

The role of foraging behaviour in recovering fur seal populations



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Thesis Summary

Large carnivores shape the structure and function of ecosystems as top-down effects on food webs can help maintain species diversity and resilience. This role is becoming more apparent as conservation efforts encourage the recovery and range expansion of many large carnivores. Many of the semi-aquatic pinnipeds are recovering well from past over-exploitation, particularly fur seals (*Arctocephalus* spp.). As populations return to pre-exploitation numbers and return to historical ranges, ecological theory predicts intra and interspecific competitive interactions will have a greater impact on ecosystem structure and function. The recovery of these populations provides an opportunity to explore the importance of competitive interactions, by investigating the behaviour of fur seals at the core of their ranges, where populations are at relatively high density and comparing them with those at the margins of their expanding ranges. The comparative approach can be further refined by separating fundamental limitations arising from morphological or reproductive constraints from ecological pressures by investigating the less well-known foraging behaviour of juveniles and males.

In this thesis I investigated inter-individual differences in foraging behaviour of three fur seal species, with a focus on adult males; Antarctic fur seals *A. gazelle*, Australian fur seals *A. pusillus doriferus*, and New Zealand fur seals *A. forsteri*. I tracked the foraging behaviour of individuals from large, established breeding colonies and haul-out sites with small populations at the joint range periphery of two species. Fur seals display a variety of foraging strategies (e.g. avoiding areas with high putative competition, focusing their search effort in areas of high biological production, partitioning niche space from congeneric species, high individual specialisation within benthic foraging species) that are consistent with foraging and niche theory, and that likely support intraspecific coexistence at large colonies and interspecific coexistence at range margins. Some important differences in foraging behaviour occur among individuals at a species range margin that distinguish them from individuals in the core of the species range. At this range periphery, the niche partitioning among males of sympatric fur seals offers insights into the processes driving foraging behaviour as species expand their range. Furthermore, an established network of protected areas could have useful management applications to mitigate negative interactions between humans and fur seals at their range periphery, and thereby support population expansion and recolonization of historical breeding areas. These insights provide direction for future research to support the conservation of fur seals and a more harmonious coexistence with humans.

Author's Declaration

I, Marcus Salton, certify that this thesis entitled “The role of foraging behaviour in recovering fur seal populations” is an original piece of work and has not been submitted in whole or in part for a higher degree at any institution other than Macquarie University. This work was undertaken in the Marine Predator Research Group in the School of Natural Sciences at Macquarie University, in collaboration with Phillip Island Nature Parks, New South Wales Marine Parks Authority and Australian Antarctic Division, under the supervision of Professor Robert Harcourt (Macquarie University), Dr Ian Jonsen (Macquarie University), Dr Roger Kirkwood (Phillip Island Nature Parks, SARDI Aquatic Sciences), Dr David Slip (Taronga Conservation Society Australia) and Dr Vincent Raoult (University of Newcastle, Macquarie University).

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This thesis was prepared and written by me. All assistance in the preparation of this thesis has been acknowledged and all references and sources of information used in this thesis are listed within.

Marcus Salton
July 2022

Statement of Contributions

Chapter Two: “Environmental drivers of foraging behaviour during long-distance foraging trips of male Antarctic fur seals”.

This chapter presents an analysis of horizontal and vertical movement patterns of male Antarctic fur seals from an established breeding colony in the subantarctic (Heard Island) to determine drivers of their post-breeding foraging behaviour. Dr Nick Gales collected the data with support of a field team. Myself, Dr Sophie Bestley and Prof Robert Harcourt conceived and designed the study. Dr Sophie Bestley collated and pre-processed tracking and habitat data. I further processed the data and performed all analyses with feedback from Dr Sophie Bestley. I wrote and prepared the manuscript, which was submitted to the journal *Animal Behaviour* in 2021. Dr Sophie Bestley, Prof Robert Harcourt, Dr Nick Gales, Dr Ian Jonsen, Dr Rebecca McIntosh and Dr Kaja Wierucka contributed critically to the draft manuscript for publication; Dr Sophie Bestley, Prof Robert Harcourt, Dr Nick Gales are listed as co-authors on the paper.

Chapter Three: “Mechanisms for sex-based segregation in foraging behaviour by a polygynous marine carnivore”.

This chapter presents an analysis of movement behaviours in relation to sex and life stage (juvenile and adult) foraging constraints, to determine mechanisms for sex-based segregation in foraging of Australian fur seals at a well-established breeding colony (Seal Rocks, Victoria). Myself and Dr Roger Kirkwood collected the data with support of various field teams. Myself, Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt conceived the study. I processed and analysed the data with feedback from Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt. I wrote and prepared the manuscript, which was submitted to the journal *Marine Ecology Progress Series* in 2019. Dr Roger Kirkwood, Dr David Slip, Prof Robert Harcourt and Dr Rebecca McIntosh contributed critically to the draft manuscript for publication; Dr Roger Kirkwood, Dr David Slip, Prof Robert Harcourt are listed as co-authors on the paper.

Chapter Four: “Using accelerometers to develop time-energy budgets of wild fur seals from captive surrogates”.

This chapter presents the development and validation of behavioural signatures from accelerometry to identify time-energy budgets of wild fur seals. Myself, Dr Monique Ladds, Dr David Hocking, Dr David Slip and Prof Robert Harcourt conceived, designed and carried out the captive and wild experiments with the help of support teams in captive facilities and at wild fur seal colonies. Myself, Dr Monique Ladds and Adam Thompson analysed the data, and myself and Dr Monique Ladds prepared the figures and tables. Myself, Dr Monique Ladds, Adam Thompson and Dr David Hocking wrote the manuscript and Dr Rebecca McIntosh, Dr David Slip and Prof Robert Harcourt reviewed the draft of the manuscript, which was submitted to the journal *PeerJ* in 2017.

Chapter Five: “Niche partitioning and individual specialisation in resources and space use of sympatric fur seals at their range margin”.

This chapter presents an analysis of male Australian and New Zealand fur seals from two sites with small populations at the margin of both species range, to assess whether niche size and partitioning, and individual specialisation aligns with low putative competition at their range margin. Myself, Dr Vincent Raoult, Dr Ian Jonsen and Prof Robert Harcourt conceived and designed the study. Myself, Matt Carr, Justin Clarke, Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt collected the data. Myself and Ian Jonsen processed the data and I analysed the data with feedback from Dr Vincent Raoult, Dr Ian Jonsen and Prof Robert Harcourt. I wrote and prepared the manuscript, which was submitted to the journal *Oecologia* in 2022. Dr Vincent Raoult, Dr Ian Jonsen and Prof Robert contributed critically to the draft manuscript for publication and are all listed as coauthors on the publication.

Chapter Six: “Protected area use by two sympatric marine predators repopulating their historical range”.

This chapter presents an analysis of male Australian and New Zealand fur seals from a non-breeding haul-out site at the margin of both species range, to determine whether the behaviour is consistent with males from breeding colonies in the core of their range and if their important habitats at the range margin are receiving protection. Myself, Matt Carr, Justin Clarke, Dr David Slip and Prof Robert Harcourt conceived and designed the study. Matt Carr, Justin Clarke, Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt collected the data. I processed the data, and myself and Dr Max Tarjan analysed the data with feedback from Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt. I wrote and prepared the manuscript, which was submitted to the journal *Endangered Species Research* in 2020. Matt Carr, Justin Clarke, Dr Max Tarjan, Dr Roger Kirkwood, Dr David Slip and Prof Robert Harcourt contributed critically to the draft manuscript for publication and are all listed as coauthors on the publication.

Supplementary Material 1: “Understanding meta-population trends of the Australian fur seal, with insights for adaptive monitoring”.

This chapter presents an analysis of Australian fur seal population surveys to determine the current status and trend of the species, and assess the various survey methods to provide insights for adaptive monitoring. All authors equally contributed to the summed parts to deliver the project, and to the writing of the manuscript, with the exception of the lead author – Dr Rebecca McIntosh - who was involved more extensively throughout the project and writing. The manuscript was submitted to the journal *PLoS ONE* in 2017.

Conference Presentations and Awards

Conference presentations:

Salton, M., Kirkwood, R., Slip, D. and Harcourt, R. 2013 “Utilising juvenile Australian fur seals to unravel constraints on foraging”. Presentation at: 20th Biennial Conference of the Society for Marine Mammalogy.

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Field support team members:

June 2012: Matt Carr, Justin Clarke, François Van Zyl, Robert Harcourt, David Slip
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Dedicated to those seals who died in the process of science. Your deaths shall not be in vain.

1. Chapter One

Thesis Introduction



Drawing credit: Marcus Salton

1.1 General Introduction

Recovery of carnivores and the role of foraging

Humans are exerting unprecedented pressure on natural environments (McCauley et al. 2015; Newbold et al. 2015; Poloczanska et al. 2016) threatening both the survival of many species and ecosystem function (Worm et al. 2005; Halpern et al. 2008; Elahi et al. 2015). Persistent conservation efforts resulted in some population recoveries and the recolonisation of historical ranges, including by a number of large carnivore species (Wabakken et al. 2001; Lotze et al. 2011; Chapron et al. 2014; Gompper et al. 2015; Karamanlidis et al. 2015; López-Bao et al. 2017; Bouley et al. 2018; Cimatti et al. 2021). From both declines and recoveries of populations of large carnivores it has become apparent that they can play an important role in regulating ecosystem structure and functions and biodiversity (Dalerum et al. 2008; Baum & Worm 2009; Ray et al. 2013; Ripple et al. 2014). Despite these conservation efforts and realisations, negative human interactions persist that threaten population

growth and range expansion of large carnivores in both terrestrial and marine environments (Reeves et al. 2013; Wolf & Ripple 2016, 2017; Sandom et al. 2018; Dias et al. 2019).

Understanding the drivers of population size and species distributions is of ecological interest (Hanski 1999; Krebs 2001), and has implications for natural resource managers and other stakeholders such as exploitative industries, tourism operators, conservationists and traditional land owners (Treves & Karanth 2003; Expósito-Granados et al. 2019; Serenari 2021). Even when threats to populations are identified, it can be difficult to determine the mechanisms that regulate recovery and range expansion. The mechanisms that drive recovery involve various demographic parameters (Hone & Sibly 2002; Sæther & Engen 2002; Sibly & Hone 2002; Benton et al. 2006), and these parameters are influenced by both intrinsic (i.e. intraspecific, density-regulated) and extrinsic factors (i.e. community and environment interactions) (Krebs 2002; De Little et al. 2007; Baylis et al. 2015b; Martinez Cano et al. 2016). For example, survival through immature stages is of importance in determining populations trends (York 1994; Gaillard et al. 1998; Wilson & Martin 2012; Pardo et al. 2016), and may be influenced by intraspecific exploitative and interference competition, by prey availability and by predation (Promislow & Harvey 1990; Lindström 1999; Maness & Anderson 2013). For many species extrinsic factors are important in regulating population growth, and intrinsic factors are particularly relevant once the population reaches maturity, or carrying capacity (Fowler 1987; Wolff 1997; Sæther et al. 2002; Bowen et al. 2003; De Little et al. 2007). However, the complex relationships between the drivers of population regulation and the lack of information on large carnivores during recovery leaves considerable uncertainty in the mechanisms driving their population growth and expansion.

Intrinsic and extrinsic factors influence an animal's foraging behaviour by dictating their ability to acquire the necessary energy and nutrients for growth and reproduction while surviving lethal threats. Accordingly, foraging behaviour can be a useful behavioural metric of population status and potential carrying capacity (Morris & Mukherjee 2007; Wildermuth et al. 2013). For example, central-place foragers may deplete or reduce the availability of prey around colonies, known as "Ashmole's halo" effect, which forces individuals to extend their foraging distance and range to acquire energy for activities, such as reproduction, ultimately regulating population size (Ashmole 1963; Birt et al. 1987; Lewis et al. 2001; Gaston et al. 2007; Weber et al. 2021). During population recovery of birds and mammals, an increase in intraspecific competition for food and mates may also drive the dispersal of individuals, typically, juveniles and adults not constrained by parental care, away from source populations towards range margins (Dobson 1982; Pusey 1987; Travis et al. 1999; Matthysen 2005). At the same time, range margins may contain different habitats that do not provide the preferred food resources, and might be inhibited by new competitors and predators. The colonising individual will require behavioural adaptation in order to coexist and remain in the new area (Shreeve et al. 1996; Duckworth 2008; Kawecki 2008; Chevin & Lande 2011; Hamel et al. 2013; Fisher et al. 2014; Hughes et

al. 2019). Given the current state of the environment, these new habitats likely include humans, and if not managed appropriately can result in human-carnivore conflict at range margins that may have further unintended consequences for expansion of the species' range (Treves & Karanth 2003; Graham et al. 2010; Wallace et al. 2011; Miller 2015; Morehouse & Boyce 2017; Nattrass et al. 2020). In addition, climate warming is a likely cause of shifting geographic ranges and local abundance for many species, by altering availability of preferred habitat, and is expected to have different effects on species that are adapted to different environments, further complicating future ecosystem dynamics for recovering species (Martinez Cano et al. 2016; Santini et al. 2016b; Elmhagen et al. 2017).

Fur seals and their recovery

Fur seals are otariids (fur seals and sea lions), one of the most sexually dimorphic mammalian taxa, with males on average three times larger than females (Weckerly 1998). They are polygynous (Trillmich & Trillmich 1984), with distinct sex-specific strategies to maximise lifetime reproductive success. Males must acquire competitive size, skill, and energy reserves to establish and defend a breeding territory and mate with a number of sexually mature females (McCann 1980; Boness 1991; Carey 1991; Kiyota 2005; Franco-Trecu et al. 2014); though there is evidence of alternative mating strategies within some populations (Gemmell et al. 2001; Lancaster et al. 2007; Kiyota et al. 2008; Caudron et al. 2010).

Parental care is entirely left to females, who act as central place foragers while supporting their pup between 4 and 36 mo (depending on the species) (Bonner 1984; Kovacs & Lavigne 1992; Boyd 1998). Fur seals have a prolonged juvenile stage, with sexual maturity at 3-6 years of age for females and 3-7 years for males, though males typically do not have sufficient size or experience to compete for breeding territory until 8-10 years old (York 1983; Stewardson et al. 1998; Dickie & Dawson 2003; McKenzie et al. 2007b).

Fur seal (*Arctocephalus* spp.) populations were decimated by humans for their pelts in the 1700s and 1800s, but gradually received various forms of protection in the late 1800s and 1900s, with all populations now protected to some extent (Hofman & Bonner 1985; Bonner 1989; Wickens & York 1997). Presently, many fur seal populations have increased in size, colonised or recolonised new areas, and some have seemingly reached a "maturity" phase where the rate of increase has declined (Antarctic fur seal; Subantarctic fur seal; Australian fur seal; New Zealand fur seal; Cape fur seal; South American fur seal; Campbell et al. 2014; Shaughnessy et al. 2015; Wege et al. 2016; McIntosh et al. 2018b; Baylis et al. 2019; Cárcamo et al. 2019; Franco-Trecu et al. 2019; Milano et al. 2020; Khoyetskyy & Pishniak 2021). However, other fur seal species have smaller populations with a limited range (Juan Fernández *A. philippii*, Guadalupe *A. townsendi*), and some have suffered recent declines and are listed as vulnerable or endangered by the International Union for Conservation of Nature (northern *Callorhinus ursinus* and Galapagos fur seals *A. galapagos*, respectively, at the last assessment in 2015) (Lee et al. 2014; Alava et al. 2017; Osman & Moreno 2017; García-Aguilar et al. 2018; Páez-Rosas et al. 2021). Variation in

population growth rates and range expansions have been attributed to reduced availability of food resource by fisheries, other anthropogenic impacts (e.g. bycatch, pollution and disturbance) and a changing climate (Swartzman & Haar 1983; Trites 1992; Pauly et al. 1998; Reid & Forcada 2005; Kovacs et al. 2012; Alava 2017; Alava et al. 2017; Pirotta et al. 2018; McHuron et al. 2019; Gálvez et al. 2020; Perez-Venegas et al. 2021). At this juncture, precise mechanisms regulating different populations remain uncertain, however, partly due to specific information gaps about fur seal foraging behaviour.

During population recovery of fur seals there appear to be several processes that limit population growth and expansion. Growth and survival of pups is related to population size and rate of population change, most likely due to density dependent effects at the colony and associated with foraging efficiency (Bradshaw et al. 2000a; Reid & Forcada 2005; Oosthuizen et al. 2016). An increased density at colonies can result in higher mortality of pups from lethal interactions with non-maternal females and fighting males, and potentially longer periods of separation from mothers leading to death by starvation (Doidge et al. 1984; Harcourt 1992). Starvation of pups also correlated with increased foraging trip duration of lactating females, suggesting that food availability within range of these females is also important (Reid & Forcada 2005). The post-weaning survival rate, which is variable and often low (Trites 1989; Wickens & York 1997; Beauplet et al. 2005), is another potentially important driver of fur seal population trends (Trites & Larkin 1989) as it influences recruitment and population growth rate (Lindström 1999; Sæther et al. 2013; Benson et al. 2018). In addition, population growth improves with an increase in adult survival rates (Gibbens & Arnould 2009).

Accordingly, much effort has been given to understanding what factors limit pup survival and female foraging behaviour. The central-place nature of female foraging has facilitated recovery of telemetry devices that are required to measure fur seal foraging behaviour, and this has produced a strong bias toward females in fur seal foraging studies (Carter et al. 2016). From such work, it has become apparent that different fur seals adopt different foraging modes (e.g. benthic and epipelagic diving), with benthic foragers often exceeding their species' aerobic dive limit (i.e. high foraging effort) (Costa et al. 2001; Arnould & Costa 2006; Ladds et al. 2020). The higher energetic expenditure on foraging may explain why benthic foraging species also have slower population growth rates and smaller population sizes (Costa 1991; Arnould & Costa 2006; Ladds et al. 2020; Costa & Valenzuela-Toro 2021). While the importance of juvenile survival in regulating populations is recognised, there is relatively little known about the foraging ecology and movements of this age class, partly because their smaller size and unpredictable attendance patterns at terrestrial sites (haul-outs) are less conducive to telemetry studies.

Fur seals are reliant on haul-outs for breeding, moulting, rest, and socialising, and on the marine environment for food resources. Accordingly, there are factors that influence their population growth and range expansion both on land (e.g. limited space, appropriate habitat features, thermal tolerance,

disturbance and predation) and at sea (e.g. access to prey, predation). Many of the fur seal haul-outs are in remote locations making them difficult for researchers to access and monitor, yet even more challenging is determining fur seal at-sea foraging behaviour and intra and interspecific interactions, including interactions with humans. It is also difficult to monitor known individuals throughout their lives, particularly accurately determining individual reproductive success, which is important to understand demographic parameters that influence population dynamics. These challenges have limited the breadth of study on certain aspects of fur seal biology and ecology, but are being overcome in order to accurately understand human impacts and the effects of climate change on fur seal recovery and range expansion. In particular, it is becoming more necessary to understand these impacts on temperate otariids in a rapidly warming environment as they are sensitive to high temperatures (Gentry 1973), with thermal energetic costs often higher for pups and juveniles (Liwanag 2010). Ocean warming is also altering prey distributions and abundances and thereby the habitat uses of marine predators (Amador-Capitanachi et al. 2020; Evans et al. 2020; Niella et al. 2020; d'Entremont et al. 2021; Florko et al. 2021; Niella et al. 2021), though the details of these processes and their impact on population processes are not yet available for most fur seal species.

Fur seal foraging behaviour during recovery

Foraging behaviours are shaped by physiological and behavioural constraints that result from different morphology, size and life history strategies (Marchetti & Price 1989; Costa 1993; Stephens et al. 2007). Fur seals are air breathing mammals, and have evolved physiological adaptations associated with oxygen and fuel stores, and metabolic processes that consume these stores, that enable individuals to effectively exploit marine habitats (Costa et al. 2004). Their physiological capacity takes years to develop fully (Horning & Trillmich 1997; Baker & Donohue 2000; Baylis et al. 2005; Spence-Bailey et al. 2007; Verrier et al. 2011) because physiological processes scale with body size (Schreer & Kovacs 1997; Schreer et al. 2001; Halsey et al. 2006). Accordingly, age and body size are important drivers of sex-life stage differences in energy and nutritional requirements, foraging experience and efficiency, and vulnerability to competitive interactions and predation (Stillman et al. 2000; Nagy 2005; Dial et al. 2008; Kim et al. 2012; Preisser & Orrock 2012; Hintz & Lonzarich 2018; Sheppard et al. 2018; Mazza et al. 2019; Baert et al. 2021). Sex differences in reproductive strategies are also important in shaping life history strategies, with sex-specific trade-offs between long-term survival and reproductive output, and therefore greater propensity for risk in males in order to successfully reproduce (Isaac 2005; Aloise King et al. 2013; Schindler et al. 2015; Hämäläinen et al. 2018). In summary, within a species there are differences in behaviour between juveniles and adults, between breeding and non-breeding adults, and between breeders with different contributions to the care of offspring.

With an increase in individuals at a colony, niche theory predicts there should be behavioural adjustments that mitigate the increased intraspecific competition occurring within the limited niche

space (Hardin 1960; MacArthur & Levins 1967). Given the long lactation period and central-place foraging behaviour, female fur seals, in particular, are predicted to adjust their foraging behaviour during population recovery in response to localised resource depletion (Ashmole's halo described above), and indeed lactating female northern fur seals increased their foraging trip duration, trip distance, foraging range and diving effort during a 4-fold increase in population size over 15 years (Kuhn et al. 2014). Similarly, female Antarctic fur seals at a larger colony had longer distant foraging trips compared to females from a much smaller colony (Staniland et al. 2011). Long trips are more energetically expensive and coincide with higher pup mortality (Costa et al. 1989; Reid & Forcada 2005; Staniland et al. 2007; Seguel 2018). Changes in foraging behaviour of juveniles and adult males associated with increased population density remain uncertain.

As outlined above, sex-life stage cohorts are expected to adopt different strategies to exploit available resources (Svanbäck & Bolnick 2007). Juvenile and adult male fur seals, being free of the constraints resulting from pup care, are expected to range more widely than females, either to avoid competition with the more spatially constrained females and/or to capitalise on more distant, profitable, feeding grounds that are inaccessible to females (Staniland 2005; Page et al. 2006; Staniland & Robinson 2008). Alternatively, fur seals could partition other parts of their niche, including type/s of prey, dive depth, timing of foraging (Page et al. 2005b, 2005a; Hofmeyr et al. 2010; Drago et al. 2015; Kernaléguen et al. 2015b; Juárez-Ruiz et al. 2018; Jones et al. 2020). This behavioural diversification of foraging strategies reduces intraspecific competition and promotes coexistence (Kobler et al. 2009; Bolnick et al. 2011). New types of foraging strategies used by populations in order to mitigate competition are expected to become apparent as populations recover and colonise/recolonise peripheral parts of their range.

While juveniles and adult males of many fur seal species forage from breeding colonies throughout the year, flipper tagging and some telemetry studies suggest they are important vectors of population dispersal (Warneke 1975; Baker et al. 1995; Skern-Mauritzen et al. 2009; Zeppelin et al. 2019; Shaughnessy & Goldsworthy 2020). Indeed, juveniles and males are often found at range margins, and are in larger numbers as breeding colonies are establishing; with females becoming more abundant as colonies mature (Oosthuizen 1991; Hofmeyr et al. 1997; Bradshaw et al. 2000b; Burleigh et al. 2008b; Goldsworthy et al. 2009; Kirkwood et al. 2009; Bester 2021). The limited work investigating juvenile foraging behaviour supports ontogenetic constraints on their foraging behaviour associated with their immature development and naivety (Horning & Trillmich 1997; Page et al. 2006); similar to birds and other mammals (Marchetti & Price 1989; Rubenstein 1993; Riotte-Lambert 2013). However, it remains unclear what the key drivers of their mortality are during this life stage. The limited information about juveniles and males is from breeding colonies, leaving a deficit of knowledge about dispersal and range expansion, particularly whether the behaviour differs between source populations within centralised parts of the species range and sink populations at their range periphery.

During the colonisation or recolonization phase of population recovery, the numbers of animals in a source population increases to a point where constraints on available niche space drives dispersal of individuals to new, low-density colonies (Roux 1987; Travis et al. 1999; Matthysen 2005). Based on the source-sink hypothesis, the source population should rely on good quality habitat while the dispersers move towards more distant lower quality habitat (Dias 1996). However, for species that were extirpated throughout much of their historical range, the contemporary source populations may exist within poor quality, marginal habitat and dispersing individuals may in fact establish new colonies in higher quality habitat (Baker & Johanos 2004; Augé et al. 2011). At the edge of a species' geographic range, population size is small and thereby intraspecific competition low, reducing selection pressures associated with population density, but where interspecific competition can be an important factor shaping range limits (Hersteinsson & Macdonald 1992; Case & Taper 2000; Holt & Keitt 2000; Holt 2003; Case et al. 2005; Pigot & Tobias 2013; Fisher et al. 2014). Therefore, a comparison of foraging behaviours adopted by individuals at range margins to those in more centralised parts of the species' range will develop the understanding of ecological processes driving species distributions and range limits.

Most predators live in communities that are typically occupied by other predators who share space and resources and can pose a threat to survival. In a similar way that conspecifics occupy a similar niche, congeneric species share similar life-history traits and foraging behaviours and so often seek a similar niche. Accordingly, it is not unusual for congeneric species to live in sympatry. Across their geographic ranges several species of fur seal live in sympatry with other fur seal species, or closely related sea lions. Competition and predation can influence foraging behaviour of interacting species by driving individuals to forage on different food resources, in different habitats and at different times of day (Schoener 1974; Creel 2001; Chase et al. 2002; Chesson & Kuang 2008; Cozzi et al. 2012). These drivers are particularly strong between species with similar foraging needs and constraints, such as congeneric species living in sympatry (Palomares & Caro 1999; Linnell & Strand 2000; Caro & Stoner 2003; Cooper et al. 2009). Stronger and more frequent interspecific interactions are expected as populations increase and species' ranges expand into new areas, which can limit recovery and shape recolonisation (Berger & Gese 2007; Grether et al. 2017).

When congeneric species live in sympatry, they must also partition niche space in order to coexist, particularly in the presence of resource limitations, or risk competitive exclusion (MacArthur & Levins 1967; Pacala & Roughgarden 1982; Luiselli 2006; Parra 2006; Harihar et al. 2011). These interspecific interactions are important to understand during population recoveries, particularly where conservation efforts are promoting recovery of one or both species. For example, as tiger *Panthera tigris* populations recovered in the Chilla Range of Rajaji National Park, India, where its historical large prey were absent, these tigers fed on medium-sized prey, which likely escalated competition with the congeneric leopard *Panthera pardus*, and probably led to the measured decline in leopard density (Harihar et al. 2011).

Dietary, spatial and temporal niche partitioning also occurs among several similar species of seabird allowing their respective populations to coexist within the same colony while breeding (Wilson 2010; Navarro et al. 2013; Petalas et al. 2021). Accordingly, it is not surprising that niche partitioning is prevalent in various forms (spatial, temporal, dietary) among sympatric fur seals (Robinson 2002; Bailleul et al. 2005; Page et al. 2005b, 2005a; Page et al. 2006; Luque et al. 2007; Luque et al. 2008; Hoskins et al. 2017), though the role of this segregation during recovery remains unclear. For female fur seals, contrasting durations of lactation may influence niche partitioning between sympatric species (Bailleul et al. 2005; Luque et al. 2007). Similarly, the timing of breeding could influence niche partitioning between sympatric male fur seals, though such interactions remain largely unexplored. Partitioning could allow coexistence or be an artefact of competitive exclusion, and thereby limit population growth and potentially exclude one species (Franco-Trecu 2014).

Interactions among species can also take the form of predation and predator avoidance, with interspecific killing common among mammalian carnivores (Palomares & Caro 1999). For example, during recovery of lions (*Panthera leo*) in Namibia one pride rediscovered various rich marine food resources, including seabirds and Cape fur seals (Stander 2019), which now threatens the persistence of the prey populations. Similarly, as sea otters recolonised part of their range on the west coast of North America, they avoided apparently suitable habitat, and resided in potentially suboptimal habitat, due to the presence of Stellar sea lions and harbour seals. As seal was the preferred prey of killer whales, this association resulted in an increased risk of predation for sea otters (Fisher et al. 2014). Therefore, in order to effectively plan and manage recovery of species and their range expansion, it is important to consider the community structure and how that might change.

Humans are another species with which large carnivores must coexist as they recover and expand their range. Despite legal protection for fur seals, interactions with humans persist that have population level consequences jeopardising fur seal recovery and range expansion, and require adaptive management (Back 2010; Cammen et al. 2019; Senko et al. 2020; Keen et al. 2021; Martin et al. 2022; Thakur & Koul 2022). As fur seal populations increase in density and abundance, and expand into new areas, interactions with humans can intensify and create new management concerns, both between humans and seals and between humans that have different perspectives or commercial interests (Hausmann et al. 2013; Pirotta et al. 2018; Davis et al. 2020; Swan et al. 2020; Tixier et al. 2021; Heredia-Azuaje et al. 2022). Protected areas are one management tool used in terrestrial and marine contexts to regulate human activities spatially and temporally to support the preservation and recovery of habitats and species, including large carnivores (Linnell & Strand 2000; Linnell et al. 2005b; Stoms et al. 2005; Chapron et al. 2014; Watson et al. 2014b). Effective networks of protected areas can support dynamic management of key refugia for recovering carnivores by redirecting human activities away from discrete habitats that support the recovery of these species.

1.2 Thesis Aims

In this thesis, I investigate the foraging strategies of juvenile and adult male fur seals both at established breeding colonies and at their range margin to assess the role of foraging behaviour in enabling coexistence and range expansion during species recovery. The foraging niche of individuals within a species is discussed in the context of intraspecific variation in physiological and behavioural constraints that have been shaped by their morphology and age-specific strategies. By investigating adult male foraging behaviour of two sympatric fur seal species at a joint range margin, I assess whether information derived from breeding colonies is still applicable at their range periphery and which mechanisms allow sympatric male fur seals to coexist. The implications of their foraging behaviour for the efficacy of existing management tools for population recovery is also investigated.

Aims

- 1) Investigate foraging strategies used by fur seals to mitigate the intraspecific competitive pressures expected at large, established breeding colonies;
- 2) Determine whether inferences about foraging behaviour obtained from individuals within core parts of a species' range are applicable to individuals at the frontline of range expansions;
- 3) Assess the influence of interspecific competition that is expected to limit range margins;
- 4) Explore the application of a current network of protected areas for these wide-ranging carnivores at an expanding margin of their range.

1.3 Thesis Structure

The thesis is comprised of this introduction, five data chapters, a general discussion and a data chapter as supplementary material. The data chapters are written as standalone papers. Each data chapter builds upon components of the study by adding new layers of insight into the role of foraging behaviour for the recovery of fur seals.

2. Chapter Two

Environmental drivers of foraging behaviour during long-distance foraging trips of male Antarctic fur seals

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Abstract

Animals may use long-distance foraging trips to capitalize on spatiotemporal variation in food availability, allowing individuals to maximize resource gain from foraging effort. This is particularly important for dimorphic species with polygynous mating where males face strong selection pressures to attain large size and access to reproductive females. We tracked 17 male Antarctic fur seals, *Arctocephalus gazella*, during their prolonged post-breeding trips and assessed links between their movements and environmental predictors of profitable feeding areas. Males made one of two types of trips: a long trip to the Antarctic ice edge or shorter trips to areas where the southern Antarctic Circumpolar Current fronts generate high biological activity. The trip type was not determined by body size but was related to departure date from the breeding area, suggesting that males must trade off opportunities at the breeding area (reproductive, social interactions) and foraging opportunities between breeding seasons. Regardless of trip structure, males focused search effort far from foraging areas of central-place foraging seabirds and seals including female Antarctic fur seals provisioning offspring. Males showed clear spatiotemporal patterns in dive behaviour, with deep dives in shelf waters during the day and predominantly shallower dives in pelagic waters at night. Diel dive patterns showed monthly changes in photoperiod and lunar phase, consistent with feeding on vertically migrating prey. However, males did not use area-restricted search to focus dive effort, instead performing a mix of foraging and nonforaging behaviour within and between restricted search areas. We discuss the scale and type of inference that can be made from movement models, given the behavioural constraints that govern long-distance trips in vast, heterogeneous environments like the Southern Ocean.

2.1 Introduction

Long-distance movements for foraging, dispersing or migrating are ubiquitous throughout the animal kingdom and key for many ecological and evolutionary processes (Bowler & Benton 2005). The causes and consequences can be examined by investigating animals before and after the movements (Liedvogel et al. 2013) but advances in animal telemetry now allow researchers to record the movements and behaviour of animals throughout their long-distance trips; this has been pivotal for our understanding of the mechanisms that drive this behaviour (Ropert-Coudert & Wilson 2005). Seasonal, long-distance movements are often an adaptation to capitalize on spatiotemporal variation in resource availability (Alerstam et al. 2003). Intraspecific variation is common, and may be explained by intrinsic factors such as age, sex, body size, personality, constraints imposed by physiological ability, reproductive roles and energy requirements (Alerstam et al. 2003) or by intrinsic individual differences (Patrick et al. 2014). However, characterizing the movements of predators and linking them to resource availability remains difficult due to a limited capacity for directly observing both the predator's foraging behaviour and the prey's distribution in the wild, particularly for long-distance movements across vast ocean expanses.

Oceanic food resources are distributed heterogeneously in space and time (Nakata et al. 2004) and consequently animals may cover great distances to satisfy their energy needs (Block et al. 2011; Sequeira et al. 2018). Marine predators often consume prey at depth, making it particularly difficult to observe and quantify their foraging behaviour at sea (Kuhn & Costa 2006). Foraging theory predicts that animals should increase their search effort in areas where resources are abundant (MacArthur & Pianka 1966), depending on predation risk and nutrient requirements (Pyke et al. 1977). It also predicts that animals should continue to search within profitable areas until the capture rate in the foraging patch falls to the average rate for the habitat (Charnov 1976). While identifying these search type movement patterns in tracking data can be challenging (Turchin 1998), analytical methods can distinguish movements that are slow and sinuous, indicative of area-restricted search (ARS; or a resident state), from faster and more linear movements (i.e. a directed state) along an animal's foraging path (Jonsen et al. 2005; Barraquand & Benhamou 2008; Pinaud 2008). ARS by marine predators often coincides with environmental features that stimulate biological activity, such as upwellings, currents and frontal systems (Block et al. 2011). It has also been linked to periods of intense feeding behaviour (Weimerskirch et al. 2007), suggesting that ARS may provide an indication of profitable feeding areas during movements at sea. Subsequently, ARS analysis has been used to identify areas of ecological importance (Hindell et al. 2011) for conservation and management efforts (Tancell et al. 2013; Hays et al. 2019). However, the inferences drawn from ARS methods applied to two-dimensional horizontal movement can be limited for animals that feed in dynamic, three-dimensional habitats (Bailleul et al. 2008; Bestley et al. 2015).

In marine environments, spatiotemporal variability in resource distribution occurs in horizontal and vertical space. The foraging strategies predators use to exploit these dynamic resources can be inferred from changes in their movement behaviour recorded using fine-scale sensors, such as dive recorders and accelerometers (Harcourt et al. 2000; Carroll et al. 2014; Yoshino et al. 2020). These sensors have revealed how marine predators allocate their time to different foraging (i.e. diving) and nonforaging (i.e. rest, recovery and prey processing) behaviours throughout long-distance trips (Boyd 1996; Russell et al. 2015). However, to combine sensors that record vertical and horizontal movement behaviour often requires a compromise between device size, battery longevity and the need to recover the device to access the data (McIntyre 2014; Wilmers et al. 2015). Consequently, assessments of vertical and horizontal movement behaviour have been limited to certain taxa and are often difficult to achieve throughout long-distance trips.

Long-distance trips are common among pinnipeds when unconstrained to a terrestrial site for breeding or moulting; this is particularly the case for males after their summer breeding period, when females are solely responsible for parental care (Boyd et al. 1998; Hückstädt et al. 2014; Salton et al. 2019; Salton et al. 2021). Males in sexually dimorphic, polygynous species, like otariids (fur seals and sea lions; (Weckerly 1998), are under high selection pressure to reach a large size so they can acquire and maintain access to breeding territory, and so might be particularly likely to need to find the most productive foraging areas (Lindenfors et al. 2002). Indeed, it is well known that male otariids make lengthy trips at sea (Boyd et al. 1998; Campagna et al. 2001; Page et al. 2006; Weise et al. 2010; Lowther et al. 2013; Baylis et al. 2018; Salton et al. 2019) to recover condition from fasting when ashore and to acquire resources for growth and reproduction. While the movements of male otariids are well studied, how long-distance movement patterns relate to individual factors such as body size or how environmental variation is linked to profitable feeding habitat remains unclear.

This study investigated the long-distance movements of male Antarctic fur seals, *Arctocephalus gazella*, a sexually dimorphic and polygynous pinniped. Male Antarctic fur seals establish and defend breeding territories during October to December; while this gives them access to females to mate with it means they must fast (McCann 1980), losing weight at up to 1.5 kg/day (Boyd & Duck 1991), and risk lethal injuries (Baker & McCann 1989). Most pups (90%) are born between 29 November and 25 December, but as late as 8 January (Page et al. 2003), and females come into oestrus and are mated 7 days postpartum (Duck 1990). After breeding, male Antarctic fur seals spend most of their time at sea (Doidge et al. 1986) and can disperse widely to areas far from their sub-Antarctic breeding sites, presumably to access higher quality feeding areas. At this time, their foraging locations are segregated from those of lactating females (which remain close to the breeding site), perhaps due to local depletion of food by females or because males can forage more successfully in more distant regions (Boyd et al. 1994). In East Antarctica, males on long-distance trips use distant, productive ice edge habitat (Raymond

et al. 2015; Patterson et al. 2016) as well as open water (Bestley et al. 2015), yet the drivers behind intraspecific variation in the use of these habitats (e.g. age, body size, reproductive status) are unknown. Male Antarctic fur seals are known to adopt ARS behaviour and rest while at sea (Bestley et al. 2015; Bestley et al. 2016), but how ARS behaviour relates to the spatiotemporal distribution of resources is unknown. There is less information on their dive behaviour postbreeding, but they appear to undertake a combination of deep and shallow dives, depending on habitat (Green 1997; Lowther et al. 2020).

The objectives of this study were to (1) characterize the behaviour of male Antarctic fur seals during their long-distance, postbreeding trips and identify drivers of individual variation (e.g. body size, date of departure from the breeding site); (2) determine whether their ARS behaviour is consistent with targeting profitable feeding areas, as indicated by key environmental parameters (e.g. frontal zones and different ice habitat); and (3) establish whether dive behaviour is related to spatiotemporal patterns in environmental features that drive prey availability (habitat and diel changes in light). Following foraging theory, we expected ARS and dives to be more frequent while seals were away from our study site (Heard Island), as close to the island intra- and interspecific competition is likely to be high in the mid to late austral summer because of the many seabirds and seals foraging close to the breeding area on similar prey (Woehler & Green 1992; Green et al. 1998; Hindell et al. 2011; Patterson et al. 2016). We also expected ARS and dives to be more frequent in habitats with abundant prey, such as the ice edge, where melting sea ice releases ice algae and allows increased light penetration, enhancing primary productivity and biological activity (Brierley & Thomas 2002), particularly in January–February when light levels and ice melt rate are favourable for phytoplankton (Arrigo et al. 2008). Moreover, we expected variation in dive depth to closely align with diel changes in solar illumination and lunar phase, as light levels map diel vertical movements of dominant Southern Ocean prey for marine predators (Croxall et al. 1985; Duhamel et al. 2000; Bost et al. 2002).

2.2 Methods

Tag deployment

We used telemetry data collected from 17 male Antarctic fur seals that were captured and sedated while hauled out at Heard Island (53°10' S, 73° 30' E) between 18 December 2003 and 14 January 2004 (further details under Ethical Note, Frydman & Gales 2007). The males were likely to have been breeders (or at least competitors of territory) given their proximity to the breeding area, their body size and the timing of capture which was prior to the arrival of itinerant males (Boyd & Duck 1991; Page et al. 2003). Males were weighed with a spring balance (200 ± 0.1 kg, Salter Australia Ltd, Rowville, Victoria, Australia) and their standard body length (nose to tail) was measured (± 1 cm) before either a satellite relay data logger (SRDL, $N = 5$; Sea Mammal Research Unit, University of St Andrews, St Andrews, U.K.) or a Kiwisat ($N = 12$; Sirtrack Ltd, Havelock North, New Zealand) tag was attached (see Ethical Note for further capture and handling details). Data were collected until the battery of the tag failed or the tag fell off, which was between 31 and 183 days (see Appendix 2.1 for details).

The SRDL and Kiwisat tags collected location information via the ARGOS system (CLS, Saint-Agne, France). Location data were obtained at irregular time intervals (median interval of 30 min) and included Argos location estimates of classes 3, 2, 1, 0, A and B (with decrease degree of location accuracy, Argos 1989). The SRDL tags also had pressure and salinity sensors, with onboard data processing, and were used to transmit a summary of data on three categorized behaviours: diving (>5 m depth), cruising (<5 m depth and no dives for 5 min) and hauled out (dry for 10 min), summarized as percentages of time within 6 h periods (Fedak et al. 2002). Cruising may encompass multiple behaviours such as travelling and resting at the surface. The SRDL tags also transmitted an optimized and unbiased sample of individual dive records (Fedak et al. 2002; Bestley et al. 2015). These records included information on dive characteristics, such as maximum dive depth (m) and dive duration (s). A third dive characteristic, 'dive residuals', was derived from the other two characteristics (i.e. residuals from a linear model of duration relative to depth), and used to identify relatively long-duration dives for a given depth (i.e. relatively higher effort; following Bestley et al. 2015).

Post-breeding Trip Characteristics

To address our first objective and characterize the behaviour of male Antarctic fur seals during their long-distance, post-breeding trips, the location data were interrogated and processed. Investigating the time at sea showed some males made local trips around Heard and Kerguelen Islands (collectively referred to as the 'breeding area') before they undertook clear movements away from the breeding area, off the Kerguelen Plateau and towards the Antarctic continent (the post-breeding trip). Only post-breeding trips were analysed. Trip start time was identified from the last location recorded on land before a trip was initiated. The end time was the time of the first on-land location recorded when the

seal returned to the breeding area (a 'complete trip'; mean \pm SD: 89 ± 56 days, $N = 11$ individuals), or the time of the last location transmitted at sea for that seal. Individuals started their post-breeding trips 1–49 days after tag deployment (mean \pm SD: 16 ± 13 d, $N = 17$ individuals; Appendix 2.1) with trips initiated between 29 December 2003 and 5 February 2004.

A hierarchical switching state-space model (SSSM) was used to predict the most likely movement path and associated behavioural states from the error-prone Argos locations (Breed et al. 2009; Bestley et al. 2015). This model estimates locations at a specified, regular time step and also the probability of being in one of two unobserved movement states: faster, linear movements ('directed') and slower, more sinuous movements ('resident'), which we refer to as residence probabilities (Jonsen et al. 2005). The SSSM was implemented as described by Bestley et al. (2015) with a 3 h time step, and individual tracks were processed in batches based on similar trip duration and formation. The SSSM was fitted using the software package WINBUGS (freely available online: <https://www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-winbugs>). We used the diagnostics outlined by Bestley et al. (2015) to assess the goodness-of-fit.

The SSSM location estimates were used to calculate four parameters that summarized each male's post-breeding trip: maximum distance from Heard Island (Great Circle distance using trip R package v1.1-17; Sumner 2013), total distance travelled during a trip, trip duration and minimum latitude (i.e. furthest south). It was not possible to accurately calculate the four parameters when tags ceased transmitting at sea, and we therefore only used males that made a complete trip ($N = 11$) in the following grouping analysis. Based on these parameters, individuals were grouped using a classification tree (binary recursive partitioning model) using the tree R package v1.0-35 (Ripley 2014). This identified that while all males moved in a southerly direction, their trips could be categorized into two types based on whether they crossed 65.65°S : either a long post-breeding trip ('long trip') or a short post-breeding trip ('short trip'). This information was used to categorize incomplete trips. Two-sample t tests were then applied to assess whether body mass, body length, body condition (mass adjusted for length, kg/m, Arnould 1995) and trip start date differed between males that made long versus short trips.

Spatial Predictors of ARS Behaviour

To assess our second objective and determine whether ARS patterns were consistent with targeting profitable feeding areas, we investigated competition and biological activity as potential drivers of ARS behaviour. The distance a male travelled from Heard Island was deemed an indicator of competition avoidance (Kuhn et al. 2014; Weber et al. 2021).

To estimate the relative importance of biological activity, nine habitats were defined based on environmental features known to influence biological activity (Moore & Abbott 2000; Bestley et al. 2020). 'Shelf' habitat defined locations over the shallow section of the Kerguelen Plateau (0–500 m)

using bathymetry from GEBCO (global 30 arc-second grid, GEBCO 2014). Beyond the shelf, locations were categorized according to frontal zones identified by Sokolov and Rintoul (2009) extracted at a daily resolution using *raadtools* v0.3.1.9001 (Sumner 2014). These frontal zones were Polar Front (north: 'PF_N'; middle: 'PF_M'; south 'PF_S'), Southern Antarctic Circumpolar Current Front (north: 'SACCF_N'; south: 'SACCF_S') and Southern Boundary Current ('SB'). The 'ice' habitat was defined from daily sea ice concentration and the approximate ice edge (15% concentration) derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (Cavalieri et al. 2015). Locations were allocated within ice habitat if the ice concentration was greater than zero, the location was south of the ice edge or less than 50 km from the ice edge (to account for the spatiotemporal accuracy of the ice and seal data). This classification should encapsulate locations where the dominant driving force of biological activity is the ice. Some locations were not assigned to a habitat: they typically occurred between the southern extent of the Sokolov and Rintoul (2009) frontal zones and the ice habitat. We expected these locations to have a similar biological distribution to the Southern Boundary Current and defined them as 'SB/near-ice'. For the SRDL tags, we could identify when seals were hauled out on ice. Therefore, for the analysis of dive data from SRDL tags (see Spatiotemporal predictors of diving) we divided ice habitat into two categories: ice habitat where males were known to have hauled out (Ice_Haul) and were known not to have hauled out (Ice_NoHaul).

Dynamic air-sea physical processes that affect ice concentration, distribution and decay subsequently influence biological activity within ice habitat (Smith Jr 1987; Brierley & Thomas 2002). We therefore conducted a separate analysis specifically for males in ice habitat that assessed whether within-ice habitat dynamics might explain changes in movement state while males were within the vicinity of the ice. Four variables were derived from the product of sea ice concentration and ice edge (outlined above) and used to predict the movement state of the males when they were south of 62°S: distance to ice edge (km), ice concentration (log transformed), time since the ice melted (days) and ice melt rate (calculated as a north-to-south first difference from the time-since-melt raster, providing a spatial gradient in the rate of ice retreat; (Andrews-Goff et al. 2018)).

Generalized additive mixed models (GAMM; Wood 2006) were used to assess whether the probability of animals being in a resident state was explained by each of these drivers independently: distance from Heard Island (continuous variable), habitat (factor) and features of the ice environment (continuous). The continuous variables were fitted as smoothing functions to account for expected nonlinear trends. To account for repeated measures, all models were fitted with individual as a random effect (intercept only, to elevate convergence issues with the models) including an AR1 autoregressive correlation structure nested within individual to account for the serial time dependence. These residence probability models were fitted with a binomial error distribution and a logit link function, implemented

using the mgcv R package v1.7.28 (Wood 2011). All model selection and parameter inference approaches are described at the end of the Methods.

ARS behaviour may also be associated with seal behaviours other than foraging. Antarctic fur seals are known to spend periods hauled out on ice (Ribic et al. 1991) and it is likely that, like other fur seals, they also spend prolonged periods at sea at the water's surface, either resting or digesting prey (Bestley et al. 2016; Ladds et al. 2018). To assess whether these behaviours influence ARS probabilities, the duration of two SRDL data summary behaviours, cruising and hauled out, were calculated within directed and resident states for each habitat. Each 6 h period with behavioural data was assigned a location estimate from the SSSM using the middle time step of the 6 h period. If a seal was hauled out away from the breeding area, the duration of the period hauled out was quantified by summing the number of consecutive 6 h periods with 100% time spent hauled out. Any nonconsecutive periods spent hauled out were excluded, such that these calculations are minimum estimates. Similarly, the duration of 6 h summaries that had consecutive 100% cruise time were calculated.

Spatiotemporal Predictors of Diving

Our third objective was to establish whether seal dive behaviour was related to spatiotemporal patterns in environmental features that drive prey availability. Only the SRDL tags ($N = 5$ individuals) collected dive data. Associating the three dive characteristics (dive depth; dive duration; dive residuals) with profitable foraging areas required estimating the dive location. This was achieved by cross-referencing the time a dive occurred with the times of the estimated SSSM locations and, where necessary, applying a linear interpolation between locations. To test the effect of habitat on the dive characteristics, six linear mixed models (LMM) were fitted using the nlme R package v3.1-108 (Pinheiro et al. 2013) to assess whether each of the three dive characteristics varied among habitat types, separately for directed and resident movement states. Dive depth and duration were log transformed to normalize the residuals and the estimates were presented back transformed to their original units. All models included individual as random effect (intercept only, to elevate convergence issues with the models) to account for repeated measure of dives per male ($N = 5$ individuals).

We also examined changes in light levels that are likely to influence diurnal movement of prey. We assessed whether dive frequency ($N = 5$ SRDL tags only) differed with diel light levels by using solar position at a seal's location as a proxy for solar illumination. Solar position (continuous variable) is calculated using solar azimuth and elevation based on location, local date and time (Indian/Kerguelen time zone: UTC +5 h), using the maptools R package v0.8-29 (Bivand & Lewin-Koh 2014). From solar position, a categorical variable for diel period was defined with four levels: positive values of solar elevation angle identified 'day'; values between zero and -12 deg below the horizon identified nautical twilight ('dusk' from 0 to -12 and 'dawn' from -12 to 0); and values below -12 deg identified 'night'. The length of diel periods dramatically changes from summer to winter and not all SRDL tags transmitted

data into the austral winter months (some tags fell off earlier than others). Therefore, to assess changes in dive frequency we included a variable for month and used only a subset of the data, from January to March, where dives were recorded for all seals with SRDL tags. To investigate lunar phase effects on the diel pattern we calculated a categorical predictor for lunar phase. Lunar phase is based on the fraction of the moon illuminated, as defined in equation 32.2 of Meeus (1982). The fractional part illuminated was calculated based on location and local time using the *oce* R package v0.9-13. (Kelley 2014). These values were categorized into lunar phases using even sampling intervals centred on the fractional part that defines each lunar phase. Therefore, values 0.875 to 1 and 0 to 0.125 were categorized as ‘new’, 0.125 to 0.375 as ‘waxing’, 0.375 to 0.625 as ‘full’ and 0.625 to 0.875 as ‘waning’.

We tested for temporal change in both dive frequency and dive behaviour using diel periods and solar position, respectively. The categorical predictors for month and lunar phase were incorporated into models as interaction terms. Dive frequency was the number of dives recorded for an individual within each of the categorized diel periods (four-level factor) within a given month (three-level factor) or lunar phase (four-level factor). Generalized linear mixed models (GLMMs) were fitted to these dive frequency models using the *lme4* R package v0.999999.0 (Bates et al. 2012) with a random effect for individual (intercept only, to elevate convergence issues with the models) and a Poisson error distribution with a log link function. An offset was included in the model that accounted for the average duration of the diel period for an individual within each month or moon phase (i.e. longer days during high summer months). Dive characteristics were tested against predictor variables of solar illumination (continuous) and its interaction with lunar phase (four-level factor) using LMMs. Dive depth and duration were log transformed to normalize the residual errors and the estimates were presented back transformed to their original units. These LMMs also included individual male as the random effect (intercept only, to elevate convergence issues with the models).

Model Selection and Parameter Inference

For GAMMs examining residence probabilities, a separate model was fitted for each of the three sets of predictor variables (distance to Heard Island, habitat and features of the ice environment). Inference about whether or not the predictor(s) was informative was based on *P* values that were calculated using the Bayesian estimated covariance matrix of the parameter estimates (Wood 2011).

The LMMs and the GLMMs (dive frequency) were initially fitted with maximum-likelihood estimation and Akaike’s information criterion (AIC) was used to compare the full model with each reduced model (e.g. without the interaction term and competing fixed effects), including the null (no fixed effects; (Zuur et al. 2009). Inference about the suitability of models was drawn from the differences in AIC relative to the model with the lowest AIC (i.e. ΔAIC). The best model had the lowest AIC and highest Akaike weight (w_i). Factor level comparisons were based on modelled estimates and associated *P* values that were calculated using restricted maximum likelihood, to correct for biases in the estimates (Zuur et al. 2009).

