty acid profiles reflected the dietary differences of seals in each of the three clusters, with cluster one consisting of individuals that consumed greater proportions of elasmobranchs, cluster two consisting of individuals that consumed high proportions of arrow squid, and cluster three consisting of seals that exhibited the broadest dietary composition.
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Figure 5.4: Results of the hierarchical clustering analysis of blubber fatty acids indicated inter-individual variation within the diet of male Australian fur seals (n=41). Clustering was determined using Ward’s linkage criterion and used the individual scores of the five retained PC’s determined in a PCA (accounting for 82.6 % of the total variation; see text for details). Bayesian Information Criteria determined that the optimal number of clusters within the dataset was three, each containing 21, 5 and 15 seals, respectively.
Figure 5.5: Mean proportion (± SE) of the individual fatty acids for each cluster group male of Australian fur seals (see Fig. 5.4 and text for details). Clusters 1 to 3 each contained 21, 5 and 15 seals, respectively. Each group was characterised by differences in their saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA).
Chapter 5: Variation in the diet of male Australian fur seals

Discussion

Trophic interactions

The results indicated that male Australian fur seals are opportunistic foragers that consume a broad variety of demersal/benthic prey species. The dietary composition of the study animals reflected their relatively restricted foraging range and primarily benthic foraging behaviour (Chapters 2 and 3). Many of the prey species identified in the QFASA models (arrow squid; greenback flounder; silver dory, Cyttus australis; southern calamari, Sepioteuthis australis; whiptail, Caelorinchus maurofasciatus; king snapper, Pristipomoides filamentosus; and silver warehou, Seriolella punctata) are frequently reported in studies that examine Australian fur seal diet, emphasizing the importance of these prey to the species (Gales & Pemberton 1994, Hume et al. 2004, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Hoskins et al. 2017). However, the results suggested that many other species also constitute an important part of male Australian fur seal diet.

Most notably, QFASA results indicated that elasmobranchs (sharks, skates and rays) were consumed in high proportions. Elasmobranchs are seldom reported in studies that investigate Australian fur seal diet using hard part analysis (e.g. Page et al. 2005b, Littnan et al. 2007, Kirkwood et al. 2008), which highlights the value of biochemical analysis techniques (Tollit et al. 2009). Presumably, the cartilaginous skeleton of elasmobranchs do not survive digestion and therefore, are infrequently detected using traditional hard part analysis (Tollit et al. 1997, Bowen 2000, Staniland 2002, Bowen & Iverson 2013). Furthermore, most traditional studies reflect the diet of adult females because the collection of scats occurs at breeding colonies.
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Despite these limitations, traditional hard part analysis techniques remain a valuable tool to investigate broad-scale dietary information and temporal trends in diet across a population (Kirkwood et al. 2008, Baylis et al. 2013, Tollit et al. 2015, Harrington et al. 2017). However, the use of biochemical techniques, such as QFASA, DNA, and stable isotope analysis can overcome the biases of predators that consume soft-bodied or cartilaginous prey and has the further ability to incorporate demographic information, enabling the dietary assessment of different age- and sex-classes (Iverson et al. 2004, Budge et al. 2006, Casper et al. 2007, Tollit et al. 2009).

The present study, however, is limited in its ability to detect potential new prey species. The interpretation of the fatty acid profiles was limited by the prey species that have previously been reported within the diet of Australian fur seals and by the availability of prey fatty acid profile data. Consequently, it was not possible to identify new prey of males in this study and species that were not considered within the scope of this study may have been consumed. Prey consumed by seals in the present study may also exhibit slightly different fatty acid signatures to those reported by Nichols et al. (1998) and Mooney et al. (2002) due to temporal variation between the two studies. Furthermore, calibration coefficients of Australian fur seals were not available for the present study and may influence dietary interpretation. The present study should be seen to provide a preliminary assessment into the diet of individual male Australian fur seals and should be interpreted accordingly. While the results of the present study are compelling regarding the diet of males, it would be useful to undertake additional investigations as new data becomes available.
Inter-individual and temporal variation in male diet

Results indicated that dietary composition varied between individuals. Male and female Australian fur seals exhibit a high degree of spatial overlap in their foraging areas within the Bass Strait region (Kernaléguen et al. 2015a) (Chapters 2-4). Given their restricted foraging range, the species presumably encounters a high degree of intraspecific competition when compared to other species that exhibit sex-specific foraging areas (e.g. Antarctic fur seals) (Boyd et al. 1998). Australian fur seals may utilise different foraging strategies to target a variety of prey resources, thereby reducing intraspecific competition for resources within Bass Strait. Indeed, several studies have documented inter-individual variation in foraging strategy (dive behaviour and habitat consistency) and individual differences in dietary composition Australian fur seals (Arnould et al. 2011, Hoskins et al. 2015b) (Chapters 2 and 3). Individual variability in behaviour and diet serves to broaden the trophic niche of a species and has important implications its ability to respond to environmental fluctuations that affect prey distribution, abundance, and availability (Svanbäck & Bolnick 2007, Araújo et al. 2011, Bolnick et al. 2011).

