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The diet of Weddell seals (*Leptonychotes weddellii*) in Terra Nova Bay using stable isotope analysis

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Abstract

Stable isotope analyses were used to investigate the diet of Weddell seals in Terra Nova Bay (Ross Sea) and the potential variation of their foraging behaviour with age, sex and body mass. For this purpose, skin samples were collected from adult breeding seals and pups, together with muscle samples of their potential prey. Our results showed variation in foraging behavior between age classes, with pups reporting lower $\delta^{13}\text{C}$ values than adults, while no significant differences in $\delta^{15}\text{N}$ were recorded. In addition, contrary to expectations, a mixing model analysis showed that adult seals foraged mainly on shallow benthic prey, such as *Trematomus* spp. (34.1%) and *Dissostichus mawsoni* (21.1%), rather than on pelagic fish, such as *Pleuragramma antarcticum* (9.8%). Overall, with this paper we provide novel diet information on a seal colony not previously sampled, adding new insight into the feeding ecology of a top Antarctic predator.

Keywords: Weddell seal diet, *Leptonychotes weddellii*, stable isotopes, Terra Nova Bay, Antarctica

1. Introduction

The Ross Sea is a region of the Southern Ocean, consisting of an extensive ice shelf with variable topography and several ice-free areas during the austral summer (Smith et al. 2007). It is a highly productive ecosystem, mostly due to the abundant macronutrients on the Antarctic continental shelves (Moore et al. 2013), and therefore hosts a large number of top predators, such as Adelie penguins (*Pygoscelis adeliae*), emperor penguins (*Aptenodytes forsteri*), killer whales (*Orcinus orca*), minke whales (*Balaenoptera bonaerensis*), leopard seals (*Hydrurga leptonyx*) and Weddell seals (*Leptonychotes weddellii*).

Within the Ross Sea, Terra Nova Bay has been recognised as an area of high ecological and scientific value (Antarctic Treaty Secretariat 2013), and it has been lately made an Antarctic Special Protected Area (ASPANo 161). The high biodiversity of Terra Nova Bay is likely the consequence of its peculiar environmental conditions, as during the Antarctic summer the site is fully ice-free – which is a rare feature in the Antarctic (Stocchino & Luseti 1988,

1990) – and shows a perennial coastal polynya (i.e., area of open water surrounded by ice, see Smith & Barber 2007), which is characterized by high levels of primary productivity and intense spring blooms (Baumann 1989). Coastal polynyas are, in fact, one of the most important components of the polar regions (Massom et al. 1988), as they represent two-thirds of the continental-shelf biological production (Arrigo & van Dijken 2003).

Among others, the coasts of Terra Nova Bay host a breeding colony of Weddell seals (*Leptonychotes weddellii*), which has been only lately target of scientific researches (Zappes et al. 2017). With an estimated population of 730,000 individuals on the continent (Erickson & Hanson 1990), these pinnipeds have an important role in the Antarctic, as they inhabit the fast-ice shelf and forage in both benthic and pelagic waters, diving to depths of over 600 m in the ocean (Kooyman 1981; Lake et al. 2003). However, the diet of Weddell seals from the Ross Sea is not homogeneous throughout the seasons. They feed primarily on fish from the Nototheniidae family (i.e., toothfish) and cephalopods (Dearborn 1965; Plötz et al. 1991; Burns et al. 1998),

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although some variations in food resources are expected, as they move from the open ocean to the coast, where they breed. So far, most studies on their diet analysed scats or stomach contents (but see Goetz et al. 2017, Botta et al. 2018) and have been restricted to the colonies of McMurdo; sampling is normally done when they are tied to the fast ice to breed (September–November), and hence easily accessible from research stations (Davis et al. 1982; Casaux et al. 1997; Lake et al. 2003; Daneri et al. 2012). However, since the results of these methods are based on the remains of the hard parts of prey, they might not reflect the whole predator diet, as soft prey or those only partially eaten (Ainley & Siniff 2009) may not be present in the analysed samples (Ponganis & Stockard 2007; Kooyman 2013).

To deal with visually undetected prey, the analysis of stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in various tissues of predators is therefore often used. These isotopic ratios vary according to animal diet and trophic level (Hobson & Welch 1992) and, as a consequence of retention of the heavier isotope, tissues of predators show generally higher $\delta^{15}\text{N}$ values than those of their prey (Minagawa & Wada 1984; Checkley & Entzeroth 1985). Values of $\delta^{15}\text{N}$ can vary from 1.5‰ to 5‰ between trophic levels (Peterson & Fry 1987; Hammill et al. 2005), and it can be therefore used as an indicator of the position of consumers in the food web. On the contrary, the isotope $\delta^{13}\text{C}$ has a relatively small enrichment between trophic levels (usually 0.5–1‰) (McConnaughey & McRoy 1979; Zhao et al. 2004) and it is mainly used as an indicator of the main food sources (e.g., pelagic *vs* benthonic) of an organism and its habitat (e.g., Hobson & Welch 1992; France 1995; Post 2002).

In the last decades, the number of studies using carbon and nitrogen stable isotopes has been growing, as they represent a valuable tool not only to analyse the individual diet, but also to answer a wide range of questions linked to animal ecology. They have been applied to investigate various aspects of foraging ecology and habitat use, migratory and dispersal behaviour, ecotoxicology, historic and paleoecology, also in several species of marine mammals (Boecklen et al. 2011).

An important aspect of isotopes is that their rates of turnover vary with the metabolic activity of the sampled tissue, meaning that changes in diet can take anywhere from a few days to many weeks to appear in different animal tissues (Tieszen et al. 1983; Hobson & Clark 1992; Hobson 1993). For this reason, the isotopic analysis of metabolically inactive tissues such as hair, skin, whiskers, nails and feathers will reflect the diet of individuals only during their period of growth (Hobson

et al. 1996). Isotopic analysis of skin, with its rate of turnover between liver (faster) and muscles (slower), will provide medium-term dietary information (1383 intermediate days before sampling, Cipro et al. 2012).

In this paper, we analysed the diet of Weddell seals of Terra Nova Bay for the very first time, to investigate if their feeding behavior varied with sex, age and weight. For this purpose, we analysed stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) in skin samples of seals and in muscle samples of their potential prey. The analysis of skin, which has a rate of turnover higher than muscles, would reflect their feeding behaviour during those weeks when they are not hauled out and they are therefore difficult to study (e.g., during winter, when the seals are under the ice-shelf), and provide new important insight into their diet.

