

Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals

Laëtitia Kernaléguen^{1,2*}, John P. Y. Arnould¹, Christophe Guinet² and Yves Cherel²

¹School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, 3125 Burwood, Vic., Australia; and ²Centre d'Etudes Biologiques de Chizé, UMR 7372 du CNRS-Université de La Rochelle, BP 14, 79360 Villiers-en-Bois, France

Summary

1. The degree of individual specialization in resource use differs widely among wild populations where individuals range from fully generalized to highly specialized. This interindividual variation has profound implications in many ecological and evolutionary processes. A recent review proposed four main ecological causes of individual specialization: interspecific and intraspecific competition, ecological opportunity and predation.

2. Using the isotopic signature of subsampled whiskers, we investigated to what degree three of these factors (interspecific and intraspecific competition and ecological opportunity) affect the population niche width and the level of individual foraging specialization in two fur seal species, the Antarctic and subantarctic fur seals (*Arctocephalus gazella* and *Arctocephalus tropicalis*), over several years.

3. Population niche width was greater when the two seal species bred in allopatry (low interspecific competition) than in sympatry or when seals bred in high-density stabilized colonies (high intraspecific competition). In agreement with the niche variation hypothesis (NVH), higher population niche width was associated with higher interindividual niche variation. However, in contrast to the NVH, all Antarctic females increased their niche width during the interbreeding period when they had potential access to a wider diversity of foraging grounds and associated prey (high ecological opportunities), suggesting they all dispersed to a similar productive area.

4. The degree of individual specialization varied among populations and within the annual cycle. Highest levels of interindividual variation were found in a context of lower interspecific or higher intraspecific competition. Contrasted results were found concerning the effect of ecological opportunity. Depending on seal species, females exhibited either a greater or lower degree of individual specialization during the interbreeding period, reflecting species-specific biological constraints during that period.

5. These results suggest a significant impact of ecological interactions on the population niche width and degree of individual specialization. Such variation at the individual level may be an important factor in the species plasticity with significant consequences on how it may respond to environmental variability.

Key-words: competition, diet, foraging ecology, niche variation hypothesis, niche width, otariid, pinniped, stable isotopes, vibrissae, whisker

Introduction

Traditionally, resource use has been investigated at the species or population level, and the Hutchinson's concept of

niche (Hutchinson 1957) has been seen as an attribute of the species or population as a whole. However, individual niche variation in resource use is a widespread phenomenon in many vertebrate and invertebrate taxa (reviewed by Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011). Individual specialization occurs when individuals of similar sex and age class use a small subset of the population's resources (Bol-

*Correspondence author. E-mail: laetitia.kernaléguen@gmail.com

nick *et al.* 2003). This interindividual variability has long been of particular concern in evolutionary studies as it provides the raw material for natural selection. More recently, it has also been shown to substantially affect the population and community dynamics (Hughes *et al.* 2008; Bolnick *et al.* 2011) and is recognized as playing a major role in many ecological processes.

The development of new indices that measure the degree of individual specialization (Bolnick *et al.* 2002; Araújo *et al.* 2008) has enabled to investigate how the level of individual variation varies among populations and ecological contexts, providing new insights into the mechanisms of individual specialization (e.g. Svanbäck *et al.* 2008; Darimont, Paquet & Reimchen 2009; Tinker *et al.* 2012). In a recent review, Araújo, Bolnick & Layman (2011) identified four ecological causes of individual specialization: interspecific competition, intraspecific competition, ecological opportunity and predation. These factors are likely to alter resource availability which, in turn, modifies the population niche width and the degree of interindividual variation.

For example, in foraging ecology, optimal foraging theory predicts that individuals should only feed on the most valuable resources that maximize the energy intake per unit handling time (MacArthur & Pianka 1966). If the more profitable prey become less abundant (increase of intraspecific competition) or the population has access to a greater diversity of prey (decrease of interspecific competition or predation, increase of ecological opportunities), individuals should broaden their diet to include a larger range of prey. Individuals may vary in their ability to find, handle and/or digest prey due to differences in morphology (Knudsen *et al.* 2007), physiology [e.g. digestive capacity (Afik & Karasov 1995), energy requirement (Belovsky 1978)] or behaviour [e.g. learned skills on how to capture/handle different types of prey (Estes *et al.* 2003)]. As a consequence, individuals may vary in the profitability of alternative prey or ranking order (Svanbäck & Bolnick 2005). If individuals feed on different alternative prey, their respective diet will diverge as they increase their foraging niche. In reverse, if the less-preferred prey are items that were originally eaten by others, the degree of interindividual variation will decrease as individuals broaden their diet (Svanbäck & Bolnick 2005; Tinker *et al.* 2012).

In addition, individuals might face functional trade-offs that limit the number of prey they can efficiently consume (Taper & Chase 1985; Afik & Karasov 1995; Robinson 2000). If individual niche is limited in size, expansion of population niche width, like in ecological release, will occur via an increase of interindividual differences rather than all individuals increasing the range of resources they use. Accordingly, the niche variation hypothesis (NVH) (Van Valen 1965) states that populations with wider niches are more variable than populations with narrower niches.

A major limitation in investigating the determinants of individual specialization is that estimating the individual variance requires repeated measurements on the same

individuals, over a sufficient period of time to account for daily, seasonal or even multiyear variation of resource use. Correspondingly, few studies have been conducted and in particular on long-lived species with large home ranges. The use of the isotopic niche as a proxy of the trophic niche enables to overcome this methodological limitation (Bearhop *et al.* 2004; Araújo *et al.* 2007; Newsome *et al.* 2007). For example, in otariids (fur seal and sea lion), the isotopic signature of continuously growing whiskers can provide a fine scale chronology of $\delta^{13}\text{C}$ (proxy of foraging habitat in marine environments, Hobson, Piatt & Pitocchelli 1994; Cherel & Hobson 2007) and $\delta^{15}\text{N}$ (proxy of trophic level, DeNiro & Epstein 1981) values over several years (Cherel *et al.* 2009; Lowther *et al.* 2011; Kernaléguen *et al.* 2012; Franco-Trecu, Auriolles-Gamboa & Inchausti 2013).