Models that included habitat as a predictor and movement state (response or predictor) were fitted to a subset of the data: exclusively movements within habitats in which more than one male adopted a resident movement state. The subset was necessary to allow model convergence. Given that distinct trip structures were observed (i.e. long and short trips), it was also important to account for biases in habitat use among males with different trip structures (i.e. some males did not use ice habitat). To do this, separate models were implemented for males that adopted the two different trip structures, including a separate model for males that made second post-breeding trips. This accounted for the different males being only able to use certain habitats, and distinct temporal changes in the spatial distribution of habitats due to the seasonal advance of the sea ice. This method was chosen over the use of interactions because we were ultimately interested in how the response variable differed between the habitats. A slight modification of this approach was required when we assessed habitat effects on dive behaviour: there were too few individuals with dive data to fit separate models for males with different trip structures. The test statistics represent differences in habitat levels relative to a reference habitat level, which we specified as the most northern habitat where both movement states were recorded: the northern extension of the southern Antarctic Circumpolar Current front (SACCF).

All analyses were conducted in R v2.15.1 (R Development Core Team 2012). All parameter estimates are reported as back-transformed estimates to the original units along with their standard errors. The parameter test statistics and log-ratio tests were considered significant at $P < 0.05$.

Ethical Note

The 17 male Antarctic fur seals were captured while hauled out on Heard Island. Each seal was approached as it rested and was netted with a handheld hoop net (Furhman Diversified Inc, Seabrook, TX, U.S.A.), after which three people physically restrained the animal by holding the pectoral flippers to the side of the body and the head and neck to the ground. The net was designed with a hole at the apex large enough to allow the snout to protrude for unimpeded breathing and enable mask induction of gas anaesthetic, while keeping the eyes covered with sufficient net material to block the vision of the animal. Isoflurane and oxygen were delivered through a mask connected to a vaporizer (Isotec III, Ohmeda Ltd, Hatfield, U.K.) and Bain nonrebreathing circuit in a similar system to that described by Gales et al. (2005). Isoflurane anaesthesia was maintained using the mask delivery system, during which time the tag was glued (Araldite 2017 epoxy adhesive, Araldite, Basel, Switzerland) to the mid-dorsal pelage between the scapulae, and standard body measurements were recorded (Committee on Marine Mammals 1967). The devices weighed <700 g and were equivalent to <1% of the seal's weight and < 1% of adult seals' body cross-section, making them unlikely to significantly adversely affect swimming and diving (Skinner et al. 2012). Once the glue became reasonably set (5–10 min) the anaesthesia ceased, and the animals were released and observed during recovery. All animal handling procedures were

approved and carried out under the guidelines of the University of Tasmania Animal Ethics Committee and the Australian Antarctic Animal Ethics Committee.

2.3 Results

Eight males made long and nine made short post-breeding trips from Heard Island (Appendix 2.1). Complete long trips ($N = 4$) lasted 157 ± 25 days during which time males spent 29–55% of their time associated with the ice (Fig. 2.1a). Males on long trips typically returned to the breeding area mid-year (mean \pm SD = 9 June \pm 27 days, $N = 4$ trips). In contrast, short trips ($N = 7$) lasted 50 ± 6 days and did not reach the ice; the males returned to the breeding area around 3 months earlier (mean \pm SD = 10 March \pm 10 days, $N = 7$ trips; Fig. 2.1b). Some males that made a short trip were recorded undertaking a second short trip, after a period hauled out at Heard Island (mean \pm SD = 18 \pm 4 days hauled out, $N = 4$ trips), when they again moved south to comparable latitudes (by which time the ice had advanced north) and adopted resident states in ice habitat (Fig. 2.1c).

Whether a male made a long or short trip was not associated with body mass, body length or body condition (i.e. mass/length; Appendix 2.2). However, the males that made a long trip departed the breeding area earlier (mean \pm SD = 6 January \pm 9 days, $N = 8$ individuals) than those that made a short trip (mean \pm SD = 20 January \pm 8 days, $N = 9$ individuals; Appendix 2.1). Long trips reached a greater maximum distance from Heard Island, entailed a longer time at sea and traversed greater total distances compared to short trips (Appendix 2.1). Males alternated between directed and resident states throughout post-breeding trips. All males displayed lengthy directed periods at the start and end (for complete trips) of the trip, and with more resident states at the southern extent (Fig. 2.2). Consequently, males on long trips spent a greater proportion of time in a resident state than those on short trips (Appendix 2.1).

Spatial Predictors of ARS Behaviour

Males rarely entered a resident state during the initial traverse away from the breeding area or in the return phase of their trip (i.e. through the Kerguelen shelf habitat and polar frontal zones; Fig. 2.2). Residence probabilities were strongly positively related to distance travelled from Heard Island (GAMM: $P < 0.001$; Table 2.1, Model 1) and influenced by habitat type, but were dependent on the type of trip (i.e. long versus short; Table 2.1, Models 2.1, 2.2 and 2.3).

Males on long trips had high residence probabilities in Southern Boundary/near-ice habitat and ice habitat (59–60%), and similar probabilities in other habitats (38–41%; Table 2.1, Model 2.1). Males on long trips adopted at least one resident state prior to reaching the ice, and all arrived at the ice by 8 February (mean \pm SD = 27 \pm 2 days after departing the breeding area, $N = 8$ individuals). Males on short trips also had a higher residence probability in their southernmost habitat (SB/near-ice 68%), and similar probabilities in other habitats (47–50%; Table 2.1, Model 2.2). However, later in the season once the ice had advanced north, the four individuals that made a second short trip had equivalent residence probabilities in all habitats south of the polar front (47–50%; Table 2.1, Model 2.3; Fig. 2.2). For all males

that used ice habitat ($N = 12$ individuals), none of the sea ice features examined (distance to ice, ice concentration, time since ice melt or ice melt rate) explained variation in residence probabilities (GAMM: $|T| < -0.48$, $|P| > 0.07$; Table 2.1, Model 3).

During post-breeding trips, males with SRDL tags ($N = 5$ individuals) dived during both resident and directed states (Appendix 2.2) but overall spent relatively little time diving (13–22%) and more time cruising (55–88%) or hauled out (11–47%). Two of the SRDL-tagged males made long trips and recorded periods hauled out while in ice habitat, for up to 2 days at a time (Fig. 2.2, Appendix 2.2). These short periods hauled out in the ice habitat occurred during directed and resident states.

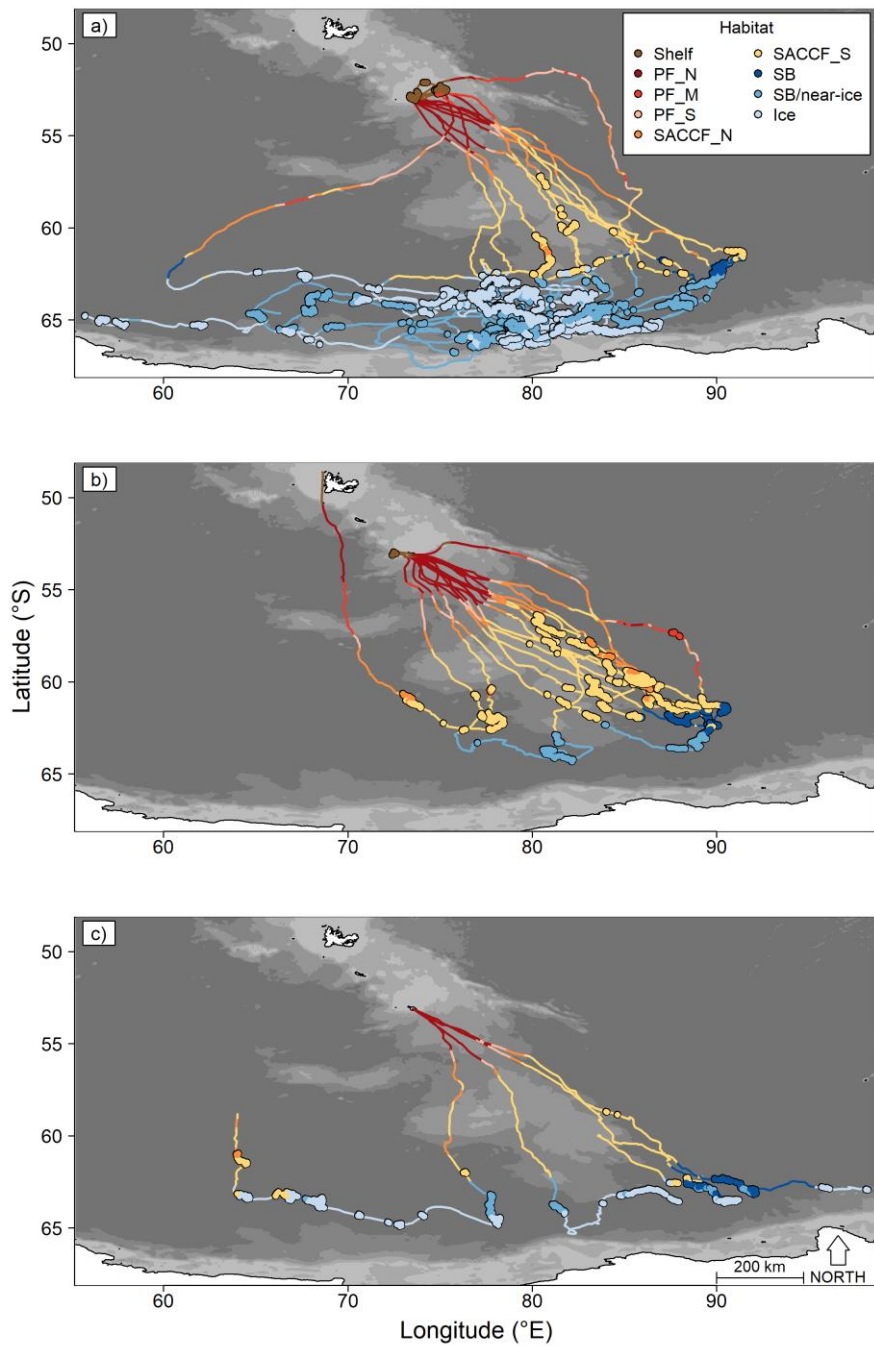


Figure 2.1 Post-breeding trips for male Antarctic fur seals departing Heard Island ($N = 16$ males) and Kerguelen Island ($N = 1$ male) from 29 December 2003 to 3 July 2004. Males made either (a) a single 'long' trip ($N = 8$) or (b, c) multiple short trips: (b) first short trip ($N = 9$) and (c) second short trip ($N = 4$). Lines indicate directed movement states and enlarged sections along lines indicate resident movement state from a switching state-space model. Habitats encountered during trips (see inset legend): shelf; Polar Front zones (north: PF_N; middle: PF_M; south: PF_S), Southern Antarctic Circumpolar Current Front zones (north: SACCf_N; south: SACCf_S), Southern Boundary Current (SB), near-ice/Southern Boundary Current (SB/near-ice) and ice. Bathymetry (GEBCO) is shaded at four intervals: 0–500 m, 500–1000 m, 1000–2000 m and >2000 m depth.

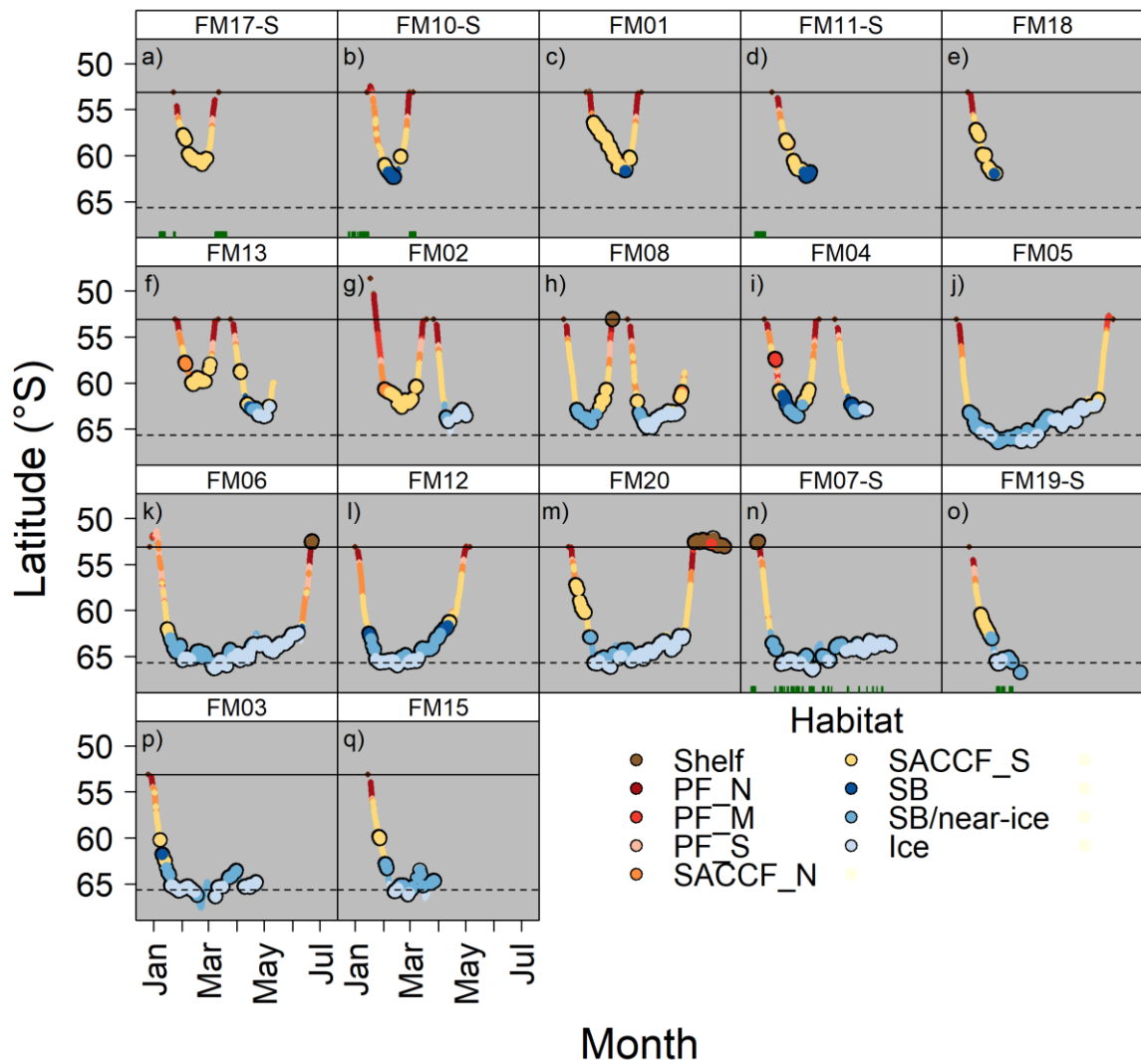


Figure 2.2 Latitudinal movements during post-breeding trips of male Antarctic fur seals. Individuals (IDs are shown above each panel) made (a – e) a single short trip, (f – i) multiple short trips or (j – q) a single long trip. Locations were derived from a switching state-space model, with dots indicating resident states. For habitat abbreviations see Fig. 1. The solid horizontal line identifies the latitude of the deployment site, and the dotted horizontal line represents the boundary between long and short trips. For the five males with SRDL tags, (a), (b), (d), (n) and (o), green vertical lines show the occurrence of 6 h periods hauled out (derived from the 6 h binned behaviour data).

Table 2.1 Summary of generalized additive mixed models that assessed three types of predictors of residence probabilities (pResident) for male Antarctic fur seals on post-breeding trips from Heard Island. The first model tested the effect of a continuous variable for distance to Heard Island (HI). The second model tested a factor variable for habitat, with factor level comparisons to a reference level (SACCF_N; for habitat abbreviations see Fig. 1). The second model was fitted on three subsets of the data, based on trip structure: long trips; short trips 1st; short trips 2nd. The third model tested four continuous variables relating to features of the ice environment: distance to ice, ice concentration, time since the ice melted and ice melt rate. Each model was fitted with binomial errors and logit link, a random effect for individual male (to account for repeated measures), and an autoregressive correlation structure to account for serial dependence in the switching state-space model time series. NIL: did not enter ice the habitat.

Model	Response	Predictor	Estimate (%) (SE)	t/F	P
(subset)					
1	pResident	Distance to HI	0.003 (0.0004)	69.99	<0.001
2.1	pResident (long trip)	[SACCF_N]	38 (22)	-2.15	0.03
		SACCF_S	41 (13)	0.94	0.35
		SB	41 (23)	0.46	0.64
		SB/near-ice	59 (19)	4.36	< 0.001
		Ice	60 (19)	4.65	< 0.001
2.2	pResident (short trip 1st)	[SACCF_N]	47 (23)	-0.58	0.56
		SACCF_S	48 (8)	0.47	0.64
		SB	50 (19)	0.74	0.46
		SB/near-ice	68 (34)	2.56	0.01
		Ice	NIL	NIL	NIL
2.3	pResident (short trip 2nd)	[SACCF_N]	54 (35)	0.49	0.62
		SACCF_S	49 (20)	-1.08	0.28
		SB	50 (27)	-0.68	0.49
		SB/near-ice	50 (29)	-0.64	0.52
		Ice	47 (26)	-1.08	0.28
3	pResident	[Intercept]	0.339	3.29	0.001
		Distance to ice	-0.351	-1.89	0.06
		Ice concentration	0.071	1.47	0.14
		Time since melt	-0.075	-1.25	0.21
		Melt rate	-0.008	-0.48	0.63

Spatiotemporal Predictors of Diving

A total of 16 317 dives were recorded for males with SRDL tags and the dive characteristics varied among habitats. Males were capable of diving down to 232 m and for up to 12.3 min, but most dives were within the upper 40 m of the water column (mean \pm SD: $89 \pm 4\%$ of an individual's dives, $N = 5$ individuals) and lasted less than 2 min (mean \pm SD: $85 \pm 3\%$ of an individual's dives, $N = 5$ individuals). The deepest dives (i.e. >200 m, $N = 10$ dives) all occurred in shelf habitat (i.e. close to the sea floor), and while in shelf habitat few dives were <40 m ($N = 2$ of 49 dives in shelf habitat). Only 268 dives were recorded in the Polar Frontal zones and most of these dives were in the top 40 m ($N = 172$ dives; 64%). South of the Polar Front, dives were predominantly within the upper 40 m of the water column ($N = 14$ 397 of 16 000 dives; 90%). Variation in dive depth and duration among habitats south of the Polar Front was notably small, particularly during resident states (Appendix 2.3). Both positive and negative dive residuals occurred south of the Polar Front, with significantly negative residuals (i.e. shorter dive durations than expected for a given depth) within the Southern Boundary Current near ice habitat and ice habitat without periods hauled out (Appendix 2.3).

Dives occurred on almost all days of post-breeding trips (80–100% of days per individual). Day length varied by month from January to March (depending on location; mean \pm SD: 17 ± 0.5 h to 14 ± 0.7 h, respectively). Accordingly, the number of hours during night, dusk and dawn increased from January to March, at which time most dives were recorded at high latitudes near the ice. Dives consistently occurred during the darkest part of the 24 h cycle, regardless of the month (GLMM, significant interaction, ΔAIC -322.51; Table 2.2, Fig. 2.3). In January, dives were more likely to occur during dawn and dusk, and, despite the short night, were more likely to occur at night than during the day (mean \pm SD: dawn: 21.8 ± 0.1 dives/h; dusk: 26.7 ± 0.1 dives/h; night: 9.1 ± 0.1 dives/h; day: 4.2 ± 0.4 dives/h). By March, the frequency of dives was greatest during the night and dusk, with fewer occurring during dawn and daytime (mean \pm SD night: 19.9 ± 0.1 dives/h; dusk: 19.0 ± 0.2 dives/h; dawn: 8.0 ± 0.2 dives/h; day: 1.7 ± 0.2 dives/h).

The frequency of dives in different diel periods was dependent on lunar phase (GLMM, significant interaction, ΔAIC -142.18). Night dives were least frequent under a full moon compared with any other lunar phase (mean \pm SD: full: 16 ± 0.1 dives/h; new: 41 ± 0.1 dives/h; waxing: 39 ± 0.1 dives/h; waning: 33 ± 0.1 dives/h). In addition, all three dive characteristics (dive depth, dive duration and dive residuals) were influenced by solar illumination and this relationship was dependent on lunar phase. Dives were deeper and longer at higher light values, consistent with the deepest dives occurring during daylight (78% of dives deeper than 100 m occurred during the day and 18% at dawn, $N = 45$ dives). There was a significant lunar phase influence on night diving (Table 2.3). At low values of solar illumination, night dives were shallower, and they lasted longer under a new moon than under a full moon (dive depth: new moon intercept = 2.88, slope = 0.01; full moon, intercept = 2.85, slope = 0.006; dive duration: new

moon, intercept = 3.96, slope = 0.004; full moon, intercept = 3.98, slope = 0.007). Under a new moon, night dive residuals were also more likely to be positive (i.e. greater duration for a given depth; dive residuals: new moon, intercept = -0.02, slope = -0.01; full moon, intercept = 0.09, slope = 0.01).

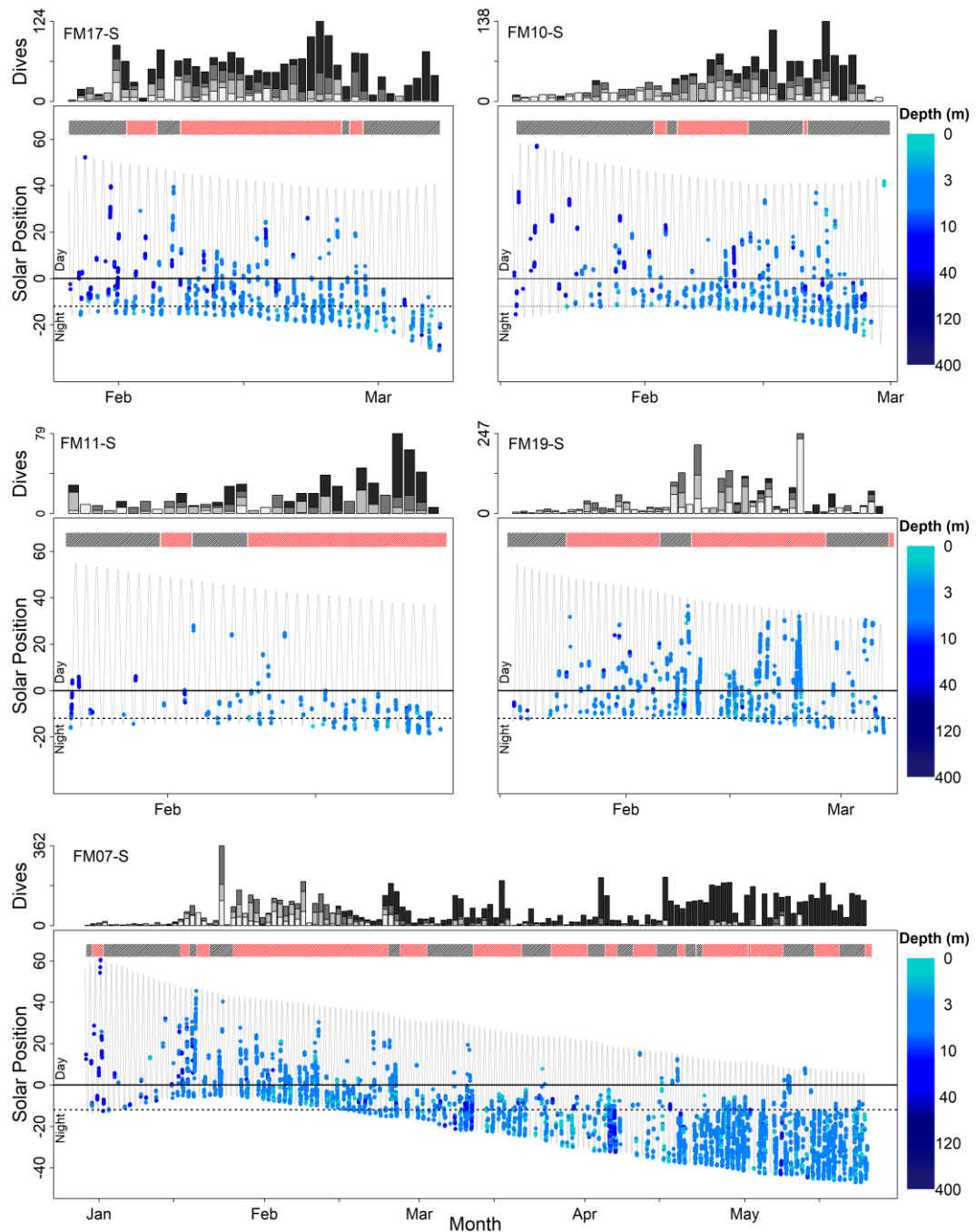


Figure 2.3 Temporal pattern in dives of male Antarctic fur seals ($N = 5$) relative to the position of the sun during their post-breeding trips. IDs are shown at the top of each panel. Vertical bars indicate daily dive frequency and are separated into diel periods by colour (from white to black: day, dawn, dusk, night). The black wave line is the solar position through time relative to an individual's location throughout its trip, with dives indicated as coloured points (coloured according to their depth). Positive values of solar position indicate daylight, values between 0 and -12 (solid and dotted horizontal lines, respectively) indicate nautical twilight and values below -12 indicate night. Black and red horizontal rectangles above the black wave line indicate changes in movement state (directed and resident, respectively).

Table 2.2 Model selection to test for the effects of diel period and month (Model 1) and diel period and lunar phase (Model 2) on the frequency of dives by male Antarctic fur seals. An offset was used to account for different length diel periods that are typical of high-latitude environments and as seals moved latitudinally over time. logLik: log-likelihood; AIC: Akaike information criterion; Δ AIC: difference in AIC; w_i : Akaike weight (see Methods). $N = 5$ individuals, 16 317 dives.

Model	Response	Fixed effects	logLik	AIC	Δ AIC	w_i
1	Dive	Diel + Month + Diel*Month + offset	-1069.9	2175.4	0	1
		Diel + Month + offset	-1240.7	2497.9	322.5	0
		Diel + Month + Diel*Month	-1372.1	2779.7	604.3	0
		Diel + Month	-1959.0	3934.6	1759.2	0
		Month	-1984.6	3978.1	1802.7	0
		Diel + offset	-4242.5	8496.4	6320.9	0
		Month + offset	-4824.9	9658.7	7483.3	0
		Diel	-5460.5	10 932.4	8756.9	0
		Null	-5486.1	10 976.5	8801.1	0
		Offset	-8013.9	16 032.1	13 856.7	0
2	Dive	Diel + Lunar + Diel*Lunar + offset	-851.1	1746.3	0	1
		Diel + Lunar + offset	-935.1	1888.4	142.1	0
		Diel + offset	-1074.3	2159.4	413.1	0
		Diel + Lunar + Diel*Lunar	-11719	2387.9	641.6	0
		Diel + Lunar	-1289.7	2597.4	851.1	0
		Diel	-1369.8	2750.5	1004.1	0
		Lunar	-1383.5	2777.8	1031.4	0
		Lunar + offset	-1459.2	2922.6	1176.3	0
		Null	-4689.7	990.3	7643.9	0
		Offset	-4795.2	9594.5	7848.2	0

Table 2.3 Model selection to test for the effects of solar illumination (Solar) and lunar phase (Lunar) on dive depth (Model 1), dive duration (Model 2) and dive residuals (Model 3) for male Antarctic fur seals. logLik: log-likelihood; AIC: Akaike information criterion; Δ AIC: difference in AIC; w_i : Akaike weight (see Methods). $N = 5$ individuals, 16 317 dives.

Model	Response	Fixed effects	logLik	AIC	Δ AIC	w_i
1	Dive depth	Solar + Lunar + Solar:Lunar	-16 416.5	32 853.0	0	1
		Solar + Lunar	-16 436.9	32 888.0	34.9	0
		Solar	-16 451.2	32 910.3	57.3	0
		Lunar	-16 654.3	33 320.7	467.6	0
		Null	-16 668.4	33 342.9	489.9	0
2	Dive duration	Solar + Lunar + Solar*Lunar	-20 069.2	40 158.3	0	1
		Solar	-20 084.5	40 177.0	18.6	0
		Solar + Lunar	-20 082.7	40 179.5	21.1	0
		Null	-20 109.6	40 225.1	66.8	0
		Lunar	-20 107.5	40 227.0	68.6	0
3	Dive residuals	Solar + Lunar + Solar*Lunar	-21 380.5	42 781.1	0	1
		Solar + Lunar	-21 461.7	42 937.5	156.4	0
		Solar	-21 521.7	43 051.5	270.1	0
		Lunar	-21 567.5	43 147.1	365.9	0
		Null	-21 624.8	43 255.5	474.4	0

2.4 Discussion

The foraging behaviour of post-breeding male Antarctic fur seals is not constrained by offspring provisioning which frees them to undertake long-distance trips to highly productive feeding habitats. Tracked male Antarctic fur seals showed two distinct trip types, either a long trip south to the marginal ice zone or short trip(s) within oceanic waters. Trip type was related to departure date but not to body size. Resident states were more likely to occur away from the breeding area and within habitats at the southern extent in ice habitat during long trips and in southern Antarctic Circumpolar Current front habitat during short trips. Dive behaviour varied among habitats and followed a diel pattern amplified by changes in solar and lunar light. These findings suggest that date of departure from the breeding ground has consequences for post-breeding habitat use, including dive behaviour, and that during the post-breeding period these males forage for prey whose behaviour is influenced by solar and lunar illumination.

The two trip types offered different foraging opportunities. Long trips to ice habitat are consistent with animals targeting the highly productive marginal ice zone (Bost et al. 2004; Bailleul et al. 2007; Lawton et al. 2008; Labrousse et al. 2015). Blooms at the marginal ice zone can be several magnitudes more productive than blooms in open water (Smith & Nelson 1986; Arrigo et al. 2008) providing important feeding grounds for marine predators (Ainley & DeMaster 2013). We found significant negative dive residuals in ice habitats suggesting relatively efficient prey encounters in that habitat. Further north, where the Southern Boundary Current and Southern Antarctic Circumpolar Current Front interact with the southern extent of the Kerguelen Plateau, persistent phytoplankton blooms also occur (Sokolov & Rintoul 2007; Schallenberg et al. 2018). The productivity of these blooms can also be several magnitudes higher than the surrounding waters (Sullivan et al. 1993), and there is evidence of other marine predators including migratory humpback whales, *Megaptera novaeangliae* (Bestley et al. 2019) foraging in this area. Notably though, short post-breeding trips of male Antarctic fur seals included a relatively high proportion of directed state movement behaviour. An earlier comparison between directed and resident states for these males suggested that the directed state is more costly, in terms of horizontal and vertical movement (Bestley et al. 2015), and may therefore result in a lower prey encounter rate for males on short trips. This suggests that while both long and short trips provide opportunities to feed in highly productive habitats, opportunity costs may differ between trip types. For example, by remaining at the breeding area longer, males undertaking short trips may have a lower prey encounter rate but gain other benefits such as increased reproductive opportunities, see below.

Trip duration in some otariids has been associated with body size (Weise et al. 2010; Salton et al. 2019), but this was not the case for Antarctic fur seals (this study), Australian sea lions, (*Neophoca cinerea*, Lowther et al. 2013) or New Zealand fur seals, (*Arctocephalus forsteri*, Page et al. 2006). Rather, the distinction between males making a long or short trip arose from their departure date from the

breeding area: seals that made long trips departed earlier. Late departures may allow males to gain access to receptive females that come into oestrus later in the breeding season (Shaughnessy & Goldsworthy 1990; Page et al. 2003), but it seems that by doing so these males cannot reach the ice in time for the February peak of productivity at the marginal ice zone (Arrigo et al. 2008). Instead, these individuals must concentrate feeding further north in the food web supported by the bloom associated with the southern Kerguelen Plateau. It seems males may make a trade-off between accessing foraging areas and other opportunities gained from remaining closer to the breeding area (e.g. foraging, reproductive, social).

The spatial distribution of ARS behaviour at sea is consistent with male seals passing through areas of low profitability and focusing their effort on more productive foraging areas. During the austral summer, seabirds and seals provisioning offspring on Heard Island are largely constrained to foraging in local waters (Hindell et al. 2011). This may lead to depletion of local resources (Ashmole 1963; Birt et al. 1987; Kuhn et al. 2014) and increase local foraging competition (Woehler & Green 1992; Green et al. 1998; Hindell et al. 2011). This could reduce the rate of energy return for fur seal males foraging in local habitats, and from their behaviour it seems that it is more profitable for them to forage in areas beyond the reach of most provisioning seals and seabirds. The residence probabilities were highest in the southern extent of the Southern Antarctic Circumpolar Current Front, the Southern Boundary Current and near the sea ice. By focusing their search efforts in these productive areas, males may increase their rate of energy return, to help restore condition lost while they fasted during breeding (Boyd & Duck 1991) and prepare for their annual moult (Page et al. 2003). Similar long-distance foraging patterns are seen in other marine predators at Heard Island that are not constrained to central-place foraging (Labrousse et al. 2015; Patterson et al. 2016).

Although ice habitat appears important on a large scale, the specific ice environment features we examined did not show any relationship with residence probabilities, which could reflect processes that operate at different scales within a hierarchical patch system (Fauchald 1999). Foraging animals have been shown to adjust their behaviour in response to hierarchical spatial distributions of food resources and environmental factors (Fritz et al. 2003; Weimerskirch et al. 2005; Benoit-Bird et al. 2013). The ability to distinguish a behavioural response at different hierarchical scales is limited by the spatiotemporal precision at which animal foraging behaviour is measured (Fritz et al. 2003). The location data used in this study have a resolution ranging from hundreds of metres to several kilometres, which limits inferences about movement behaviour (Hays et al. 2001). While the SSM approach used here can improve inferences drawn from tracking data (Breed et al. 2012), the spatial resolution of our approach seems best suited for detecting behavioural responses to regional scale processes, and less adequate for within-region processes. Within-ice features at a larger scale, such as polynyas, can be used to predict habitat use of male Antarctic fur seals (Raymond et al. 2015). The within-ice features examined in this

study, relating to sea ice dynamics, influence biological processes at a relatively fine spatiotemporal scale: perhaps as fine as tens of metres and hours (Massom & Stammerjohn 2010). Identifying behavioural responses of marine predators to these dynamic processes may require movement measurements at a comparable scale, and ideally integration of the dive behaviour, as shown for southern elephant seals, *Mirounga leonina* (Bailleul et al. 2008; Labrousse et al. 2015), or finer-scale environmental features, as shown for emperor penguins, (*Aptenodytes forsteri*, Labrousse et al. 2019). This highlights the importance of grounding inferences from movement data to comparable hierarchical spatial scales of food resources and environmental factors.

Patterns of diving behaviour were consistent with seals capitalizing on spatiotemporal variability in prey distributions throughout their wide-ranging post-breeding trips and can provide information on targeted prey. Males made deeper dives over the shelf during the day when photoperiod was longest (i.e. in summer) suggesting that they were targeting benthopelagic prey, such as mackerel icefish, *Champsocephalus gunnari*, which form deep shoals (100–250 m) at dawn and during the day (Frolkina 2002), and that was a dominant prey species found in Antarctic fur seal scats at Heard Island during austral summer 1987–1988 (Green et al. 1989). As photoperiod decreased, and the nights lengthened, seals moved into pelagic habitats and dived to shallow depths at night. The longer duration dive for a given depth at night, particularly under a new moon, also suggests that males invested more effort in their dives under low ambient light levels. This diel pattern indicates feeding upon vertically migrating prey, such as myctophids and krill (Croxall et al. 1985; Boyd & Croxall 1992; Horning & Trillmich 1999; Lea et al. 2002; Lea et al. 2009), which aggregate at shallow depths during periods of low ambient light levels (Duhamel et al. 2000; Bost et al. 2002; Hays 2003). For air-breathing marine vertebrates, shallow dives are more cost effective than deeper dives (Butler & Jones 1997). By foraging on shallow aggregations of prey, particularly as photoperiod decreases, males are more likely to maximize their rate of energy return and thereby restore condition lost during breeding (Boyd & Duck 1991).

Although animal movement patterns are driven by the distribution of resource patches, wide-ranging predators may forage opportunistically, and other factors can motivate residency. To sustain directed movement between breeding and distant foraging areas, wide-ranging predators like male Antarctic fur seals may need to feed opportunistically while travelling. After reaching a profitable feeding area, marine predators will also need to rest at some point, to recover from diving and process prey (Boyd 1996; Weimerskirch & Guionnet 2002; Sparling et al. 2007; Russell et al. 2015). Ideally resting behaviours should occur close to the foraging area, to minimize travel costs. Resting could occur on the ice or at the surface of the water: the latter would be consistent with the long cruise periods undertaken by males while in open-water habitat. Males may also haul out on ice to evade predators such as killer whales, (Ribic et al. 1991; Orcinus orca, Pitman & Durban 2012). The relatively short periods spent

hauled out while at the ice edge habitat is consistent with maximizing foraging time and/or primarily resting in surface waters.

In conclusion, the large sexual size dimorphism and highly polygynous mating system of otariids means males of these species are under strong selection pressures to attain large size and sufficient energy storage to successfully retain a territory during breeding. Consequently, these males must seek highly productive foraging areas between breeding seasons to restore condition lost during breeding. Male Antarctic fur seals appear to achieve this by avoiding areas with high competition for food resources and focusing their foraging effort in areas of high biological activity further away. The two types of post-breeding trips observed in this study may reflect males making a trade-off between prime post-breeding foraging opportunities associated with sea ice and reproductive opportunities gained by remaining in the breeding area after other males leave.

2.5 Appendices

Appendix 2.1 Summary of animal measurements and post-breeding trip(s) characteristics for 17 male Antarctic fur seals from Heard Island. Animal identities with ‘-S’ are those that carried an SRDL tag. Complete trips are those that returned to the breeding area (see Methods). Seals that made a ‘long trip’ are presented first, in order of their start date, and then the seals that made a ‘short trip’. The mean \pm SE for five test variables and the results of Welch two-sample tests between the groups (long versus short trips) are presented. Maximum distance is from Heard Island, and percentage of time in resident state (rather than directed state) is from a switching state-space model.

ID (trip number)	Mass (kg)	Length (m)	Body condition (kg/m)	Trip start date	Complete trip	Maximum distance (km)	Total distance (km)	Trip duration (days)	Minimum latitude (S)	Time in resident state (%)
FM03 (1)	82.7	1.63	50.7	29 Dec	×	1649	6874	115	67.60	40.3
FM07-S (1)	118.9	1.66	71.6	29 Dec	×	1524	6907	147	66.49	58.1
FM06 (1)	67.8	1.39	48.8	30 Dec	✓	1520	11 859	175	66.35	50.8
FM05 (1)	100.8	1.67	60.4	31 Dec	✓	1504	9608	166	66.49	60.6
FM12 (1)	106.4	1.7	62.6	3 Jan	✓	1556	6773	120	66.01	66.8
FM19-S (1)	87.1	1.69	51.5	14 Jan	×	1529	2724	54	66.79	60.4
FM20 (1)	104.6	1.75	59.8	16 Jan	✓	1487	9122	169	66.22	64.7
FM15 (1)	91.2	1.63	56.0	18 Jan	×	1510	4375	72	66.59	34.4
Mean \pm SE	95 \pm 16	1.6 \pm	58 \pm 8	6 Jan \pm 9 days						60.7 \pm 3.5
FM04 (1)	73.8	1.6	46.1	11 Jan	✓	1474	3857	54	63.70	48.4
FM08 (1)	96.7	1.7	56.9	12 Jan	✓	1346	3966	52	64.35	33.4
FM18 (1)	74.3	1.6	46.4	13 Jan	×	1230	1758	28	61.98	58.4
FM10-S (1)	97.2	1.59	61.1	16 Jan	✓	1423	3432	45	62.41	23.1
FM11-S (1)	98.55	1.64	60.1	19 Jan	×	1350	1831	39	62.29	60.7
FM02 (1)	110.7	1.73	64.0	20 Jan	✓	1090	3518	56	62.63	48.8
FM17-S (1)	70.1	1.55	45.2	25 Jan	✓	1088	2651	44	60.98	55.4
FM13 (1)	116.7	1.64	71.2	27 Jan	✓	1109	2837	42	60.16	41.1
FM01 (1)	114.6	1.56	73.5	5 Feb	✓	1350	3778	55	61.66	58.9
Mean \pm SE	95 \pm 18	1.6 \pm	58 \pm 11	20 Jan \pm 8 days						44 \pm 4.7
FM08 (2)	96.7	1.70	24 Dec	21 Mar	×	1338	3897	60	64.92	62.3
FM04 (2)				28 Mar	×	1806	2393	32	63.20	36.4
FM13 (2)				28 Mar	×	1547	2845	45	63.67	50
FM02 (2)				30 Mar	×	1446	2233	33	65.32	32.9
<i>df</i>	15	10.7	14.4	14.434						8.97
<i>t</i>	0.02	0.38	-0.14	-3.3214						2.79
<i>P</i>	0.981	0.708	0.893	0.005						0.021

Appendix 2.2 Summary of foraging (i.e. diving) and nonforaging (i.e. cruising and hauled out) behaviours that occurred during each movement state throughout the post-breeding trips of five male Antarctic fur seals with SRDL tags. Males are grouped according to trip type (long or short trip). Variables include the number of movement states (D = directed; R= resident), number of dives, percentage of time in a behaviour (diving, cruising or hauled out; see Methods) and the duration of behaviours (see Methods). Means are presented \pm SD and calculations of duration include the range (within brackets). Behaviour summary data were available for a portion of each movement state: mean \pm SD = 76.86 \pm 25.48 [0–99% coverage]. NA: not available.

ID (Trip type)	State	No. of states	State duration (days)	No. of dives	Time diving (%)*	Time cruising (%)*	Time hauled out (%)*	Duration cruising (days)	Duration hauled out (days)
FM19-S (long)	D	3	7 \pm 2 [4–8]	182 \pm 127	22 \pm 8	74 \pm 11	11	0.5 \pm 0.2 [0.2–0.7]	0.5
	R	3	15 \pm 4 [12–18]	766 \pm 692	19 \pm 12	54 \pm 26	54	0.4 \pm 0.2 [0.3–0.5]	2
FM07-S (long)	D	15	4 \pm 3 [1–14]	226 \pm 203	15 \pm 6	67 \pm 24	38 \pm 28	0.4 \pm 0.1 [0.3–0.5]	0.9 \pm 0.5 [0.2–2]
	R	15	6 \pm 7 [1–29]	443 \pm 583	18 \pm 7	56 \pm 25	47 \pm 17	0.4 \pm 0.2 [0.3–0.7]	0.8 \pm 0.5 [0.2–2]
FM17-S (short)	D	4	4 \pm 3 [1–9]	176 \pm 123	16 \pm 10	88 \pm 11	NA	0.6 \pm 0.1 [0.5–0.7]	NA
	R	3	7 \pm 9 [1–18]	449 \pm 632	16 \pm 5	84 \pm 5	NA	0.5 \pm 0.0 [0.5–0.5]	NA
FM10-S (short)	D	4	8 \pm 6 [1–16]	307 \pm 217	16 \pm 8	83 \pm 6	NA	0.9 \pm 0.9 [0.5–2]	NA
	R	3	5 \pm 5 [1–8]	170 \pm 223	22 \pm 8	78 \pm 8	NA	0.4 \pm 0.2 [0.3–0.5]	NA
FM11-S (short)	D	2	7 \pm 3 [5–9]	56 \pm 5	13 \pm 0	87 \pm 0	NA	0.5 \pm 0.0 [0.5–0.5]	NA
	R	2	11 \pm 11 [3–18]	262 \pm 344	18 \pm 7	84 \pm 7	NA	0.5 \pm 0.0 [0.5–0.5]	NA

*Percentage of total behaviour summary data recorded during each movement state that was allocated to that behaviour.

Appendix 2.3 Summary of factor level comparisons for six linear mixed models that assessed whether three dive characteristics (dive depth; dive duration; dive residuals) varied among habitat types, separately for when male Antarctic fur seals were in directed or resident states. Dive depth and duration were log transformed to normalize the residuals and the estimates are presented back transformed to their original units. All models included a random effect to account for repeated measure of dives per male ($N = 5$ individuals), which accounted for 65–89% of the variance explained by the models. The northern SACCF level [SACCF_N] was used as a reference for factor level comparisons. For habitat abbreviations see Fig. 1. Ice_Haul: ice habitat where males were known to have hauled out; Ice_NoHaul: ice habitat where males were known not to have hauled out.

Response	Habitat	Directed state			Resident state		
		Estimate (SE)	<i>t</i>	<i>P</i>	Estimate (SE)	<i>t</i>	<i>P</i>
Dive depth (m)	[SACCF_N]	36.3 (0.13)	27.71	< 0.001	16.1 (0.09)	32.04	< 0.001
	SACCF_S	20.4 (0.05)	-11.57	< 0.001	18.2 (0.08)	1.53	0.13
	SB	21.7 (0.06)	-8.60	< 0.001	13.7 (0.09)	-1.75	0.08
	SB/near-ice	13.2 (0.09)	-11.38	< 0.001	15.1 (0.09)	-0.73	0.46
	Ice_Haul	10.1 (0.09)	-14.92	< 0.001	12.7 (0.08)	-2.93	0.003
	Ice_NoHaul	14.2 (0.09)	-10.80	< 0.001	23.8 (0.08)	4.75	< 0.001
Dive duration (min)	[SACCF_N]	1.63 (0.13)	34.8	< 0.001	0.81 (0.12)	31.25	< 0.001
	SACCF_S	0.98 (0.06)	-8.08	< 0.001	0.92 (0.11)	1.18	0.24
	SB	1.07 (0.07)	-5.60	< 0.001	0.73 (0.12)	-0.91	0.36
	SB/near-ice	0.82 (0.11)	-6.32	< 0.001	0.64 (0.12)	-2.03	0.04
	Ice_Haul	0.78 (0.11)	-8.79	< 0.001	0.97 (0.11)	-1.46	0.14
	Ice_NoHaul	0.65 (0.11)	-6.94	< 0.001	0.69 (0.11)	1.62	0.10
Dive residuals	[SACCF_N]	0.02 (0.12)	0.17	0.868	0.15 (0.14)	1.09	0.28
	SACCF_S	-0.14 (0.07)	-1.92	0.06	-0.08 (0.14)	-1.60	0.11
	SB	-0.14 (0.09)	-1.54	0.12	0.003 (0.15)	-1.05	0.29
	SB/near-ice	0.23 (0.12)	1.89	0.06	-0.36 (0.15)	-3.39	< 0.001
	Ice_Haul	-0.001 (0.12)	2.67	0.01	0.07 (0.14)	-0.58	0.57
	Ice_NoHaul	0.32 (0.12)	-0.01	0.99	-0.56 (0.14)	-4.90	< 0.001

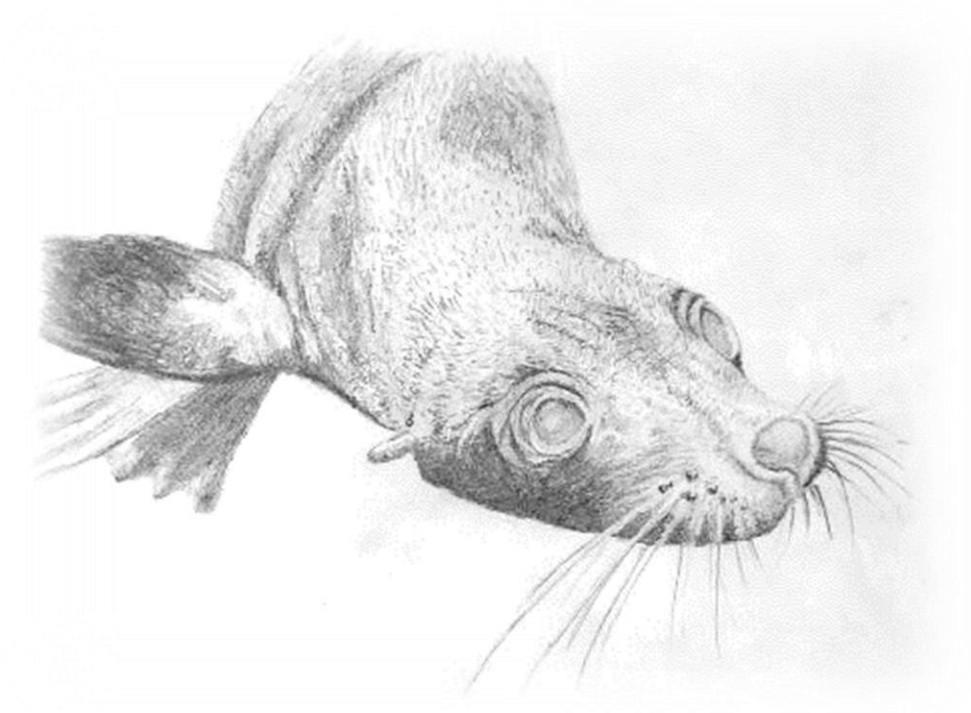
3. Chapter Three

Mechanisms for sex-based segregation in foraging behaviour by a polygynous marine carnivore

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Drawing credit: Marcus Salton

Abstract

Sexual segregation in foraging is often attributed to constraints arising from sexual size dimorphism, such as differing physiological abilities and energy requirements, or to reproductive commitments including nutritional requirements and behavioural limitations such as parental care. In species with sexual size dimorphism and a polygynous mating system, there are sex differences in both body size and reproductive commitments, so distinguishing the mechanism underlying sexually segregated foraging is particularly difficult. We investigated movements of the sexually dimorphic, polygynous Australian fur seal *Arctocephalus pusillus doriferus*, and compared foraging strategies of juveniles to adults in order to investigate foraging constraints associated with differences in body size separately from those also associated with reproduction. Foraging trip duration, range, core area, and distance to core area from the breeding site were similar between the sexes in juveniles and adults, but juveniles were overall more constrained than adults. After foraging trips, juveniles and adult females were more likely to return to the breeding site than to other sites, probably because of physiological limitations (juveniles) or reproductive commitments (adult females). Freedom from reproductive commitments allowed adult males to reside in areas away from the breeding site and thereby meet the higher energy requirements arising from their larger body size, without competing with adult females. Consequently, intraspecific differences in foraging strategies of Australian fur seals are shaped first by foraging constraints associated with body size, and to a lesser extent by reproductive behaviour.

3.1 Introduction

Intraspecific foraging differences are an important feature of foraging ecology, with implications for population dynamics and conservation strategies (Bolnick et al. 2011). Foraging differences are often found between breeding males and females, and this is exemplified in sexually dimorphic species (Ruckstuhl & Neuhaus 2005). Sex differences in body size and reproductive roles can influence foraging behaviour in a number of ways. For example, the behaviour of females with dependent offspring may be constrained by the need to protect their offspring from predation (Hay et al. 2008; Weir et al. 2008), the larger size of males may allow them to access different food resources (Bugalho et al. 2001), sex-specific nutrient requirements may differ between the sexes at different times of the reproductive cycle (Beck et al. 2007; Miranda et al. 2012), and lactation or parental care may limit activities (Thompson et al. 1989; Miquelle et al. 1992; Ruckstuhl & Kokko 2002). The underlying mechanisms that drive sexually segregated foraging behaviour have been extensively debated because it is often difficult to separate the influence of body size from reproductive roles (Wearmouth & Sims 2008). The conflation of body size and reproductive activity has been investigated in ungulates (Main et al. 1996; Bowyer 2004; Ruckstuhl & Neuhaus 2005; Ruckstuhl 2007) and some marine taxa (Wearmouth & Sims 2008). For example, in polygynous mammals where females are smaller than males and responsible for all parental care, males may exploit a larger foraging range due to the resource requirements arising from larger body size. Alternatively, they may be free to forage more widely because they are not constrained to returning to the breeding site to care for offspring.

To assess whether reproductive strategies or physiological requirements most influence foraging behaviour, some studies have examined the differences between males and females that have contrasting reproductive strategies (Breed et al. 2006; Ruckstuhl 2007; Main 2008). However, an alternative approach to teasing apart this question is to compare juveniles and adults. Juveniles have no immediate reproductive demands, and so foraging range is primarily constrained by the limits associated with their immature development and naivety (Marchetti & Price 1989). Ontogenetic constraints mean that juveniles are often less efficient foragers (Fowler et al. 2007a; Fayet et al. 2015), poorer competitors (Sol et al. 1998), have lower fasting endurance (Lindstedt & Boyce 1985), and are more vulnerable to predation (Grignolio et al. 2007). The lack of reproductive constraints also means they may have more time to explore. As a consequence, to avoid competition with adults, juveniles could either exploit the same foraging area but different resources than adults (Jeglinski et al. 2013), or move to different foraging areas (Fayet et al. 2015). In juvenile seals, foraging should be influenced largely by age (e.g. experience and individual learning) and body size (e.g. energy requirements and breath-hold capacity) (Stewart 1997; Field et al. 2005). Studying juveniles allows foraging constraints associated with size to be investigated in individuals free of conflicting foraging constraints associated with reproductive behaviour. Accordingly, comparing foraging behaviour between males and females

and between juveniles and adults provides a study design that should be able to tease out the mechanisms that result in intra-specific differences in foraging.