2. Materials and methods

2.1. Sampling

Skin samples were collected from seals of Terra Nova Bay during the austral spring of 2014 (middle November–early December), on the fast ice of Victoria Land, from Tethys Bay to Kay Island (coordinates: 74°04–38'S, 164°13–19'E, Figure 1). Animal handling caused only minor disturbance to the seals, and sampling procedures were approved by the Italian Ministry of Foreign Affairs, within the PNRA Research Project 2013/AZ.01 – “Protocol on Environmental Protection to the Antarctic Treaty”, Annex II, art.3. Skin samples (about 1–1.5 cm thickness and without fur) were collected from 56 seals – 32 adults (9 males and 23 females) and 24 pups (11 males and 13 females) (Table I) – and then frozen at -80°C , until laboratory analysis. As Weddell seals are not aggressive animals,

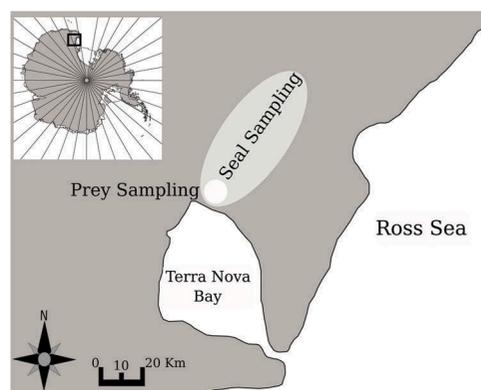


Figure 1. Sampling areas close to Terra Nova Bay. The white circle area corresponds to the area where seals were sampled, while the grey area shows where preys were sampled.

Table I. Sex (F = females; M = males), age (A = adults; P = pups), class of body mass (Class I < 200 kg; Class II < 400 kg; Class III \geq 400 kg), $\delta^{15}\text{N}$ (‰), $\delta^{13}\text{C}_{\text{lipid-free}}$ (‰), and C:N values (\pm standard deviations) and trophic level (TL) of Weddell seals sampled in Terra Nova Bay (Ross Sea).

Sex	Age	Class of weight (kg)	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}_{\text{lipid-free}}$ (‰)	SD	C:N	SD	TL
F	A	Class II	14.9	0.8	-22.2	0.1	2.8	0.2	4.9
F	A	Class II	16.4	0.7	-20.2	0.0	2.5	0.3	5.4
F	A	Class II	15.2	0.2	-21.2		3.0	0.3	5.0
F	A	Class II	16.2	0.3	-21.1	0.8	2.7	0.1	5.4
F	A	Class II	15.1	0.5	-21.6	0.1	2.9	0.0	5.0
F	A	Class II	15.3	0.5	-21.2	0.2	2.7	0.1	5.1
F	A	Class II	16.1	0.3	-20.9	0.1	2.8	0.0	5.3
F	A	Class II	15.7	0.6					5.2
F	A	Class II	16.2	0.3	-21.0	0.1	2.8	0.0	5.4
F	A	Class II	15.6	0.0					5.2
F	A	Class II	14.3	0.6	-21.3	0.0	2.9	0.0	4.7
F	A	Class II	16.4	0.5	-19.9	0.0	3.7	0.0	5.4
F	A	Class II	16.0	0.3	-21.1		2.8	0.0	5.3
F	A	Class II	15.9	0.3	-21.5	0.4	2.5	0.2	5.3
F	A	Class II	14.8	0.6	-22.1	0.2	2.6	0.2	4.9
F	A	Class III	15.4	0.2	-21.3	0.3	2.5	0.2	5.1
F	A	Class III	15.4	0.4	-21.8	0.3	2.6	0.1	5.1
F	A	Class III	15.5	0.2					5.1
F	A	Class III	15.8	0.1	-20.7	0.0	2.8	0.0	5.2
F	A	Class III	16.1	0.0	-19.2	0.2	2.7	0.1	5.3
F	A	Class III	15.8	0.5	-21.6	0.9	2.9	0.1	5.2
F	A		14.6	0.2					4.8
F	A		14.6	0.5					4.8
M	A	Class II	16.7	0.4	-20.7		2.9	0.2	5.5
M	A	Class II	15.5	0.5	-21.6	0.4	2.6	0.3	5.1
M	A	Class II	16.2	0.1	-20.6	0.4	2.6	0.1	5.4
M	A	Class III	15.0	0.1	-20.9	0.8	2.7	0.0	5.0
M	A	Class III	16.3	0.4	-20.9	0.5	2.7	0.1	5.4
M	A	Class III	15.5	0.3	-21.5	0.2	2.9	0.0	5.1
M	A	Class III	16.3	0.1	-20.9	0.3	2.9	0.1	5.4
M	A		15.6	0.4					5.2
M	A		16.3	0.5					5.4
F	P	Class I	15.1	0.6	-21.2	0.2	2.8	0.0	5.0
F	P	Class I	17.0	0.0	-21.9	0.5	3.8	0.6	5.6
F	P	Class I	16.2	0.1	-22.6	0.4	3.0	0.3	5.4
F	P	Class I	15.0	0.1					5.0
F	P	Class I	16.6		-21.3		3.3	0.1	5.5
F	P	Class I	16.1	0.1	-21.9	0.2	2.8	0.1	5.3
F	P	Class I	15.6	0.2	-21.9	0.0	2.7	0.1	5.2
F	P	Class I	15.8	0.1	-22.1	0.0	2.7	0.1	5.2
F	P	Class I	16.1	0.3	-22.0	0.1	2.5	0.1	5.3
F	P	Class I	15.7	0.5					5.2
F	P	Class I	15.9	0.1					5.3
F	P	Class I	15.7	0.0					5.2
F	P	Class I	15.3	0.5					5.1
M	P	Class I	15.7	0.1	-21.3	0.8	2.9	0.1	5.2
M	P	Class I	16.2	0.2	-22.1	0.2	2.6	0.2	5.4
M	P	Class I	15.7	0.4	-21.7	0.1	2.9	0.0	5.2
M	P	Class I	15.3	0.2	-22.5		3.4	0.1	5.1
M	P	Class I	16.1	0.1	-22.1	0.3	3.7	0.3	5.3
M	P	Class I	16.4	0.5	-21.2	0.3	2.6	0.5	5.4
M	P	Class I	15.9	0.1	-22.0	0.2	3.3		5.3
M	P	Class I	16.0	0.3	-21.8	0.2	2.7	0.1	5.3
M	P	Class I	14.4	0.1	-20.8		3.7		4.8
M	P	Class I	16.1	0.0	-20.6	0.2	3.7	0.0	5.3
M	P	Class I	16.6	0.6					5.5

their sedation with diazepam was not needed; indeed, the sampling procedure lasted only a few minutes and did not cause any pup abandonment by their mothers. During handling, the head of the seal was covered with a canvas bag, and a small piece of skin from the hind flippers was taken. The seal was then positioned in a pole net and weighted with a digital scale. Each individual was classified according to its body mass: Class I < 200 kg; Class II < 400 kg; Class III \geq 400 kg (Table I). According to literature, potential prey species of Weddell seals (reported in Table III) were selected; a portion of white muscle close to the dorsal fin was extracted from each fish specimen and stored frozen (-20°C) for isotopic analysis.

