

# Habitat use and diving behaviour of male Australian fur seals

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

**KEY WORDS:** *Arctocephalus* · Foraging behaviour · Habitat use · Diving behaviour · Diel trends · Intraspecific competition · At-sea distribution · Pinniped · Australian fur seal · Bass Strait

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## INTRODUCTION

Marine predators have a significant influence on the structure and function of oceanic ecosystems, through the consumption of large amounts of prey biomass and the redistribution of nutrients and other resources across habitat boundaries (Estes et al. 2016). As a consequence, knowing where marine predators forage and how individual strategies vary enables us to better understand ecosystem processes, and has important implications for the management and conservation of marine predator populations (Lomnicki 1978, Costa et al. 2010a). In the marine environment, spatial and temporal distributions of

prey resources are highly variable (Harris et al. 1988, Perry et al. 2005), and predators must employ a variety of foraging strategies in order to obtain sufficient resources for survival, growth, and reproduction (Boyd et al. 1994, Costa et al. 2010a). For example, in times of lower prey availability, predators may alter their foraging areas to more profitable habitats, switch their diet to more abundant prey resources, or alternatively, increase their foraging effort (Georges et al. 2000, Hall-Aspland et al. 2005, Womble & Sigler 2006, Thomas et al. 2011, Kuhn & Costa 2014, Blanchet et al. 2015, O'Toole et al. 2015, Thorne et al. 2015). However, the foraging behaviour of marine predators is often difficult to observe, largely due to

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their cryptic nature and the fact that such behaviour usually occurs at depth (Boyd et al. 1994). Consequently, animal movements and diving behaviour provided by animal-borne data loggers allows us to infer their habitat use (Austin et al. 2004, Pinaud et al. 2005, Mattern et al. 2007, Fuller et al. 2008, Kuhn et al. 2010, Banks et al. 2014).

Otariid seals (fur seals and sea lions) are large marine predators that have been the focus of significant tracking efforts using animal-borne data loggers (e.g. Campagna et al. 2001, Page et al. 2005, Weise et al. 2010, Chilvers et al. 2013, Kuhn & Costa 2014, Arthur et al. 2015). Otariid seals display some of the most extreme sexual dimorphism of any mammal, with males up to 4 times the mass of females (Staniland 2005). Consequently, males are important consumers of prey biomass, and therefore potentially play a significant role in trophic dynamics (Estes et al. 2016). In addition, unlike lactating females that are obligate central place foragers due to the need to provision nutritionally dependent offspring, male otariids play no role in parental care (Bonner 1984, Gentry & Kooyman 1986). Therefore, males are less restricted than lactating females in their foraging range, giving them access to a wider range of habitats and niches, and potentially a greater capacity to connect ocean ecosystems over large spatial scales (Boyd et al. 1998, Estes et al. 2016). Yet despite otariids being the subject of considerable tracking effort, our understanding of otariid foraging ecology is largely derived from ecological studies that have examined lactating females (e.g. Thompson et al. 1998, Harcourt et al. 2002, Call et al. 2008, Lowther et al. 2011, Staniland et al. 2012, Baylis et al. 2015b). Comparatively few studies have investigated the foraging ecology of male otariids, presumably because their larger body size makes them difficult to capture and device recovery is often unreliable, as males are not constrained to a central place (Campagna et al. 2001, Page et al. 2005, Weise et al. 2006, 2010, Lowther et al. 2013, Baylis et al. 2016).

The Australian fur seal *Arctocephalus pusillus doriferus* is the largest of all fur seal species, with males and females weighing on average 279 and 76 kg, respectively (Warneke & Shaughnessy 1985, Arnould & Warneke 2002). Its breeding distribution is restricted almost entirely to islands within Bass Strait (Kirkwood et al. 2010), the shallow (mean depth: 50 to 70 m) continental shelf region between mainland Australia and Tasmania (Sandery & Kämpf 2007). Despite Bass Strait being typically recognised as a nutrient-poor region of low primary productivity,

it is influenced by numerous oceanographic features that feed it with seasonal secondary productivity (Gibbs et al. 1986, Sandery & Kämpf 2007, Kämpf 2015). With an estimated population of ca. 120 000 individuals (Kirkwood et al. 2010), the Australian fur seal is an important consumer of marine resources in southeastern Australia.

In addition to a limited breeding distribution, numerous studies on the foraging ecology of adult female Australian fur seals revealed that they feed almost exclusively on benthic/demersal prey, during foraging trips that are typically restricted to the continental shelf of Bass Strait (Arnould & Hindell 2001, Arnould & Kirkwood 2007, Kirkwood & Arnould 2011, Hoskins & Arnould 2014, Hoskins et al. 2015b). To date, only a few studies have investigated the foraging behaviour of male Australian fur seals, and information on male dive behaviour has been derived from a single animal (Hindell & Pemberton 1997, Kirkwood et al. 2006, Kernaléguen et al. 2015). Prior studies suggest that the foraging range of males is limited to the continental shelf, and that male Australian fur seals are relatively shallow divers (mean depth:  $20 \pm 14.3$  m; max. depth: 102 m; Hindell & Pemberton 1997). However, information on whether diving behaviour varies between individuals, spatially or temporally is not known.

Furthermore, as several studies have documented the presence of intra- and inter-individual variation in habitat use, diving behaviour, and dietary specialisations in adult female Australian fur seals (Arnould et al. 2011, Hoskins & Arnould 2014, Kernaléguen et al. 2016), individual differences in foraging strategies may also be apparent in males and act to reduce the pressures of intra-specific competition (Kernaléguen et al. 2012). Given that male Australian fur seals likely play a significant role in the trophic dynamics and relationships of the Bass Strait marine region, the aims of the present study, therefore, were to investigate (1) the spatial distribution and diving behaviour of male Australian fur seals; (2) how such behaviour varies temporally (seasonally and diel); and (3) the inter- and intra-individual variation in male foraging behaviour.

## MATERIALS AND METHODS

### Animal handling and instrumentation

The study was conducted at the Australian fur seal colony on Kanowna Island, in central northern Bass Strait, southeastern Australia ( $39^{\circ} 10' S$ ,  $146^{\circ} 18' E$ ;

see Fig. 1) which has an annual pup production of ca. 3400 individuals (Kirkwood et al. 2010). Fieldwork was carried out in June and July of 2013 and 2014, with individuals from 2013 included in a previous study (Kernaléguen et al. 2015). Males were chemically restrained using a 1:1 mixture of tiletamine-zolazepam (Zoletil, Virbac; ca. 1.5 mg kg<sup>-1</sup> of estimated mass), remotely administered via darts propelled by a CO<sub>2</sub> powered tranquiliser gun (Dan Inject JM Standard; Baylis et al. 2015a). Anaesthesia was maintained during the handling procedure using isoflurane delivered via a portable gas vaporizer (Stinger™, Advanced Anaesthesia Specialists).

Each seal was instrumented with a satellite-linked GPS-dive behaviour data logger (Mk10-AF Splash Tag, Wildlife Computers), glued to the dorsal fur along the mid-line just posterior to the scapula using quick setting 2-part epoxy (RS Components). Devices were programmed to record depth at 5 s intervals and GPS locations every 10 min. These data were transmitted to the CLS ARGOS system with transmission schedules being optimised to maximise the number of uplinks (Costa et al. 2010b). Specifically, at sea the devices were programmed to transmit GPS and dive behaviour messages every 90 s, while on land they were programmed to transmit every 30 s over 6 h intervals when satellites were overhead. In addition to device instrumentation, morphometric data (standard length, axis, axillary girth, and flipper length; ±0.5 cm), and biological samples (blubber biopsy, whisker, and blood) were taken for use in concurrent studies. Mass and age were estimated from previously determined allometric relationships between body mass and morphometric measurements for the species (Arnould & Warneke 2002). Upon completion of handling, individuals were monitored as they recovered from anaesthesia and left to resume normal behaviours.

