

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

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1 **ABSTRACT**

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

20 Key Words: competition, stable isotopes, foraging ecology, marine predator, recovery

21 INTRODUCTION

22 Understanding the factors that limit species' distributions is a key theme in ecology. An important
23 factor that limits the distribution of many plants and animals is interrelations among species which
24 determine food supply, threat of predation, disease and competition (Krebs 2001). In the case of
25 competition, two species living in a community can compete for resources to a point where one
26 species compromises the fitness of another, but can coexist by partitioning resources or risk
27 competitive exclusion (MacArthur & Levins 1967; Pacala & Roughgarden 1982; Luiselli 2006).

28 Interspecific competition is ubiquitous in plants and animals, though particularly prevalent at higher
29 trophic levels and/or among larger animals where available resources may be more limited (Connell
30 1983; Schoener 1983). Many populations of large carnivores are currently recovering and expanding
31 their range due to persistent conservation efforts (Wabakken et al. 2001; Chapron et al. 2014;
32 Gompper et al. 2015; Martinez Cano et al. 2016). During such recoveries, the interrelations with
33 species in the existing community and with other recovering carnivores are often unknown, but can
34 involve interspecies competition with detrimental impacts to some species, including human conflict
35 (Gompper 2002; Thornton et al. 2004; Kilgo et al. 2010; Reddy et al. 2019; Engebretsen et al. 2021;
36 Franchini et al. 2021). Therefore, determining factors that mitigate competition and mechanisms for
37 coexistence remain important in ecology and will support conservation management.

38 Niche theory suggests it is possible for competing species to coexist if they occupy different niches
39 (Hardin 1960; MacArthur & Levins 1967). Within a species, similar individuals manage to coexist by
40 partitioning resources, with individuals that have contrasting morphology, physiological capacity,
41 energy requirements or social status typically adopting different strategies to exploit available
42 resources (Svanbäck & Bolnick 2007). Individuals can also use a subset of the population's resources
43 for reasons unrelated to sex, age and morphological variation, i.e. inter-individual variation (Bolnick et
44 al. 2003; Araújo et al. 2011), with more specialised individuals using a smaller subset and more
45 generalised individuals using a larger subset of the population resources. The level of inter-individual
46 variation can be positively related to population density – a proxy for intraspecies competition
47 (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007; Araújo et al. 2008; Tinker et al. 2012;
48 Newsome et al. 2015). At the edge of a species' geographic range, population size is small and thereby

49 intraspecies competition tends to be low, reducing selection pressures associated with population
50 density, but here interspecies competition can be an important factor setting range limits (Hersteinsson
51 & Macdonald 1992; Case & Taper 2000; Case et al. 2005; Pigot & Tobias 2013).

52 By progressing the study of how species coexist, particularly at a species' expanding margin of their
53 range, we can better assess and predict the interrelations between species as they recover and move
54 into new communities. There are now well-established methods for quantifying ecological niche size
55 and partitioning, including variance and ellipse-based metrics, and spatial, resource and temporal
56 dimensions (Pielou 1972; Petraitis 1979; Bearhop et al. 2004; Peres-Neto et al. 2006; Jackson et al.
57 2011; Swanson et al. 2015; Frey et al. 2017), which have been used to demonstrate that individuals
58 can coexist by partitioning parts of their niche space, resources and time (Luiselli 2006; Navarro et al.
59 2013; Dehnhard et al. 2020). These niche dimensions have often been assessed in isolation, but with
60 the proliferation of stable isotope analyses and telemetry devices more studies are demonstrating the
61 importance of a multifaceted approach to understanding niche partition (Kleynhans et al. 2011; Matich
62 & Heithaus 2014; Baylis et al. 2015; Giménez et al. 2018; Riverón et al. 2021; Schwarz et al. 2021).
63 There have also been advances in measuring intra and interspecific variability in resource and space
64 use (Bolnick et al. 2002; Araújo et al. 2007; Zaccarelli et al. 2013; Carneiro et al. 2017; Bonnet-
65 Lebrun et al. 2018) that require serial sampling individuals to determine individual specialisation
66 (Newsome et al. 2010; Eerkens et al. 2016). Animals can be monitored over long periods of time by
67 using telemetry devices and sampling tissues that accumulate isotopes, with both approaches capable
68 of quantifying individual specialisation (Bearhop et al. 2006; Newsome et al. 2009; Elorriaga-
69 Verplancken et al. 2013; Kernaléguen et al. 2016; Bonnet-Lebrun et al. 2018). Commonly analysed
70 isotopes include nitrogen, as an indicator of trophic position of prey, and carbon, as an indicator of
71 geographic origin of prey (Kelly 2000; McCutchan Jr et al. 2003). In marine systems, carbon isotopes
72 can reflect nearshore vs. offshore foraging and prey originating from benthic vs. epipelagic
73 environments (Michener & Kaufman 2007; Newsome et al. 2010). Therefore, the tools are now
74 available to provide detailed assessments of how large predators coexist as they recover and expand
75 their range.

76 Otariids, fur seals and sea lions, were ubiquitously overharvested for their fur from the eighteenth to
77 twentieth century, with extinction of many populations and dramatic range reductions (Bonner 1989;
78 Gerber & Hilborn 2001). With persistent conservation efforts, many species have been recovering in
79 recent decades and reoccupying parts of their historic range (Wickens & York 1997; Gerber & Hilborn
80 2001; Kirkman et al. 2013; Crespo 2021; Salton et al. 2021). There are many incidences of two otariid
81 species living in sympatry during such recoveries (Majluf & Trillmich 1981; Lyons et al. 2000; Wege
82 et al. 2016; Elorriaga-Verplancken et al. 2021), and while this seems to be possible by partitioning
83 their niche (Robinson 2002; Franco-Trecu et al. 2012; Páez-Rosas et al. 2012; Jeglinski et al. 2013;
84 Pablo-Rodríguez et al. 2016; Hoskins et al. 2017) different levels of individual specialisations in diet
85 and foraging among species may also play a role (Franco-Trecu 2014; Kernaléguen et al. 2015a;
86 Kernaléguen et al. 2015b; Riverón et al. 2021). Some sympatric species display disparate population
87 growth rates and range expansion, which could be attributed to interrelations between the similar
88 species (Wickens & York 1997; Villegas-Amtmann et al. 2013; Franco-Trecu 2014; Elorriaga-
89 Verplancken et al. 2021).