2.2. Isotopic analysis

Prior to isotopic analysis, samples were oven-dried at 60°C for 24 h and powdered with mortar and pestle. Since lipids in an organism typically show lower $^{13}\text{C}:^{12}\text{C}$ ratio than protein and carbohydrate (e.g., McConnaughey & McRoy, 1979), lipids were removed from samples, to obtain realistic $\delta^{13}\text{C}$ values. However, because lipid extraction can also have effects on $\delta^{15}\text{N}$ values (e.g., Pinnegar & Polunin 1999; Sotiropoulos et al. 2004; Murry et al. 2006), each sample was divided in two aliquots: one aliquot was used directly (i.e., without lipid extraction procedure) to determine the values of $\delta^{15}\text{N}$, while the other aliquot was stored in a pre-weighed glass vial containing a solution of chloroform/methanol/water,

following the methods of Folch et al. (1957) and Bligh and Dyer (1959). Briefly, the tissue was homogenized in a 2:1 chloroform/methanol mixture, 20 times the tissue volume. The homogenate was sonicated for 10 min at 35 kHz, and then centrifuged at 12,000 g for 5 min, to separate the remaining tissue. The supernatant was removed and the tissue washed in ultra-pure water (20X volume of water to tissue), sonicated and centrifuged again to remove remaining chloroform/methanol, which may influence $\delta^{13}\text{C}$. The lipid-extracted tissue was oven-dried at 60°C to a constant weight. When the aliquot of skin was not sufficient to use the lipid extraction procedure, a direct determination of $\delta^{15}\text{N}$ was done and only $\delta^{15}\text{N}$ values were reported (Table I).

The samples were weighed into tin capsules (0.5 mg) in three replicates (when possible) and analysed at the GeoChemistry Laboratory (ISMAR-CNR, Naples, Italy), using an Elemental Analyzer “ThermoFisher Flash EA 1112” interfaced with a Delta Plus XP mass spectrometer. Obtained values for seals and their prey are reported as $\delta^{15}\text{N}$, $\delta^{13}\text{C}_{\text{lipid-free}}$ and C:N ratio in Tables I and II, respectively.

Stable isotope ratios were expressed in delta notation (δ), according to the equation: $\delta^{15}\text{N}$ (or $\delta^{13}\text{C}$) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R_{sample} is the ratio of $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$, while R_{standard} is the atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$ and the Vienna PeeDee Belemnite (VPDB) limestone for $\delta^{13}\text{C}$ (DeNiro & Epstein 1978). Isotopes ratio units were expressed as *per mil* (‰) differences from the

Table II. Means and standard deviation (SD) for classes of weight (Class I and Class II/III) and sex (M = male; F = female).

Sex	Age	Class of weight (kg)	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}_{\text{lipid-free}}$ (‰)	SD	C:N	SD
M	P	Class I	15.9	0.6	-21.6	0.2	3.2	0.5
F	P	Class I	15.9	0.6	-21.9	0.2	3.0	0.4
M + F (mean)	P	Class I	15.9	0.6	-21.7	0.2	3.1	0.4
M	A	Class II/Class III	15.9	0.6	-21.0	0.2	2.8	0.1
F	A	Class II/Class III	15.5	0.6	-21.1	0.7	2.8	0.3
M + F (mean)	A	Class II/Class III	15.6	0.6	-21.1	0.3	2.8	0.2

Table III. Nitrogen and carbon stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}_{\text{lipid-free}}$) and C:N ratios for food sources of Weddell seal. The $\delta^{13}\text{C}_{\text{lipid-free}}$ mean (\pm SD) of $\delta^{13}\text{C}$ values corrected for lipid contents .

Species	n	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}_{\text{lipid-free}}$ (‰)	SD	C:N	SD
<i>Chionodraco hamatus</i>	6	12.9	1.2	-26.8	0.7	2.9	0.1
<i>Dissostichus mawsoni</i>	4	15.0	0.4	-25.5	1.5	3.4	0.3
<i>Pagothenia borchgrevinki</i>	5	11.5	0.7	-22.9	1.3	3.0	0.1
<i>Pleuragramma antarcticum</i>	12	10.6	0.6	-24.3	0.6	3.2	0.2
<i>Trematomus eulepidotus</i>	3	12.5	0.4	-21.4	0.6	2.9	0.4
<i>Trematomus hansonii</i>	6	13.5	0.5	-23.3	0.5	3.1	0.1
<i>Trematomus pennellii</i>	1	14.6	0.6	-22.6	0.8	3.3	0.1
<i>Trematomus newnesi</i>	1	14.4	0.6	-23.9	0.8	2.8	0.5

standard. A previous calibration was made using urea with both its elementary composition (Nitrogen = 46,65% and Carbon = 20%) and isotopic values ($\delta^{15}\text{N} = 0.02\text{‰}$, $\delta^{13}\text{C} = -47.37\text{‰}$). The analytical precision, using replicate measurements of laboratory standards, was 0.05‰ for $\delta^{15}\text{N}$ and 0.10‰ for $\delta^{13}\text{C}$.

To calculate the trophic level of Weddell seals, we used the relationship $\text{TL} = (\text{D} - 3.1)/2.3 + 1$ (Nyssen et al. 2002): D is the $\delta^{15}\text{N}$ value of seals, 3.1‰ refers to the mean $\delta^{15}\text{N}$ value of Suspended Particulate Organic Matter (SPOM) in the Ross Sea, and TL is the organism trophic level (see Table I). The enrichment factor of ^{15}N for skin was of 2.3‰ and 2.8‰ for ^{13}C (Hobson et al. 1996).

2.3. Statistical methods

We used ANOVA to evaluate possible differences in isotopic values among seals in terms of sex, age and body mass. Normality and homogeneity of variances were checked by means of Levene's and Shapiro-Wilk tests, respectively. Holm p-value correction was used for *post hoc* testing, in case of multiple comparisons. Correlation analysis (Pearson correlation) was also carried out to verify the presence of significant relationship among the considered variables. To calculate the contribution of each specific prey item to the overall diet of *L. weddellii*, we created and run a Bayesian mixing model within the framework MixSIAR (<https://github.com/brianstock/MixSIAR/>). In particular, MixSIAR estimates the proportion of each prey to the consumer diet, taking into account the variability observed in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both consumers and prey, thus also providing an estimate of the variability in the estimated proportion (Stock et al. 2018). We excluded pups from the mixing model analysis because the isotopic signal in their skin will mainly reflect their nursing period. Potential seal prey were grouped together (by averaging $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) prior to running SIAR, according to their ecological characteristics (e.g., benthic and pelagic fish) and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values; species showing comparable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were considered as a single source, only if they showed similar size and belonged to the same habitat.

Finally, before MixSIAR analysis, potential prey and consumers were plotted in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space (Figure 4), considering a Trophic Enrichment Factor (TEF) of 2.8‰ for $\delta^{13}\text{C}$ and 2.3‰ for $\delta^{15}\text{N}$ for the skin, as reported by Hobson et al. (1996). In the plot, in order to assume that the identified prey are consistent with the seal diet, consumers have to be surrounded by sources (Figure 4).

All statistical analyses were carried out using R statistical environment (R Core Team 2017).