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

## Data processing and analyses

GPS location data were first filtered using a basic speed filter (max. swim speed of 8 m s<sup>-1</sup>) to remove any erroneous locations (McConnell et al. 1992), and then linearly interpolated every 10 min in the R package 'trip' (Sumner 2013). For each austral season (winter: Jun to Aug; spring: Sep to Nov; summer: Dec to Feb), the at-sea spatial distribution was quantified using 95% (home range; HR) and 50% (core range; CR) utilisation distribution probabilities (UD). Each seal contributed equally to the overall UD calculation for each season (i.e. the UD for each seal was standardized to a value of 1). Overlap in UD between each season was calculated using the utilisation distribution overlap index (UDOI; Fieberg & Kochanny 2005). Smoothing parameters for the UD were calculated using the ad hoc method (Worton 1989), and bathymetry data were used as a habitat grid to avoid unrealistic probabilities spanning across land. Spatial analyses were conducted within the R package 'adehabitatHR' (Calenge 2006).

Due to device malfunction, only the maximum depth and dive frequency were available in the satellite-transmitted data from animals that were not recaptured. Hence, with the exception of these 2 variables, analyses on diving behaviour were restricted to individuals for which the full archive was available. Data from these tags was corrected for any drift in depth readings, and subsequently summarised for basic per dive metrics (dive duration, post-dive interval, dive depth, descent and ascent rate, and bottom time) using the 'diveMove' package in R (Luque & Fried 2011). Consistent with prior Australian fur seal studies, we defined a dive as >10 m in depth (Arnould & Hindell 2001, Hoskins & Arnould 2013). In addition, as female Australian fur seals begin foraging within 2.6 ± 0.4 h of leaving the colony (Arnould & Hindell 2001), a male foraging trip was defined as any continuous at-sea period ≥2 h.

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

Arnould & Hindell 2001, Hoskins & Arnould 2013), and were determined in the present study. For archival individuals that were tracked over winter and spring, seasonal differences in mean dive behaviour (dive duration, descent/ascent rates, and dive rate) and trip duration were analysed using paired *t*-tests.

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

## RESULTS

### Habitat use

A total of 16 individuals were instrumented with biogging equipment over the study (2013:  $n = 6$ ; 2014:  $n = 10$ ), with 2 individuals equipped over both years (seal ID 4/9 and seal ID 2/16). Body length and axillary girth measurements indicated that the tagged males were reproductively mature individuals (Warneke & Shaughnessy 1985, Stewardson et al. 1998; Table 1). Data were collected across 3 austral seasons (winter, spring and summer) for an average of  $106.7 \pm 12.5$  d ind.<sup>-1</sup> (range: 30 to 187 d), with half of the units ( $n = 8$ ) being recovered to provide the raw archival data. Of the remaining devices, one (seal ID 14) did not transmit diving behaviour data, and thus was excluded from dive-related analyses. The proportion of total archived dives for which information was transmitted was  $32.1 \pm 5.3\%$  (range: 12.1 to 55.7%) and there was no temporal bias (time of day or season) in the transmitted data. No difference in mean dive depth was detected between the archival and transmitted dive data ( $t_7 = -1.20$ ,  $p > 0.05$ ). Consequently, the transmitted data (dive depth and dive frequency) obtained from individuals that were not recaptured (i.e. no archival record) were considered represen-

Table 1. Deployment summary and basic dive data for all 16 male Australian fur seals *Arctocephalus pusillus doriferus* tagged at Kanowna Island in winter 2013 and 2014. Deployment date is given as dd/mm/yyyy. Individuals for which archive data was successfully obtained are indicated by (\*). Seals IDs 4 and 9, and 2 and 16 were the same individual tagged in consecutive years. Proportion of benthic dives were calculated using intra-depth zone (IDZ) score (see 'Materials and methods: Data processing and analyses' for details). Mass and age were estimated from body length following Arnould & Warneke (2002)

Seal ID	Deployment date	Deployment duration (d)	Length (cm)	Axillary girth (cm)	Est. mass (kg)	Est. age (yr)	No. of dives analysed	Modal max. depth (m)	Max. depth (m)	Benthic dives (%)
1	30/05/2013	76	162.0	123.0	129.9	4.5	1604	76.5	86.5	92.3
2*	30/05/2013	68	163.0	115.0	109.2	4.5	7766	77.0	86.0	75.5
3*	02/06/2013	51	189.0	126.0	138.2	7.5	4768	78.5	85.0	87.4
4*	02/06/2013	52	171.0	139.0	177.8	5.5	4707	83.5	86.5	90.2
5*	02/06/2013	149	173.0	121.0	124.5	5.5	15 227	83.0	86.0	83.4
6	03/06/2013	86	194.0	130.0	149.7	8.5	1895	84.5	86.5	96.8
7	28/07/2014	140	167.0	–	–	4.7	4627	82.5	259.5	79.4
8*	30/07/2014	96	177.0	–	–	5.7	8152	82.5	86.5	92.5
9*	01/08/2014	90	188.0	134.0	161.8	6.7	6833	75.0	86.5	82.6
10	02/08/2014	171	173.0	143.5	193.0	5.7	2742	84.5	86.5	79.8
11	02/08/2014	166	152.0	130.0	149.7	3.7	3834	78.5	221.5	74.2
12*	02/08/2014	88	179.0	129.5	148.2	6.7	7681	79.5	83.5	85.6
13	03/08/2014	187	185.5	157.0	243.2	6.7	2388	76.5	86.5	95.4
14	03/08/2014	30	176.0	135.0	165.0	5.7	–	–	–	–
15	03/08/2014	172	207.0	–	–	10.7	2036	70.5	283.5	84.0
16*	05/08/2014	85	165.5	118.0	116.7	5.7	9601	84.0	86.5	65.5
Mean $\pm$ SE		$106.7 \pm 12.5$	$176.4 \pm 3.5$	$130.8 \pm 3.1$	$154.4 \pm 9.9$	$6.1 \pm 0.4$	$5590.7 \pm 956.6$	$79.8 \pm 1.1$	$119.8 \pm 18.3$	$85.6 \pm 2.4$

Table 2. Dive parameters for archival individual Australian fur seals *Arctocephalus pusillus doriferus*. Values are presented as mean  $\pm$  SE. 'W' and 'S' refer to winter and spring, respectively

Seal ID	Trip duration (d)		Dive duration (min)		Descent rate (m s <sup>-1</sup> )		Ascent rate (m s <sup>-1</sup> )		Proportion of time spent diving (%)		Dive frequency (no. dives h <sup>-1</sup> )		Dive rate (m h <sup>-1</sup> )	
	W	S	W	S	W	S	W	S	W	S	W	S	W	S
2	3.0 $\pm$ 0.4	-	2.9 $\pm$ <0.1	-	1.36 $\pm$ <0.01	-	1.45 $\pm$ <0.01	-	35.0	-	7.3	-	939.4	-
3	5.0 $\pm$ 0.7	-	4.2 $\pm$ <0.1	-	1.27 $\pm$ <0.01	-	1.29 $\pm$ <0.01	-	39.4	-	5.6	-	739.2	-
4	4.3 $\pm$ 0.9	-	4.3 $\pm$ <0.1	-	1.54 $\pm$ <0.01	-	1.55 $\pm$ <0.01	-	40.6	-	5.6	-	876.9	-
5	3.3 $\pm$ 0.7	3.0 $\pm$ 0.4	4.0 $\pm$ <0.1	4.4 $\pm$ <0.1	1.47 $\pm$ <0.01	1.51 $\pm$ 0.01	1.68 $\pm$ <0.01	1.68 $\pm$ 0.01	46.7	49.5	7.0	6.8	977.5	931.3
8	2.8 $\pm$ 1.4	1.4 $\pm$ 0.3	4.4 $\pm$ <0.1	3.8 $\pm$ <0.1	1.39 $\pm$ 0.01	1.47 $\pm$ 0.01	1.36 $\pm$ <0.01	1.48 $\pm$ 0.01	31.7	40.0	4.3	6.4	681.0	768.3
9	4.8 $\pm$ 0.6	2.5 $\pm$ 1.0	3.9 $\pm$ <0.1	3.9 $\pm$ <0.1	1.51 $\pm$ 0.01	1.47 $\pm$ <0.01	1.67 $\pm$ 0.01	1.53 $\pm$ 0.01	39.2	46.4	6.0	7.2	863.6	1211.6
12	3.1 $\pm$ 0.3	2.6 $\pm$ 0.5	4.5 $\pm$ <0.1	4.3 $\pm$ <0.1	1.25 $\pm$ 0.01	1.19 $\pm$ 0.01	1.39 $\pm$ 0.01	1.34 $\pm$ 0.01	44.4	41.9	5.9	5.9	917.9	893.3
16	5.7 $\pm$ 0.7	5.6 $\pm$ 1.1	3.0 $\pm$ <0.1	2.5 $\pm$ <0.1	1.50 $\pm$ 0.01	1.43 $\pm$ 0.01	1.48 $\pm$ 0.01	1.48 $\pm$ 0.01	34.0	26.5	6.8	6.3	911.0	750.0
Mean $\pm$ SE	3.7 $\pm$ 0.3	2.6 $\pm$ 0.2	3.8 $\pm$ <0.1	3.7 $\pm$ <0.1	1.4 $\pm$ <0.1	1.4 $\pm$ <0.1	1.5 $\pm$ <0.01	1.5 $\pm$ <0.1	38.9 $\pm$ 1.8	40.8 $\pm$ 4.0	6.1 $\pm$ 0.3	6.5 $\pm$ 0.2	863.3 $\pm$ 36.1	910.9 $\pm$ 82.9