90 Here, we investigate how two otariids, the Australian fur seal, *Arctocephalus pusillus doriferus*, and
91 the New Zealand fur seal, *A. forsteri* (also known as long-nosed fur seal, Shaughnessy & Goldsworthy
92 2015), coexist in sympatry at an expanding margin of both species' range. These species have recently
93 reestablished seasonal occupation of their north-eastern range margin (Warneke 1975; Irvine et al.
94 1997; Shaughnessy et al. 2001; Burleigh et al. 2008; Salton et al. 2021) following broader population
95 recovery and range expansion (Arnould et al. 2003; Shaughnessy et al. 2015; McIntosh et al. 2018).
96 Their populations at this margin remain small and predominantly consists of juveniles and sub-adult
97 males (Burleigh et al. 2008), though both breed on Montague Island, NSW (36° 14' S, 150° 13' E), in
98 small numbers (McIntosh et al. 2018). The two species are typically considered 'generalists' due to
99 their broad diets (Page et al. 2005a; Kliska 2016), but in some areas Australian fur seals do exhibit
100 individual specialisations in diet and foraging (Kernaléguen et al. 2012; Kernaléguen et al. 2016; Knox
101 et al. 2018). The two species have apparently distinct foraging modes, with Australian fur seals
102 primarily foraging during benthic dives over the continental shelf (Knox et al. 2017; Salton et al.
103 2019) and New Zealand fur seals foraging during pelagic dives on and off the continental shelf (Page
104 et al. 2005b; Page et al. 2006; Salton et al. 2021). There is some evidence that the two species have

105 different diets and foraging behaviour in this part of their range (Hardy et al. 2017; Salton et al. 2021),
106 though the mechanisms for coexistence remains unclear. Given the small population sizes of both
107 species, we expect intraspecies competition to be low and, accordingly, interspecies interactions to
108 drive niche partitioning. To understand the mechanisms for coexistence in a situation with purported
109 low intraspecies competition we aim to 1) estimate niche sizes, in isotopic and movement space, and
110 the degree of partitioning between species at a population level, and 2) the degree of individual
111 specialization at the intra-population level and how it relates to their population niche size. Then, 3)
112 we assess the relationship between individual specialisation in isotopic space and individual
113 specialisation in movement space, and the importance of intrinsic differences in body size.

114 **METHODS**

115 **Ethics statement**

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

127 **Study species, study site and data collection**

128 The data were collected during the male's inter-breeding period between 25-May and 22-Aug in 2011
129 to 2014, inclusive, when they are free of immediate reproductive constraints and thereby no
130 requirement to attend a specific terrestrial site and can range widely. The breeding period for male
131 Australian fur seals is between late October and late December and for male New Zealand fur seals
132 between early November and early January (Crawley & Wilson 1976; Warneke & Shaughnessy 1985).
133 Males move away from their inter-breeding areas towards breeding colonies at the approach of
134 breeding seasons, and it is assumed the reverse occurs at the end of breeding, consistent with the
135 seasonal pattern of attendance at these inter-breeding areas (Shaughnessy et al. 2001; Burleigh et al.
136 2008) and resighted seals marked with flipper tags at colonies (Warneke 1975). Male fur seals were
137 captured at two study sites, Jervis Bay (35° 3' S, 150° 50' E) and Montague Island (36° 14' S, 150°
138 13' E) on the southeast coast of Australia (Fig. 1). This coastline has a narrow continental shelf (17-72
139 km width) with the shelf break between 130 and 170 m (Geoscience Australia, data.gov.au, 2017-06-
140 24). The populations of both fur seal species have recently been growing in this north-eastern region

141 of both species' range after near extirpation from over harvesting, and at the time of this study the
142 populations remained small (Warneke 1975; McIntosh et al. 2018).

143
144 The movement of males were recorded with Mk10-AF Fastloc-GPS devices (Wildlife Computers; 105
145 $\times 60 \times 20$ mm, 240 g) at Jervis Bay and CTD-SRDL-9000 (Conductivity-Temperature-Depth Satellite
146 Relay Data Logger, Sea Mammal Research Unit, St Andrews, UK; 120 x 72 x 60 mm, 545 g) at
147 Montague Island. Both devices collected Argos satellite-derived locations (collected at irregular time
148 intervals, with a median fix rate of 1 fix per 1.1 h), and Mk10 devices also recorded GPS locations
149 (collected at 2 min intervals, with a median fix rate of 1 fix per 1.5 h), both of which were transmitted
150 via the Argos satellite network (Collecte Localisation Satellites, Saint-Agne, France). Dive data were
151 collected with both devices (but not Mk10-AF in 2011), with depth (± 0.5 m) sampled every 5 s when
152 the device was wet. Single dives were defined by a minimum depth of 5 m and minimum duration of
153 10 s, then the maximum depth per dive was extracted.

154 To account for potential inter-annual variability in resource use (Rodríguez-Malagón et al. 2021), we
155 sampled individual vibrissae from both species across each year of the study. The longest whisker was
156 sampled (plucked) from each seal while a tracking device was being attached. One whisker was
157 sampled from a dead seal incidentally in 21 November 2012. In the laboratory, vibrissae were hand-
158 washed in 100% ethanol and cleaned in an ultrasonic bath of distilled water for 5 minutes. Vibrissae
159 were then dried, measured and cut into 3 mm-long consecutive sections starting from the proximal
160 (facial) end, following Cherel et al. (2009). The first 10 sections were sampled from all individuals.