As generalist predators with a restricted foraging range, the behaviour and dietary composition of Australian fur seals is expected to fluctuate proportionately to the distribution, abundance, and availability of prey within their foraging areas (Boyd et al. 1994, Croxall et al. 1999). Indeed, the study animals exhibited temporal variation in their dietary composition which is consistent with prior studies investigating temporal trends in Australian fur seal diet (Kirkwood et al. 2008, Arnould et al. 2011, Kernaléguen et al. 2015a, Kliska 2015). With the exception of
Chapter 5: Variation in the diet of male Australian fur seals

the 2012 pre-breeding period, each season was characterised by a dominant prey type (2013 non-breeding: blue mackerel and dusky shark; 2013 pre-breeding: alfonsino; 2014 non-breeding: arrow squid and greenback flounder). The prevalence of these prey species within the diet of fur seals was presumably influenced by local environmental conditions. For example, warmer oceanic temperatures provide favourable conditions for cephalopod growth (Jackson & Domeier 2003) and may have contributed to an increase in available biomass of arrow squid during the non-breeding season of 2014 (Kirkwood et al. 2008) (Chapter 4). However, given the energetic content of available prey species may differ, fluctuations in prey availability, abundance and distribution may have important implications for the growth, reproductive success and ultimately the survival of predators.

Predators must balance a trade-off between searching for preferred, nutrient-rich prey and targeting lower quality but abundant resources to meet their energetic demands (Boyd et al. 1994, Womble & Sigler 2006, Schrimpf et al. 2012). Being capital breeders, a larger body size provides males with an advantage when defending territories from other males (Arnould & Duck 1997, Kiyota 2005, Lourie et al. 2013). The diet of male seals during the pre-breeding season may have substantial implications for their fasting endurance which, in turn, influences their ability to hold a territory and their overall reproductive success (Warneke & Shaughnessy 1985, Costa 1991). During the pre-breeding season males may forage upon a broader range of resources to maximise their net energetic intake and body energy accumulation (Beck et al. 2007). Indeed, throughout the pre-breeding season study animals consumed a broader range of prey resources. This may be a consequence of male...
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Australian fur seals moving to adjacent shelf-slope waters during the pre-breeding season, where they presumably target different resources (Chapter 2). In contrast, during the non-breeding season males are not subjected to the same metabolic costs of preparing for an extensive fasting period and may exhibit a narrower trophic niche as they target preferred prey resources within central Bass Strait. However, further investigation into prey handling costs, prey size, and energetic content of prey is required to assess the implications of variation in the dietary composition and trophic niche of male Australian fur seals.

In summary, the present study revealed that male Australian fur seals forage opportunistically on a broad range of benthic/demersal prey species. Several prey species have been frequently reported in prior studies emphasizing the importance of these prey to Australian fur seals. However, the presence of elasmobranchs throughout this study suggests that males may consume these prey species in greater proportions when compared to the rest of the population. Males exhibited inter-individual variation in dietary composition which serves to broaden the trophic niche of a species in response to increased intraspecific competition. Furthermore, substantial temporal variation existed within the diet of males which presumably reflects the distribution, availability and abundance of resources within Bass Strait at the time of sampling. Temporal variability in dietary composition has important implications for the growth and reproductive success of males. However, further information on the net energetic gain of specific prey is needed to assess the nutritional implications of consuming certain species.
Chapter 5: Variation in the diet of male Australian fur seals

Table S5.1: List of 75 Australian fur seal prey species included as potential prey in the QFASA model. Fatty acid data for each species were obtained from the literature (Nichols et al. 1998, Mooney et al. 2002).