Fur seals experience contrasting levels of interspecific and intraspecific competition and ecological opportunity. They represent thus an interesting model to investigate to what degree these ecological interactions affect the population niche width and the level of individual specialization, in the marine environment. First, in the Southern Ocean, two closely related species, the Antarctic (*Arctocephalus gazella*, Peters, 1875) and subantarctic fur seal (*Arctocephalus tropicalis*, Gray, 1872), occur both in allopatry and sympatry during the pup-rearing period. The two species have a similar diet when foraging in the same water masses (Klages & Bester 1998; Robinson *et al.* 2002; Cherel *et al.* 2007). However, species-specific resource partitioning is observed in sympatry (Bailleul *et al.* 2005; Kernaléguen *et al.* 2012), suggesting an adaptation of the foraging behaviour to the co-occurrence of the competitor species. Secondly, fur seals have been intensively hunted during the 18th and 19th centuries, with commercial sealing resulting in local extinction of the two species. Many populations are still recovering with increasing sizes, suggesting they have not reached their carrying capacity yet (Bonner & Laws 1964). Other populations have stabilized and are very likely to experience a higher degree of intraspecific competition (Gilpin & Ayala 1973). Finally, lactating females are central place foragers during the pup-rearing period, they feed at sea but need to come back regularly to the colony to suckle their single pup. After weaning, during the interbreeding period, females are not as spatially constrained; they can disperse and have potentially access to a greater diversity of foraging habitat and associated prey (ecological opportunity).

In this study, the isotopic signature of serially sampled whiskers of Antarctic and subantarctic lactating females were determined to measure the population niche width and the degree of individual foraging specialization under contrasting conditions of interspecific and intraspecific competition and ecological opportunity. These ecological interactions together with predation correspond to the four ecological drivers of individual specialization identified by Araújo, Bolnick & Layman (2011). We predicted that (i) population niche width should be lower in sympatry and

that, in agreement with the NVH, the associated degree of individual specialization should be also lower in sympatry than in allopatry; (ii) high-density, stabilized populations should be characterized by a greater population niche width and higher interindividual variation; and (iii) within a same population, the niche width and level of individual specialization should vary within the annual cycle and be lower during the pup-rearing than interbreeding period.

Materials and methods

STUDY SITES

Fieldwork was carried out on two species at three study sites in the southern Indian Ocean (Fig. 1). Mare aux Elephants, Crozet Islands (46°22'S, 51°40'E, hereafter called Crozet), located in the subantarctic zone, between the subtropical and polar fronts, hosts sympatric populations of Antarctic and subantarctic fur seals during the pup-rearing period. These two populations are still recovering from past sealing and increasing in size (Guinet, Jouventin & Georges 1994). Cap Noir, Kerguelen Archipelago (49°07'S, 70°45'E, hereafter called Kerguelen), located just north of the polar front, hosts allopatric breeding Antarctic fur seals with a population that is also increasing (long-term demographic unpublished data). Lastly, Mare aux Elephants, Amsterdam Island (37°50'S, 77°30'E, hereafter called Amsterdam), in the subtropical zone north of the subtropical front, hosts allopatric breeding subantarctic fur seals in a high-density and stabilized population (Guinet, Jouventin & Georges 1994) (Fig. 1).

FIELDWORK AND ISOTOPIC ANALYSIS

During the 2002 pup-rearing period, 10 lactating females of unknown age were selected at random in each colony, captured using a hoop net and restrained on a board while a whisker was cut as close to the skin as possible. Females from Crozet (and their corresponding whisker isotopic results) are the same individuals as those in the study by Kernaléguen *et al.* (2012). Seals breeding in Crozet were also weighed using a suspension scale (± 0.1 kg). In the laboratory, whiskers were hand-washed in

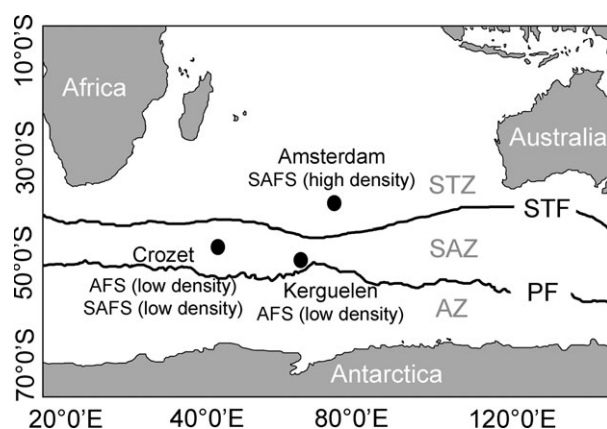


Fig. 1. Location of Crozet, Kerguelen, Amsterdam and of the main oceanic fronts and zones in the southern Indian Ocean. SAFS, subantarctic fur seal; AFS, Antarctic fur seal; STF, subtropical front; PF, polar front; STZ, subtropical zone; SAZ, subantarctic zone; AZ, Antarctic zone.

100% ethanol and cleaned in distilled water for 5 min in an ultrasonic bath. They were dried, measured and cut into 3-mm-long consecutive sections starting from the proximal (facial) end, following Chérel *et al.* (2009). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each whisker section were determined by a continuous flow mass spectrometer (Thermo Scientific, Delta V Advantage, Waltham, MA, USA) coupled to an elemental analyser (Thermo Scientific, Flash EA 1112). Results are presented in the conventional δ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors $< 0.10\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

POPULATION NICHE BREADTH AND INTERINDIVIDUAL VARIABILITY

The degree of individual specialization was calculated using Roughgarden's WIC/TNW index for continuous data (Bolnick *et al.* 2002). Roughgarden (1972) suggested that the population Total Niche Width (TNW, corresponding to the population variance) can be partitioned into the Within Individual Component (WIC, intra-individual variance) and the between-individual component (BIC, interindividual variance), where $\text{TNW} = \text{WIC} + \text{BIC}$. The WIC/TNW ratio is a measurement of the degree of individual specialization: high values (approaching 1) indicate that individuals use the full range of the population resources and low values (approaching 0) characterize specialist individuals. Each 3-mm-long section integrated an average period of time of 42 ± 15 days (see Results) and was considered as one observation. Thus, WIC corresponded to the average variance between sections calculated at the whisker level, and BIC corresponded to the variance between whiskers' mean isotopic values (Fig. 2). If x_{ij} is the j th $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value of the i th individual, then,

$$\text{TNW} = \text{Var}(x_{ij})$$

$$\text{WIC} = E[\text{Var}(x_{ji})]$$

$$\text{BIC} = \text{Var}[E(x_{ji})].$$

Roughgarden's indices for each population were calculated using the program INDSPEC1 (Bolnick *et al.* 2002; <http://www.esapubs.org/archive/ecol/E083/056/default.htm>). In order to test the significance of WIC/TNW ratios, additional 1000 replicate populations were generated under the null hypothesis that individuals are generalists which sample randomly from the population's distribution. Replicate data sets were generated with INDSPEC1 by resampling using a nonparametric Monte Carlo procedure (Bolnick *et al.* 2002). WIC/TNW has no published statistical properties (Bolnick *et al.* 2002; Araújo, Bolnick & Layman 2011), so it was not possible to test whether two populations had significantly distinct WIC/TNW ratios. Population niche widths TNW were compared with a Fisher's test after checking for the normality of the data.