161 Vibrissae growth rate estimates for Australian fur seal males are 0.17 ± 0.04 mm d⁻¹ (Kernaléguen et
162 al. 2015b), and while they are not known for male New Zealand fur seals we assume it is similar based
163 on growth rate estimates of other male fur seals; *Arctocephalus australis* 0.13 mm d⁻¹, *Arctocephalus*
164 *gazelle* 0.14 ± 0.02 mm d⁻¹, *Arctocephalus tropicalis* 0.14 ± 0.04 mm d⁻¹, (Kernaléguen et al. 2012;
165 Vales et al. 2015). Hence, a 3mm section corresponds to approximately 18 days (Kernaléguen et al.
166 2015b). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each whisker section were determined by a PDZ Europa ANCA-
167 GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon,
168 Cheshire, UK) at the University of California Davis (UC-Davis) Stable Isotope Facility. Results are
169 presented in the conventional δ notation relative to Vienna PeeDee Belemnite marine fossil limestone

170 and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory
171 standards indicate measurement errors of $< 0.58\text{‰}$ and $< 0.20\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values,
172 respectively.
173 Vibrissae were sampled for carbon and nitrogen isotope analysis from 9 male Australian fur seals
174 (AuFS) and 35 male New Zealand fur seals (NZFS). Location and dive recording devices were
175 deployed on 10 male AuFS and 38 male NZFS. Location and dive data were recorded for 15-259 days
176 (mean \pm SE 131.9 ± 15.5 days and 101.4 ± 10.7 days per individual, respectively), which was
177 equivalent to 15 ± 1.2 weeks with location and dive data, 635 ± 53 locations (from SSM, at 3hr
178 interval) and 1151 ± 221 dives per individual. Based on body length of the seals, male AuFS were
179 larger than male NZFS (body length mean \pm SE 192 ± 7.9 cm, $N = 9$ individual, vs. 137 ± 5.7 , $N = 39$
180 individuals, respectively; Wilcoxon rank sum test $W=339$, $P < 0.001$).

181 **Data processing**

182 All data processing, analysis and figure development were conducted in R v4.1.1 (R Core Team
183 2020).
184 Locations were subjected to standard quality-control checks, including removal of erroneous and
185 duplicated locations, removal of locations after a tag fell off a seal, and reclassification of Argos Z-
186 class locations to B-class ($n = 86/ 56978$ locations). Then a continuous-time correlated random walk
187 state-space model (Jonsen et al. 2020) was fitted to the quality-controlled locations using
188 the *'fit_ssm'* function in the *'foieGras'* R package (Jonsen & Patterson 2020). This approach
189 accounted for observation errors in the Argos location data, and provided location estimates with
190 standard errors at regular 3 hr time intervals along each individual's track (Jonsen et al.
191 2013). Foraging 'distance to land' was used as an index of horizontal movement behaviour. To
192 calculate this index, SSM-estimated locations were projected using Albers equal-area based on the
193 extent of the seal's movements, determined using <https://projectionwizard.org/>, then distance to the
194 Australian coastline (GEODATA Coast 100K 2004, Geosciences Australia) was calculated using the
195 *'gDistance'* function in the *'rgeos'* R package (Bivand & Rundel 2021). Locations within 100 m of
196 land were assumed to be indicative of the seal being on land or not foraging and removed.
197 To best represent the foraging behaviour of animals at the expanding range margin, we analysed only
198 the 10 most recent whisker sections to represent an individual's isotopic niche and the first 10 weeks

199 of tracking data to represent their movement niche. This avoids details of their seasonal migrations
200 that may influence the stable isotope values preceding the period at the range margin (Online
201 Resource, Fig. S1; Kernaléguen et al. 2015b; Salton et al. 2021). Based on the whisker growth rate
202 estimates (presented above), the isotope data corresponds to diet approximately 180 days prior to
203 sampling (i.e. approximately the first six months of the year). Each whisker section represented a
204 unique sample of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values per individual. For movement data, distance to land and
205 maximum dive depth were averaged per week for each individual, and these weekly averaged values
206 represented individual samples of movement behaviour.

207 **Niche partitioning and Individual specialisation**

208 Species differences in the two isotope variables ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and two movement variables (distance
209 to land and dive depth) were tested using linear mixed models. For each of the four variables, a linear
210 mixed model was fitted with species a fixed categorical effect and sample nested in individual identity
211 as a random effect, using the ‘*lme*’ function in the ‘nlme’ R package (Pinheiro et al. 2021). All models
212 included a temporal autocorrelation (corAR1 of form $\sim 1|ID$) to account for serial sampling of
213 individuals. When there were model convergence issues (i.e. $\delta^{15}\text{N}$), these were corrected by removing
214 the nested sample component of the random effect. Akaike Information Criterion (AIC) and analysis
215 of variance tests were used to compare the model with fixed effects to the null model, with $P < 0.05$
216 indicative of a significant difference from the null model; following the protocol outlined by Zuur et
217 al. (2009). Distance to land and dive depth were log transformed to account for these indexes being
218 highly positively skewed, and the model estimates are presented back-transformed with their
219 confidence interval (alternatively, isotope estimates are presented with their modelled standard error).
220 The 95% and 50% spatial utilisation distribution (UD) probabilities were calculated for the inter-
221 breeding period. Smoothing parameters for the UD were calculated using the plug-in bandwidth
222 selector function ‘*Hpi*’ and associated ‘*kde*’ function in the ‘*ks*’ R package (Duong 2021), and the
223 Australian coastline was used as a habitat grid to ensure realistic UD probabilities over water. UDs
224 were calculated for each individual and then standardised to produce a population level 95% and 50%
225 UD for AuFS and NZFS. Percentage UD overlap was calculated using the equation $[(\text{area}_{ab}/\text{UD}_a) \times$
226 $(\text{area}_{ab}/\text{UD}_b)]^{0.5}$, where area_{ab} is the area of overlap in the home ranges of species a and b , and UD_a and
227 UD_b refer to the UD of species a and b , respectively (Atwood & Weeks 2003; Hoskins et al. 2017).

228 To test for partitioning in the circadian pattern of dive behaviour, we assessed whether dive frequency
229 and dive depth differed with three diel periods; day, twilight and night. Solar position was calculated
230 using solar azimuth and elevation based on location, local date and time (Australian eastern standard
231 time: UTC +10 h), using the ‘*solarpos*’ function in the ‘*maptools*’ R package (Bivand & Lewin-Koh
232 2021). From solar position, a categorical variable for diel period was defined with three levels:
233 positive values of solar elevation angle identified ‘day’; values between zero and -12 deg below the
234 horizon identified nautical ‘twilight’; and values below -12 deg identified ‘night’. Generalized linear
235 mixed models were fitted to assess whether dive frequency was explained by diel period, for each
236 species separately, using the ‘*lmer*’ function in the ‘*lme4*’ R package (Bates et al. 2015) with a random
237 effect for individual (intercept only, to elevate convergence issues with the models) and a Poisson
238 error distribution with a log link function. Linear mixed models were fitted to assess whether dive
239 depth (log transformed) was explained by diel period, for each species separately, using the ‘*lmer*’
240 function in the ‘*lme4*’ R package (Bates et al. 2015) with a random effect for individual (intercept
241 only, to elevate convergence issues with the models). AIC and analysis of variance were again used to
242 compare the model with fixed effects to the null model, with $P < 0.05$ indicative of a significant
243 difference from the null model.