3. Results

Results from all 56 Weddell seals, classified according to sex (males and females), age (pups and adults), and body-mass class (Class I < 200 kg; Class II < 400 kg; Class III \geq 400 kg) are reported in Table I. Overall, isotope ratios in seal samples ranged from 14.3‰ to 17.0‰ (mean \pm SD: 15.7‰ \pm 0.6) for $\delta^{15}\text{N}$, and from -22.6‰ to -19.2‰ (mean \pm SD: -21.3‰ \pm 0.7) for $\delta^{13}\text{C}_{\text{lipid-free}}$. Average trophic level was 5.2 (Table I).

No significant differences were found between adults (males and females) and pups, in terms of C:N and $\delta^{15}\text{N}$. On the contrary, the ANOVA analysis highlighted the presence of significant differences ($F_{(2,40)} = 5.67$, $p < 0.01$) in $\delta^{13}\text{C}_{\text{lipid-free}}$ among the above-mentioned groups. More specifically, while average adult $\delta^{13}\text{C}_{\text{lipid-free}}$ values were similar between males and females (-21.0‰ \pm 0.2 and -21.1‰ \pm 0.7, respectively), they were significantly different from those of pups (-21.6‰ \pm 0.2 for male and -21.9‰ \pm 0.2 for female; Figure 2 and Table II).

Also, when looking at body-mass classes, the only significant difference was in $\delta^{13}\text{C}_{\text{lipid-free}}$ ($F_{(2,40)} = 5.82$, $p < 0.01$). Class I was significantly depleted in $\delta^{13}\text{C}_{\text{lipid-free}}$ when compared to Class II and Class III, which were instead characterized by similar average values (Figure 3).

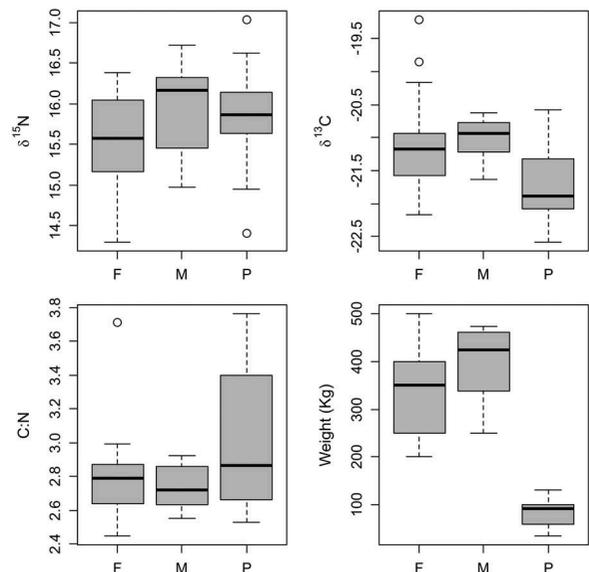


Figure 2. Mean, 25–75 percentiles (box) and non-outlier range (whiskers) of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, C:N and body mass for adult males (M), adult females (F) and pups (P).

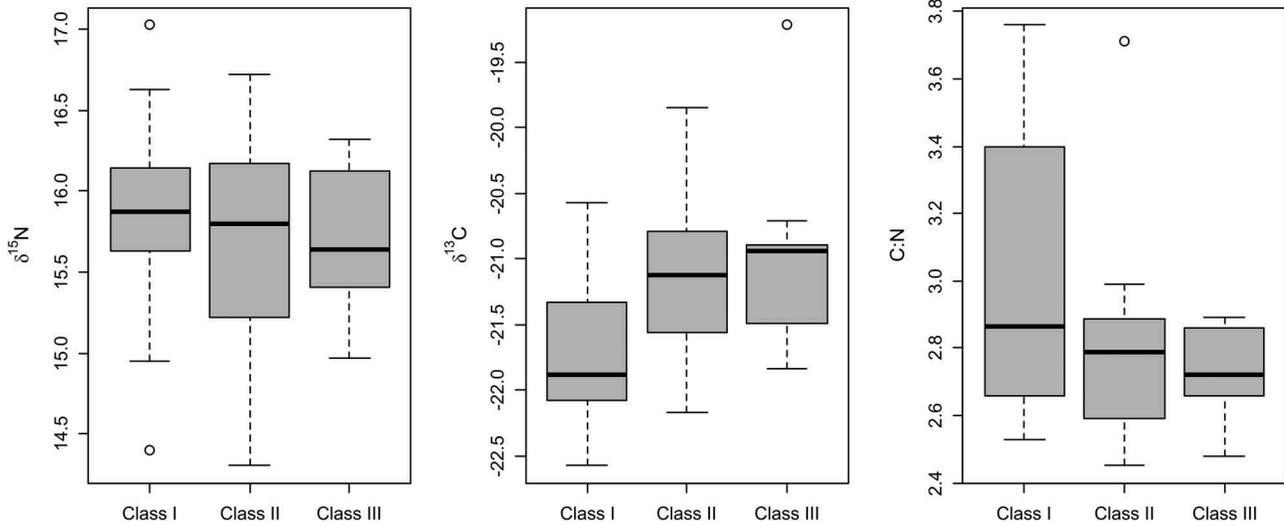


Figure 3. Mean, 25–75 percentiles (box) and no-outlier range (whisker) of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and C:N by body mass (Class I < 200 kg; Class II < 400 kg; Class III \geq 400 kg).

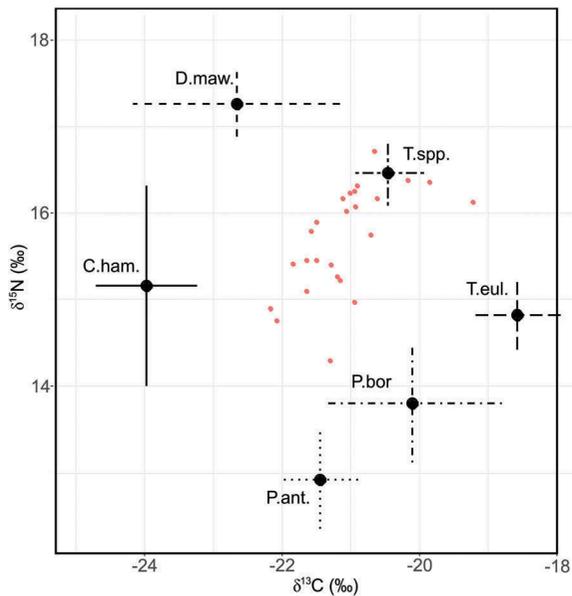


Figure 4. Relationship between sources (D.maw = *Dissostichus mawsoni*; T.spp. = *Trematomus* spp.; P.ant. = *P. antarctica*; C.ham. = *Chionodraco hamatus*; P.bor. = *Pagothenia borchgrevinkii*; T.eul. = *Trematomus eulepidotus*) and consumers (A = adult seals and P = pup seals) considering the TEF (see text for details).