Otariids (fur seals and sea lions) are the most sexually dimorphic mammalian taxa, with males on average being 3 times larger than females (Weckerly 1998). They are polygynous (Trillmich & Trillmich 1984), with distinct sex-specific strategies to maximise lifetime reproductive success. Males must acquire competitive size, skill, and energy reserves in order to establish and defend a breeding territory and mate with a number of sexually mature females (McCann 1980; Boyd & Duck 1991). Parental care is entirely left to females, who act as central place foragers while supporting their pup for between 4 and 36 mo (depending on the species) (Bonner 1984; Kovacs & Lavigne 1992; Boyd 1998). Otariids also have a long juvenile development stage, with females typically maturing at age 3 to 4 yr and males at age 5 to 6 yr; however, males typically are not large enough to establish and defend a breeding territory until age 8 to 9 yr (Atkinson 1997; Wickens & York 1997). In many otariids, foraging behaviours differ between adult males and females, and between adults and juveniles (Boyd et al. 1998; Sterling & Ream 2004; Staniland 2005; Page et al. 2006; Fowler et al. 2007b; Staniland & Robinson 2008; Geschke & Chilvers 2010; Jeglinski et al. 2013), yet the mechanisms that drive these differences are still unclear.

Australian fur seals *Arctocephalus pusillus doriferus* are one of the most sexually dimorphic otariids, with males and females weighing on average 279 and 76 kg, respectively (Warneke & Shaughnessy 1985). Lactation in Australian fur seals lasts approximately 10 mo (Arnould & Hindell 2001) and sexual maturity is reached at age 3 to 6 yr (Arnould & Warneke 2002; Gibbens & Arnould 2009). Most of the Australian fur seal population is concentrated in Bass Strait, Tasmania and the southeast Australian coastline (Kirkwood et al. 2010). Foraging behaviour of adult female and adult male Australian fur seals has been extensively investigated (Arnould & Hindell 2001; Littnan & Arnould 2002; Kirkwood et al. 2006; Arnould & Kirkwood 2007; Robinson et al. 2008a; Kirkwood & Arnould 2012; Hoskins & Arnould 2014; Kernaléguen et al. 2015b; Knox et al. 2017, 2018), but only one study (Kernaléguen et al. 2015b) compared foraging behaviour of males and females. Juvenile foraging ranges have not been documented for Australian fur seals apart from a mark-resight study covering 1960–1970 (Warneke 1975). Studies of juveniles are not common for otariids because of the difficulty of recovering data loggers from animals unconstrained by haul-out fidelity (Page et al. 2006).

In this study, we compared the foraging strategies of juvenile and adult male and female Australian fur seals from a breeding site in northern Bass Strait, Australia. Given that lactating females must return to suckle their pup, we expected adult females to both forage closest to, and return most frequently to, the breeding site. Consistent with ontogenetic constraints, we expected juveniles to either share foraging areas with adults but use the space differently, or to forage in different areas to adults. Neither juveniles nor adult males need to return to the breeding site to provision pups, so we hypothesised they would be more likely to use haul-outs close to their feeding areas and so reduce transit time between

feeding and rest sites and maximise the rate of energy gain while at sea. We predicted this would drive sexual segregation and so reduce competition with females, and free juveniles and adult males from relying on potentially depleted resources around breeding sites (Ashmole 1963; Kuhn et al. 2014). As some juveniles may benefit from prolonged maternal care (Hume et al. 2001), we anticipated that some individuals could exhibit unusually small ranges. For most juveniles, though, foraging range and core foraging area were expected to reflect the body size of juveniles (Lindstedt et al. 1986; Tucker et al. 2014), with smaller seals having a smaller size range.

3.2 Methods

Data compilation and collection

We compiled historic data for 9 adult male and 10 female Australian fur seals *Arctocephalus pusillus doriferus* tracked from their breeding site at Seal Rocks, northern Bass Strait, Australia (38.526° S, 145.099° E), between 1999 and 2003 (Kirkwood et al. 2006; Arnould & Kirkwood 2007; Kirkwood & Arnould 2012). In those studies, individuals were selected based on morphological and behavioural characteristics: males, the most dominant present, to sample breeding individuals; and females, nursing a pup. All seals were captured and restrained (using methods appropriate for their body size) and were sedated while a device was attached (Kirkwood et al. 2006; Arnould & Kirkwood 2007). Their straight-line body length was measured (± 1 cm) and their mass either estimated (adult males, to the nearest 10 kg) or weighed to ± 1 kg using a spring scale (females). All animals were captured during winter, and devices were either recovered after approximately 6 wk or remained on the seals until they fell off.

We used a similar protocol to track between 3 and 6 juveniles each year from 2004 to 2012, resulting in 18 males and 20 females. We selected seals based on their body length < 1.5 m, no indication of lactation (in the case of females), the presence of obvious canines (indicating they were at least 1 yr old), and their location—we took seals closest to our location at the time to minimise disturbance to other seals resting at the colony. This provided a haphazard component to the selection process. Their straight-line body length was measured (± 1 cm) and their mass calculated using a spring scale (± 1 kg). Across all studies, 2 types of tracking devices were deployed: Kiwisat100 (Sirtrack; $13 \times 6 \times 4$ cm) and Mk10 (Wildlife Computers; $11 \times 7 \times 3$ cm). Both tracking devices collected positional data via the Argos satellite system (CLS, France). Positions of location classes Z, A, and B were not collected for males (Kirkwood et al. 2006), Z and B were not collected for females (Arnould & Kirkwood 2007), and Z class locations were omitted from juvenile data (1% of locations), due to the extra cost (in earlier years), inaccuracy, and the frequent collection of higher-quality estimates. Improvements in movement models over time made collection of location classes with higher error (i.e. A and B) worthwhile in later years. Erroneous positions were filtered following the methods of Austin et al. (2003) using a maximum speed of 9 km h^{-1} for all seals. A continuous-time correlated random walk model was fitted to the filtered data using R package ‘crawl’ v.1.4 (Johnson 2013) and the model output was used to predict hourly positions along each seal’s track. The error estimate for each Argos location class was specified using refined estimates for Australian fur seals (Costa et al. 2010). Intervals on land were incorporated into the model to avoid predicting movements while a seal was stationary. Intervals on land were identified from the wet/dry conductivity sensor, dive data that were collected by Mk10 devices, and the direction of travel and proximity (< 20 km, due to low frequency and accuracy of locations) to sites where seals were known to haul out (Kirkwood et al. 2006; Kirkwood & Arnould 2012). Intervals at sea were defined as ‘trips’ and intervals on land as ‘hauled-out’. When individuals spent < 7 h in the water and traversed < 10

km, there were too few locations (<5 locations), most of poor location accuracy, to determine accurately whether an individual had departed the site, on a short trip, or had remained within the waters adjacent to the site (e.g. among rockpools, rafting with other seals close to shore). We considered these periods in the water to be part of a period hauled out on land. Therefore, trips reflect travel and foraging between 2 sites, not exclusively an animal leaving and returning to the breeding site (site of deployment), as is usually the case in otariid foraging studies (Boyd 1996; Arnould & Hindell 2001; Harcourt et al. 2002).

Calculation of response variables

All trips by an individual seal were analysed to compile key information on foraging behaviour and to derive the response variables for analyses. Trip duration was calculated as the time elapsed between departure from a site ('hauled-out') and arrival at the next site where they hauled-out. To estimate the foraging areas of each seal, we used kernel utilisation distribution methods to delineate 'foraging range' (95% utilisation distribution; km²) and 'core area' (50% utilisation distribution; km²) using the R package 'ks' v.1.8-13 (Duong 2013). We used plug-in bandwidth selection because visual inspections indicated this method consistently represented the distribution of the predicted hourly positions of each individual. To measure displacement of a seal's foraging area from the breeding site, we calculated the minimum, straight-line distance between Seal Rocks and the centre of the core area ('distance to core area'). If a seal's core area comprised multiple polygons, then the distance to the core area (D) was calculated as:

$$D = \sum [d(i) \times (\text{core area size}(i) / \text{total core area size})] \quad (1)$$

where i is a core area polygon, d is the distance between Seal Rocks and the centre of a polygon, core area size is the area (km²) of the polygon, and total core area size is the summed area of all polygons that made up the core area.

Data analysis

All analyses were performed with R v.2.15.1 (R Development Core Team 2012). Preliminary analysis highlighted that the among-individual variation in foraging parameters within a year was greater than the among-year variation, and variations in response variables were similar to a previous study of female Australia fur seals (Arnould & Hindell 2001). Therefore, we pooled data from all years for analyses.

To avoid spurious effects from analysing multiple correlated parameters, we assessed the relationship between the 2 measures of body size, i.e. body length and body mass. To do this, body mass was tested as a predictor of body length using a linear model (LM) fitted by maximum likelihood. Akaike's information criterion (AIC) was used to compare a model with body mass and a null model without body mass. If the AIC was reduced by more than a factor of 2 from the null model ($\Delta\text{AIC} > 2$), then the

predictor was considered informative (Burnham & Anderson 2002) and that there was a linear relationship between the predictor and response variables. If there was a relationship, 1 parameter was selected for subsequent analyses.

One response variable was specified at the trip level ('trip duration', multiple measures per individual) and other response variables were calculated at the individual level ('foraging range', 'core area', 'distance to core area', and 'frequency of returns to the breeding site', 1 measure per individual). To test trip duration, a linear mixed model (LMM) was fitted, with individual identity as the random effect, in the R package 'nlme' v.3.1.108 (Pinheiro et al. 2013). To test variables calculated at the individual level, LMs (foraging area variables) and general linear models (GLMs) with binomial errors (for frequency of returns to the breeding site) were fitted. In the GLMs, we used a 2-column matrix with the number of successes and failures, where a success was a return to the breeding site and a failure was a use of an alternative site. Log-transformations were applied to LMs and LMMs where necessary to normalise residual error.

Two sets of predictors were tested against each response variable. First, the importance of the predictor variables sex (male and female) and life stage (juvenile and adult) was tested, and their interaction term included to assess whether a sex difference was consistent between life stage groups. Second, the importance of body size as a (continuous) predictor variable was tested, including an interaction between body size and life stage to assess whether a relationship with body size was dependent on life stage group. AIC was used to compare models fitted by maximum likelihood, and again inference was drawn from the ΔAIC to identify the best model (lowest AIC and highest Akaike weight, w_i). If an interaction term was retained in the best model, then separate models were fitted for each level of life stage (i.e. adults and juveniles). Therefore, for each set of predictors, 5 models were fitted for each response variable (e.g. sex and life stage with the additive and multiplicative interactions and the null model). In the event of a significant interaction, a further 4 models tested the effect of sex (or body size) for each level of the life stage predictor (adults and juveniles) and the associated null models.

The best models were refit with restricted maximum likelihood (REML) to get the most accurate estimates of predictors and presented ± 1 SE; model estimates based on log-transformed and binomial data were back-transformed to original units. For the second set of predictors, if body size was not retained in the best model but was more informative than the null (i.e. $\Delta AIC < -2$), then we also refit the model with body size, applying REML, and estimated the global relationship with body size. The goodness of fit, or strength, of the best model was assessed using R^2 for linear models and general linear models and both marginal R^2 (mR^2) and conditional R^2 (cR^2) for mixed models, using the R package 'MuMIn' v.1.9.13 (Barton 2013).

3.3 Results

Size dimorphism

The length and mass of seals varied among sex and life stage groups, but the difference between sexes was not consistent between life stage groups (LM; $\Delta\text{AIC} = -54.34$ and $\Delta\text{AIC} = -98.37$, respectively, compared to the models without the sex– life stage interaction). Adults were sexually dimorphic both in terms of length (LM; $\Delta\text{AIC} = -54.48$ compared to the null) and mass (LM; $\Delta\text{AIC} = -41.48$ compared to the null), but juveniles were not (length, LM; $\Delta\text{AIC} = 1.09$ compared to the null; mass, LM; $\Delta\text{AIC} = 0.66$ compared to the null) (Table 3.1, Fig. 3.1). Length and mass were highly positively correlated (LM; $\Delta\text{AIC} = -117.21$ compared to the null). As we were more confident in our measurement of length (mass of adult males was estimated), we used length in subsequent analyses of body size.

Foraging locations

Individuals were tracked for between 20 and 191 d: juvenile females, 63.6 ± 1.1 d; juvenile males, 62.1 ± 4.8 d; adult females, 94.7 ± 16.2 d; and adult males, 105.4 ± 21.1 d. Seals mainly used the western half of Bass Strait, but some travelled to the eastern and western extents of Victoria, and to southern Tasmania (Fig. 3.2). Seals were located mainly in waters shallower than the 200 m bathymetry contour (i.e. on the continental shelf); locations beyond the continental shelf slope were rare.

Trip duration

We recorded 825 trips, of which 291 were from juvenile females, 286 from juvenile males, 138 from adult females, and 110 from adult males. On average, an individual made 14.4 ± 1.1 trips (range: 1–38 trips), and the mean number of trips was similar for each sex–life stage group (Table 1). Trip duration varied greatly (range: 0.3–24.1 d), and mean trip duration for individual seals ranged from 1.0 to 15.7 d.

Trip duration varied between life stage groups without a sex effect (Model 3, $w_i = 0.54$; Model 2, $w_i < 0.01$), but a weak interaction effect suggested the difference between sexes depended on life stage (Model 5, $w_i = 0.16$ for the interaction effect) (Table 3.2). Juvenile trip durations (2.50 ± 0.10 d) were almost half those of adults (5.20 ± 0.18 d). Within life stage groups, males tended to have longer trips than females, more so in adults (Table 3.1).

There was a high level of inter-individual and intra-individual variation in trip duration (Fig. 3a). Many juveniles made trips of similar duration to adults, but most trips by juveniles were relatively shorter. Similarly, adults made short trips that were of comparable duration to juveniles, but most trips by adults were longer. One juvenile female (body length: 135 cm) consistently travelled on much longer trips than the other juvenile females (15.7 ± 2.8 d, range: 12.0–24.1 d, compared to other juvenile females: 3.6 ± 0.4 d, range: 0.3–15.0 d), but model outcomes were unchanged when this outlier was removed.

Trip duration was explained more by life stage (Model 3, $w_i = 0.55$) than body size (Model 2, $w_i = 0.13$), and there was a possible interaction between life stage and body size (Model 5, $w_i = 0.10$) (Table 3.3), i.e. larger individuals had longer trips, particularly adult males (Fig. 3.3a).

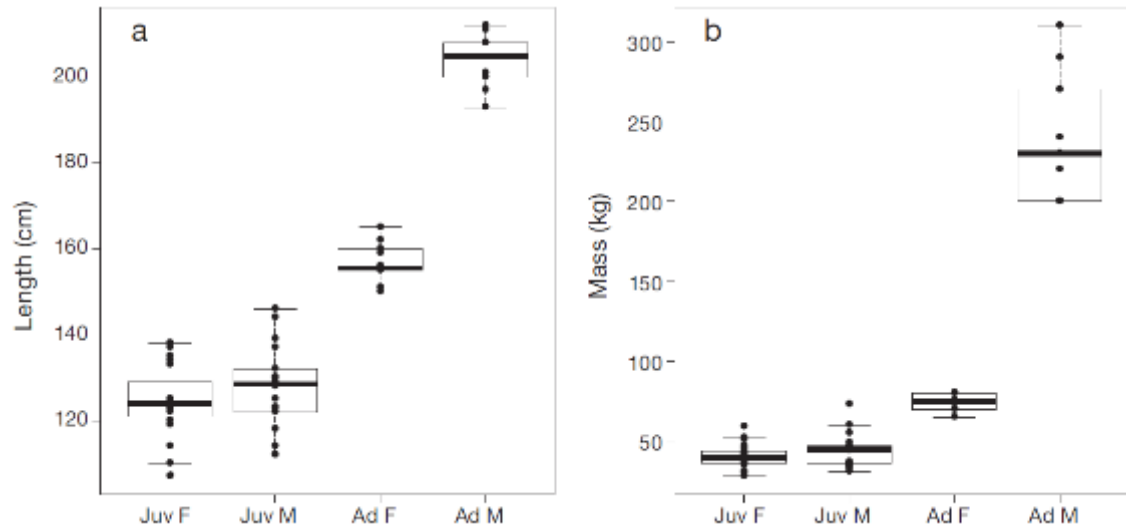


Figure 3.1 (a) Body length and (b) body mass of juvenile female (Juv F), juvenile male (Juv M), adult female (Ad F), and adult male (Ad M) Australian fur seals *Arctocephalus pusillus doriferus* from Seal Rocks, Victoria, Australia. Lines from bottom to top represent the minimum, first quartile, mode, third quartile, and maximum, and dots indicate each sample value.

Table 3.1 Summary of deployments on Australian fur seals *Arctocephalus pusillus doriferus*: (a) body size, (b) foraging behaviours, and (c) frequency of returns to the breeding site. Averages are of individual means and presented ± 1 SE with the range of individual means in parentheses.

	Juveniles		Adults	
	Females	Males	Females	Males
No. of individuals	20	18	10	9
Years tracked	2004–2012	2004–2012	2001–2003	1999–2001
(a) Body size				
Length (m)	1.24 ± 0.02 (1.07–1.38)	1.27 ± 0.02 (1.12–1.46)	1.56 ± 0.02 (1.45–1.65)	2.00 ± 0.04 (1.68–2.12)
Mass (kg)	41 ± 1.7 (28–59)	44 ± 2.5 (31–73)	75 ± 1.7 (60–90)	234 ± 13.7 (180–310)
(b) Foraging behaviours				
No. of trips per individual	14.9 ± 2.1 (3–34)	16.5 ± 2.3 (2–35)	14.0 ± 3.2 (1–39)	12.6 ± 2.2 (2–23)
Trip duration (d)	3.6 ± 0.4^a (1.0–15.7)	3.7 ± 0.6 (0.8–9.5)	6.0 ± 0.5 (3.0–8.6)	6.6 ± 0.6 (2.3–8.1)
Foraging range (km ²)	4634 ± 257 (317–20932)	4696 ± 1282 (165–19023)	8879 ± 1523 (447–16030)	13325 ± 2672 (4148–28591)
Core area (km ²)	626 ± 215 (35–3602)	640 ± 178 (15–2598)	1434 ± 265 (99–2796)	2041 ± 461 (485–5285)
Distance to core area (km)	79 ± 14 (9–251)	104 ± 25 (4–384)	100 ± 22 (49–268)	300 ± 121 (100–1238)
(c) Frequency of returns to breeding site (proportion of trips)	0.73 ± 0.08 (0–1)	0.62 ± 0.10 (0–1)	0.81 ± 0.08 (0.18–1)	0.25 ± 0.08 (0–0.64)

^aRemoved 1 outlier individual to calculate the mean (see text Section 3.3), but not removed in models

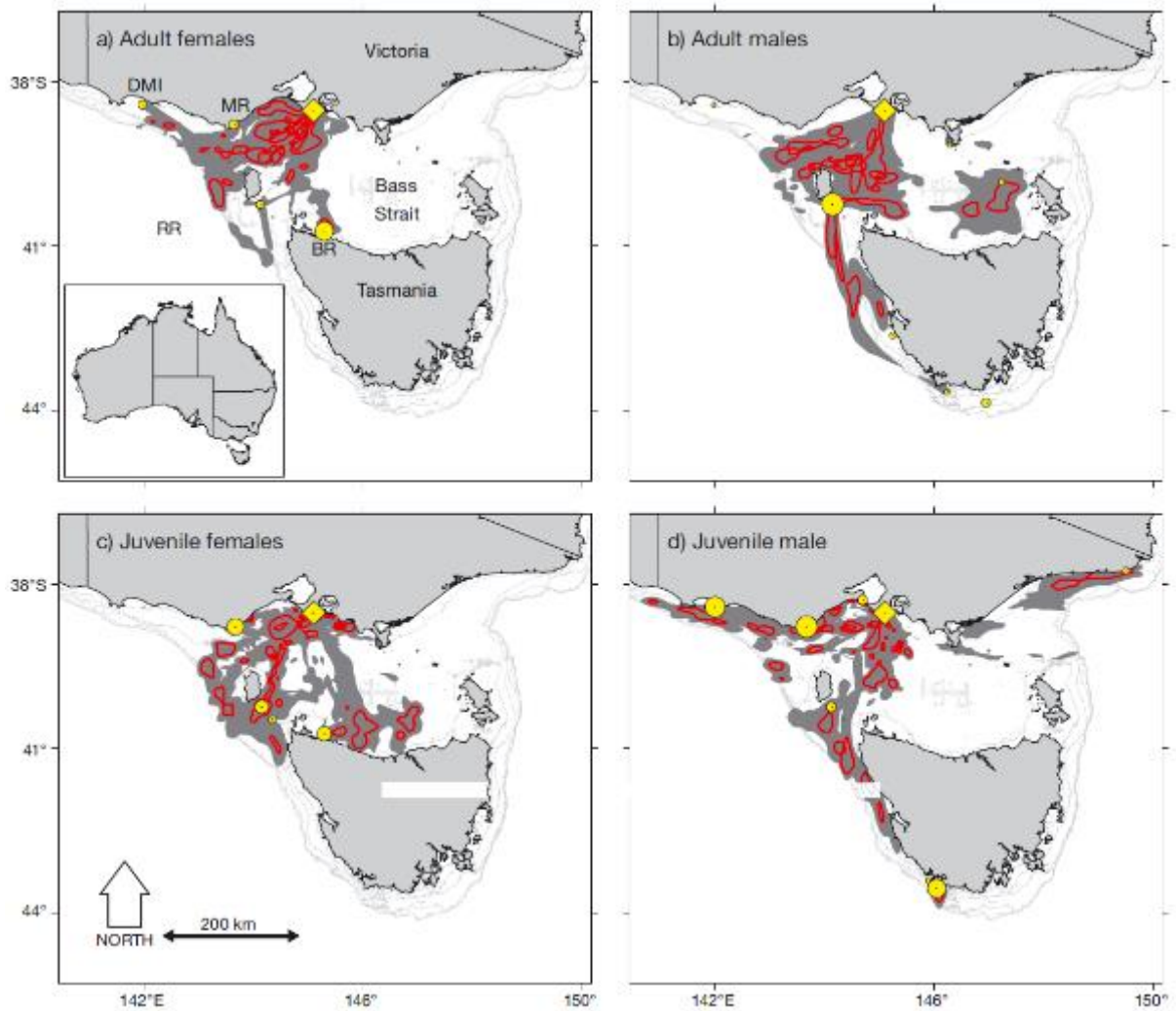


Figure 3.2 Combined individual foraging ranges (dark grey) and core areas (red lines) of (a) adult female, (b) adult male, (c) juvenile female, and (d) juvenile male Australian fur seals *Arctocephalus pusillus doriferus* from Seal Rocks (yellow diamond), Victoria, Australia between June and December. Yellow dots: other sites that the seals used; dot size: their relative log-frequency of use. The 4 main alternative sites used by seals are shown in panel (a): Marengo Reef (MR), Reid Rocks (RR), Bull Rock (BR), and Deen Maar Island (DMI) (inset: Australia). Grey dotted lines: bathymetry contours at 50 m intervals to 200 m; thick grey dotted line: the shelf slope.

Table 3.2 Model selection results for the test of the predictors sex, life stage, and their interaction against 4 foraging behaviours and frequency of returns to the breeding site of Australian fur seals *Arctocephalus pusillus doriferus* from Seal Rocks, Victoria, Australia. Five models were tested for each response variable (Models 1–5), and when an interaction was important, an additional 4 models were tested (Models 6–9). LogL: log likelihood; AIC: Akaike’s information criterion; w_i : Akaike weight; R^2 and mR^2 : R^2 for the fixed effects and the fixed and random effect, respectively; n and N: number of observations of the response variable and number of individuals, respectively. Models with $\Delta AIC > 10$ are not presented.

Response variable	Model	Parameter	LogL	AIC	ΔAIC	w_i	R^2 (mR^2)	n (N)
Trip duration	3	Life stage	–892.5	1793	0	0.54	0.125 (0.527)	825 (57)
	4	Life stage + Sex	–892.1	1794.2	1.2	0.30		
	5	Life stage \times Sex	–891.7	1795.4	2.4	0.16		
Foraging range	3	Life stage	–574.9	1156.2	0	0.52	0.209	57
	4	Life stage + Sex	–574.4	1157.5	1.3	0.27		
	5	Life stage \times Sex	–573.5	1158.1	1.9	0.21		
Core area	3	Life stage	–471.3	949	0	0.59	0.229	57
	4	Life stage + Sex	–470.9	950.6	1.6	0.26		
	5	Life stage \times Sex	–470.3	951.7	2.7	0.15		
Distance to core area	3	Life stage	–79.9	166.2	0	0.44	0.141	57
	5	Life stage \times Sex	–77.9	167	0.8	0.29		
	4	Life stage + Sex	–79.3	167.5	1.3	0.23		
	1	Null	–84.2	172.6	6.4	0.02		
	2	Sex	–83.7	173.9	7.7	<0.01		
Frequency of returns to breeding site	5	Life stage \times Sex	–173.1	699.9	0	1.00	–	57
	7	Adult Sex	–44.3	143.6	0	1.00	0.243	19
	9	Juvenile Sex	–275.7	555.7	<0.01	0.99	0.028	38

Table 3.3 Model selection results for the test of predictors body size (length), life stage, and their stage interaction against 4 foraging behaviours and frequency of returns to the breeding site of Australian fur seals *Arctocephalus pusillus doriferus* from Seal Rocks, Victoria, Australia. Five models were tested for each response variable (Models 1–5), and when an interaction was important, an additional 4 models were tested (Models 6–9). LogL: log likelihood; AIC: Akaike’s information criterion; w_i : Akaike weight; R^2 and mR^2 : R^2 for the fixed effects and the fixed and random effect, respectively; n and N: number of observations of the response variable and number of individuals, respectively. Models with $\Delta AIC > 10$ are not presented.

Response variable	Model	Parameter	LogL	AIC	ΔAIC	w_i	R^2 (mR^2)	n (N)
Trip duration	3	Life stage	–892.5	1793.0	0	0.55	0.101 (0.527)	825 (57)
	4	Length + Life stage	–892.4	1794.8	1.8	0.22		
	2	Length	–893.9	1796.0	2.9	0.13		
	5	Length \times Life stage	–892.2	1796.5	3.4	0.10		
Foraging range	2	Length	–571.1	1148.6	0	0.66	0.308	57
	4	Length + Life stage	–571.0	1150.8	2.3	0.21		
	5	Length \times Life stage	–570.4	1152.0	3.5	0.12		
	3	Life stage	–574.9	1156.2	7.6	0.01		
Core area	2	Length	–92.9	943.6	0	0.65	0.298	57
	4	Length + Life stage	–93.1	945.8	2.3	0.21		
	5	Length \times Life stage	–92.1	947.4	3.8	0.10		
	3	Life stage	–92.0	949.0	5.4	0.04		
Distance to core area	2	Length	–73.4	159	0	0.60	0.243	57
	4	Length + Life stage	–73.3	160.8	1.8	0.24		
	5	Length \times Life stage	–72.2	161.8	2.8	0.15		
	3	Life stage	–76.1	166.2	7.2	0.02		
Frequency of returns to breeding site	5	Length \times Life stage	–314.9	638.7	0	0.97	– 0.271 0.146	57 19 38
	4	Length + Life stage	–319.5	645.4	6.8	0.03		
	7	Adult Length	–65.9	136.6	0	1.00		
	9	Juvenile Length	–249.0	502.4	0.0	1.00		

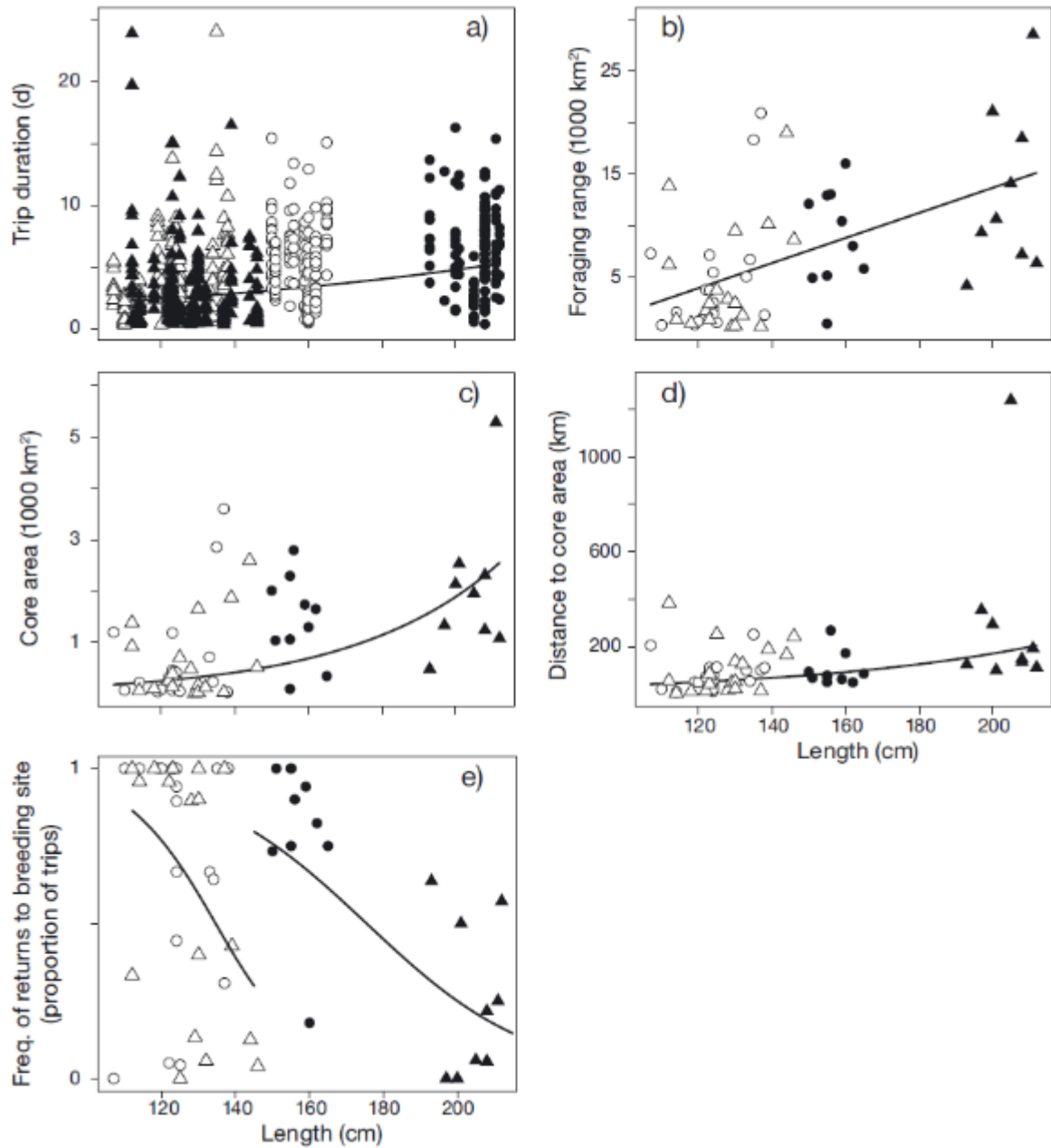


Figure 3.3 Regressions between body size (length) of Australian fur seals *Arctocephalus pusillus doriferus* from Seal Rocks, Victoria, Australia, and (a) trip duration, (b) foraging range, (c) core area, (d) distance to core area (from the breeding site, Seal Rocks), and (e) frequency of returns to the breeding site. Panel (e) shows returns to the breeding site (1) as opposed to alternative site (0); expressed as a proportion for visualisation, but models used the number of successes and failures (see text Section 2.3). Open circles: juvenile females; open triangles: juvenile males; filled circles: adult females; and filled triangles: adult males. Solid lines are the modelled regressions, and were calculated for juveniles and adults separately in panel (e) to account for an interaction term in the model. The response was log-transformed in models (a), (c), and (d) to normalise residuals, and presented back-transformed to original units. All points for the same body length come from the same individual.

Foraging range, core area, and distance to core area

Overall, sex and life stage groups foraged in similar areas of Bass Strait (Fig. 3.2). However, the size of foraging ranges and core areas and the distance to core areas (from the breeding site) differed between life stage groups (Model 3: $w_i = 0.52$, $w_i = 0.59$, and $w_i = 0.44$, respectively; Table 2). The foraging range, core area, and distance to core area of juveniles ($4663 \pm 958 \text{ km}^2$, $632.9 \pm 155 \text{ km}^2$, and $56.1 \pm 0.2 \text{ km}$, respectively) were less than half those of adults ($10985 \pm 1660 \text{ km}^2$, $1722 \pm 269 \text{ km}^2$, and $130.2 \pm 0.3 \text{ km}$, respectively). Weak interactions between sex and life stage for each response variable suggest the difference in these foraging parameters between sexes depended on life stage (Model 5: $w_i = 0.21$, $w_i = 0.15$, and $w_i = 0.29$, respectively; Table 3.2). The size of foraging ranges, core areas, and the distance to core areas were similar between sexes for juveniles, but slightly greater in adult males than in adult females (Table 3.1).

Within life stage groups, the size of a foraging range and core area and the distance to core area were highly variable among individuals, with some juveniles being comparable to adults (Fig. 3.3b–d). This variability was partly attributed to a positive relationship with body size (Model 2: $w_i = 0.66$, $w_i = 0.65$, and $w_i = 0.60$, respectively; Table 3.3). Therefore, smaller juveniles had smaller foraging ranges that were closer to the breeding site, and larger juveniles had foraging ranges similar to adults. Weak interactions with life stage suggest the relationships are stronger in adults (Model 5: $w_i = 0.12$, $w_i = 0.10$, and $w_i = 0.15$, respectively; Table 3.3), such that larger individuals ranged more widely and further from the breeding site; this applied particularly to adult males (Fig. 3.3b–d).

Frequency of returns to the breeding site

Seals used 20 different sites throughout the study (Fig. 3.2). The seals returned to the breeding site on 527 trips and occupied alternative sites at the end of 298 trips. The most frequently used alternative sites were all in western Bass Strait: Marengo Reef (74 visits), Reid Rocks (73 visits), Bull Rock (37 visits), and Deen Maar Island (also known as Lady Julia Percy Island, 36 visits) (Fig. 3.2). Adult and juvenile females only used sites in this area of Bass Strait, while adult and juvenile males also used sites in eastern Bass Strait and southern Tasmania.

Some seals always returned to the breeding site, while others never returned during the period they were tracked. The proportion of returns to the breeding site varied among sex and life stage groups, and the difference between sexes depended on life stage (Model 5, $w_i = 0.97$; Table 3.2). The sex difference was stronger in adults than juveniles (Model 7, $w_i = 1.00$, $R^2 = 0.243$; and Model 9, $w_i = 0.99$, $R^2 = 0.028$, respectively; Table 3.2), with adult females much more likely to return to the breeding site than adult males (mean frequency of returns: 0.679 ± 0.181 and 0.221 ± 0.290 , respectively). There was less difference between juvenile females (0.728 ± 0.130) and juvenile males (0.594 ± 0.176).

Frequency of returns to the breeding site was related to body size, with larger individuals less likely to return to the breeding site at the end of a foraging trip (Fig. 3.3e). The relationship was different between life stage groups (Model 5, $w_i = 0.97$; Table 3), being stronger in juveniles (Fig 3.3e) and less variable in adults (Model 7, $w_i = 1.00$, $R^2 = 0.271$; and Model 7, $w_i = 1.00$, $R^2 = 0.146$, respectively; Table 3.3).

3.4 Discussion

We studied intraspecific differences in foraging strategies in the sexually dimorphic and polygynous Australian fur seal *Arctocephalus pusillus doriferus*, where foraging of lactating adult females (due to their need to return to the colony and suckle pups) was expected to differ from juveniles and adult males. Investigation of foraging behaviours and frequency of returns to the breeding site revealed consistent differences between life stages, yet few sex differences within these groups. Despite using similar foraging areas, juveniles and adults had distinct foraging behaviours within that space, which was consistent with them having foraging constraints associated with body size and reproductive behaviours.

Despite no reproductive commitments, and in contrast to juvenile northern fur seals *Callorhinus ursinus* (Sterling & Ream 2004) and New Zealand fur seals *A. forsteri* (Page et al. 2006), juvenile Australian fur seals did not make longer-duration foraging trips than adults. Instead, juvenile Australian fur seals had shorter trips than adults and travelled shorter distances to reach their core foraging areas. This accords with findings from other otariids, including Galapagos fur seals *A. galapagoensis* (Horning & Trillmich 1997), and sea lion species *Neophoca cinerea* (Fowler et al. 2007b), *Zalophus wollebaeki* (Jeglinski et al. 2013), *Phocarctos hookeri* (Chilvers 2008; Leung et al. 2012), *Otaria byronia* (Campagna et al. 2001; Hückstädt et al. 2014), and *Eumetopias jubatus* (Merrick & Loughlin 1997; Milette & Trites 2003; Raum-Suryan et al. 2004; Call et al. 2007). While juvenile Australian fur seals and juvenile sea lions are large enough to exploit benthic habitat and often make deep, 'benthic-type' dives as seen in other otariid species (Pitcher et al. 2005; Fowler et al. 2006; Spence-Bailey et al. 2007; Leung et al. 2013; Hückstädt et al. 2014), their incomplete morphological and physiological development still restricts their capacity to make 'adult-like' deep benthic dives (Kooyman & Ponganis 1998; Costa et al. 2004). This probably limits them to feeding in shallow, coastal environments that are close to resting and breeding sites (Fowler et al. 2007b) and so may result in shorter foraging trips. Juvenile Australian fur seals spend on average half of their time in the water, compared to 75% for adult females (Ladds et al. 2018). By contrast, northern and New Zealand fur seals are not only smaller than Australian fur seals and sea lions, but feed on shallow-swarming pelagic prey associated with frontal systems and continental slopes rather than shallow, continental shelves (Boyd et al. 1994; Harcourt et al. 2002), and so may be advantaged by longer foraging trips (Page et al. 2006). Both the small juvenile Galapagos fur seal and larger Galapagos sea lion also make pelagic dives but have short foraging trips (Horning & Trillmich 1997, 1999; Jeglinski et al. 2013), probably because both species haul-out in close proximity to deep pelagic habitat with very productive upwelling (Jeglinski et al. 2013). Thus, the body size of an otariid and proximate geographic features play important roles in shaping intraspecific differences in time and distances travelled when foraging.

In Australian fur seals, body size did indeed influence trip duration, size of foraging range, size of core area, and distance travelled to core area. While a relationship between body mass and diving behaviour is well established for pinnipeds and other diving birds and mammals (Halsey et al. 2006), an allometric relationship with range size has rarely been documented (Thompson et al. 1998). Among terrestrial and marine mammals, body size is positively related to home range size (McNab 1963; Tucker et al. 2014). This correlation is largely driven by the increase in total energy required as body mass increases (Nagy 2005), and the ability of larger individuals to travel further than smaller individuals to acquire the resources that provide this energy (McNab 1963). The largest foraging ranges were exhibited by the largest Australian fur seals, the adult males, while juveniles and females, which have higher mass-specific metabolic rates (Ladds et al. 2017b), had smaller ranges, suggesting a need to concentrate on closer, but productive areas. A significantly larger body size means that, like other dimorphic mammals, adult male Australian fur seals still have overall larger gross energy requirements, and this may be reflected in a larger foraging range (Tucker et al. 2014). Difference in reproductive behaviour may also be relevant (Lindstedt et al. 1986): the adult males need not return to provision offspring, so can range more widely than lactating females and use productive feeding areas more distant from the breeding site, such as off the western coast of Tasmania (Kämpf & Kavi 2017). Juveniles are equally free of reproductive commitments, so their smaller ranges are likely shaped more by foraging constraints associated with their smaller body size.

Despite this allometric relationship with foraging patterns, there was significant spatial overlap between adult male and female foraging ranges. This was surprising given that sex segregation in foraging is common among sexually dimorphic, polygynous mating species (Ruckstuhl 2007; Wearmouth & Sims 2008). The absence of sex segregation might be due to low levels of competition, as Australian fur seals are still recovering from severe depletion in the last century (McIntosh et al. 2018b) and have a relatively diverse diet (Deagle et al. 2009; Hardy et al. 2017). Resources within Bass Strait may be sufficient for both the adult males and females. If so, the foraging areas may diverge if local resources can no longer support the size of the population. Alternatively, intraspecific competition may be alleviated by dietary niche segregation, as for other seals (Page et al. 2005a; Tucker et al. 2007). Adult male Australian fur seals appear to feed more on higher trophic-level prey than females (Kernaléguen et al. 2015b). The larger body size of adult males may allow them to access and/or handle larger prey (Page et al. 2005a). Larger and older seals also have greater oxygen stores and subsequent capacity for greater submergence time (Weise & Costa 2007), which likely influences their ability to hunt benthic prey (Arnould et al. 2011).

Intraspecific differences in haul-out site preference were consistent with expectations due to differences in reproductive behaviour. Because lactating females must return often to the colony to suckle their pup, their time away from the breeding site was limited by the fasting ability of their pup,

resulting in adult females returning to the breeding site more frequently than juveniles and adult males. Adult males, being free of parental care, could utilise alternative sites. By using haul-out sites that are closer to feeding areas than the breeding site, seals could minimise travel time and distance between feeding and non-feeding areas, and thereby maximise their rate of energy gain while foraging (Charnov 1976). Indeed, the non-breeding sites most frequently used by the seals were located in the more productive western edge of Bass Strait (Gibbs et al. 1986), and away from major breeding colonies (i.e. Seal Rocks and Deen Maar Island) (Kirkwood et al. 2010), that are likely associated with local depletion of prey (Ashmole 1963; Kuhn et al. 2014). While reproductive behaviour partially explains sex and life stage differences in site use, body size further explains individual variation within sex and life stage groups, particularly in juveniles.

While juveniles were expected to disperse (Warneke 1975; Dobson 1982), many actually returned frequently to the breeding site. It is possible that some individuals do disperse and were not present at the colony when deployments occurred, while other juveniles remain close to the breeding site throughout the year and were sampled. In addition to morphological and physiological limitations on foraging (discussed above in this section), smaller juveniles may remain close to breeding sites to opportunistically suckle from their mother (or other lactating females), as Australian fur seals exhibit extended maternal care (Hume et al. 2001). As juveniles grow, the increase in their physiological diving capacity (Spence-Bailey et al. 2007) and foraging experience may allow them to develop greater independence, becoming less reliant on maternal care. This is reflected by their returning less frequently to the breeding site, and extending their foraging range as body size increased.

This study sampled sex and life stage groups in different years, and it is possible that environmental fluctuations influenced foraging behaviour of all seals within certain years. For each sex and life stage group, individuals were sampled over multiple years and a mixture of body sizes were sampled within each year. Therefore, each sex and life stage group included individuals exposed to environmental conditions in different years. Environmental fluctuations are known to influence foraging trip duration and time spent diving by female Australian fur seals in Bass Strait (Hoskins & Arnould 2014) but have not yet been linked to changes in foraging range size and distribution. Given that differences among sex and life stage groups were consistent with studies of otariid seals, and that body size within groups was important, the differences in foraging parameters found in this study appear to be driven by intrinsic factors rather than extrinsic factors.

In summary, by tracking the movements of Australian fur seal juveniles, and comparing their movements with those of adult females and males, we reveal intraspecific differences in foraging behaviour and frequency of return to the breeding site. Our results suggest that for this species, foraging strategy is primarily determined by size, and somewhat surprisingly, reproductive behaviour

plays a lesser role. This suggests that the fasting ability of pups must be well adapted to longer absences of their mothers.

4. Chapter Four

Using accelerometers to develop time-energy budgets of wild fur seals from captive surrogates

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Photo credit: Marcus Salton

Abstract

Accurate time-energy budgets summarise an animal's energy expenditure in a given environment, and are potentially a sensitive indicator of how an animal responds to changing resources. Deriving accurate time-energy budgets requires an estimate of time spent in different activities and of the energetic cost of that activity. Bio-loggers (e.g. accelerometers) may provide a solution for monitoring animals such as fur seals that make long-duration foraging trips. Using low resolution to record behaviour may aid in the transmission of data, negating the need to recover the device.

This study used controlled captive experiments and previous energetic research to derive time-energy budgets of juvenile Australian fur seals (*Arctocephalus pusillus doriferus*) equipped with tri-axial accelerometers. First, captive fur seals and sea lions were equipped with accelerometers recording at high (20 Hz) and low (1 Hz) resolutions, and their behaviour recorded. Using this data, machine learning models were trained to recognise four states—foraging, grooming, travelling and resting. Next, the energetic cost of each behaviour, as a function of location (land or water), season and digestive state (pre- or post-prandial) was estimated. Then, diving and movement data were collected from nine wild juvenile fur seals wearing accelerometers recording at high- and low- resolutions. Models developed from captive seals were applied to accelerometry data from wild juvenile Australian fur seals and, finally, their time-energy budgets were reconstructed.

Behaviour classification models built with low resolution (1 Hz) data correctly classified captive seal behaviours with very high accuracy (up to 90%) and recorded without interruption. Therefore, time-energy budgets of wild fur seals were constructed with these data. The reconstructed time-energy budgets revealed that juvenile fur seals expended the same amount of energy as adults of similar species. No significant differences in daily energy expenditure (DEE) were found across sex or season (winter or summer), but fur seals rested more when their energy expenditure was expected to be higher. Juvenile fur seals used behavioural compensatory techniques to conserve energy during activities that were expected to have high energetic outputs (such as diving).

As low resolution accelerometry (1 Hz) was able to classify behaviour with very high accuracy, future studies may be able to transmit more data at a lower rate, reducing the need for tag recovery.

Reconstructed time-energy budgets demonstrated that juvenile fur seals appear to expend the same amount of energy as their adult counterparts. Through pairing estimates of energy expenditure with behaviour this study demonstrates the potential to understand how fur seals expend energy, and where and how behavioural compensations are made to retain constant energy expenditure over a short (dive) and long (season) period.

4.1 Introduction

An animal's fitness can be assessed by its ability to survive and reproduce in a given environment (Orr 2009). Time-energy budgets are a useful measure of one aspect of animal fitness, as they describe the energy spent and energy gained over a specific period in an animal's life (Boyd & Hoelzel 2002). Animals gain energy by eating and metabolising food, and expend energy largely through basal metabolic rate (BMR), digestion, thermoregulation and activity, with excess energy available for growth and reproduction (Costa 1999). Time-energy budgets that quantify both the time animals spend engaged in different activities and the energetic costs associated with those activities can be used to determine whether animals are in positive energy balance (Travis 1982).

Air-breathing marine mammals, such as fur seals, that forage on aquatic prey have challenging constraints when acquiring energy. They dive repeatedly, may travel long distances to foraging sites (an energetically intensive strategy), and must return to the surface to breathe, only diving for as long as their oxygen stores allow (Gerlinsky et al. 2014). As relatively small marine mammals, fur seal thermoregulatory costs at sea are high compared to terrestrial counterparts, because water conducts heat 25 times faster than air (Hind & Gurney 1997) and the heat increment of feeding (HIF) also consumes energy (Rosen & Trites 1997). However, thermoregulation and HIF are negligible in comparison to resting metabolic rate and activity that contribute to the largest variation in energy expenditure (Dalton et al. 2015). How fur seals acquire and allocate energy to key processes may be understood through constructing time-energy budgets developed by calculating daily energy expenditure (DEE) and resolved by recording the duration of various activities and multiplying these by their associated energetic cost (Goldstein et al. 2015).

Calculating the costs associated with different activities from wild fur seals is difficult and often expensive, but estimates of the energetic costs associated with different activities have been made from laboratory experiments using captive surrogates and respirometry (Ladds et al. 2017c). While respirometry measures metabolic rate (and thus energy expenditure) accurately, its field applications are limited (Halsey 2011). If a proxy of the metabolic costs incurred by different activities can be developed using animal-borne sensors that identify these activities, such as accelerometers, then we can potentially measure activity-specific field metabolic rates as well (Cooke et al. 2014). But as the energetic outputs will vary for animal size, age and the time of year, this technology must be validated (Nathan et al. 2012).

Accelerometers have been used to define the behavioural state of a range of animals, validated through captive experiments (Vázquez Diosdado et al. 2015; Wang et al. 2015). They can measure specific events, such as prey-capture (Volpov et al. 2015), identify a range of behaviours (Whitney et al. 2010) and define movement patterns (Shepard et al. 2008b). Dynamic body acceleration (DBA) or stroke rate,

measured from accelerometers was promoted as a way to directly estimate energy expenditure in wild fur seals (Jeanniard-du-Dot et al. 2017). However, this approach has recently been shown to be flawed, as the apparent relationship between DBA and energy expenditure is in fact time correlated with time, as both the independent variable (energy) and dependent variable (DBA or strokes) are both summed, thus introducing time into both sides of the equation (Halsey 2017; Ladds et al. 2017a). Thus, a new way of estimating energy expenditure is needed.

Accelerometers can record at high resolution (multiple samples per second), to give a detailed picture of behaviour, but processing this amount of data post-collection is time-consuming and the amount of data collected may limit opportunities for uploading data remotely (Nathan et al. 2012). In addition, battery and memory limitations mean that if animals are at sea for long periods the period that can be sampled at a high resolution maybe relatively short compared to the total trip due to logger memory constraints (Halsey et al. 2009). Limiting the amount of accelerometry data that needs to be collected allows for smaller devices to be deployed, or for additional data from other sensors (such as temperature or orientation) to be collected. Fur seals make long-duration foraging trips over multiple days or weeks, and so analysing such trips maybe made simpler with low resolution (<10 Hz) recording.

In the pursuit of finding an appropriate and valid methodology of measuring wild fur seal energy expenditure and behaviour, the authors have conducted studies to investigate: the metabolic rate of fur seals during activity (Ladds et al. 2017c); metabolic rates over seasons, sizes, sexes and species (Ladds et al. 2017b); and how to classify behaviours from accelerometry (Ladds et al. 2016; Ladds et al. 2017d). What is missing now is a model connecting behaviour to its energetic cost and the application of the model to a wild population. To address this gap, we focus on the Australian fur seal (*Arctocephalus pusillus doriferus*). Australian fur seals are endemic to Australia, occupying much of the South-Eastern coast (Kirkwood & Goldsworthy 2013). While much is known about adult females (Arnould & Hindell 2001; Knox et al. 2014), few, if any, studies have focussed on juveniles.

This paper takes a five-step approach to achieving our goal. (1) Conduct behavioural experiments with captive seals and train machine learning models to automatically recognise four important behaviours (grooming, resting, travelling and foraging) with high (20 Hz) and low (1 Hz) resolution accelerometry. (2) Estimate the energetic cost of each behaviour based on previous research. (3) Collect accelerometer data from a sample of wild fur seals at high and low resolutions. (4) Apply the captive behaviour machine learning model to determine how much time is spent in each behaviour. (5) Apply the energetic cost of the behaviour in two locations (land and water) as a function of time and season to build an overall estimate of energy expenditure.

4.2 Methods

Behaviour validation experiments with captive fur seals and sea lions

To validate the use of accelerometers for classifying behaviours of wild fur seals we used captive surrogates at three Australian marine facilities; Dolphin Marine Magic Coffs Harbour, Underwater World Sunshine Coast, and Taronga Zoo Sydney, from August to November 2014 and in August 2015. We used two adult Australian fur seals (*Arctocephalus pusillus doriferus*; one male, one female), three New Zealand fur seals (*Arctocephalus forsteri*; two male adults, one male juvenile), one subantarctic fur seal (*Arctocephalus tropicalis*; juvenile male), and six Australian sea lions (*Neophoca cinerea*; two adult males, three adult females, one juvenile female). Fur seals had accelerometers attached with tape to the fur, while sea lions wore a custom fitted harness with the accelerometer sewn into a pocket (for details of the animals used see Ladds et al. 2017d, Table 1). We pooled data from all four species for training machine learning models because fur seals and sea lions (otariids) are conservative in morphology and including species and/or attachment method as a factor only improves the accuracy of such models by ~5% (Ladds et al. 2017d). This study was conducted under permits from Macquarie University ethics committee (ARA-2012_064) and Taronga ethics committee (4c/10/13).

Tri-axial accelerometers (CEFAS Technology Ltd, Lowestoft, UK) were set to record -8 g to +8 g at 1 Hz and 25 Hz simultaneously, with a wet/dry sensor active, and behaviours typical of wild fur seals were video-recorded during training sessions. We observed two types of sessions; feeding and behaviour. The feeding sessions aimed to provide seals with large food items that required some form of processing prior to eating. Behaviour sessions also incorporated some feeding events with small fish that did not require processing. Fish were thrown in the pool so that seals had to “capture” them mid-water as they sank. These two behaviours constituted foraging. During each behaviour session seals were instructed to perform a series of natural behaviours from their known behavioural repertoire, such as porpoising, swimming and grooming. While seals could not reach depths they would achieve in the wild, their pools provided adequate space to perform behaviours typical of wild fur seals. Captive fur seals had access to both land and water during trials, similar to a wild fur seal near their haul-out. In addition, seals were trained to swim consistently below the water for several minutes to replicate a deep dive for another project. The experimental set-up and training allowed us to record behaviours that lasted from less than a second (grabbing fish from the water column) to several minutes (swimming or resting).