tative of the dive behaviour and used in dive-related analyses.

A total of 26 688 GPS locations were obtained across the 16 deployments (1668  $\pm$  227 ind.<sup>-1</sup>). On average, individuals travelled a total of 3561  $\pm$  405 km (range: 770 to 6251 km) over the instrumentation period, covering 34.2  $\pm$  1.9 km d<sup>-1</sup>. All of the individuals returned to Kanowna Island at least once (4.2  $\pm$  1.0 times) over the study period. While the majority (94%) of individuals frequented other colonies and haul-out sites (2.9  $\pm$  0.3 sites), 1 individual (seal ID 12) returned only to Kanowna Island from where it made 12 foraging trips to approximately the same location, 50 to 80 km to the southwest.

For the 8 recaptured individuals (for which complete archived data record was available), foraging trips lasted on average 3.1  $\pm$  0.2 d. There was no significant difference in the mean trip duration between winter and spring ( $t_4 = 2.24$ ,  $p > 0.05$ ; Table 2). The longest continuous at-sea period lasted 11.5 d in spring (seal ID 16: 6–18 Oct 2014). The kernel UD analysis revealed that the winter foraging range of all males remained within the continental shelf of Bass Strait (Fig. 1). This restricted foraging range was also evident for the majority of the spring. However, in the period immediately prior to the breeding season (late spring), 3 males (seal IDs 7, 11, and 15) dispersed from central Bass Strait and foraged along the edge of the continental shelf on either side of Tasmania, where they remained until their devices stopped transmitting. During the breeding season, 1 individual (seal ID 13) established a breeding territory at Kanowna Island (T. C. Knox pers. obs.). The GPS of another male (seal ID 10) revealed that it spent the majority of its time hauled out at Seal Rocks, where it is also presumed to have held a territory during the breeding period. Post-breeding movements showed that these 2 individuals remained to forage within Bass Strait until their devices stopped transmitting.

## Dive behaviour

A total of 64 735 dives were obtained from devices that were recovered ( $n = 8$ ; 8092  $\pm$  1177) and used for analysis. Mean dive durations ranged between 2.7  $\pm$  0.9 to 4.4  $\pm$  0.8 min between individuals, with the longest recorded dive lasting 9.8 min (seal ID 8; Table 1). No seasonal difference in mean dive duration was detected ( $t_4 = 1.0$ ,  $p > 0.05$ ). All individuals displayed predominantly benthic diving behaviour, with 85.6  $\pm$  2.4% (range: 65.5 to 96.8%) of dives falling within the IDZ of the preceding dive (Fig. 2,

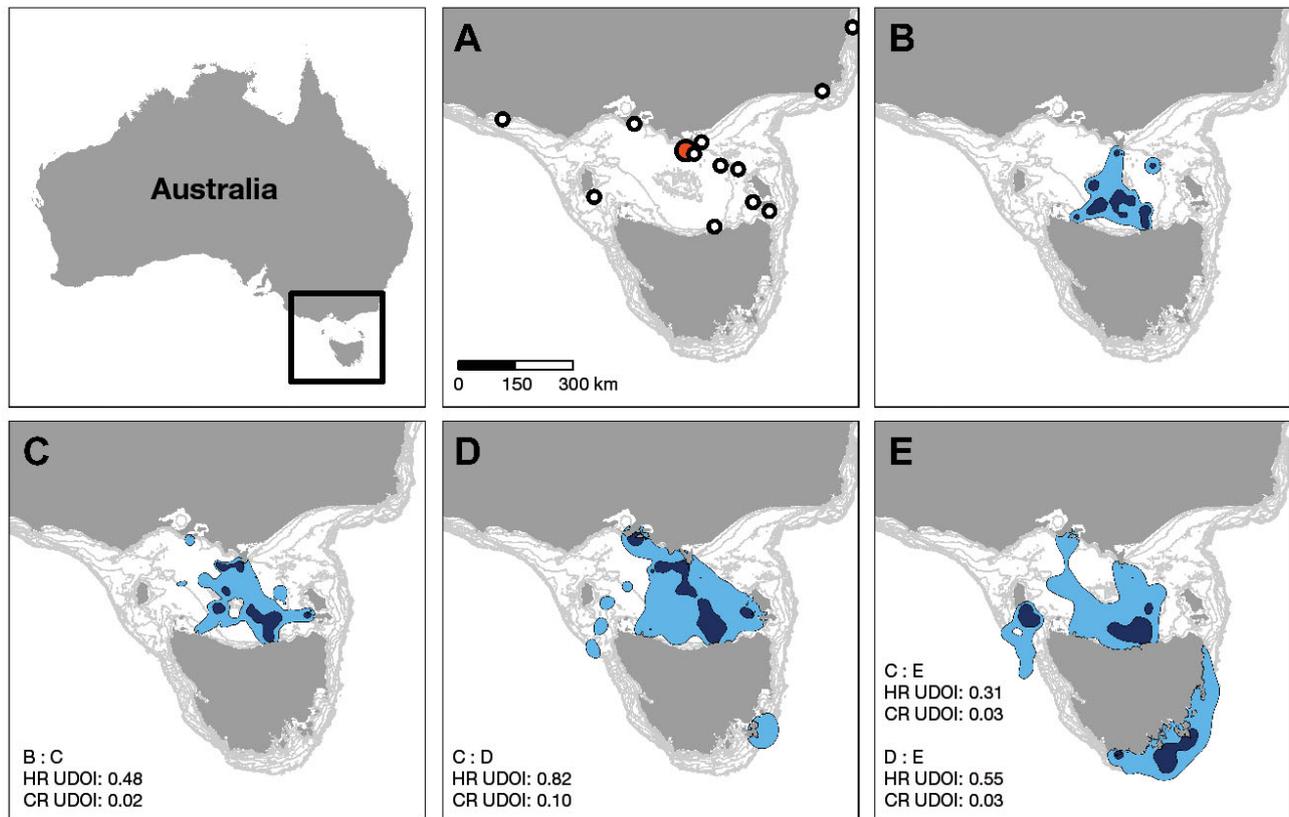


Fig. 1. (A) Kanowna Island (filled orange circle) and other breeding colonies (open circles) of Australian fur seals *Arctocephalus pusillus doriferus* within the southeastern Australian region. The 95% home range (HR: light blue shading) and 50% core range (CR: dark blue) utilisation distribution probabilities are shown for (B) winter 2013 ( $n = 6$ ), (C) winter 2014 ( $n = 10$ ), (D) spring 2014 ( $n = 10$ ), and (E) summer 2014 ( $n = 5$ ). The HR and CR utilisation distribution overlap index (UDOI) between each season is reported in the corresponding panel. Grey lines: bathymetry (in 20 m intervals) to the edge of the continental shelf

