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Foraging niche separation in sympatric temperate-latitude fur seal species

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ABSTRACT: To reduce interspecific competition, sympatric species must segregate their resources in a variety of dimensions. Otariid seals (fur seals and sea lions) breed sympatrically in several regions and, where this occurs, differences in lactation length and body size (which influence foraging behaviour and diet) are apparent. However, congeneric Australian fur seals *Arctocephalus pusillus doriferus* (AUFS) and New Zealand fur seals *A. forsteri* (NZFS) breed sympatrically on several islands within south-eastern Australia, and display complete overlap in breeding period. How these populations segregate resources is unknown. We assessed the foraging ecology and diet of adult females of both species breeding on Kanowna Island, south-eastern Australia. Foraging locations and diving behaviour differed between species, with AUFS diving deeper (consistent with benthic foraging; 70.6 ± 2.3 m [SD]), while NZFS predominantly dived to shallow depths (16.9 ± 3.7 m), suggesting an epipelagic foraging mode. A bimodal pattern in foraging range was observed in NZFS, with animals either foraging near the colony (15.7 ± 13.0 km) or travelling beyond the continental shelf (363.4 ± 17.2 km), while AUFS foraged within 79.8 ± 8.8 km of the colony. Although dietary composition was similar, the relative importance of prey differed. NZFS predominantly consumed pelagic species, while AUFS primarily consumed a variety of benthic/demersal species (niche overlap 0.39). These differences coincide with the divergence in population demography of the 2 species (AUFS exhibit lower, more stable fecundity compared to NZFS) and are consistent with predictions that foraging mode influences life history traits in otariid seals.

KEY WORDS: Benthic diving · Pelagic diving · Spatial distribution · Diet overlap · Australian fur seal · New Zealand fur seal

INTRODUCTION

Sympatry, defined as the occurrence of 2 or more species breeding in the same location (Cain 1953), can lead to interspecific competition when the species use a common, limiting resource (Pianka 1974). Such interspecific competition is usually most severe between closely related species, since these generally exhibit a high degree of similarity (Hardin 1960, Ashmole 1968, Pianka 1974). Competition can compromise the fitness of the species involved (Pacala & Roughgarden 1985) and may ultimately lead to the competitive exclusion of one species. A limit in the degree of niche overlap should therefore exist in sympatric species (Hardin 1960, Pianka 1974).

Several species of otariid seals (fur seals and sea lions) occur in sympatry throughout the world (Dellinger & Trillmich 1999, Costa et al. 2006, Jeglinski et al. 2013, Villegas-Amtmann et al. 2013). The areas of sympatry, however, represent only a small propor-

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tion of the allopatric ranges (Riedman 1990). If sympatry has occurred through evolutionary time, selective pressure would have facilitated divergence between closely related species, and interspecific differences in habitat use by sympatric species could thus be expected (Ashmole 1968). However, the duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry has resulted from recent population recoveries and recolonisation following the cessation of commercial sealing (Costa et al. 2006). If sympatry is a result of recent events, it is possible that divergence is not yet evident and/or that competitive exclusion is occurring (Pianka 1974).

Congeneric Australian fur seals *Arctocephalus pusillus doriferus* (AUFS) and New Zealand fur seals *A. forsteri* (NZFS) have similar breeding seasons and display complete overlap in lactation (approximately 10 mo: Warneke & Shaughnessy 1985, Goldsworthy 2006). Both are temperate-latitude species, with NZFS have a breeding distribution ranging from the south-western coast of Australia to southern New Zealand (Riedman 1990), while the breeding range of AUFS is predominantly restricted to 10 offshore islands within Bass Strait, south-eastern Australia (Kirkwood et al. 2005, 2010). Both species existed in south-eastern Australia prior to commercial exploitation, which resulted in the near extinction of both species from the region (Warneke & Shaughnessy 1985). They are now both in the process of recovery (population increases — NZFS: 0.31–5.0% yr^{-1}, AUFS: 3.1–29.2% yr^{-1}; Littnan & Mitchell 2002, Kirkwood et al. 2010), and sympatric colonies of the 2 species have recently been discovered at several locations within south-eastern Australia (Kirkwood et al. 2009, 2010). These colonies represent the sole known locations where 2 closely related (both being *Arctocephalus* seals), temperate-latitude, otariid seals with almost identical breeding patterns occur in sympatry anywhere in the world (Costa et al. 2006).

Previous studies have shown that similar species may exist sympatrically in areas where resources are not limiting (Hunt & Hunt 1973). Consequently, sympatry may be possible because the 2 species are partitioning the resources so that they are not limiting. Alternatively, AUFS and NZFS may be able to occur in sympatry because full recolonisation following commercial harvesting has not yet occurred and that competition may increase as populations grow (Kirkwood et al. 2010). Previous studies have shown that AUFS are a predominantly benthic foraging species whose foraging is restricted to on-shelf regions (Hoskins & Arnould 2013, Hoskins et al. 2015), whereas NZFS, in other parts of their range, are pelagic foragers (Page et al. 2005b). Dietary studies of both species (comparing adult male AUFS with NZFS at a NZFS colony/AUFS haul-out) have indicated that there is the potential for moderate dietary overlap (Page et al. 2005a). However, there is currently no information about how NZFS may behave within the large, shallow, on-shelf region of Bass Strait or how these species may behave when breeding in sympatry. Knowledge of whether and how these species may be partitioning resources is crucial for understanding how they may respond to environmental change. This is especially important as the waters of south-eastern Australia are some of the fastest warming in the world (Lough & Hobday 2011), with potentially dramatic consequences for prey abundance and distribution in the region (Frusher et al. 2014), while both species are still recovering from severe exploitation. The aims of this study were to compare the diet and foraging behaviour of AUFS and NZFS at a sympatric site in Bass Strait.

MATERIALS AND METHODS

Animal capture and instrumentation

The study was conducted in the winters (June to August) of 2006 to 2008 at Kanowna Island (39° 10′ S, 146° 18′ E) in central northern Bass Strait, south-eastern Australia (Fig. 1). Winter was chosen, as this is the period of highest nutritional demand for female AUFS and NZFS, while also coinciding with reduced availability of marine resources (Kirkwood et al. 2005), maximising the potential for competition to be occurring between the species. The island is populated by breeding colonies of AUFS and NZFS, with annual pup productions of ~3200 and ~75 ind., indicating ~15 000 and ~330 ind., respectively (Kirkwood et al. 2009, 2010). Breeding areas occur in geographically distinct areas on the island. The areas used by AUFS are dominated by smooth granite leading into tussock grass, whereas NZFS breed in a boulder-filled area close to the water's edge and backed by a large cliff.