Population isotopic niche width and the degree of individual specialization were calculated during the pup-rearing season (December to March for Antarctic fur seals; December to August for subantarctic fur seals) and during the interbreeding period (April to November and September to November for Antarctic and subantarctic fur seals, respectively) separately (Fig. 2). Whisker isotopic values were assigned to one of each period by placing the

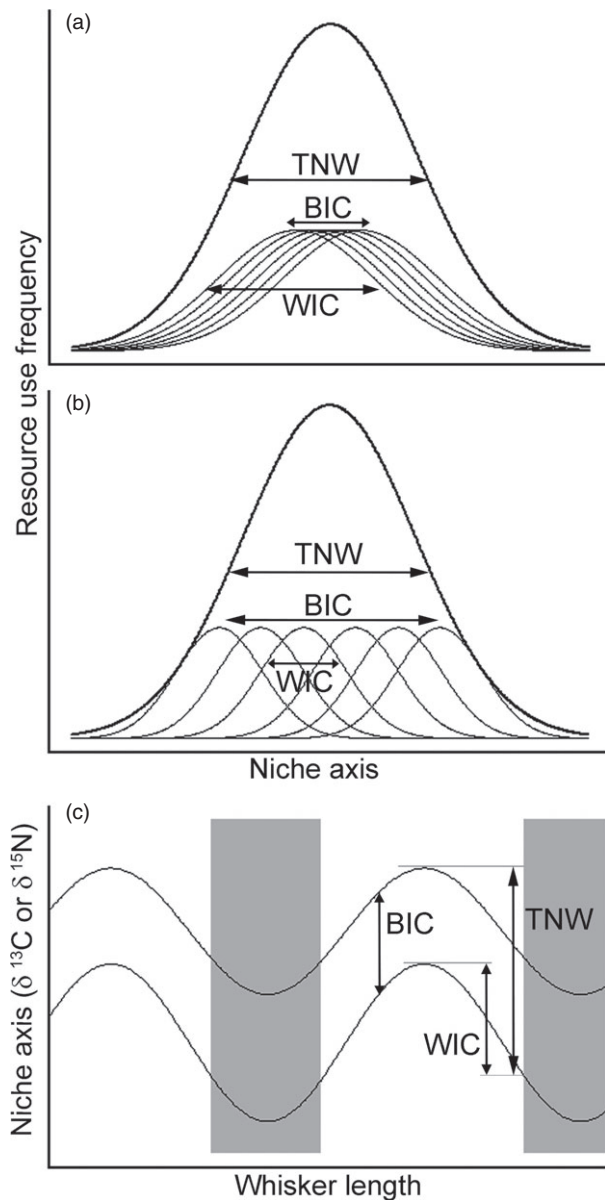


Fig. 2. Schematic diagrams illustrating (i) the calculation of Roughgarden (1972) indices of individual specialization (a and b, adapted from Bolnick *et al.* (2003)) and (ii) how these indices have been calculated from whisker isotopic values (c). (a and b) represent the population's (thick curve) and individuals' (thin curves) niches in a generalist and specialist populations, respectively. The total niche width (TNW) is decomposed into its within- and between-individual components (WIC corresponding to the intra-individual variance and BIC corresponding to the inter-individual variance, respectively). Theoretical isotopic ratio ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) along the length of two whiskers is represented in (c). TNW, BIC and WIC were calculated during the pup-rearing (in white) and the interbreeding (in grey) periods separately. Analyses were performed on the three most recent years depicted in whiskers to account for the interannual variability, and so each individual contributed equal weight in the analyses.

annual breeding cycles along the length of each whisker (conversion of the whisker length into a time-scale). In many cases, isotopic signature of otariid whiskers present regular annual cycles along their length (Hirons, Schell & St Aubin 2001; Cherel *et al.*

2009; Kernaléguen *et al.* 2012). Periodicity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was first assessed using the wavelet analysis following Kernaléguen *et al.* (2012). This analysis allowed us to detect (i) whether the isotopic signature of whiskers consisted of a repeated periodic signal and, more importantly, (ii) whether the period of the cyclic pattern was consistent along the length of the whisker (Cazelles *et al.* 2008). In addition, isotopic ratios of whole blood collected at different stages of the breeding cycle of females (unpublished data) allowed us to identify the summer and winter signatures in whiskers. A blood sample was collected during the pup-rearing period on the same individuals, when the whisker was taken. Additional blood samples were collected on random females in December 2002, when females returned to the colony after their winter trip, at Crozet (on both species) and Amsterdam; and in August 2002, on subantarctic fur seal females at Crozet and Amsterdam.

The temporal integration of whiskers varied greatly between individuals (from 2.7 to 7.3 years, see Results). The population niche width and the degree of individual specialization were calculated only on the three most recent years depicted in whiskers to account for the interannual variability, and so each individual contributed equal weight in the analyses. However, whiskers of two subantarctic fur seals breeding at Amsterdam integrated only 2.7 and 2.8 years. One Antarctic fur seal from Crozet exhibited extremely low $\delta^{13}\text{C}$ values at the distal end of its whisker, most likely reflecting an ontogenic shift. Since the aim of this study was to compare the foraging ecology of lactating females, the isotopic data corresponding to the third year of this specific whisker were not taken into account in the variance analyses.

Results

BODY CONDITION AND WHISKER ISOTOPIC RESULTS

Antarctic and subantarctic fur seal females breeding at Crozet weighed on average 34.5 ± 4.4 kg (range: 27.4–41.0 kg) and 28.1 ± 4.5 kg (range: 23.6–38.0 kg), respectively. Mean whisker length was 132 ± 38 mm, corresponding to an average of 44 ± 13 isotopic measurements per individual. In total 1760 samples were analysed. Overall isotopic data of whiskers were spread over a large range, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varying from -25.8‰ to -14.3‰ and from 8.4‰ to 15.1‰ , respectively (Table 1). Wavelet analyses indicated that all seals exhibited significant periodic oscillations along the length of their whisker in $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ signals (Fig. 3). Importantly, in all individuals, the cycle duration was constant along the length of each whisker and similar in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, supporting the assumption of a constant whisker growth rate in otariid species (Hirons, Schell & St Aubin 2001; Cherel *et al.* 2009; Kernaléguen *et al.* 2012). Whiskers recorded an average of 4.8 ± 1.0 years and each 3 mm section integrated an average period of time of 42 ± 15 days (Table 1).