Correlation analysis evidenced the absence of significant relationships between $\delta^{15}\text{N}$ –C:N, $\delta^{13}\text{C}_{\text{lipid-free}}$ –C:N and $\delta^{15}\text{N}$ –body mass, while a positive correlation ($r = 0.46$, $r^2 = 0.21$, $p < 0.01$) was found between $\delta^{13}\text{C}_{\text{lipid-free}}$ and body mass.

Isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}_{\text{lipid-free}}$) and their C:N ratios found in the muscles of potential prey are reported in Table III.

Table IV. Results of MixSIAR model: percentages of food sources for Weddell seal adults and standard deviation (SD).

Species	Adults (% Mean)	SD
<i>Trematomus</i> spp.*	34.1	0.2
<i>Trematomus eulepidotus</i>	14.7	0.1
<i>Dissostichus mawsoni</i>	21.1	0.1
<i>Chionodraco hamatus</i>	10.8	0.1
<i>Pleuragramma antarctica</i>	9.8	0.1
<i>Pagothenia borchgrevinkii</i>	9.6	0.1

**Trematomus* spp. = *Trematomus hansoni*, *Trematomus pennellii* and *Trematomus newnesi*

The results from the mixing model showed a well-defined preference for *Trematomus* spp. and *Dissostichus mawsoni*, as they together accounted for about 55% of seal diet (34.1% and 21.1%, respectively – see Table IV).

4. Discussion

This is the first study on the diet of Weddell seals of Terra Nova Bay, and our results (TL > 5 and mean $\delta^{15}\text{N} = 15.7\text{‰}$) confirmed that this species occupies a top trophic position among phocids within the Antarctic ecosystem (e.g., Pinkerton & Bradford-Grieve 2014; Goetz et al. 2017; Botta et al. 2018). As upper trophic-level species, its responses to changes in the low levels of the food chain due to environmental variations would be amplified and affect its diet, reproductive performance, and population size (Erikstad et al. 1998; Orzack & Tuljapurkar 2001; Hindell et al. 2003; Le Boeuf & Crocker 2005; Reid et al. 2005).

Each year, Weddell seal females haul out on the coast of the Ross Sea during the austral spring (September–November), give birth and nurse their pup for about 6–7 weeks (Lindsey 1937; Mansfield 1954; Fenwick 1973; Hill 1987; Reijnders et al. 1990), until weaning age (minimum weaning age = 33 days, Kaufman et al. 1975). Furthermore, lactating females spend most of their time with their pups, and only go to sea for short and close-by dives (Hindell et al. 2002), while males are very busy maintaining their breeding territories, and likely fast for a large part of the breeding season. Our samples were collected in middle November/early December, and thus referred to the diet of seals during a period of few weeks, from the end of fall/winter (while they were feeding at sea) up to the beginning of the pupping/breeding season (when seals might have been in their fasting period) (Figure 5). Since skin isotope content will reflect the diet from 13 to 83 days before sampling (Cipro et al. 2012), our isotopic values were probably an integration of both feeding and fasting periods. During lactation, marine mammals can excrete ^{15}N into their milk, rather than diverting it back into their tissues (Kurle & Worthy 2002), with a consequent enrichment of $\delta^{15}\text{N}$ values in pups' tissues; nevertheless, values of $\delta^{15}\text{N}$ were not related with seal age, sex or body mass, indicating that all seals were foraging at a similar trophic level. On the contrary, significant differences were found in $\delta^{13}\text{C}$ values between pups and adults. The combination of similar $\delta^{15}\text{N}$ with depleted $\delta^{13}\text{C}$ values in pups compared to their mothers (Table II) suggests that the lipid extraction from pup-tissue samples could have led to lower $\delta^{13}\text{C}$ values, being the milk of mothers very rich in lipid content (Costa & Williams 1999; Stegall et al. 2008). Skin samples of adult Weddell seals (females and males) exhibited a large range of $\delta^{13}\text{C}$ values, which could be used to distinguish benthic from pelagic, and nearshore

from offshore sources (Wada et al. 1987; Shell et al. 1989; France & Peters 1997; Zhao et al. 2004).

As the other Antarctic and sub-Antarctic pinnipeds (Costa & Gales 2000; Fabiani et al. 2003; Hoffman et al. 2006), Weddell seals show, in fact, excellent diving ability (Thomas & Terhune 2009): they can reach deep depths and far distances in the open sea, and use the entire water column to forage in shallow-shelf waters (Plötz et al. 2001; Hindell et al. 2002; Costa et al. 2010; Casaux et al. 2011; Heerah et al. 2013; Raymond et al. 2015). The large range of $\delta^{13}\text{C}$ values found in our seal samples could be therefore associated with the consumption of ^{13}C -enriched benthic and ^{13}C -depleted pelagic prey (France 1995; Cherel & Hobson 2007), as also reported in an analysis of scat samples by Casaux et al. (2011). Mean $\delta^{13}\text{C}$ values in adults were not significantly different between females and males. Enriched $\delta^{13}\text{C}$ values and results from our mixing model suggested that adult seals were mainly feeding on benthic prey belonging to *Trematomus* spp. (34.1%) and on benthopelagic fish, such as *D. mawsoni* (about 21.1%). Many studies in literature indicate that large quantities of *Trematomus* spp. and Antarctic toothfish (*D. mawsoni*) are annually taken by Weddell seals and killer whales (*Orcinus orca* Linn.) in McMurdo Sound, the most southern branch of the Ross Sea (Murphy 1962; Dearborn 1965; Calhaem & Christoffel 1969; Thomas et al. 1981; Burns et al. 1998; Davis et al. 1999, 2003; Fuiman et al. 2002; Wu & Mastro 2004; Kim et al. 2005; Ainley et al. 2006a; Ponganis & Stockard 2007; Goetz et al. 2017). Ainley and Siniff (2009) showed that sub-adult Weddell seals can eat large Antarctic toothfish, up to one-third as big as them. Seals do not always consume the entire fish, and this can explain why hard parts of it (i.e., otoliths and bones) are rarely found in their stomach or scats, making the results of these types of analyses not totally reliable (Ainley & Siniff 2009). As *D. mawsoni* is also a high-level predator – therefore

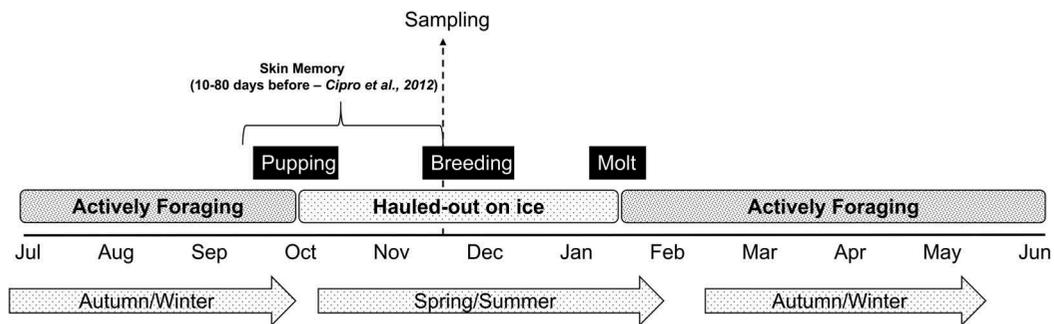


Figure 5. Annual cycle for Weddell seals in the Ross Sea (considering pupping, breeding and molting periods). Sampling event and the time frame integrated by the skin samples are shown.

showing higher isotopic values – its consumption could explain the high-nitrogen isotope values observed in the Weddell seals of Terra Nova Bay, and might be linked to periods when Weddell seals are in need of more energy (for example, during breeding and fasting).

