

**Cephalopod diet of juvenile male southern elephant seals
Mirounga leonina at Marion Island, South Indian Ocean**

M.N. Bester¹, M. Connan²

¹Mammal Research Institute, Department of Zoology and Entomology, University of
Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa

Corresponding author: +27(0)726015470; +27(0)124202534 (fax)

E-mail: mnbester@zoology.up.ac.za

orcid.org/0000-0002-2265-764X

²Department of Zoology, Marine Apex Predator Research Unit, Institute for Coastal and
Marine Research, Nelson Mandela University, Gqeberha, South Africa

E-mail: maelle.connan@gmail.com

orcid.org/0000-0002-1308-9118

Abstract

Southern elephant seals *Mirounga leonina* have a circumpolar distribution and migrate across broad geographic regions. Therefore they can provide important insights into the responses of top predators to changes in the environment, especially those effected by climate change. For this, determining trophic interactions is key, and thus it is important to investigate the diet of all populations of *M. leonina* in the Southern Ocean. Limited literature exists on the diet of southern elephant seals at the Prince Edward Islands in the sub-Antarctic. During August and September 1976, the stomach contents of two juvenile male southern elephant seals were opportunistically collected at Marion Island (46°54'S, 37°51'E), and later analysed. Accumulated cephalopod beaks (n = 137) representing 18 taxa in nine decapod families were found. Onychoteuthidae was numerically the most abundant (28.7%), followed by Brachioteuthidae (21.8%), Neoteuthidae (12.6%) and Histioteuthidae (9.2%). *Slosarczykovia circumantarctica* (Brachioteuthidae) was the most abundant species (19.5%) followed by *Batoteuthis skolops* (Batoteuthidae) at 12.6%. Allometric equations using lower rostral lengths showed that the southern elephant seals ingested cephalopods with mantle length between 5.2 and 39.9 cm and weighing between 0.003 and 2.62 kg. There was only one very digested crustacean, and no recognizable fish remains in the stomach contents. The continuation of the investigation relies on examination of natural mortalities and dietary items obtained by stomach lavage of individuals, complemented by, for example, stable isotope compositions captured along the length of vibrissae and within dentinal growth layer groups of teeth as proxies for the elephant seals' trophic ecology.

Key words: Cephalopod beaks, Diet, Prince Edward Islands, Southern elephant seal, Stomach contents

Introduction

The Southern Ocean is experiencing extensive changes due to various factors including climate change, all of which are threatening global marine biodiversity (Block et al. 2011). Such changes are especially relevant for apex predators that have to find alternative food locations or have an increase in energy costs due to more complex foraging trips away from their breeding grounds (Constable et al. 2014; Reisinger et al. 2021). The southern elephant seals

Juvenile SES cephalopod diet

Mirounga leonina (SES) in particular can provide insights into responses to environmental conditions across broad geographic regions due to their circumpolar distribution, and their extensive migrations (Hindell et al. 2016). Juvenile SES at sub-Antarctic Marion Island predominantly forage in pelagic waters more than 3000 m deep to the southwest of the island, mainly within the Polar Frontal Zone (PFZ) (Tosh et al. 2012, 2015). Most foraging takes place between 43°S and 56°S, around the sub-Antarctic Front (SAF) and Antarctic Polar Front (APF), respectively (Tosh et al. 2012), but this might not have been the case in the early 1970s, given the general shift towards lower productivity of ecosystems within sub-Antarctic waters (Lea et al. 2002). In order to understand how top predators respond to the changing environment, trophic interactions are key (Trathan et al. 2007). Although the diet of SES has been studied elsewhere in the Southern Ocean (e.g., Green and Burton 1993; van den Hoff 2004; Daneri et al. 2015), such information from the Marion Island population is limited (Ryan and Bester 2008; Lübcker et al. 2017).

Here we report on the examination of stomach contents of two juvenile SES collected opportunistically at Marion Island in 1976. Although limited, these opportunistic observations are important in the context of potential climate change induced modifications of the marine ecosystem.