POPULATION NICHE BREADTH AND INTERINDIVIDUAL VARIABILITY

During the pup-rearing period, $\delta^{13}\text{C}$ TNW of Antarctic females was similar between the allopatric and sympatric

Table 1. Whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, C/N mass ratios, overall length, time integration of 3-mm-long section and number of cycles recorded in whiskers

	<i>N</i>	Length (mm)	$\delta^{13}\text{C}$ (‰) \pm SD [range]	$\delta^{15}\text{N}$ (‰) \pm SD [range]	C/N mass ratio	Section (day)	Number of cycles [range]
Antarctic FS Crozet	10	145 \pm 45	-17.1 \pm 1.1 [-25.8; -16.1]	10.6 \pm 0.6 [8.4; 12.4]	2.86 \pm 0.04	40 \pm 11	5.1 \pm 1.2 [3.2; 7.3]
Antarctic FS Kerguelen	10	97 \pm 24	-18.1 \pm 0.7 ^a [-21.6; -16.8]	10.4 \pm 0.5 ^a [8.4; 11.7]	2.83 \pm 0.04	59 \pm 17	5.0 \pm 0.9 [4.0; 6.5]
subantarctic FSCrozet	10	133 \pm 27	-16.7 \pm 0.4 ^b [-18.2; -15.7]	10.5 \pm 0.6 ^b [8.6; 12.4]	2.88 \pm 0.02	36 \pm 9	4.2 \pm 0.9 [2.7; 6.5]
Subantarctic FS Amsterdam	10	152 \pm 34	-15.2 \pm 0.4 [-16.0; -14.3]	13.4 \pm 0.7 [11.4; 15.1]	2.87 \pm 0.03	35 \pm 7	4.7 \pm 0.9 [3.0; 6.5]

Antarctic FS, Antarctic fur seal; subantarctic FS, subantarctic fur seal.

Values are means \pm standard deviation.

^aTwo samples were removed because they corresponded to the suckling period of one female when she was pup.

^bFourteen samples were removed because they corresponded to the suckling period of two females when they were pups.

sites ($F_{59,90} = 0.87$, $P = 0.53$), while the $\delta^{15}\text{N}$ TNW was greater by a factor of two in allopatry than in sympatry ($F_{59,90} = 0.53$, $P < 0.001$) (Table 2, Fig. 4). Significant individual specialization occurred in both populations (all $P < 0.03$) but varied in magnitude depending of the level of interspecific competition. The degree of individual specialization was greater in allopatry considering both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ WIC/TNW indexes of 0.52 and 0.49, respectively, in allopatry and 0.80 and 0.73 in sympatry).

Subantarctic fur seals from Crozet and Amsterdam had a similar $\delta^{13}\text{C}$ TNW during the pup-rearing period ($F_{238,243} = 0.96$, $P = 0.73$), while the $\delta^{15}\text{N}$ TNW was twice higher in Amsterdam than in Crozet ($F_{238,243} = 0.50$, $P < 0.001$). Subantarctic females also exhibited significant individual foraging specialization ($P < 0.001$ for all WIC/TNW ratios). The degree of individual specialization was lower in Amsterdam than in Crozet when considering $\delta^{13}\text{C}$ values (WIC/TNW indexes of 0.57 and 0.85 in Crozet and Amsterdam, respectively). However, an opposite trend was found when considering $\delta^{15}\text{N}$ values (WIC/TNW indexes of 0.73 and 0.61 in Crozet and Amsterdam, respectively).

The overall population niche breadth TNW of Antarctic females from Crozet and Kerguelen increased during the interbreeding season (increase in at least one isotopic ratio, $F_{90,183} = 0.22$, $F_{90,183} = 0.47$ for Crozet $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TNW, respectively, both $P < 0.002$; and $F_{59,135} = 0.33$, $P < 0.001$ and $F_{59,135} = 0.69$, $P = 0.10$ for Kerguelen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TNW, respectively). Concurrently, the degree of individual specialization was lower during the interbreeding period, for both isotopic ratios and populations, with the exception of WIC/TNW $\delta^{13}\text{C}$ ratio of females breeding at Crozet.

In contrast, subantarctic fur seals exhibited a similar TNW during both periods ($F_{72,238} = 1.10$ and $F_{72,243} = 0.89$ for Crozet $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TNW, respectively, both $P > 0.60$; and $F_{72,238} = 0.33$ and $F_{72,243} = 0.69$ for Amsterdam $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TNW, respectively, both $P > 0.50$). Greater interindividual differences were found during the interbreeding period, for both isotopic ratios and populations. All WIC/TNW indices were significant during the interbreeding period (all $P < 0.003$) except for the $\delta^{15}\text{N}$ WIC/TNW index of Antarctic fur seals breeding at Crozet (WIC/TNW = 0.93, $P = 0.20$).

Discussion

Isotopic signature of whiskers highlighted significant individual foraging specialization in fur seal populations. The degree of interindividual variation varied depending on the intensity of interspecific and intraspecific competition and over the breeding cycle, as the diversity of accessible foraging grounds differed. However, potential effect of confounding factors such as oceanographic differences between the sites could not be ruled out due to the lack of replication. The effect of predation

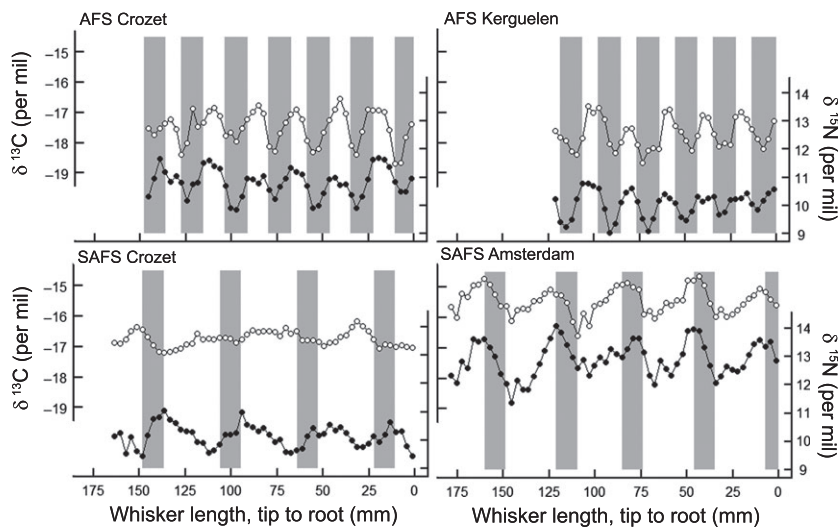


Fig. 3. Whisker $\delta^{13}\text{C}$ (open circles) and $\delta^{15}\text{N}$ (filled circles) values of one representative female of each population. Pup-rearing and interbreeding periods are represented in white and grey, respectively. The proximal end (time zero), that is the youngest part of the whisker, appears on the right of plots. AFS, Antarctic fur seal; SAFS, subantarctic fur seal.