On the other side, pelagic prey such as *P. antarcticum* (9.8%) only partially contributed to the diet of our adult seals. This result clearly disagrees with precedent data that described *P. antarcticum* as the main prey of Weddell seals, representing up 90% of fish biomass in the Antarctic sea (e.g., Eastman 1985; Everson 1985; Burns et al. 1998). The large consumption of both benthopelagic and benthonic fish in Weddell seals of Terra Nova Bay could be somehow linked to the presence of polynya in the area. Antarctic coastal polynyas are areas of reduced sea-ice cover within the coastal sea-ice zone, largely maintained by offshore winds and oceanic currents that push the ice away from the coast (Tamura et al. 2008). The physical importance of Antarctic coastal polynyas has been described in recent studies (e.g., Tamura et al. 2008; Herraiz-Borreguero et al. 2015), and they are surely important for local wildlife. Seals that live in Terra Nova Bay have, in fact, direct access to the open ocean all year round, and they might have, therefore, evolved local feeding strategies.

Notwithstanding their incredible diving skills, swimming and foraging come with a cost for Weddell seals (Williams et al. 2004), and it is likely that travelling shorter distances and diving to shallower depths would be less energetic demanding. For this reason, seals of Terra Nova Bay might prefer to catch benthic or benthopelagic prey (i.e., *Trematomus* spp. and *D. mawsoni*) found near the coast, instead of undertaking longer trips for pelagic prey (i.e., *P. antarcticum*, Testa 1994). This could be even more true during the pre-breeding season, when seals might search for more energy-rich prey such as *D. mawsoni*, to afford the large loss in body condition during reproduction.

As the philopatric behaviour of seals of this colony has been lately confirmed with the analysis of genetic markers (Zappes et al. 2017), the predatory behaviour and prey preference might have somehow contributed to the evolution and maintenance of the genetic differentiation between Terra Nova Bay and the close-by seal colonies.

In conclusion, while $\delta^{15}\text{N}$ values indicated that all Weddell seals (males, females and pups) of Terra Nova Bay were foraging at the same trophic level, the significant difference between age- and body-mass classes in $\delta^{13}\text{C}_{\text{lipid-free}}$ suggested that seals rely on various “food sources”. Adults seemed to concentrate their efforts on *D. mawsoni* and *Trematomus* spp.,

showing feeding preferences different from those found in previous studies – which detected *P. antarcticum* as seals’ main prey. These differences could represent peculiar feeding strategies, evolved in areas where the access to benthic and benthopelagic species is more suitable than to prey on smaller pelagic species, such as the polynya area of Terra Nova Bay. Nevertheless, as ours are the very first data on the diet of Terra Nova Bay seals and sampling time was somehow restricted, we believe that further studies would be required. The implementation of isotopic analyses on larger seal and prey samples, and over a longer time frame, would provide a better understanding of the foraging behavior of these marine mammals, of their position in the Antarctic food web and of the potential threats to the whole Antarctic ecosystem.

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Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Antarctic Treaty Secretariat. 2013. Antarctic specially protected area No 161 (Terra Nova Bay, Ross Sea): Revised Management Plan. Available: <https://ats.aq/devAS/Meetings/Mesure/540>. Accessed Sep 2014 14.
- Ainley DG, Ballard G, Dugger KM. 2006a. Competition among penguins and cetaceans reveals trophic cascades in the Ross Sea, Antarctica. *Ecology* 87:2080–2093.
- Ainley DG, Siniff DB. 2009. The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. *Antarctic Science* 21:317–327. DOI: 10.1017/S0954102009001953.
- Arrigo KR, van Dijken GL. 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *Journal of Geophysical Research: Oceans* 108(C8). DOI: 10.1029/2002JC001739.
- Baumann P. 1989. PAH, metabolites and neoplasia in feral fish populations. In: Varanasi U, editor. *Metabolism of polycyclic aromatic hydrocarbons in the aquatic environment*. Boca Raton (FL): CRC Press.