Methods

To provide food for captive feral house cats *Felis catus* within the feral cat eradication programme (Bester et al. 2000), two juvenile male SES (< 3 years old) were shot and killed on Marion Island (46°54'S, 37°51'E) following Bonner (1993). The animals were dispatched with a single shot each from a rifle firing 0.22 inch (5.6 mm) calibre ammunition on 2 August and 2 September 1976 during their winter haul-out (Condy 1979) which is rarely as long as 40 days in duration (Carrick et al. 1962) but most commonly between 10 and 20 days in under-yearlings (Wilkinson and Bester 1990). The stomach of each SES was opened and any prey remains (almost all cephalopod beaks in this case) were removed and preserved in 70% ethanol. The prey remains were sorted and stored in the collection of the Prey Identification Service (PIDS) at the Port Elizabeth Museum, South Africa.

The individual cephalopod lower and upper beaks (both non-eroded and eroded) were identified to the lowest taxonomic level possible with reference to keys in Clarke (1986),

Juvenile SES cephalopod diet

updated with descriptions in Cherel (2020) and Xavier and Cherel (2021) and a reference collection at PIDS. Within each SES stomach content, the minimum number of individual cephalopods per taxa was determined as followed: upper and lower beaks were paired by size within taxa, each pair representing one individual, and each unpaired beak represented a different individual. The percentage numerical abundance (%NA), the number of each cephalopod taxa present in both stomach contents combined, was then calculated. The lower rostral length (LRL) of each intact lower beak, and the upper rostral length of each intact upper beak were measured to the nearest 0.01 mm with a digital Vernier caliper. The LRLs were then used in allometric equations given in Xavier and Cherel (2021) and Jackson et al. (1997) to estimate mantle length (mm) and wet weight (g).

Finally, a literature survey was done to gather prey remain studies conducted on SES in the Southern Ocean. Extensive improvements and updates of the classification and identification of Southern Ocean cephalopod species from beaks have recently been published (Cherel 2020); all identifications were thus updated with this new classification as much as possible.

Results and discussion

The stomachs of both juvenile male SES contained a combined total of 137 accumulated cephalopod beaks (corresponding to a minimum of 87 individuals), a very digested unidentified crustacean, and no recognizable fish remains. Cephalopod beaks were subsequently identified to 18 taxa (14 of it to species level) that represented nine families of decapods (Online Resource 1). At the family level, the Onychoteuthidae was the most abundant (28.7%), followed by the Brachioteuthidae (21.8%), Neoteuthidae (12.6%) and Histioteuthidae (9.2%) (Online Resource 1). *Slosarczykovia circumantarctica* (Brachioteuthidae) was the most abundant species (19.5%) followed by *Batoteuthis skolops* (Batoteuthidae) at 12.6% (Online Resource 1). Estimated mantle lengths of ingested cephalopods ranged from 5.2 cm (*S. circumantarctica*) to 39.9 cm (*Moroteuthopsis ingens*) corresponding to wet weights from 3 g to 2.6 kg (Online Resource 1). The cephalopod species consumed had a circumpolar distribution characteristic of the Antarctic and Polar Frontal zones and were also found in more restricted areas further north up to the sub-Antarctic zone (Cherel 2020). Most foraging of juvenile SES from Marion Island occurs in the aforementioned areas (between 43°S and 56°S) especially in the area west of Marion Island (Tosh et al. 2012).