Table 2. Population isotopic niche breadth and intra-individual and interindividual variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values during the pup-rearing and the interbreeding periods, based on whisker's isotopic signature during 3 years. The total niche width (TNW) is decomposed into its within- and between-individual components (WIC corresponding to the intra-individual variance and BIC corresponding to the interindividual variance, respectively). Roughgarden's WIC/TNW index (1972) provides a measurement of the degree of individual specialization of the population; low and high values characterize specialist and generalist individuals, respectively

	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	TNW	WIC	BIC	WIC/TNW	TNW	WIC	BIC	WIC/TNW
Pup-rearing Antarctic FS								
Crozet	0.12	0.09	0.02	0.80	0.08	0.06	0.03	0.73
Kerguelen	0.13	0.07	0.08	0.52	0.16	0.08	0.08	0.49
Interbreeding Antarctic FS								
Crozet	0.52	0.37	0.19	0.70	0.26	0.24	0.02	0.93
Kerguelen	0.28	0.19	0.10	0.67	0.23	0.19	0.05	0.82
Pup-rearing subantarctic FS								
Crozet	0.14	0.08	0.08	0.57	0.27	0.20	0.08	0.73
Amsterdam	0.15	0.13	0.02	0.85	0.54	0.33	0.21	0.61
Interbreeding subantarctic FS								
Crozet	0.13	0.05	0.09	0.37	0.25	0.15	0.09	0.63
Amsterdam	0.17	0.09	0.07	0.57	0.48	0.25	0.26	0.52

Antarctic FS, Antarctic fur seal; subantarctic FS, subantarctic fur seal.

could not be tested as no accurate data are currently available on the density of predator species or rates of predation.

Since individual foraging specialization plays a major role in many natural processes, it is important to better understand how ecological interactions influence the amount of interindividual variation (Araújo, Bolnick & Layman 2011). However, this question has been little documented, especially in the wild and on species with large home ranges (Tinker, Bentall & Estes 2008; Darimont, Paquet & Reimchen 2009). A major limitation is the difficulty in acquiring repeated diet data on the same individuals to account for temporal variability in foraging behaviour. In that context, subsampling whiskers provided a unique opportunity to address this question in fur seals as they provided longitudinal isotopic data at a fine scale over numerous years.

INTERSPECIFIC COMPETITION

As expected, the overall isotopic niche breadth (TNW) of Antarctic fur seals was much greater in allopatry (Kerguelen) than in sympatry (Crozet, during the pup-rearing period). The increase occurred via $\delta^{15}\text{N}$ values (a proxy of the trophic level) which exhibited double the variation in Kerguelen, whereas the variation in $\delta^{13}\text{C}$ values (a proxy of the foraging habitat) was similar between the two populations. This niche expansion, also known under the name of 'ecological release', has been extensively described in many island vertebrates (e.g. Van Valen 1965; Diamond 1970; Prodon, Thibault & DeJaifve 2002). The underlying hypothesis is that populations from species-poor habitats (e.g. islands) have access to a larger range of resources that would be depleted or monopolized in a highly competitive environment (e.g. mainland).

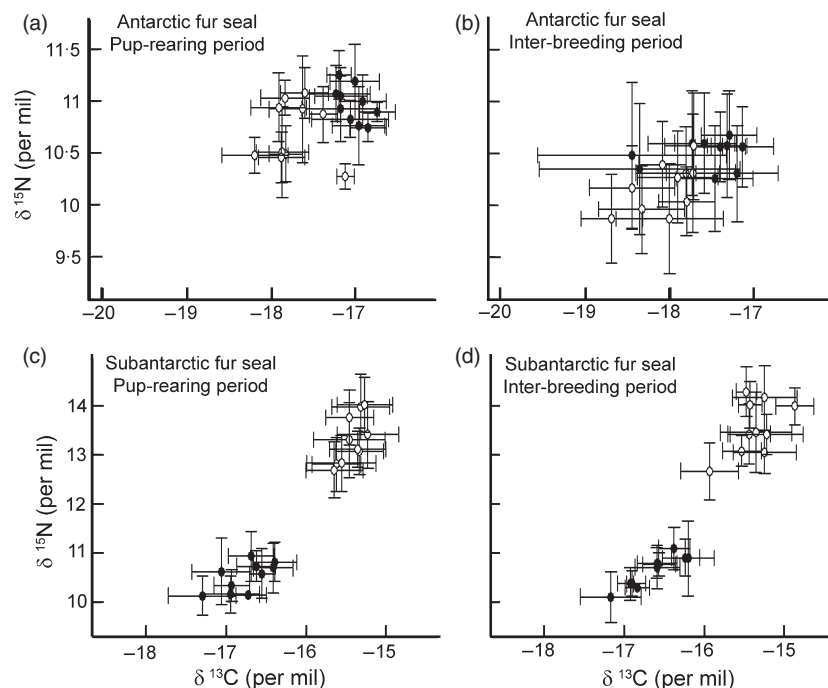


Fig. 4. Interindividual variability of carbon and nitrogen values of whiskers of females from Crozet (black circles) and Amsterdam or Kerguelen (open circles) during the pup-rearing period (a and c) and the interbreeding period (b and d). Values are mean \pm standard deviation.

Previous tracking and isotopic studies have shown a spatial segregation in foraging niche between the two sympatric species at Crozet (Bailleul *et al.* 2005; Cherel *et al.* 2007; Kernaléguen *et al.* 2012). Hence, a smaller $\delta^{13}\text{C}$ TNW was also expected at Crozet. Isotopic $\delta^{13}\text{C}$ values of marine organisms exhibit a latitudinal gradient in the Southern Ocean, allowing discrimination of foraging habitats (Cherel & Hobson 2007; Jaeger *et al.* 2010). However, $\delta^{13}\text{C}$ values at the base of the trophic chain are not linearly related to latitudes but display stepwise changes, with little variation within a given water mass and abrupt changes at frontal zones (François *et al.* 1993; Trull & Armand 2001). In accordance with tracking studies (Bonadonna *et al.* 2001; Guinet *et al.* 2001; Bailleul *et al.* 2005), $\delta^{13}\text{C}$ values showed that females from both islands foraged exclusively in one water mass during the pup-rearing period, the subantarctic zone. A limit of the isotopic method is that if resource pools differ little in isotopic values, consumers will have similar isotopic composition even if they differ substantially in their foraging habitats and prey.

Antarctic fur seal females breeding at Crozet and Kerguelen are known to feed primarily on myctophid fish (Cherel *et al.* 2007; Lea *et al.* 2008). Based on the isotopic values of females (this study) and their known diet from scat analyses (Cherel *et al.* 2007), higher $\delta^{15}\text{N}$ TNW in allopatry is likely to reflect the consumption of a higher proportion of squid, and/or of myctophids with higher $\delta^{15}\text{N}$ values (Cherel *et al.* 2010). The co-occurrence of the competitive species in Crozet might also impact the species composition of fur seals' diet. For example, the main prey of Antarctic females breeding at Kerguelen (Cap Noir colony), *Gymnoscopelus fraseri*, is also the primary component of the diet of subantarctic, but not Antarctic

females at Crozet, where the latter species feed mainly upon *Gymnoscopelus piabilis* (Cherel *et al.* 2007; Lea *et al.* 2008). However, the isotopic method might fail to distinguish diet based on different fish species as they may have similar $\delta^{15}\text{N}$ signatures.