Behaviours were manually matched to the accelerometry by two investigators. Where behaviours recorded by the investigators did not match, they reviewed the video such that both reached agreement. Twenty-six behaviours were grouped into four behavioural categories—foraging, travelling, grooming and resting, in three locations—land, water surface and underwater (for details of the behaviours and their groups see (for details of the behaviours and their groups see Ladds et al. 2016,

Table 2). Foraging behaviours consisted of searching for prey and prey handling limited to dead fish. Grooming was any behaviour used in body maintenance or thermoregulation. To thermoregulate at sea, fur seals float with either their hind flippers (jughandling) or their fore flippers (sailing) in the air. Grooming involves the use of flippers to scratch or rub the body, including the face to clean whiskers. Resting was any period of stillness, while travelling was any period involving movement that was not foraging or grooming (Ladds et al. 2017d).

Estimate the energetic cost of each behaviour

Resting energy expenditure

Energy consumption when resting in water is related to water temperature for postabsorptive (not digesting) female and subadult Australian and New Zealand fur seals (Ladds et al. 2017b). However, postprandial (digesting) resting metabolic rate (RMR) for pups of northern fur seal (*Callorhinus ursinus*) (Liwanag 2010) and juvenile South American fur seals (*Arctocephalus australis*) (Dassis et al. 2014) is 1.6 times the postabsorptive rate and stays at this level for about 3.5 h. For simplicity, we assumed that fur seals were postabsorptive while on land, and postprandial in the water.

Resting in water:

$$\text{sSMR } R_{\text{water}} (\text{l O}_2 \text{ kg}^{-1}) = 1.6 (0.00195 + 0.00029 (\text{water temp.}) (\text{duration})) \quad (1)$$

Because no measure of RMR on land for juvenile Australian fur seals was available we used the mass specific standard metabolic rate (sSMR) of a subadult New Zealand fur seal in water (Ladds et al. 2017b). As northern fur seal pups and southern sea lion subadult males both had ~30% lower RMR on land than in water (Donohue et al. 2000; Dassis et al. 2012), this assumption was applied to our RMR estimation on land. In addition, to account for a seasonal effect on sSMR in New Zealand fur seals (Ladds et al. 2017b), we calculated a summer and a winter energy consumption (Eqs. (2.1)–(2.2)).

Winter RMR on land:

$$\text{sSMR } R_{\text{winter,land}} (\text{l O}_2 \text{ kg}^{-1}) = (0.007 \times 0.7) (\text{duration}) \quad (2.1)$$

Summer RMR on land:

$$\text{sSMR } R_{\text{summer,land}} (\text{l O}_2 \text{ kg}^{-1}) = (0.009 \times 0.7) (\text{duration}) \quad (2.2)$$

Active energy expenditure from foraging and travelling

We combined foraging and travelling as, despite having many studies of the energetic cost of diving in seals e.g., (Williams et al. 2004; Rosen et al. 2017), there is yet to be a study evaluating the cost of

travelling at the surface. The time an animal spent active (foraging and travelling) was multiplied by the average energy expenditure estimated in Ladds et al. (2017b). In their study seals swam below the surface stroking constantly, thus the energetic cost of activity was estimated (as opposed to foraging or travelling per se) (Williams et al. 2004; Ladds et al. 2017c; Rosen et al. 2017).

There have been no estimates of the cost of travelling on land for any pinniped, though experimentally the cost of movement on land is probably much greater than in water. In semi-aquatic water rats (*Hydromys chrysogaster*) the metabolic cost of running was around 13–40% more than swimming when moving at equal speeds, and for platypus (*Ornithorhynchus anatinus*), the cost of walking was 2.1 times the cost of swimming (Fish et al. 2001). As terrestrial locomotion in otariids is more similar to platypus than water rat, we assumed that the cost of movement on land is twice that in water. As activity compensates for some of the additional costs of cold water (Liwanag et al. 2009) we assumed that the energy expenditure for winter and summer was the same (Eq. (3.1)).

Energy expended from activity (foraging and travelling):

$$A_{\text{water,winter/summer}} (\text{l O}_2 \text{ kg}^{-1}) = 0.0303 (\text{duration}) \quad (3.1)$$

$$A_{\text{land,winter/summer}} (\text{l O}_2 \text{ kg}^{-1}) = 2 (0.0303 (\text{duration})) \quad (3.2)$$

Grooming energy expenditure

The energy expended from grooming was estimated to be between 1.5 and 2 times the postprandial RMR and between 0.9 and 1.2 times postabsorptive RMR in northern fur seal pups depending on activity level (Liwanag 2010). Considering our model generally only labelled active grooming, we assumed that grooming had an energetic cost twice that of in-water RMR (Eqs. (4.1)–(4.2)).

Energy expended from grooming in winter in water:

$$G_{\text{winter,water}} (\text{l O}_2 \text{ kg}^{-1}) = (0.007 \times 2) (\text{duration}) \quad (4.1)$$

Energy expended from grooming in summer in water:

$$G_{\text{summer,water}} (\text{l O}_2 \text{ kg}^{-1}) = (0.009 \times 2) (\text{duration}) \quad (4.2)$$

For grooming on land fur seals were assumed to be postabsorptive so they were assumed to have the same energetic output as resting or slightly higher.

Wild fur seal data collection

We tracked juvenile Australian fur seals from two colonies, Seal Rocks (Phillip Island, Victoria Australia, 38° 52'S–145°11'E, $n = 6$) during austral winter of 2013 and Lady Julia Percy (Victoria, Australia, 38°52'S–142°00'E, $n = 8$) during austral summer of 2014. These sites are the largest breeding colonies for

Australian fur seals, with each site containing approximately 25% of the total population of the species (Kirkwood et al. 2010). In Australian fur seals, suckling ceases after 1 year, puberty occurs in females at approximately 3 years old and in males at 4–5 years old (Arnould & Warneke 2002). We used animals between one and three years of age that were independently foraging (i.e. juveniles) for this study.

We identified juveniles by their mature pelage (i.e., lacking the lanugo of pre-moult pups) and size (<1.5 m and 40 kg) and captured individuals using a modified hoop-net and isofluorane gas sedation (Gales & Mattlin 1998), then measured standard length (straight-line), girth and mass. Numbered tags were applied to the trailing edge of both fore-flippers (Super Tags[®], Dalton I.D. Systems Ltd, Henley-on-Thames, UK) to aid with identification and recapture. One of two types of location device (Kiwisat100, Sirtrack Ltd, New Zealand or Mk10; Wildlife Computers), a VHF transmitter (Sirtrack Ltd, 6 cm × 3 cm × 2 cm), and a tri-axial accelerometer G6A + (CEFAS technology Ltd, Lowestoft, UK) were glued directly to the fur on the dorsal midline of each fur seal (Fig. 1) using quick-setting epoxy (Araldite 2017; Aeropia Ltd, Crawley, UK or Araldite 268; Huntsman Advanced Materials, Victoria, Australia). A time-depth recorder (TDR) was also attached, either as part of the Mk10 device or a separate device (Mk9, Wildlife Computer; Fig. 1). The total instrument package mass (179 g–239 g) equated to <1% of the seal's body mass and attached to maintain the lowest profile possible to minimise a drag effect. We observed animals until they had fully recovered from anaesthesia and released them at the site of capture. A minimum of 15 days lapsed before recapture (via hoop net and manual restraint), and devices were retrieved by cutting the hair beneath the glued instrument.

For the duration of the deployment, defined as from attachment until removal of a device, TDRs recorded depth (m) every second, and any drift in the depth sensors or error spikes were corrected prior to analyses using Zero-Offset Correction (Wildlife Computers, Redmond, WA, USA). Tri-axial accelerometers recorded acceleration on the X, Y, and Z axes at 1 sample per second (1 Hz) and temperature at 0.5 Hz. Accelerometers also recorded at a high resolution (20 Hz) when diving (depth > 1.5 m). This would sometimes continue after a diving event, giving high resolution data both at the surface and during diving.

To give an indication of time duration at sea, data from the TDRs were summarised into trips and dives. Trips started when a seal entered the water and ended when the seal hauled out, and excluded periods in water with minimal diving or dives <10 m (e.g. when seals rest at the water surface adjacent to colonies). Dives were defined as periods spent underwater below a minimum depth of 5 m to account for wave action at the surface. Fur seal physical parameters, trip duration, number of trips, average dive duration, mean maximum depth and maximum depth were derived from these parameters (Table S1).

Predicting behaviours of wild fur seals from accelerometers

As the high-resolution data were only recorded for wild seals while at sea, the high-resolution captive data were subsampled to include only those behaviours that occurred in the water. Low resolution (1 Hz) data were recorded continuously for both the wild and captive seals. The wet/dry sensor of the accelerometers from the wild fur seals (hereafter wild data) was used to indicate when individuals were in water or on land to improve the predictability of the models. We tested the accuracy of both high and low resolution accelerometry to classify behaviours.

To determine the behavioural state of surrogates using accelerometers, gradient boosting models (GBM) were trained in R using the package 'xgboost' (Chen et al. 2016). GBM models are an extension of a random forest, whereby they build a classification tree on a subset of the data, then use a subsequent tree to learn from the errors of the previous trees. Trees are built successively until a stopping criteria is met, and the trees built are averaged together to provide an estimate of classification (Friedman 2002). Captive data were pooled and split into one of three epochs (the number of samples on which summary data are calculated) for training the GBM. For high resolution (20 Hz) data epochs of 13, 25 and 75 samples were tested, which correspond to 0.65, 1.25 and 3.75 s of data, respectively. For low resolution (1 Hz) data epochs of 7.0, 15.0 and 21.0 samples were tested, which corresponded to 7.0, 15.0 and 21.0 s of data respectively. Training and testing longer epochs was not possible because there were too few events lasted for longer than a few seconds, meaning there were not enough examples to train a model. Down-sampling (randomly selecting behaviours from a pool until a specified number is met) was used to ensure that the behaviour categories had an even number of samples (Ladds et al. 2017d).

We coded 52 summary statistics and added five covariates describing some characteristic of the individual or the event to the second stage of model testing. These were included as they have previously been demonstrated to make a small improvement on prediction performance of the models (Ladds et al. 2017d). The covariates included were device attachment method (harness or tape), age, mass, sex and species of the individual. We included where the behaviour occurred (surface, underwater or land) in all models. Location was determined first by the wet/dry switch which indicated whether a seal was in the water or on land, then once a seal was more than 1 m under the surface (as determined by the depth device) they were classified as underwater. Summary statistics calculated included: mean, median, standard deviation, skewness, kurtosis, minimum, maximum, absolute value, inverse covariance, autocorrelation trend (the coefficient derived from a linear regression) for each of the three axes. We also calculated q as the square-root of the sum-of-squares of the three axis (Nathan et al. 2012), and included pair-wise correlations of the three axes ($x-y$, $y-z$, $x-z$) (Ravi et al. 2005). The inclination as azimuth were calculated as per Nathan et al. (2012). We calculated three measures of dynamic body acceleration (DBA) by first using a running mean of each axis over 3 s to create a value for static acceleration. We then subtracted the static acceleration at each point from the raw acceleration

value to create a value for partial dynamic body acceleration (PDBA). The values of PDBA on each axis were used to calculate overall dynamic body acceleration (ODBA) (Wilson et al. 2006; Shepard et al. 2008a) and vectorial dynamic body acceleration (VeDBA) (Qasem et al. 2012). The integral of the start and end point of ODBA and VeDBA for each epoch ODBA and VeDBA was calculated using the package “MESS” in R (Ekstrøm 2014; R Core Team 2015).



Figure 4.1 Juvenile Australian fur seal with three devices attached. Devices are CEFAS accelerometer, time depth recorder (TDR) and VHF. Source: DP Hocking.

GBM models were run with the full suite of summary statistics derived from captive data and run over a grid of parameters (for details see Table 4.2 and additional file 2 in Ladds et al. 2017d). The combination of parameters that resulted in the highest accuracies was chosen for implementation on the high and low resolution wild data. Within each epoch, wild data were categorized using predictions from the GBM model built with captive data that produced the highest cross-validation accuracy and kappa values. Accuracy is a measure of the proportion of true positives identified by the model, while kappa is a performance measure that accounts for investigators' observations agreeing or disagreeing by chance. Behaviour events were categorised for the duration of each deployment. Events were considered different when either the location or the behaviour category changed for an epoch, and the change occurred for longer than 15 s. A sensitivity analysis was conducted on the probability of each event being assigned to a behaviour group. For wild data, each event was assigned a probability of it being each behaviour category and then classified as the behaviour that had the highest probability. To

evaluate how well our models classified behaviours, behaviours that were selected with less than 80% chance of occurring were examined, and the behaviour with the next highest probability was extracted. This allowed us to see when the model may have ‘confused’ two categories.

Apply the model to create time-energy budgets

To build time-energy budgets, we estimated DEE (MJ) which was assumed to be a function of the energy expenditure (EE) of a given behaviour event, its duration, the season it occurred in and where it occurred (land or water) summed over 24 h periods (Table 1, Eq (5)). An example of how this is calculated over a single dive is given in Fig 4.2. Details of the calculations and assumptions made for the energetic models are in Table 1. The overall energetics model is defined by the sum of all of the behaviour events ($e = e...E$) that occur in a 24 h period (from midnight to midnight) for A (activity), G (grooming) and R (resting) as a function of season s ($s = \text{winter, summer}$) and location l ($l = \text{land, water}$):

$$\text{DEE (l O}_2\text{)} = \sum_e^E R_{s,l} + \sum_e^E A_{s,l} + \sum_e^E G_{s,l}. \quad (5)$$

For reporting and comparison with other energetics papers, the total oxygen used was converted into MJ. First, the total energy expended was converted to kilocalories using a factor of 5 kcal per l O₂, then converted to kilojoules using a conversion factor of 4.186 J cal⁻¹ (Williams et al. 2007).

Table 4.1 Energy budget calculations and references for each behavioural and digestive state, accounting for location (land or water—where water includes surface and underwater) and season (winter or summer). All measures converted to l O₂ kg⁻¹ from original measure. Temperature in °C, duration in minutes, NZM3 is the reference to the seal used.

Energy expenditure	Digestive state	Location	Austral season	Energy expenditure equation (l O ₂ kg ⁻¹)	Reference
Resting	Postprandial	Water	Temp. related	$S R_{\text{water}} = 1.6(0.002 + 0.0003 \times \text{water temp.})(\text{duration})$	Ladds et al. (2017c, Fig 5D), Liwanag (2010), Dassis et al. (2014)
Resting	Postabsorptive	Land	Winter	$R_{\text{land,winter}} = 0.0049(\text{duration})$	Ladds et al. (2017c, Table 2 NFM3), Donohue et al. (2000), Dassis et al. (2014)
Resting	Postabsorptive	Land	Summer	$R_{\text{land,summer}} = 0.0063(\text{duration})$	Ladds et al. (2017c, Table 2 NFM3), Liwanag (2010), Dassis et al. (2014)
Foraging/ travelling	N/A	Water	N/A	$A_{\text{water}} = 0.0303(\text{duration})$	Ladds et al. (2017c), Table 1 NFM1)
Foraging/ travelling	N/A	Land	N/A	$A_{\text{land}} = 0.0606(\text{duration})$ $A_{\text{land}} = 0.0606 \text{duration}$	Ladds et al. (2017c), Table 1 NFM1), Fish et al. (2001)
Grooming	Postprandial	Water	Winter	$G_{\text{mwater,winter}} = 0.014(\text{duration})$	Ladds et al. (2017c, Table 2 NFM3), Liwanag (2010)
Grooming	Postprandial	Water	Summer	$G_{\text{water,summer}} = 0.018(\text{duration})$	Ladds et al. (2017c, Table 2 NFM3), Liwanag (2010)
Grooming	Postabsorptive	Land	Winter	$G_{\text{land,winter}} = 0.007(\text{duration})$	Ladds et al. (2017c, Table 2 NFM3), Donohue et al. (2000), Dassis et al. (2014)
Grooming	Postabsorptive	Land	Summer	$G_{\text{land,summer}} = 0.009(\text{duration})$	Ladds et al. (2017b, Table 2 NFM3), Liwanag (2010), Dassis et al. (2014)

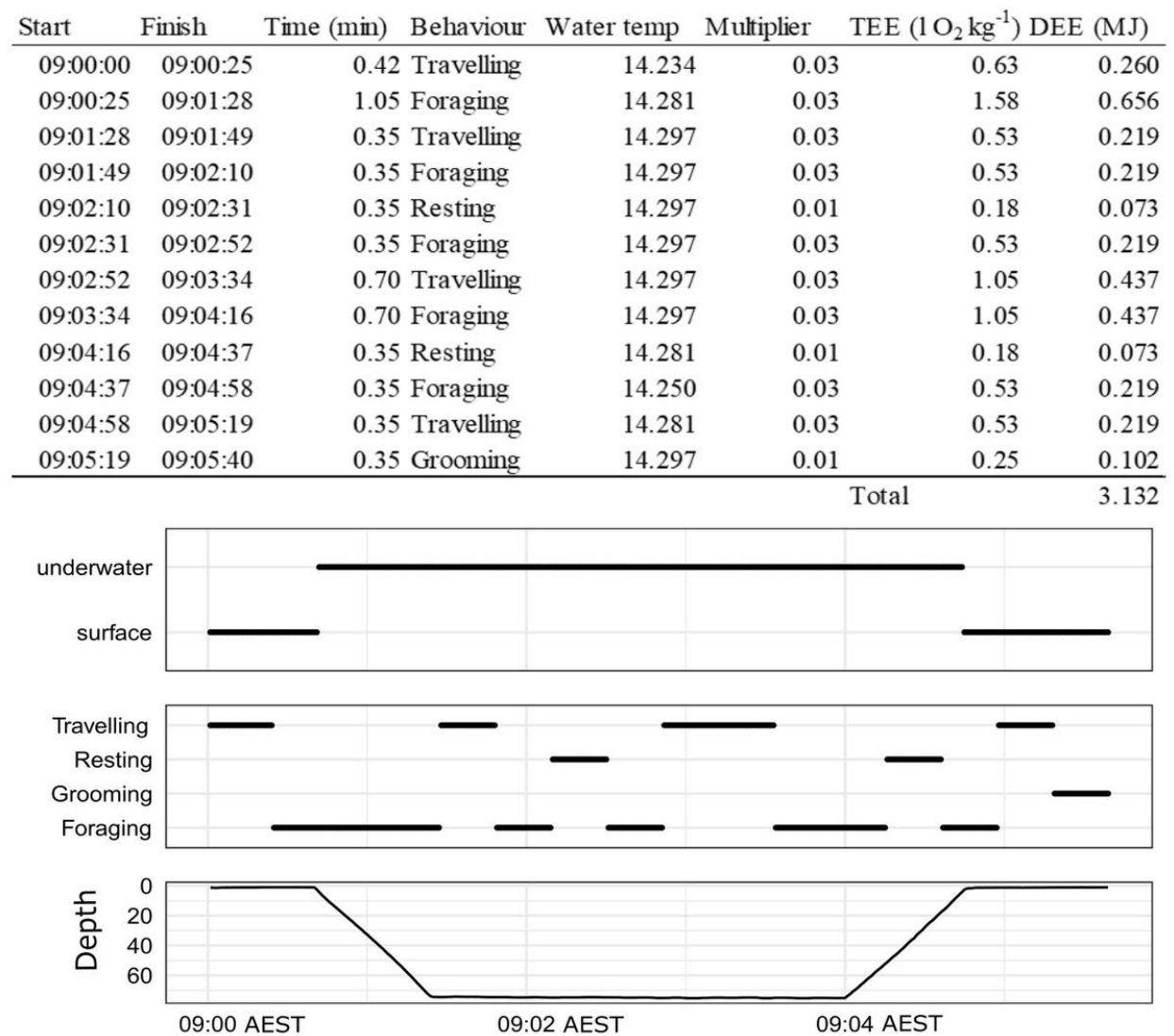


Figure 4.2 An example of how DEE is calculated for a single dive of a wild male juvenile Australian fur seal from Seal Rocks (winter), Victoria, Australia. Panels show location (underwater or surface), behaviour state (travelling, resting, grooming, foraging) and depth. See Table 1 for definitions and details of each behaviour state.

Statistical analysis

As it was not feasible to validate the captive model after applying it to the wild data, we conducted a sensitivity analysis on the probability of each event being assigned to a behaviour group. To do so, we adjusted the proportion of time wild fur seals spent in different behaviours (increasing some while decreasing others, such that the total proportion of time spent in the three behaviours always summed to 1) and investigated how it affected the overall DEE. We calculated 1,000 simulated proportions based on the actual range of time spent in each behavioural category, where each simulated proportion represented a day. We applied the energetics model to the simulated proportions and grouped the activities according to three behaviour categories: active (travelling and foraging) grooming and resting; then by two location categories: water and land. We then plotted the total DEE for the day against the simulated proportions for each of the five categories. As fur seals were of different sexes and were

tagged in different seasons we tested for differences in DEE between sexes and seasons using *post-hoc* general linear hypothesis and a multiple comparison test via the Tukey method within the function *glht* from the package “multcomp” (Hothorn et al. 2013). Individual fur seal identification was included in models as a random factor and significance was set at $p < 0.05$. All analyses were completed in R (Version 3.1.3; R Core Team 2015) and values reported as mean \pm SEM. The datasets generated and analysed during the current study are available in the “Time-energy budgets from accelerometers” repository: https://github.com/MoniqueLadds/Time-energy_budgets_from_accelerometers.git.

4.3 Results

Behaviour validation experiments with captive fur seals and sea lions

Most epochs (99%) were assigned to a behaviour category with over 80% probability (Fig. 4.3). We investigated those behaviours that were assigned with a less than 80% (~1% of total epochs) probability to understand where the model may have 'confused' behaviours. When the model was uncertain that an epoch was in the behaviour category "foraging" (less than chance), it generally predicted the epoch should be assigned as "travelling" and almost never "resting" or "grooming" (Fig. 4.3A). When there was uncertainty if an epoch should be categorised as "travelling", with less than 50% chance, the behaviour category with the next highest probability was "foraging" (Fig. 4.3B). Grooming was rarely confused for other behaviours, but when there was uncertainty the model calculated "resting" with the next greatest probability (Fig. 4.3C). There was also little confusion with assigning an epoch to resting, but occasionally the model assigned a higher probability of foraging.

The models correctly classified surrogate behaviour (travelling, foraging, grooming, resting) with high accuracy (>68%), but the number of samples in an epoch used affected the results, where longer epochs (sampling time of behaviour) resulted in higher accuracies (Table 4.2). The best low-resolution model (1 Hz) used 21 samples for an epoch, and the best high-resolution model (20 Hz) used 75 samples for an epoch, both of which had the highest training, testing and kappa scores for their behaviour category. Given that the 1 Hz data classified behaviours with very high accuracy (90% out-of-sample using epochs of size 21, Table 4.2) and recorded for the duration of deployments on wild fur seals (20 Hz data only recorded while fur seals were diving and for a short time after), only the 1 Hz data for the activity budgets were analysed.

Wild fur seal data collection

Three fur seals from Seal Rocks and six fur seals from Lady Julia Percy were successfully recaptured (recapture rates of 50% and 67% respectively) and accelerometer data obtained. Fur seals made between two and 45 trips with durations of between 30 min and nine days. Diving parameters (Appendix 4.1) were very similar between individuals from both sites. Fur seals in winter (from Seal Rocks) made fewer and longer foraging trips than fur seals in summer (from Lady Julia Percy). All other diving parameters were very similar between winter and summer fur seals (Appendix 4.1). Similarly, there were few differences in diving parameters for male and female juvenile fur seals.

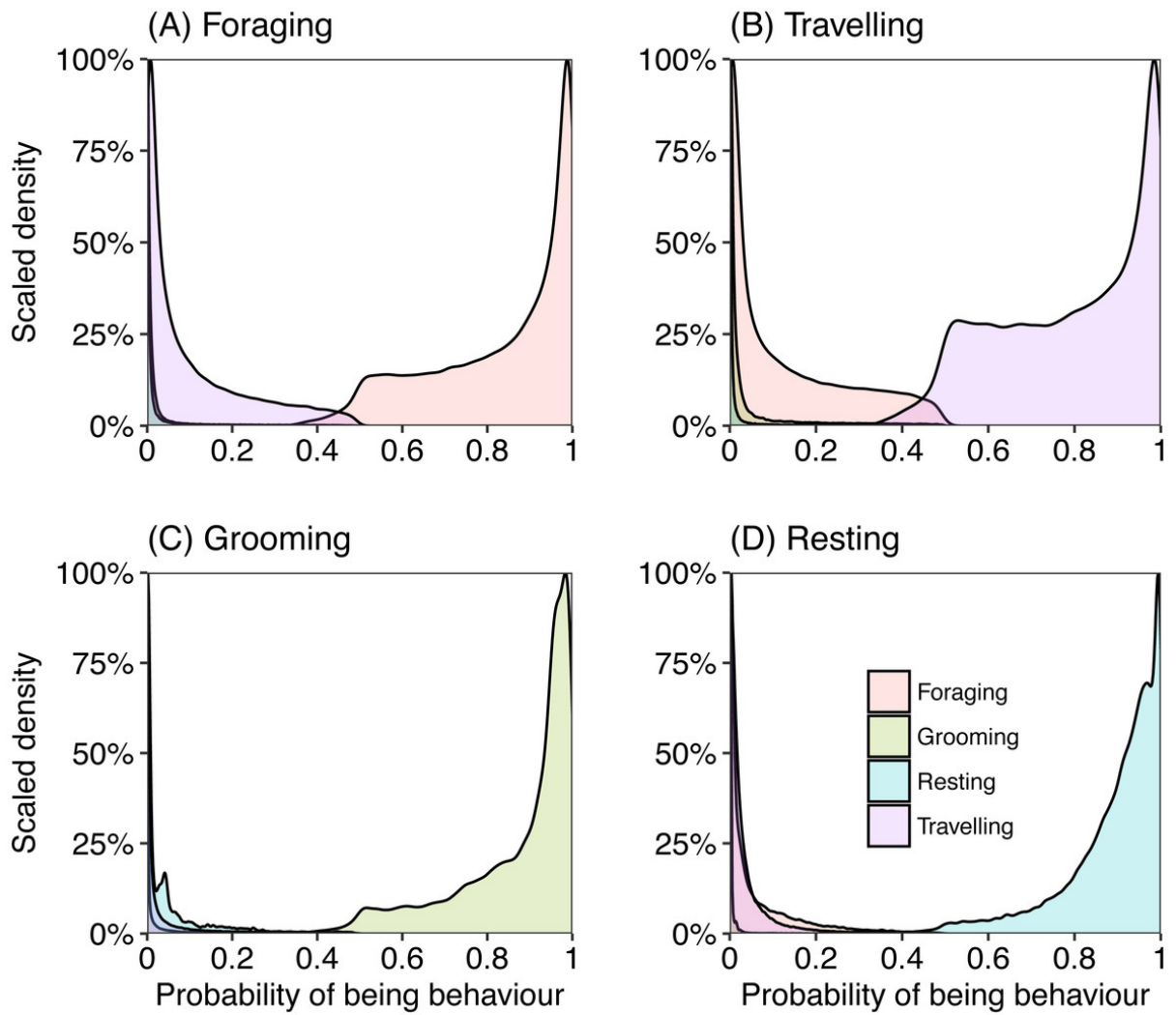


Figure 4.3 Cross-validation (training) and out-of-sample (testing) accuracy for gradient boosting models (GBM) trained across a range of epochs using two datasets for all behaviours (ALL) and for behaviour in water (Water).

Predicting behaviours of wild fur seals from accelerometers

Figure 4.4 is an example of the output produced by the activity model for a wild fur seal, showing the end of a foraging bout, travelling back to land and then a short period of resting on land (hauled out). This figure demonstrates the strengths and weaknesses of the GBM built from surrogates. The model was very good at predicting when the wild individual was resting, as there was very little movement in the accelerometer. But this feature resulted in the dive ascent also being classified as resting as the seal rose slowly through the water column with limited body movement (Fig. 4.4B). Grooming was also classified accurately; it predominantly occurred immediately prior to or following a dive, or during the first hour or so after hauling out. Foraging and travelling were frequently misclassified by the model (Fig. 4.3); most commonly, the descent of a dive was classified as foraging when it most likely should have been travelling, and foraging appeared periodically during long trips returning to the haul out site.

Apply the model to create time-energy budgets

Overall, the time that fur seals spent in the three different locations was between 31–63% on land, between 3–25% underwater and between 28–47% at the surface of the water. The pressure sensor on the accelerometers on two of the wild fur seals (LJP_A10283 and LJP_A10284) failed for a portion of the deployment, which resulted in a significant underestimation of the time spent underwater. Each fur seal spent approximately half of their deployment resting (range 32–55%), predominantly on land (Fig. 5) and another 22% (range 17–33%) was used for grooming. Approximately 20% (range 13–25%) of fur seals' time was foraging and approximately 12% travelling (range 8–22%).

There were no significant differences in the DEE for females ($18.22 \pm 5.91 \text{ MJ d}^{-1}$) and males ($18.86 \pm 6.01 \text{ MJ d}^{-1}$; *post-hoc* comparisons: $Z = -0.35$, $p = 0.72$) or for winter deployments ($20.77 \pm 7.00 \text{ MJ d}^{-1}$) and summer ($17.55 \pm 5.30 \text{ MJ d}^{-1}$; *post-hoc* comparisons: $Z = 1.10$, $p = 0.27$), which also represented site and year. Therefore, it was justifiable to pool the samples. The average DEE for wild individuals and locations pooled was $18.73 \pm 5.73 \text{ MJ d}^{-1}$ (range: $8.24\text{--}32.04 \text{ MJ d}^{-1}$) and mass-specific DEE was $0.50 \pm 0.14 \text{ MJ kg}^{-1} \text{ d}^{-1}$ (range: $0.08\text{--}0.81 \text{ MJ kg}^{-1} \text{ d}^{-1}$; Table 3). The maximum DEE was from a wild individual that spent 12 h continuously diving at sea (Appendix 4.2).

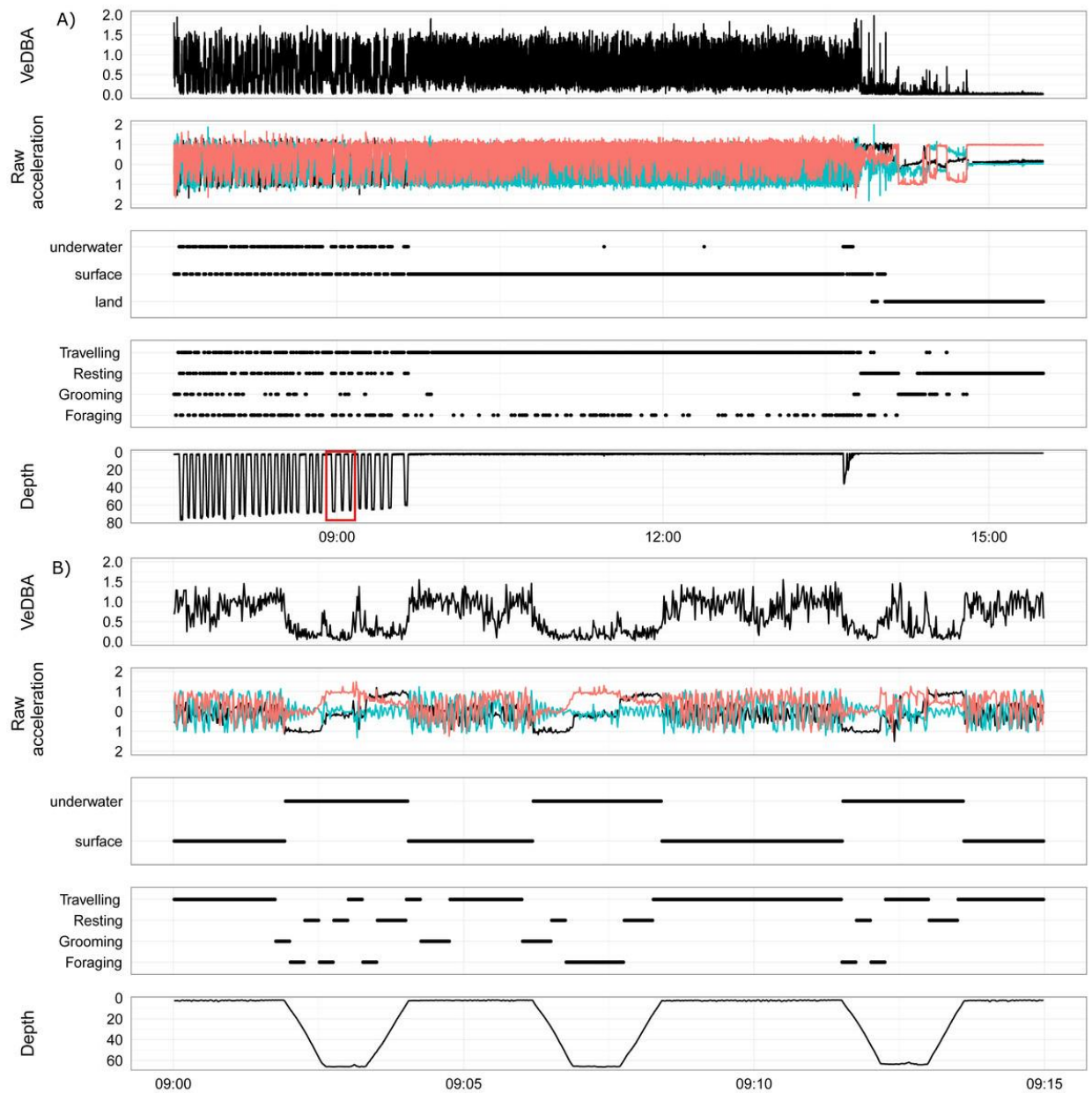


Figure 4.4 An example foraging bout, transition and haul-out of a female juvenile Australian fur seal from Lady Julia Percy, Victoria, Australia. (A, B) show VeDBA, raw acceleration of the x, y and z axis, location (underwater, surface or land), behaviour state (travelling, resting, grooming, foraging) and depth (time is in AEST). (A) Shows the end of a foraging bout, transiting back to land and then a short period of the haul out. The red box highlights the area of the dive that is displayed in (B). (B) shows three dives from the foraging bout.

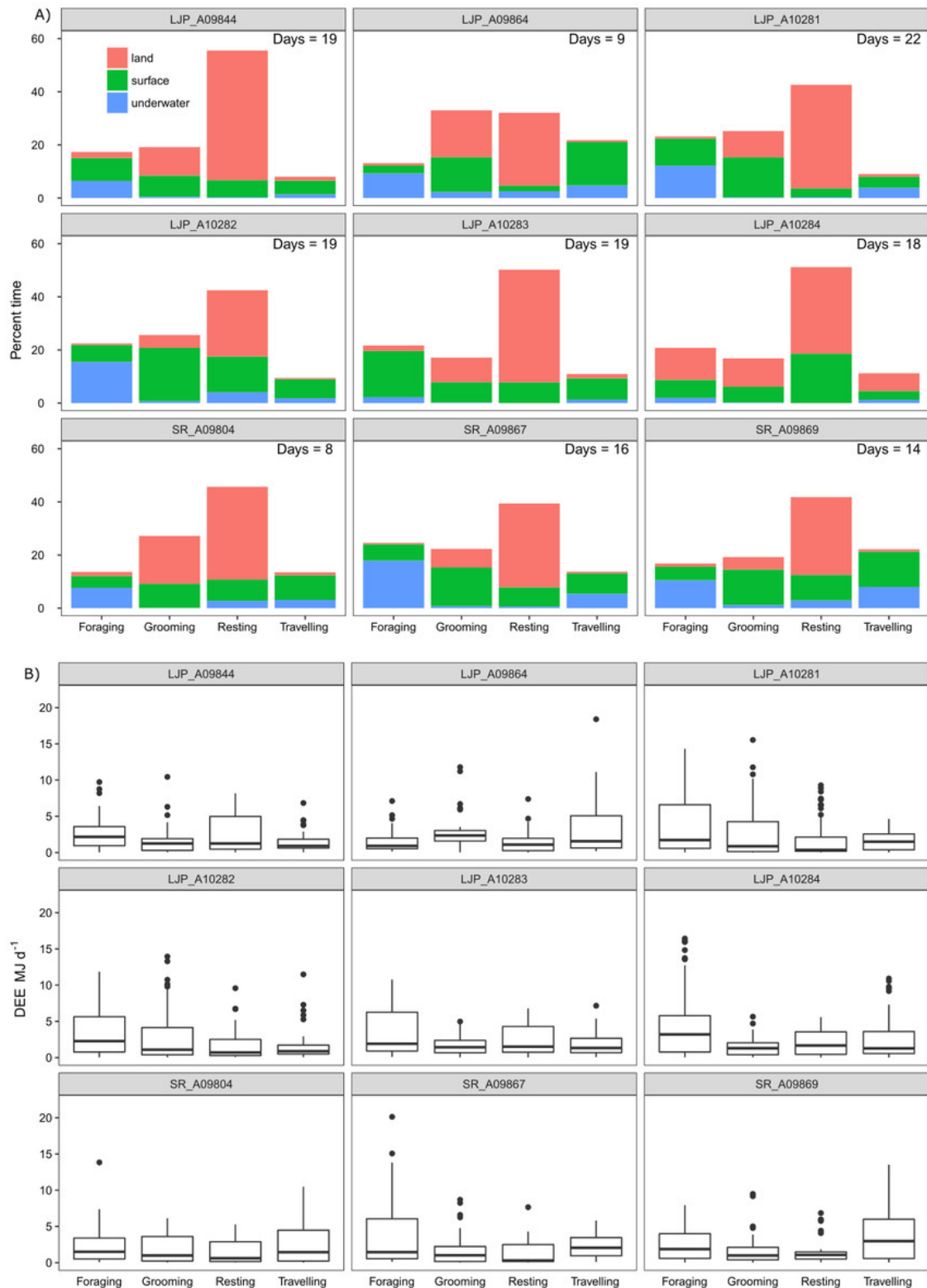


Figure 4.5 Activity (A) and energy (B) budgets for nine wild juvenile Australian fur seals—six deployed in summer and three deployed in winter. (A) Bars represent % of time spent in each type of activity over the duration of the deployment for the number of days presented in the top right-hand corner of plots. Colours represent the location of the behaviour. (B) Boxplots represent the minimum, 25% (Q1), median, 75% (Q3) and the upper limit (Q3 + 1.5 × the interquartile range (Q3 - Q1)) of DEE (MJ d⁻¹) with outliers of the upper limit represented by points.

Table 4.2 Daily energy expenditure (DEE MJ d⁻¹) for different behaviours on land, at the surface and underwater for nine juvenile Australian fur seals.

Behaviour	Average DEE (MJ d ⁻¹)	SD DEE	Max DEE	% total DEE	% Activity Budget
Land					
Resting	2.62	1.37	6.66	14.7%	35%
Grooming	1.05	0.86	3.77	5.9%	10%
Travelling ^a	1.22	1.52	7.69	6.9%	4%
Surface					
Resting	1.29	1.59	12.30	7.3%	9%
Grooming	1.59	1.46	7.80	8.9%	12%
Foraging	2.53	1.97	7.37	14.2%	8%
Travelling	2.46	2.38	12.24	13.8%	8%
Underwater					
Resting	0.27	0.41	2.15	1.5%	1%
Grooming	0.25	0.34	1.62	1.4%	2%
Foraging	3.30	3.46	17.41	18.5%	9%
Travelling	1.19	1.30	5.86	6.7%	3%
Total					
Resting	4.18	3.37	21.11	21.4%	45%
Grooming	2.89	2.65	13.20	14.8%	24%
Foraging	5.83	5.43	24.78	29.8%	16%
Travelling	6.68	7.91	37.36	34.1%	15%

^aAny foraging that was classified as occurring on land was assumed to be travelling.

The most energetically expensive behaviour was foraging, making up over a third of the DEE (Table 4.3). Resting on land made up ~15% of the overall energetic budget though this was the largest part of the activity budget (~45%). Fur seals spent little time resting at sea (~10%) and this behaviour represented ~9% of the overall energetic budget. The least costly activities were underwater grooming (1.4%) and resting (1.5%) which were likely to be mistaken behaviour classification. Grooming only made up one seventh of DEE, less than resting, and most grooming activity was at the surface (12%). Travelling and foraging made up two-thirds of the energetic budget, though they only represent roughly a third of the activity budget.

The sensitivity analysis revealed that the proportion of time spent in different behaviours (active, grooming or resting) and locations (water or land) altered the expected DEE for a juvenile Australian fur seal. DEE increased with more time spent active where DEE increased up to 27 MJ d⁻¹ when a seal was active more than 50% of the time (Fig. 4.6A). DEE decreased to 13 MJ d⁻¹ as seals spent more time resting (Fig. 4.6C). There was no clear relationship between the time spent grooming (Fig. 4.6B) or time spent on land or in water (Figs. 4.6D–4.6E) and DEE.

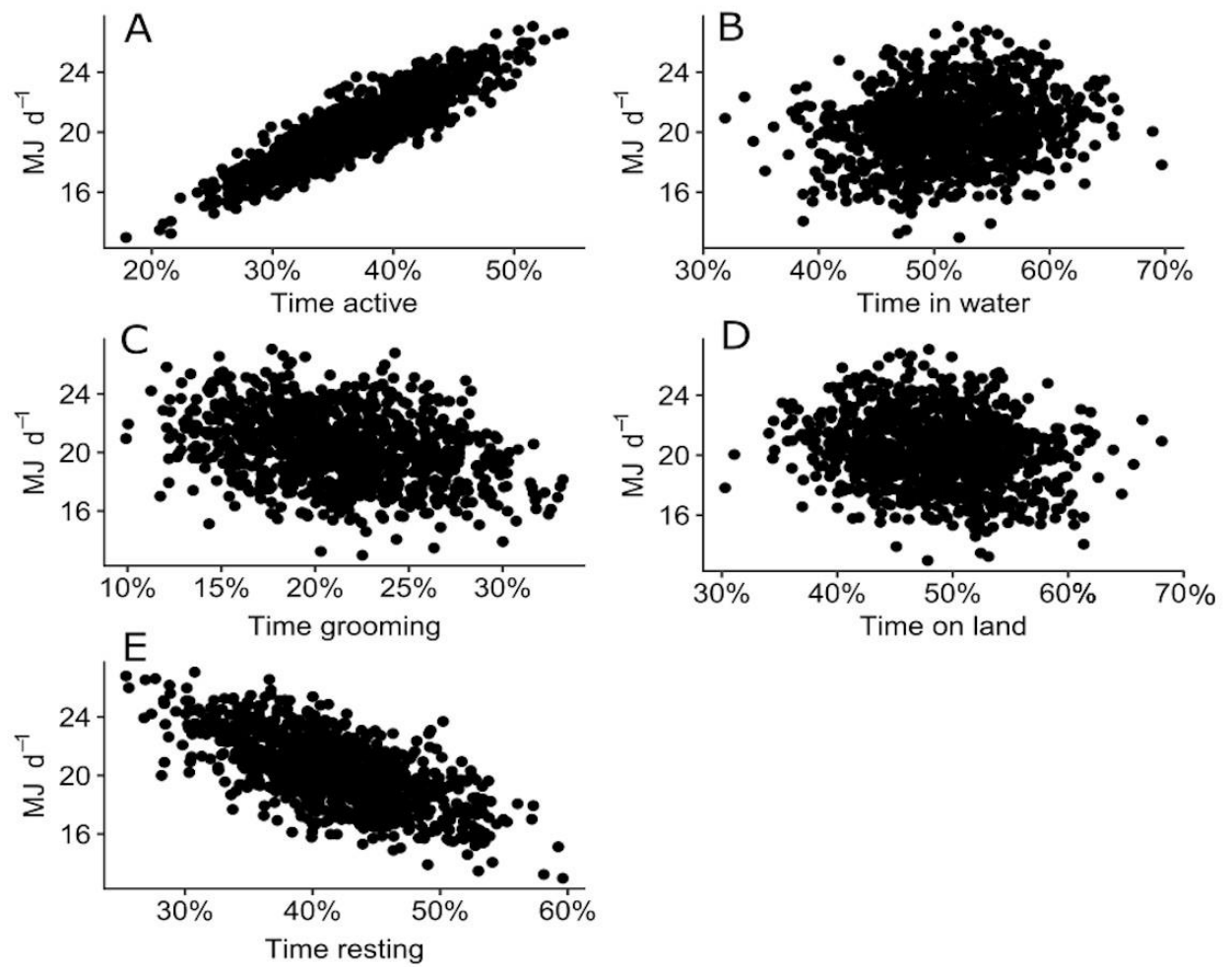


Figure 4.6 Plot of 500 simulated points of total DEE for wild juvenile Australian fur seals against percentage of time spent: (A) active (travelling and foraging); (B) grooming; (C) resting; (D) in water; (E) on land.

4.4 Discussion

Behaviour segmenting with accelerometers and machine learning

Supervised machine learning models trained with accelerometry data from captive animals reliably and accurately classified all four behaviour categories tested: foraging, grooming, resting and travelling. We expected that higher resolution data would enable the models to perform better at distinguishing the different behaviour types (Halsey et al. 2009), but were unable to compare this directly as we had too few long-duration behaviours recorded in water at high resolutions (>7 s). Despite this limitation, low resolution sampling produced very high out-of-sample (i.e., test) validation accuracies over a range of epoch sizes (72–90%; Table 2). The sample window size (epoch) influenced the result, with longer epochs tending to produce greater accuracies. The overall value of the summary statistic and its variation would be lower for long duration behaviours, i.e., low energy, repetitive behaviours are easier to distinguish (Vázquez Diosdado et al. 2015). Shorter epochs are more likely to pick up irregular movements of the animal that arise from short duration, high energy activities (such as burst attacks on prey), that were rarely seen in the captive experiments (Bom et al. 2014). Instead, foraging was defined by handling of dead prey and actively searching the bottom of the pool for food hidden in the substrate (Ladds et al. 2017d). From this definition, foraging became the most difficult behaviour category for the model to classify.

The trained model based on captive animals predicted the behaviour of the wild fur seals, with minimal anomalies. Overall, the activity budgets matched expectations of wild fur seals (Battaile et al. 2015), where they spent most time resting ($\sim 45\%$), and the rest of their time was split evenly among other activities—grooming ($\sim 22\%$), foraging ($\sim 20\%$) and travelling ($\sim 12\%$). The model classified some behaviours incorrectly, primarily from two events—classifying the descent of the dive as foraging, when it was more likely travelling, and from identifying bouts of foraging during long bouts of surface swimming transiting back to the colony, when the fur seals were more likely grooming or simply changing direction. Explicitly defining some behaviours from accelerometers for other species has also been challenging. For example, using supervised machine learning models the foraging behaviour of plovers could not be classified (Bom et al. 2014), nor grooming of pumas (Wang et al. 2015). The total time that fur seals spent foraging and travelling is likely accurate because foraging and travelling were most often confused, thus combining the behaviours reduces the overall error, and is considered sufficient to summarise their activity budget. One major limitation of this study was the use of dead prey to induce foraging, so future studies should use live prey to help refine and improve the accuracy of models.

Time-energy budgets

Juvenile fur seals had an average DEE that was 4.2 times the predicted BMR, which was about the same as estimated mass-specific energy expenditure measured from adult female Antarctic fur seals and northern fur seals (4.7 times BMR; Jeanniard-du-Dot et al. 2017) and slightly lower than adult female Californian sea lions (*Zalophus californianus californianus*) (5.2 times BMR; Ponganis et al. 1997). DEE did not differ for sex or for season (winter vs. summer) allowing us to pool the data. Sample size was too small and without adequate replication for further division. Even so, sex differences were not expected for juveniles, as any differences in diving abilities (Fowler et al. 2006), physiological parameters (Burns et al. 2004) or survival (Beauplet et al. 2005) have been attributed to age or size rather than sex (Weise & Costa 2007).

Grooming

Juvenile fur seals in this study spent approximately 25% of their time at-sea grooming, compared to northern fur seals that spend around ~30% of their time at sea rolling at the surface and another 9% in other grooming activities (Battaile et al. 2015). Fur seals groom for general body maintenance and this can offset some of the costs of thermoregulation (Liwanag 2010; Iwata et al. 2013). Through rubbing the fur, fur seals encourage small air-bubbles to be accumulate between their layers of fur, providing further insulation. This also helps maintain positive buoyancy which in turn saves energy while diving (discussed below; Fish et al. 2002) and increases metabolic rate in cold water (Liwanag 2010). Fur becomes compressed while diving, reducing its effectiveness to provide insulation, warmth and buoyancy (Fish et al. 2002), and to counteract this fur seals roll at the surface while rubbing their body with their fore flippers in order to trap air bubbles into their pelage (Liwanag 2010). Indeed, our models identified many cases of grooming following a dive (e.g. Fig. 4.4).

Other thermoregulatory behaviours are sailing and jughandling which allows heat to escape their hairless flippers in warm water, or to avoid heat loss in cold water (Bartholomew & Wilke 1956). Due to the sedentary style of this behaviour, the total energetic cost of daily grooming was not different from resting, despite having up to twice the energy demand (Liwanag 2010). Fur seals appear to allow for its increased energetic cost by resting more often (Table 4.3). General body maintenance, such as rubbing whiskers, can occur after consuming large prey items. Wild polar bears (*Ursus maritimus*) have been observed to clean regularly while consuming prey where they pause eating at regular intervals to rinse and lick their fore paws and face (Stirling 1974). Fur seals also spent significant time grooming on land (~15% of all land activity) using their flippers and occasionally their teeth to maintain their fur, further indicating the importance of this behaviour.

Resting

Juvenile fur seals spent around half of their time resting, which contributed around ~14% to their overall energetic budget. Due to the large cost of travelling and foraging, fur seals must use long haul-out periods to rest and recuperate. This is particularly true of juveniles who have an additional cost of growth, and use this time for reintegrating tissue and laying down fat (Kirsch et al. 2000). Juvenile Australian fur seals spent on average 72% of their time on land resting, which was ~16% of their overall activity budget. During long periods ashore, fur seals generally remain motionless for energy conservation while fasting. For example, over the breeding season, adult male northern and subantarctic fur seals spent >90% of observed time (during the day only) motionless, either sitting or lying (Stirling 1971).

The fur seals in this study spent ~12% of their time at-sea resting, similar to Northern fur seals and Antarctic fur seals (*Arctocephalus gazella*, Battaile et al. 2015), with ~2% of this time underwater. Some phocid seals rest underwater (Mitani et al. 2010), but it is highly unlikely that these seals did so as Australian fur seal dives were generally only a few minutes, and their trip durations relatively short (Maresh et al. 2015). Instead, the behaviour classified as resting underwater may be explained by the model classifying the ascent part of the dive as resting. Long periods of gliding on the ascent part of the dive, likely results from the fur seals being positively buoyant. During underwater glides, metabolic rate is at or lower than RMR (Fahlman et al. 2008), which conserves their on-board oxygen stores (Williams et al. 2004; Ponganis et al. 2011). Therefore, classifying this part of the dive as resting, and thus having a lower metabolic rate associated, actually strengthens the validity of the models.

Active behaviours (Foraging and Travelling)

Derivation of our energetic budget distinguishes between two sedentary behaviours (resting and grooming) and two active behaviours (foraging and travelling). While there has been a proposition that accelerometers can be used to measure energetics from active behaviours (Jeanniard-du-Dot et al. 2017), these relationships are confounded by time (Halsey 2017). To account for this, we estimated active energy expenditure as a function of time spent active at sea. This approach assumed that fur seals were postabsorptive at sea and postprandial on land and the cost of foraging and travelling were equivalent. These assumptions are supported by evidence that seals partially delay digestion while diving (Rosen & Trites 1997). The cost of foraging and travelling in this study could not be separated because the model sometimes confused the behaviours. Regardless, the two behaviours are inextricably linked due to the common movement of the behaviours (Ladds et al. 2017d), and the energetic cost would likely be similar.

Estimating the energetic cost of locomotion on land was difficult because this has not been measured for otariids. Movement on land is likely far more costly than in water because seal morphology has adapted them for efficiency in the ocean (Beentjes 1990), a hypothesis with experimental evidence from

the platypus and the water rat (Fish et al. 2001). Therefore, the cost of travelling on land was assumed to be twice as costly for fur seals as swimming in water. As a result, the average EE of activity on land was 1.51 MJ d^{-1} , or $\sim 5\%$ of the overall energetic budget. Given the assumed high cost of travelling on land and that travelling on land represented only $\sim 4\%$ of the overall activity budget, juvenile fur seals likely minimise the time spent active on land to save energy for foraging.