Juvenile SES cephalopod diet

Cephalopod remains in SES stomach contents have been published for nine populations, including the present study (Online Resource 1). The squid *Moroteuthopsis longimana* (previously *Kondakovia longimana*), was previously isolated from the stomach of a SES at Marion Island (Ryan and Bester 2008). Whereas *S. circumantarctica* is commonly taken by SES from Heard Island (Green and Burton 1993; Slip 1995), Macquarie Island (Green and Burton 1993; van den Hoff 2004; Field et al. 2007), South Georgia (Rodhouse et al. 1992) and the South Shetland islands (Piatkowski et al. 2002; Daneri et al. 2015; Burdman et al. 2015), it has not as yet been recorded for the South Orkney islands (Clarke and MacLeod 1982) and East Antarctica (van den Hoff et al. 2003) (Online Resource 1). On the other hand, *B. skolops* has only been recorded in very low number in the diet of SES at South Georgia (Rodhouse et al. 1992). It is likely that beaks identified as *Psychroteuthis glacialis* by Slip (1995) at Heard Island included beaks of both *Mastigoteuthis psychrophila* and *B. skolops*, but the relative proportions of the two species remain unknown (Cherel 2020)(Online Resource 1). Given that *B. skolops* presents a circumpolar distribution in the Antarctic and Polar Frontal zones, it is surprising that it has not been recorded from SES more widely in the Southern Ocean (e.g., Macquarie and King George islands).

Cephalopods comprise a large proportion of the diet in some seals, but no seal is a specialist cephalopod feeder, with elephant seals the only seals that are regular squid eaters (Klages 1996). Similar to juvenile SES (n = 32) which were stomach lavaged successfully at King George Island, South Shetland islands (Burdman et al. 2015), there was a total absence of fish remains in the stomach contents of the two juvenile seals (this study). However, SES are predominant squid and fish eaters (Laws 1956; de Bruyn et al. 2016), and the differential retention of squid beaks and fish otoliths in stomachs (Tollit et al. 1997; Harvey and Antonelis 1994), is likely to have biased the actual composition of the SES diet. Furthermore, only one crustacean was isolated, although crustaceans were, for example, more conspicuous in the stomach contents of male juvenile (< 3 years) and sub-adult (4 – 7 years) SES in East Antarctica (Burton and van den Hoff 2002; van den Hoff et al. 2003). Moreover, diet composition may differ between sites, season, age group, sex (Online Resource 1) and with differences in diving behaviour (e.g., benthic versus pelagic) of SES from different populations (James et al. 2012). In addition, studies on SES are based, amongst others, on stomach lavage (Daneri et al. 2000; van den Hoff 2004), stomachs collected from sacrificed animals (Clarke and MacLeod 1982; Green and Burton 1993), natural mortalities and stable isotopic compositions of this top predator and potential prey (Cherel et al. 2008), all of which can produce different outcomes.

Juvenile SES cephalopod diet

Previous attempts to isolate prey hard remains from SES stomachs at Marion Island entailed (a) examining natural mortalities, and (b) a pilot study on stomach lavage of live, immobilised individuals (Bester et al. 2011). Natural mortalities rarely delivered any positive results, presumably because the morbid SES were fasting on land, and perhaps had been fasting for some time before hauling out. Similarly, the low percentage of SES stomachs that were found to contain prey suggested that most of those SES hauled out in the Vincennes Bay region, East Antarctica, had time to digest and defecate all their prey parts before sampling (van den Hoff et al. 2003).

Without any information on SES diet from Marion Island, an earlier attempt to calculate annual food consumption of SES here (Condy 1981) relied on published dietary information from SES populations elsewhere in the Southern Ocean. More recently, stable isotope analyses of SES vibrissae from Marion Island predicted that up to 76% of juvenile SES diet comprised crustaceans, followed by myctophid fish (Lübcker et al. 2017). It did, however, also indicate that the Ommastrephid *Martialia hyadesi* (not isolated in the present study, but commonly taken by SES at other islands; Online Resource 1) and the Onychoteuthid *M. longimana* showed up in the stable isotope analyses as it did in the stomach contents (this study). In addition, although mesopelagic fish and squid dominated juvenile (1 – 3 years old) SES stomach lavage samples at Macquarie Island (Online Resource 1), the stable isotope composition of their sampled vibrissae also emphasized the contribution of crustaceans to their diet (Walters et al. 2014).