Adult females nursing pups were selected at random from within their respective colonies. Capture and handling of AUFS females followed standard protocols for this species (Hoskins et al. 2015). All NZFS were remotely immobilised using Zoletil® (Virbac), following McKenzie et al. (2013). General anaesthesia was maintained using Isofluorane (1–2%) during handling (Gales & Mattlin 1998).

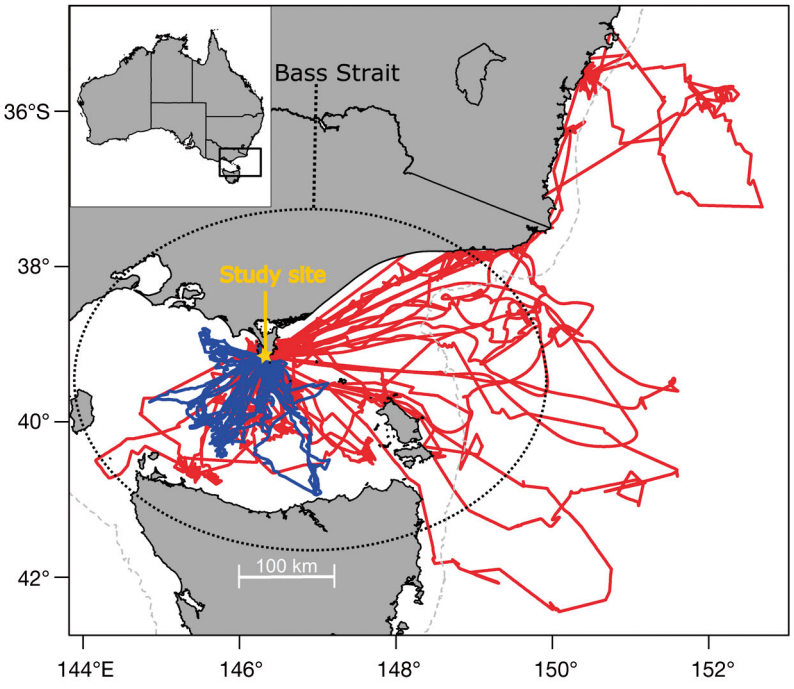

Fig. 1. Filtered foraging tracks for female Australian fur seals *Arctocephalus pusillus doriferus* (blue) and New Zealand fur seals *A. forsteri* (red) foraging from Kanowna Island, Bass Strait, Australia, during the Austral winters of 2006 to 2008. Grey dashed line delineates shelf waters

Once anaesthetised, devices were then glued to the mid-dorsal pelage with quick-setting epoxy (RS Components).

The at-sea movements and diving behaviour of lactating females were determined using a combination of FastLoc GPS loggers (FastLoc 1, 5 × 10 × 2 cm; Sirtrack) and electronic time-depth recorders (TDRs; MK10, 8 × 6 × 4 cm, Wildlife Computers) in AUFS and satellite-linked TDRs (Splash Tag, 8 × 5 × 2 cm, Wildlife Computers) in NZFS. The TDRs were programmed to sample depth (± 0.5 m) every 5 s when wet, and Splash Tags were programmed to transmit location and dive behaviour information every 45 s when seals were at the surface, while the FastLoc GPS loggers were programmed to collect a position every 15 min. To assist in relocating the animals for recapture, a VHF radio transmitter (6 × 3 × 2 cm, Sirtrack) was also attached in line with the other instruments.

Individuals were then released and left to conduct normal foraging trips. AUFS females were recaptured after 1 to 12 foraging trips and devices were removed by cutting the fur beneath them. Due to logistical difficulties, NZFS were not recaptured and the devices were shed within 1 to 2 mo (as confirmed by subsequent resights).

Processing and statistical analyses of biologging data

The at-sea locations of NZFS were obtained through the Argos system (www.argos-system.org). These data were subsequently filtered using a correlated random walk, state-space model which included movement, error and stopping models (Johnson et al. 2008). Location precision was assumed to be the same as found by Costa et al. (2010). After filtering, foraging tracks were interpolated to provide an estimated position every 10 min. Filtering and interpolation of NZFS data was carried out using the R package crawl (v. 1.5; Johnson 2015).

As NZFS could not be recaptured, diving behaviour was determined from data transmitted via satellite. Summary information of the number of dives recorded during 2 h intervals in pre-defined histogram bins was obtained: maximum dive depth (0, 0–10, 10–20, 20–30, … , 90–100, 100–150, 150–200 and >200 m); and duration (0, 0–10, 10–20, 20–30, … , 90–100, 100–150, 150–200 and >200 s). In order to calculate the means of these parameters, the median value for each bin (e.g. 15 m for a 10–20 m bin) was taken.

At-sea locations for AUFS were collected using FastLoc GPS, which provides locations at much greater accuracies than Argos (mean Argos accuracy, all classes combined: 19.44 ± 116.89 km [SD; median 1.91 km]; mean Fastloc accuracy: 0.35 ± 8.65 km [median 0.02 km]; Costa et al. 2010, Dujon et al. 2014). However, some erroneous locations can still occur; therefore, the location data for AUFS were filtered using a basic speed filter to remove serious outliers from tracks (threshold used: 10 m s^{-1}; McConnell et al. 1992). These data were subsequently interpolated to provide a position estimate every 10 min along each foraging track.

The TDR records for AUFS were analysed using the diveMove package in R. Data were zero-offset corrected following the methods of Luque & Fried (2011), and foraging dives were identified as all submergences to >2 m depth. Per-dive summary statistics (dive duration, depth and time) were then calculated from these filtered data. To allow the use of equivalent quality datasets for comparison between the 2 species, these individual dive statistics were

subsequently coarsened into the same 2-hourly binned data that was transmitted by satellite for NZFS.

Individual foraging trips were identified using the location data for both AUFS and NZFS following the criteria used by Hoskins et al. (2015). The foraging trip duration (s), total distance travelled (m), maximum distance from colony (m) and mean bearing from colony (°) were then calculated for all foraging tracks. Where data did not exist for both tracking and diving behaviour (e.g. due to battery failure of 1 device on AUFS), these data were truncated to include only times where both tracking and diving data existed. Additionally, to exclude the potential of seasonal differences in behaviour affecting the results (Hoskins & Arnould 2013), data were truncated to only those foraging trips that occurred during the Austral winter (June through August).