244 Isotopic and movement niche size and partitioning between species were estimated using Bayesian
245 ellipse-based metrics calculated in the ‘SIBER’ R package (Jackson et al. 2011). SIBER applies a
246 ‘typical’ individual approach to calculate the core niche of a population, and incorporates uncertainties
247 relating to sampling biases and small sample sizes (Jackson et al. 2011; Syväranta et al. 2013). We
248 used the 40% Bayesian standard ellipse area (SEA_b) to represent the most reliable population-level
249 niche, with the variance estimated through 10^4 posteriori draws, and a 95% SEA_b to capture individual
250 variation and enable more accurate cross-study comparisons. Repeated sample measurements per
251 individual were not independent, yet the small sample size of individual Australian fur seals produced
252 highly variable niche estimates for that population, albeit consistent niche size compared to the whole
253 dataset (Sup 1). Independent sampling is a required assumption for use of Bayesian SEA_b (Jackson et
254 al. 2011), but incorporating a large number of individuals as in this case was preferable to other
255 methods of assessing isotope niche. SEA_b results should nevertheless be interpreted in combination
256 with results from mixed effect models. Overlap of isotopic and movement niches was calculated per

257 species based on the posterior distributions of the fitted ellipses using the ‘*baysianOverlap*’ function (n
258 = 360, draws = 50).

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

275 Online Resource, Figure S1. Isotopic biplots for each of the four niche parameters for each individual
276 male Australian fur seals (*A. pusillus doriferus*, red) and New Zealand fur seals (*A. forsteri*, yellow)
277 calculated with three different datasets (one per row).

278 RESULTS

279 Isotopic and movement niche

280 The two species had broad, overlapping isotopic niches of similar size. Bayesian estimation of the
281 isotopic niche space of the two species shows similar sized isotopic niches, based on the 40% SEA_b
282 and 95% SEA_b, yet Australian fur seals had a narrower range of $\delta^{15}\text{N}$ values (trophic levels) and wider
283 range of $\delta^{13}\text{C}$ (nutritional sources) compared to New Zealand fur seals (Fig. 2; Table 1). Bayesian
284 trophic niche (40% SEA_b) overlap was negligible at ~5%, suggesting strong resource partitioning
285 between the two pinniped populations. There were significant differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values
286 between male AuFS and NZFS, with AuFS having higher $\delta^{15}\text{N}$ values and higher but ecologically
287 similar $\delta^{13}\text{C}$ values (models were significantly different to the null model, $\delta^{15}\text{N}$ $\Delta\text{AIC} = 17.65$ $\text{Chisq} =$
288 19.65 $P < 0.001$; $\delta^{13}\text{C}$ $\Delta\text{AIC} = 3.16$ $\text{Chisq} = 5.16$ $P = 0.023$; Table 1). Based on the 40% SEA_b,
289 partitioning of their iso-niche space was primarily in $\delta^{15}\text{N}$ values that relate to trophic level (Fig. 2,
290 Table 1).

291 Male AuFS remained close to the coast over the continental shelf while NZFS travelled across the
292 continental shelf and off the shelf over deep water. Consequently, male NZFS had a much larger 95%
293 utilisation distribution than AuFS (Table 1), and the percentage overlap or 95% UD shared with the
294 other species was ~80% for AuFS and ~10% for NZFS. However, the 50% UD for both species was
295 predominantly over the continental shelf, of similar size, and showed approximately 50% species
296 overlap (Fig. 1; Table 1). Accordingly, the mean distance that an individual travelled from land per
297 week was highly positively skewed for male AuFS and NZFS, and not significantly different between
298 the two species (distance to land not significantly different to the null model, $\Delta\text{AIC} = 1.6$ $\text{Chisq} = 0.32$
299 $P = 0.574$; Table 1). The two species also shared vertical movement space, but on average male AuFS
300 dived deeper than NZFS (dive depth significantly different to the null model, $\Delta\text{AIC} = 7.9$ $\text{Chisq} = 9.89$
301 $P = 0.002$; Fig. 1; Table 1). The movement behaviour of AuFS (i.e. predominantly deep dives over the
302 continental shelf) was consistent with a benthic foraging mode, and the movement behaviour of NZFS
303 (shallow dives over the shelf and deep water) was consistent with epipelagic foraging mode. However,
304 four male NZFS with weekly average maximum depth >100 m also remained close to land (<20 km)

305 during those weeks, suggesting benthic foraging; this was the case for all weeks recorded for one of
306 these four NZFS, suggesting it only used a benthic foraging mode during its inter-breeding period.

307 With the horizontal and vertical movements combined, NZFS had a much larger movement niche
308 space (40% and 95% SEA_b; Table 1), due to a wider range in horizontal movement (distance to land)
309 yet similar range in vertical movement (dive depth) among individuals of each species. Based on the
310 40% SEA_b, the two species overlapped in movement niche space (though AuFS share more of their
311 movement niche space with NZFS, and NZFS have more space that is segregated from AuFS space).
312 The divergence in movement niche was primarily due to segregation in dive depth (Fig. 2).

313 The two species also had different circadian patterns in dive frequency, with NZFS diving
314 significantly more at night and AuFS diving similarly between night and day, but significantly less
315 during twilight (Online Resource; Fig. S2, S3). Neither species had a diel pattern in dive depth (Online
316 Resource; Fig. S2, S3).

317 Table 1 Population-level isotope niche space statistics ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and movement niche
 318 space statistics (distance to land and dive depth), including Bayesian Standard Ellipse Area
 319 (SEA_b), of male Australian fur seals (*A. pusillus doriferus*) and New Zealand fur seals (*A.*
 320 *forsteri*). Isotopic space calculated from 3 mm segments from one vibrissae per individual.
 321 Movement space calculated from weekly mean statistics per individual.