Juvenile Australian fur seals spent around half of their time in water (36–69%). During the breeding season, adult female Australian fur seals spend around 75% of their time in the water (Arnould & Hindell 2001), while pups are only in the water for around 29% of their time (Spence-Bailey et al. 2007). Of the time juveniles are in the water, approximately 56% (35–62%) is spent foraging and travelling, which contributes to most ($\sim 75\%$) of their DEE (Fig. 4.4, Table 4.3). The large cost of travelling and foraging is predominantly from the mechanical power of flipper strokes during swimming, rather than diving, which can be offset using a range of behavioural compensatory techniques that lower metabolic rate (Davis & Williams 2012).

Conclusions

We constructed time-energy budgets for wild fur seals across multiple foraging trips using accelerometers recording at a low resolution (1 Hz), validating the activity budgets from experiments with captive surrogates. Sensitivity analyses revealed that the average DEE for a 50 kg wild juvenile Australian fur seal over multiple foraging trips was between 18 and 25 MJ d^{-1} which equated to 1.9 to 6.4 times Kleiber (1975) prediction for the BMR for similarly sized terrestrial mammals. This was within than the field metabolic rate (FMR) range of 3.3 to 6.7 times Kleiber reported for adult female otariids in other studies (Costa et al. 1989; Fowler et al. 2007a; Jeanniard-du-Dot et al. 2017).

An important finding from this study is that time-energy budgets were able to be created from low resolution (1 Hz) accelerometry with very high accuracy (90%). Previous studies interpreting the foraging behaviour (Battaile et al. 2015) or energy expenditure (Jeanniard-du-Dot et al. 2017) of wild fur seals have used high ($>20 \text{ Hz}$) resolution data, at a cost of space and battery power from the device. Through validating low resolution accelerometry, this study will advance the use of accelerometers in the field as remote uploads are more feasible with less data, and battery life can be prolonged. Using low resolution data also significantly decreases the computational time and power required for analysis. Finally, as the drive towards smaller tags continue, using low resolution settings supports the use of smaller tags, without restricting the time with which they can be deployed.

While there is potential to fine-tune the model presented here to estimate a detailed time-energy budget on a minute or hourly basis, the current methodology provides a validated and representative estimate of daily time-energy budgets for wild fur seals. Through pairing estimates of energy expenditure with behaviour this study demonstrates the potential to understand not only how fur seals

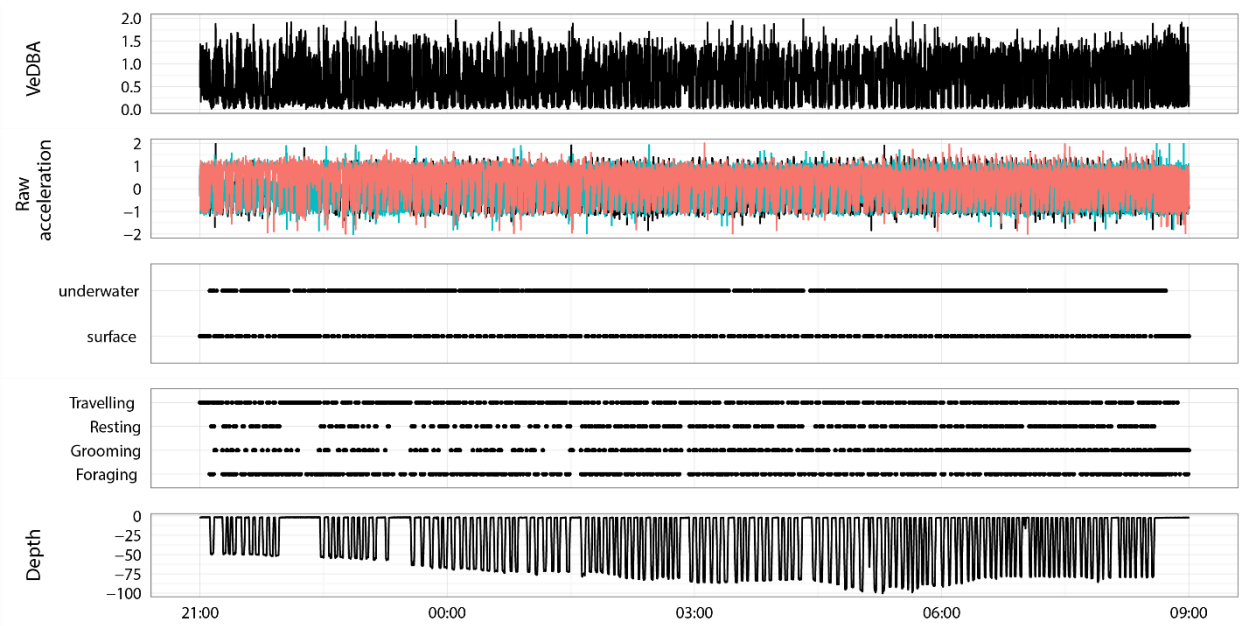
expend energy, but also where and how behavioural compensations are made to retain constant energy expenditure over short (a dive) and long (season) time period.

4.5 Appendices

Appendix 4.1 Summary statistics of daily energy expenditure (DEE MJ d⁻¹) and dive trip details for nine juvenile Australian fur seals. Fur seal details and average, standard deviation, minimum and maximum DEE for the length of deployment.

ID	Sex	Mass (kg)	Number of trips	Av. trip duration (days) (SD)	Number of dives	Av. max. dive depth (m) (SD)	Av. dive duration (s) (SD)	Max depth (m)	Av. DEE (MJ d ⁻¹) (SD)	Range DEE	Av. Kleiber multiple	Days
Winter												
A09804	Male	41 130	2	5.8 (4.6)	2907	40.3 (31.8)	114.8 (85.6)	85	21.2 (10.0)	12.3-37.1	4.5	8
A09867	Female	43 139	6	1.6 (0.4)	3113	33.2 (8.6)	128.6 (31.3)	63	24.7 (7.8)	12.0-37.3	5.0	16
A09869	Male	45 133	7	1.1 (0.7)	2158	51.4 (29.6)	121.9 (59.1)	81	25.2 (8.6)	11.4-37.0	5.0	14
Summer												
A09844	Female	35 107	14	0.3 (0.2)	1071	29.7 (21.3)	121.9 (79.4)	62	22.6 (4.5)	17.2-33.0	5.4	19
A09864	Female	30 110	4	1.2 (0.9)	1261	73.2 (23.0)	140.3 (39.9)	105	27.8 (6.7)	18.0-35.6	7.4	10
A10281	Female	42 119	12	0.8 (0.8)	2499	34.9 (9.5)	122.6 (38.3)	54	26.2 (7.8)	15.5-37.7	5.4	22
A10282	Female	30 107	6	0.8 (1.0)	1461	39.0 (8.9)	173.2 (70.9)	50	25.2 (6.5)	14.9-33.8	6.7	19
A10283	Male	34 110	45	0.1 (0.1)	1552	10.2 (7.8)	49.6 (36.2)	44	25.6 (3.0)	18.8-31.8	6.2	19
A10284	Female	35 108	21	0.2 (0.2)	1277	23.1 (12.7)	90.9 (47.7)	46	30.4 (6.8)	15.8-38.9	7.2	18

Appendix 4.2 An example of 12 hours of diving from a 40 kg juvenile Australian fur seal. Panels show VeDBA, raw acceleration, location (underwater or surface), behaviour category (travelling, resting, grooming, foraging) and depth.



5. Chapter Five

Niche partitioning and individual specialisation in resources and space use of sympatric fur seals at their range margin

This chapter has been submitted for publication in *Oecologia* as:

Salton, M., Raoult, V., Jonsen, I. & Harcourt, R. G. Niche partitioning and individual specialisation in resources and space use of sympatric fur seals at their range margin



Drawing credit: Marcus Salton

Abstract

Ecological theory predicts niche partitioning between high level predators living in sympatry as a strategy to minimise the selective pressure of competition. Accordingly, male Australian fur seals *Arctocephalus pusillus doriferus* and New Zealand fur seals *A. forsteri* that live in sympatry should partition their broad niches (in habitat and trophic dimensions) in order to coexist. However, at the northern end of their distributions in Australia both are recolonising their historic range after a long absence due to over-exploitation, and their small population sizes suggest competition should be weak and allow overlap in niche space. We found some niche overlap, yet clear partitioning in diet trophic level ($\delta^{15}\text{N}$ values from vibrissae), movement space (horizontal and vertical telemetry data) and circadian activity patterns (timing of dives) between males of each species, suggesting competition remained an active driver of niche partitioning among individuals in these small, peripheral populations. Consistent with individual specialisation theory, broad niches of populations were associated with high levels of individual specialisation for both species, despite putative low competition. Specialists in isotopic space were not necessarily specialists in movement space, further emphasising their diverse individual strategies for niche partitioning. Males of each species displayed distinct foraging modes, with Australian fur seals primarily benthic and New Zealand fur seals primarily epipelagic, though unexpectedly high individual specialisation for New Zealand fur seals might suggest marginal populations provide exceptions to the pattern generally observed among other fur seals.

5.1 Introduction

Understanding the factors that limit species' distributions is a key theme in ecology. An important factor that limits the distribution of many plants and animals is interrelations among species which determine food supply, threat of predation, disease and competition (Krebs 2001). In the case of competition, two species living in a community can compete for resources to a point where one species compromises the fitness of another, but can coexist by partitioning resources or risk competitive exclusion (MacArthur & Levins 1967; Pacala & Roughgarden 1982; Luiselli 2006). Interspecific competition is ubiquitous in plants and animals, though particularly prevalent at higher trophic levels and/or among larger animals where available resources may be more limited (Connell 1983; Schoener 1983). Many populations of large carnivores are currently recovering and expanding their range due to persistent conservation efforts (Wabakken et al. 2001; Chapron et al. 2014; Gompper et al. 2015; Martinez Cano et al. 2016). During such recoveries, the interrelations with species in the existing community and with other recovering carnivores are often unknown, but can involve interspecific competition with detrimental impacts to some species, including human conflict (Gompper 2002; Thornton et al. 2004; Kilgo et al. 2010; Reddy et al. 2019; Engebretsen et al. 2021; Franchini et al. 2021). Therefore, determining factors that mitigate competition and mechanisms for coexistence remain important in ecology and will support conservation management.

Niche theory suggests it is possible for competing species to coexist if they occupy different niches (Hardin 1960; MacArthur & Levins 1967). Within a species, similar individuals manage to coexist by partitioning resources, with individuals that have contrasting morphology, physiological capacity, energy requirements or social status typically adopting different strategies to exploit available resources (Svanbäck & Bolnick 2007). Individuals can also use a subset of the population's resources for reasons unrelated to sex, age and morphological variation, i.e. inter-individual variation (Bolnick et al. 2003; Araújo et al. 2011), with more specialised individuals using a smaller subset and more generalised individuals using a larger subset of the population resources. The level of inter-individual variation can be positively related to population density – a proxy for intraspecific competition (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007; Araújo et al. 2008; Tinker et al. 2012; Newsome et al. 2015). At the edge of a species' geographic range, population size is small and thereby intraspecific competition tends to be low, reducing selection pressures associated with population density, but here interspecific competition can be an important factor setting range limits (Hersteinsson & Macdonald 1992; Case & Taper 2000; Case et al. 2005; Pigot & Tobias 2013).

By progressing the study of how species coexist, particularly at a species' expanding margin of their range, we can better assess and predict the interrelations between species as they recover and move into new communities. There are now well-established methods for quantifying ecological niche size and partitioning, including variance and ellipse-based metrics, and spatial, resource and temporal

dimensions (Pielou 1972; Petraitis 1979; Bearhop et al. 2004; Peres-Neto et al. 2006; Jackson et al. 2011; Swanson et al. 2015; Frey et al. 2017), which have been used to demonstrate that individuals can coexist by partitioning parts of their niche space, resources and time (Luiselli 2006; Navarro et al. 2013; Dehnhard et al. 2020). These niche dimensions have often been assessed in isolation, but with the proliferation of stable isotope analyses and telemetry devices more studies are demonstrating the importance of a multifaceted approach to understanding niche partition (Kleynhans et al. 2011; Matich & Heithaus 2014; Baylis et al. 2015a; Giménez et al. 2018; Riverón et al. 2021; Schwarz et al. 2021). There have also been advances in measuring intra and interspecific variability in resource and space use (Bolnick et al. 2002; Araújo et al. 2007; Zaccarelli et al. 2013; Carneiro et al. 2017; Bonnet-Lebrun et al. 2018) that require serial sampling individuals to determine individual specialisation (Newsome et al. 2010; Eerkens et al. 2016). Animals can be monitored over long periods of time by using telemetry devices and sampling tissues that accumulate isotopes, with both approaches capable of quantifying individual specialisation (Bearhop et al. 2006; Newsome et al. 2009; Elorriaga-Verplancken et al. 2013; Kernaléguen et al. 2016; Bonnet-Lebrun et al. 2018). Commonly analysed isotopes include nitrogen, as an indicator of trophic position of prey, and carbon, as an indicator of geographic origin of prey (Kelly 2000; McCutchan Jr et al. 2003). In marine systems, carbon isotopes can reflect nearshore vs. offshore foraging and prey originating from benthic vs. epipelagic environments (Michener & Kaufman 2007; Newsome et al. 2010). Therefore, the tools are now available to provide detailed assessments of how large predators coexist as they recover and expand their range.

Otariids, fur seals and sea lions, were ubiquitously overharvested for their fur from the eighteenth to twentieth century, with extinction of many populations and dramatic range reductions (Bonner 1989; Gerber & Hilborn 2001). With persistent conservation efforts, many species have been recovering in recent decades and reoccupying parts of their historic range (Wickens & York 1997; Gerber & Hilborn 2001; Kirkman et al. 2013; Crespo 2021; Salton et al. 2021). There are many incidences of two otariid species living in sympatry during such recoveries (Majluf & Trillmich 1981; Lyons et al. 2000; Wege et al. 2016; Elorriaga-Verplancken et al. 2021), and while this seems to be possible by partitioning their niche (Robinson 2002; Franco-Trecu et al. 2012; Páez-Rosas et al. 2012; Jeglinski et al. 2013; Pablo-Rodríguez et al. 2016; Hoskins et al. 2017) different levels of individual specialisations in diet and foraging among species may also play a role (Franco-Trecu 2014; Kernaléguen et al. 2015a; Kernaléguen et al. 2015b; Riverón et al. 2021). Some sympatric species display disparate population growth rates and range expansion, which could be attributed to interrelations between the similar species (Wickens & York 1997; Villegas-Amtmann et al. 2013; Franco-Trecu 2014; Elorriaga-Verplancken et al. 2021).

Here, we investigate how two otariids, the Australian fur seal, *Arctocephalus pusillus doriferus*, and the New Zealand fur seal, *A. forsteri* (also known as long-nosed fur seal, Shaughnessy & Goldsworthy 2015), coexist in sympatry at an expanding margin of both species' range. These species have recently

reestablished seasonal occupation of their north-eastern range margin (Warneke 1975; Irvine et al. 1997; Shaughnessy et al. 2001; Burleigh et al. 2008b; Salton et al. 2021) following broader population recovery and range expansion (Arnould et al. 2003; Shaughnessy et al. 2015; McIntosh et al. 2018b). Their populations at this margin remain small and predominantly consists of juveniles and sub-adult males (Burleigh et al. 2008b), though both breed on Montague Island, NSW (36° 14' S, 150° 13' E), in small numbers (McIntosh et al. 2018b). The two species are typically considered 'generalists' due to their broad diets (Page et al. 2005a; Kliska 2016), but in some areas Australian fur seals do exhibit individual specialisations in diet and foraging (Kernaléguen et al. 2012; Kernaléguen et al. 2016; Knox et al. 2018). The two species have apparently distinct foraging modes, with Australian fur seals primarily foraging during benthic dives over the continental shelf (Knox et al. 2017; Salton et al. 2019) and New Zealand fur seals foraging during pelagic dives on and off the continental shelf (Page et al. 2005b; Page et al. 2006; Salton et al. 2021). There is some evidence that the two species have different diets and foraging behaviour in this part of their range (Hardy et al. 2017; Salton et al. 2021), though the mechanisms for coexistence remains unclear. Given the small population sizes of both species, we expect intraspecific competition to be low and, accordingly, interspecific interactions to drive niche partitioning. To understand the mechanisms for coexistence in a situation with purported low intraspecific competition we aim to 1) estimate niche sizes, in isotopic and movement space, and the degree of partitioning between species at a population level, and 2) the degree of individual specialization at the intra-population level and how it relates to their population niche size. Then, 3) we assess the relationship between individual specialisation in isotopic space and individual specialisation in movement space, and the importance of intrinsic differences in body size.

5.2 Methods

Ethics statement

All research protocols were conducted under Office of Environment and Heritage Animal Ethics Committee Approval (100322/03) and Macquarie University Ethics Committee Approval 2011/054. Capture and handling methods are outlined in Salton et al. (2019). While sedated, standard body length was measured using standard methods (± 1 cm, Kirkwood et al. 2006), and the telemetry device was glued to the dorsal midline of each seal with a quick-setting epoxy (Araldite® K-268, Huntsman Advanced Materials; Quick Set Epoxy Resin 850-940, RS components, Australia). Devices remained on the seals until they fell off, once their fur weakened towards the annual moult. Access to the study site at Jervis Bay was under the guidance and support of the Australian Navy, New South Wales National Parks and Wildlife Service, Jervis Bay Marine Park and the Beecroft Ranger Station. Access to the study site at Montague Island was under the guidance and support of New South Wales National Parks and Wildlife Service.

Study species, study site and data collection

The data were collected during the male's inter-breeding period between 25-May and 22-Aug in 2011 to 2014, inclusive, when they are free of immediate reproductive constraints and thereby no requirement to attend a specific terrestrial site and can range widely. The breeding period for male Australian fur seals is between late October and late December and for male New Zealand fur seals between early November and early January (Crawley & Wilson 1976; Warneke & Shaughnessy 1985). Males move away from their inter-breeding areas towards breeding colonies at the approach of breeding seasons, and it is assumed the reverse occurs at the end of breeding, consistent with the seasonal pattern of attendance at these inter-breeding areas (Shaughnessy et al. 2001; Burleigh et al. 2008b) and resighted seals marked with flipper tags at colonies (Warneke 1975). Male fur seals were captured at two study sites, Jervis Bay (35° 3' S, 150° 50' E) and Montague Island (36° 14' S, 150° 13' E) on the southeast coast of Australia (Fig. 5.1). This coastline has a narrow continental shelf (17-72 km width) with the shelf break between 130 and 170 m (Geoscience Australia, data.gov.au, 2017-06-24). The populations of both fur seal species have recently been growing in this north-eastern region of both species' range after near extirpation from over harvesting, and at the time of this study the populations remained small (Warneke 1975; McIntosh et al. 2018b).

The movement of males were recorded with Mk10-AF Fastloc-GPS devices (Wildlife Computers; 105 × 60 × 20 mm, 240 g) at Jervis Bay and CTD-SRDL-9000 (Conductivity-Temperature-Depth Satellite Relay Data Logger, Sea Mammal Research Unit, St Andrews, UK; 120 x 72 x 60 mm, 545 g) at Montague Island. Both devices collected Argos satellite-derived locations (collected at irregular time intervals, with a median fix rate of 1 fix per 1.1 h), and Mk10 devices also recorded GPS locations (collected at 2 min

intervals, with a median fix rate of 1 fix per 1.5 h), both of which were transmitted via the Argos satellite network (Collecte Localisation Satellites, Saint-Agne, France). Dive data were collected with both devices (but not Mk10-AF in 2011), with depth (± 0.5 m) sampled every 5 s when the device was wet. Single dives were defined by a minimum depth of 5 m and minimum duration of 10 s, then the maximum depth per dive was extracted.

To account for potential inter-annual variability in resource use (Rodríguez-Malagón et al. 2021), we sampled individual whiskers from both species across each year of the study. The longest whisker was sampled (plucked) from each seal while a tracking device was being attached. One whisker was sampled from a dead seal incidentally in 21 November 2012. In the laboratory, whiskers were hand-washed in 100% ethanol and cleaned in an ultrasonic bath of distilled water for 5 minutes. Whiskers were then dried, measured and cut into 3 mm-long consecutive sections starting from the proximal (facial) end, following Cherel et al. (2009). The first 10 sections were sampled from all individuals. Vibrissae growth rate estimates for Australian fur seal males are 0.17 ± 0.04 mm d⁻¹ (Kernaléguen et al. 2015b), and while they are not known for male New Zealand fur seals we assume it is similar based on growth rate estimates of other male fur seals; *Arctocephalus australis* 0.13 mm d⁻¹, *Arctocephalus gazelle* 0.14 ± 0.02 mm d⁻¹, *Arctocephalus tropicalis* 0.14 ± 0.04 mm d⁻¹, (Kernaléguen et al. 2012; Vales et al. 2015). Hence, a 3mm section corresponds to approximately 18 days (Kernaléguen et al. 2015b). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each whisker section were determined by a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, UK) at the University of California Davis (UC-Davis) Stable Isotope Facility. Results are presented in the conventional δ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards indicate measurement errors of $< 0.58\text{‰}$ and $< 0.20\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively.

Whiskers were sampled for carbon and nitrogen isotope analysis from 9 male Australian fur seals (AuFS) and 35 male New Zealand fur seals (NZFS). Location and dive recording devices were deployed on 10 male AuFS and 38 male NZFS. Location and dive data were recorded for 15-259 days (mean \pm SE 131.9 ± 15.5 days and 101.4 ± 10.7 days per individual, respectively), which was equivalent to 15 ± 1.2 weeks with location and dive data, 635 ± 53 locations (from SSM, at 3hr interval) and 1151 ± 221 dives per individual. Based on body length of the seals, male AuFS were larger than male NZFS (body length mean \pm SE 192 ± 7.9 cm, $N = 9$ individual, vs. 137 ± 5.7 , $N = 39$ individuals, respectively; Wilcoxon rank sum test $W=339$, $P < 0.001$).

Data processing

All data processing, analysis and figure development were conducted in R v4.1.1 (R Core Team 2020).

Locations were subjected to standard quality-control checks, including removal of erroneous and duplicated locations, removal of locations after a tag fell off a seal, and reclassification of Argos Z-class locations to B-class ($n = 86 / 56978$ locations). Then a continuous-time correlated random walk state-space model (Jonsen et al. 2020) was fitted to the quality-controlled locations using the *'fit_ssm'* function in the *'foieGras'* R package (Jonsen & Patterson 2020). This approach accounted for observation errors in the Argos location data, and provided location estimates with standard errors at regular 3 hr time intervals along each individual's track (Jonsen et al. 2013). Foraging 'distance to land' was used as an index of horizontal movement behaviour. To calculate this index, SSM-estimated locations were projected using Albers equal-area based on the extent of the seal's movements, determined using <https://projectionwizard.org/>, then distance to the Australian coastline (GEODATA Coast 100K 2004, Geosciences Australia) was calculated using the *'gDistance'* function in the *'rgeos'* R package (Bivand & Rundel 2021). Locations within 100 m of land were assumed to be indicative of the seal being on land or not foraging and removed.

To best represent the foraging behaviour of animals at the expanding range margin, we analysed only the 10 most recent whisker sections to represent an individual's isotopic niche and the first 10 weeks of tracking data to represent their movement niche. This avoids details of their seasonal migrations that may influence the stable isotope values preceding the period at the range margin (Appendix 5.1; Kernaléguen et al. 2015b; Salton et al. 2021). Based on the whisker growth rate estimates (presented above), the isotope data corresponds to diet approximately 180 days prior to sampling (i.e. approximately the first six months of the year). Each whisker section represented a unique sample of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values per individual. For movement data, distance to land and maximum dive depth were averaged per week for each individual, and these weekly averaged values represented individual samples of movement behaviour.

Niche partitioning and Individual specialisation

Species differences in the two isotope variables ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and two movement variables (distance to land and dive depth) were tested using linear mixed models. For each of the four variables, a linear mixed model was fitted with species a fixed categorical effect and sample nested in individual identity as a random effect, using the *'lme'* function in the *'nlme'* R package (Pinheiro et al. 2021). All models included a temporal autocorrelation (corAR1 of form $\sim 1 | \text{ID}$) to account for serial sampling of individuals. When there were model convergence issues (i.e. $\delta^{15}\text{N}$), these were corrected by removing the nested sample component of the random effect. Akaike Information Criterion (AIC) and analysis of variance tests were used to compare the model with fixed effects to the null model, with $P < 0.05$ indicative of a significant difference from the null model; following the protocol outlined by Zuur et al. (2009). Distance to land and dive depth were log transformed to account for these indexes being highly positively

skewed, and the model estimates are presented back-transformed with their confidence interval (alternatively, isotope estimates are presented with their modelled standard error).

The 95% and 50% spatial utilisation distribution (UD) probabilities were calculated for the inter-breeding period. Smoothing parameters for the UD were calculated using the plug-in bandwidth selector function '*Hpi*' and associated '*kde*' function in the '*ks*' R package (Duong 2021), and the Australian coastline was used as a habitat grid to ensure realistic UD probabilities over water. UDs were calculated for each individual and then standardised to produce a population level 95% and 50% UD for AuFS and NZFS. Percentage UD overlap was calculated using the equation $[(\text{area}_{ab}/\text{UD}_a) \times (\text{area}_{ab}/\text{UD}_b)]^{0.5}$, where area_{ab} is the area of overlap in the home ranges of species *a* and *b*, and UD_a and UD_b refer to the UD of species *a* and *b*, respectively (Atwood & Weeks 2003; Hoskins et al. 2017).

To test for partitioning in the circadian pattern of dive behaviour, we assessed whether dive frequency and dive depth differed with three diel periods; day, twilight and night. Solar position was calculated using solar azimuth and elevation based on location, local date and time (Australian eastern standard time: UTC +10 h), using the '*solarpos*' function in the '*mapproj*' R package (Bivand & Lewin-Koh 2021). From solar position, a categorical variable for diel period was defined with three levels: positive values of solar elevation angle identified 'day'; values between zero and -12 deg below the horizon identified nautical 'twilight'; and values below -12 deg identified 'night'. Generalized linear mixed models were fitted to assess whether dive frequency was explained by diel period, for each species separately, using the '*lmer*' function in the '*lme4*' R package (Bates et al. 2015) with a random effect for individual (intercept only, to elevate convergence issues with the models) and a Poisson error distribution with a log link function. Linear mixed models were fitted to assess whether dive depth (log transformed) was explained by diel period, for each species separately, using the '*lmer*' function in the '*lme4*' R package (Bates et al. 2015) with a random effect for individual (intercept only, to elevate convergence issues with the models). AIC and analysis of variance were again used to compare the model with fixed effects to the null model, with $P < 0.05$ indicative of a significant difference from the null model.

Isotopic and movement niche size and partitioning between species were estimated using Bayesian ellipse-based metrics calculated in the '*SIBER*' R package (Jackson et al. 2011). SIBER applies a 'typical' individual approach to calculate the core niche of a population, and incorporates uncertainties relating to sampling biases and small sample sizes (Jackson et al. 2011; Syväranta et al. 2013). We used the 40% Bayesian standard ellipse area (SEA_b) to represent the most reliable population-level niche, with the variance estimated through 10^4 posteriori draws, and a 95% SEA_b to capture individual variation and enable more accurate cross-study comparisons. Repeated sample measurements per individual were not independent, yet the small sample size of individual Australian fur seals produced highly variable niche estimates for that population, albeit consistent niche size compared to the whole dataset (Sup 1). Independent sampling is a required assumption for use of Bayesian SEA_b (Jackson et al. 2011), but

incorporating a large number of individuals as in this case was preferable to other methods of assessing isotope niche. SEA_b results should nevertheless be interpreted in combination with results from mixed effect models. Overlap of isotopic and movement niches was calculated per species based on the posterior distributions of the fitted ellipses using the '*baysianOverlap*' function (n = 360, draws = 50).

The degree of individual specialisation in male AuFS and NZFS for each of the four niche parameters were measured and compared using Roughgarden's WIC/TNW index for continuous data (Bolnick et al. 2002). The approach considers the total niche width (TNW), or variance in total niche parameter for all individuals, to be a sum of the within-individual component (WIC) and the between-individual component (BIC). The WIC is the average of individual niche widths, for example the variance in isotopes within each individual's whisker, and the BIC is the variance in mean parameter estimates (e.g. isotope values) among individuals. The 'WTcMC' function in the 'RInSp' R package (Zaccarelli et al. 2013) was used to calculate the specialisation index (SI) for each population, weighting each individual equally to account for slight variances in the number of samples per individual. The SI varied between 0 (specialist) and 1 (generalist), and we apply Monte Carlo resampling (using 1000 replicates) to test the null hypothesis that all individuals sample equally from a generalist population. Relationships between the SI for the four niche parameters and with individual body length were tested using linear models, separately for each species, with t-statistics used to assess the fitted linear model, with $P < 0.05$ indicative of a significant relationship. A lack of relationship between the SI of each niche parameter and body size ensured the measure of individual specialisation aligned with the definition by Bolnick et al. (2002).

5.3 Results

Isotopic and movement niche

The two species had broad, overlapping isotopic niches of similar size. Bayesian estimation of the isotopic niche space of the two species shows similar sized isotopic niches, based on the 40% SEA_b and 95% SEA_b, yet Australian fur seals had a narrower range of $\delta^{15}\text{N}$ values (trophic levels) and wider range of $\delta^{13}\text{C}$ (nutritional sources) compared to New Zealand fur seals (Fig. 5.2; Table 5.1). Bayesian trophic niche (40% SEA_b) overlap was negligible at ~5%, suggesting strong resource partitioning between the two seal populations. There were significant differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between male AuFS and NZFS, with AuFS having higher $\delta^{15}\text{N}$ values and higher but ecologically similar $\delta^{13}\text{C}$ values (models were significantly different to the null model, $\delta^{15}\text{N}$ $\Delta\text{AIC} = 17.65$ $\text{Chisq} = 19.65$ $P < 0.001$; $\delta^{13}\text{C}$ $\Delta\text{AIC} = 3.16$ $\text{Chisq} = 5.16$ $P = 0.023$; Table 5.1). Based on the 40% SEA_b, partitioning of their iso-niche space was primarily in $\delta^{15}\text{N}$ values that relate to trophic level (Fig. 5.2, Table 5.1).

Male AuFS remained close to the coast over the continental shelf while NZFS travelled across the continental shelf and off the shelf over deep water. Consequently, male NZFS had a much larger 95% utilisation distribution than AuFS (Table 5.1), and the percentage overlap or 95% UD shared with the other species was ~80% for AuFS and ~10% for NZFS. However, the 50% UD for both species was predominantly over the continental shelf, of similar size, and showed approximately 50% species overlap (Fig. 5.1; Table 5.1). Accordingly, the mean distance that an individual travelled from land per week was highly positively skewed for male AuFS and NZFS, and not significantly different between the two species (distance to land not significantly different to the null model, $\Delta\text{AIC} = 1.6$ $\text{Chisq} = 0.32$ $P = 0.574$; Table 5.1). The two species also shared vertical movement space, but on average male AuFS dived deeper than NZFS (dive depth significantly different to the null model, $\Delta\text{AIC} = 7.9$ $\text{Chisq} = 9.89$ $P = 0.002$; Fig. 5.1; Table 5.1). The movement behaviour of AuFS (i.e. predominantly deep dives over the continental shelf) was consistent with a benthic foraging mode, and the movement behaviour of NZFS (shallow dives over the shelf and deep water) was consistent with epipelagic foraging mode. However, four male NZFS with weekly average maximum depth >100 m also remained close to land (<20 km) during those weeks, suggesting benthic foraging; this was the case for all weeks recorded for one of these four NZFS, suggesting it only used a benthic foraging mode during its inter-breeding period.

With the horizontal and vertical movements combined, NZFS had a much larger movement niche space (40% and 95% SEA_b; Table 5.1), due to a wider range in horizontal movement (distance to land) yet similar range in vertical movement (dive depth) among individuals of each species. Based on the 40% SEA_b, the two species overlapped in movement niche space (though AuFS share more of their movement niche space with NZFS, and NZFS have more space that is segregated from AuFS space). The divergence in movement niche was primarily due to segregation in dive depth (Fig. 5.2).

The two species also had different circadian patterns in dive frequency, with NZFS diving significantly more at night and AuFS diving similarly between night and day, but significantly less during twilight (Appendix 5.2; Appendix 5.3). Neither species had a diel pattern in dive depth (Appendix 5.2; Appendix 5.3).

Figure 5.1 Utilisation distributions (a) 95% (b) 50% and box-whisker plots of movement niche parameters for male Australian fur seals (*A. pusillus doriferus*; AuFS, red) and New Zealand fur seals (*A. forsteri*; NZFS, yellow) from Jervis Bay and Montague Island (sites combined). Continental shelf (<500m depth) is light blue. Inset map in panel a) shows approximate range of each species. In panels c) and d), boxes represent 1st and 3rd quartiles and median as a thick line, and whiskers are 1.5x inter quartile range. Panel c) is cropped between 100 - 200 km for clarity (16 points for NZFS not visible). Notches in the boxes indicate 95% confidence interval around the median and overlap in notches between groups suggests the medians are not significantly different.

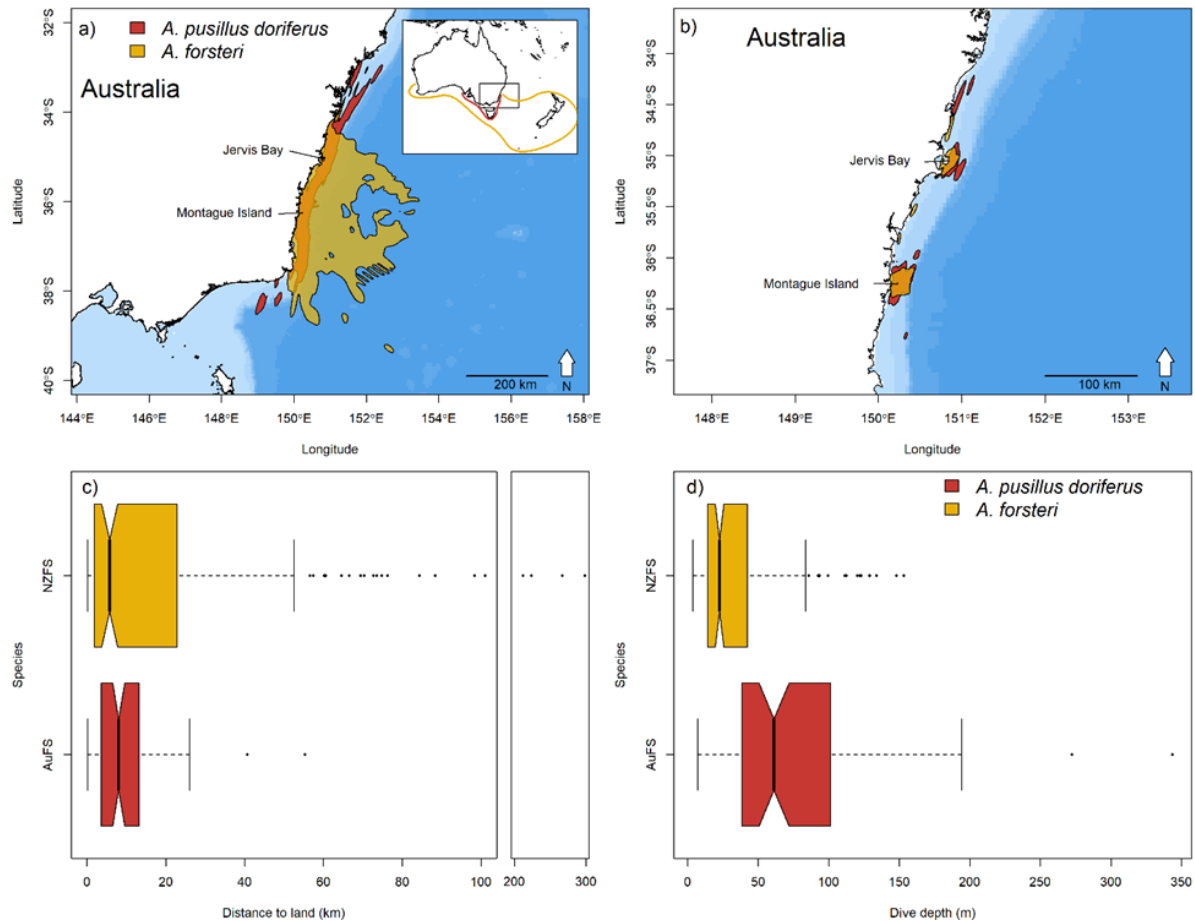


Figure 5.2 Isotopic and movement niche bi-plots (a and c) and respective posterior density plots (b and d) from Bayesian standard ellipse area (SEAb; solid lines 40%, dashed line 95%; density plots are of 40% SEAb) of male Australian (*Arctocephalus pusillus doriferus*; red) and New Zealand fur seals (*A. forsteri*; yellow). In isotope bi-plot, points represent isotope values from the ten most recent whisker samples from each individual. For clarity, a sample of 50 modelled ellipses (40% SEAb) per species are shown. Bi-plots represent the size and overlap of the niche space, and density plots compare size (similar niche size have more overlap) and variance among 40% SEAb estimates (height-width of density plot).

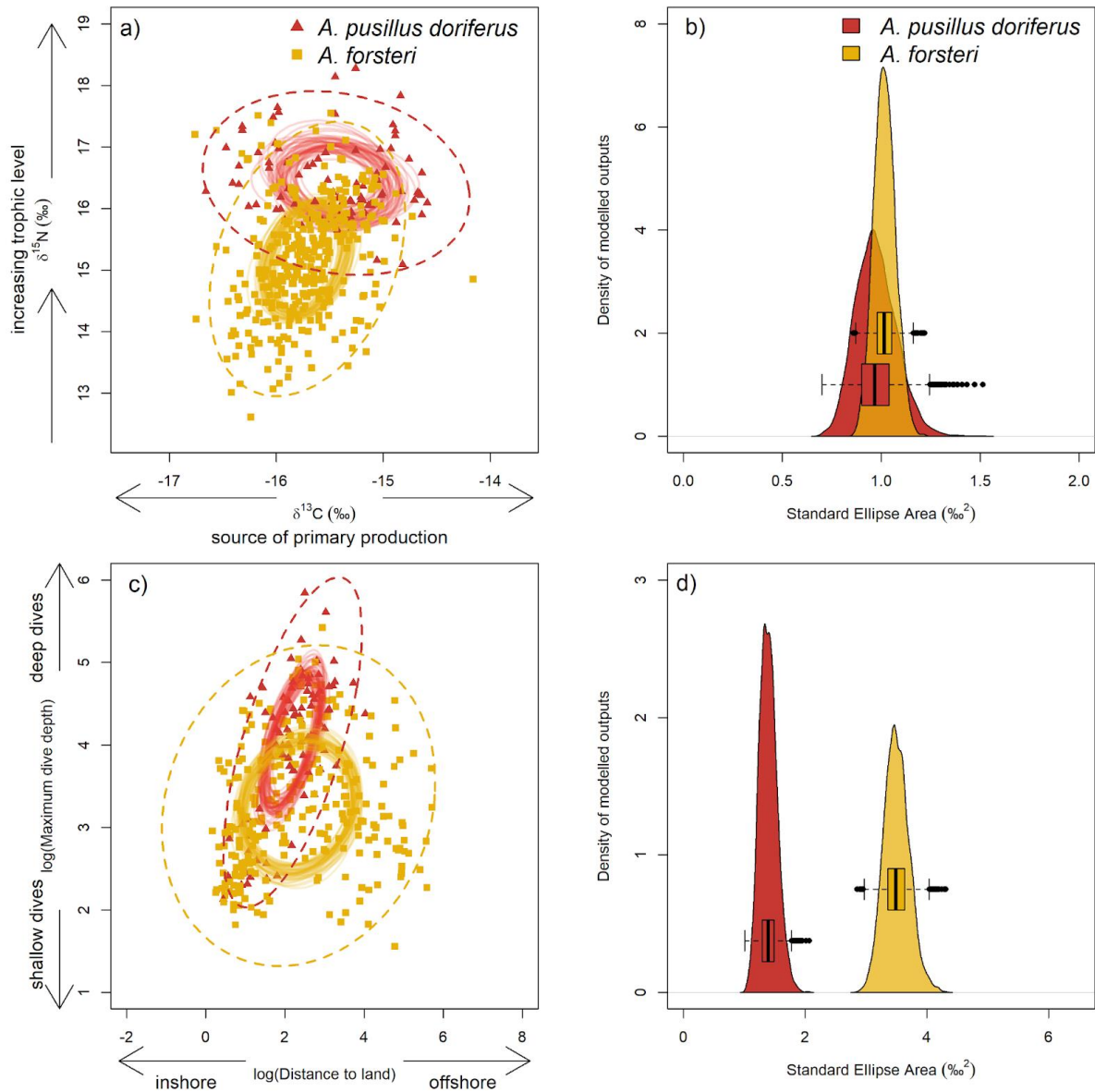


Table 5.1 Population-level isotope niche space statistics ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and movement niche space statistics (distance to land and dive depth), including Bayesian Standard Ellipse Area (SEAb), of male Australian (*A. pusillus doriferus*) and New Zealand fur seals (*A. forsteri*). Isotopic space calculated from 3 mm segments from one vibrissae per individual. Movement space calculated from weekly mean statistics per individual. Mean \pm SE and range are calculated at the individual level (i.e. mean of each individual's average value across its whisker segments or weekly movement data). Movement space parameters were log-transformed, and subsequently their back-transformed estimates of means are accompanied by 95% confidence intervals (CI).

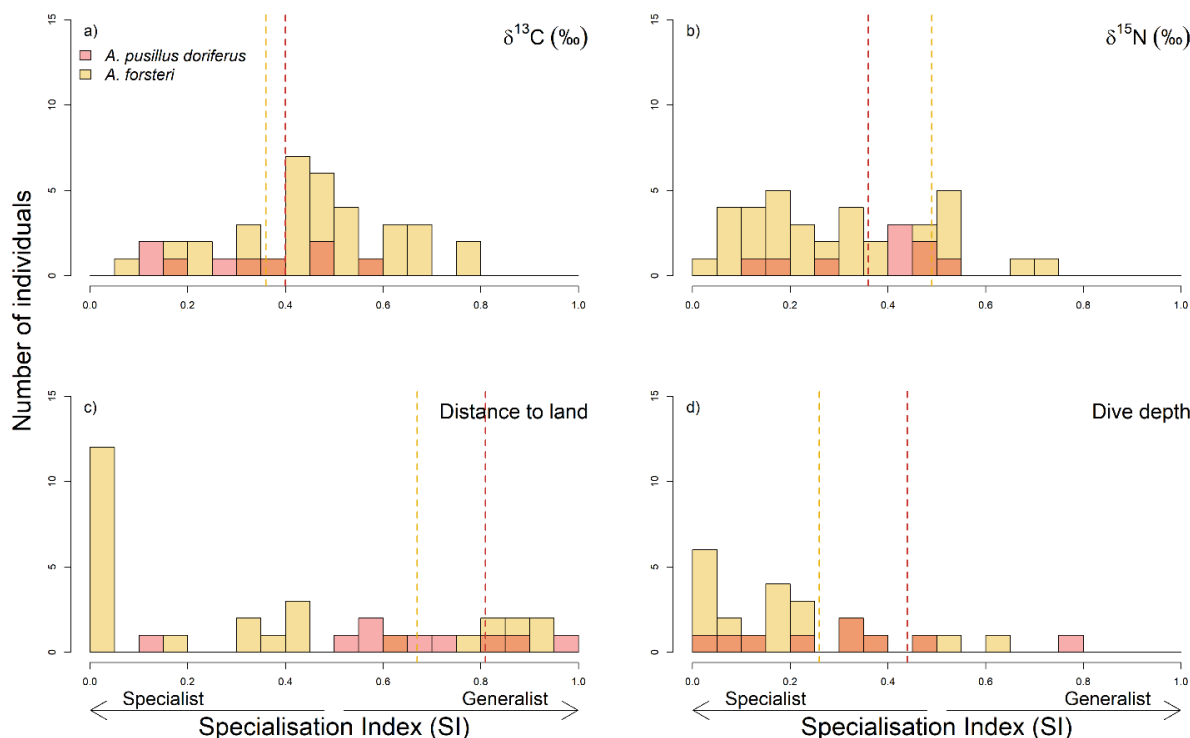
		<i>A. pusillus doriferus</i>	<i>A. forsteri</i>
N individuals with isotope data		9	35
$\delta^{15}\text{N}$ ‰ values	mean \pm se	16.4 \pm 0.2	15.2 \pm 0.2
$\delta^{13}\text{C}$ ‰ values	mean \pm se	-15.4 \pm 0.1	-15.7 \pm 0.1
SEAb size ‰ ²	40%, mean \pm se (n = 50) 95% (n = 1)	1.0 \pm 0.11 5.8	1.0 \pm 0.04 6.1
SEAb overlap (%)	mean \pm se (n = 50)	5.8 \pm 1.04	5.7 \pm 4.12
SEAb width (isotope range)	$\delta^{13}\text{C}$ ‰ $\delta^{15}\text{N}$ ‰	-16.2 to -14.7 15.6 to 17.4	-16.3 to -15.2 14.1 to 16.2
N individuals with location data		10	39
Distance to land (km)	mean CI	6.3 3.4 – 11.0	6.3 1.4 – 20.6
Size and overlap of 95% UD	Size (km ²) Overlap (%)	17,478 71	72,375 17
Size and overlap of 50% UD	Size (km ²) Overlap (%)	1577 52	1109 73
N individuals with dive data		10	35
Maximum dive depth (m)	mean CI	58.1 35.5 – 85.5	25.3 9.0 – 68.1
SEAb size ‰ ²	40%, mean \pm se (n = 50) 95% (n = 1)	1.4 \pm 0.2 8.2	3.5 \pm 0.2 20.9
SEAb overlap (%)	mean \pm se (n = 50)	48.3 \pm 10.0	19.6 \pm 4.4
SEAb width (movement range)	Distance to land (km) Dive depth (m)	2.3 - 23.5 17.4 – 164.4	1.0 – 53.1 9.2 – 67.3

Individual Specialisation

The individual specialisation index (SI) of $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values and dive depth for AuFS and NZFS indicated these male fur seals were specialists in each of these niche dimensions ($P < 0.001$; Table 5.2). However, there was high variability in the SI among individuals for each species (Fig. 5.3), with some individuals tending towards the generalist end of the spectrum but most individuals at the specialist end of the spectrum. For distance to land, AuFS were generalists and NZFS were specialists, though both species had high variability in the SI among individuals with their values spread across the SI spectrum (Fig. 5.3). There were a relatively large number of highly specialised male NZFS for 'distance to land'; 12 individuals with SI values < 0.05 . These individuals include some who travelled off the continental shelf into deep water during each week, and other individuals who only moved between islands and the coastline (i.e. remained very close to land).

There were no correlations between an individual's SI in any dimension and its body length (Appendix 5.4); all $P > 0.05$. An individual's SI in one dimension (e.g. $\delta^{13}\text{C}$) was not related to its SI in another dimension (e.g. $\delta^{15}\text{N}$).

Table 5.2 Density plot of specialisation index (SI) in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each individual male Australian (*A. pusillus doriferus*; red) and New Zealand fur seals (*A. forsteri*; yellow). Vertical dotted lines show the population-level SI (from Table 5.1).



5.4 Discussion

Our results indicate that male Australian and New Zealand fur seals that are reoccupying the north-eastern extent of their respective ranges share broad ecological niche space but have significant partitioning in isotopic and movement dimensions of their niche, despite expectations of low drivers of competition. Given their broad niches, it was not surprising that males of both species showed high levels of individual specialisation in isotopic and movement space, particularly given their increased intraspecific competition over recent decades. Highly specialised individuals in isotopic space were not necessarily highly specialised in movement space, further emphasising their diverse strategies for niche partitioning. There was support for a link between foraging mode and individual specialisation, as for other fur seals, though unexpected high specialisation for epipelagic NZFS males suggests exceptions be apparent among marginal populations of a species' distribution.

Niche partitioning

As populations increase in size so can intraspecific competition for the most valuable food resources, which should drive individuals to broaden their niche (diet and/or foraging behaviour) to maintain optimal foraging (MacArthur & Pianka 1966; Roughgarden 1972; Bolnick 2001; Svanbäck & Bolnick 2007). Among marine predators, increased intraspecific competition has been associated with broader dietary niche and foraging niche attributed to the need to access different prey, prey at deeper depths and greater distances from their colony (Lewis et al. 2001; Kuhn et al. 2014; Ratcliffe et al. 2018). Along the same lines, subantarctic fur seals in a large population that has reached carry capacity had a wider niche than those from a smaller population that is still increasing (Kernaléguen et al. 2015a). In contrast, at their range margin where population sizes are still small, these male fur seals continued to display a broad dietary niche ($\delta^{15}\text{N}$ values) and movement niche (horizontal and vertical behaviour), and this is consistent with an earlier dietary analysis of fur seal scats (Hardy et al. 2017). Alternatively, to enhance intraspecific competition individuals may expand their foraging niche in response to interspecific competition or decreased availability of most valuable food resources (Chiaradia et al. 2003; Moleón et al. 2009; Prati et al. 2021) and both these alternatives typically characterise a species' range margins (MacArthur 1984; Case et al. 2005; Guo et al. 2005). Therefore, individuals may need to maintain a broad niche when moving between their range core and margins to mitigate different types of competition (intra and interspecific) and variable abundance of favourable prey throughout a species' distribution.

Interspecific competition was expected at this range margin, where two congeneric species live in sympatry. However, their populations are small so interspecific competition should be low thereby allowing these species to share the most profitable resources and overlap niche space. These male fur seals did indeed overlap in the prey source of primary productivity ($\delta^{13}\text{C}$ values), trophic level of their

prey ($\delta^{15}\text{N}$ values; Kelly 2000; Davenport & Bax 2002) and horizontal and vertical niche space, consistent with males of both species being high order predators that frequently return to land to rest and digest, and have foraging habitat at a range of depths (Page et al. 2005a; Hardy et al. 2017; Knox et al. 2017; Salton et al. 2021). Although the two species had overlapping niches, they had clear partitioning in their dietary niche and dive behaviour, with AuFS typically feeding on higher trophic level prey than NZFS (based on $\delta^{15}\text{N}$ values; Davenport & Bax 2002) and generally diving deeper than NZFS. Similar means of niche partitioning (different dietary composition and foraging behaviour) were found between sympatric female AuFS and NZFS at a breeding colony (Hoskins et al. 2017) and between sympatric male AuFS and NZFS at a New Zealand fur seal breeding colony (Page et al. 2005a). However, at breeding colonies this partitioning is expected because the larger populations suggest that absolute competition (intra and interspecific competition combine) should be higher compared to the small populations at this range margin (Shaughnessy et al. 2015; McIntosh et al. 2018b). It is possible that competition in the core of their range drove niche partitioning ancestrally, and neither species is plastic enough in foraging to relax their constraints when seasonally present at the range margin, even in the absence of resource limitations.

Individual specialisation

Niche expansion can occur when all individuals of a population exploit a wider niche or via increased between-individual variation. The latter is termed the Niche Variation Hypothesis (Van Valen 1965), and has supporting quantitative evidence from numerous taxa (Bolnick et al. 2007). Consistent with this hypothesis, fur seal populations that feed only on a few prey species are often made up of generalist individuals and populations with a broad dietary niche often have high levels of individual specialisation (Kernaléguen et al. 2015a; Riverón et al. 2021), including Australian fur seals (Kernaléguen et al. 2015b; this study) and New Zealand fur seals (this study). In addition to the Niche Variation Hypothesis, the level of individual specialisation in a population can be positively related to population density (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007; Tinker et al. 2008), presumably because smaller populations have less intraspecific competition driving niche expansion, which appears to be the case for some fur seals (Franco-Trecu 2014; Kernaléguen et al. 2015a). Therefore, individuals at range margins, within small populations, may have lower individual specialisation than conspecifics at the range core. Contrary to this, the level of individual specialisation in $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values among male AuFS at this range margin (0.40 and 0.36, respectively) was higher (more specialised) compared to male AuFS in the core of the species' range (0.93 and 0.56, respectively; Kernaléguen et al. 2015b). This disparity could be associated with the shorter temporal scale used to measure individual specialisation in our study (10 whisker segments, rather than whole whiskers), which often exaggerates the apparent level of individual specialisation (Araújo et al. 2007; Novak & Tinker 2015; Kernaléguen et al. 2016). Alternatively, it could provide further support for behavioural differences between disperses and

residents, with disperses having high heterogeneity in behaviour that supports population expansion into novel environments (Cote et al. 2010).