The spatial intensity of use was assessed through kernel density estimates of the interpolated foraging tracks. Kernels were first estimated per individual before these individual kernels were summed over the region and normalised to produce a density estimate per group. The total area and area of overlap between groups was then calculated for areas occupying the 50% kernel density area. Percentage overlap was then calculated using the equation:

$$[(\text{area}_{ab}/\text{home range}_a) \times (\text{area}_{ab}/\text{home range}_b)]^{0.5} \quad (1)$$

where area_{ab} is the area of overlap in the home ranges of species *a* and *b*, and home range_a and home range_b refer to the 50% kernel home ranges of species *a* and *b*, respectively (Atwood & Weeks 2003). All kernels were calculated using the R package *adehabitatHR* (v. 0.4.14; Calenge 2006).

The tracking and diving data followed a nested design with multiple foraging trips per individual, nested inside different years, with the potential for temporal and/or spatial autocorrelation between variables. As such, comparisons between species were made using a mixed-effects modelling framework. Linear mixed-effects (LME) models were used to compare differences between summary foraging metrics (maximum distance from the colony [km], total distance travelled [km], foraging trip duration [d], mean direction of travel from the colony [°], dive depth [m] and dive duration [s]) and each species. Each foraging metric was used as a response variable, with species used as a categorical predictor variable. To account for repeated measurements and potential inter-annual differences in variance, individual and year were used as nested random effects, with animal ID nested within year. Where necessary (after inspection of the residuals) a constant variance structure with separate variances per individual seal was used to account for heteroscedasticity in residual spread. The significance of the blocked year random effect was assessed using Akaike's information criterion (AIC; Akaike 1998). The individual level random effect was assumed necessary due to the data structure, and so was left in all models.

Additionally, diel variation in diving behaviour was assessed using generalised additive mixed-effects models (GAMMs), with one model using total time spent diving per 2-hourly block as the response variable and another GAMM using mean dive depth per 2-hourly block as a response variable. Categorical parametric coefficients were fitted to each species grouping, and hour of the day was fitted as a smooth predictor variable using cyclic cubic regression splines with individual splines fitted to each species. Within individual, temporal auto-correlation between time blocks was assessed using an auto-regressive correlation structure of the order 1. The complete random structure consisted of foraging trip nested inside individual ID nested inside year. Significance of random effects and the auto-correlation structure were assessed using AIC. Significance of individual smooth splines was then assessed using models fitted with the final random effects structure via AIC.

Models were fitted within R using the *nlme* package (v. 3.1-127; Pinheiro & Bates 2006) for LMEs and the *mgcv* package (v. 1.8-7; Wood 2004) for GAMMs following the methods of Pinheiro & Bates (2006) and Wood (2006). Where given in the text, parameter estimates from individual models are shown as estimate ± SE.

Diet analysis

The diets of the 2 species were investigated by analysing hard prey remains in scats and regurgitates collected at their respective colonies. Only fresh, whole scats produced by adults (differentiated from those of pups by size) were collected. Similarly, only fresh regurgitates that showed no evidence of being scattered or disturbed were collected from each colony. As the study areas are almost exclusively frequented by adult females nursing pups at this time of the year, the diets are presumed to represent that of lactating females. After collection, samples were stored frozen (–20°C) until analysis.

In the laboratory, scat and regurgitate profiles were analysed separately to avoid biases associated with differential regurgitation of prey remains (Hume et al. 2004). Sagittal otoliths, fish teeth, fish

spines and cephalopod beaks were examined under a dissecting microscope and identified by comparison to reference atlases and collections (Clarke 1986, Smale et al. 1995, Lu & Ickeringill 2002, Furlani et al. 2007). Otoliths were graded according to their level of erosion (1: unidentifiable to 5: pristine; Robinson et al. 2002), and only the lengths of those rated >3 were measured to estimate prey size. Seabird prey were identified by their feathers and, in one case, by the presence of intact bill and feet. Hard prey remains that could not be quantified, such as fish teeth and seabird feathers, were assigned a numerical abundance of 1 for each unique species (Gales & Pemberton 1994).

The frequency of occurrence of prey remains was calculated as the proportion of samples with identifiable prey remains in which a particular prey type occurred (i.e. only counting each species once per sample) while the numerical abundance was expressed as the total number of prey items encountered in samples (i.e. including all unique prey items). Prey size was estimated from the remains measured (±0.1 mm) using an eye-piece graticule under a dissecting microscope and published regression equations (O'Sullivan & Cullen 1983, Gales & Pemberton 1990, 1994, Cullen et al. 1991, Lu & Ickeringill 2002, Furlani et al. 2007). To avoid obtaining size estimates from the same prey individual, only the otoliths of the side with the greater number of intact otoliths per sample were measured. Depending on the regression equations available, rostrum, crest or hood length of intact upper or lower cephalopod beaks were measured. Size of prey that could not be identified to species was estimated using species within the same family for which regression equations were available.

Dietary overlap in fish prey between AUFS and NZFS was analysed using Schoener's (1968) niche overlap index (O):

$$O = 1 - {}^{1}/_{2} \times \sum_{j=1}^{n} |p_{1j} - p_{2j}| \quad (2)$$

where p_{1j} and p_{2j} refer to the proportion of the total number of the j^{th} prey species for AUFS and NZFS, respectively. An overlap index of 1 indicates complete dietary overlap, while an index of 0 indicates no interspecific overlap. Additionally, the diversity of fish prey consumed by each seal species was calculated using Shannon's diversity index (H'):

$$H' = -\sum (p_j \log p_j) \quad (2)$$

where p_j is the proportion of the total number of individuals of the j^{th} family. A more diverse diet is represented by a greater H' value (Shannon & Weaver 1949). Due to the limited number of regurgitates collected, only data obtained from scats were used to calculate both indices, and since cephalopod beaks and seabird feathers tend to be regurgitated, both were calculated purely on non-composite fish prey remains. These indices were calculated based on the families of fish prey, as some taxa could only be identified to family level.