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alfonsino</td>
<td>Beryx splendens</td>
</tr>
<tr>
<td>Arrow squid</td>
<td>Nototodarus gouldi</td>
</tr>
<tr>
<td>Australian angel shark</td>
<td>Squatina australis</td>
</tr>
<tr>
<td>Australian bonito</td>
<td>Sarda australis</td>
</tr>
<tr>
<td>Baby octopus</td>
<td>Octopus australis</td>
</tr>
<tr>
<td>Banded morwong</td>
<td>Cheilodactylus spectabilis</td>
</tr>
<tr>
<td>Barracouta</td>
<td>Thrysites atun</td>
</tr>
<tr>
<td>Bay flounder</td>
<td>Ammotretis rostratus</td>
</tr>
<tr>
<td>Black bream</td>
<td>Acanthopagrus butcheri</td>
</tr>
<tr>
<td>Blue grenadier</td>
<td>Macruronus novaezelandieae</td>
</tr>
<tr>
<td>Blue mackerel</td>
<td>Scomber australasicus</td>
</tr>
<tr>
<td>Blue morwong</td>
<td>Nemadactylus valenciennesi</td>
</tr>
<tr>
<td>Blue warehou</td>
<td>Seriolella brama</td>
</tr>
<tr>
<td>Blue-throated Wrasse</td>
<td>Notolabrus tetricus</td>
</tr>
<tr>
<td>Broadnose shark</td>
<td>Notorynchus cepedianus</td>
</tr>
<tr>
<td>Butterfly gurnard</td>
<td>Lepidotrigla vanessa</td>
</tr>
<tr>
<td>Calamari spp.</td>
<td>Sepioteuthis spp.</td>
</tr>
<tr>
<td>Crimsonband wrasse</td>
<td>Notolabrus gymnogenis</td>
</tr>
<tr>
<td>Cuttlefish</td>
<td>Sepia hedleyi</td>
</tr>
<tr>
<td>Dark banded whiptail</td>
<td>Caelorinchus maurofasciatus</td>
</tr>
<tr>
<td>Dusky flathead</td>
<td>Platycephalus fuscus</td>
</tr>
<tr>
<td>Dusky shark</td>
<td>Carcharhinus obscurus</td>
</tr>
<tr>
<td>Eastern Australian salmon</td>
<td>Arripis trutta</td>
</tr>
<tr>
<td>Eastern school whiting</td>
<td>Sillago flindersi</td>
</tr>
<tr>
<td>Gemfish</td>
<td>Rexea solandri</td>
</tr>
<tr>
<td>Greenback flounder</td>
<td>Rhombosolea tapirina</td>
</tr>
<tr>
<td>Grey morwong</td>
<td>Nemadactylus douglasii</td>
</tr>
<tr>
<td>Gummy shark</td>
<td>Mustelus antarcticus</td>
</tr>
<tr>
<td>Hapuku</td>
<td>Polyprion oxygeneios</td>
</tr>
<tr>
<td>Indian goatfish</td>
<td>Parupeneus indicus</td>
</tr>
<tr>
<td>Jack mackerel</td>
<td>Trachurus declivis</td>
</tr>
<tr>
<td>Jackass morwong</td>
<td>Nemadactylus macropterus</td>
</tr>
<tr>
<td>John dory</td>
<td>Zeus faber</td>
</tr>
<tr>
<td>King dory</td>
<td>Cyttus traversi</td>
</tr>
<tr>
<td>King george whiting</td>
<td>Sillaginoades punctata</td>
</tr>
<tr>
<td>King snapper</td>
<td>Pristipomoides filamentosus</td>
</tr>
<tr>
<td>Largespot herring</td>
<td>Herklotsichthys koningsbergeri</td>
</tr>
<tr>
<td>Leatherjacket</td>
<td>Aluterus monoceros</td>
</tr>
<tr>
<td>Luderick</td>
<td>Girella tricuspidata</td>
</tr>
<tr>
<td>Maori rockcod</td>
<td>Epinephelus undulatostriatius</td>
</tr>
</tbody>
</table>
### Chapter 5: Variation in the diet of male Australian fur seals