Population-level statistics	<i>A. pusillus doriferus</i>	<i>A. forsteri</i>
Isotope niche space	(n=9)	(n=35)
$\delta^{15}\text{N}$ (‰) ^a	16.4 ± 0.2	15.2 ± 0.2
$\delta^{13}\text{C}$ (‰) ^a	-15.4 ± 0.1	-15.7 ± 0.1
SEA_b 40% area (‰ ²) ^{a, d}	1.0 ± 0.11	1.0 ± 0.04
SEA_b 95% area (‰ ²) ^{a, e}	5.8	6.1
SEA_b 40% overlap (%) ^{a, d}	5.8 ± 1.04	5.7 ± 4.12
SEA_b 95% width $\delta^{13}\text{C}$ (‰) ^b	-16.2; -14.7	-16.3; -15.2
SEA_b 95% width $\delta^{15}\text{N}$ (‰) ^b	15.6; 17.4	14.1; 16.2
Movement niche space	(n=10)	(n=35)
Maximum dive depth (m)	58.1 (35.5 to 85.5)	25.3 (9.0 to 68.1)
SEA_b 40% area (‰ ²) ^{a, d}	1.4 ± 0.2	3.5 ± 0.2
SEA_b 95% area (‰ ²) ^{a, e}	8.2	20.9
SEA_b 40% overlap (%) ^{a, d}	48.3 ± 10.0	19.6 ± 4.4
SEA_b 95% width Distance to land (km) ^b	2.3; 23.5	1.0; 53.1
SEA_b 95% width Dive depth (m) ^b	17.4; 164.4	9.2; 67.3
Movement niche space, horizontal only	(n=10)	(n=39)
Distance to land (km) ^c	6.3 (3.4 to 11.0)	6.3 (1.4 to 20.6)
Area of 95% UD (km ²)	17,478	72,375
Overlap of 95% UD (%)	71	17
Area of 50% UD (km ²)	1577	1109
Overlap of 50% UD (%)	52	73

322 ^a Mean ± SE and range are calculated at the individual level (i.e. mean of each individual's
 323 average value across its whisker segments or weekly movement data)

324 ^b Range of values

325 ^c Movement space parameters were log-transformed, and subsequently their back-transformed
 326 estimates of means are accompanied by 95% confidence intervals.

327 ^{d, e} A sample of 50 SEA_b were used to calculate 40% areas and overlap, and one sample of 1
 328 SEA_b was used to calculate 95% areas and widths

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

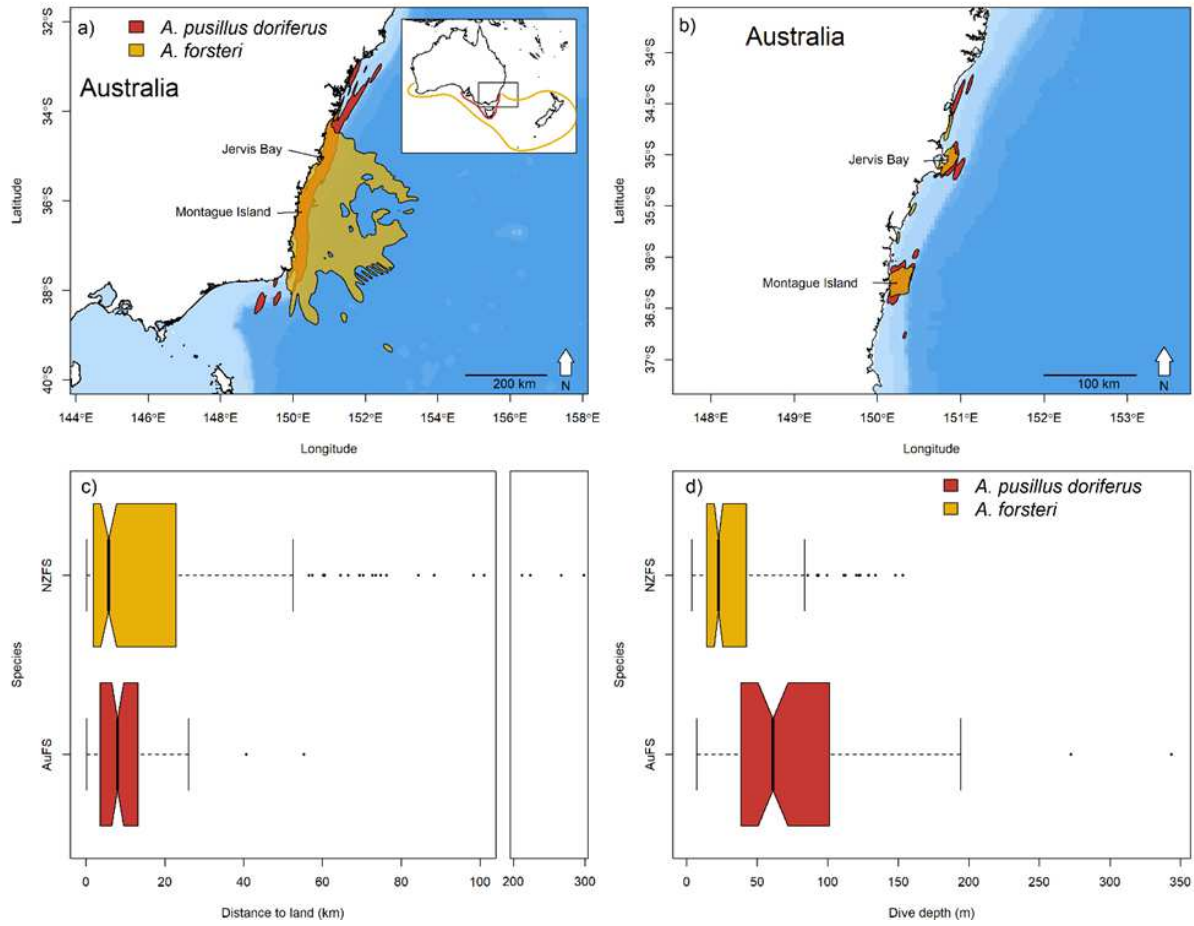
338 Fig. 2 Isotopic and movement niche bi-plots (left) and posterior density plots (right) from
339 Bayesian standard ellipse area (SEA_b; solid lines 40%, dashed line 95%; density plots are of
340 40% SEA_b) of male Australian fur seals (*Arctocephalus pusillus doriferus*; red) and New
341 Zealand fur seals (*A. forsteri*; yellow). In isotope bi-plot, points represent isotope values from
342 the ten most recent whisker samples from each individual. For clarity, a sample of 50
343 modelled ellipses (40% SEA_b) per species are shown. Bi-plots represent the size and overlap
344 of the niche space, and density plots compare size (similar niche size have more overlap) and
345 variance among 40% SEA_b estimates (height-width of density plot).