- Bligh EG, Dyer WJ. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* 37(8):911–917.
- Boecklen WJ, Yarnes CT, Cook BA, James AC. 2011. On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution and Systematics* 42:411–440. DOI: 10.1146/annurev-ecolsys-102209-144726.
- Botta S, Secchi ER, Rogers TL, Prado JHF, de Lima RC, Carlini P, Negrete J. 2018. Isotopic niche overlap and partition among three Antarctic seals from the Western Antarctic Peninsula. *Deep-Sea Research Part II* 149:240–249.
- Burns JM, Trumble SJ, Castellini MA, Testa JW. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology* 19:272–282. DOI: 10.1007/s003000050245.
- Calhaem I, Christoffel DA. 1969. Some observations of the feeding habits of a Weddell seal, and measurements of its prey, *Dissostichus mawsoni*, at McMurdo Sound, Antarctica, New Zealand. *Journal of Marine and Freshwater Research* 3:181–190.
- Casaux R, Baroni A, Carlini A. 1997. The diet of the Weddell seal *Leptonychotes weddellii* at Harmony Point, South Shetland Islands. *Polar Biology* 18:371–375. DOI: 10.1007/s003000050202.
- Casaux R, Bertolin ML, Carlini A. 2011. Feeding habits of three seal species at the Danco Coast, Antarctica: A re-assessment. *Polar Biology* 34:1615–1620. DOI: 10.1007/s00300-011-0994-1.
- Checkley DM, Entzeroth LC. 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. *Journal of Plankton Research* 7:553–568.
- Cherel Y, Hobson KA. 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.
- Cipro CVZ, Bustamante P, Taniguchi S, Montone RC. 2012. Persistent organic pollutants and stable isotopes in pinnipeds from King George Island, Antarctica. *Marine Pollution Bulletin* 64(12):2650–2655. DOI: 10.1016/j.marpolbul.2012.10.012.
- Costa DP, Williams TM. 1999. Marine mammal energetics. In: Reynolds JE, Rommel SA, editors. *Biology of marine mammals*. Washington, DC: Smithsonian Institution Press. pp. 176–217.
- Costa DP, Gales NJ. 2000. Foraging energetics and diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. *Journal of Experimental Biology* 203:3655–3665.
- Costa DP, Huckstadt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA. 2010. Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integrative and Comparative Biology* 50:1018–1030. DOI: 10.1093/icb/icq054.
- Daneri GA, Carlini AR, Negri A, Allcock AL, Corbalan A. 2012. Predation on cephalopods by Weddell seals, *Leptonychotes weddellii*, at Hope Bay, Antarctic Peninsula. *Polar Biology* 35:585–592. DOI: 10.1007/s00300-011-1104-0.
- Davis R, Castellini M, Horning M, Davis M, Kooyman G. 1982. Winter ecology of Weddell seals at White Island. *Antarctic Journal of the United States* 17:183–184.
- Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–995.
- Davis RW, Fuiman LA, Williams TM, Horning W, Hagey WP. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. *Marine Ecology Progress Series* 264:109–122.
- Dearborn JH. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. *Journal of Mammalogy* 46:37–43. DOI: 10.2307/1377814.
- DeNiro MJ, Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica and Cosmochimica Acta* 42:495–506. DOI: 10.1016/0016-7037(78)90199-0.
- Eastman JT. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4:155–160. DOI: 10.1007/BF00263878.
- Erickson AW, Hanson MB. 1990. Continental estimates and population trends of Antarctic ice seals. In: Kerry KR, Hempel G, editors. *Antarctic ecosystems, ecological change and conservation*. Berlin and Heidelberg: Springer-Verlag. pp. 253–264.
- Erikstad KE, Fauchald P, Tveraa T, Steen H. 1998. On the cost of reproduction in long-lived birds: The influence of environmental variability. *Ecology* 79:1781–1788.
- Everson I. 1985. Biology of fish. In: Laws RM, editor. *Antarctic ecology*. Vol. 2. Fish biology. London: Academic Press. pp. 491–532.
- Fabiani A, Hoelzel AR, Galimberti F, Muelbert MMC. 2003. Long-range paternal gene flow in the southern elephant seal. *Science* 299:676. DOI: 10.1126/science.299.5607.676.
- Fenwick GD. 1973. Breeding biology and population dynamics of the Weddell seal, *Leptonychotes weddellii*: A review. *Mauri Ora* 1:29–36.
- Folch J, Lees M, Stanley GHS. 1957. A simple method for the isolation and purification of total lipides from animal tissues. *The Journal of Biological Chemistry* 226:497–509.
- France R. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: Foodweb implications. *Marine Ecology Progress Series* 124:307–312. DOI: 10.3354/meps124307.
- France RL, Peters RH. 1997. Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1255–1258.
- Fuiman LA, Davis RW, Williams TM. 2002. Behavior of mid-water fishes under the Antarctic ice: Observations by a predator. *Marine Biology* 140:815–822. DOI: 10.1007/s00227-001-0752-y.
- Goetz KT, Burns JM, Huckstadt LA, Shero MR, Costa DP. 2017. Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 140:36–44. DOI: 10.1016/j.dsr2.2016.05.017.
- Hammill M, Lesage V, Carter P. 2005. What do harp seals eat? Comparing diet composition from different compartments of the digestive tract with diets estimated from stable-isotope ratios. *Canadian Journal of Zoology* 83:1365–1372. DOI: 10.1139/z05-123.
- Heerah K, Andrews-Goff V, Williams G, Sultan E, Hindell M, Patterson T, Charrassin JB. 2013. Ecology of Weddell Seals during winter: Influence of environmental parameters on their foraging behavior. *Deep Sea Research Part II: Topical Studies in Oceanography* 88:23–33. DOI: 10.1016/j.dsr2.2012.08.025.
- Herraiz-Borreguero L, Coleman R, Allison I, Rintoul SR, Craven M, Williams GD. 2015. Circulation of modified Circumpolar Deep Water and basal melt beneath the Amery Ice Shelf, East Antarctica. *Journal of Geophysical Research: Oceans* 120(4):3098–3112.
- Hill SEB. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. PhD dissertation. Minneapolis: University of Minnesota.

- Hindell MA, Bradshaw CJA, Sumner MD, Michael KJ, Burton HR. 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: Relevance to management and oceanographic zones. *Journal of Applied Ecology* 40:703–715.
- Hindell MA, Harcourt R, Waas JR, Thompson D. 2002. Fine-scale, three dimensional spatial use of diving lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* 242:275–284. DOI: 10.3354/meps242275.
- Hobson KA. 1993. Trophic relationships among high Arctic seabirds: Insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series* 95:7–18. DOI: 10.3354/meps095007.
- Hobson KA, Clark A. 1992. Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *Condor* 94:189–197.
- Hobson KA, Schell DM, Renouf D, Noseworthy E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: Implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences* 53:528–533. DOI: 10.1139/f95-209.
- Hobson KA, Welch HE. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 84:9–18. DOI: 10.3354/meps084009.
- Hoffman JI, Trathan PN, Amos W. 2006. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. *Molecular Ecology* 15:3841–3847. DOI: 10.1111/j.1365-294X.2006.03053.x.
- Kaufman G, Siniff DB, Reichle R. 1975. Colony behavior of Weddell seals, *Leptonychotes weddellii*, at Hutton Cliffs, Antarctica. *Rapport et Procès-Verbaux Réunions du Conseil International Pour L'exploration de la Mer* 169:228–246.
- Kim SL, Conlan K, Malone DP, Lewis CV. 2005. Possible food caching and defence in the Weddell seal: Observations from McMurdo sound, Antarctica. *Antarctic Science* 17:71–72.
- Kooyman GL. 1981. *Weddell seal, consummate diver*. New York: Cambridge University Press.
- Kooyman GL. 2013. An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. In: Llano GA, Schmitt WL, editors. *Washington: Biology of the Antarctic Seas III*. American Geophysical Union. pp. 227–261.
- Kurle CM, Worthy GAJ. 2002. Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: Implications for dietary and migratory reconstructions. *Marine Ecology Progress Series* 236:289–300. DOI: 10.3354/meps236289.
- Lake S, Burton H, van den Hoff J. 2003. Regional, temporal and fine scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series* 254:293–305. DOI: 10.3354/meps254293.
- Le Boeuf BJ, Crocker DE. 2005. Ocean climate and seal condition. *BMC Biology* 3:9.Reid
- Lindsey AA. 1937. Weddell seals in the Bay of Whales, Antarctica. *Journal of Mammalogy* 18:127–143. DOI: 10.2307/1374459.
- Mansfield AW. 1954. The breeding behaviour and reproductive cycle of the Weddell seal (*Leptonychotes weddellii* Lesson). Vol. 18. Falkland Island Dependencies Survey, Scientific Report. London, UK: Her Majesty's Stationery Office. pp. 1–41.
- Massom RA, Harris PT, Michael KJ, Potter MJ. 1988. The distribution and formative processes of latent-heat polynyas in East Antarctica. *Annals of Glaciology* 27:420–426. DOI: 10.3189/1998AoS27-1-420-426.
- McConnaughey T, McRoy CP. 1979. Food-web structure and the fractionation of the carbon isotopes in the Bering Sea. *Marine Biology* 53:257–262.
- Minagawa M, Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Cosmochimica Acta* 48:1135–1140. DOI: 10.1016/0016-7037(84)90204-7.
- Moore CM, Mills MM, Arrigo KR, Berman-Frank I, Bopp L. 2013. Processes and patterns of oceanic nutrient limitation. *Nature Geoscience* 6:701–710. DOI: 10.1038/NNGEO1765.
- Murphy RC. 1962. The oceanic life of the Antarctic. *Scientific American* 207:187–210.
- Murry BA, Farrell JM, Teece MA, Smyntek PM. 2006. Effect of lipid extraction on the interpretation of fish community trophic relationships determined by stable carbon and nitrogen isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2167–2172. DOI: 10.1139/f06-116.
- Nyssen F, Brey T, Lepoint G, Bouqueneau JM, De Broyer C, Dauby P. 2002. A stable isotope approach to the western Weddell Sea trophic web: Focus on benthic amphipods. *Polar Biology* 25:280–287. DOI: 10.1007/s00300-001-0340-0.
- Orzack SH, Tuljapurkar S. 2001. Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology* 82:2659–2665.
- Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293–320. DOI: 10.1146/annurev.es.18.110187.001453.
- Pinkerton MH, Bradford-Grieve JM. 2014. Characterizing food-web structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. *ICES Journal of Marine Science*. DOI: 10.1093/icesjms/fst230.
- Pinnegar JK, Polunin NVC. 1999. differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: Implications for the study of trophic interactions. *Functional Ecology* 13:225–231.Folch.
- Plötz J, Bornemann H, Knust R, Schroder A, Bester M. 2001. Foraging behavior of Weddell seals, and its implications. *Polar Biology* 24:901–909. DOI: 10.1007/s003000100297.
- Plötz J, Ekau W, Reijnders PJH. 1991. Diet of Weddell seals *Leptonychotes weddellii* at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. *Marine Mammal Science* 7:136–144. DOI: 10.1111/j.1748-7692.1991.tb00560.x.
- Ponganis PJ, Stockard TK. 2007. Short note: The Antarctic toothfish: How common a prey for Weddell seals? *Antarctic Science* 19:441–442. DOI: 10.1017/S0954102007000715.
- Post DM. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83:703–718. DOI: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.
- R Development Core Team. 2017. R: A Language and Environment for Statistical Computing. Available: <https://www.R-project.org/>.
- Raymond B, Lea MA, Patterson T, Andrews-Goff V, Sharples R, Charrassi JB, Cottin M, Emmerson L, Gales N, Gales R, Goldsworthy SD. 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* 38:121–129.
- Reid K, Croxall JP, Briggs DR, Murphy EJ. 2005. Antarctic ecosystem monitoring: Quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science* 62:366–373.
- Reijnders PJH, Plötz J, Zegers J, Gräfe M. 1990. Breeding biology of Weddell seals (*Leptonychotes weddellii*) at Drescher Inlet, Riiser Larsen ice shelf, Antarctica. *Polar Biology* 10:301–306. DOI: 10.1007/BF00238429.