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maori wrasse</td>
<td>Ophthalmolepis lineolata</td>
</tr>
<tr>
<td>Pilchard</td>
<td>Sardinops neopilchardus</td>
</tr>
<tr>
<td>Pink ling</td>
<td>Genypterus blacodes</td>
</tr>
<tr>
<td>Pot-bellied Leatherjacket</td>
<td>Pseudomonacanthus peroni</td>
</tr>
<tr>
<td>Red morwong</td>
<td>Cheilodactylus fuscus</td>
</tr>
<tr>
<td>Red mullet</td>
<td>Upeneichthys vlamingii</td>
</tr>
<tr>
<td>Redfish</td>
<td>Centroberyx affinis</td>
</tr>
<tr>
<td>Reef leatherjacket</td>
<td>Meuschenia freycineti</td>
</tr>
<tr>
<td>Reef ocean perch</td>
<td>Helicolenus percoides</td>
</tr>
<tr>
<td>Ruby snapper</td>
<td>Etelis coruscans</td>
</tr>
<tr>
<td>Sand flathead</td>
<td>Platycephalus bassensis</td>
</tr>
<tr>
<td>Sandy sprat</td>
<td>Hyperlophus vittatus</td>
</tr>
<tr>
<td>School shark</td>
<td>Galeorhinus galeus</td>
</tr>
<tr>
<td>Silver dory</td>
<td>Cyttus australis</td>
</tr>
<tr>
<td>Silver trevally</td>
<td>Pseudocaranx dentex</td>
</tr>
<tr>
<td>Silver warehou</td>
<td>Seriolella punctata</td>
</tr>
<tr>
<td>Skipjack tuna</td>
<td>Katsuwonus pelamis</td>
</tr>
<tr>
<td>Smallspot herring</td>
<td>Herklotsichthys lippa</td>
</tr>
<tr>
<td>Snapper</td>
<td>Pagrus auratus</td>
</tr>
<tr>
<td>Southern calamari</td>
<td>Sepioteuthis australis</td>
</tr>
<tr>
<td>Southern garfish</td>
<td>Hyporhamphus melanochr</td>
</tr>
<tr>
<td>Southern rockcod</td>
<td>Pseudophycis barbata</td>
</tr>
<tr>
<td>Spikey dogfish</td>
<td>Squalus megalops</td>
</tr>
<tr>
<td>Spot-tail Shark</td>
<td>Carcharhinus sorrah</td>
</tr>
<tr>
<td>Spotted golden goatfish</td>
<td>Parapeneuys heptacanthus</td>
</tr>
<tr>
<td>Stargazer</td>
<td>Kathetostoma canaster</td>
</tr>
<tr>
<td>Striped trumpeter</td>
<td>Latris lineata</td>
</tr>
<tr>
<td>Sweep</td>
<td>Scorps lineolatus</td>
</tr>
<tr>
<td>Tailor</td>
<td>Pomatomus saltatrix</td>
</tr>
<tr>
<td>Tiger flathead</td>
<td>Neoplatycephalus richardsoni</td>
</tr>
<tr>
<td>Trumpeter</td>
<td>Latridopsis forsteri</td>
</tr>
<tr>
<td>Velvet leatherjacket</td>
<td>Meuschenia scaber</td>
</tr>
<tr>
<td>Yelloweye mullet</td>
<td>Aldrichetta forsteri</td>
</tr>
<tr>
<td>Yellowfin bream</td>
<td>Acanthopagrus australis</td>
</tr>
</tbody>
</table>
Chapter 5: Variation in the diet of male Australian fur seals

Chapter 6: General Discussion
Chapter 6: General Discussion

Understanding the ecological role of the Australian fur seal (Arctocephalus pusillus doriferus) requires knowledge of many aspects of their ecology including spatial, temporal and sex differences in their foraging behaviour and dietary composition. The main aim of this thesis was to investigate the foraging ecology of male Australian fur seals and place this within the broader context of seal ecology. The preceding chapters have found that males exhibit a high degree of spatial overlap with the foraging areas of female Australian fur seals (Chapter 2). However, the larger body size of males enables them to access resources that females cannot, thereby contributing to small-scale sexual segregation in foraging niche (Chapter 4). Furthermore, males exhibited inter-individual variation in their fine-scale habitat use (i.e. site fidelity; Chapter 3) and temporal diving strategies (Chapter 2). These behaviours presumably reflect individuals utilising different foraging strategies to target prey resources, resulting in substantial inter-individual variation in resource use within the species (Chapter 5). The purpose of the current chapter is to synthesise the major findings of these combined studies and to discuss their implications in the broader context of pinniped ecology. Furthermore, it discusses the potential impacts for the Australian fur seal population in Bass Strait and outlines areas for future research.