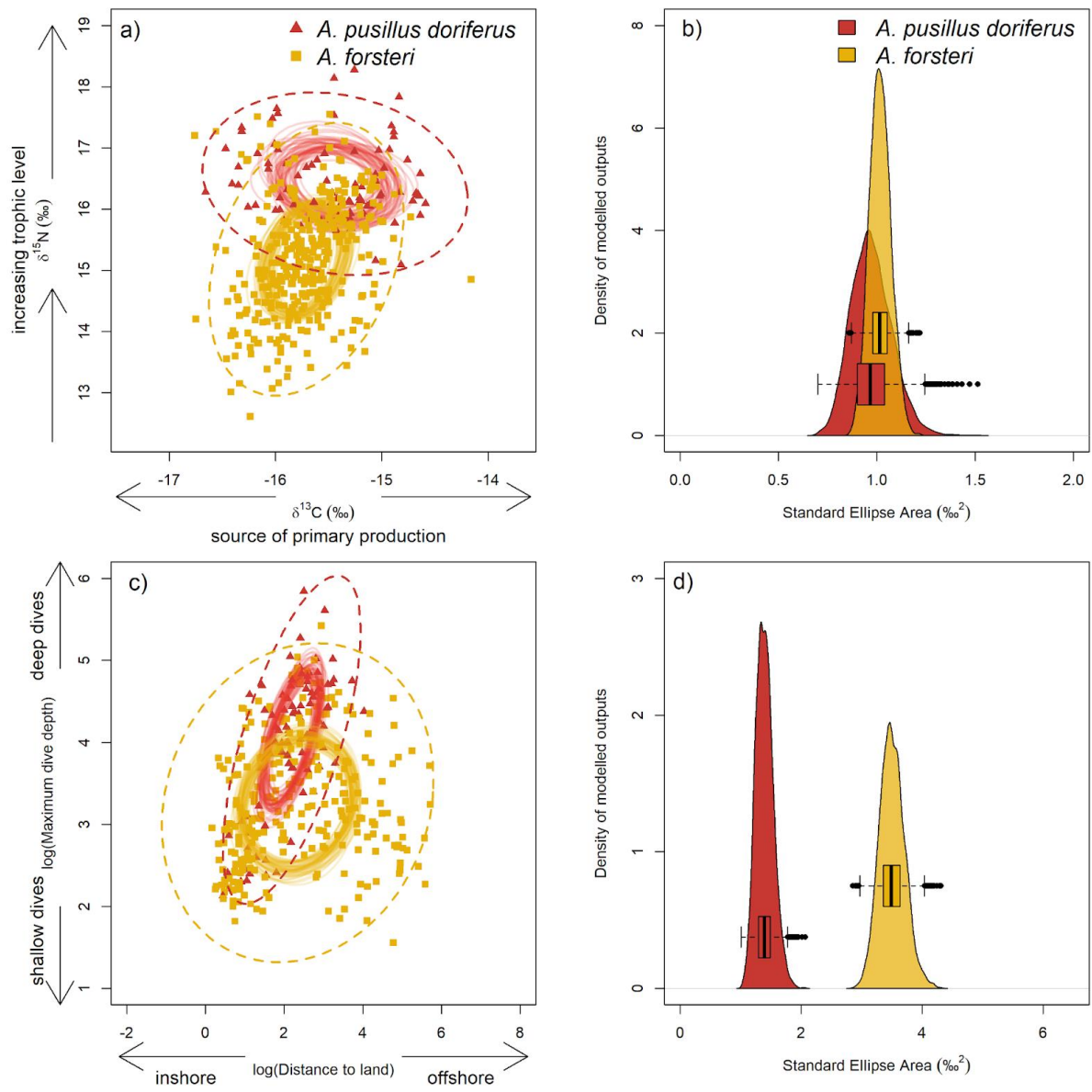
346 Fig. 3 Density plot of specialisation index (SI) in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each individual
347 male Australian fur seals (, red) and New Zealand fur seals (*A. forsteri*, red). Vertical dotted
348 lines show the population-level SI (from Table 1).

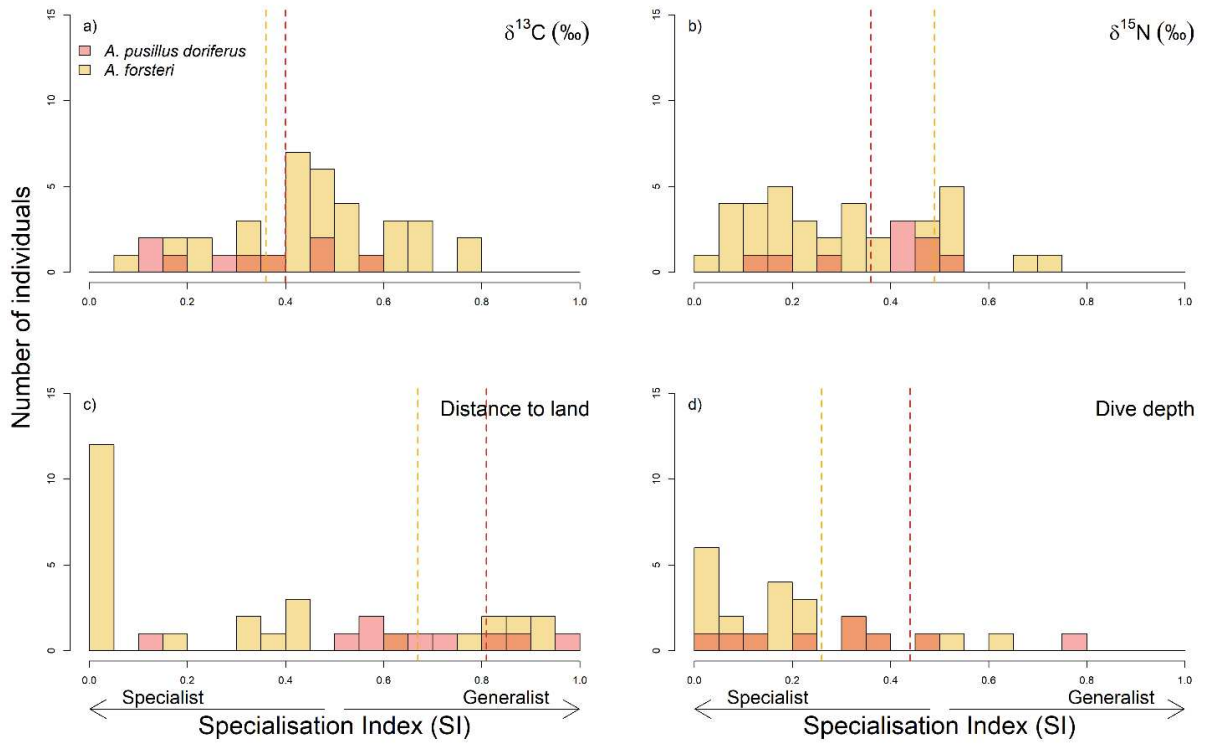
349 Online resource, Fig. S2 Different circadian patterns in dive frequency and but not dive depth between
350 male Australian fur seals (*A. pusillus doriferus*, red) and New Zealand fur seals (*A. forsteri*, yellow).