RESULTS

Foraging locations and diving behaviour

Diving behaviour and tracking information was successfully recorded from 12 and 10 individual female AUFS and NZFS, respectively. On average, 3.5 ± 2.6 foraging trips (range: 1–12 foraging trips) were recorded per individual. The foraging distribution of AUFS was substantially more restricted than that of NZFS, with the former exploiting areas exclusively over the continental shelf in central Bass Strait (Fig. 1). In contrast, NZFS ranged over a much greater area, predominantly exploiting waters to the east and south-east of the colony (Fig. 1).

Visual inspection of the NZFS tracking data revealed a bimodal distribution in foraging strategy. During a foraging trip, individuals appeared to adopt 1 of 2 strategies, either foraging in areas near the colony or foraging much farther afield in areas east of Kanowna Island, including deep waters beyond the continental shelf. Individuals were observed to adopt both foraging strategies on successive foraging trips. Multidimensional scaling (MDS) of all tracking metrics confirmed this bimodal distribution when reducing the dimensionality of the data to 2 (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m566p229_supp.pdf). This was further highlighted when visualising the density distribution of the maximum distances achieved from the colony for female NZFS (Fig. S2). Following this ordination analysis, the NZFS data were divided into 2 groups, short and long foraging trips, for subsequent analyses.

The core foraging ranges, defined as those areas in which each species spent 50% of the time during foraging trips (Robinson et al. 2002), were restricted to the continental shelf for both AUFS and NZFS undertaking short foraging trips (Fig. 2a). However, when undertaking a long foraging trip, the core foraging range of NZFS expanded to occupy areas off the continental shelf, east of Bass Strait (Fig. 2a). Significant spatial overlap in core foraging ranges occurred

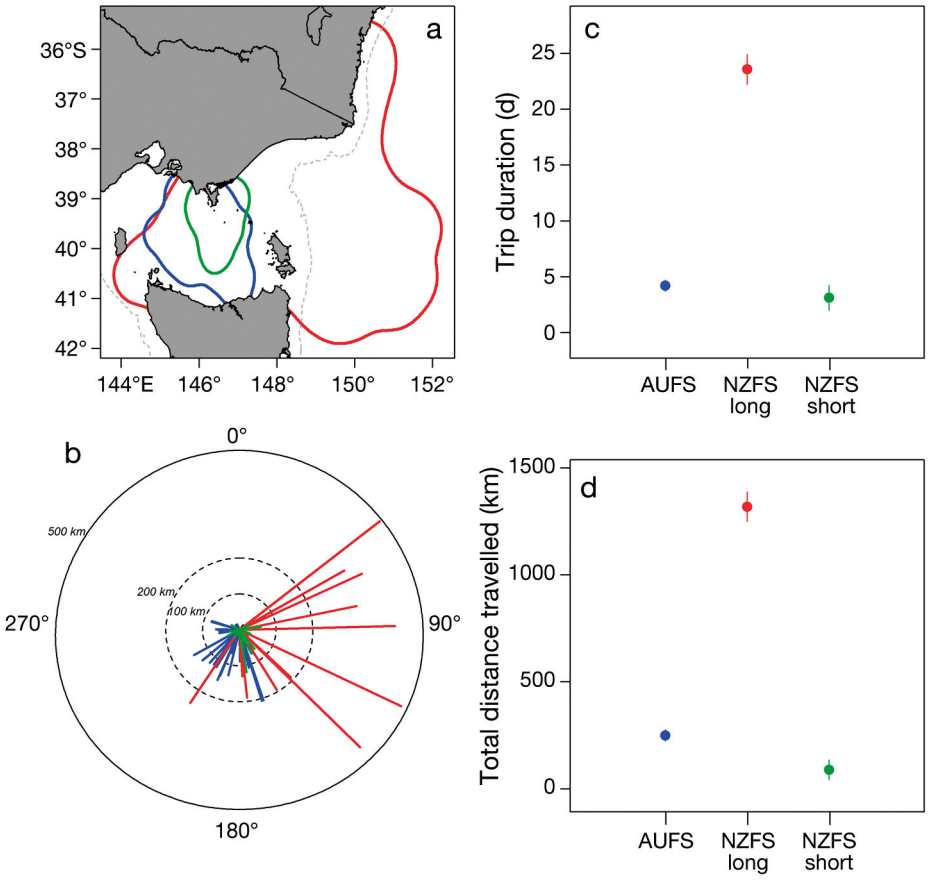

Fig. 2. Comparisons of summary tracking metrics for female Australian fur seals *Arctocephalus pusillus doriferus* (AUFS) and New Zealand fur seals *A. forsteri* (NZFS) tracked from Kanowna Island, Bass Strait, Australia. On all plots, blue: AUFS; red: NZFS undertaking long foraging trips; green: NZFS undertaking short foraging trips. (a) Comparisons of the 50% kernel density estimates. Grey dashed line delineates shelf waters. (b) Simplified travel information showing the maximum distance from colony and the mean bearing of travel for each foraging trip. (c) Linear mixed-effects model estimated mean foraging trip duration. (d) Linear mixed-effects model estimated total distance travelled during a foraging trip

between AUFS and NZFS undertaking short trips (58.4%; Fig. 2a), with almost the entire core range of NZFS on short trips being contained within the range of AUFS. As such, AUFS foraged over a greater area (AUFS foraging area: 49 534 km^2, NZFS short trip foraging area: 22 501 km^2). Almost the entire core foraging area of AUFS was contained within the core foraging areas of NZFS undertaking long foraging trips. The core AUFS foraging area was far more restricted than NZFS undertaking long foraging trips (NZFS long trip core foraging area: 294 556 km^2, spatial overlap 40.2%).

LMEs fitted to estimate the differences in metrics describing the spatial movements of each species revealed significant differences between all 3 groups (AUFS, and NZFS undertaking long and short trips) for the maximum distance reached from the colony, total distance travelled and mean travel direction (Fig. 2b–d, Table S1). In contrast, there was a significant difference in foraging trip duration between AUFS and NZFS on long foraging trips, but no difference between AUFS and NZFS on short foraging trips (Fig. 2c, Table S1). This suggests that NZFS on short trips were travelling at much slower rates and/or more often choosing to remain in smaller areas than AUFS.