Sexual niche segregation in seals

Pinnipeds exhibit substantial differences in reproductive strategies that place different limitations on the foraging behaviour of species. In some species, these reproductive constraints contribute to sex-specific foraging behaviour. The capital
breeding phocid seals (true seals) utilise their energy stores acquired prior to parturition. Phocid lactation periods are characteristically short in duration, ranging from a few days to a few months (Kovacs and Lavigne 1986). Outside of this short lactation period, female phocids are not restricted in their foraging range. In contrast, female otariids (seals and sea lions) and odobenids (walruses) are income breeders, where females acquire resources throughout a comparatively long lactation period to nourish their young through milk provisioning (Kovacs and Lavigne 1992). While walrus calves are able to travel with their mother to foraging areas and suckle in remote locations, otariid pups cannot. Therefore, females must alternate foraging trips with returning to the natal colony to provision their offspring and are restricted in their foraging range and duration by their pups’ ability to fast (Boness and Bowen 1996; Schulz and Bowen 2004).

However, male pinnipeds do not provide parental care and, therefore, there has been a long-standing assumption that the male reproductive strategy promotes dispersal (Stirling 1983; Gentry et al. 1986). Such dispersal should lead to spatial segregation in otariids. Indeed, initial observations of habitat use in otariid species which exhibit a pelagic foraging strategy suggested males disperse during non-breeding periods while females remain to forage in closer proximity to breeding areas (Table 6.1). For example, male Antarctic fur seals (*Arctocephalus gazella*) and California sea lions (*Zalophus californianus*) were shown to undertake extended post-breeding migrations (Boyd et al. 1998; Weise et al. 2006; Weise et al. 2010). However, more recently, some studies have suggested this is not the case for all otariid species.
Table 6.1: Seven species of otariid have documented varying degrees of sexual segregation in foraging habitats. Data on male habitat use for the remaining otariid species is not available. Table adapted from Staniland (2005).

<table>
<thead>
<tr>
<th>Species</th>
<th>Male mass (kg)</th>
<th>Female mass (kg)</th>
<th>Segregation in foraging habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>California sea lion <em>Zalophus californianus</em></td>
<td>275-390</td>
<td>91-110</td>
<td>Females forage in close proximity to breeding colonies, while males migrate northward along Californian coastline after breeding foraging pelagically (Melin 1995; Weise et al. 2006; Weise et al. 2010).</td>
</tr>
<tr>
<td>Northern fur seal <em>Callorhinus ursinus</em></td>
<td>180-270</td>
<td>30-50</td>
<td>Males and females are segregated in different regions of the North Pacific Ocean and Bering Sea (Loughlin et al. 1999; Sterling et al. 2014).</td>
</tr>
<tr>
<td>New Zealand fur seal <em>Arctocephalus forsteri</em></td>
<td>120-185</td>
<td>25-50</td>
<td>Males and females forage in spatially separated habitats (continental shelf and shelf-slope habitats) (Page et al. 2005a; Page et al. 2006).</td>
</tr>
<tr>
<td>Antarctic fur seal <em>Arctocephalus gazella</em></td>
<td>90-210</td>
<td>25-55</td>
<td>Females forage in close proximity to breeding grounds, while males migrate ~ 900 km away from South Georgia (Boyd et al. 1998).</td>
</tr>
<tr>
<td>Southern sea lion <em>Otaria flavescens</em></td>
<td>300</td>
<td>150</td>
<td>Patagonia – males travelled twice the distance to foraging areas as females (Campagna et al. 2001).</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Falkland Islands – high degree of spatial overlap, males forage benthically hauling out on islands within the Falklands archipelago (Baylis et al. 2016; Baylis et al. 2017).</td>
</tr>
<tr>
<td>Australian sea lion <em>Neophoca cinerea</em></td>
<td>250-300</td>
<td>70-110</td>
<td>Males and females make short foraging trips within the continental shelf edge of south-eastern Australia (Lowther et al. 2011; Lowther et al. 2013).</td>
</tr>
<tr>
<td>Australian fur seal <em>Arctocephalus pusillus doriferus</em></td>
<td>220-360</td>
<td>36-110</td>
<td>Males remain to forage in the continental shelf exhibiting a high degree of spatial overlap with females – (Kernaléguen et al. 2015a) (Chapters 2-4).</td>
</tr>
</tbody>
</table>
Chapter 6: General Discussion