The level of specialisation in a niche dimension varied among individuals, suggesting disproportionate effects of the drivers of specialisation on individuals. Accordingly, we tested whether the level of individual specialisation in one niche dimension was linearly related to the specialisation in other niche dimensions, and found this was not the case for any of the four niche dimensions. Therefore, a seal may have a highly specialised dietary niche ($\delta^{15}\text{N}$ values) but forage across a range of habitats to access their prey (less specialised movement niche). Alternatively, a seal may principally forage epipelagically in inshore habitat (specialised movement niche) on a broad range of prey (less specialised dietary niche). This suggests that individuals respond to the drivers of specialisation in different ways, potentially specialising in various niche dimensions but not necessarily all of them. This emphasises the behavioural plasticity of individuals to selection pressures, and highlights the importance of considering multiple niche dimensions when assessing ecological drivers and consequences of individual specialisation.

While species-specific foraging modes were apparent (i.e. benthic versus pelagic), both species were specialists in isotopic and movement space based on Monte Carlo resampling tests for a null, generalist population. Benthic environments typically have a high diversity of prey, with each prey species having relatively low abundance, compared to the low diversity of pelagic species that are highly abundant (Gray 1997). Therefore, the benthic environment offers greater opportunity and motivation (e.g. to alleviate competition for limited resources) for predators to specialise on particular prey, whereas the pelagic environment has less potential and perhaps motivation for individuals to diverge from the average population diet. Empirical evidence shows pelagic foraging fur seals using offshore habitats have narrow isotopic niche, with generalist individuals and low specialisation, while benthic foraging fur seals using inshore habitats have a broader population isotopic niche with specialist individuals (Riverón et al. 2021). In our study, male AuFS were consistent with that predicted from elsewhere, displaying benthic inshore foraging and consisting of a population of individual specialists. However, male NZFS movement behaviour was typical of epipelagic foraging, and they also had high individual specialisation. These male NZFS exploited predominantly inshore but also offshore habitats, and some male NZFS remained close to the coast displaying an apparent benthic foraging mode. Ecological diversification often occurs in marine mammals that foraging in inshore areas (Wolf et al. 2008; Chilvers & Wilkinson 2009; Aurióles-Gamboa et al. 2013), perhaps due to the greater diversity of isotopic pathways in coastal environments (Ray 1991) and greater habitat complexity (Sequeira et al. 2018). Given these populations are small, perhaps there is some interspecific competition release that creates space for some male NZFS to exploit the benthic and inshore habitats, thereby increasing potential for inter-individual diversification. This may change as populations increase, and male AuFS come to dominate the inshore environment and NZFS forage more epipelagically further from the coast (Page et al. 2006).

Ecological Implications

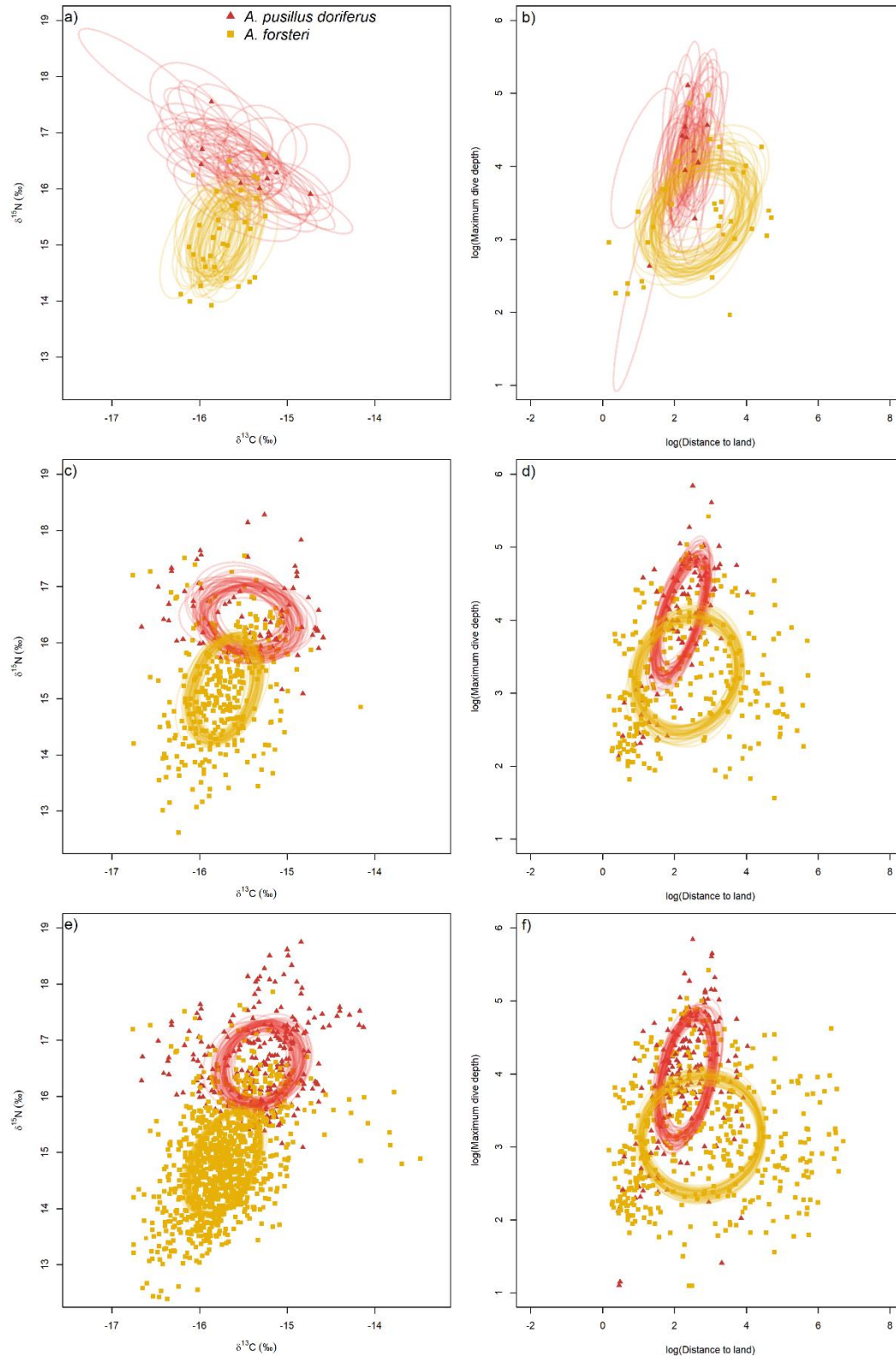
As species expand their range into new habitat they must compete for resources with the native community, which already compete among themselves. The size of a community can influence the level of niche overlap, with increasing number of species associated with less overlap (Pianka 1974), and if the community is sufficiently large it can prevent newly introduced species from becoming established (Case 1990). This has implications for the success of biological invasions (MacArthur 1984; Freed & Cann 2014), and potentially the recovery and range expansion associated with conservation efforts of a native species. Given the smaller populations of both species at this expanding range margin, there was potential for high niche overlap associated with competition release. Somewhat contradictory, the niche overlap and individual specialisation between and within these male fur seals suggests there is available niche for each of these species and potential for further mitigation of inter and intraspecific competition, and therefore potential for population growth and range expansion. Indeed, prior to this study both populations of fur seals in Australia had positive population trajectories (Shaughnessy et al. 2015; McIntosh et al. 2018b). Ongoing assessments of niche partitioning and individual specialisation within and between these sympatric and congeneric species at this range margin will further develop ecological understanding of the mechanisms for successful population growth and range expansion, and should consider the role of a rapidly warming environment.

Individual specialisation and behavioural plasticity provide opportunities for a population to adapt to environmental change (Brent 1978; Bolnick et al. 2003; Tuomainen & Candolin 2011; Edelaar & Bolnick 2019). Accordingly, the high individual specialisation amongst these male fur seals may contribute to their successful re-occupation of this margin of their range amidst extreme rate of ocean warming (Ridgway 2007) and a dense human population. However, species have physiological limits, for example otariids in temperate regions are sensitive to high temperatures (Gentry 1973), and thermal energetic costs are often higher for pups and juveniles (Liwanag 2010). Species are also limited by habitat needs, in this case particular terrestrial features at haul-out and breeding sites (Bradshaw et al. 1999; Stevens & Boness 2003), and several of their haul-out sites at this margin of their range are currently not zoned as protected areas (Salton et al. 2021). Therefore, while males have reoccupied this part of the species' range, these additional limitations could influence the successful reestablishment of a breeding population and future occupation by males. Furthermore, ocean warming is altering prey distribution and abundance and thereby the habitat uses of marine predators (Amador-Capitanachi et al. 2020; Evans et al. 2020; Niella et al. 2020; d'Entremont et al. 2021; Florko et al. 2021; Niella et al. 2021). There have been recent losses of habitat and habitat-forming species at this margin of the seals' range (Wernberg et al. 2011). Thus, while these predators demonstrate capability to exploit a dynamic environment and a high level of adaptiveness to change, a rapidly warming environment presents several risks that could limit population growth and expansion at this margin of their range. These risks

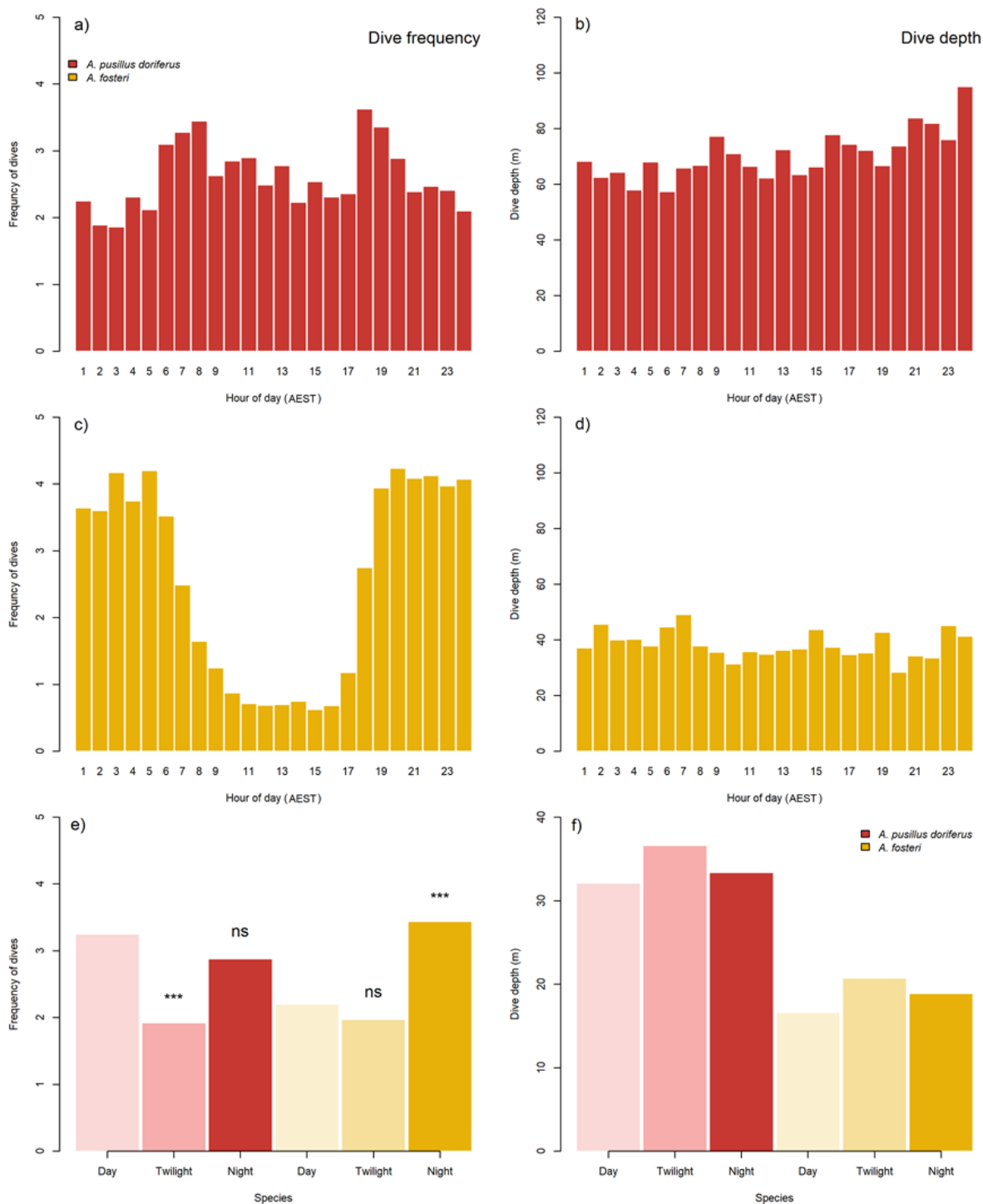
would compromise the success of current conservation efforts that have seen these species reoccupy parts of their historic range. To mitigate such compromises, we encourage actions that support species to adapt to climate change (Hobday et al. 2016; Roberts et al. 2017; Miller et al. 2018; Wilson et al. 2020).

5.5 Appendices

Appendix 5.1 Isotopic biplots for each of the four niche parameters for each male Australian (*A. pusillus doriferus*, red) and New Zealand fur seal (*A. forsteri*, yellow), calculated with three different datasets (one per row). Dataset 1: a) and b) average values per individual. Dataset 2: c) and d) first 10 whisker segments or first 10 weeks of movement data, which is used in the analysis and presented in Figure 1. Dataset 3: e) and f) all whisker segments and all weeks of movement data. Standard Ellipse Area (40%) showing first 50 draws for clarity.



Appendix 5.2 Different circadian patterns in dive frequency and but not dive depth between male Australian (*A. pusillus doriferus*, red) and New Zealand fur seals (*A. forsteri*, yellow). a) and c) dive frequency per hour of day (Australian Eastern Standard Time; AEST). b) and d) average dive depth per hour of day (mean per individual). e) and f) modelled values of dive frequency and dive depth, respectively, per diel period (mean individual, per week). Modelled significant differences relatively to reference factor level (diel period 'day') are represented by *** (P<0.001) or ns (not significant).



Appendix 5.3 Model results for diel pattern in dive frequency and dive depth (using means per week for each individual) of male Australian fur seals (*A. pusillus doriferus*) and New Zealand fur seals (*A. forsteri*), including models tested (top) and modelled fixed effects (bottom). Dive depth was log transformed to normalise residuals (log values presented). Levels of fixed effects were tested against the reference level 'Day'. Diel was not significant for dive depth, so the fixed effect levels were not tested.

		<i>A. pusillus doriferus</i>			<i>A. forsteri</i>		
Models tested							
Response	Fixed effects	logLik	AIC	P	logLik	AIC	P
Dive frequency	Diel	-1456.7	2931.4		-4897.6	9813.2	
	Null	-1471.8	2957.5	< 0.001	-4927.8	9869.6	< 0.001
Dive depth	Diel	-10065	20151		-29528	59076	
	Null	-10066	20149	0.399	-29530	59076	0.111
Modelled fixed effects							
Response	Diel period	Estimate (SE)	z	P	Estimate (SE)	z	P
Dive frequency	Day	3.2 (0.2)	21.4		2.2 (0.2)	11.9	
	Twilight	-1.3 (0.1)	-12.1	<0.001	-0.2 (0.1)	-1.7	0.082
	Night	-0.4 (0.3)	-1.3	0.202	1.2 (0.2)	7.4	<0.001
Dive depth	Day	3.5 (0.3)	na		2.9 (0.2)	na	
	Twilight	0.1 (0.2)	na		0.2 (0.1)	na	
	Night	0.04 (0.2)	na		0.1 (0.1)	na	

Appendix 5.4 Linear model results comparing individual specialisation indices of male Australian fur seals (AuFS) and New Zealand fur seals (NZFS) in isotopic space ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and movement space (Dive depth and Distance to land), and compared to their body size (Length).

Response	Predictor	Species	T value	P value
$\delta^{15}\text{N}$	Length	AuFS	-2.694	0.054
$\delta^{15}\text{N}$	Length	NZFS	-0.669	0.508
$\delta^{13}\text{C}$	Length	AuFS	-1.074	0.343
$\delta^{13}\text{C}$	Length	NZFS	0.968	0.341
Dive depth	Length	AuFS	-1.948	0.123
Dive depth	Length	NZFS	1.747	0.091
Dist. to land	Length	AuFS	0.906	0.416
Dist. to land	Length	NZFS	-1.962	0.059
$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	AuFS	1.217	0.291
$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	NZFS	1.745	0.091
Dive depth	$\delta^{15}\text{N}$	AuFS	1.366	0.244
Dive depth	$\delta^{15}\text{N}$	NZFS	-0.723	0.475
Distance to land	$\delta^{15}\text{N}$	AuFS	0.027	0.980
Distance to land	$\delta^{15}\text{N}$	NZFS	0.539	0.594
Dive depth	$\delta^{13}\text{C}$	AuFS	0.337	0.753
Dive depth	$\delta^{13}\text{C}$	NZFS	-1.321	0.196
Distance to land	$\delta^{13}\text{C}$	AuFS	0.681	0.533
Distance to land	$\delta^{13}\text{C}$	NZFS	-1.408	0.169
Distance to land	Dive depth	AuFS	-1.271	0.273
Distance to land	Dive depth	NZFS	0.045	0.964

Appendix 5.5 Summary of male fur seals (Australian, aufs; New Zealand, nzfs) sampled (i.e. whisker) and/or tracked (with a Wildlife computer Mk10, Jervis Bay, 'jb'; or SMRU, Montague Island, 'mi') between 2011 and 2014. Whiskers were cut into 3mm segments: some whole whiskers others only the ten segments closest to the root of the whisker (most recent). Whiskers were sampled when a tracking device was attached, unless it was a dead seal (had died within days of collecting the whisker).

ID	Location	Species	Year	Body length (cm)	Date deployment/sample	Data types	Deployment duration (d)	N# dives
JB-1-2011	jb	nzfs	2011	100	21/06/2011	Loc	201	NA
JB-2-2011	jb	nzfs	2011	80	23/06/2011	Loc	30	NA
JB-3-2011	jb	nzfs	2011	75	4/07/2011	Loc	91	NA
JB-4-2011	jb	nzfs	2011	90	7/07/2011	Loc	60	NA
JB-2-2012	jb	nzfs	2012	100	28/06/2012	SI, Loc, Div	166	4439
JB-3-2012	jb	nzfs	2012	90	28/06/2012	SI, Loc, Div	113	2541
JB-8-2013	jb	nzfs	2013	70	19/07/2013	SI, Loc, Div	166	3828
JB-11-2013	jb	nzfs	2013	90	10/07/2013	SI, Loc, Div	187	3314
JB-12-2013	jb	nzfs	2013	150	11/07/2013	SI, Loc, Div	154	1844
JB-15-2013	jb	nzfs	2013	100	30/07/2013	SI, Loc, Div	10	40
JB-16-2013	jb	nzfs	2013	100	9/08/2013	SI, Loc, Div	141	3810
JB-17-2013	jb	nzfs	2013	110	22/08/2013	SI, Loc, Div	168	1458
JB-10-2013	jb	nzfs	2013	90	9/07/2013	SI, Loc, Div	118	2328
JB-7-2013	jb	nzfs	2013	100	19/06/2013	SI, Loc, Div	207	6229
JB-14-2013	jb	nzfs	2013	100	26/07/2013	SI, Loc, Div	106	2017
JB-9-2013	jb	aufs	2013	250	20/06/2013	SI, Loc, Div	156	3662
JB-13-2013	jb	aufs	2013	200	25/07/2013	SI, Loc, Div	190	3836
MI-3-2012	mi	nzfs	2012	162	23/06/2012	SI, Loc, Div	259	674
MI-4-2012	mi	nzfs	2012	183	23/06/2012	SI, Loc, Div	233	887
MI-1-2012	mi	nzfs	2012	154	12/06/2012	SI, Loc, Div	178	665
MI-2-2012	mi	nzfs	2012	152	12/06/2012	Loc, Div	146	1071
MI-5-2012	mi	nzfs	2012	165	23/06/2012	Loc, Div	69	340
MI-7-2012	mi	nzfs	2012	185	23/06/2012	SI, Loc, Div	67	226
MI-60-2012	mi	nzfs	2012	NA	21/11/2012	SI	NA	NA
MI-16-2013	mi	nzfs	2013	167	28/05/2013	SI, Loc, Div	120	558
MI-4-2013	mi	nzfs	2013	165	25/05/2013	SI, Loc, Div	115	370
MI-3-2013	mi	nzfs	2013	163	25/05/2013	SI, Loc, Div	94	367
MI-1-2013	mi	nzfs	2013	162	25/05/2013	SI, Loc, Div	50	112
MI-5-2013	mi	nzfs	2013	160	25/05/2013	SI, Loc, Div	49	234
MI-9-2013	mi	nzfs	2013	155	26/05/2013	SI, Loc, Div	29	234
MI-7-2013	mi	nzfs	2013	167	26/05/2013	SI, Loc, Div	25	164
MI-12-2013	mi	nzfs	2013	170	27/05/2013	SI, Loc, Div	17	122
MI-8-2013	mi	nzfs	2013	NA	26/05/2013	SI	NA	NA
MI-2-2014	mi	nzfs	2014	164	2/08/2014	SI, Loc, Div	35	18
MI-1-2014	mi	nzfs	2014	174	2/08/2014	SI, Loc, Div	15	70
MI-5-2014	mi	nzfs	2014	138	3/08/2014	SI, Loc, Div	91	191
MI-4-2014	mi	nzfs	2014	176	3/08/2014	SI, Loc, Div	70	137
MI-3-2014	mi	nzfs	2014	155	3/08/2014	SI, Loc, Div	23	38
MI-8-2014	mi	nzfs	2014	157	4/08/2014	SI, Loc, Div	78	183
MI-7-2014	mi	nzfs	2014	155	4/08/2014	SI, Loc, Div	58	193
MI-6-2014	mi	nzfs	2014	172	4/08/2014	SI, Loc, Div	30	50
MI-9-2014	mi	nzfs	2014	150	5/08/2014	SI, Loc, Div	61	184
MI-10-2014	mi	nzfs	2014	162	5/08/2014	SI, Loc, Div	34	104
MI-6-2012	mi	aufs	2012	180	24/06/2012	SI, Loc, Div	141	876
MI-9-2012	mi	aufs	2012	177	25/06/2012	Loc, Div	109	480
MI-8-2012	mi	aufs	2012	190	24/06/2012	Loc, Div	62	253
MI-6-2013	mi	aufs	2013	173	25/05/2013	SI, Loc, Div	185	1223
MI-10-2013	mi	aufs	2013	180	26/05/2013	SI, Loc, Div	166	1114
MI-14-2013	mi	aufs	2013	200	28/05/2013	Loc, Div	152	338
MI-15-2013	mi	aufs	2013	180	28/05/2013	SI, Loc, Div	110	638
MI-13-2013	mi	aufs	2013	NA	27/05/2013	Loc, Div	47	352
MI-11-2013	mi	aufs	2013	NA	27/05/2013	SI	NA	NA
MI-2-2013	mi	aufs	2013	NA	25/05/2013	SI	NA	NA

6. Chapter Six

Protected area use by two sympatric marine predators repopulating their historical range

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Photo credit: Marcus Salton

Abstract

As large carnivores recover from over-exploitation, managers often lack evidence-based information on species habitat requirements and the efficacy of management practices, particularly where species repopulate areas from which they have long been extirpated. We investigated the movement and habitat use of two semi-aquatic carnivores (Australian fur seals *Arctocephalus pusillus doriferus* and New Zealand fur seals *A. forsteri*) at the northern end of their distributions in Australia, where after long absence both are recolonising their historic range. We also assess male fur seal habitat use overlap with terrestrial and marine protected areas (PAs). While at the margin of the range during winter and early spring, the males remained inshore close to terrestrial sites and where interactions with humans often occur. From early spring, the males from the range margin showed uniform movement toward colonies in the core of the species' range prior to their breeding seasons. This contrasts with males tracked from the core of the species' range that return periodically to colonies during the year, and highlights the importance of range-wide monitoring of a species to inform conservation planning. Habitat use of some males included over 90% of a marine PA at the margin of the species' range. Most terrestrial haul-outs used were within terrestrial PAs, while sites not protected were on the margin of the range. Despite wide-ranging habits, their dependence on coastal sites, where human access and activities can be regulated and more readily enforced, suggests terrestrial and marine PAs will continue to play an important role in managing the recovery of these fur seals.

6.1 Introduction

Conservation efforts have increased the population size of many large carnivores, and have either expanded their ranges or allowed recovery into historical ranges (Chapron et al. 2014; Gompper et al. 2015; Karamanlidis et al. 2015; Martinez Cano et al. 2016). These changes often result in increased conflicts between humans and carnivores and among humans (e.g., conservationists and industries) (Treves & Karanth 2003; Miller et al. 2013). Interactions at expanding range margins can be challenging for humans, who are more often ill prepared to manage such change (Ciucci & Boitani 1998; Trouwborst et al. 2015; Morehouse & Boyce 2017). While lethal methods are often deployed to alleviate conflict, they are counter-productive for conservation of recovering species and do not necessarily reduce conflicts (Stahl et al. 2001; Treves 2009). Non-lethal management alternatives (e.g. Shivik 2004) are important to resolve human-carnivore conflicts and create a future where humans and competing wildlife coexist (Woodroffe et al. 2005). Accordingly, there is growing interest in identifying habitat selection of large carnivores and locating potential ‘conflict hotspots’ (Miller 2015). This can help prioritise limited management resources into areas with high-risk human-carnivore interactions. In this study, we investigate the movements of individuals from recovering populations of large semi-aquatic carnivores, fur seals, which are often seen by fishermen as competitors. We focus on a region where two species have recently greatly expanded their geographic ranges after a long absence resulting from sealing in the 19th and early 20th Century. We quantify habitat use and compare marine and terrestrial areas in relation to their protected status for conservation planning.

Protected areas are a widely used, multi-purpose management tool (Watson et al. 2014b). Protected areas may conserve biodiversity and ecosystem functions, protect natural and cultural features, preserve human assets (e.g. forests and water resources) and minimise human impacts. By regulating human access and activities, protected areas can play a role in mitigating negative interactions with wildlife and aid the recovery of large carnivores (Linnell et al. 2005a; Chapron et al. 2014; Santini et al. 2016a). Protected areas are used in terrestrial and marine contexts and when positioned along a coastline they can assist in managing human impacts on adjacent marine and terrestrial habitats (Stoms et al. 2005). These areas are typically not designed specifically to mitigate interactions between humans and wide-ranging species, because their small boundaries do not sufficiently capture the species’ large foraging range (Hooker et al. 2011). However, despite many large carnivores ranging widely to feed, they often use discrete areas for essential activities such as breeding, moulting, resting, predator avoidance, and for these activities, discrete protected areas may have beneficial effects (Huon et al. 2015; McAllister et al. 2015; Pérez-Jorge et al. 2015).

Protected area design often includes multiple use zoning where human activities are restricted to different extents depending upon intent. For example, within Australia’s marine park network there may be four or more tiers of protection zone, ranging from no-take zones to areas where only certain types

of fishing (e.g. commercial) are prohibited (Roberts et al. 2018). These zones can focus human activities into areas where they will cause least disruption to animals, whilst allowing compatible activities to continue. With effective mitigation of negative human-carnivore interactions, protected areas can help sustain populations (Barnes et al. 2016), directly improve their demographic parameters (Gormley et al. 2012), and support ecosystem recovery (Prato et al. 2013). This suggests that conservation management of carnivores moving back into their historical range could be improved if existing protected areas with suitable habitat for essential activities by these carnivores could be identified.

Semi-aquatic species have a strong reliance on coastal habitats where we now also have high density human populations, so it is not surprising that they have a long history of interactions with humans. Many species have been harvested, or culled to reduce fisheries and aquaculture interactions, but are now recovering (Gerber & Hilborn 2001; Kirkwood & Goldsworthy 2013; Magera et al. 2013). In Australia, the New Zealand fur seal *Arctocephalus forsteri* (also Long-nosed fur seal, Shaughnessy & Goldsworthy 2015) and the Australian fur seal *A. pusillus doriferus*, are both recovering from past exploitation (Littnan & Mitchell 2002; Kirkwood et al. 2010; Shaughnessy et al. 2015; McIntosh et al. 2018b). Both species are protected by national law under the Environmental Protection and Biodiversity Conservation Act 1999 and are the subjects of a national strategy to minimise adverse interactions with human activities (National Seal Strategy Group). As with other semi-aquatic species, interactions between fur seals and humans occur on land and at sea, with fisheries, aquaculture, and tourism industries, and the general public (Kirkwood et al. 2003; Shaughnessy et al. 2003; Hamer & Goldsworthy 2006; Robinson et al. 2008b), and are likely to increase as seal populations continue to recover and industries develop (Schumann et al. 2013). These interactions can result in economic loss or injury to humans, and stress, changed behaviour, injury or death of seals. Therefore it is important to have accurate information to correctly assess seal-human interactions and their consequences as seal populations recover (Costalago et al. 2019).

Currently there is little information on the movements and habitat use of the two fur seal species in Australasia on which to base management plans, as most information is focused on females (Harcourt et al. 2001; Harcourt et al. 2002; Littnan & Arnould 2002; Page et al. 2006; Arnould & Kirkwood 2007; Baylis et al. 2008a; Baylis et al. 2008b; Baylis et al. 2012; Kirkwood & Arnould 2012; Hoskins & Arnould 2013, 2014; Hoskins et al. 2015; Hoskins et al. 2017). Most studies on male movements and habitat use are from the core of the species' range (Kirkwood et al. 2006; Page et al. 2006; Kernaléguen et al. 2015b; Knox et al. 2017, 2018). These studies have focused on foraging behaviour and at-sea habitat use: Australian fur seals occupy mostly shelf waters (Kernaléguen et al. 2015b; Knox et al. 2017) and New Zealand fur seals occupy a combination of shelf and pelagic waters (Page et al. 2006). Their at-sea movements can be strongly associated with fishing activities, such as fish farms, which generate a predictable source of food (Robinson et al. 2008a). While there is some segregation in behaviour and

foraging niche between these two fur seal species (Page et al. 2005a; Page et al. 2006; Hardy et al. 2017; Hoskins et al. 2017), both interact similarly with human activities and accordingly management practices tend not to differentiate between them. With studies focused on the foraging behaviour and broader habitat use (e.g. benthic versus pelagic), there is limited information on how seals use discrete terrestrial 'haul-out' sites and the waters adjacent to those sites, where interactions with tourism and recreational activities often occur, and can have lethal consequences (Back et al. 2018). Importantly, movements and habitat use of male fur seals at the periphery of both species' geographic range are unknown: this is the case in New South Wales, along the east coast of Australia where the population is growing and a breeding population recently established (Warneke 1975; Warneke 1982; Irvine et al. 1997; Shaughnessy et al. 2001; Littnan & Mitchell 2002; Kirkwood et al. 2010; McIntosh et al. 2014; Hardy et al. 2017). This continuing expansion on the margin of their range is therefore likely to see an increase in human-wildlife conflict, and humans appear to be less experienced and prepared for this type of conflict (Shaughnessy et al. 2008).

The east coast of Australia is subject to significant coastal development and human use of marine resources. Networks of marine protected areas have been established to protect representative marine habitats and biological diversity, and maintain ecosystem processes (Lynch et al. 2013), but not designated specifically to protect seals. As fur seals have expanded northward along the east coast, they have established haul-outs within one of these marine protected areas, Jervis Bay Marine Park (JBMP). The seals are now seasonally abundant in JBMP (Burleigh et al. 2008b), but _ it is unclear what habitats they require and whether these habitats are within existing marine and terrestrial protected areas.

This study investigates the on-land and at-sea movements and habitat use of fur seals from two species that reside in the expanding margin of their range. By evaluating the frequency of visitation to different habitats, we identify areas likely to be important to the seals and where interactions with humans could be most acute. By overlaying haul-out site use and foraging ranges with the distribution of terrestrial and marine protected areas, we assess whether important areas used by seals at the margin of their range are receiving protection. The seals at this range margin are seasonally abundant, so the tracking study also aims to determine how long the seals are in residence and where they go when they leave. This may help conservation managers to identify habitats into which the population might expand and so connectivity between core and periphery populations is also investigated.

6.2 Methods

Animal handling and data collection

The movements of male New Zealand (NZFS; *Arctocephalus forsteri*) and Australian fur seals (AuFS; *Arctocephalus pusillus doriferus*) from Lamond Head, Jervis Bay, Australia (35°3'S, 150°50'E) (Fig. 6.1) were recorded with Mk10-AFs Fastloc-GPS devices (Wildlife Computers, Redmond, WA, USA; 105 × 60 × 20 mm, 240 g). Individuals were selected based on their proximity to a suitable access point to their rocky platform terraces at the base of a 30-meter high cliff face. Species were distinguished by their pelage, facial structure and cusps on their post-canine teeth (Kirkwood & Goldsworthy 2013). To attach the device, each seal was sedated with a light intra-muscular injection of zoletil (dose rate based on estimated seal weight was 1 to 1.5 mg/kg) that was delivered remotely with the aid of a pneumatic dart-gun, then approached and restrained in a catch net before being maintained under sedation with a mix of oxygen and isoflurane (approximately 1.5% to 2% isoflurane; adjusted as required) delivered via a portable vaporiser (Gales & Mattlin 1998). While sedated, seals were measured using standard methods (Kirkwood et al. 2006) and the telemetry device glued to the dorsal midline of each seal with a quick-setting epoxy (Araldite® K-268, Huntsman Advanced Materials, Australia; Quick Set Epoxy Resin #850-940, RS Components, Australia). Measurements were used to approximate the life stage of individuals (juvenile or adult) (Warneke & Shaughnessy 1985; Arnould & Warneke 2002; McKenzie et al. 2007a; McKenzie et al. 2007b). Deployments occurred in 2011, 2012 and 2013 from June to August, when seal numbers ashore tend to increase (Burleigh et al. 2008b). The devices transmitted GPS location (collected at 2-minute intervals, and median fix rate received via satellite transmission was 1 fix per 1.5 hours), behaviour data (e.g. dive and surface interval events, including their duration) and histogram summary data (e.g. percentage time at different depths and performing dives in 6-hr intervals) via the Argos satellite network (Collecte Localisation Satellites, France) until the battery failed or the tag fell off the seal. Fastloc-GPS locations were post-processed with satellite ephemeris and almanac data (Fastloc-GPS Solver version 1.0.56, Wildlife Computers, Redmond USA), which retained locations with at least four satellite acquisitions and an accuracy typically within 10s of meters (Dujon et al. 2014).

Movements on land and at-sea

To distinguish when a seal was at sea (i.e. on a “trip”) or on land (i.e. “hauled out”) we used a combination of data sources from the telemetry device to complete gaps in individual data sources. First, locations were pre-defined as wet or dry by the device, based on the conductivity sensor. Second, between location time-stamps we used behaviour data on single dives (movements below 2 m for greater than 10 s), post-dive surface intervals (i.e. an interval when the tag was at the surface and wet), and surface intervals ashore (i.e. an interval when the tag was at the surface and dry for 20 consecutive minutes and ceased when wet for > 30 s of a minute). Third, between location time-stamps and in the absence of behaviour data, we used histogram data summaries of time spent in dive and surface

behaviours and periods hauled-out. A seal was indicative of being at sea between time-steps where the device was recorded as wet, dives or post-dive surface intervals were recorded, and 100% of a 6-hr histogram summary was spent in dive and surface behaviours. A seal was indicative of being on land when the device was recorded as dry and where 100% of a 6-hr histogram summary was spent hauled out. To better estimate the time on land and at sea, the transition between land and water was estimated to occur at the mid-point between an interval on land and at sea. If no location was recorded while a seal was defined as being on land, a haul-out location (or 'site') was assigned based on the proximity of recent locations to known haul-out sites.

On-land locations were pre-processed to account for variance in location accuracy when quantifying terrestrial habitat use. Locations were visually clustered into groups or "sites", based on known site locations and applying a maximum 200 m diameter per group (which was the size of most point clusters and consistent with the size of known haul-out sites, M. Salton pers. comm.). Then we calculated the length of time on land, or "visits" ashore, the frequency of visits to each site, and the number of individuals visiting each site. Sites were defined as being either a non-breeding site or breeding site based on a recent pup census throughout the species' range (McIntosh et al. 2014) and knowledge from experienced observers (R. Kirkwood pers. obs. and A. Irvine pers. comm.).

At-sea habitat use was quantified using two parameters: trip duration and foraging range. Trip duration was the time elapsed between a departure and a return to land. The foraging range was quantified using Permissible Home Range Estimation (Tarjan & Tinker 2016). This method incorporates underlying environmental information into probability estimates to define a permissible foraging range. Land was used as the environmental predictor (i.e. proximity to coast/land). Distance-from-land values were measured as the Euclidean distance from the closest shoreline feature (GEODATA Coast 100K 2004, Geoscience Australia). Areas on land were assigned a distance value of zero. The distance-from-land values were log-transformed to normalize the empirical data distribution. The smoothing parameter was calculated using the univariate plug-in selector of Wand & Jones (1994) for the distance-from-land values, employed in the R package *ks* v1.8.13 (Duong 2013). Probability values were estimated across two scales depending on location as a compromise between resolution and processing time: (i) a 500 by 500 m grid for areas <40 km from shore, and (ii) a 5,000 by 5,000 m grid for areas >40 km from shore. The at-sea distribution for each individual was quantified at the margin of the range (i.e. New South Wales, at the edge of the breeding range and where several haul-out sites are established) and core of the range (where numerous breeding sites are located) using the 90% utilisation distribution (home range; HR) and 50% utilisation distribution (core range; CR). To test change in foraging trips and the size of the distributions between the margin and core of their range, we used a Student's t-test and a Wilcoxon's test, respectively, with the latter based on paired individuals (i.e. those we recorded distributions in both parts of the range) and accounted for non-normal distributions and unequal

variance. The variability among individuals was assessed by calculating the total area used by all individuals and the percentage of that area used by two or more individuals (e.g. the area where at least two distributions overlapped).

Overlap with protected areas

We used different approaches to assess whether terrestrial and at-sea habitat used by the seals overlapped with protected areas, because haul-out sites were discrete locations while at-sea areas were spatial areas (i.e. polygons). Haul-out sites were classed as inside or outside a protected area, where a protected area is any spatial management area listed under the IUCN global protected area programme (Dudley 2008). The primary interest was at the margin of the range, but we also assessed how seal used sites and the overlap of sites with terrestrial protected areas when the seals dispersed from the margin of the range. For at-sea habitat use, we quantified how much of a fur seals' foraging range overlapped with the marine protected area that was consistently occupied by the seals at the margin of the range: Jervis Bay Marine Park (JBMP). All data were processed and analysed with R v2.15.1 (R Development Core Team). Means are presented with \pm standard error.

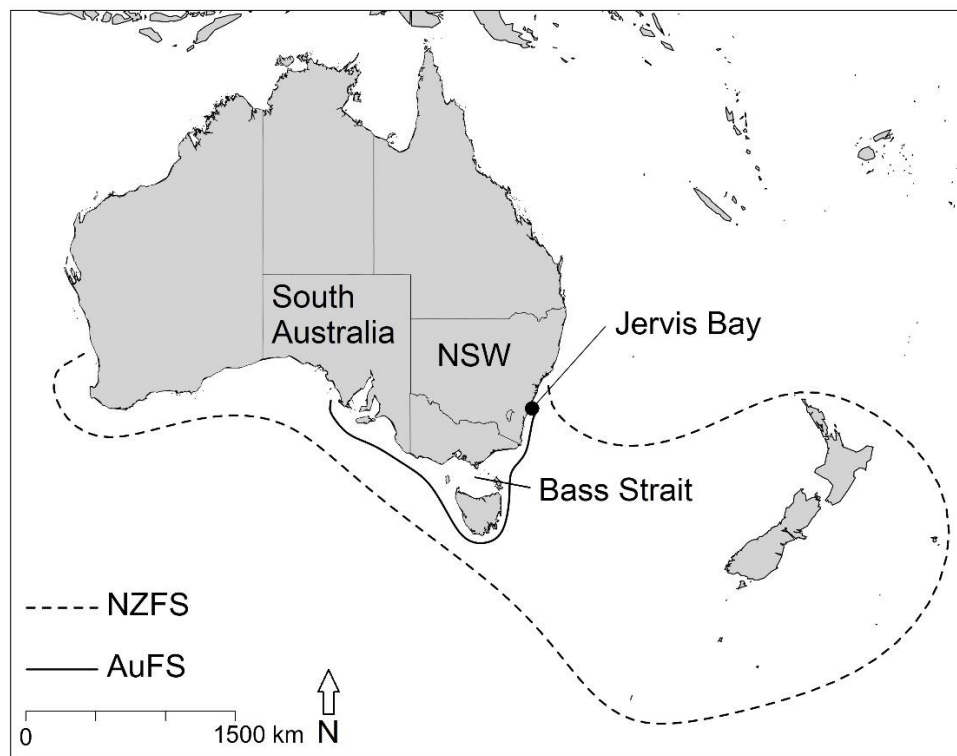


Figure 6.1 Approximate species range for Australian *Arctocephalus pusillus doriferus* and New Zealand fur seals *A. forsteri* (solid line and dotted line, respectively) and the site of deployment (Lamond Head, Jervis Bay) in New South Wales (NSW Marine Parks Authority).

6.3 Results

Eleven adult male NZFS were tagged (4 in 2011, 2 in 2012, 5 in 2013) and 4 adult male AuFS were tagged in 2013. NZFS weighed 95 ± 6 kg and AuFS weighed 160 ± 39 kg (Table 1). The 15 seals were tracked for 129 ± 51 d (range: 21-204 d) and the period of tracking covered from 21st June to 25th January in 2011, 2012 and 2013 (Table 1). We recorded 865 trips (range: 17-91 trips per seal) and from these it was calculated that individuals spent 70 ± 7 % of their time at sea (range: 58-82 %) (Table 6.1) and otherwise they were on land.

Behaviour at the margin of the range

All seals remained at the northern margin of the range (i.e. New South Wales, Australia) during the austral winter months. From 17 September, both species departed the margin of the range and moved south towards the core of the range where there are established breeding colonies (mean departure date AuFS 13 October ± 10 d, NZFS 15 October ± 6 d).

The seals used 26 haul-out sites while at the margin of the range and spent 14.8 ± 1.0 h ashore (range: 25 minutes – 4.2 d). Each individual visited between four and ten sites (6.2 ± 1.9 sites). Most sites were non-breeding sites, with records of pups only on Montague Island (Fig. 6.2). The deployment site was revisited by 13 of 15 individuals (post-deployment): several sites were visited by five to seven individuals (Fig. 6.2). Most were used by both species ($n = 16$ sites), with nine only visited by NZFS and one only by AuFS. Generally, sites were visited infrequently, with some only visited once (five sites) or fewer than ten times (11 sites). The deployment site (Lamond Head) was the most frequented site (a non-breeding site, 391 visits, or 59.3 % of all visits to sites at the margin of the range). This may be indicative of high site fidelity or favourable site conditions (note: males tracked from Montague Island in 2012 and 2013 often visited this site when they came ashore in this area, Harcourt and Slip unpublished data). The next most frequented sites had 38, 36 and 32 visits and were 145 km, 18 km, and 65 km away from the deployment site (Fig. 2).

While at the margin of the range, NZFS trips at sea were either on the continental shelf or pelagic waters east of the shelf and AuFS foraging trips were concentrated on the shelf (Fig. 6.3). Seals moved up to 250 km north of Jervis Bay to the coastline off the highly populated city of Sydney. The size of individual HR area at the margin of the range were $2,467 \pm 843$ km², and similar in size for both species (Table 6.2). The individual HR and CR areas overlapped, and the area of high overlap for CR areas was predominantly in the coastal waters within 20 km of the frequently used haul-out sites (Fig. 6.3). While at the margin of the range, at-sea trip durations were 1.7 ± 0.2 d (range: 38 minutes – 35.1 d) for individuals of both species, and approximately one fifth of their at-sea trips were <0.5 d in duration (Table 6.2), during which time individuals remained within inshore waters adjacent to terrestrial sites (average individual mean maximum distance of 8 ± 6 km from site of departure).

Behaviour at core of the range

After seals departed the margin of the range, ten tags continued to transmit data (6 NZFS and 4 AuFS). During this period the seals used 31 haul-out sites and spent 22.2 ± 2.6 h ashore (range: 25 minutes – 3.9 d). The sites used by the seals were spread across multiple jurisdictional boundaries, comprising 3 Australian states (Victoria, Tasmania and South Australia) and New Zealand (Fig. 3). Most sites were non-breeding sites, with only ten of the 31 sites known for breeding activity. Individuals visited between one and ten different sites throughout the core of their range. Eight of the ten seals visited at least one breeding site, where they spent 21.5 ± 3.4 h ashore (range: 25 minutes – 3.9 d). Most sites were visited by only one individual (20 sites), but some sites were visited by up to three individuals (6 sites). Seven sites were visited by both species, 12 sites only by NZFS and 12 sites only by AuFS. Most sites were visited infrequently, either once (8 sites) or fewer than 10 times (26 sites). The most frequently used site was The Skerries (breeding site, 79 visits, or 34.5 % of all visits to sites at the core of the range). The next most frequently used sites were Althorpe Island (non-breeding site, 23 visits, or 10.0 %), Gabo Island (non-breeding site, 18 visits, or 7.9 %), Cape Linois (non-breeding site, 15 visits, or 6.6 %).

While at the core of the range, NZFS trips to sea were primarily in pelagic waters east of the continental shelf between Australia and New Zealand, and AuFS trips remained on the continental shelf but also around the shelf break, with one individual venturing off the shelf. The fur seals displayed a change in foraging behaviour from the margin of the range to the core of the range; while their foraging trip duration was not significantly different (Student's paired t-test $T = -2.23$, $P = 0.052$), they had significant expansion of their HR (Wilcoxon signed-rank test $V = 0$, $Z = -3.3$, $P < 0.001$, $R = 0.99$) (Fig. 6.3, Table 6.2). There was high variability among individual HR and CR and only a small percentage of the total area was used by two or more individuals (HR 29.5% and CR 11.0%).

During October, one New Zealand fur seal (NZ_13) traversed the Tasman Sea. The seal left Montague Island (on the 2nd October) and reached Nee Islets, New Zealand on 10 November. This seal spent 15 d around the Nee Islets and a total of 9.5 d hauled out there. The seal left the Nee Islets on 24 November, traversed the Tasman Sea and hauled out at Cape Hauy, Tasmania, on 18 December for 1.2 d.

Table 6.1 Deployment summary for male New Zealand fur seals (NZ) *Arctocephalus forsteri* and Australian fur seals (Au) *A. pusillus doriferus* at Lamond Head, Jervis Bay in austral winters of 2011 to 2013

Seal ID	Length (m)	Girth (m)	Date attached	Deployment Duration (d)	Time at sea (%)	GPS locations
NZ_1	1.56	1.05	21/06/11	194.5	74.3	1341
NZ_2	1.75	0.98	25/06/11	21.2	58.5	168
NZ_3	1.59	1.06	05/07/11	86.9	61.5	483
NZ_4	1.58	1.09	09/07/11	55.4	72.5	339
NZ_5	1.64	1.05	01/07/12	159.2	68.7	266
NZ_6	1.61	0.99	30/06/12	112.0	62.6	339
NZ_7	1.51	0.93	22/06/13	158.2	72.8	593
NZ_8	1.65	1.01	10/07/13	166.0	82.5	639
NZ_9	1.7	1.11	11/07/13	104.7	77.5	385
NZ_10	1.59	1.12	27/07/13	102.3	65.6	189
NZ_11	1.58	1.06	10/08/13	135.3	64.9	416
Au_1	1.49	0.99	19/06/13	204.3	73.1	441
Au_2	1.85	-	20/06/13	153.4	66.8	898
Au_3	1.42	0.9	11/07/13	112.5	75.4	481
Au_4	2.06	1.63	31/07/13	178.1	66.9	1204

Table 6.2 Foraging behaviour parameters (mean \pm SE) of male New Zealand (NZ) *Arctocephalus forsteri* and Australian fur seals (Au) *A. pusillus doriferus* when they were at the margin of the range (i.e. New South Wales) and the core of their range. Parameters include home range (HR; 90% utilisation distribution) and core range size (CR; 50% utilisation distribution). For seals at the margin of the range, we also investigated how much of Jervis Bay Marine Park (JBMP) was used, and the overlap of individual HR and CR with JBMP.

Region and parameter	New Zealand fur seals	Australian fur seals
Margin of the range		
Number of seals	11	4
Haul-out duration (h)	14.2 \pm 1.3	16.4 \pm 1.5
Trip duration (d)	1.4 \pm 0.2	1.8 \pm 0.4
HR size (km ²)	2612 \pm 1133	2068 \pm 778
CR size (km ²)	587 \pm 266	427 \pm 208
Trips <0.5 days (% of individual's total no. trips)	23.9 \pm 5.6	19.9 \pm 2.9
JBMP area used (%)	28.1 \pm 7.2	41.4 \pm 19.6
HR overlap with JBMP (%)	10.1 \pm 3.7	9.9 \pm 5.3
CR overlap with JBMP (%)	12.5 \pm 8.2	16.4 \pm 15.8
Core of the range		
Number of seals	6	4
Haul-out duration (h)	18.9 \pm 2.3	28.7 \pm 5.3
Trip duration (d)	3.4 \pm 0.9	4.1 \pm 1.5
HR size (km ²)	153,140 \pm 40,517	88,394 \pm 57,877
CR size (km ²)	33,972 \pm 8,607	22,039 \pm 14,816
Trips <0.5 days (% of individual's total no. trips)	43.1 \pm 8.4	28.3 \pm 16.4

Protected areas

Of the 57 sites used by the seals, most ($n = 47$) were within terrestrial protected areas (i.e. national parks, reserves, naval exclusion area) (Fig. 6.2). All 10 sites that were outside terrestrial protected areas were non-breeding haul-out sites at the margin of the range (Fig. 6.2). Six of the sites outside terrestrial protected areas were along the Jervis Bay coastline and the other four were north of Jervis Bay towards Sydney. There was no difference in the average number of visits to sites outside terrestrial protected areas, 7.5 ± 7.6 visits, compared to sites inside terrestrial protected areas, 7.3 ± 8.5 visits (excluding the deployment site, which was an extreme outlier). A total of 591 visits were recorded at 13 sites in Jervis Bay Marine Park (JBMP) (range: 1-391 visits per site). After the deployment site, the frequency of use of other sites in Jervis Bay was relatively low and did not appear to be influenced by whether the site was inside or outside a protected area (Fig. 6.2).

While at the margin of the range, individuals of both species used a large percentage of the Jervis Bay Marine Park (JBMP) (up to 93% of the park, Table 6.2; Fig. 6.4). As expected for a wide-ranging species, only a percentage of an individual's HR overlapped with JBMP, however, there was great individual variability with the CR of some individuals being almost entirely within JBMP (up to 92% of an individual's CR overlapped within the park, Table 6.2). When a seal's home range or core range overlapped with JBMP, the overlap occurred mostly within the coastal waters adjacent to haul-out sites (Fig. 6.4).