On average, NZFS on long foraging trips travelled much greater distances from the colony (NZFS long trip: 363.4 ± 17.2 km, AUFS: 79.8 ± 8.8 km, NZFS short trip: 15.7 ± 13.0 km) and travelled greater total distances than other groups, with AUFS travelling distances intermediate between the 2 NZFS groups (NZFS long trip: 1319.1 ± 69.1 km, AUFS: 250.0 ± 27.2 km, NZFS short trip: 88.3 ± 47.0 km).

On average, AUFS travelled in a south-westerly direction (214.1 ± 13.3°), whereas NZFS travelled in either an easterly (92.5 ± 19.6°) or south-easterly (140.2 ± 19.6°) direction during long and short trips, respectively (Fig. 2b, Table S1). Foraging trip duration was similar between AUFS (4.2 ± 0.5 d) and NZFS undertaking short foraging trips (3.1 ± 1.1 d). However, when undertaking long foraging trips, NZFS spent significantly longer at sea (23.6 ± 1.3 d; Fig. 2c, Table S1).

Models fitted to the diving behaviour for AUFS and NZFS identified significant differences in both dive duration and dive depth between the 2 species but no differences between the 2 groupings (short and long trips) of NZFS (Table S2). As there was no difference between the 2 NZFS groupings, models were refitted after clustering NZFS back into a single group to pro-

vide estimates of diving behaviour for both AUFS and NZFS. Estimates from these models showed that, while diving, AUFS averaged depths 53 m deeper (AUFS: 70.6 ± 2.3 m, NZFS: 16.9 ± 3.7) on dives that lasted 50 s longer (AUFS: 211.3 ± 7.8 s, NZFS: 160.4 ± 12.4 s) than NZFS.

When assessing diel variation in diving behaviour, the model with the most parsimonious fit was one that showed diel differences in diving patterns between AUFS and NZFS but no differences in diving between NZFS undertaking either long or short foraging trips (Table S2). Although AUFS and NZFS spent a similar amount of time diving during the night, their behaviour diverged during daylight hours, with AUFS increasing their time diving and NZFS doing the opposite (Fig. 3a). This resulted in an overall greater amount of time spent diving during a 24 h period for AUFS compared to NZFS (Table S2). Throughout a 24 h period, AUFS and NZFS occupied different parts of the water column (Table S2). On average, NZFS dived to depths between 6.7 and 19.2 m, with deeper dives occurring during the night (Fig. 3b). In contrast, AUFS were estimated to dive between 53 and 73 m, with the shallowest dives occurring during the first part of the night (Fig. 3b).

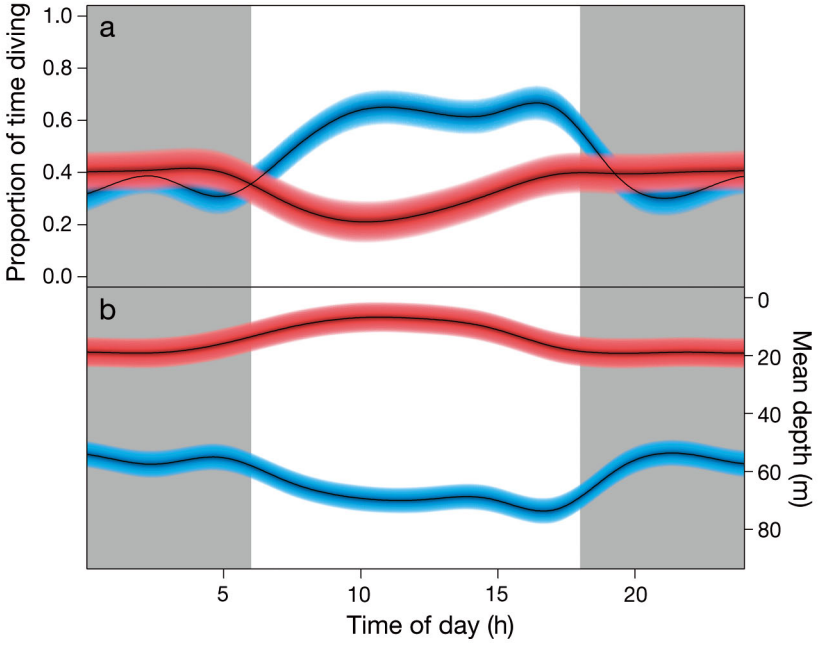

Fig. 3. Results of the smooth components (black lines: mean response, coloured bands: 95% confidence intervals) of generalised additive mixed-effects models fitted to time-series diving data for female Australian fur seals *Arctocephalus pusillus doriferus* (AUFS, blue) and New Zealand fur seals *A. forsteri* (NZFS, red) recorded foraging from Kanowna Island, Bass Strait, Australia. Models were fitted to show the daily temporal trend of (a) the time spent diving and (b) mean dive depth for each 2-hourly block of summary dive information received via satellite (NZFS) or coarsened logged dive behaviour information (AUFS). Estimates from the model assessing the diel patterns in time spent diving have been divided by the total duration of each 2-hourly block (7200 s) to be shown as proportions in panel a. Grey shading indicates night

Diet

Overall, a total of 137 scats and 5 regurgitates, and 104 scats and 9 regurgitates from AUFS and NZFS, respectively, were sampled. Nine scat samples (6 AUFS, 3 NZFS) which contained no diagnostic prey remains were excluded from further analyses. A total of 3645 sagittal otoliths (1313 from AUFS and 2332 from NZFS) and 220 cephalopod beaks (112 from AUFS and 108 from NZFS) were obtained from faecal samples, and 44 cephalopod beaks were recovered from regurgitates (15 from AUFS and 29 from NZFS). Of these, 3318 (91.0%) otoliths and 224 (84.8%) cephalopod beaks were identifiable, representing a minimum of 30 fish, 7 cephalopod and 3 seabird taxa. Fish remains in regurgitates consisted solely of leatherjacket dorsal spines. Two seabird taxa were also identified from both scats and regurgitates.