Table 2). In some cases, shorter than normal dives followed by subsequent shallow dives near the surface were apparent (Fig. 2B). This behaviour was indicative of handling large prey at or near the surface, as seen using animal-borne cameras on female Australian fur seals (Volpov et al. 2015). The modal maximum depth ranged from 70.5 to 84.5 m ( $79.8 \pm 1.1$  m; Table 1). Throughout the winter tracking period of both 2013 and 2014, the maximum depth achieved was 86.5 m ( $86.1 \pm 0.2$  and  $85.2 \pm 0.7$  m, respectively). While this depth was consistent across the majority (70%) of individuals tracked throughout spring and summer (max. depth: 85.6 and 85.5 m, respectively), 3 of the individuals (seal IDs 7, 11, and 15) for which transmitted data was obtained achieved depths  $\geq 220$  m during the same period (max. depth: 283.5 m; Table 1). Two of these individuals (seal IDs 7 and 15) appeared to switch to a predominantly pelagic foraging mode, with only 44.5 and 48.7% of dives, respectively, considered to be benthic.

On average, individuals spent  $39.3 \pm 2.1\%$  of their time at sea diving (mean range: 28.5 to 47.9%) and made  $6.2 \pm 0.2$  dives  $\text{h}^{-1}$  (Table 2). Vertical travel rates showed comparatively little variation between individuals, ranging from 681 to 977.5  $\text{m h}^{-1}$  in winter and 750 to 1211.6  $\text{m h}^{-1}$  in spring, with no difference detected between seasons ( $t_4 = -0.47$ ,  $p > 0.05$ ; Table 2). Mean descent ( $1.40 \pm <0.01$   $\text{m s}^{-1}$ ) and ascent ( $1.46 \pm <0.01$   $\text{m s}^{-1}$ ) rates were nearly identical between seasons ( $t_4 = -1$ ,  $p > 0.05$  in both cases) and males showed relatively little individual variation, with mean values for individual males ranging from 1.20 to 1.54 and 1.29 to 1.68  $\text{m s}^{-1}$  for descent and ascent rates, respectively.

Hierarchical clustering of the dissimilarity matrix created from the 2 h mean proportion of dives produced a dendrogram of 3 well-defined groups based on their seasonal preferences of diving: nocturnal, no preference, and diurnal (Fig. 3). Across all individuals and seasons, there were 12 (40%) instances where nocturnal preferences of diving were detected, while

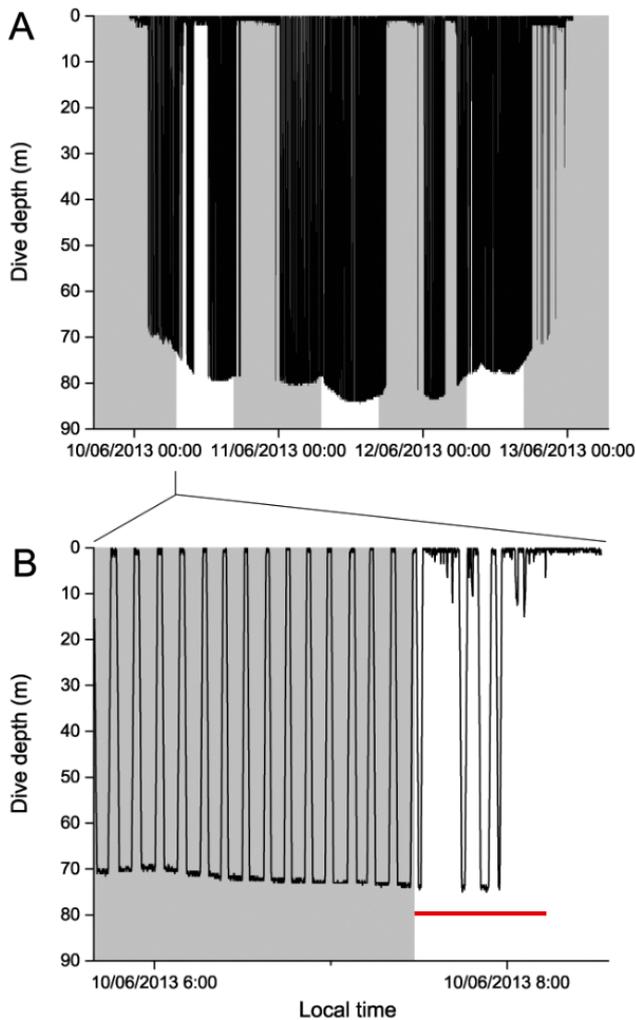


Fig. 2. (A) Representative dive profile of a typical Australian fur seal *Arctocephalus pusillus doriferus* foraging trip (mean:  $3.1 \pm 0.2$  d; max.: 11.5 d). Dives were primarily benthic ( $85.6 \pm 2.4\%$ ) across all individuals (modal max. depth: 83.5 m), lasting on average  $3.8 \pm 0.1$  min. (B) In some cases, shorter than normal dives, followed by subsequent shallow dives near the surface were apparent (highlighted by red bar) and may be indicative of handling large prey such as squid, octopus, or stingrays at or near the surface (as seen using animal-borne cameras on female Australian fur seals; Volpov et al. 2015)

the remaining 60% were clustered evenly across the nocturnal diving group, or the group that did not display a preference for time of day (30% each). In the winter and spring months, the majority of individuals preferred to dive during the night, with nocturnal diving preferences recorded for 40 and 60% of individuals, respectively (Fig. 3B). In addition, diurnal diving preferences were observed to be the least prevalent strategy during these months, with only 27% of individuals recorded diving during the day in winter and 20% in spring. In contrast to the behav-

ours observed in winter and spring, a preference for nocturnal diving was not observed at all during the summer, with 66% of the tracked males showing a preference for diurnal diving during this time (Fig. 3B). The majority (80%) of males switched their foraging strategies between seasons (Figs. 3B & 4), while only 1 seal (seal 7) was consistent in its foraging strategy across all 3 seasons. The 95% HR UD analysis revealed that all 3 diel foraging strategies occurred throughout large areas of central Bass Strait; however, the 50% CR UD contour suggested that there was little overlap in core area use between the 3 strategies (Fig. 5).

## DISCUSSION

### Habitat use

Throughout the austral winter and most of the spring, male Australian fur seals typically foraged benthically, and their movements were restricted to the shallow continental shelf of Bass Strait. The findings of the present study differ from the wide ranging movements of male otariids that are characterised by a pelagic foraging mode, such as New Zealand fur seals *Arctocephalus forsteri* (Page et al. 2006) and Californian sea lions *Zalophus californianus* (Weise et al. 2010). However, these results are similar to male otariids of other species, which have a predominantly benthic foraging mode, such as Australian sea lions *Neophoca cinera* (Lowther et al. 2013) and southern sea lions *Otaria flavescens* (Baylis et al. 2016). This suggests that the foraging ranges of male otariids are influenced by their foraging mode (pelagic or benthic) and the available habitat. In addition, these findings provide further evidence to suggest that despite the available continental shelf habitat adjoining Bass Strait, male Australian fur seals have a foraging range that is largely restricted to Bass Strait (Kirkwood et al. 2006, Kernaléguen et al. 2015).