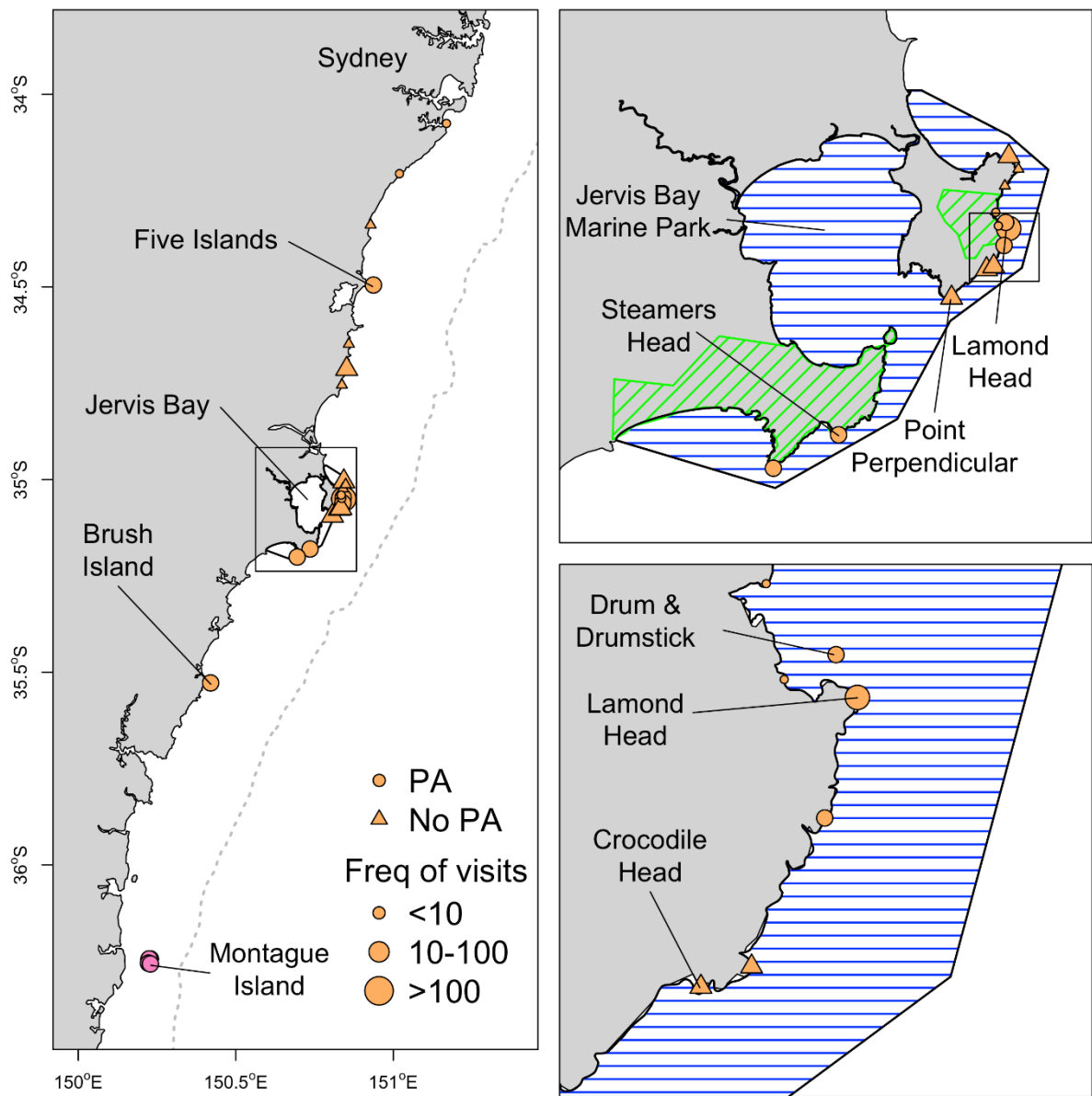


Figure 6.2 (a-c) Sites visited by male fur seals and their overlap with a terrestrial protected area (PA); overlap (circle) or no overlap (triangle). Icon size indicates the frequency of visits to a site (see inset legend) and colour indicates non-breeding haulout site (orange) or a colony (pink) (rare breeding attempts at Montague Island). Diagonal hashed areas (green) indicate a terrestrial PA (southern Jervis Bay) and a naval exclusion zone (north Jervis Bay). Horizontal area (blue) is Jervis Bay Marine Park. The dotted line indicates the 200m bathymetric contour and approximate edge of the continental shelf.

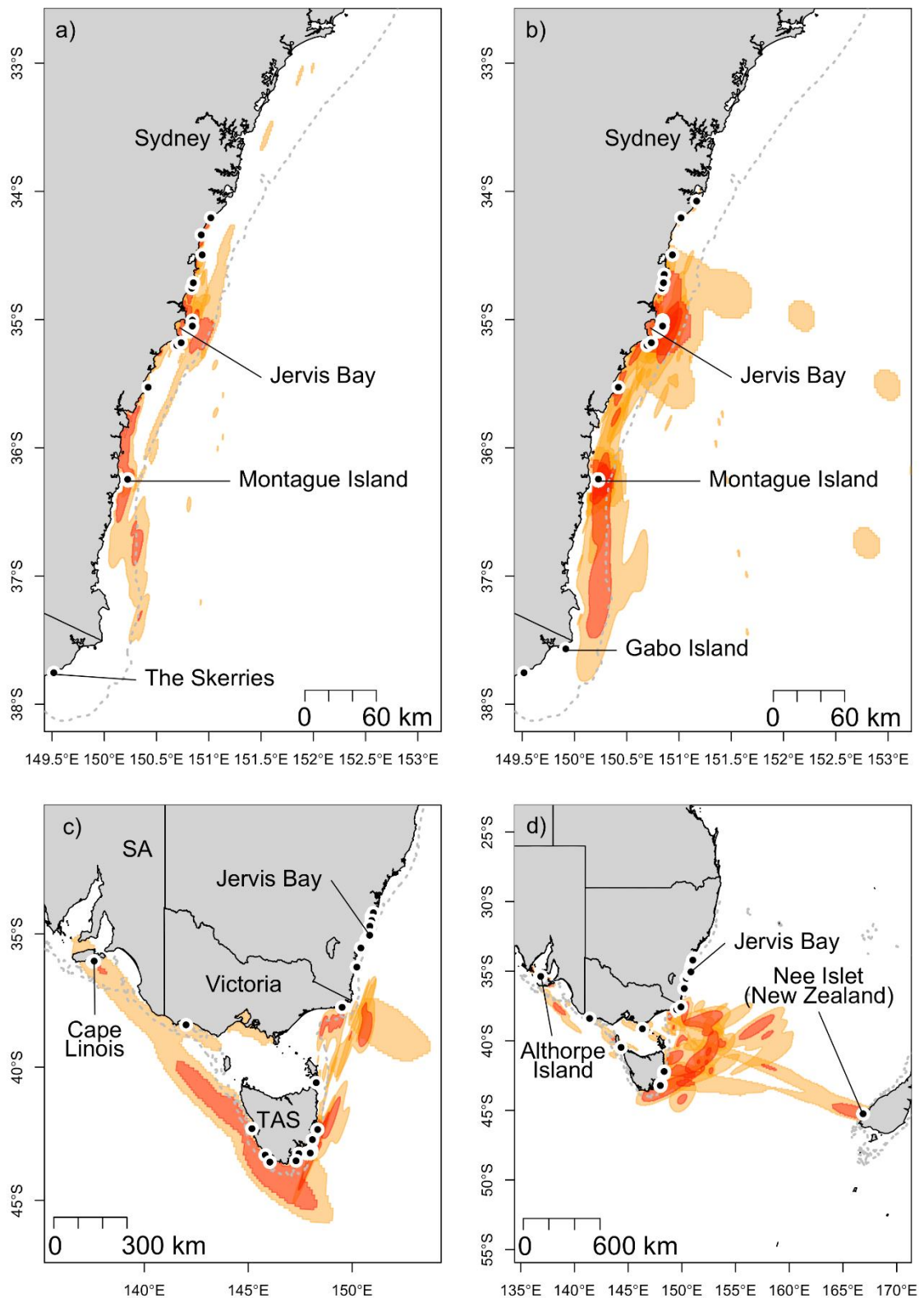


Figure 6.3 The home range (orange) and core range (red) utilisation distributions of each individual male fur seal tracked from Jervis Bay in 2011 to 2013. (a) Australian fur seals *Arctocephalus pusillus doriferus* at the margin of the range ($n = 4$), and (c) core of the range ($n = 4$); (b) New Zealand fur seals *A. forsteri* at the margin of the range ($n = 11$), and (d) core of the range ($n = 8$). At the time of tracking, The Skerries was the north-eastern extent of the breeding sites for these fur seals (i.e. core geographic range), with rare breeding attempts at Montague Island. Darker shades indicate greater overlap among individuals. Dotted lines are the 200m bathymetric contour and approximate edge of the continental shelf. SA: South Australia, TAS: Tasmania

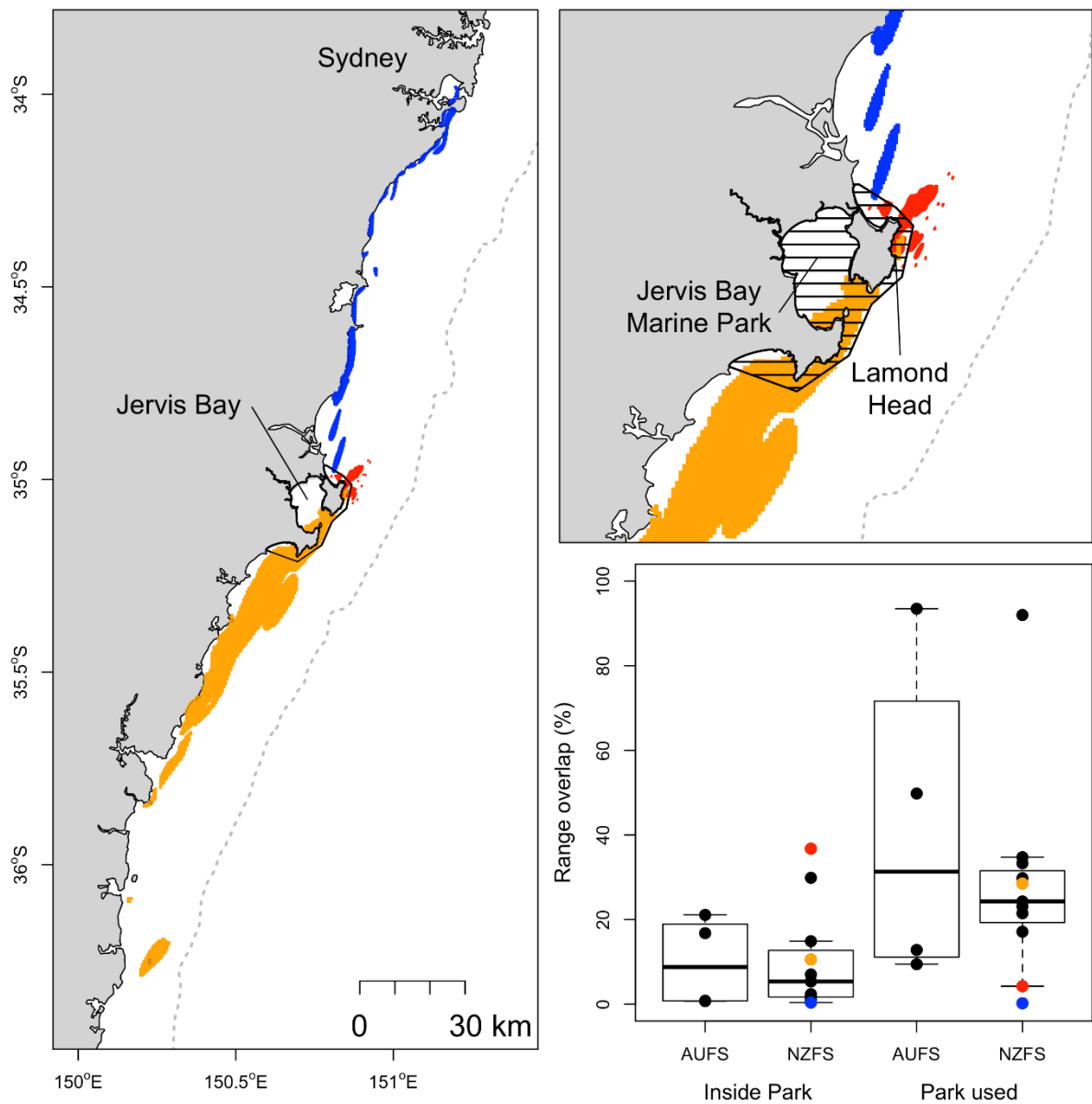


Figure 6.4 Overlap of individual male fur seal home ranges with Jervis Bay Marine Park. The home range of three individuals are presented with different colours (red, orange, blue), and the same colours used to represent these individuals in the box-and-whisker plot. Box-and-whisker plots (minimum, maximum and three quartiles) summarise the percentage of the range contained within the park (Inside park) and the percentage of the park that utilised by each seal (Park used) (dot per individual). Dotted line is the 200m bathymetric contour and approximate edge of the continental shelf.

6.4 Discussion

We tracked the movements and habitat use of sympatric male Australian (AuFS; *Arctocephalus pusillus doriferus*) and New Zealand fur seals (NZFS; *A. forsteri*) at the northern end of their distribution where both species are expanding their range, to identify areas important to these predators and determine if they are receiving protection there. Habitat use of the study males was similar to that of males that reside at the core of the species range, but they used much larger ranges and had consistent seasonal movements away from the margin to the core of their distribution. Despite being wide-ranging predators, the males consistently used discrete terrestrial sites and adjacent inshore waters while at the margin of the range, and these habitats were either coincidentally, or actively, selected for reduced disturbance, falling within established terrestrial and marine protected areas.

Many large marine carnivores, such as seals, crocodiles, turtles, and seabirds, range widely at sea, but return periodically to land to rest, breed, and moult, and this can bring them into close contact with coastal human populations. Consistent use of particular discrete inshore habitats makes terrestrial and marine protected areas a viable management option for mitigating human-carnivore conflict, at least where the two areas coincide. Protected areas are often designed with human and ecosystem values in mind (Thackway & Cresswell 1997), and not specifically for wide-ranging carnivores, and yet in this study they appear to capture most of terrestrial habitat used by the seals. The seals received protection throughout much of their range as a result of management of activities in protected areas, with the exception of some sites at the expanding northern margin of the species range. Wide-ranging marine carnivores may opt to use protected areas specifically because of functions offered within their boundaries (e.g. less human activity or different activities, such as prohibited rock fishing). Alternatively, the areas humans zoned for protection have features that are coincidentally also favoured by the carnivores (e.g. remote areas, low human visitation, limited commercial activity). When marine carnivores are on land they can be disturbed by visual, audible and olfactory cues whether approached from land or sea (Boren et al. 2002; Burleigh et al. 2008a; Tripovich et al. 2012; Watson et al. 2014a; Cowling et al. 2015; Marcella et al. 2017; Back et al. 2018; Speakman et al. 2020) or from the air by piloted and remotely operated aircraft (Born et al. 1999; Borrelle & Fletcher 2017; Arona et al. 2018; Bevan et al. 2018; McIntosh et al. 2018a), which at worst may have lethal consequence (Back et al. 2018). An effective way to reduce disturbance to marine carnivores on land is to restrict access and modify behaviour of humans, for example installing barriers and/or interpretive signage (Cassini 2001; Cassini et al. 2004; Granquist & Sigurjonsdottir 2014; Marschall et al. 2017) and regulating approach distances for different aircraft types with minimum height restrictions (Hodgson & Koh 2016). Protected areas allow strict regulation of human access and activities and have proven applicable for conserving large carnivores through reduced negative interaction with humans (Hooker & Gerber 2004; Barnes et al. 2016; Santini et al. 2016a). Minimising human disturbance to provide refugia may be particularly

important for low-density populations, such as those at the margin of a range where individuals may consider themselves more at risk due to decreased vigilance and dilution effects (Stevens & Boness 2003). A network of established protected areas along the coastal fringe may enhance recovery and range expansion of wide-ranging carnivores, like these seals, by providing important stepping-stones of refuge as they expand their range (Kirkman 2010; Huisamen et al. 2011).

With tracking studies of wide-ranging marine carnivore focussing on foraging trips at sea, there has been less focus on what these carnivores are doing during short trips within inshore habitat. In this study, the considerable time spent on land and within inshore waters adjacent to terrestrial sites by all individuals of both species is indicative of the importance of this habitat to these marine carnivores at the margin of their range. Terrestrial sites are important to male fur seals for a variety of reasons (to breed, moult, rest, digest, and refuge from marine predators), though at the margin of the range the benefit is unlikely associated with reproduction because there are no reproductively active females in the area. During the non-breeding period, social interactions between males are likely to play an important role in gaining experience that determines hierarchy and breeding success (Stirling 1970; Miller 1974; McCann 1980). Little is known about the importance of inshore waters adjacent to terrestrial sites. Male NZFS and AuFS move between land and inshore waters to thermoregulate (Mattlin 1978; Garlepp et al. 2014), which may be more important for seals in warmer climates at lower latitudes (Stevens & Boness 2003). The inshore environment may also provide valuable foraging grounds, with the diet of both fur seal species at Jervis Bay having a high prevalence of benthic, demersal and reef-associated prey associated with inshore habitats (Hardy et al. 2017). Inshore habitats may also be selected for features (e.g. shallow reefs and kelp beds) that improve evasion from predators (Wirsing et al. 2007; Wcisel et al. 2015). Supporting these critical functions with protection of terrestrial sites and inshore waters will facilitate recolonization of these habitats throughout their historic range. The coastal margins of these seals' range, the focus of this study, supports a large, dense, human population, with active fishing, aquaculture and tourism industries. Mitigating at-sea interactions with fur seals in the relatively discrete area found adjacent to terrestrial haul-out sites would be challenging at this margin of these seal species' range, but likely benefit the recovery of the seals by reducing disruption to critical on-land and inshore behaviours.

Protecting the entire foraging range of wide-ranging marine carnivores is often impractical. By understanding the movements of carnivores, it is possible to identify life stages or periods within a breeding cycle that are contained in discrete areas more suitable for protected area zoning. For example, this study showed when male seals were at the expanding margin of their range they used relatively small at-sea areas, with a large percentage overlap with the existing marine protected area, Jervis Bay Marine Park, and the park captured the core range areas that were adjacent to terrestrial sites. Through spatial zoning within their boundaries, marine protected areas can be used to direct

marine-based activities (fishing, aquaculture, tourism) and land-based fishing and tourism activities into areas away from sites important to species of conservation concern. Jervis Bay Marine Park is an example of a park that is internally zoned to spatially regulate activities throughout the park, and since its establishment several predators have returned and established populations in the park (Lynch et al. 2013; Bruce et al. 2014, this study). By identifying the areas within the park that are important to each marine carnivore, management authorities can apply evidence-based information to improve zoning within the park (i.e. modify boundaries or activities within zones) to better mitigate interactions between users and the carnivores. In the absence of such information, this study suggests zoning the coastal marine environment close to terrestrial sites could capture important inshore habitat for wide-ranging marine carnivores that regularly come ashore, and provide the opportunity to mitigate interactions between these carnivores and human activities that disrupt their behaviours that occur in terrestrial and inshore habitat.

Factoring novel and consistent intraspecific variation in foraging behaviour into movement models for carnivores is an important consideration to predict accurately the habitat use of populations, and necessary to correctly inform conservation planning. In this study, the uniform movement of the male AuFS and NZFS seals from overwintering at the margin of the range towards colonies prior to breeding contrasts with males tracked within the core of the range in other studies. Long-range movements from the winter grounds have occurred in only a small number of individuals tracked from the core of the range in other studies: NZFS, (Page et al. 2006); AuFS, (Kirkwood et al. 2006; Robinson et al. 2008a; Knox et al. 2017). This sort of intraspecific variation in movements is rarely seen in other otariids, with males either all migrating away from colonies post-breeding (Robertson et al. 2006; Staniland & Robinson 2008) or all showing high fidelity to a colony throughout the non-breeding period (Lowther et al. 2013; Baylis et al. 2018). This appears analogous to partial migrating species, where segregation in overwinter movement behaviour may be associated with individual characteristics such as age, body size, competitive ability and personality (Lundberg 1988; Chapman et al. 2011). Breeding status may explain the more consistent movement and colony fidelity of males tracked from the core of the range (Kirkwood et al. 2006), with those less involved in breeding in the subsequent season (e.g. holding or challenging for breeding territory) ranging more widely over winter. This idea is supported by this study, with all males on the margin of the range having minimal association with colonies in the subsequent breeding season and insufficient body size to be competitive for breeding territory (Lourie et al. 2014): though other strategies exist (Caudron et al. 2010). High intra- and inter-specific competition and local depletion of food resources at the core of a species range, close to breeding areas, may be a strong motivation for some individuals to disperse from breeding colonies (Ashmole 1963; Boyd et al. 1998; Weise et al. 2006; Kuhn et al. 2014). As a trade-off, however, lower densities of periphery populations are thought to reflect poorer quality habitat towards margins of a range (Holt 1987; Lawton 1993; Guo et al. 2005), which is thought to explain divergent foraging behaviour from individuals at the core of the

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range (Augé et al. 2011). The movements of individuals at the periphery of a population's range can clearly diverge from the patterns identified in individuals at the core of their range. This study emphasises that caution is required when modelling habitat use of carnivores recolonising their historic range when using information derived from individuals at the core of their species' range.

This study identifies important considerations to improve conservation and management of recovering wide-ranging marine carnivore populations, based on analysis of movements and habitat use of males of two fur seals species occupying an expanding margin of their species' range. The dependence of many marine carnivore species on discrete habitats that are of similar size to existing protected areas means recovering populations of marine carnivores can benefit from an established network of protected areas – terrestrial and marine – at the frontier of their range. Improvements can be made to the designation and zoning of protected areas by integrating specific habitat use information of individuals at expanding range margins into the review of management plans. This will help account for unique intra-specific behaviour of individuals at range peripheries. As marine carnivores recolonise their historic range, it is necessary to consider ecosystem consequences, and the utility of protected areas, where high-level predators become established and exert influence on trophic dynamics within protected areas (Hooker et al. 2011; Kelaher et al. 2015). Having a network of protected areas along the coastal fridge at the margins of a carnivore's range could help to minimise and mitigate adverse interactions between industry and recovering marine carnivores, and thereby support a key conservation and management objectives for marine carnivore populations. For these protected areas, it is important to ensure enforcement of regulations, as activities can persist illegally and reduce the effectiveness of the protected area (Harasti et al. 2019). Given that wide-ranging marine carnivores will often move beyond discrete habitats, point-source management methods, such as seal exclusion devices on trawl nets (Shaughnessy et al. 2003), will likely continue to play a role in mitigating at-sea interactions between humans and recovering marine carnivore populations.

Despite promising recovery of populations for both fur seal species throughout their range (Kirkwood et al. 2010; Shaughnessy et al. 2015; Watson et al. 2015), recent population estimates based on pup numbers identified a reduction in the Australian fur seal population at core breeding colonies (McIntosh et al. 2018b). The implications of population fluctuations within the core of a species range for the colonisation of the margin by periphery populations is still unknown. In this case, resource partitioning, on land and at sea, between two recovering, sympatric predators requires further investigation, and studying this at the expanding margin of both species' range, where neither species currently has apparent priority, may have useful insights for carnivore population recovery and recolonization (Hardy et al. 2017). Importantly, the implications for large-scale environmental change, such as strengthening of the East Australian Current (Suthers et al. 2011), on the recovery of large carnivore populations and

changes in their distribution are still largely unknown, but potentially significant (Niella et al. 2020), and should be considered when planning for recovery and expansion of marine carnivore populations.

7. Chapter Seven

Thesis Discussion



Photo credit: Marcus Salton

7.1 General Discussion

With continued successful recovery of many large carnivores (Lotze et al. 2011; Chapron et al. 2014; Gompper et al. 2015; Karamanlidis et al. 2015; Martinez Cano et al. 2016), including many fur seal species (Gerber & Hilborn 2001; Magera et al. 2013), ecological theory predicts the role of intra and interspecific competition in shaping foraging behaviour will become pronounced. In this thesis, by exploring the behaviour of juvenile and male fur seals, who are free from the constraints imposed by parental, I identified foraging strategies used by fur seals to mitigate 1) the intraspecific competitive pressures expected at breeding colonies, and 2) interspecific competition expected at a range periphery. Juveniles and males are expected at the forefront of fur seal population dispersal and range expansions. By investigating the behaviour of these fur seals at the species' expanding range margin, I also aimed to assess whether inferences relating to foraging behaviour that are obtained from individuals at established breeding colonies are applicable to marginal populations. Finally, given the wide-ranging movements of these large carnivores while foraging, I explored the efficacy of a current network of protected areas to sustain the recovery of fur seals foraging at the frontline of a range expansion. This discussion provides an overview and synthesis of the main findings, offering insights into the role of foraging behaviour during population recovery and range expansion of fur seals.

Intraspecific foraging behaviour

Intraspecific competition is expected to increase as populations recover, grow in size and density, and therefore concentrate more conspecifics into finite niches. The population growth rate is likely to be influenced by resource availability (Fishman 1997), in which case monitoring foraging behaviour can reveal a population's status during recovery (Wildermuth et al. 2013). For example, foraging trip duration, trip distance, foraging range and diving effort of central-place foraging lactating female fur seals has been associated with differences in colony size (Staniland et al. 2011; Kuhn et al. 2014). Male and juvenile fur seals are not bound to the central place by the parental duties of raising offspring. Therefore, to avoid exploitative competition they could adopt longer trips to more distant foraging areas segregated from that of females. Indeed, this appears to be the case for juvenile and adult male New Zealand, Antarctic and northern fur seals that make long distant foraging trips away from the foraging areas of females (Boyd et al. 1998; Loughlin et al. 1999; Sterling & Ream 2004; Ream et al. 2005; Page et al. 2006; Warren et al. 2006; Staniland & Robinson 2008; Zeppelin et al. 2019; Lowther et al. 2020; March et al. 2021). I found this was also the case for male Antarctic fur seals at an established colony at Heard Island (Ch 1; Salton et al. 2022). Not only did these males make long-distance post-breeding trips, they also adopted a directed movement state when close to the colony (out-bound and in-bound) with resident movement states (indicative of foraging areas) concentrated in distant locations characterised by high biological production (Ch 1; Salton et al. 2022). These distant areas can sustain productivity several magnitudes higher than waters closer to the colony (Sullivan et al. 1993; Arrigo et al. 2008). Similarly, juvenile New Zealand fur seals in South Australia (where the species is abundant) move quickly away from their colony and more slowly at the distal ends of their trip, and focus their time in areas associated with ocean features (e.g. the subtropical front) that generate high biological production (Page et al. 2006). This suggests the behaviour of these adult males and juveniles is consistent with the marginal value theorem (Charnov 1976). The animal's transit through areas of putative high exploitative competition where prey capture rates are expected to be relatively low, to focus their efforts at patches in the more distant areas of high biological production with a higher rate of energy return. Maximising the rate of energy intake post-breeding is important for adult males to help restore condition lost while fasting during breeding (Boyd & Duck 1991), and to gain condition to sustain them through their post-breeding moult and prepare for subsequent breeding. The immature development and naivety of juveniles limits their foraging behaviour and competitive ability (Marchetti & Price 1989; Lindström 1999), and they have high mortality risk (Lindström 1999; Benson et al. 2018), so they too need productive foraging areas to support their growth and survival. These fur seals also display inter-individual dietary segregation as a means of partitioning their niche among conspecifics (Page et al. 2005a; Zeppelin & Orr 2010; Kernaléguen et al. 2012; Jones et al. 2020). Dietary partitioning between juvenile conspecifics could be influenced by some feeding on what they can catch locally while others feed on distant prey, with the time and energy costs of accessing distant areas potentially offset by

more energy dense prey at distant foraging grounds (Staniland et al. 2007; Lea et al. 2008; Casper et al. 2010). Spatial and dietary partitioning should reduce intraspecific competition and thereby support a higher carrying capacity at their breeding colonies.

While there is evidence of intraspecific exploitative competition being a driver of segregated foraging range in some fur seals, Australian, South American and Cape fur seals the males and females often have overlapping foraging ranges (Skern-Mauritzen et al. 2009; Kernaléguen et al. 2015b; Baylis et al. 2018), and juvenile Galápagos fur seals have similar trip durations to adult females (Horning & Trillmich 1997). At two well-established Australian fur seal breeding colonies (Supplementary material 1; McIntosh et al. 2018b), I found juveniles made shorter duration trips and had smaller foraging ranges than adults (females and males), and adult males had similar foraging trip durations and foraging ranges compared to adult females (Ch 3 & Ch 4; Ladds et al. 2018; Salton et al. 2019). One of these colonies (Seal Rocks, Victoria) is located in the nutrient impoverished Bass Strait (Gibbs et al. 1986; Gibbs et al. 1991), and there juveniles and males were more likely to use alternative haul-out sites while females typically returned to the breeding colony between foraging trips (Ch 3; Salton et al. 2019). By using alternative haul-out sites, juveniles and males could reduce the transit time, and thus energetic costs, between rest sites and foraging areas, providing them with closer access to the more productive margins of Bass Straits (Gibbs et al. 1991; Kämpf 2015; Kämpf & Kavi 2017). The daily energy expenditure of juvenile Australian fur seals is lower when they spend more time resting and higher when active (e.g. travelling and foraging) (Ch 4; Ladds et al. 2018). Therefore, by resting closer to foraging areas, the juveniles and males could minimise the proportion of time spent travelling to foraging areas, and thereby increase their rate of energy return while foraging. A similar strategy is used by other male fur seals on long distance trips, where they haul-out on land, on ice, or rest at the surface of the water near foraging grounds (Ch 2 & Ch 6; Baylis et al. 2018; Lowther et al. 2020; Salton et al. 2021; Salton et al. 2022). Being primarily benthic foragers (Arnould & Kirkwood 2007; Hoskins et al. 2015; Knox et al. 2017), Australian fur seals may be too spatially constrained on the shallow basin of Bass Strait and narrow continental shelf around southern Australia to effectively segregate foraging space among sex-life stage groups (Ch 3; Kernaléguen et al. 2015b; Salton et al. 2019). Dietary analysis suggests adult males may feed at a higher trophic level than adult females (Kernaléguen et al. 2015b), and analyses of diving behaviour indicate juveniles are unable to make adult-like dives due to physiological constraints while males are capable of deeper dives than females (Ch 4; Arnould & Hindell 2001; Spence-Bailey et al. 2007; Knox et al. 2017; Ladds et al. 2018). Therefore, these seals appear to reduce intraspecific competition by targeting different prey types, foraging at different depths and resting at alternative haul-out sites, which may explain their ability to sustain a reasonable density within a relatively nutrient impoverished habitat.

Diversification of foraging strategies reduces intraspecific competition (Kobler et al. 2009; Bolnick et al. 2011) and accordingly enhances niche partitioning among sex-life stage groups. Associated niche expansion is positively related to population density and expected in large, established populations (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007; Svanbäck et al. 2008; Tinker et al. 2008; Kobler et al. 2009; Svanbäck & Persson 2009; Sánchez-Hernández & Cobo 2013). Inter-individual variability in foraging has been found amongst male fur seals from large breeding colonies for various species (Kernaléguen et al. 2012; Kernaléguen et al. 2015b; Knox et al. 2017; Baylis et al. 2018; Lowther et al. 2020). I found male Antarctic fur seals at Heard Island had two distinct departure times and distinct foraging areas away from the breeding colony (Ch 2; Salton et al. 2022). At Heard Island, males made a trade-off between leaving the breeding colony earlier to capitalising on the more distant biologically productive ice habitat, or remained at the breeding colony longer, potentially to maximise breeding opportunities, then forage in closer but less biologically productive open ocean (Ch 2; Salton et al. 2022). At the range margins of Australian and New Zealand fur seals, where populations are small and intraspecific competition should be low, I expected less variation among individuals, but males of both species had broad niches and high individual specialisation in various niche dimensions (dietary, diving and space use). In fact, the male Australian fur seals were more specialised than males from a larger, well-established breeding colony (Ch 5; Kernaléguen et al. 2015b), and these results were consistent with diet reconstructed from scat analysis at the same locations compared to breeding colonies throughout the seal's range (Hardy et al. 2017); discussed further below. Similarly, female fur seals also show high inter-individual variability in various foraging behaviours (Cherel et al. 2009; Kernaléguen et al. 2016; Juárez-Ruiz et al. 2018; Foo et al. 2019; de Lima et al. 2021). Diversification of prey type, foraging habitat and diving behaviour should reduce intraspecific competition and the ability to do this may be an important aspect of fur seal behaviour that has supported the growth of large, dense populations at numerous fur seal colonies.

In addition to intraspecific competition, segregation of foraging space between females and males can also align with morphological and physiological differences and associated energy requirements (Ch 3; Salton et al. 2019). Ontogenetic effects on foraging (e.g. physiological development, experience, propensity toward risk) can also explain the protracted trips of juveniles in some species (Ch 3; Salton et al. 2019). The many drivers of foraging behaviour present a challenge to quantify the importance of intraspecific competition in shaping individual foraging strategies. However, as discussed here, the evidence suggests that the foraging strategies of male and juvenile fur seals have in part been shaped by intraspecific competition, and its effects are particularly prominent among fur seals in large breeding aggregations. In addition, the extension of female fur seal foraging trips at larger populations of the same species (Staniland et al. 2011), and among females at one colony that increased 4-fold over 15 years (Kuhn et al. 2014), further supports the theory the flexibility in foraging strategy assists fur seals to form dense populations.

Populations at the range margin

Juveniles (particularly males) and adult males are generally responsible for dispersal and initial occupation of new sites in birds and mammals (Greenwood 1980; Pusey 1987; Matthysen 2005), including fur seals (Warneke 1975; Oosthuizen 1991; Bradshaw et al. 2000b; Goldsworthy et al. 2009; Kirkwood et al. 2009; Shaughnessy et al. 2010; Huisamen et al. 2011). Prior to this thesis, the limited information on juvenile and adult male foraging behaviour was derived from individuals at breeding colonies, and it remained unclear whether behaviour at marginal parts of the species' range differed from individuals at more central breeding colonies. Generally, there are intrinsic differences in the behaviour of individuals that disperse (Cote et al. 2010). In theory the habitat beyond a species range margin is typically unsuitable for maintenance and hence delineates the distribution of the species (Guo et al. 2005; Holt et al. 2005; Gaston 2009). In these margins individuals forage on poor food resources (quantity or quality) and should diversify their diet (Shreeve et al. 1996; Marti 1997). However, lower intraspecific competition at a range periphery can also be associated with ecological release (Lawton 1993; Svanbäck & Bolnick 2007), but interspecific interactions can result in novel competition and predation that shape the behaviour and persistence of species at range margins (Case & Taper 2000; Holt & Keitt 2000; Berger & Gese 2007; Fisher et al. 2014). As a consequence, there are several potential drivers of diversification in the diet and foraging behaviour of individuals at range margins compared to individuals in centralised parts of a species range.

I found the foraging behaviour of male Australian and New Zealand fur seals at a margin of both species' range maintained some similarities but with key differences from that of males at more centralised breeding colonies. Benthic foraging over the continental shelf and epipelagic foraging over the shelf, shelf edge and deep water continued to characterise the movements of male Australian and New Zealand fur seals, respectively, at the range margin (Ch 5). However, males foraging at the range margin had much shorter trip durations and smaller core foraging areas compared to males from breeding colonies (Ch 3, Salton et al. 2019; Ch 5; Ch6, Salton et al. 2021; Page et al. 2006; Knox et al. 2017, 2018), suggesting they were able to obtain the resources they needed within close proximity to their haul-out sites. The niche size and levels of individual specialisation in various niche dimensions were also more similar compared to males from breeding colonies (Ch 5), despite having small populations and low putative intraspecific competition. This was unexpected, given niche size typically increases with intraspecific competition (MacArthur & Pianka 1966; Roughgarden 1972; Bolnick 2001; Svanbäck & Bolnick 2007), and appears to be the case at different sized breeding colonies of congeneric subantarctic fur seals (Kernaléguen et al. 2015a). Alternatively, individuals may expand their foraging niche in response to interspecific competition or decreased availability of valuable food resources (Chiaradia et al. 2003; Moleón et al. 2009; Prati et al. 2021), both of which typically characterise a species' range margins (MacArthur 1984; Case et al. 2005; Guo et al. 2005). High individual specialisation aligns with

dispersers having high heterogeneity in behaviour to support population expansion into novel environments (Cote et al. 2010). Importantly, I detected uniform movement of males away from the range margin, towards breeding colonies immediately prior to the breeding season (Ch 6; Salton et al. 2021); the complete abandonment of winter foraging grounds for the entire summer breeding period has not been recorded for males from breeding colonies. When males from the range margin visited breeding colonies their haul-out periods ashore were much shorter than those of males holding or challenging territories (Kirkwood et al. 2006), suggesting males from the range margin were not returning to the core of the range to breed. Similar behaviour was observed for three of eleven males tracked from a non-breeding area at their southern range margin in Australia (south-eastern Tasmania), where males were captured at fish farms and translocated to elsewhere in Tasmania (Robinson et al. 2008b).

This disparity in foraging behaviour between males at range margins and males from more centralised breeding colonies is rare in otariids, with males typically all dispersing away from breeding areas post-breeding (Boyd et al. 1998; Loughlin et al. 1999; Salton et al. 2022) or maintaining high fidelity to a colony throughout the non-breeding period (Lowther et al. 2013; Baylis et al. 2018). Prior information on the movements of other male otariids derives from breeding colonies, making it difficult to assess whether the patterns of foraging behaviour identified in this study persist across species, or even across other parts of these species' range margins. Clearly the foraging behaviour of male fur seals at their range margin can differ from that of males at breeding colonies, which emphasises that caution is required when modelling habitat use of carnivores recolonising their historic range if using information derived from individuals at the core of their species' range.

Interspecific foraging interactions

Interspecific interactions are important to understand during population recoveries, particularly where conservation efforts aim to allow and/or promote recovery of similar species living in sympatry. Interspecific interactions are thought to drive the foraging niche partition that is prevalent in various forms (spatial, temporal, dietary) among sympatric fur seals (Robinson 2002; Bailleul et al. 2005; Page et al. 2005b, 2005a; Page et al. 2006; Luque et al. 2007; Luque et al. 2008; Hoskins et al. 2017). This partitioning could support coexistence, but may also limit the niche space of one or both species to the point where it suppresses recovery of the species (Franco-Trecu 2014).

Current information on foraging niche partitioning of sympatric fur seals has focused on lactating females, with evidence from males derived from breeding colonies where intraspecific interactions may confound competition for niche space (Page et al. 2005a; Kernaléguen et al. 2012). Male Australian and New Zealand fur seals living in sympatry at a joint species range margin have small population sizes, and therefore interspecific competition and overlapping foraging niche was expected to be minimal. I found these males shared parts of their niche, particularly foraging space while they were at the range margin,

but had significant partitioning in the diet and diving aspects of their niche (Ch 5). Some dietary overlap but significant partitioning was also evident between these species at the same range margin from analysis of prey DNA in their scats (Hardy et al. 2017). This partitioning suggests there is potential for exploitative competition and/or competitive exclusion among sympatric fur seals despite small populations, such as those at a range margin.

At their western range margin, an increase in the Australian fur seals' population appears to be displacing an established New Zealand fur seal population (Shaughnessy et al. 2010), yet it is not clear what drives this displacement. One possibility is the male Australian fur seals, a thigmotactic species, are crowding the personal space of the New Zealand fur seals, which are not thigmotactic. Alternatively, it could be associated with competitive interactions at sea. I found niche overlap between males of these species was highest in their inshore habitat over the continental shelf, an obligative feeding area for both male and female Australian fur seals due to their benthic foraging mode (Hoskins et al. 2015; Volpov et al. 2015; Knox et al. 2017). By contrast male New Zealand fur seal foraging behaviour includes epipelagic foraging over the shelf break and off the continental shelf over deep water, similar to males tracked from a New Zealand fur seal breeding colony in South Australia (Page et al. 2006). Australian fur seals are larger and have a greater physiological capacity to make deeper and longer dives compared to smaller New Zealand fur seals (Costa et al. 2004; Page et al. 2005b; Spence-Bailey et al. 2007; Knox et al. 2017). Accordingly, their adaptations to exploit inshore environments may allow Australian fur seals to more efficiently exploit this environment, and when the density of seals increases the New Zealand fur seals move away to exploit prey patches further away as a consequence of competitive exclusion.

Interspecific competition for space and food resources can also take place across taxa; for example, fur seals and penguins (Barlow et al. 2002). This can be particularly problematic for many fur seals that rely on sparse, remote islands for breeding, like sub-Antarctic islands in the Southern Ocean (Croxall & Wood 2002). The limited breeding space is required by other seabirds and seals and forces them to coexist, which can require adjustment of foraging niche space to obtain the resources needed for survival, growth and reproduction. These aggregations of large predators have complex interspecific interactions to which predators have developed behaviour mechanisms for coexistence, that demonstrate they have spatial awareness of multiple competitors at a range of spatial scales (Vanak et al. 2013). In light of this, the consistent directed movement state of male Antarctic fur seals close to Heard Island (Ch 2; Salton et al. 2022) could be driven by high cumulative competition (intra and interspecific combined), as many of the breeding marine predators at Heard Island have restricted foraging ranges within close proximity to the island (Hindell et al. 2011; Patterson et al. 2016). Assigning interspecific competition as a driver of population change can be challenging given the complex ecological interactions that can influence population trajectories in these multi-predator assemblages (McMahon et al. 2005), however, such interspecific interactions would exacerbate pressures on recovering populations of fur seals.

The interspecific interactions that influence foraging behaviour are also likely to change as fur seals expand into areas where they have long been extirpated. Prey species at range margins may be naïve during initial encounters with predators and lack evasive strategies, but can make behavioural adjustments within a single generation (Berger et al. 2001; Carthey & Blumstein 2018). The introduction of high-order predators into a community can drive cascading effects on the structure and function of that community, which similarly can require predators to adapt their behaviour in order to persist and establish a population (Casini et al. 2008; Baum & Worm 2009; Hammerschlag et al. 2019; Smith et al. 2021). Added to this is the influence of environmental conditions on predator foraging, which has flow-on effects to interspecific interactions (Hammerschlag et al. 2006), and these interactions are expected to alter in light of current rapid ocean warming (Gilg et al. 2009; Grigaltchik et al. 2012). Therefore, the diet and foraging strategies of predators may need to adjust quickly for a population to persist at the range margin, and what appears to be productive habitat for dispersing individuals may become less attractive for breeding females to become established. Apparent changes in community structure associated with range expansions of fur seals (Kelaher et al. 2015) may change over time as populations become established and mature concurrently with other predator populations and an evolving climate.

Management and recovery of fur seal populations

While over-exploitation was responsible for historic decimation of fur seal populations (Gerber & Hilborn 2001) and ongoing human intervention and food limitations may have limited their recovery (Arnould et al. 2003; Baylis et al. 2015b), currently, negative interactions between fur seals and humans persist, on land and at sea, and require management. Negative interactions between humans and fur seals can interrupt vital activities, increase energy expenditure, reduce breeding success, cause injury or death, and regulate population growth (Stevens & Boness 2003; Back 2010; Perez-Venegas et al. 2021). Due to sex and life-stage specific foraging behaviours and dietary niche, these interactions could target cohorts differently and affect certain aspects of population growth and range expansion (e.g. breeding success and recruitment, immigration and emigration) (Leung et al. 2012). The response of fur seals to human stimuli and the consequence of the interaction can also vary depending on the size, structure and reproductive status of the fur seal population (Stevens & Boness 2003). Accordingly, there are varying complexities associated with assessing and monitoring interactions between humans and fur seals, and the interactions require different approaches to achieve mitigation.

At expanding range margins, interactions with recovering carnivores can be a novel occurrence that human populations are often ill-prepared to manage (Trouwborst et al. 2015; Moss et al. 2016; Aronsson & Persson 2017; Morehouse & Boyce 2017). Terrestrial sites used by seals are an interface for negative interactions with humans. These sites and the adjacent inshore habitats provide important refugia for the seals (Ch6; Salton et al. 2021). This may partly explain why the terrestrial sites used by male fur seals throughout their range often coincide with designated protected areas, where human activities

can be regulated, despite that protection not always be assigned with fur seals in mind (Ch6; Salton et al. 2021). It is not always intuitive where seals will establish new terrestrial sites during their range expansion. However, by tracking the movements of individuals at the range periphery, potential sites can be identified, and these sites can then be reviewed for protection; both for fur seals and the other values they provide. A multi-zoning approach within protected areas could help maintain shared use of the area by different stakeholders, though these zones should remain dynamic spatially and temporally to allow adaptive management within the protected area as community and habitat structure inevitably change. Establishing a network of such protected areas throughout the historical range of fur seal populations would be a proactive management approach to ecosystem restoration, and provide another management tool to support the coexistence of humans with fur seals during the seals recovery and range expansion.

7.2 Perspectives and future research directions

Fur seals have a diversity of foraging strategies to mitigate potential intraspecific competition associated with increased population density during recovery, as demonstrated in this study. These strategies can be shaped by sex-life stage differences in morphology and reproductive constraints, but inter-individual variability within cohorts indicates finer-scale individual plasticity in behaviour that could further reduce intraspecific competition and support coexistence at large colonies.

There has been a growth in the study of male fur seals, though there remains considerable uncertainty in the drivers of foraging behavioural change through time associated with intrinsic and extrinsic factors. There is also uncertainty about how different foraging strategies translate into inter-individual differences in reproductive success. A major constraint to performing such studies is the risk of death associated with anaesthesia of these large carnivores in field settings, and the collection of biotelemetry information at the appropriate fine-scale resolution required to accurately assess their ecological interactions (with prey, conspecifics, other species and humans) (Nathan et al. 2008; Nathan et al. 2012; Nathan et al. 2022). There has similarly been a surge in understanding juvenile fur seal foraging behaviour, and while the risks of handling these individuals for biotelemetry studies are lower, their small size limits the payload and therefore sensor type and battery life that are required to gain the fine-resolution data that will better progress our understanding of their ecological interactions, particularly during long-range dispersals. Combining accelerometers and machine learning models, such as those presented in this study, shows promise in providing the resolution to understand ecological interactions of these deep diving, marine predators (Sutton et al. 2021).

A clear deficit of knowledge remains in the foraging ecology of fur seals at their range margins, which is important to understand given their behaviour can differ from those of individuals foraging in central parts of the species range. The foraging behaviour of these high-trophic level carnivores at range

margins are shaped by different drivers compared to the range core, and potential novel interactions with humans and changes in ecosystem structure and function should motivate further study in this aspect of fur seal foraging ecology. While lessons can be taken from similar work in terrestrial systems, the drivers of foraging behaviour of marine predators are somewhat unique and more cryptic. Fortunately, many marine predator populations are showing signs of recovery and provide diverse field settings that will enable targeted studies of specific ecological interactions across different settings, and in so doing help develop generalised models to apply across species.

As conservation efforts allow and/or promote further recovery and expansion of large carnivore populations, changes to interspecific interactions can be expected. These interactions could compromise parallel conservation efforts for recovery of marine predators. For example, the recent predation of Antarctic fur seals by leopard seals that are expanding their range, which is dramatically reducing the population size and growth rate of the fur seals (Krause et al. 2022). Also, the miss-targeting of sea otters, particularly immature and male otters (demographics associated with range expansion) by predatory white sharks and sea otters will likely impact the range expansion of these recovering sea otter populations (Moxley et al. 2019). The ability for high-trophic predators to re-shape the structure and function of a community (Terborgh & Estes 2013) can change lower-trophic level dynamics in ways that are not fully understood (Valenzuela et al. 2013; Kelaher et al. 2015; Estes et al. 2016; Smith et al. 2021). Human stakeholders can hold different opinions on the changes, leading to conflict and re-assessment of priorities as successful recoveries create new or exacerbate existing issues (Carter & Linnell 2016; Jacobsen & Linnell 2016; Bombau & Szteren 2017; Lute et al. 2018). Resolving such conflicts is likely to direct future research on populations of high trophic level wildlife that show signs of recovery and re-occupation of former ranges.

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Appendix

Ethics approval

 MACQUARIE UNIVERSITY	ANIMAL RESEARCH AUTHORITY
AEC Reference No.: 2011/054	Date of Expiry: 12 December 2012
Full Approval Duration: 13 December 2011 to 12 December 2014 (36 months)	
Principal Investigator: Professor Rob Harcourt Dept of Environment and Geography Macquarie University NSW 2109 (02) 9850 7970 robert.harcourt@mq.edu.au 0421 780 434	Other principal Investigators: Iain Field 0427 355 879 David Slip 0432 886 278 Associate Investigators: Gemma Carrol 0422 775 086 Matt Carr 0417 041 086 Justin Clarke 0412 025 434
In case of emergency, please contact: Animal Welfare Officer - 9850 7758 Principal investigator – 0421 780 434 <i>or the Associate Investigators named above</i>	
The above-named are authorised by MACQUARIE UNIVERSITY AEC to conduct the following research:	
Title of the project Marine predators, marine parks and marine hotspots: Is zoning and effective conservation tool in a changing environment?	
Type of animal research and description of project: Wildlife research/conservation: This project aims to identify the underlying physical and biological drivers of Areas of Ecological Significance, by observing the movement of eight predator species and analysis in relation to the dynamic oceanographic conditions of the region and the static boundaries of marine reserves.	
All procedures must be performed in accordance with the AEC approved protocol.	
Species of animal: <i>Arctophthalmus forsteri</i> New Zealand Fur Seal; <i>Arctophthalmus pusillus doriferus</i> Australian fur seal; <i>Eudyptula minor</i> Little Penguin <i>Puffinus pacificus</i> Wedge tailed shearwater; <i>Puffinus griseus</i> Sooty shearwater; <i>Sterna bengalensis</i> Lesser crested tern; <i>Larus novaehollandiae</i> Silver gull	
Number: (Adults / Juveniles): 120/150; 120/150; 90/0; 150/0; 150/0; 150/0; 150/0	
Location: Montague Island, Jervis Bay and Batemans Bay marine parks	
Conditions of Initial Approval: 1. No more than 5% of blood volume (BV) is sampled. (A suggested estimate of BV is 60ml per Kg of body weight) 2. Copies of NPWS and MPA permit/licences are submitted to animal.ethics@mq.edu.au prior to research beginning	
Amendments considered and approved by the AEC since Initial approval: As approved by and in accordance with the establishment's Animal Ethics Committee. MACQUARIE UNIVERSITY AEC	
Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.	
This authority remains in force from 13 December 2011 to 12 December 2012 , unless suspended, cancelled or surrendered, and will only be renewed upon receipt of a PROGRESS REPORT before the end of this period.	
<hr/> Prof Michael Gillings Chair, Animal Ethics Committee	Date: <u>8 December 2011</u>

Supplementary material

Supplementary material 1

Understanding meta-population trends of the Australian fur seal, with insights for adaptive monitoring

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Understanding meta-population trends of the Australian fur seal, with insights for adaptive monitoring

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Abstract

Effective ecosystem-based management requires estimates of abundance and population trends of species of interest. Trend analyses are often limited due to sparse or short-term abundance estimates for populations that can be logistically difficult to monitor over time. Therefore it is critical to assess regularly the quality of the metrics in long-term monitoring programs. For a monitoring program to provide meaningful data and remain relevant, it needs to incorporate technological improvements and the changing requirements of stakeholders, while maintaining the integrity of the data. In this paper we critically examine the monitoring program for the Australian fur seal (AFS) *Arctocephalus pusillus doriferus* as an example of an ad-hoc monitoring program that was co-ordinated across multiple stakeholders as a range-wide census of live pups in the Austral summers of 2002, 2007 and 2013. This 5-yearly census, combined with historic counts at individual sites, successfully tracked increasing population trends as signs of population recovery up to 2007. The 2013 census identified the first reduction in AFS pup numbers (14,248 live pups, -4.2% change per annum since 2007), however we have limited information to understand this change. We analyse the trends at breeding colonies and perform a power analysis to critically examine the reliability of those trends. We then assess the gaps in the monitoring program and discuss how we may transition this surveillance style program to an adaptive monitoring program than can evolve over time and achieve its goals. The census results are used for ecosystem-based modelling for fisheries management and emergency response planning. The ultimate goal for this program is to obtain the data we need with minimal cost, effort and impact on the fur seals. In conclusion we identify the importance of power analyses for interpreting trends, the value of regularly assessing long-term monitoring programs and proper design so that adaptive monitoring principles can be applied.

Introduction

In the marine environment, monitoring the abundance and trends of a top predator can provide measures of ecosystem health and management success [1–5]. While population assessments for marine predators are challenging, they are generally easier and more accurate for species that breed on land, such as seabirds and pinnipeds, than for species that are wholly aquatic, such as cetaceans [6–9]. However, challenges remain: the proportion of the population that is ashore can be difficult to determine, breeding colonies can be difficult to access and in some cases, geographically dispersed [10–12]. Trends analyses can be limited by sparse or short-term abundance estimates for populations that can be logistically difficult to monitor regularly over time [13, 14], and few include a power analysis of the trend to understand its reliability [15–17]. An additional consideration is that surveying seabird and pinniped colonies may cause disturbance and potentially reduce breeding success, particularly if a greater frequency of surveys is required to improve the reliability of the trend. Especially when capacity is limited, monitoring may be focused on single sites. The limited spatial coverage of such studies reduces the usefulness of the data for broader applications such as trophic modelling or for informing ecosystem management [1, 18–20]. Ideally, survey design needs to take into account potential variation in population dynamics over space and time (depending on research or monitoring objectives), and ensure compatibility of survey methods over space and time [2, 5, 21].

In the case of fur seals, population estimates are frequently based on the number of live pups that are confined to the breeding colony (hereafter referred to as ‘colony’) for the first few weeks of life [22]. They are easy to distinguish from older fur seals due to their smaller size, behaviour and dark natal pelage, and the timing of births each year is synchronous and predictable. For example, the median birth date for Australian fur seals (AFS) *Arctocephalus pusillus doriferus* is late November, but colonies may not be accessible because of aggressive breeding bulls until late December or January [23]. Therefore, the year allocated to a breeding season represents the year the season began (e.g. a breeding season that begins in November 2013 and is surveyed in January 2014 is referred to as the 2013 breeding season). Fur seals are important upper trophic level predators that, in Australia, are protected marine species and pose specific management challenges that include fisheries and aquaculture interactions; economic value through tourism; potential impacts on other important marine species such as seabirds; and emergency situations such as oil spills [1, 24–26]. For these reasons, it is important to obtain accurate and relevant abundance information and interpret change in fur seal populations.