On average, a greater number of fish were found in the scats of NZFS (15.0 ± 1.9 items) versus AUFS (10.4 ± 1.3 items), whereas other groups were found in similar amounts (AUFS: crustaceans: 0.57 ± 0.1, cephalopods: 0.9 ± 0.1; NZFS: crustaceans: 0.67 ± 0.2 and cephalopods: 0.9 ± 0.2, seabirds: 0.34 ± 0.1). The gross composition of the diets of both species was broadly similar, with both consuming fish and cephalopods in relatively similar proportions (Fig. 4; Tables S3 & S5). In scats and regurgitates combined, fish contributed 84.5 and 86.4% to the prey of AUFS and NZFS, respectively, while cephalopods comprised 8.4 and 6.4%, respectively. However, only NZFS consumed seabirds (little penguins *Eudyptula minor*, shearwaters *Puffinus* spp. and fairy prions *Pachyptila turtur*). Evidence of these occurred in 29.7% of scats and 55.6% of regurgitates (Fig. 4). Crustacean remains, comprising amphipods, isopods and/or claws and carapace fragments of decapods, represented 6.7 and 4.6% of the number of prey items ingested

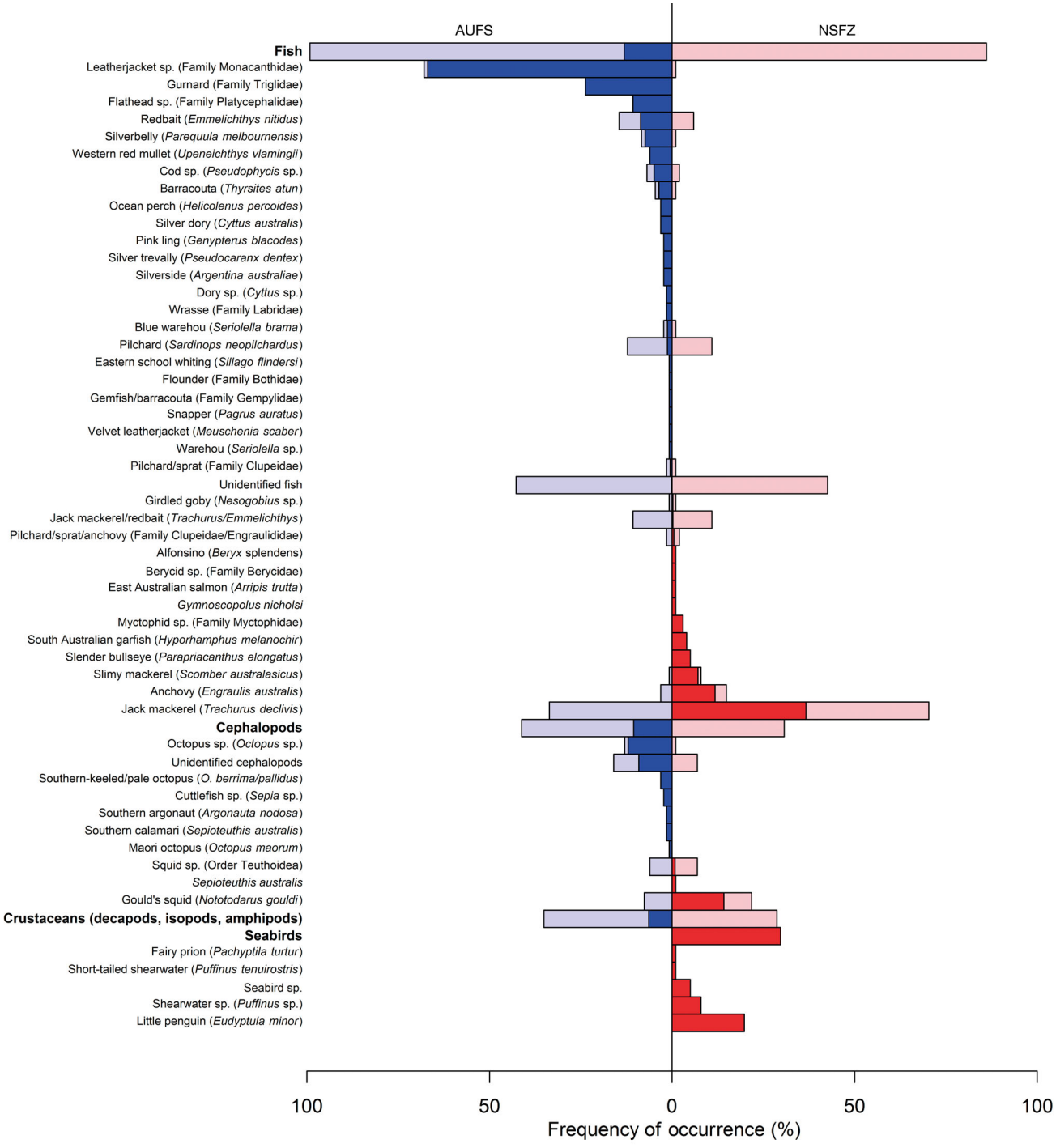

Fig. 4. Frequency of occurrence dietary composition for Australian fur seals *Arctocephalus pusillus doriferus* (AUFS, blue) and New Zealand fur seals *A. forsteri* (NZFS, red) from scat samples collected on Kanowna Island, Bass Strait, south-eastern Australia. Pale bars show frequency of occurrence of each prey species; solid bars indicate the difference in frequency of occurrence between AUFS and NZFS

by AUFS and NZFS, respectively (Fig. 4), with whole specimens being <16.3 mm. Due to their small size and the observation that jack mackerel *Trachurus declivis* may harbour parasitic isopods (Maxwell 1982), it was considered unlikely that these crustaceans were ingested as prey. Consequently, crustaceans were not considered in further analyses.

The fish prey consumed by AUFS and NZFS were broadly similar, with at least 12 taxa consumed by both seal species. Jack mackerel, redbait *Emmelich-*

thys nitidus and pilchard *Sardinops neopilchardus* were among the most frequently occurring prey taxa in scats of both seal species, with jack mackerel numerically dominant in both. However, differences in the relative importance and diversity of prey taxa were apparent between seal species, evidenced by a niche overlap index of 0.53. Differential consumption of jack mackerel and leatherjackets (Family Monocanthidae) was primarily responsible for interspecific dietary differences, with jack mackerel comprising a greater proportion of the prey remains in NZFS (54.0%) than in AUFS (34.3%) while leatherjackets constituted a greater proportion in AUFS (14.5%) than in NZFS (0.1%; Fig. 4). Leatherjackets also dominated by frequency of occurrence in AUFS samples. In addition, the greater consumption of anchovy *Engraulis australis* by NZFS and of gurnard (Family Triglidae) by AUFS were important in contributing to dietary differences between the species (Fig. 4). A minimum of 23 fish species (excluding groups where the species could not be clearly identified, such as redbait/jack mackerel) occurred in scats of AUFS, whereas 18 were identified from scats of NZFS (Fig. S3, Tables S3 & S5), and the fish prey diversity index was substantially greater for AUFS (0.79) than for NZFS (0.48).