There are a number of reasons why male Australian fur seals may choose to remain within the continental shelf of Bass Strait throughout the winter period. Despite the region being considered nutrient-poor (Gibbs et al. 1986, Sandery & Kämpf 2007, Kämpf 2015), the benthic habitat of Bass Strait may still provide sufficient prey resources to support the Australian fur seal population during winter (Arnould & Hindell 2001, Hoskins et al. 2015b, Kernaléguen et al. 2015). Additionally, Bass Strait has many offshore islands dispersed throughout the region that are free from predators. The males of the present study visited many of

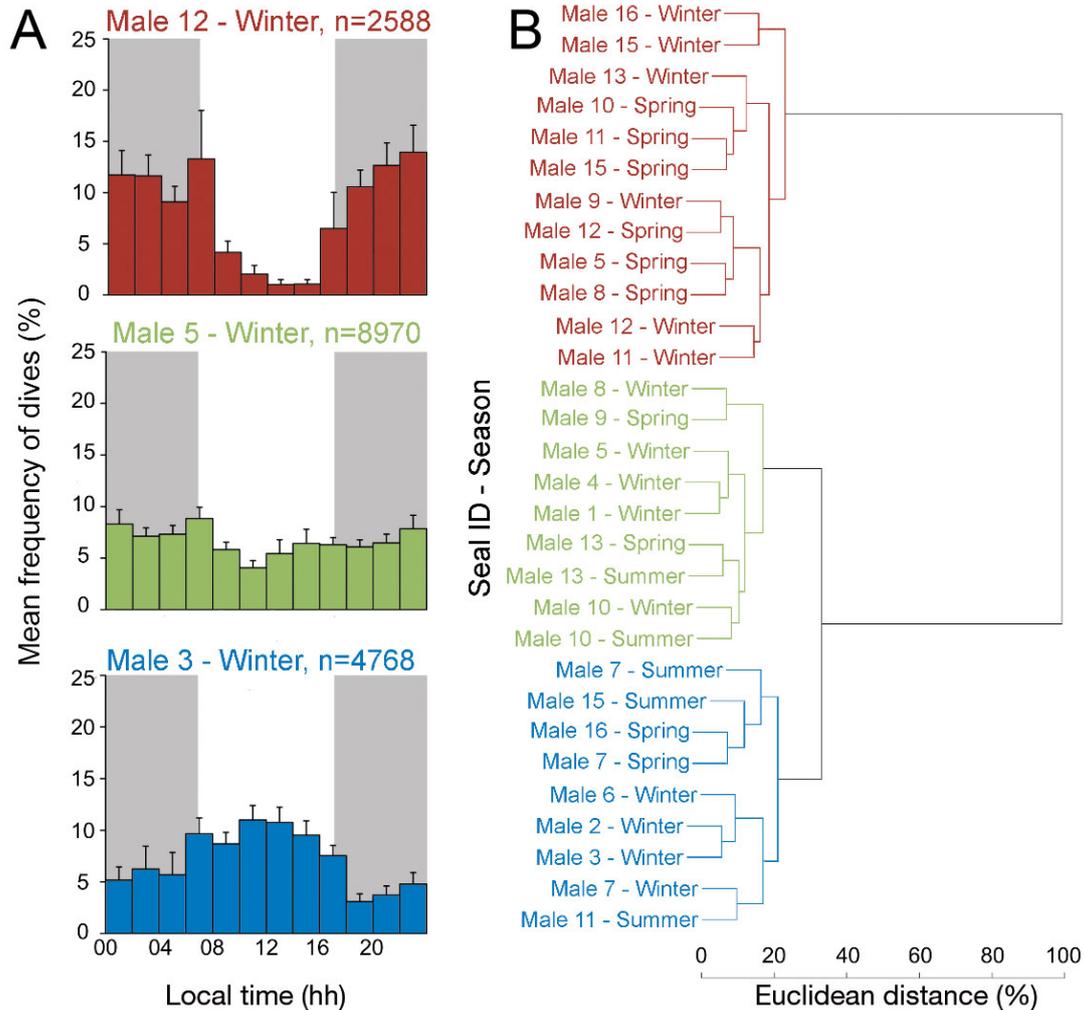


Fig. 3. Inter-individual variation within the diving strategies of male Australian fur seals *Arctocephalus pusillus doriferus*. (A) Representative examples of the mean frequency of dives per day ( $\% \pm \text{SE}$ ). (B) Clustering analysis revealed 3 distinct diel strategies: nocturnal (red), no preference (green), and diurnal (blue). Mean day and night hours are indicated by background shading

these land locations between foraging trips. By hauling out at these land sites, male Australian fur seals are able to rest in relatively close proximity to their foraging grounds within Bass Strait, consequently minimising their at-sea energetic costs and reducing their risk of predation (Boyd et al. 1998, Arnould & Kirkwood 2007, Staniland et al. 2012).

The only times male Australian fur seals foraged outside of Bass Strait was in late spring and summer. Spring movements of male Australian fur seals away from foraging areas in close proximity to the breeding colony may reflect these areas being suboptimal for larger males at a time of great nutritional importance. Male otariid seals fast throughout the breeding season (up to 60 d) while they maintain a territory, and consequently, lose a significant proportion of their body mass (Stirling 1983, Warneke &

Shaughnessy 1985). Hence, for territorial males, foraging conditions immediately prior to the breeding season (late spring) are critical for them to acquire the reserves necessary for territorial tenure and to replenish their body mass after the extended fasting during the breeding period (Staniland & Robinson 2008). As a consequence, prior to the breeding season, territorial Australian fur seal males may be required to search for more productive foraging areas or seek more energetically profitable prey outside of central Bass Strait.

Alternatively, intra-specific competition for resources close to the breeding colony may cause a local depletion of resources (Ashmole 1963, Boyd et al. 1998, Weise et al. 2006). Therefore, the foraging efficiency of males may be enhanced by travelling further away from foraging areas that are within

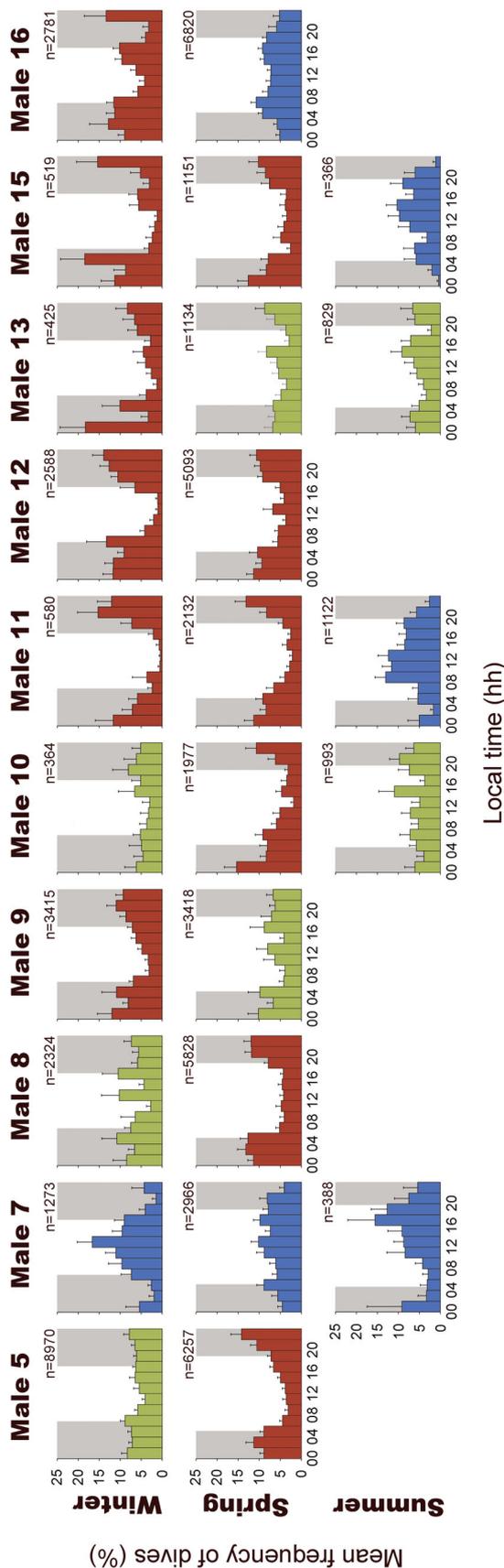


Fig. 4. Intra-individual variation in the diving strategies of male Australian fur seals *Arctocephalus pusillus doriferus*, showing mean frequency of dives (%  $\pm$  SE) per day for each individual. Bar colour corresponds to the foraging strategy determined by cluster analysis (blue: diurnal diel strategy; green and red: mixed and nocturnal diel strategies, respectively). Grey shading: mean day and night hours for each season

close proximity to breeding colonies and likely reduce intra-specific competition with adult female Australian fur seals. This notion is broadly consistent with other male otariid species such as Californian sea lions *Z. californianus* and Antarctic fur seals *Arctocephalus gazella* which travel extended distances (>1000 km) to forage in more productive waters after the breeding season, while females remain to forage in areas closer to the breeding colony (Boyd et al. 1998, Weise et al. 2006, 2010). Indeed, 3 males who did not attend a breeding colony over the breeding season left central Bass Strait and foraged in areas along the coast of Tasmania known to support large aggregations of seabirds and other marine mammals (Brothers & Pemberton 1990, Brothers et al. 1998).