Predominantly benthic foraging otariids, such as the Australian sea lion (*Neophoca cinerea*), southern sea lion (*Otaria flavescens*) and now, the Australian fur seal, have all exhibited a relatively restricted foraging range within the continental shelf (Lowther et al. 2013; Baylis et al. 2016) (*Chapters 2-4*). The contrasting observations between pelagic and benthic foraging otariids suggest that the spatial range of males may be influenced by their foraging mode (pelagic or benthic), the available habitat and the prey resources it provides. Males may not disperse to foraging grounds further afield to maximise their net energetic intake while foraging (Pyke et al. 1977; Ropert-Coudert et al. 2004). Given their predominantly benthic foraging strategy, these seals are presumably targeting prey species found along the sea floor (Arnould and Costa 2006). The distribution of preferred prey resources for these males may be more accessible within the shallower waters of continental shelf habitats. While their body size suggests (and dive behaviour confirms, *Chapter 2*) that they are capable of diving to deeper depths (Weise and Costa 2007; Weise et al. 2010), the additional time and energy required to access benthic prey in deeper shelf-edge habitats may be an unnecessary metabolic expense for these species (Costa et al. 2001; Costa et al. 2004; Horning 2012). In addition, continental shelf habitats characteristically have a greater number of offshore islands that can be used as haul-out locations when compared to oceanic off-shelf habitats (*Chapter 3*). Haul-out locations provide males an opportunity to rest between foraging trips and, when they are located nearby profitable foraging areas, they reduce the costs of transit and their risk of at-sea predation (McConnell et al. 1999; Womble et al. 2009). Indeed, male Australian sea lions, southern sea lions and Australian fur seals have all been shown
Chapter 6: General Discussion

to utilise haul-out locations to access nearby foraging areas in a similar manner to a central place forager (Lowther et al. 2013; Baylis et al. 2017) (Chapter 3).

By not dispersing away from breeding areas, males of these species exhibit greater spatial overlap with female conspecifics (Kernaléguen et al. 2015a; Baylis et al. 2016) (Chapter 2 and 4). Therefore, it might be assumed that they will experience greater intra-specific competition from females. However, just like terrestrial predators, body size plays a role in determining the type and size of prey that can be efficiently handled and consumed (Shine 1991; Fish et al. 2003) such that larger size males may not share the same prey selection criteria as smaller conspecifics (Chapter 4). Furthermore, in the marine environment, an air breathing predator must forage within the physiological limitations of a single breath hold (Boyd and Croxall 1996; Andrews and Enstipp 2016) and there is a strong positive relationship between body size and physiological capacity in diving mammals (Weise and Costa 2007; Weise et al. 2010; Halsey et al. 2006). Correspondingly, larger individuals may be able to consume more prey, search for more cryptic prey or capture and/or handle larger prey that are more difficult to subdue, in a single dive. Indeed, across all pinniped species, it is commonly reported that larger size males can dive considerably longer than female conspecifics (Le Boeuf et al. 1993; Beck et al. 2003; Page et al. 2005a) and, where sex-specific dietary data exists, males and females have been shown to consume different prey (Beck et al. 2005; Lewis et al. 2006; Meynier et al. 2008; Kernaléguen et al. 2012; Kernaléguen et al. 2016a) (Chapter 4). Sexual segregation can have some obvious consequences for the management of seals and their prey resource, therefore, differences in the trophic
niche of each sex should be accounted for explicitly when examining a species’ foraging ecology.

Individual variation in behaviour and resource use

Intraspecific competition is believed to be a major driver in determining the overall niche breadth of a predator and the degree of individual specialisation that occurs within the species (Svanbäck and Bolnick 2007). In pinniped species where males exhibit a restricted foraging range, such as Australian fur seals (Chapters 2 and 3), individuals may experience a greater degree of intra-specific competition for prey resources. For this reason, individuals may use different foraging strategies to target alternate resources, resulting in a reduction in intraspecific competition (Ebenman 1987; Bolnick et al. 2011). In the present study, individual males differed in their diel foraging strategies (Chapters 2 and 3), potentially using different strategies to target different prey and in their fatty acid profiles, suggesting dietary variation (Chapters 4 and 5).

Given that certain prey species may be optimal based on their nutritional content alone, high levels of competition for these resources may reduce their availability and abundance within foraging areas (Ashmole 1963; Birt et al. 1987). In turn, this may influence the metabolic costs of acquiring these prey resources (Bolnick et al. 2003; Svanbäck and Bolnick 2007; Araújo et al. 2011). In periods where preferred prey are higher in abundance and availability, a predator species may narrow its overall foraging niche as the costs of acquiring these resources are reduced. Conversely, in periods of lower availability, the increased metabolic costs associated with targeting
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the same prey resources may lead to niche divergence within a species. However, optimal foraging theory suggests that individuals will make decisions on where, when and, how to forage, that maximises their foraging efficiency and ultimately their fitness (Charnov 1976; Stephens and Krebs 1987). Within a population and even within sex classes, conspecifics can differ considerably in their morphology, physiology, experiences and breeding status. These intrinsic attributes can also significantly affect the foraging ability of individuals and which foraging strategies they employ to find and search for prey (Werner and Gilliam 1984; Bence 1986). For this reason, individuals may differ in their optimal foraging strategies and the prey resources which they target (Bolnick et al. 2003; Araújo et al. 2011).