Individual scats showed a similar pattern as the pooled data, with more species found in each AUFS scat (3.68 ± 0.13 species) when compared against NZFS (2.90 ± 0.15 species). This trend continued when looking at different prey groups with higher numbers of species in individual scats of AUFS for fish (AUFS: 2.97 ± 0.11 species, NZFS: 2.06 ± 0.13 species) and cephalopods (AUFS: 0.71 ± 0.06 species, NZFS: 0.49 ± 0.07 species). This only exception was birds that were only consumed by NZFS (0.33 ± 0.05 species per scat).

Cephalopods were more prevalent in regurgitates than scats of both seal species. Four of the 8 cephalopod taxa identified to genus or species were consumed by both seal species (Fig. 4 and see Fig. S3). However, interspecific differences in the relative importance of cephalopod prey were apparent. Gould's squid *Nototodarus gouldi* was the principal cephalopod prey in scats and regurgitates of NZFS, whereas in AUFS samples, octopus (*Octopus* spp.) were the most important prey taxon in scats and giant cuttlefish *Sepia apama* dominated in regurgitates (Fig. S3 and Tables S4 & S6).

Only a small proportion of otoliths and beaks were sufficiently pristine for measuring (Table 1). Of the measured prey remains, regression equations were available for 13 fish and 4 cephalopod species (Table 1). The means (or modes where samples were not normally distributed: Klages & Bester 1998) of these were compared between the 2 fur seal species.

Comparisons of fish prey size between AUFS and NZFS could only be made for jack mackerel, since this was the sole species for which there were sufficient numbers of intact otoliths. The distributions of the lengths of jack mackerel consumed by AUFS and NZFS were not normally distributed. The distribution of jack mackerel consumed by AUFS showed a bimodal pattern with the highest peak at 103 mm, a second smaller peak at 179 mm and the nadir be-

Table 1. Number of otoliths or beaks measured, mean (modal) length ± SE (mm) and range of lengths of fish (mm) (FL: fork length, SL: standard length, TL: total length) and cephalopods (ML: mantle length) consumed by Australian fur seals *Arctocephalus pusillus doriferus* (AUFS) and New Zealand fur seals *A. forsteri* (NZFS) at Kanowna Island (winters, 2006 to 2008). Mode (SE not calculated for data that were not normally distributed)

Prey	AUFS			NZFS		
	n	Mean (mode)	Range	n	Mean (mode)	Range
Fish						
Jack mackerel (FL)	78	(103)	85–240	180	(85)	57–280
Redbait (FL)	14	161 ± 5	120–188	2	170 ± 22	148–191
Anchovy (SL)	3	95 ± 4	90 – 103	31	(98)	79–108
Cod (TL)[a]	3	190 ± 53	122–294	5	76 ± 10	50–103
Pilchard (SL)	6	134 ± 4	123–148	4	143 ± 9	123–161
Flathead (TL)[b]	5	122 ± 24	67–182	–	–	–
Barracouta (FL)	3	(500)	288–500	–	–	–
Leatherjacket (SL)[c]	4	133 ± 11	109–158	–	–	–
Silver trevally (SL)	1	258	–	–	–	–
Blue warehou (FL)	1	212	–	–	–	–
Girdled goby (SL)	–	–	–	16	(37)	34–45
Southern sea garfish (SL)	–	–	–	3	154 ± 27	101–183
Beryciformes (SL)[d]	–	–	–	2	120 ± 2	118–123
Cephalopods						
Gould's squid (ML)	11	52 ± 3	40–69	52	(49)	38–84
Giant cuttlefish (ML)	2	161 ± 70	91–231	4	209 ± 26	153–274
Southern calamari (ML)	2	116 ± 0	116–116	1	56	–
Octopus (ML)[e]	18	50 ± 8	6–86	–	–	–

Size estimates based on:
[a]red cod *Pseudophycis bachus*
[b]sand flathead *Platycephalus bassensis*
[c]bridled leatherjacket *Acanthaluteres spilomelanurus*
[d]blacktip sawbelly *Hoplostethus intermedius*
[e]Southern keeled octopus *Octopus berrima*

tween these 2 peaks at 147 mm (35% of jack mackerel consumed were ≥147 mm; Fig. S4). In contrast, NZFS consumed smaller jack mackerel whose lengths were focused around a primary mode at 85 mm, with only 11% of jack mackerel consumed being greater than 147 mm (Fig. S4). A non-parametric *t*-test confirmed this difference in the distribution of jack mackerel lengths consumed by AUFS and NZFS ($U = 3051.5$, $p < 0.001$; Table 1).

In addition, the average modal/mean length of fish prey consumed by AUFS (191 mm) was substantially larger than that in NZFS (110 mm). Similarly, based on size estimates using beaks recovered from scat samples, AUFS consumed larger cephalopods than those consumed by NZFS (average modal/mean mantle lengths of 73 and 51 mm in AUFS and NZFS, respectively). There were no significant differences in the mantle length of Gould's squid consumed by the 2 species (52 mm in AUFS compared to 49 mm in NZFS; $U = 264$, $p = 0.69$).

DISCUSSION

Competition can lead to the exclusion of species from a region and is usually most intense between closely related species (Hardin 1960, Ashmole 1968). Numerous studies have shown that sympatric species maintain ecological isolation by segregating their resources, thereby precluding competitive exclusion (e.g. Robinson et al. 2002, Parra 2006).The results of the present study suggest that sympatric, temperate-latitude, AUFS and NZFS in northern Bass Strait have foraging ecologies that differ in diet, habitat use (i.e. foraging range, use of shelf/off-shelf water, benthic/pelagic) and diving behaviour (i.e. dive depth, time of day). Therefore, with the exception of some key prey species (i.e. jack mackerel), it appears the species could be partitioning resources allowing them to co-exist sympatrically.

Foraging locations and diving behaviour

As has previously been documented (Kirkwood et al. 2006, Hoskins et al. 2015), AUFS in the present study foraged exclusively over the continental shelf of Bass Strait. In contrast, and consistent with studies at allopatric sites (e.g. Harcourt et al. 2002, Page et al. 2006), NZFS used both continental shelf waters and areas beyond the continental shelf edge. Our study demonstrates that when both species are foraging out of the same site, there can be considerable overlap (47–67%) in the core foraging areas of both species.