### Dive behaviour

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

Measures of dive effort by the male Australian fur seals (i.e. proportion of time diving and vertical travel rates) were similar to those reported for female Australian fur seals (ca. 41% and 997 to 1133 m h<sup>-1</sup> for

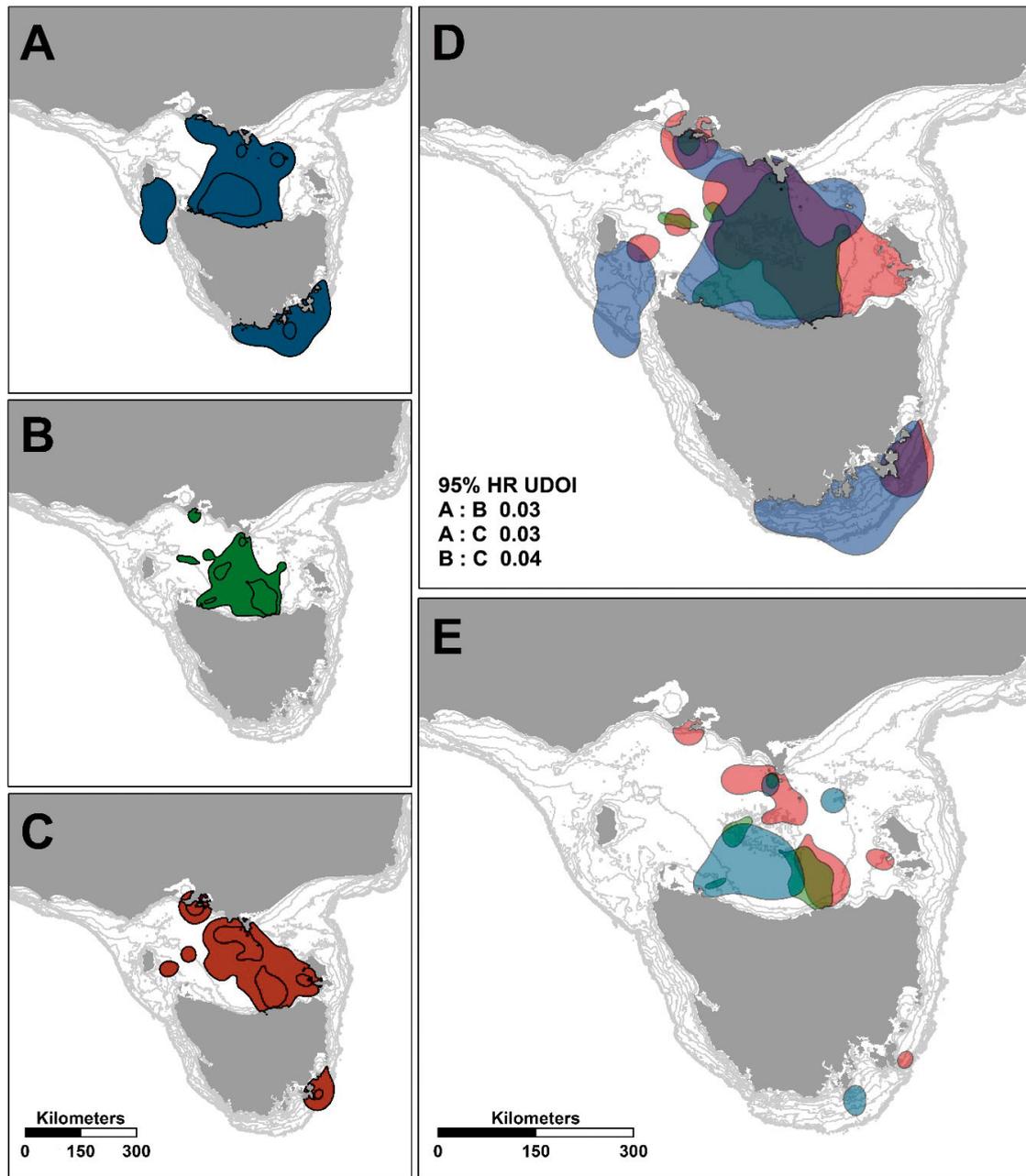


Fig. 5. The 95% home range (HR) and 50% core range (CR) utilisation distribution (UD) probabilities for each diel diving strategy of Australian fur seals *Arctocephalus pusillus doriferus*: (A) diurnal (blue), (B) mixed (green), and (C) nocturnal (red). Overlap between each diel strategy is presented in (D) 95% HR and (E) 50% CR, with the 95% HR utilisation distribution overlap index (UDOI) reported for each of the corresponding strategies (the overlap for the 50% UD was <0.01 in all cases). Grey lines: bathymetry (in 20 m intervals to the edge of the continental shelf)

mean proportion of time diving and range of vertical travel rates, respectively; Arnould & Hindell 2001, Hoskins & Arnould 2013). These results revealed that, in general, benthic-foraging Australian fur seals, irrespective of sex, will spend substantially more time diving and have greater travel rates than pelagic fur seals (15 to 24% of their time diving;

Arnould & Costa 2006) and the pelagic-foraging California sea lion (32%; Feldkamp et al. 1989). However, the dive effort of Australian fur seals is similar to other benthic-foraging sea lions (44 to 58%; Gentry & Kooyman 1986, Georges et al. 2000, Arnould & Costa 2006). Therefore, the increased effort displayed by Australian fur seals may reflect benthic

habitats being of low prey abundance, but spatially and temporally predictable (Arnould & Hindell 2001, Arnould & Costa 2006).

Mean dive durations for male Australian fur seals were greater than reported for other fur seals, and more typical of larger sea lions (e.g. Boyd et al. 1991, Harcourt et al. 1995, Georges et al. 2000, Page et al. 2005, Arnould & Costa 2006, Waite et al. 2012). In addition, male Australian fur seals have longer mean dive durations and longer foraging trip durations than female conspecifics (males: 2.7 to 4.4 min and 3.1 d, females: 2.9 to 3.1 min and 2.9 d; Arnould & Hindell 2001, Hoskins & Arnould 2013). Similar sex-related differences have been observed in New Zealand fur seals, where males have longer dive durations than females, and in southern sea lions, where males spend longer at sea than their female conspecifics (Campagna et al. 2001, Page et al. 2005). Sex differences in dive duration are consistent with an increase in physiological capacity of larger animals due to their body mass (Costa 1991, Weise & Costa 2007, Weise et al. 2010). Within Australian fur seals, males and females may forage in the same areas of Bass Strait, and to the same depth throughout the same temporal periods. However, an increase in the foraging ability of males may enable them to search longer in order to pursue more cryptic prey resources, thereby leading to sexual segregation in diet as has been previously reported (Kernaléguen et al. 2015).