Niche expansion can occur either when all individuals exploit a wider range of resources (increase of individual niche width) or when each individual keeps using a small range of available resources but diverge from each other (increase of among-individual differences). The NVH proposed by Van Valen (1965) supports the latter scenario and states that populations with wider niches are more variable than populations with narrower niches. Our data were in agreement with this prediction. The increase of $\delta^{15}\text{N}$ TNW in allopatry was achieved by higher interindividual variation, while individual niche breadth remained unchanged. However, the effect of potential confounding factors could not be ruled out because of the lack of replication due to the challenge of studying wild marine species. Interestingly, the degree of individual specialization, measured by the ratio WIC/TNW (see Materials and methods), was similar for both isotopic ratios: 0.52 and 0.49 in allopatry, and 0.80 and 0.73 in sympatry. As expected, during the interbreeding period, when seals from Crozet are no longer in sympatry, differences between the two populations decreased and results converged towards a similar level of individual specialization.

An underlying question in individual specialization is why individuals vary in their foraging strategy. If individuals were ecologically similar, they should all adopt the same optimum strategy to maximize their energy intake and, ultimately, their fitness (MacArthur & Pianka 1966; Schoener 1971). However, conspecific individuals differ in many traits including their morphology, age, social status, behaviour

or physiology (Bolnick *et al.* 2011). For instance, in this study, fur seals varied in body size which is an important factor in their diving capacity as it determines their aerobic dive limit (Kleiber 1961). Larger females can dive longer and deeper (Costa, Gales & Goebel 2001) and have potentially access to a wider range of resource. Age is another component influencing foraging behaviour in pinnipeds (McDonald *et al.* 2009; Arnould *et al.* 2011). The age of the sampled females was not known, but can potentially range from 3 to 20 years old (Lunn, Boyd & Croxall 1994). Furthermore, while females were all providing a pup the year of the study, they might not have been pregnant or lactating the previous years. Reproductive status can affect nutritional or energetic requirements which, in turn, modify individual's optimum diet (Belovsky 1978).

Like elsewhere in the Southern Ocean, Antarctic and subantarctic fur seal populations at Crozet and Kerguelen are continuing to recover from the overexploitation of the commercial sealing during the 18th and 19th centuries (Bonner & Laws 1964; Guinet, Jouventin & Georges 1994). In contrast, the population of subantarctic fur seals at Amsterdam has stabilized (Guinet, Jouventin & Georges 1994). As this population has reached its carrying capacity, the intraspecific competition level should accordingly be higher in the Amsterdam population than at Crozet (Gilpin & Ayala 1973). In addition, Authier, Cam & Guinet (2011) have reported that the probability of breeding success has decreased in Amsterdam as the population has stabilized, most probably as a consequence of increasing competition. Therefore, the impact of interspecific competition in the subantarctic fur seal (sympatry in Crozet, allopatry in Amsterdam) may be masked by effects of contrasted level of intraspecific competition between the two populations and has not been investigated in this species. Since the absolute level of competition (interspecific and intraspecific competition combined) should be much higher in Amsterdam, intraspecific competition should be the main ecological interaction explaining variations between the two populations.

INTRASPECIFIC COMPETITION

Overall isotopic niche breadth in subantarctic fur seals was much greater in Amsterdam than in Crozet, where the population is still increasing. This difference was also influenced primarily by $\delta^{15}\text{N}$ values, which exhibited double the variation in Amsterdam than in Crozet. Variation in $\delta^{13}\text{C}$ values within the two populations was alike and similar to that of Antarctic fur seal populations. Such a wider population niche is expected in a higher intraspecific competitive environment. Indeed, as the intraspecific competition intensifies, preferred prey resources become less abundant and optimal foraging theory predicts that individuals should broaden their diet to include less-preferred prey (MacArthur & Pianka 1966). Consistent with this theory, individual $\delta^{15}\text{N}$ niche breadth of subantarctic fur seals was higher in Amsterdam than in Crozet.

Inclusion of interindividual phenotypic variation in classical optimal diet theory reveals that intraspecific competition should also affect the strength of individual specialization (Svanbäck & Bolnick 2005). If individuals differ in their prey rank preferences or the profitability of alternative prey, models predict their diet should vary in different directions as competition intensifies. For example, if individuals have different 'preferred prey' (distinct preferences model), they might include in their diet secondary prey that were originally eaten by other conspecifics. As a consequence, the diet of individuals should become more similar as they feed on a larger diversity of prey. In contrast, if individuals have the same preferred prey (first choice) but vary in their ranking order of alternative prey (competitive refuge model) or vary in the profitability of these prey (willingness of adding novel prey, shared preferences model), the level of interindividual variation should increase with the predator density up to a certain level, where individuals add all alternative prey and become generalist (Svanbäck & Bolnick 2005).

Empirical and experimental studies, mostly conducted in freshwater fishes, have consistently found a positive relationship between the population density and the degree of individual specialization (e.g. Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Huss, Byström & Persson 2008). Similarly, in the present study, subantarctic fur seals exhibited a higher level of individual specialization in their $\delta^{15}\text{N}$ values when breeding in higher density. Subantarctic fur seal females are also myctophid fish eaters, although females breeding at Crozet and Amsterdam feed on different species reflecting variation in prey distribution in their respective foraging zones (Beauplet *et al.* 2004; Chérel *et al.* 2007). As for the Antarctic species, a greater diversity in $\delta^{15}\text{N}$ values most probably reflected a higher range of prey size or type (squid and/or myctophid fish).

In contrast, $\delta^{13}\text{C}$ values revealed a higher degree of individual specialization in Crozet, even though both populations exhibited a similar $\delta^{13}\text{C}$ TNW. Isotopic values indicated that females foraged exclusively in one water mass, the subantarctic or subtropical zone, during the whole pup-rearing period. As expected, subantarctic females breeding at Crozet had also a similar TNW that Antarctic females foraging in the same water mass. Higher interindividual variation is predicted by models under certain circumstances (e.g. distinct preferences model, Svanbäck & Bolnick 2005). However, the lack of variation between the two populations' TNW together with the small isotopic $\delta^{13}\text{C}$ variation in the environment suggest that results are more likely to be a methodological artefact. However, further studies in contrasted geographic and isotopic environments are required to better address this question.

ECOLOGICAL OPPORTUNITY

During the pup-rearing period, lactating females are central place foragers, alternating at-sea foraging trips with

periods on land to suckle their pup. Following the lactation period, during the interbreeding period, females are not constrained by the need to feed their pup. Consequently, their foraging grounds and associated prey are much less spatially limited. With lactation periods varying substantially between Antarctic (4 months) and subantarctic (10 months) fur seals, their interbreeding periods, and the opportunity for exploiting a greater diversity of foraging resources, also differ between the two species.