There were clear differences in diving behaviour between AUFS and NZFS. The overwhelming majority of dives conducted by female AUFS in this study were to depths reflective of the local bathymetry. Furthermore, while diving occurred at all times of the day, it was more frequent during daylight hours. These features combined are consistent with foraging behaviour previously recorded for the species (Hoskins & Arnould 2013) and are indicative of a benthic foraging mode. Such foraging behaviour is unique among arctocephaline fur seals, being more akin to sea lion foraging behaviour, and has been ascribed to a lack of proficiency in capturing small, pelagic schooling prey (Arnould & Costa 2006).

In contrast, diving by NZFS was predominantly to depths shallower than 30 m. Corresponding data on at-sea locations indicate that, on average, these animals were foraging in waters >60 m in depth, demonstrating that they primarily performed mid-water, epipelagic dives. Such behaviour is consistent with that previously recorded for this species elsewhere throughout its range (Harcourt et al. 2002).

Interestingly, NZFS adopted a bimodal foraging strategy, with females either foraging close to the colony or travelling much longer distances to forage off the continental shelf. This behaviour has not been previously reported in this species. It is possible that individuals from Kanowna Island have adopted this strategy as a response to increased competition for limited resources while foraging on the continental shelf, allowing NZFS to access prey resources that are not accessible to AUFS. If the AUFS and NZFS colonies within Bass Strait continue to expand, this strategy could help to reduce competition between the species.

Differences in vertical habitat use can coincide with dietary divergence. For example, Luque et al. (2007) demonstrated fine-scale differences in dive depth that were associated with dietary differences between Antarctic fur seals *Arctocephalus gazella* and subantarctic fur seals *A. tropicalis* at Crozet Islands. Likewise, in the present study, interspecific differences in the prey consumed may reflect the foraging habitats used by each species; benthic/demersal prey were more prevalent in the diet of AUFS than in the diet of NZFS. However, as jack mackerel was a dominant prey item of both seal species, it is possible that prey species typically considered pelagic sometimes occupy demersal habitats. Indeed, while jack mackerel is nominally regarded as a pelagic schooling species in deep

waters beyond the continental shelf edge (May & Blaber 1989), individuals occupying shelf waters may move to the benthos in winter, with larger fish typically occupying greater depths (Kailola et al. 1993). The benthic versus epipelagic foraging strategies employed by AUFS and NZFS, respectively, may thus be reducing interspecific overlap in resource use. However, the main prey species for both AUFS and NZFS is shared (jack mackerel) so there is likely still some competition occurring. A similar pattern of niche separation has been reported for Galapagos fur seals and sea lions (Villegas-Amtmann et al. 2013). In that situation, the larger sea lions are constrained to a smaller home range, diving deeper on the Galapagos platform, whereas the fur seals forage widely off the shelf making shorter shallower dives.

Diet

In the present study, AUFS used a broader spectrum of fish prey taxa than NZFS, consuming 19 species in total, 7 of which comprised 58.5% of the prey remains. This is consistent with previous findings that the species has a broad diet and is considered a generalist predator (Hume et al. 2004, Kirkwood et al. 2008). In contrast, NZFS consumed only 13 fish species, of which 2 were primary prey (contributing 59.6% of all prey identified). Interspecific differences in fish prey consumed by AUFS and NZFS at Kanowna Island were largely due to differential consumption of some common prey taxa (e.g. jack mackerel). Such dietary partitioning by using similar prey in different proportions is common in sympatric predators (e.g. Johnson & Franklin 1994) and has been suggested as the primary means by which Antarctic, subantarctic and NZFS can coexist at Macquarie Island (Green et al. 1990).

The niche overlap index used in this study did not account for interspecific differences in prey size, a factor which can contribute to niche separation (Schoener 1974). Such a dietary separation has been observed in sympatric Antarctic and subantarctic fur seals at Marion Island (Klages & Bester 1998). In the present study, a lack of available regression equations for prey size constrained the number of species for which estimates could be obtained. Combined with the paucity of measurable specimens, these factors preclude the ability to provide detailed reconstructions of prey sizes for the majority of the diet. Nonetheless, the prey sizes observed in the present study are consistent with those previously reported for both species (Gales & Pemberton 1994, Page et al. 2005a). Notably, in the present study, scats of AUFS contained the remains of fewer prey, which were larger, whereas those of NZFS contained greater numbers of smaller prey. Generally, even for prey consumed by both species, AUFS were found to feed on larger specimens.

The results of our study indicate that dietary segregation between sympatric AUFS and NZFS in Bass Strait involves differences in prey species, proportions of commonly consumed species and size of prey. Female AUFS are on average 1.8 times the mass of NZFS (AUFS: 76 kg, NZFS 42 kg; Warneke & Shaughnessy 1985, Page et al. 2005b), which may account for the increased prey size and is consistent with theories on body size and foraging mode for otariid seals (Arnould & Costa 2006). The dietary differences identified in this study are also consistent with theories that suggest benthic foraging otariid species rely on more diverse, larger prey found at a lower, more evenly dispersed abundance when compared to pelagic foraging species that consume greater numbers of lower diversity, smaller prey that are found in large local aggregations within the water column (Arnould & Costa 2006).

In summary, our results have documented significant differences in the diet, foraging behaviour and habitat use of sympatric populations of AUFS and NZFS breeding in Bass Strait. The divergence in resource use, with AUFS foraging on the benthos for larger prey on the continental shelf and NZFS consuming smaller, pelagic schooling prey both over and beyond the continental shelf, is consistent with previously noted relationships between foraging mode and population demography in seals (Arnould & Costa 2006). The study was conducted in winter when lactating females experience the greatest nutritional demand with potentially the lowest food availability (Arnould & Hindell 2002) and, hence, it is possible that divergence in resource use may differ at other times of the year. There are numerous historical breeding sites within Bass Strait that have yet to be recolonised and, as AUFS and NZFS prefer different breeding habitat (Kirkwood et al. 2005), competition for breeding sites is unlikely to regulate the two populations. Furthermore, the foraging ecologies of the two species appear sufficiently divergent to maintain ecological separation. However, both use jack mackerel as their primary prey resource, leading to the potential for competition between the species as the populations of both species continue to grow in Bass Strait.

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