The differences in the aforementioned results obtained from the two methods are not entirely unexpected as squid beaks tend to accumulate in seal stomachs (Croxall 1993; Field et al. 2007) and clearly bias stomach content analyses towards prey with indigestible hard parts (e.g., Bester and Laycock 1985; Harvey and Antonelis 1994; Ferreira and Bester 1999; Field et al. 2007). In addition, only accumulated squid beaks were found, and no fresh prey, probably because of the quick digestion of approximately 13 hours in SES (Krockenberger and Bryden 1994) and the likely long haul-out period in winter (Carrick et al. 1962; Wilkinson and Bester 1990). Nevertheless, stomach lavage as methodology to study the diet of elephant seals still provides important diet information. Although stable isotope compositions provide longer-term data, it is without the taxonomic and/or numerical resolution (Hobson et al. 1997) of stomach content analyses. Therefore, all avenues of sample collection and analyses should be explored to

Juvenile SES cephalopod diet

portray SES diet composition, as there is no single ideal way to present the results of seal dietary studies (Croxall 1993).



Fig. 1. Location of Marion Island and the islands and continents in the Atlantic and Indian sectors of the Southern Ocean which are mentioned in the text. SAF: Sub-Antarctic Front (dashed line); APF: Antarctic Polar Front (black line); PFZ: Polar Frontal Zone; AZ: Antarctic Zone; Isl: Island; isl: islands. Oceanic fronts follow Park and Durand (2019) and Park et al. (2019). Map built using SMap r package (Maschette et al. 2019)

Conclusions

Cephalopods feature in the diet of juvenile SES at Marion Island. The SI analyses of vibrissae of SES (Lübcker et al. 2017) that are routinely collected within the MIMMP (<https://www.marionseals.com/>) need to be continued, and the current stable isotope analyses of dentinal growth layer groups in fur seal teeth (Pretorius 2020) extended to SES following Martin et al. (2011). Employing alternative methods, such as DNA sequencing of scat samples, together with the traditional analyses would allow for the determination of species, sex and age together with prey identification (Reed et al. 1997; King et al. 2008; Emami-Khoyi et al. 2016; Xavier et al. 2018) that would otherwise be unknown. However, the process is costly and the samples need to be collected soon after the food was ingested (Deagle et al. 2005). (Fig. 1)

Author Contributions

MNB sacrificed the SES under permit and collected the prey samples from their stomachs and deposited these at the PIDS, Port Elizabeth Museum. MNB and MC sourced relevant scientific literature, MC identified the prey items, summarised the findings together with published SES diet studies elsewhere, and prepared the map. MNB drafted the first version of the manuscript. Both authors read, edited and approved the final manuscript.

Acknowledgements

We thank Steve Kirkman for his original work at Marion Island and his attempts to secure dietary samples from SES through stomach lavage. The late Grant Craig ably assisted in the field during the Marion 33 (1976/77) expedition. The late Norbert Klages from the Prey Identification Service (PIDS), Port Elizabeth Museum, sorted and stored the prey remains of the two juvenile SES. Greg Hofmeyr from the Port Elizabeth Museum at Bayworld facilitated the loan. We thank Yves Cherel for his advice in the identification of one of the beaks. Logistic support at Marion Island was provided by the then South African Department of Transport (SADT), within the South African National Antarctic Programme. Two reviewers provided insightful comments on the manuscript for which we are grateful.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: Field procedures in 1976 were approved by the Director-General, SADT, under advice from the South African Scientific Committee for Antarctic Research, pursuant to the provisions of the South African Sea Bird and Seals Protection Act, 1973 (Act 46 of 1973), and the Convention for the Conservation of Antarctic Seals of 1972. No formal animal ethics committee existed at the University of Pretoria in 1976.

Data Availability

The stomach content data, together with appropriate species identification, has been entered into an Excel file. This data base is available upon request.