Whiskers isotopic values exhibited synchronous annual cycles in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicating temporal variation in foraging strategy. Individuals fed in different foraging habitat throughout the year and changed accordingly their diet. As a consequence, population and individuals niche breadths were not only determined by the diversity of resource used at a time but were also influenced by the duration of the studied period (pup-rearing or interbreeding period). Accordingly, subantarctic females from both locations had a smaller individual niche breadth during the short interbreeding period (2 months) than during the longer pup-rearing period (10 months). Similarly, individual niche widths of Antarctic fur seals were higher during the interbreeding (8 months) than pup-rearing (4 months) period.

The index of individual specialization was less influenced by this artefact as it is calculated as a ratio (individual to population variance, WIC/TNW, see Materials and methods). Subantarctic fur seals exhibited among the highest levels of specialization found in the present study during the interbreeding period, when they were no longer central place forager and could disperse. The degree of interindividual variation was consistently higher than during the pup-rearing period. This result is in agreement with recent studies which have consistently found higher dietary interindividual variation when resource diversity increases, either temporally (Herrera *et al.* 2008) or spatially (Layman *et al.* 2007; Darimont, Paquet & Reimchen 2009; Evangelista *et al.* 2014). Higher levels of individual specialization were always associated with higher population niche breadth. In the present study, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TNW were similar during the pup-rearing and interbreeding periods. However, pup-rearing TNW also included higher intra-individual temporal variation of foraging behaviour. Hence, results also suggested individuals used relatively a greater diversity of resource during the short interbreeding period, both in terms of foraging grounds and diet.

In contrast, Antarctic females showed less interindividual variation during the interbreeding period, except for the $\delta^{13}\text{C}$ values of females breeding at Crozet. In contradiction with the NVH (Van Valen 1965), the increase of TNW was mainly achieved by higher individual niche breadth, suggesting that females dispersed to the same productive area after weaning. The interbreeding period (when females gain condition in preparation for the next lactation period) lasts 8 and 2 months in the Antarctic and subantarctic fur seal, respectively. Consequently, the

shorter period available to the latter species may lead to increased interindividual divergence in foraging area or prey selection to avoid competition. Moreover, the difference in the duration of the interbreeding period between the two species might also affect the calculation of individual specialization indices. Estimations of population and individual niche width variances are dependent of the sample size (amount of time averaging) and may have different asymptotic properties as it increases. So, it is possible that the longer interbreeding period for the Antarctic fur seals results in more time averaging and thus a lower estimate of individual specialization (Bearhop *et al.* 2004). However, the latter hypothesis may not explain the opposite trend found in the two species.

Interestingly, isotopic niche of Antarctic females from both sites greatly overlapped during the interbreeding period, indicating females exploited the same resources in the same water mass. Simultaneously, difference in the degree of individual specialization between females breeding at Crozet and Kerguelen decreased during the interbreeding period, and $\delta^{15}\text{N}$ WIC/TNW ratios were similar in both populations. These results confirmed the level of individual specialization is mainly driven by the local environment, even at a short-term scale, and does not seem a characteristic of a population.

In summary, the results of the present study highlighted the importance of examining variation in several aspects of the ecological niche (spatial, dietary and temporal, as determined by whisker stable isotopes) as contrasting trends may be observed depending on the parameter investigated. In accordance with Araújo, Bolnick & Layman (2011) predictions, for the two Antarctic fur seal populations, levels of interindividual variation were similar during the interbreeding period, when their isotopic niches overlapped and were presumed to experience a similar degree of competition and ecological opportunity. However, during the pup-rearing season, when both populations were constrained to contrasting levels of interspecific competition, the degree of individual specialization diverged, confirming an effect of competition on the level of interindividual variation. Higher levels of interindividual variation were found in lower interspecific and higher intraspecific competition environments. The influence of ecological opportunity, however, differed between the species and was primarily influenced by the local environment and specific biological cycle and constraints of the two species.

Acknowledgements

The authors thank F. Bailleul, F. Pawlowski, J. Kingston, S. Luque, L. Dubroca, M. C. Martin, S. Jenouvrier and D. Pinaud for their contribution in the field, P. Richard and G. Guillou for their help in the preparation of isotopic samples and B. Cazelles for his precious help for the wavelet analyses. The present work was supported financially and logistically by the ANR-VMC IPSOS-SEAL, the Institut Polaire Français Paul Emile Victor (IPEV, programme no. 109) and the Terres Australes et Antarctiques Françaises. The ethics committee of IPEV approved all field procedures.

Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k231g> (Kernaléguen et al. 2015).