We also found strong inter-individual variation in temporal patterns of diving, and some evidence to suggest that the core area use of these strategies differed in their location. Diel variation is a common feature in the diving behaviour of pelagic foraging otariids, as it is typically associated with diurnal and nocturnal movements of vertically migrating prey (Boyd & Croxall 1992, Boyd et al. 1994, Harcourt et al. 1995, Georges et al. 2000). However, it appears to be less apparent in benthic-foraging otariids whose cryptic prey species do not normally migrate (Costa & Gales 2003). Furthermore, few studies of otariids have examined individual or spatial variation within such diel strategies, with most examining temporal patterns in dive behaviour at the population level (Boyd et al. 1991, Lea et al. 2002). Australian fur seals are considered opportunistic foragers that consume a broad range of fish, cephalopods, and elasmobranchs (Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009, Arnould et al. 2011, Kernaléguen et al. 2016). However, the inter-individual variation in dive strategies observed in the present study may be indicative of individuals targeting specific resources

at certain periods of the day or night. Furthermore, the intra-individual (seasonal) variation within the diel strategies may also be indicative of individuals focussing their effort on profitable prey resources that are only temporally abundant within a particular season (Kirkwood et al. 2008, Kernaléguen et al. 2016). There was also some evidence to suggest spatial separation of foraging strategies within Bass Strait. This was surprising, given that Bass Strait is considered both uniform in habitat and distribution of prey (Gibbs et al. 1986, Gibbs 1992, Sandery & Kämpf 2007, Kämpf 2015). Spatial separation of foraging strategies may reflect male individuals targeting specific prey resources in certain areas of Bass Strait, or may be due to competitive exclusion by conspecifics (Hardin 1960, Van Valen 1965, Banks et al. 2014, Hoskins et al. 2015b). However, the spatial separation of foraging strategies could also be a result of low sample size. Consequently, additional tracking studies are ultimately required to characterise and assess any spatial separation of foraging strategies.

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

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## LITERATURE CITED

- Arnould JPY, Costa DP (2006) Sea lions in drag, fur seals incognito: insights from the otariid deviants. In: Trites AW, DeMaster DP, Fritz LW, Gelatt LD, Rea LD, Wynne KM (eds) Sea lions of the world. Alaska Sea Grant College Program, University of Alaska, Fairbanks, AK, p 111–125
- Arnould JPY, Hindell MA (2001) Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can J Zool* 79:35–48
- Arnould JPY, Kirkwood R (2007) Habitat selection by female Australian fur seals (*Arctocephalus pusillus doriferus*). *Aquat Conserv* 17:S53–S67
- Arnould JPY, Warneke RM (2002) Growth and condition in Australian fur seals (*Arctocephalus pusillus doriferus*) (Carnivora: Pinnipedia). *Aust J Zool* 50:53–66
- Arnould JPY, Cherel Y, Gibbens J, White JG, Littnan CL (2011) Stable isotopes reveal inter-annual and inter-individual variation in the diet of female Australian fur seals. *Mar Ecol Prog Ser* 422:291–302
- Arthur B, Hindell M, Bester M, Trathan P and others (2015) Return customers: foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. *PLOS ONE* 10:e0120888
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103b:458–473
- Austin D, Bowen WD, McMillan JI (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* 105:15–30
- Banks J, Lea MA, Wall S, McMahon CR, Hindell MA (2014) Combining bio-logging and fatty acid signature analysis indicates spatio-temporal variation in the diet of the southern elephant seal, *Mirounga leonina*. *J Exp Mar Biol Ecol* 450:79–90
- Baylis AMM, Page B, Staniland IJ, Arnould JPY, McKenzie J (2015a) Taking the sting out of darting: risks, restraint drugs and procedures for the chemical restraint of Southern Hemisphere otariids. *Mar Mamm Sci* 31:322–344
- Baylis AMM, Orben RA, Arnould JPY, Peters K, Knox T, Costa DP, Staniland IJ (2015b) Diving deeper into individual foraging specializations of a large marine predator, the southern sea lion. *Oecologia* 179:1053–1065
- Baylis AMM, Orben RA, Costa DP, Arnould JPY, Staniland IJ (2016) Sexual segregation in habitat use is smaller than expected in a highly dimorphic marine predator, the southern sea lion. *Mar Ecol Prog Ser* 554:201–211
- Blanchet MA, Lydersen C, Ims RA, Kovacs KM (2015) Seasonal, oceanographic and atmospheric drivers of diving behaviour in a temperate seal species living in the high Arctic. *PLOS ONE* 10:e0132686
- Bonner WN (1984) Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symp Zool Soc Lond* 51:253–272
- Boyd IL, Croxall JP (1992) Diving behaviour of lactating Antarctic fur seals. *Can J Zool* 70:919–928
- Boyd IL, Lunn NJ, Barton T (1991) Time budgets and foraging characteristics of lactating Antarctic fur seals. *J Anim Ecol* 60:577–592
- Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J Anim Ecol* 63:703–713
- Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can J Fish Aquat Sci* 55:845–852
- Brothers N, Pemberton D (1990) Status of Australian and New Zealand fur seals at Maatsuyker Island, Southwestern Tasmania. *Aust Wildl Res* 17:563–569
- Brothers N, Gales R, Hedd A, Robertson G (1998) Foraging movements of the shy albatross *Diomedea cauta* breeding in Australia; implications for interactions with long-line fisheries. *Ibis* 140:446–457
- Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- Call KA, Ream RR, Johnson D, Sterling JT, Towell RG (2008) Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. *Deep-Sea Res II* 55:1883–1896
- Campagna C, Werner R, Karesh W, Marin MR, Koontz F, Cook R, Koontz C (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *J Zool* 255:205–220
- Chilvers BL, Childerhouse SJ, Gales NJ (2013) Winter foraging behaviour of lactating New Zealand sea lions (*Phocarctos hookeri*). *NZ J Mar Freshw Res* 47:125–138
- Costa DP (1991) Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am Zool* 31:111–130
- Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol Monogr* 73:27–43
- Costa DP, Huckstadt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA (2010a) Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integr Comp Biol* 50:1018–1030
- Costa DP, Robinson PW, Arnould JPY, Harrison AL and others (2010b) Accuracy of ARGOS locations of pinnipeds at-sea estimated using fastloc GPS. *PLOS ONE* 5:e8677
- Deagle BE, Kirkwood R, Jarman SN (2009) Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Mol Ecol* 18:2022–2038
- Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016) Megafaunal impacts on structure and function of ocean ecosystems. *Annu Rev Environ Resour* 41:83–116
- Feldkamp SD, DeLong RL, Antonelis GA (1989) Diving patterns of California sea lions, *Zalophus californianus*. *Can J Zool* 67:872–883
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359
- Fuller WJ, Broderick AC, Phillips RA, Silk JRD, Godley BJ (2008) Utility of geolocating light loggers for indicating at-sea movements of sea turtles. *Endang Species Res* 4: 139–146
- Gentry RL, Kooyman GL (eds) (1986) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ
- Georges JY, Tremblay Y, Guinet C (2000) Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. *Polar Biol* 23:59–69
- Gibbs CF (1992) Oceanography of Bass Strait: implications