Several intrinsic factors have been shown to be important in determining the prey selection and foraging areas of pinnipeds. For example, age influences the dive behaviour and foraging movements of adult grey seals (Halichoerus grypus) and Antarctic fur seals (Arctocephalus gazella; Beck et al. 2003; Austin et al. 2004; McDonald et al. 2009), while overall body size impacts the diving ability of male Californian sea lions (Zalophus californianus; Weise et al. 2010). In Australian fur seals, similar intrinsic relationships have been observed within the behaviour and diet of females (Arnould et al. 2011; Arnould et al. 2015; Hoskins et al. 2015b). However, the same morphological characteristics were not determined to be important for male Australian fur seals. This may be due to all males in the present study being large enough in size to access sufficient prey resources within the relatively shallow benthic habitats of Bass Strait. Therefore, all males may have been operating within the physiological limitations of the smallest male sampled (Chapter 2).
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Site fidelity is presumably an advantageous strategy for males as it reduces the metabolic costs of transiting to profitable foraging areas (Switzer 1993; Piper 2011). In benthic environments, predators may be able to utilise sea floor characteristics to return to profitable foraging areas. Given the predominantly benthic foraging behaviour of male Australian fur seals, prior experiences may contribute to the overall foraging success of males (Chapters 2 and 3). Like other benthic foraging pinnipeds (e.g. southern sea lions and Australian sea lions; Lowther et al. 2011; Baylis et al. 2017), male Australian fur seals exhibited varying degrees of fidelity to foraging sites. For these long-lived species, it may confer a considerable energetic advantage over the life time of these individuals (Bonadonna et al. 2001; Bradshaw et al. 2004; Baylis et al. 2011; Merkle et al. 2015; Wakefield et al. 2015).

If particular foraging strategies, such as foraging in a specific site, are profitable in the long term, individuals may become highly specialised (Sims et al. 2008; Araújo et al. 2011). However, a potential consequence of specialisation is that individuals may lack the ability to respond to increased environmental variability or perturbations (Bolnick et al. 2003; Wakefield et al. 2015). While one male in Chapter 3 did exhibit a high degree of fidelity to a single foraging site, the degree of fidelity for other males was variable across the temporal period of the study. Furthermore, males altered their diel diving strategies and showed broad-scale variation in their foraging movements between seasons (Chapter 2) and exhibited substantial dietary variation throughout the period of the study (Chapter 5). Correspondingly, it implies that male Australian fur seals exhibit a high degree of behavioural flexibility in order to respond to fluctuations in their food supply.
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The high degree of individual variation observed in the previous chapters suggests that population-level approaches when describing otariid foraging behaviour and diet may be an oversimplification. Few studies have investigated male otariid foraging behaviour and diet at an individual level, with most treating all individuals as ecologically equivalent (e.g. Call and Ream 2012; Sterling et al. 2014; Baylis et al. 2017). Therefore, it remains unclear if the level of inter-and intra-individual variation observed in male Australian fur seals is representative of males in other pinniped species. Addressing individual variation in male habitat use and diet may have important implications for predicting how a species, or a population, may be able to respond to increased environmental variability and future environmental perturbations (Bolnick et al. 2003; Bolnick et al. 2011).

Future research directions

Knowledge of a species foraging behaviour and how it may vary within the population, has important implications for its management and overall understanding of trophic dynamics. The current study investigated the foraging ecology of Australian fur seals. In doing this, it determined that while males may utilise other habitats prior to breeding, male Australian fur seals do not segregate spatially from female conspecifics throughout winter (Chapters 2 to 4). However, body size differences place different constraints on the foraging ability of males and females and may contribute to sex-based resource partitioning (Chapter 4). Furthermore, the results of the present study suggest that male Australian fur seals exhibit substantial
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inter- and intra-individual variation in their habitat use, behaviour (Chapters 2 and 3) and dietary composition (Chapter 5).