Ideally, to interpret population trends and drivers of change, which can be unique to a location or region, the selected index of change (in this case live pups) should be determined annually [2, 27,

[28]. Longer intervals between estimates may obscure short-term fluctuations and could delay recognition of changes in the population, as well as factors that influence population change [29]. Performing frequent e.g. annual estimates can be logistically challenging, for reasons such as inconsistent funding or adverse weather and, depending on the technique, can have implications for the welfare of animals. Also, while an index of population abundance is important, it can only detect change and does not allow for an understanding of the causes behind detected change in population. To understand density dependent effects: age-structure, mortality and density are useful parameters; and to understand how the environment may be affecting the population: foraging ecology, animal health and diet can be highly informative [2, 30–33]. In this paper we aim to determine whether the monitoring program for the AFS is achieving its goals: to determine the pup abundance of the AFS and provide trends for the population.

In Australia, it is thought that up to 26 AFS colonies existed prior to the onset of commercial harvesting in the early 1800s [34]. The uncertainty regarding the number of colonies is caused by an inability to determine the exact location of all sealing locations and a lack of clarity as to which species was harvested [35]. At the end of commercial harvesting in 1921, fewer than 10 AFS colonies were extant with greatly reduced numbers of fur seals [35]. The number and size of colonies in south-eastern Australia have regenerated subsequently (Fig 1), but with 20 breeding sites identified in 2007 the population is still considered to be in recovery [36].

Monitoring of AFS pup numbers was rare and sporadic up to the late 1960s [37] (Warneke unpub. data) and was then opportunistic and ‘surveillance’ in style until 2002 [34, 38]. At this point, the monitoring program adapted to a coordinated range-wide census performed every five years [39]. The population seemed to double in size between 1986 and 2002, from <10,000 to approximately 22,000 fur seal pups, at a growth rate of 5% per annum [39, 40]. This may have been in response to full legislative protection of the AFS, enacted in 1975. Prior to this, recovery of the population following the end of commercial harvesting in 1921 had been minimal, perhaps to some extent due to on-going lethal interactions with fisheries [40]. There was little overall growth in the population between 2002 and 2007 [36] when the total population was estimated at 120,000 seals, although the breeding range had expanded. It was speculated that the population had approached carrying capacity within the core breeding area of Bass Strait, limited either by breeding areas and/or prey availability, and that this may have contributed to the range expansion [36].

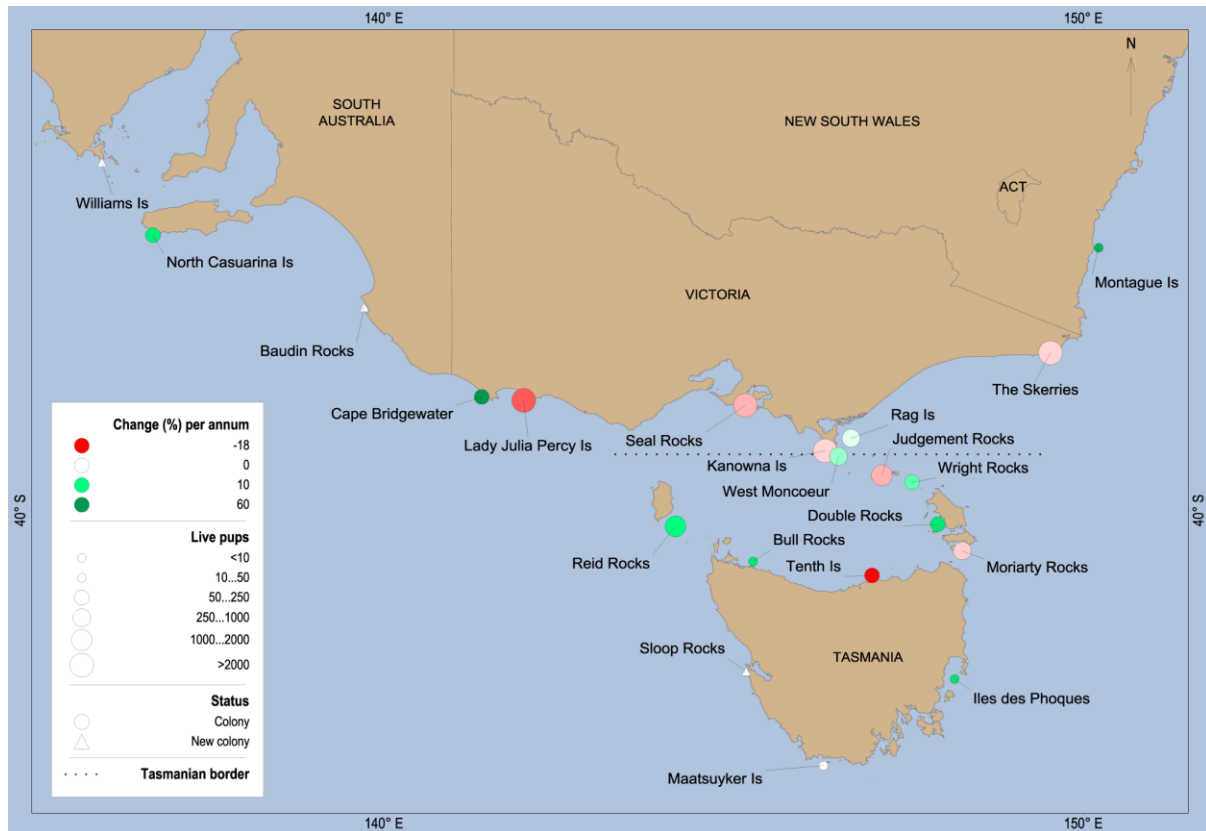


Fig 1. Map showing the range of the Australian fur seal with change (%) per annum between the 2007 census and the 2013 census. Note the pup estimate used for The Skerries and Maatsuyker Island was obtained in the 2014 breeding season and the % change per annum for Iles des Phoques were calculated from the 2002 census because the colony was not visited during the 2007 census. The number of live pups is indicated by the size of the colony shape. "Colonies" represent previously identified locations with pups and "new colonies" are those that were identified during the 2013 census.

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Surveys have used a variety of methods in response to research interest, opportunity and regional or state access to funding [23, 29, 38, 41–45]. The technique employed also varied at colonies over time, but was standardized by site for the censuses performed after 2002. In general, ground counts were used at smaller colonies (<500 pups) or colonies where the terrain was steep and dangerous for handling pups, capture-mark-resight (CMR) at larger colonies (>500 pups), and aerial surveys at colonies that were particularly difficult to access and/or had an open topography [36, 46]. At sites with high pup numbers, or more cryptic and rocky terrain where pups can hide, CMR is preferable because the resulting estimates have higher precision and accuracy than a ground or aerial count [36, 43, 47].

This 5-yearly census program was a great improvement, providing estimates of total abundance at intervals and the detection of positive population trends. However, because annual variability in pup abundance can be large [8] and surveys infrequent, the true rate of increase and the reliability of the trends are unknown. It is generally understood that the ideal longterm monitoring program is

adaptive and able to evolve over time [21]. Such a program is resilient and informative with regular review so that it can be modified to maximise success. In this study, we report results of a third range-wide census of pup abundance for the 2013 breeding season, and interpret temporal trends for each breeding colony from the long-term data. Using the updated time series, we estimate the power to detect changes in the trends and critically examine the success of this five-yearly census as a long-term monitoring program. We then provide recommendations to improve our ability to interpret the changes observed in the population and respond adaptively. This paper provides valuable information on how to design monitoring programs for pinnipeds using real data as a case study. We explore changes in the program that will facilitate a transition to an adaptive monitoring program to provide reliable and useful information for managers and stakeholders.

Materials and methods

In Victoria, the research was performed under animal ethics permit 1.2011 from the Phillip Island Nature Park Animal Ethics Committee and Wildlife Permit 10006785 from the Department of Environment and Primary Industries. In Tasmania, the research was permitted by Department of Primary Industries, Parks, Wildlife and Environment through Standard Operating Procedures for staff.

Species-wide census of pup production

The AFS has a single annual pupping period in the Austral summer and 90% of pups are born in a 3–4 week period with a peak in early December [23]. Given this breeding synchrony, it is reasonable to assume a closed population at each individual site, with equal likelihood of observing all pups at the time of the surveys since they are of a similar age and at a similar stage of development. This improves the accuracy of the abundance estimate and trend [48, 49].

To continue the five yearly monitoring program for the AFS and with the intention of obtaining temporally and spatially aligned data, a census of live pup numbers was conducted in 2013 across the range of the AFS as described by Kirkwood, Pemberton [36]. Between 2 and 6 replica assessments were performed at each colony. Some sites included sub-locations and mean estimates were calculated per sub-location then summed for a total estimate for the colony and standard errors calculated, repeating methods in Kirkwood, Pemberton [36]. To replicate the 5-year survey interval, we planned the census for the 2012 breeding season but funding constraints meant only Seal Rocks was surveyed (using) CMR in that season. Thus the main census was postponed to 2013. From December 2013 to February 2014, 20 out of 22 recognised colonies (colony descriptions are provided in Table 1). Two colonies, The Skerries and Maatsuyker Island, were not surveyed in 2013

due to a lack of resources but were surveyed one year later, in the 2014 breeding season. Additional surveys were performed at Cape Bridgewater in 2014 and 2015: this site is on mainland Victoria and consists of approximately 100 pups that are estimated via direct count. The simplified logistics of the mainland site at Cape Bridgewater enabled more frequent visits.

Temporal trends in pup abundance

Live pup numbers at several of the AFS colonies' were estimated by multiple methods over time (ground count, CMR, or aerial survey). To reduce the variability in the data caused by multiple methods being used at a site across a temporal scale, the predominant method for each site was selected and only data for that method from 1986–2013 were included for each site in the analysis. Data prior to 1986 were unreliable and not included. Eight colonies employed the CMR method, 12 used direct counts and one, aerial survey ([Table 2](#)). By only including data of the same method at a site, we reduced the variability caused by different methods.

Dependable and complete surveys of the total live pup abundance of AFSs were obtained during the three censuses 2002, 2007 and 2013. Three data points over eleven years were not considered a large enough time series for performing trends analysis for the total population combined. Additionally, the reduction in pup numbers during the 2013 census resulted in three highly variable results for the total population that could not be used with confidence. Therefore, the sub-set data with standardized methods for a colony ([Table 2](#)) were used to calculate trends separately by colony. This approach enabled the trends to be calculated over a larger temporal scale and the inclusion of data that was obtained outside the three range-wide censuses performed in 2002, 2007 and 2013. It also avoided combining data from colonies that were surveyed by different methods. Using the larger dataset improved the reliability of colony-specific trends. Additionally, trends can be site specific and vary depending on, for example, the maturity of the colony and its density and therefore much insight can be gained by analysing the trends separately [[28](#), [50](#)].

Dead pups were not counted throughout the AFS monitoring program: a major shortfall of the design. Based on mortality rates of AFS pups [[45](#), [51](#)], previous papers reporting census trends have added 15% to the CMR result to estimate total pup production, which is in effect a standardization that does not affect the trend. Correction factors have also been applied for some sites in an attempt to standardise data obtained by different methods and estimate a more accurate total number of live pups [[23](#), [39](#), [42](#), [43](#), [52](#)]. Total population abundance (adults, juveniles and pups) was then calculated by multiplying the total pup production estimate by between 3.5 and 4.5 [[1](#), [10](#), [36](#), [39](#), [45](#)]. Because correction factors and early pup mortality rates can be colony and year specific,

total population estimates based on these correction factors are of unknown accuracy. For this paper, we use only the raw data for live pups to perform the analysis.

Generalized Linear Models (GLMs) were applied to the data individually for each colony (live pup estimate ~ year) using the package “MASS” (v7.3–45) [57] in the R statistical environment (v3.1.1, R Core Team, 2013). All GLMs were fitted with a Negative Binomial distribution to correct for over-dispersion (highly inflated ϑ) [58]. The use of a Negative Binomial distribution also avoided the likelihood of standard errors being biased downward, resulting in spuriously large z-values [58]. The Negative Binomial GLM is not suitable for a small sample size, therefore dispersion parameters (ϑ) were provided to assess the confidence in pup abundance trends [58].

Table 1. Descriptions of colonies (n = 22) for the Australian fur seal and dates of pup estimates from December 2013 to February 2015.

Colony	Agency	Latitude	Longitude	Area (ha)	Height (m)	Breeding area description	Estimate method	Date of pup estimate
Victoria								
Lady Julia Percy Island (LJP)	PINP & DELWP	38°25'S	142°00'E	150	40	Inter-tidal platforms, cobble beaches and caves	CMR	07–10 Jan 2014
Seal Rocks (SR)	PINP	38°30'S	145°10'E	8	10	Cobble beaches and outcrop	CMR	28–30 Dec 2012, 28–30 Dec 2013
Kanowna Island (Kan)	Deakin Uni	39°10'S	146°18'E	130	90	Granite slopes and boulders	CMR	08–09 Jan 2014
The Skerries* (Ske)	PINP & DELWP	37°45'S	149°31'E	8	10	Boulder outcrop, three islets	CMR	19–21 Jan 2015
Rag Island (Rag)	Deakin Uni	38°58'S	146°42'E	3	15	Granite slopes and boulders	Count	20 Jan 2014
Cape Bridgewater (CB)	PINP & DELWP	38°23'S	141°24'E	1	0	Cave and inter-tidal platforms	Count	11 Jan 2014, 15 Jan 2015
Tasmania								
Reid Rocks (RR)	DPIPWE	40°14'S	144°09'E	10	8	Series of flat-topped, columnar-dolerite islets	Aerial	19 Jan 2014
West Moncoeur (WM)	DPIPWE	39°14'S	146°30'E	4	30	Steep granite slopes and boulders	Count	19 Jan 2014
Judgment Rocks (JR)	DPIPWE	39°30'S	147°07'E	14	50	Dome shaped, steep, granite, some flat areas	CMR	13–16 Jan 2014
Tenth Island (TI)	DPIPWE	40°57'S	146°59'E	1	8	Single, low basalt islet	CMR	07–08 Jan 2014
Moriarty Rocks (MR)	DPIPWE	40°35'S	148°16'E	4	7	Granite islets (East & West)	Count	20 Jan 2014
Wright Rocks (WR)	DPIPWE	39°36'S	147°33'E	4	30	Dome shaped, steep, granite	Count	17 Jan 2014
Double Rocks (DR)	DPIPWE	40°20'S	147°55'E	1	15	Flat, rectangular, granite	Count	20 Jan 2014
Bull Rock (BR)	DPIPWE	40°44'S	147°17'E	1	5	Columnar jointed basalt	Count	19 Jan 2014
Sloop Rocks (SIR)	DPIPWE	42°18'S	145°10'E	2	15	Granite islets, slopes and boulders	Count	07 Feb 2014
Iles des Phoques (IdP)	DPIPWE	42°25'S	148°09'E	8	7	Granite island	Count	30 Jan 2014
Maatsuyker* (Maat)	DPIPWE	43°38'S	146°17'E	186	284	Quartzite	Count	26 Feb 2015
South Australia								
Williams Is (WI)	SARDI & SA Museum	35°01'S	135°58'E	141	40	Upper platform of calcarenite laying over on 'a U-shaped ridge of pink granite	Count	14 Mar 2014
North Casuarina (NC)	SARDI & SA Museum	36°40'S	136°42'E	4	10	Low schist islet, calcarenite cap	CMR	28–29 Jan 2014
Cape Gantheaume	SARDI & SA Museum	35°04'S	136°42'E			Basalt rocky coastline above tidal zone	Incidental obs	Jan 2014
Baudin Rocks (Bau)	SARDI & SA Museum	37°06'S	139°43'E	5	12	Two major islets and at least 17 smaller islets of calcareous sandstone	Count	Mar 2014 (R. Roach, pers. comm.)
NSW								
Montague Island (Mon)	Macquarie Uni & Taronga Zoo	36°15'S	150°14'E	81	64	Basalt and granite island with rocky outcrops	CMR	13 Jan 2014

*Censused one year later than other colonies

Acronyms and abbreviations, listed alphabetically: Department of Environment Land Water and Planning (DELWP), Department of Primary Industries, Water and Environment (DPIPWE), Phillip Island Nature Parks (PINP), South Australian Research and Development Institute–Aquatic Sciences (SARDI), South Australian (SA), University (Uni).

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The sub-set of live pup data of Australian fur seals per colony and of consistent method, including ground counts (count), aerial surveys (aerial) and capture-mark-resight estimates (CMR).

Raw values were cross-checked, some were obtained from individual agencies and published records [29, 36, 38, 39, 42, 44, 45, 52–56]. Year is from the start of that breeding season (Nov-Dec). Full site names and abbreviations are provided below the table. The total number of pups (Total) is provided for the census years in 2002, 2007 and 2013.

Site	LJP	SR	Kan	Ske	Rag	CB	RR	WM	JR	TI	MR	WR	DR	BR	IdP	SIR	Maat	NC	WI	Bau	Mon	
Method	CMR	CMR	CMR	CMR	Count	Count	Aerial	Count	CMR	CMR	Count	Count	Count	Count	Count	Count	Count	CMR	Count	Count	CMR	Total
1986							775															
1987																						
1988																		0				
1989							1131	217			234	1					0	0				
1990								235			858											
1991		2826					885	259			897	1										
1992					0			225			665				0			0				
1993																					1	
1994									1859	354	1035							0				
1995						1		373	2365	173	689	3						0				
1996							1476		1971	386		3										
1997		4794					579	155	2548	277	345	1	0					0				
1998							210		2539	364												
1999	4867			1867			142	252	2421	287		1		2								
2000			1724	2237																		
2001														1	1							
2002	5899	4882	2301	2486	30	7	259	257	2427		1007	5		7	1						1	17,268
2003				2936																		
2004			3206																			
2005																						
2006																					2	
2007	5574	5660	2913	2705	277	7	395	204	2387	448	598	130	51	7	0		1	29			2	21,387
2008																						
2009																						
2010																						
2011																						
2012		3725																74				
2013	2659	4092	2429		295	120	1570	256	1710	138	486	187	157	21	10	16		75	2	6	19	14,248
2014				2254			95										13					
2015						146																

Colony names and abbreviations by state of Australia

Victoria; Lady Julia Percy Island (LJP), Seal Rocks (SR), Kanowna Island (Kan), The Skerries (Ske), Rag Island (Rag), Cape Bridgewater (CB).

Tasmania; Reid Rocks (RR), West Moncoeur (WM), Judgment Rocks (JR), Tenth Island (TI), Moriarty Rocks (MR), Wright Rocks (WR), Double Rocks (DR), Bull Rock (BR), Sloop Rocks (SIR), Iles des Phoques, (IdP), Maatsuyker (Maat).

South Australia; Williams Is (WI), North Casuarina (NC), Cape Gantheaume, Baudin Rocks (Bau).

New South Wales; Montague Island (Mon)

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Power analysis of population trend

An *a priori* power analysis using GPower (version 3.1.9.2, [59, 60]) was used to investigate the ability for surveys conducted at intervals of every three or five years to reliably detect changes in trends over a 30-year duration. This test is typically applied as a survey design tool prior to beginning a monitoring program. The Program GPower computes the statistical power analyses for z-tests (using the Poisson distribution for count data) and we wanted to detect an effect size of 30% change with 90% confidence ($p < 0.10$) and power of 0.80; this effect size was considered to be realistic and achievable.

To obtain the power of the GLM trends for each individual colony, we performed a *posthoc* analysis including the raw sub-set of data and the time intervals between each survey point (Table 2), and then examined the power for the same trend with a survey interval of every three years and every year for comparison. *Post-hoc* power analyses typically result in better confidence with a large sample size, and/or small survey intervals with low annual variability and a strong positive or negative trend. This prohibits a stable population from having a high power. Therefore, we used the

power of each trend by colony as well as the difference between the 95% confidence interval of that trend to examine the reliability of each trend for each colony.

The *post-hoc* power analysis was applied following procedures in [61–63], using ‘Trends’ (v3.0, Gerrodette and Brandon 2015, <https://swfsc.noaa.gov/textblock.aspx?Division=PRD&ParentMenuId=228&id=4740>, accessed 1 June 2016). To account for the differences in the number and periodicity of surveys (Table 2), each colony was analysed individually by defining the total duration of the study (i.e. 1986 to 2015), the number of surveys (n) and the survey interval. Inputs from the corresponding GLM regression results for that colony were included i.e. the rate of change or slope of the regression line; the coefficient of variation p ($CV = 1/Theta$), which provides a measure of the precision; the significance level (probability of Type 1 error); and the power level or probability of detecting a true change in population ($1 - \text{probability of Type 2 error}$). One of these five parameters could be estimated when the others were provided.

The power analysis variance structure was set to ‘constant’ because in a fur seal population, CV can be expected to increase with abundance (see Hatch 2003 for a detailed explanation). We also set the significance level to 0.05 using a two-tailed test and for the type of change, selected an exponential model (from two choices exponential or linear). We then selected either a positive or negative trend as applicable. The minimum number of samples (or surveys) required was assessed at power = 0.8. The program ‘Trends’ would not accept an input of zero slope ($\beta \text{ year} = 0.0$), therefore where this occurred, 0.01 was used. Power was not calculated for trends with $\vartheta > 5,000$ because these trends were produced from minimal data and the power of such trends could not be calculated.

Results

Species-wide census of pup abundance

The 2013 census of the AFS resulted in a total of 14,248 live pups at 20 colonies (Tables 2 & 3). This is an underestimate of species-wide pup abundance because The Skerries (2,254 live pups) and Maatsuyker Island (13 live pups) were surveyed in 2014 and their numbers not included in the 2013 census (Table 2). We combined these results from 2014 with the 2013 census results to enable a complete comparison across censuses (Table 3). The 2013 census detected a reduction from the 2007 census of 21,387 live pups at 20 colonies (Table 3). Several colonies experienced a reduction in pup abundance in the 2013 census for the first time since monitoring began, with colonies of greater pup abundance (>1500 pups: Lady Julia Percy Island, Seal Rocks, Kanowna Island, The Skerries and Judgment Rocks) showing a negative percentage change in pup numbers compared to the 2007

census ([Fig 1](#), [Table 3](#)). Reid Rocks, also with >1500 pups showed a large increase compared to 2007 ([Fig 1](#), [Table 3](#)). The largest percentage changes in pup number occurred in smaller colonies (+60 at Cape Bridgewater and -18 at Tenth Island, [Fig 1](#), [Table 3](#)). Two colonies, Walker Island and Wender Island, both with one pup in 2007, were not visited in 2013 [[36](#)]. Three colonies were new additions to the known breeding sites, Walker Island and Baudin Rocks in South Australia and Sloop Rocks in Tasmania ([Fig 1](#)). Williams Island extended the known breeding range of the AFS to the west of their former range. The standard errors for the live pup estimates show a high level of precision for the estimates in 2013 ([Table 3](#)).

Temporal trends in pup abundance

According to the trend analysis, ten colonies showed significant changes over the study period ([Table 3](#), [Fig 2](#)). However, the degrees of freedom were small and the dispersion parameter (ϑ) was highly inflated for all but three (Lady Julia Percy Island, Cape Bridgewater and Wright Rocks) of these nine colonies ([Table 4](#)). The negative binomial can better predict the trend for over-dispersed data (dispersion parameter for Poisson distribution is taken to be "1"), however when the dispersion parameter is highly inflated (e.g. $\vartheta = > 5000$) the result of the GLM is less reliable [[58](#)]. At Lady Julia Percy Island, Judgment Rocks and Tenth Island, the large reduction in pup numbers detected in the 2013 census ([Table 3](#)) had a strong influence on the trend for those colonies ([Fig 2](#)).

Table 3. Estimated Australian fur seal pup numbers from the 2013 census, compared with previous censuses in 2002 and 2007 [39, 54].

Note the 2002 Kanowna Island pup estimate is a direct count and therefore not included in the trend analysis that is based on capture-mark-resight results (CMR). Where no standard error (s.e.) is reported, single direct counts were performed. Data for The Skerries and Maatsuyker Island were obtained in 2014 not during the 2013 census, but are provided here for comparison with previous censuses. 2013 Census results without the inclusion of these two sites results in 14,248 live pups.

A

Site	2013 census			Previous census		% Change per annum 2007–2013
	No. resight estimates	Pups marked CMR	Live pups (s.e.)	2007 Live pups (s.e.)	2002 Live pups (s.e.)	
VICTORIA						
Seal Rocks	6	1787	4,092 (38)	5,660 (83)	4,882 (51)	-5.3
Lady Julia Percy Is	6	1449	2,659 (16)	5,574 (73)	5,899 (43)	-11.6
Kanowna Is	25 ^B	1110	2,429 (27)	2,913 (110)	2301 (21) ^A	-3
The Skerries	4	924	2,254 (33)	2,705 (31)	2,486 (41)	-3
Rag Is			295	277 ^A	30	1.1
Cape Bridgewater			120	7 ^A	7	60.6
SUB-TOTAL			11,849	17,136	15,605	-6.0
TASMANIA						
Judgement Rocks	6	558	1,710 (24)	2,387 (75)	2,427 (100)	-5.4
Reid Rocks			1,570 (60)	395 ^C	259 (34) ^C	25.9
Moriarty Rocks			486 (09)	598 (09)	1,007 (08)	-3.4
West Moncoeur			256 (03)	204 (06)	257 (06)	3.9
Wright Rocks			187 (02)	130 (01)	5	6.2
Double Rocks			157 (02)	51	-	20.6
Tenth Is	12	94	138 (04)	448 (20)	124	-17.8
Bull Rock			21	7	7	20.1
Sloop Rocks			16	-	-	-
Iles des Phoques			10 ^A	0	1	46.8
Maatsuyker Is			13 ^A	1 ^A	-	44.3
SUB-TOTAL			4,564	4,221	4,087	1.3
NEW SOUTH WALES						
Montague Is	7	18	19 (0.3)	2	1	45.5
SUB-TOTAL			19	2	-	45.5
SOUTH AUSTRALIA						
North Casuarina Is	6	35	75 (3.2)	29 (1.3)	-	17.2
Williams Is			2 ^A	-	-	-
Baudin Rocks			6 ^A	-	-	-
Cape Gantheaume			1 ^D	0	-	-
SUB-TOTAL			84	29	-	17.2
			16,516	21,388	19,692	-4.2

^A Direct count

^B At Kanowna Is, four, eight and 25 resight estimates were performed at two, one and five sub-locations respectively

^C Counts differ from Kirkwood et al. (2010) and do not include any multiplicative factors: data confirmed by S. Thalman, DPIPWE, no s.e. available for 2007

^D Incidental observation and a possible hybrid with *Arctocephalus forsteri*, one pup also seen in 2012–13, and a hybrid identified in 1995 [55]

Direct count ^a At Kanowna Is, four, eight and 25 resight estimates were performed at two, one and five sub-locations respectively ^c Counts differ from Kirkwood et al. (2010) and do not include any multiplicative factors: data confirmed by S.

Thalman, DPIPWE, no s.e. available for 2007 ^d Incidental observation and a possible hybrid with *Arctocephalus forsteri*, one pup also seen in 2012–13, and a hybrid identified in 1995 [55]

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Power to detect changes in trends

The *a-priori* power analysis based on the GLMs identified that when surveying every five years, we would require 15 surveys (75 years) to detect a 30% change in the population with 90% confidence ($p < 0.10$) and 0.80 power. If colonies were surveyed every three years, nine surveys would be sufficient (27 years total).

In this study, the trends with higher power and therefore greater reliability within the parameters defined in the methods were at colonies Lady Julia Percy Island, Cape Bridgewater, Judgment Rocks, Moriarty Rocks and Wright Rocks (Table 4). The high power was caused by different attributes of each trend: for Lady Julia Percy Island, it was the large influence of the 2013 data point and the associated steep decline in the slope; for Cape Bridgewater, it was because the relatively young colony had been in a phase of exponential growth; in the case of Moriarty Rocks, there was a large sample size in terms of number of surveys; and for Wright Rocks, it was because the colony, despite not being a new colony, was in a strong growth phase (Table 4, Fig 2). Furthermore, the relatively wide confidence interval for Wright Rocks (Table 4) is an example of when the confidence interval of a trend may better express the reliability (or lack thereof) of the trend rather than the power. This confidence interval is wide because the two most recent censuses (2007 and 2013) show a strong positive deviation from the previous assessments for the site (1989–2002 in Table 2) that had also been performed more frequently (Fig 2). At Judgment Rocks, the four sequential and similar pup estimates from 1996 to 1999 improved the power of the trend (power = 0.22; -CI, +CI = -0.04, +0.03, Fig 2).

For several colonies that had a greater number of surveys (Table 4, i.e. Seal Rocks, West Moncoeur, Tenth Island), the power of the trends was lower than expected (< 0.20). However, the upper and lower confidence interval for colonies Seal Rocks and West Moncoeur were small (Table 4), indicating good reliability in the trends for these colonies (Fig 2). For colony West Moncoeur, the slope of the line was zero and the small upper and lower confidence intervals identified that this trend was reliable (Table 4). Seal Rocks also had a higher confidence (small confidence intervals) in the trend than the colony at Tenth Island and some of the other colonies for which the trends had high power (Lady Julia Percy, Cape Bridgewater, Moriarty Rocks and Wright Rocks); however, Tenth Island had a larger spread of pup estimates over a shorter time period (Fig 2 and Table 2). Power

analyses were not performed for any trends with high dispersion parameters ($\theta > 5,000$) because of the small sample size and lack of reliability.

Generally, the power of a trend increased as the interval between estimates decreased (Table 4). Standardising the interval to three years between estimates therefore resulted in increased power, except for those colonies that had intervals between estimates of less than three years, or data clustered over short time periods.

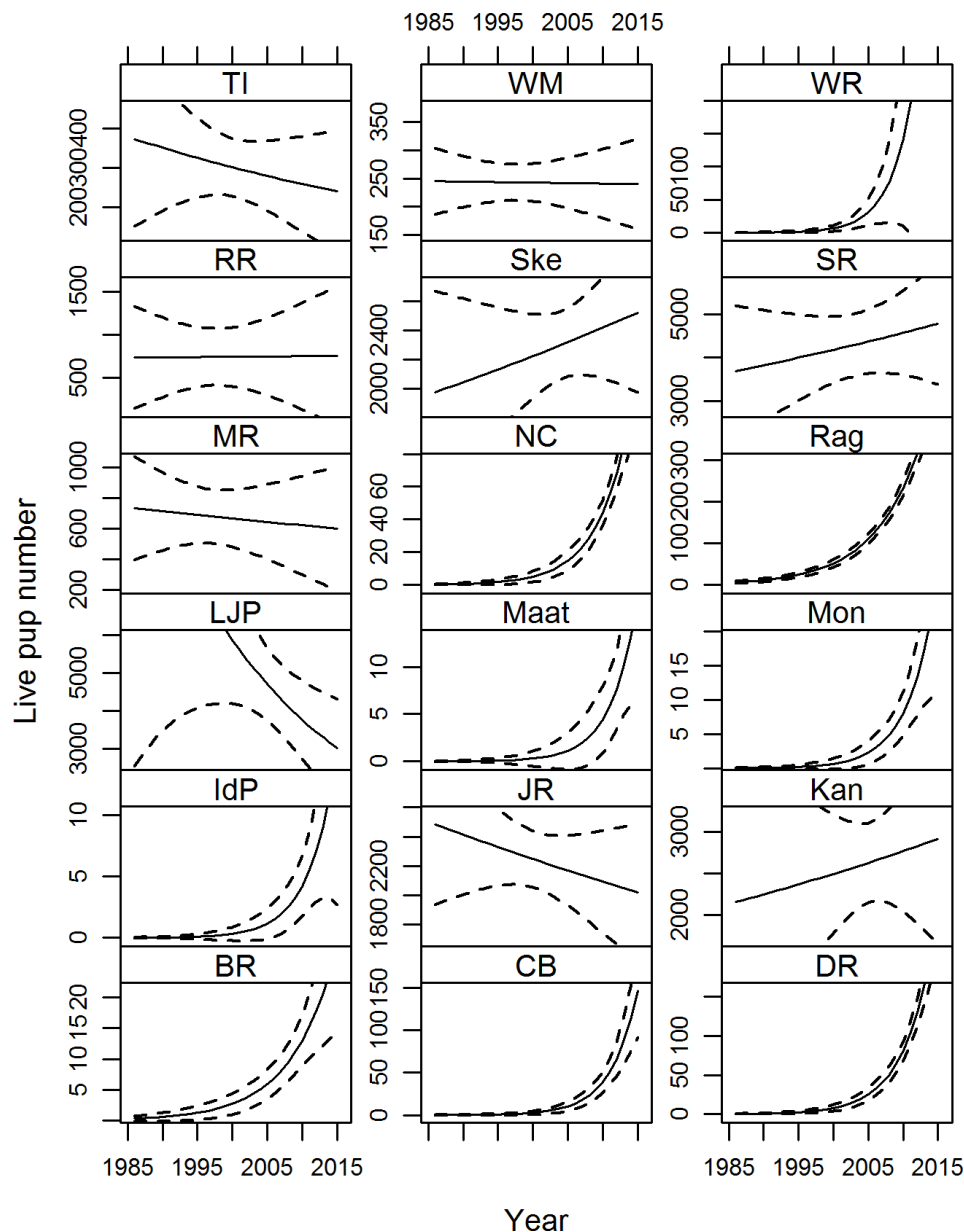


Fig 2. Smoothed predicted curves fitted to raw counts of Australian fur seal pups at breeding colonies in southeastern Australia, estimated using Generalised Linear Models with negative binomial distributions. Colony abbreviations are: Tenth Island (TI), West Moncoeur (WM), Wright Rocks (WR), Reid Rocks (RR), The Skerries (Ske), Seal Rocks (SR), Moriarty Rocks (MR), North Casuarina (NC), Rag Island (Rag), Lady Julia Percy Island (LJP), Maatsuyker Island (Maat), Montague Island (Mon), Iles des Phoques (IdP), Judgment Rocks (JR), Kanowna Island (Kan), Bull Rock (BR), Cape Bridgewater (CB), and Double Rocks (DR).

Table 4. Results of the 2007–08 and 2013–14 Australian fur seal censuses, the associated trends and power analyses. All significant trends were positive with the exception of Lady Julia Percy Island (LJP). Insignificant trends were both positive and negative as shown by β Year. The dispersion parameter is identified by theta (θ).

Negative Binomial GLM										Power analysis using "Trends" program					
Col	df	β Year	Intercept	z	P	- CI	+ CI	Dev Exp	θ	CV	MA	Trend duration (years)	Power (int = raw data)	Power (int = 3)	Power (int = 1)
Sites ordered by +/- significant trends, then ordered by df and smallest CI															
LJP	3	-0.04	97.52	-2.26	0.024	-0.09	0.00	51.07	23.13	0.208	4750	15	0.23	0.91	1.00
WR	8	0.28	-550.33	6.50	0.000	0.20	0.36	87.41	1.96	0.693	37	24	1.00	1.00	1.00
CB	5	0.27	-530.91	7.73	0.000	0.20	0.34	93.51	11.59	0.294	63	21	1.00	1.00	1.00
BR	4	0.16	-313.58	4.91	0.000	0.10	0.22	85.31	>10,000	0.003	8	15	-	-	-
Mon	4	0.25	-505.27	4.53	0.000	0.15	0.37	88.71	>5,000	0.013	5	21	-	-	-
IdP	4	0.26	-519.82	3.32	0.001	0.13	0.45	80.19	>10,000	0.005	2	13	-	-	-
Rag	3	0.15	-297.11	17.89	0.000	0.13	0.17	74.39	>10,000	0.001	151	21	-	-	-
NC	3	0.22	-431.97	7.58	0.000	0.16	0.28	93.53	>10,000	0.004	45	17	-	-	-
DR	2	0.23	-463.48	10.45	0.000	0.19	0.28	95.26	>10,000	0.002	69	17	-	-	-
Maat	2	0.27	-544.45	2.60	0.009	0.17	0.46	99.85	>10,000	0.003	5	25	-	-	-
Sites with insignificant trends ordered by "Power (int = raw data)"															
MR	9	-0.01	20.10	-0.39	0.699	-0.04	0.03	1.25	5.74	0.417	681	25	0.25	0.23	0.55
JR	8	-0.01	22.01	-0.97	0.334	-0.02	0.01	8.48	60.14	0.129	2247	20	0.22	0.25	0.60
WM	9	0.00	6.94	-0.08	0.935	-0.02	0.02	0.06	24.78	0.201	243	25	0.18	0.17	0.41
TI	7	-0.02	35.95	-0.76	0.447	-0.06	0.03	5.51	8.45	0.344	303	20	0.15	0.17	0.40
SR	6	0.01	-6.23	0.74	0.457	-0.01	0.03	6.27	25.95	0.196	4372	23	0.13	0.16	0.31
Ske	4	0.01	-9.00	0.90	0.366	-0.01	0.03	13.22	78.95	0.113	2310	16	0.12	0.09	0.28
RR	7	0.01	-19.49	0.36	0.719	-0.04	0.07	2.20	1.71	0.765	676	28	0.07	0.11	0.22
Kan	4	0.01	-13.08	0.50	0.620	-0.03	0.06	3.95	23.32	0.207	2642	14	0.06	0.07	0.09

Note: Negative Binomial Generalised Linear Models (GLM) were applied to the raw pup abundance data presented in Table 2; regression results are provided including the percentage deviance explained (*Dev Exp*) and the dispersion parameter (θ) of the GLM. Colonies (*Col*) with high *Dev Exp* and low θ (reliable results) are shaded, as are sites with no significant change detected but high power. Power analyses were not performed for sites with unreliable trends ($\theta > 5000$). Power analyses were based on the mean abundance (*MA*) for each colony, the beta value for year (β Year, the slope of the trend) and the trend duration (years). *Int = raw data* represents the power analyses performed using the raw data provided in Table 3, including the associated time intervals between surveys (in years); *int = 3* and *int = 1* are the simulated power calculations based on three and one year sampling intervals. Insignificant trends for Moriarty Rocks (MR) and Judgment Rocks (JR) showed high power (>0.20).

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Discussion

In this paper, we report the first reduction of annual pup production (-4.2% per annum, Table 3) by the AFS since species-wide protection was implemented in 1975. Between 1986 and 2002, growth was sustained at estimated rates $>5\%$ per annum resulting in a more than doubling of the pup production [39]. Between 2002 and 2007 pup production appeared to stabilize [36]. Attempting to communicate the reduction in pup numbers for the 2013 census prompted an examination of the capacity of a 5-yearly census to detect meaningful change in the population.

The observed reduction in the total number of live pups in 2013–14 relative to previous years primarily reflected reduced numbers of pups at the largest colonies. Despite the overall reduction in live pup numbers, some colonies showed an increase in numbers and three new colonies were identified (Fig 1). The reduction in pup numbers may indicate that the population has approached a regional carrying capacity, or density-dependant capacity at the established colonies as was speculated by Kirkwood, Pemberton [36], or it could be a first data-point from a sustained and as yet undetected decline. Alternatively, it could simply be because this was an unusually poor period for food availability. Such contrasting interpretations highlight a shortcoming in the ability of a 5-yearly census to quickly identify even gross changes. However, even with more frequent surveys, to gain a

detailed understanding of population changes, associated information including demographic and foraging ecology data would be required [4, 14, 33].

Interpreting changes in pup numbers

Bottom up-effects of environmental variability mediated through prey availability may have caused the reduction in AFS pup numbers in 2013–14. Indeed, food availability for predators in Bass Strait was considered to be low during this time [64, 65]. Seabirds foraging on the shelf of Bass Strait also had poor breeding seasons that year. Large numbers of short-tailed shearwaters (*Ardenna tenuirostris*), which overlap in breeding range with the fur seals, were found dead along the Australian coastline and the ‘wreck’, as such an occurrence is termed, was related to storms and starvation over the expanse of their migration [64]. Breeding success in 2013 was reduced for: short-tailed shearwaters, Australasian gannets (*Morus serrator*) and little penguins (*Eudyptula minor*) in south-eastern Australia [66–68]; little penguins (the number of chicks per breeding female for 2013 was 0.60, compared to the average of 1.08, SD 0.2 from 1997–2012) and crested terns (*Thalasseus bergii*) on Phillip Island (Unpub. data, Phillip Island Nature Parks, Australia); and shy albatross (*Thalassarche cauta*) on Albatross Island in western Bass Strait, where breeding success was only 26%, the lowest since monitoring began in 1989 [65]. At larger fur seal colonies effects of variability in prey resources may be exacerbated because of the increased likelihood of intraspecific competition for resources [28, 69–71]; while we do not have the supporting evidence, this could explain why the drop in live pup numbers were mainly associated with larger colonies such as Lady Julia Percy Island, Seal Rocks, Kanowna Island, and The Skerries.

Kirkman, Yemane [72] also reported varied trends between colonies of the conspecific Cape fur seal (*Arctocephalus pusillus pusillus*) in southern Africa. This included decreases at several of the largest colonies, stability or growth at other colonies and development of new colonies, similar to what has been shown for the AFS in this study, although the latter’s population is only 5% that of the Cape fur seal. Effects (or side-effects) of management, density dependence and shifts in prey distributions have been identified as potential causes of the declines in the case of the Cape fur seal [72].

Prey availability is the most likely regulator of population size for the AFS and while the reduction in pup abundance may be an isolated event, it is the first reduction recorded by censuses that have previously captured population growth. Tenth Island had the highest % change (-17.8% per annum) for all colonies (Fig 1, Table 3), however, this colony is known for highly variable pup estimates because it is low lying and pup numbers are affected by wave wash [29]. The reduction in

pup numbers at Lady Julia Percy Island in 2013 compared to 2007 (-11.6% per annum) is the next largest reduction in pups. An alopecia syndrome that affects thermoregulation and may reduce female survival in AFSs has been recognised at Lady Julia Percy Island [73] and may have exacerbated the pup reduction at this site. It is thought that this syndrome could be the expression of endocrine disrupting dioxin persistent organic pollutants [74]. Fluctuations in live pup counts can be caused by abnormally high early pup mortality (e.g. due to summer storms) before a census, or a high rate of aborted pregnancies prior to the breeding season, and therefore may not be a good reflection of the breeding population when considered in isolation [29, 75]. In Antarctic fur seals (*Arctocephalus gazella*), pup mortality correlates to colony density because as populations increase and space is less available, more pups may die from being crushed or separated from mothers [76]. However, it is important to appreciate that colony densities for Australian fur seals are far lower than those observed for example, in Cape fur seals and Antarctic fur seals at South Georgia, where density dependent effects on pup mortality are higher [72, 76]. Demographic assessments including counts of dead pups would be needed to differentiate recruitment issues from a short-term reduction in pup production.

Reviewing the AFS monitoring program

In 2013, we detected the first drop in live pup numbers since the beginning of the monitoring program in the 1960s. Unfortunately, lack of corroborative data prevents us from identifying the cause of this drop. To investigate the reasons behind population change, information relating to diet and demography including seal health, density and age structure are required. [32, 69, 76, 77]. However, even with such information, it can be difficult to tease apart the drivers of population change. For example, competition can act on a population of high density to reduce population growth, and also Allee effects can work the other way when there are benefits to living in group such as predator detection and avoidance [71, 78].

Oceanographic influences and food supply will vary across the range of the AFS [79–82], likely affecting diet and demography [83]. The diet of the Australian fur seal is being monitored [30], there has also been some research into disease, pup body condition and health [73, 74, 84]. Future research needs to combine these projects temporally and spatially so that we can interpret the changes we are observing in the ecosystem. Increasing the parameters to be measured without reducing the sites being visited will increase the cost, effort and logistics for the monitoring program. It is therefore necessary to prioritise several sites for more intensive monitoring.

For Australian fur seals, ecological differences exist between colonies in different locations, such as the influence of different current and upwelling systems, proximity to urbanization and varying land-use practices as well as variation in diet, and demography ([Fig 1](#), [Table 5](#)). Also, recently established colonies and those on the boundaries of the range may exhibit different demographic parameters and different trends than longer established colonies in the centre of the range [[85](#)]. These are all factors that may influence the contrasting trends that were evident between colonies ([Tables 4 and 5](#), [Fig 2](#)). Several management-agencies obtain and use the data, each with their own challenges and objectives. This adds additional complexity and makes it difficult to prioritize colonies to improve efficiency. However, in an attempt to do so, we have roughly grouped the colonies according to their attributes and trends ([Table 5](#)). It may be possible to select one colony from each group to represent those attributes as done by Kirkman, Oosthuizen [[2](#)]. While outside the scope of this paper and because of current data deficiencies, a decision-theoretic framework could be applied to assist with designing an improved monitoring program for the Australian fur seal [[86](#)].

The power analysis of the trends in this study shows that we could obtain more reliable trends by sampling more frequently than every five years. For species with extensive ranges that are spatially complex, increased effort may be necessary to obtain reliable trends; this is even more pronounced when populations reach carrying capacity and abundance estimates fluctuate around a certain level. However, increased sampling effort can lead to increased disturbance and may not be logistically possible. The Trilateral Working Group (TWG) comprising representatives from The Netherlands, Germany and Denmark performed a power analysis of their monitoring program for the harbour seal (*Phoca vitulina*) in the Wadden Sea [[17](#)]. After 45 years of annual monitoring, this group aimed to reduce sampling effort to every second or third year. Contrary to what they had hoped, their annual program lacked sufficient power to rely on the results of their trends; therefore they maintained the annual monitoring program. For the Australian fur seal, the best strategy is to balance the spatial and temporal scale of the monitoring program with increasing the parameters being sampled. We may have to accept a level of uncertainty in the trends analysis until we have more data while we incorporate those parameters that will help us to understand any changes observed in the population.

Table 5. Results of the 2013 and 2007 Australian fur seal censuses, ordered by group and then number of live pups in 2013. Colonies are grouped by similar attributes of capacity, major regional feature and trend. Potential impacts and threatening processes are identified where they exist. These attributes may be taken into account for planning and prioritising monitoring in the face of logistic or funding constraints. Information was obtained from the literature [29, 73, 79, 80, 103–107] and from results of this study. Group refers to colonies with similar abundance and trends in 2013. Storm mortality refers to storm-induced pup mortality that can cause large fluctuations in estimates. Trend summarises results from Table 4 and Fig 2. The state provides the region of management—Victoria (VIC), Tasmania (TAS), New South Wales (NSW) and South Australia (SA).

Group	Colony	Near capacity	Regional feature	Potential impacts	Trend (Fig 2)	State
1	Seal Rocks	perhaps	Close to Port Phillip Bay and the city of Melbourne and Western Port	Oil spill	Slowing growth	VIC
1	Kanowna Is.	uncertain	Wilson's Promontory and East Australian Current (EAC)	Overlap with Danish seine fishery	Growth	VIC
1	The Skerries	uncertain	EAC	Storm mortality; Overlap with Danish seine fishery	Growth	VIC
2	Lady Julia Percy	perhaps	Bonney Upwelling	Unique disease; Overlap with trawl fisheries	Decline	VIC
3	Judgement Rocks	uncertain	Eastern Bass Strait, EAC		Decline	TAS
3	Moriarty Rocks	uncertain	Eastern Bass Strait, EAC	Storm mortality	Decline	TAS
3	Tenth Is.	Yes	Eastern Bass Strait, EAC	Storm mortality	Decline	TAS
4	Reid Rocks	uncertain	West Tasmanian Upwelling	Storm mortality; Overlap with trawl fisheries	Growth	TAS
4	Rag Is.	no	EAC		Logistic growth	VIC
4	Wright Rocks	no	EAC		Logistic growth	TAS
4	Double Is.	no	NE Tasmanian upwelling		Logistic growth	TAS
4	Cape Bridgewater	no	Bonney Upwelling		Logistic growth	VIC
5	West Moncoeur	uncertain	Eastern Bass Strait, EAC		Stable	TAS
6	North Casuarina	no	Localised Upwelling		Logistic growth	SA
6	Bull Rock	no			Logistic growth	TAS
6	Montague Is.	no	Edge of range		Logistic growth	NSW
7	Sloop Rocks	no		Overlap with trawl fisheries; Aquaculture interaction	Identified 2014–15	TAS
7	Maatsuyker	no	Edge of range	Overlap with trawl fisheries; Aquaculture interaction	No trend	TAS
7	Illes des Phoques	no		Aquaculture interaction	No trend	TAS
7	Baudin Rocks	no	Bonney Upwelling		Identified 2014–15	SA
7	Williams Is.	no	Edge of range		Identified 2014–15	SA
7	Cape Gantheaume	perhaps with <i>A. forsteri</i>				SA

The ideal paradigm for the long-term monitoring of populations is adaptive monitoring [21], a paradigm that aligns with adaptive management and structured decision-making [87, 88]. Adaptive management aims to reduce uncertainty, incorporate resilience and accrue information to inform future decision making thereby improving the outcomes of management actions [88]. Adaptive or dynamic monitoring relies on a robust conceptual model of the ecosystem under study and aims to learn from that environment and account for uncertainty in the measurements and temporal variation [89]. It incorporates clear objectives, tractable questions, good statistical design, and an ability to alter the program in response to ecosystem changes, technological advances, and altered information requirements [21, 90]. Importantly, collaboration between scientists, resource managers and policy makers also ensures that the program remains relevant [21, 90, 91]. Together, these components readily differentiate the paradigm from *ad hoc*, reactive, or surveillance monitoring [88, 92, 93].

An improved monitoring program would be to survey selected sites for live and dead pups, pup body condition and health, and density of seals at least every three years and perform a range-wide census every 10 years. As a very basic requirement, dead pups should be counted at the same time as live pups to help elucidate changes in pup survival that could be related to density, the ability of mothers to provision pups, or disease [2, 70, 94, 95]. Importantly, the method of survey needs to be consistent for each site over time. Regular assessments of the program should be performed to ensure goals are being achieved. After the census, the program should be reviewed and sites prioritised for the next 10 years (for an example of a similar sampling regime, see Wege et al 2016 [14]). This approach follows the adaptive monitoring paradigm because it allows for review and change. It incorporates new information and allows changes to the sites of focus, the frequency of monitoring, the parameters being measured and the time frames of surveys. However, this monitoring program does not identify new, establishing, colonies, which is important for monitoring changes in distribution. Periodical aerial surveys may be the most cost-effective method for detecting the colonization of new sites.

There is great potential for using remote piloted aircraft (RPAs) to perform surveys as the technology becomes more accessible and cost effective [96–100]. The major benefits of using RPAs is the reduced effort and cost compared to a CMR (for example), reduced disturbance to the seals, provided height limits are tested, and the potential for an increase in the frequency of surveys as a result. Clearly, if the method at a colony is going to change, it is vital that the estimates be calibrated [101]. RPAs also allow the long-term retention of images that can be revisited for further research and the ability to monitor abundance and density of all age classes (adult females, adult males, sub-

adult males, juveniles ~1–3 years of age and pups) [102]. Such information can be used to better measure changes in abundance.

Management considerations

It is important that a revised monitoring program provides satisfactory outputs for natural resource managers and policy makers. The AFS was harvested to near extinction in the early 1800s, but is now a nationally protected species under the *Environment Protection and Biodiversity Conservation Act* (EPBC Act 1999) and considerable importance has been attached to monitoring its population recovery and responses to management approaches. Abundance data of the population are also used in ecosystem models to understand complex relationships between wildlife and commercial species and advise fisheries managers to aid effective decision making [1, 108]. Abundance data associated with known locations such as seal colonies are useful for responding to emergency situations such as identifying the impacts of oil spills on affected wildlife [26, 109]. Furthermore, spatial abundance data and knowledge of population trends enables managers to maintain updated protected areas, and facilitate and/or mitigate economically important projects, such as natural resource extraction, shipping routes and tourism ventures that seek to utilise a wildlife resource [109, 110].

Finally, population information can have localised relevance. For example, in the state of Tasmania (Fig 1) AFSs interact with the salmonid aquaculture industry, predating fish and damaging property: costing the industry an estimated \$AUS 1000 per tonne of salmon produced [111, 112]. While the rate of seal interactions varies seasonally there has been a noted increase in the number of seals interacting each year since 1990 [112]. An understanding of fur seal population trends in association with an assessment of individual seal behavior at the aquaculture site (residency rate at farm site, return rate following translocation, estimates of known seals to be interacting) are critical to understanding whether the rate of interaction is driven by intrinsic population factors or individual interaction frequency [25]. The increasing development of this industry throughout southeast Tasmania also affects the haul-out distribution of the AFS and may influence the establishment of new colonies at locations such as Iles des Phoques.

Conclusion

The monitoring of the AFS between the 1970s and 2013, incorporating periods of annual estimates at some locations, opportunistic surveys at others and three population-wide surveys, has effectively recorded change during a growth period for the seals. Into the future, however, continuation of current strategies may not reliably detect density dependent regulation of the population, or allow rapid recognition between, for example, an anomalous result and a decline.

It is understood that there are multiple reasons for monitoring a colony, which will largely be driven by the question of interest. This paper highlights key parameters that need to be measured including at the least, pup mortality and density, while also providing information to assist with the prioritising of colonies. Here we have provided an example of why monitoring programs should be assessed regularly, with the aim of improving them at regular intervals. This maximises the chance that the monitoring program is achieving its goals and responding to change. Independent research programs investigating the diet, health and pup trends need to be coordinated, with the addition of demographic information to understand this drop in live Australian fur seal pups.

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