351 Online resource, Fig. S3 Model results for diel pattern in dive frequency and dive depth (using means
352 per week for each individual) of male Australian fur seals (*A. pusillus doriferus*) and New Zealand fur
353 seals (*A. forsteri*), including models tested (top) and modelled fixed effects (bottom).

354 Online resource, Fig. S4 Linear model results comparing individual specialisation indices of male
355 Australian fur seals (AuFS) and New Zealand fur seals (NZFS) in isotopic space ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and
356 movement space (Dive depth and Distance to land), and compared to their body size (Length).







365 **Individual Specialisation**

366 The individual specialisation index (SI) of $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values and dive depth for AuFS and
367 NZFS indicated these male fur seals were specialists in each of these niche dimensions ($P < 0.001$;
368 Table 2). However, there was high variability in the SI among individuals for each species (Fig. 3),
369 with some individuals tending towards the generalist end of the spectrum but most individuals at the
370 specialist end of the spectrum. For distance to land, AuFS were generalists and NZFS were specialists,
371 though both species had high variability in the SI among individuals with their values spread across
372 the SI spectrum (Fig. 3). There were a relatively large number of highly specialised male NZFS for
373 'distance to land'; 12 individuals with SI values < 0.05 . These individuals include some who travelled
374 off the continental shelf into deep water during each week, and other individuals who only moved
375 between islands and the coastline (i.e. remained very close to land).

376 There were no correlations between an individual's SI in any dimension and its body length (Online
377 Resource; Fig. S4); all $P > 0.05$. An individual's SI in one dimension (e.g. $\delta^{13}\text{C}$) was not related to its
378 SI in another dimension (e.g. $\delta^{15}\text{N}$).

379 **DISCUSSION**

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

390 **Niche partitioning**

391 As populations increase in size so can intraspecies competition for the most valuable food resources,
392 which should drive individuals to broaden their niche (diet and/or foraging behaviour) to maintain
393 optimal foraging (MacArthur & Pianka 1966; Roughgarden 1972; Bolnick 2001; Svanbäck & Bolnick
394 2007). Among marine predators, increased intraspecies competition has been associated with broader
395 dietary niche and foraging niche attributed to the need to access different prey, prey at deeper depths
396 and greater distances from their colony (Lewis et al. 2001; Kuhn et al. 2014; Ratcliffe et al. 2018).
397 Along the same lines, subantarctic fur seals in a large population that has reached carry capacity had a
398 wider niche than those from a smaller population that is still increasing (Kernaléguen et al. 2015a). In
399 contrast, at their range margin where population sizes are still small, these male fur seals continued to
400 display a broad dietary niche ($\delta^{15}\text{N}$ values) and movement niche (horizontal and vertical behaviour),
401 and this is consistent with an earlier dietary analysis of fur seal scats (Hardy et al. 2017). Alternatively
402 to enhanced intraspecies competition, individuals may expand their foraging niche in response to
403 interspecific competition or decreased availability of most valuable food resources (Chiaradia et al.
404 2003; Moleón et al. 2009; Prati et al. 2021) and both these alternatives typically characterise a species'
405 range margins (MacArthur 1984; Case et al. 2005; Guo et al. 2005). Therefore, individuals may need
406 to maintain a broad niche when moving between their range core and margins to mitigate different

407 types of competition (intra and interspecies) and variable abundance of favourable prey throughout a
408 species' distribution.

409 Interspecific competition was expected at this range margin, where two congeneric species live in
410 sympatry. However, their populations are small so interspecific competition should be low thereby
411 allowing these species to share the most profitable resources and overlap niche space. These male fur
412 seals did indeed overlap in the prey source of primary productivity ($\delta^{13}\text{C}$ values), trophic level of their
413 prey ($\delta^{15}\text{N}$ values; Kelly 2000; Davenport & Bax 2002) and horizontal and vertical niche space,
414 consistent with males of both species being high order predators that frequently return to land to rest
415 and digest, and have foraging habitat at a range of depths (Page et al. 2005a; Hardy et al. 2017; Knox
416 et al. 2017; Salton et al. 2021). Although the two species had overlapping niches, they had clear
417 partitioning in their dietary niche and dive behaviour, with AuFS typically feeding on higher trophic
418 level prey than NZFS (based on $\delta^{15}\text{N}$ values; Davenport & Bax 2002) and generally diving deeper than
419 NZFS. Similar means of niche partitioning (different dietary composition and foraging behaviour)
420 were found between sympatric female AuFS and NZFS at a breeding colony (Hoskins et al. 2017) and
421 between sympatric male AuFS and NZFS at a New Zealand fur seal breeding colony (Page et al.
422 2005a). However, at breeding colonies this partitioning is expected because the larger populations
423 suggest that absolute competition (intra and interspecific competition combine) should be higher
424 compared to the small populations at this range margin (Shaughnessy et al. 2015; McIntosh et al.
425 2018). It is possible that competition in the core of their range drove niche partitioning ancestrally, and
426 neither species is plastic enough in foraging to relax their constraints when seasonally present at the
427 range margin, even in the absence of resource limitations.