However, the present study only assessed foraging behaviour of males from a single breeding colony, located in northern Bass Strait. Several other seal species (e.g. New Zealand fur seal, Arctocphalus forsteri; and northern fur seal, Callorhinus ursinus), including the conspecific cape fur seal (A. pusillus pusillus), have been shown to display differences in foraging areas between colonies (Robson et al. 2004; Mecereno 2006; Baylis et al. 2008; Skern-Mauritzen 2009). Furthermore, female Australian fur seals have been shown to exhibit colony-specific diets (Littnan et al. 2007). Given that the foraging habitat surrounding Kanowna Island may differ from other breeding colonies near the edges of the shallow continental shelf areas of Bass Strait (e.g. Lady Julia Percy Island and the Skerries; Fig. 1.1), males and females may exhibit greater spatial segregation at other colonies. Males of these colonies could potentially access shelf-slope waters more throughout the year, while females remain to forage in within Bass Strait (Kirkwood and Arnould 2011). Therefore, studies assessing and comparing male foraging behaviour and sexual segregation from these breeding colonies and throughout the entire year would be advantageous for our overall understanding of male foraging ecology in this species.

Furthermore, most organisms will exhibit ontogenetic shifts in their resource use associated with fluctuations in their life-history requirements (e.g. growth and reproduction) (Polis 1984; Carlisle et al. 2015). For example, several seal species exhibit sex differences in their spatial distribution, diving ability and isotopic niche straight after weaning, when males and females are of similar size and do not have
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different reproductive constraints on their foraging behaviour (Leung et al. 2012; Leung et al. 2014; Kernaléguen et al. 2016a). This has implications for our overall understanding of the processes driving sexual niche segregation in seals. Therefore, comparing the foraging behaviour and dietary composition of male and female fur seals as they mature may provide insights into the factors influencing sexual segregation within this and other otariid species.

Within populations, individuals often exhibit small-scale variations in body size and/or shape, which can lead to ecologically significant variation in their resource use (Bolnick et al. 2003; Araújo et al. 2011; Bolnick et al. 2011). The present study revealed substantial inter- and intra-individual variation in habitat use, behaviour and diet of male fur seals (Chapters 2, 3 and 5). While intrinsic factors have been shown to influence the behaviour and diet of female Australian fur seals (Arnould et al. 2011; Arnould et al. 2015; Hoskins et al. 2015b), the studies in the previous chapters were unable to find evidence to suggest the same relationships influence male behaviour and/or diet. However, it remains unclear if this is because the sampled males were operating within their physiological limits or if the present study was limited by small sample size in its ability to detect such relationships. Accordingly, the intrinsic factors influencing the inter- and intra-individual differences in male behaviour and dietary composition warrants further investigation.

Furthermore, quantitative fatty acid signature analysis (QFASA) can provide reliable estimates of the dietary composition of predators. The results of the present study (Chapters 4 and 5) are compelling regarding an assessment of male diet and how it may overlap/segregate with females of the species. However, several
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obligatory assumptions were made which may affect the dietary estimation using QFASA. For example, calibration coefficients do not exist for Australian fur seals, therefore, to account for the predator metabolism of fatty acids, calibration coefficients obtained for Steller sea lions (*Eumetopias jubatus*) were used in the QFASA models, assuming that Steller sea lion calibration coefficients are appropriate for inferring the diet of Australian fur seals. Furthermore, fatty acid data of prey were obtained from a historical data set which is assumed to be representative of species consumed by the study animals. If temporal variability in the fatty acid signatures of prey exists, this may impact dietary interpretation. Hence, the present study should be seen to provide a preliminary assessment of the diet of male Australian fur seals and how it overlaps/seggregates with females. While the results are convincing, they should be interpreted accordingly and it would be useful to undertake additional investigations as new data becomes available.

Lastly, clear species-, sex- and age- class biases continue to exist within the literature for several pinniped species (Schipper et al. 2008; McIntrye 2014). Even in comparatively well-studied species, such as elephant seals (*Mirounga sp.*), Antarctic fur seals (*Arctocephalus gazella*) and sub-Antarctic fur seals (*A. tropicalis*), an understanding of male ecology in general, is lacking. These biases are presumably due to the large body size of males making them difficult to capture and device recovery being unreliable as males are not constrained to a central place. However, improved technological advances in bio-logging equipment and dietary estimation techniques can overcome many of these challenges. For example, the development of satellite linked Fast-loc GPS technology, such as that used throughout this thesis.
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(Chapters 2-4), enables fine-scale behavioural data (spatial and behavioural data) to be transmitted without the need for device recovery. Furthermore, diet is able to be assessed using biochemical techniques (e.g. QFASA) of samples collected remotely (see Chapter 5). Future studies should aim to collect data on males and other age classes, as the current paucity of data can have important implications for the assessment of a species’ current population status, potential threats, and the conservation and management actions required (Kovacs et al. 2012).
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