- Schell DM, Saupé SM, Haubenstock N. 1989. Bowhead Whale (*Balaena mysticetus*) growth and feeding as estimated by ¹³C techniques. *Marine Biology* 103:433–443.
- Smith WO, Ainley DG, Cattaneo-Vietti R. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:91–111. DOI: [10.1098/rstb.2006.1956](https://doi.org/10.1098/rstb.2006.1956).
- Smith Jr WO, Barber DG. 2007. *Polynyas: Windows to the world*. 1st ed. Amsterdam: Elsevier Oceanography Series, Elsevier Science.
- Sotiropoulos MA, Tonn WM, Wassenaar LI. 2004. Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: Potential consequences for food web studies. *Ecology of Freshwater Fish* 13:155–160. DOI: [10.1111/eff.2004.13.issue-3](https://doi.org/10.1111/eff.2004.13.issue-3).
- Stegall VK, Farley SD, Rea LD, Pitcher KW, Rye RO, Kester CL, Stricker CA, Bern CR. 2008. Discrimination of carbon and nitrogen isotopes from milk to serum and vibrissae in Alaska Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology* 86:17–23.
- Stocchino C, Lusetti C. 1988. Le costanti armoniche di marea di Baia Terra Nova (Mare di Ross, Antartide). F.C. 1128. Genova: Istituto Idrografico della Marina.
- Stocchino C, Lusetti C. 1990. Prime osservazioni sulle caratteristiche idrologiche e dinamiche di Baia Terra Nova (Mare di Ross, Antartide). F.C. 1132. Genova: Istituto Idrografico della Marina.
- Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX. 2018. Analyzing mixing systems using a new generation of bayesian tracer mixing models. *PeerJ* 6:e5096.
- Tamura T, Ohshima KI, Nihashi S. 2008. Mapping of sea ice production for Antarctic coastal polynyas. *Geophysical Research Letters* 35(7):L07606. DOI: [10.1029/2007GL032903](https://doi.org/10.1029/2007GL032903).
- Testa JW. 1994. Over-winter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the southwestern Ross Sea, Antarctica. *Canadian Journal of Zoology* 72(10):1700–1710. DOI: [10.1139/z94-229](https://doi.org/10.1139/z94-229).
- Thomas JA, Leatherwood S, Evans WE, Jehl JR, Awbrey FT. 1981. Ross sea killer whale distribution, behavior, color patterns, and vocalizations. *Antarctic Davis Journal of the United States* 16(1):157–158.
- Thomas JA, Terhune J. 2009. Weddell seal –*Leptonychotes weddellii*. In: Perrin W, Würsig B, Thewissen J, editors. *Encyclopedia of marine mammals*. 2nd ed. Amsterdam: Academic Press. pp. 1217–1220.
- Tieszen LL, Boutton TW, Tesdahl KG, Slade A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ⁶C analysis of diet. *Oecologia* 57:32–37.
- Wada E, Terazaki M, Kabaya Y, Nemoto T. 1987. ¹⁵N and ¹³C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep Sea Research* 34:829–841.
- Williams TM, Fuiman LA, Horning M, Davis RW. 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: Pricing by the stroke. *Journal of Experimental Biology* 207(6):973–982. DOI: [10.1242/jeb.00822](https://doi.org/10.1242/jeb.00822).
- Wu N, Mastro J. 2004. *Under Antarctic ice: The photographs of Norbert Wu*. Berkeley, CA: University of California Press. p. 176.
- Zappes IA, Fabiani A, Sbordoni V, Rakaj A, Palozzi R, Allegrucci G. 2017. New data on Weddell seal (*Leptonychotes weddellii*) colonies: A genetic analysis of a top predator from the Ross Sea, Antarctica. *PloS One* 12(8):e0182922. DOI: [10.1371/journal.pone.0182922](https://doi.org/10.1371/journal.pone.0182922).
- Zhao L, Castellini MA, Mau TL, Trumble SJ. 2004. Trophic interactions of Antarctic seals as determined by stable isotope signatures. *Polar Biology* 27:368–373. DOI: [10.1007/s00300-004-0598-0](https://doi.org/10.1007/s00300-004-0598-0).