428 **Individual specialisation**

429 Niche expansion can occur when all individuals of a population exploit a wider niche or via increased
430 between-individual variation. The latter is termed the Niche Variation Hypothesis (Van Valen 1965),
431 and has supporting quantitative evidence from numerous taxa (Bolnick et al. 2007). Consistent with
432 this hypothesis, fur seal populations that feed only on a fewer prey species are often made up of
433 generalist individuals and populations with a broad dietary niche often have high levels of individual
434 specialisation (Kernaléguen et al. 2015a; Riverón et al. 2021), including Australian fur seals
435 (Kernaléguen et al. 2015b; this study) and New Zealand fur seals (this study). In addition to the Niche

436 Variation Hypothesis , the level of individual specialisation in a population can be positively related to
437 population density (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007; Tinker et al. 2008),
438 presumably because smaller populations have less intraspecies competition driving niche expansion,
439 which appears to be the case for some fur seals (Franco-Trecu 2014; Kernaléguen et al. 2015a).
440 Therefore, individuals at range margins, within small populations, may have lower individual
441 specialisation than conspecifics at the range core. Contrary to this, the level of individual
442 specialisation in $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values among male AuFS at this range margin (0.40 and 0.36,
443 respectively) was higher (more specialised) compared to male AuFS in the core of the species' range
444 (0.93 and 0.56, respectively; Kernaléguen et al. 2015b). Some of this disparity could be associated
445 with the shorter temporal scale used to measure individual specialisation in our study (10 whisker
446 segments, rather than whole vibrissae), which often exaggerates the apparent level of individual
447 specialisation (Araújo et al. 2007; Novak & Tinker 2015; Kernaléguen et al. 2016); though niche size
448 and overlap were similar for the 10 segment and whole whisker datasets (Online Resource; Fig. S1).
449 Alternatively, it could provide further support for behavioural differences between dispersers and
450 residents, with dispersers having high heterogeneity in behaviour that supports population expansion
451 into novel environments (Cote et al. 2010).
452 The level of specialisation in a niche dimension varied among individuals, suggesting disproportionate
453 effects of the drivers of specialisation on individuals. Accordingly, we tested whether the level of
454 individual specialisation in one niche dimension was linearly related to the specialisation in other
455 niche dimensions, and found this was not the case for any of the four niche dimensions. Therefore, a
456 seal may have a highly specialise dietary niche ($\delta^{15}\text{N}$ values) but forage across a range of habitats to
457 access their prey (less specialised movement niche). Alternatively, a seal may principally forage
458 epipelagically in inshore habitat (specialised movement niche) on a broad range of prey (less
459 specialised dietary niche). This suggests that individuals respond to the drivers of specialisation in
460 different ways, potentially specialising in various niche dimensions but not necessarily all of them.
461 This emphasis the behavioural plasticity of individuals to selection pressures and highlights the
462 importance of considering multiple niche dimensions when assessing ecological drivers and
463 consequences of individual specialisation.

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

487 **Ecological Implications**

488 As species expand their range into new habitat they must compete for resources with the native
489 community, which already compete among themselves. The size of a community can influence the
490 level of niche overlap, with increasing number of species associated with less overlap (Pianka 1974),
491 and if the community is sufficiently large it can prevent newly introduced species from becoming
492 established (Case 1990). This has implications for the success of biological invasions (MacArthur

493 1984; Freed & Cann 2014), and potentially the recovery and range expansion associated with
494 conservation efforts of a native species. Given the smaller populations of both species at this
495 expanding range margin, there was potential for high niche overlap associated with competition
496 release. Somewhat contradictory, the niche overlap and individual specialisation between and within
497 these male fur seals suggests there is available niche for each of these species and potential for further
498 mitigation of inter and intraspecies competition, and therefore potential for population growth and
499 range expansion. Indeed, prior to this study both populations of fur seals in Australia had positive
500 population trajectories (Shaughnessy et al. 2015; McIntosh et al. 2018). Ongoing assessments of niche
501 partitioning and individual specialisation within and between these sympatric and congeneric species
502 at this range margin will further develop ecological understanding of the mechanisms for successful
503 population growth and range expansion, and should consider the role of a rapidly warming
504 environment.

505 Individual specialisation and behavioural plasticity provide opportunities for a population to adapt to
506 environmental change (Brent 1978; Bolnick et al. 2003; Tuomainen & Candolin 2011; Edelaar &
507 Bolnick 2019). Accordingly, the high individual specialisation amongst these male fur seals may
508 contribute to their successful re-occupation of this margin of their range amidst extreme rate of ocean
509 warming (Ridgway 2007) and a dense human population. However, species have physiological limits,
510 for example otariids in temperate regions are sensitive to high temperatures (Gentry 1973), and
511 thermal energetic costs are often higher for pups and juveniles (Liwanag 2010). Species are also
512 limited by habitat needs, in this case particular terrestrial features at haul-out and breeding sites (Ryan
513 et al. 1997; Stevens & Boness 2003), and several of their haul-out sites at this margin of their range
514 are currently not zoned as protected areas (Salton et al. 2021). Therefore, while males have reoccupied
515 this part of the species' range, these additional limitations could influence the successful
516 reestablishment of a breeding population and future occupation by males. Furthermore, ocean
517 warming is altering prey distribution and abundance and thereby the habitat uses of marine predators
518 (Amador-Capitanachi et al. 2020; Evans et al. 2020; Niella et al. 2020; d'Entremont et al. 2021; Florko
519 et al. 2021; Niella et al. 2021). There have been recent losses of habitat and habitat-forming species at
520 this margin of the seals' range (Wernberg et al. 2011). Thus, while these predators demonstrate
521 capability to exploit a dynamic environment and a high level of adaptiveness to change, a rapidly

522 warming environment presents several risks that could limit population growth and expansion at this
523 margin of their range. These risks would compromise the success of current conservation efforts that
524 have seen these species reoccupy parts of their historic range. To mitigate such compromises, we
525 encourage actions that support species to adapt to climate change (Hobday et al. 2016; Roberts et al.
526 2017; Miller et al. 2018; Wilson et al. 2020).

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537 content of this article.

538 **Ethics approval** All procedures were conducted under Office of Environment and Heritage Animal
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540 2011/054. Research Permits (SL 100111 and SL 100746) and all relevant institutional and national
541 guidelines for the care and use of animals were followed.

542 **Consent to participate** Not applicable

543 **Consent for publication** All authors read and gave approval for publication to the final version of the
544 manuscript

545 **Availability of data and material** The datasets generated during and/or analysed during the current
546 study are available from the corresponding author on reasonable request.

547 **Code availability** Not applicable

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