References

- Afik, D. & Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology*, **76**, 2247–2257.
- Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011) The ecological causes of individual specialisation. *Ecology Letters*, **14**, 948–958.
- Araújo, M.S., Bolnick, D.I., Machado, G., Giaretta, A.A. & dos Reis, S.F. (2007) Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. *Oecologia*, **152**, 643–654.
- Araújo, M.S., Guimarães, P.R., Svanbäck, R., Pinheiro, A., Guimarães, P., dos Reis, S.F. et al. (2008) Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology*, **89**, 1981–1993.
- Arnould, J.P.Y., Cherel, Y., Gibbens, J., White, J.G. & Littnan, C.L. (2011) Stable isotopes reveal inter-annual and inter-individual variation in the diet of female Australian fur seals. *Marine Ecology Progress Series*, **422**, 291–302.
- Authier, M., Cam, E. & Guinet, C. (2011) Selection for increased body length in Subantarctic fur seals on Amsterdam Island. *Journal of Evolutionary Biology*, **24**, 607–616.
- Bailleul, F., Luque, S., Dubroca, L., Arnould, J.P.Y. & Guinet, C. (2005) Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Marine Ecology Progress Series*, **293**, 273–282.
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. & MacLeod, H. (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, **73**, 1007–1012.
- Beauplet, G., Dubroca, L., Guinet, C., Cherel, Y., Dabin, W., Gagne, C. et al. (2004) Foraging ecology of subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Marine Ecology Progress Series*, **273**, 211–225.
- Belovsky, G.E. (1978) Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology*, **14**, 105–134.
- Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanback, R. (2002) Measuring individual-level resource specialization. *Ecology*, **83**, 2936–2941.
- Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. et al. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1–28.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. et al. (2011) Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, **26**, 183–192.
- Bonadonna, F., Lea, M.A., Dehorter, O. & Guinet, C. (2001) Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. *Marine Ecology Progress Series*, **223**, 287–297.
- Bonner, W.N. & Laws, R.M. (1964) Seals and sealing. *Antarctic Research*, (eds R. Priestley, R.J. Adie, G. Robin & Q. de), pp.163–190. Butterworths, London.
- Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J.O., Jenouvrier, S. et al. (2008) Wavelet analysis of ecological time series. *Oecologia*, **156**, 287–304.
- Cherel, Y. & Hobson, K.A. (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series*, **329**, 281–287.
- Cherel, Y., Hobson, K.A., Guinet, C. & Vanpe, C. (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *Journal of Animal Ecology*, **76**, 826–836.
- Cherel, Y., Kernaléguen, L., Richard, P. & Guinet, C. (2009) Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. *Biology Letters*, **5**, 830–832.
- Cherel, Y., Fontaine, C., Richard, P. & Labat, J.P. (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnology and Oceanography*, **55**, 324–332.
- Costa, D.P., Gales, N.J. & Goebel, M.E. (2001) Aerobic dive limit: how often does it occur in nature? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **129**, 771–783.
- Darimont, C.T., Paquet, P.C. & Reimchen, T.E. (2009) Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*, **78**, 126–133.
- DeNiro, M.J. & Epstein, S. (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, **45**, 341–351.
- Diamond, J.M. (1970) Ecological consequences of island colonization by southwest Pacific birds, I. Types of niche shifts. *Proceedings of the National Academy of Sciences*, **67**, 529–536.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T. & Lyon, B.E. (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology*, **72**, 144–155.
- Evangelista, C., Boiche, A., Lecerf, A. & Cucherousset, J. (2014) Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. *Journal of Animal Ecology*, **83**, 1025–1034.
- François, R., Altabet, M.A., Goericke, R., McCorkle, D.C., Brunet, C. & Poisson, A. (1993) Changes in the $\delta^{13}\text{C}$ of surface water particulate organic matter across the subtropical convergence in the SW Indian Ocean. *Global Biogeochemical Cycles*, **7**, 627–644.
- Franco-Trecu, V., Auriolles-Gamboa, D. & Inchausti, P. (2013) Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids. *Marine Biology*, **70**, 609–618.
- Gilpin, M.E. & Ayala, F.J. (1973) Global models of growth and competition. *Proceedings of the National Academy of Sciences*, **70**, 3590–3593.
- Guinet, C., Jouventin, P. & Georges, J. (1994) Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarctic Science*, **6**, 473.
- Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G. et al. (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series*, **219**, 251–264.
- Herrera, L.G., Korine, C., Fleming, T.H. & Arad, Z. (2008) Dietary implications of intrapopulation variation in nitrogen isotope composition of an old world fruit bat. *Journal of Mammalogy*, **89**, 1184–1190.
- Hirons, A.C., Schell, D.M. & St Aubin, D.J. (2001) Growth rates of vibrissae of harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology*, **79**, 1053–1061.
- Hobson, K.A., Piatt, J.F. & Pitocchelli, J. (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, **63**, 786–798.
- Hughes, A.R., Inouye, B.D., Johnson, M.T., Underwood, N. & Vellend, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters*, **11**, 609–623.
- Huss, M., Byström, P. & Persson, L. (2008) Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. *Oecologia*, **158**, 249–257.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.
- Jaeger, A., Lecomte, V.J., Weimerskirch, H., Richard, P. & Cherel, Y. (2010) Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Communications in Mass Spectrometry*, **24**, 3456–3460.
- Kernaléguen, L., Cazelles, B., Arnould, J.P.Y., Richard, P., Guinet, C. & Cherel, Y. (2012) Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PLoS ONE*, **7**, e32916.
- Kernaléguen, L., Arnould, J.P.Y., Guinet, C. & Cherel, Y. (2015) Data from: Determinants of individual foraging specialisation in large marine vertebrates, the antarctic and subantarctic fur seals. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.k231g>.
- Klages, N.T.W. & Bester, M.N. (1998) Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Marine Biology*, **131**, 559–566.
- Kleiber, M. (1961) *The Fire of Life. An Introduction to Animal Energetics*. John Wiley & Sons Inc, New York, NY.

- Knudsen, R., Amundsen, P., Primicerio, R., Klemetsen, A. & Sorensen, P. (2007) Contrasting niche-based variation in trophic morphology within Arctic charr populations. *Evolutionary Ecology Research*, **9**, 1005–1021.
- Layman, C.A., Quattrochi, J.P., Peyer, C.M. & Allgeier, J.E. (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters*, **10**, 937–944.
- Lea, M.A., Guinet, C., Chérel, Y., Hindell, M., Dubroca, L. & Thalmann, S. (2008) Colony-based foraging segregation by Antarctic fur seals at the Kerguelen Archipelago. *Marine Ecology Progress Series*, **358**, 273–287.
- Lowther, A.D., Harcourt, R.G., Hamer, D. & Goldsworthy, S.D. (2011) Creatures of habit: foraging habitat fidelity of adult female Australian sea lions. *Marine Ecology Progress Series*, **443**, 249–263.
- Lunn, N., Boyd, I. & Croxall, J. (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, **63**, 827–840.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609.
- McDonald, B.I., Goebel, M.E., Crocker, D.E., Tremblay, Y. & Costa, D.P. (2009) Effects of maternal traits and individual behavior on the foraging strategies and provisioning rates of an income breeder, the Antarctic fur seal. *Marine Ecology Progress Series*, **394**, 277–288.
- Newsome, S.D., del Rio, C.M., Bearhop, S. & Phillips, D.L. (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, **5**, 429–436.
- Prodon, R., Thibault, J.-C. & Dejaifve, P.-A. (2002) Expansion vs. compression of bird altitudinal ranges on a Mediterranean island. *Ecology*, **83**, 1294–1306.
- Robinson, B.W. (2000) Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. *Behaviour*, **137**, 865–888.
- Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. & Hindell, M.A. (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research*, **53**, 1071–1082.
- Roughgarden, J. (1972) Evolution of niche width. *The American Naturalist*, **106**, 683–718.
- Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369–404.
- Svanbäck, R. & Bolnick, D.I. (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research*, **7**, 993–1012.
- Svanbäck, R. & Bolnick, D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**, 839–844.
- Svanbäck, R. & Persson, L. (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology*, **73**, 973–982.
- Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. (2008) Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos*, **117**, 114–124.
- Taper, M.L. & Chase, T.J. (1985) Quantitative genetic models for the coevolution of character displacement. *Ecology*, **66**, 355–371.
- Tinker, M.T., Bentall, G. & Estes, J.A. (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences*, **105**, 560–565.
- Tinker, M.T., Guimarães, P.R., Novak, M., Marquitti, F.M.D., Bodkin, J.L., Staedler, M. *et al.* (2012) Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecology Letters*, **15**, 475–483.
- Trull, T. & Armand, L. (2001) Insights into Southern Ocean carbon export from the $\delta^{13}\text{C}$ of particles and dissolved inorganic carbon during the SOIREE iron release experiment. *Deep Sea Research Part II: Topical Studies in Oceanography*, **48**, 2655–2680.
- Van Valen, L. (1965) Morphological variation and width of ecological niche. *The American Naturalist*, **99**, 377–390.

Received 22 July 2014; accepted 23 January 2015

Handling Editor: John Fryxell