- for the food supply of little penguins *Eudyptula minor*. *Emu* 91:395–401
- ✦ Gibbs CF, Tomczak M, Longmore AR (1986) The nutrient regime of Bass Strait. *Aust J Mar Freshw Res* 37:451–466
- ✦ Hall-Aspland SA, Rogers TL, Canfield RB (2005) Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. *Mar Ecol Prog Ser* 305: 249–259
- ✦ Harcourt RG, Schulman AM, Davis LS, Trillmich F (1995) Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. *Can J Zool* 73:678–690
- ✦ Harcourt RG, Bradshaw CJA, Dickson K, Davis LS (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Mar Ecol Prog Ser* 227:11–24
- ✦ Hardin G (1960) The competitive exclusion principle. *Science* 131:1292–1297
- ✦ Harris GP, Davies PMN, Meyers G (1988) Interannual variability in climate and fisheries in Tasmania. *Nature* 333: 754–757
- ✦ Hindell M, Pemberton D (1997) Successful use of a translocation program to investigate diving behavior in a male Australian fur seal, *Arctocephalus pusillus doriferus*. *Mar Mamm Sci* 13:219–228
- ✦ Hoskins AJ, Arnould JPY (2013) Temporal allocation of foraging effort in female Australian fur seals (*Arctocephalus pusillus doriferus*). *PLOS ONE* 8:e79484
- ✦ Hoskins AJ, Arnould JPY (2014) Relationship between long-term environmental fluctuations and diving effort of female Australian fur seals. *Mar Ecol Prog Ser* 511: 285–295
- ✦ Hoskins AJ, Costa DP, Wheatley KE, Gibbens JR, Arnould JPY (2015a) Influence of intrinsic variation on foraging behaviour of adult female Australian fur seals. *Mar Ecol Prog Ser* 526:227–239
- ✦ Hoskins AJ, Costa DP, Arnould JPY (2015b) Utilisation of intensive foraging zones by female Australian fur seals. *PLOS ONE* 10:e0117997
- ✦ Hume F, Hindell MA, Pemberton D, Gales R (2004) Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). *Mar Biol* 144:407–415
- ✦ Kämpf J (2015) Phytoplankton blooms on the western shelf of Tasmania: evidence of a highly productive ecosystem. *Ocean Sci* 11:1–11
- ✦ Kernaléguen L, Cazelles B, Arnould JPY, Richard P, Guinet C, Cherel Y (2012) Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PLOS ONE* 7:e32916
- ✦ Kernaléguen L, Cherel Y, Knox TC, Baylis AMM, Arnould JPY (2015) Sexual niche segregation and gender-specific individual specialisation in a highly dimorphic marine mammal. *PLOS ONE* 10:e0133018
- ✦ Kernaléguen L, Dorville N, Ierodiaconou D, Hoskins AJ and others (2016) From video recordings to whisker stable isotopes: a critical evaluation of timescale in assessing individual foraging specialisation in Australian fur seals. *Oecologia* 180:657–670
- ✦ Kirkwood R, Arnould JPY (2011) Foraging trip strategies and habitat use during late pup rearing by lactating Australian fur seals. *Aust J Zool* 59:216–226
- ✦ Kirkwood R, Lynch M, Gales NJ, Dann P, Sumner M (2006) At-sea movements and habitat use of adult male Australian fur seals (*Arctocephalus pusillus doriferus*). *Can J Zool* 84:1781–1788
- ✦ Kirkwood R, Hume F, Hindell M (2008) Sea temperature variations mediate annual changes in the diet of Australian fur seals in Bass Strait. *Mar Ecol Prog Ser* 369: 297–309
- ✦ Kirkwood RJ, Pemberton D, Gales R, Hoskins AJ, Mitchell T, Shaughnessy PD, Arnould JPY (2010) Continued population recovery by Australian fur seals. *Mar Freshw Res* 61: 695–701
- ✦ Kuhn CE, Costa DP (2014) Interannual variation in the at-sea behaviour of California sea lions (*Zalophus californianus*). *Mar Mamm Sci* 30:1297–1319
- ✦ Kuhn CE, Tremblay Y, Ream RR, Gelatt TS (2010) Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements of northern fur seals. *Endang Species Res* 12:125–139
- ✦ Lea MA, Hindell MA, Guinet C, Goldsworthy S (2002) Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biol* 25:269–279
- ✦ Littnan CL, Arnould JPY, Harcourt RG (2007) Effect of proximity to the shelf edge on the diet of female Australian fur seals. *Mar Ecol Prog Ser* 338:257–267
- ✦ Lomnicki A (1978) Individual differences between animals and the natural regulation of their numbers. *J Anim Ecol* 47:461–475
- ✦ Lowther AD, Harcourt RG, Hamer DJ, Goldsworthy SD (2011) Creatures of habit: foraging habitat fidelity of adult female Australian sea lions. *Mar Ecol Prog Ser* 443:249–263
- ✦ Lowther AD, Harcourt RG, Page B, Goldsworthy S (2013) Steady as he goes: at-sea movement of adult male Australian sea lions in a dynamic marine environment. *PLOS ONE* 8:e74348
- ✦ Luque SP, Fried R (2011) Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. *PLOS ONE* 6:e15850
- ✦ Mattern T, Ellenberg U, Houston DM, Davis LS (2007) Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins. *Mar Ecol Prog Ser* 343:295–306
- ✦ McConnell BJ, Chambers B, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct Sci* 4:393–398
- ✦ O'Toole MD, Lea MA, Guinet C, Schick R, Hindell MA (2015) Foraging strategy switch of a top marine predator according to seasonal resource differences. *Front Mar Sci* 2:21
- ✦ Page B, McKenzie J, Goldsworthy SD (2005) Inter-sexual differences in New Zealand fur seal diving behaviour. *Mar Ecol Prog Ser* 304:249–264
- ✦ Page B, McKenzie J, Sumner MD, Coyne M, Goldsworthy SD (2006) Spatial separation of foraging habitats among New Zealand fur seals. *Mar Ecol Prog Ser* 323:263–279
- ✦ Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- ✦ Pinaud D, Cherel Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Mar Ecol Prog Ser* 298:295–304
- ✦ Sandery PA, Kämpf J (2007) Transport timescales for identifying seasonal variation in Bass Strait, south-eastern Australia. *Estuar Coast Shelf Sci* 74:684–696
- ✦ Staniland I (2005) Sexual segregation in seals. In: Ruckstuhl KE, Neuhaus P (eds) Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge, p 53–73

- ✦ Staniland IJ, Robinson SL (2008) Segregation between the sexes: Antarctic fur seals, *Arctocephalus gazella*, foraging at South Georgia. *Anim Behav* 75:1581–1590
- ✦ Staniland IJ, Robinson SL, Silk JRD, Warren N, Trathan PN (2012) Winter distribution and haul-out behaviour of female Antarctic fur seals from South Georgia. *Mar Biol* 159:291–301
- ✦ Stewardson CL, Bester MN, Oosthuizen WH (1998) Reproduction in the male Cape fur seal *Arctocephalus pusillus pusillus*: age at puberty and annual cycle of the testis. *J Zool* 246:63–74
- Stirling I (1983) The evolution of mating systems in pinnipeds. *Spec Publ Am Soc Mamm* 7:489–527
- Sumner MD (2013) trip: spatial analysis of animal track data. R package version 1.1-17. <http://CRAN.R-project.org/package=trip>
- ✦ Thomas AC, Lance MM, Jeffries SJ, Miner BG, Acevedo-Gutiérrez A (2011) Harbor seal foraging response to a seasonal resource pulse, spawning Pacific herring. *Mar Ecol Prog Ser* 441:225–239
- ✦ Thompson D, Duck CD, McConnell BJ, Garrett J (1998) Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *J Zool* 246:135–146
- ✦ Thorne LH, Hazen EL, Bograd SJ, Foley DG and others (2015) Foraging behavior links climate variability and reproduction in North Pacific albatrosses. *Mov Ecol* 3: 27
- ✦ Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Prog Ser* 204:257–267
- ✦ Van Valen L (1965) Morphological variation and width of ecological niche. *Am Nat* 99:377–390
- ✦ Volpov BL, Hoskins AJ, Battaile BC, Viviant M and others (2015) Identification of prey captures in Australian fur seals (*Arctocephalus pusillus doriferus*) using head-mounted accelerometers: field validation with animal-borne video cameras. *PLOS ONE* 10:e0128789
- ✦ Waite JN, Trumble SJ, Burkanov VN, Andrews RD (2012) Resource partitioning by sympatric Steller sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry. *J Exp Mar Biol Ecol* 416–417:41–54
- Warneke RM, Shaughnessy PD (1985) *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. In: Ling JK, Bryden MM (eds) *Studies of sea mammals in south latitudes*. South Australian Museum, Adelaide
- ✦ Weise MJ, Costa DP (2007) Total body oxygen stores and physiological diving capacity of California sea lions as a function of sex and age. *J Exp Biol* 210:278–289
- ✦ Weise MJ, Costa DP, Kudela RM (2006) Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. *Geophys Res Lett* 33: L22S10
- ✦ Weise MJ, Harvey JT, Costa DP (2010) The role of body size in individual-based foraging strategies of a top marine predator. *Ecology* 91:1004–1015
- ✦ Womble JN, Sigler MF (2006) Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. *Mar Ecol Prog Ser* 325:281–293
- ✦ Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168

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