References

- Bester MN, Bloomer JP, Bartlett PA et al (2000) Final eradication of feral house cats *Felis catus* from Marion Island. *S Afr J Wildl Res* 30:53-57. <https://hdl.handle.net/10520/EJC117086>
- Bester MN, de Bruyn PJN, Oosthuizen WC et al (2011) The Marine Mammal Programme at the Prince Edward Islands: 38 years of research. *Afr J Mar Sci* 33:511-521. <https://doi.org/10.2989/1814232X.2011.637356>
- Bester MN, Laycock PA (1985) Cephalopod prey of the sub-Antarctic fur seal, *Arctocephalus tropicalis*, at Gough Island. In: Siegfried WR, Condy P, Laws RM (eds) Proceedings of the IVth SCAR Symposium on Antarctic Biology. Springer-Verlag, Berlin, pp 551-554
- Block BA, Jonsen ID, Jorgensen SJ et al (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86-90. <https://doi.org/10.1038/nature10082>

Juvenile SES cephalopod diet

- Bonner WN (1993) Killing methods. In: Laws RM (ed) Antarctic seals: research methods and techniques. Cambridge University Press, Cambridge, pp 155–160
- Burdman L, Daneri GA, Negrete J et al (2015) Cephalopoda as prey of juvenile Southern elephant seals at Isla 25 de Mayo/King George, South Shetland Islands. *Iheringia, Sér Zool* 105(1):12-19. <https://doi.org/10.1590/1678-4766201510511219>
- Burton H, van den Hoff J (2002) Humans and the southern elephant seal *Mirounga leonina*. *Aust Mammal* 24:127–139. <https://doi.org/10.1071/AM02127>
- Carrick R, Csordas SE, Ingham SE, Keith K (1962) Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *CSIRO Wildl Res* 7:119-160. <https://doi.org/10.1071/CWR9620119>
- Cherel Y (2020) A review of Southern Ocean squids using nets and beaks. *Mar Biodiv* 50:98
doi: 10.1007/s12526-020-01113-4
- Cherel Y, Ducatez S, Fontaine C et al (2008) Stable isotopes reveal the trophic position and meso-pelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Mar Ecol Prog Ser* 370:239–247. <https://doi.org/10.3354/meps07673>
- Clarke MR (1986) A handbook for the identification of cephalopods beaks. Clarendon Press, Oxford
- Clarke MR, MacLeod N (1982) Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. *Brit Antarct Surv Bull* 57:27-31
- Condy PR (1979) Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.), at Marion Island. *S Afr J Zool* 14:95–102.
https://hdl.handle.net/10520/AJA00445096_1208
- Condy PR (1981) Annual food consumption, and seasonal fluctuations in biomass of seals at Marion Island. *Mammalia* 45:21–30. <https://doi.org/10.1515/mamm.1981.45.1.21>

Juvenile SES cephalopod diet

- Constable AJ, Melbourne-Thomas J, Corney SP et al (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob Chang Biol* 20:3004-3025. <https://doi.org/10.1111/gcb.12623>
- Croxall JP (1993) Diet. In: Laws RM (ed.) *Antarctic seals: research methods and techniques*. Cambridge University Press, Cambridge, pp 268–290
- Daneri GA, Carlini AR, Rodhouse PGK (2000) Cephalopod diet of the southern elephant seal, *Mirounga leonina*, at King George Island, South Shetland Islands. *Antarct Sci* 12:16–19. <https://doi.org/10.1017/S0954102000000031>
- Daneri GA, Carlini AR, Marschoff ER et al (2015) The feeding habits of the Southern elephant seal, *Mirounga leonina*, at Isla 25 de Mayo/King George Island, South Shetland Islands. *Polar Biol* 38:665-676. <https://doi.org/10.1007/s00300-014-1629-0>
- Deagle BE, Tollit DJ, Jarman SN et al (2005) Molecular scatology as a tool to study diet: analysis of prey DNA in scats from captive Steller sea lions. *Mol Ecol* 14:1831-1842. <https://doi.org/10.1111/j.1365-294X.2005.02531.x>
- De Bruyn PJN, Bester MN, Oosthuizen WC et al (2016) A conservation assessment of *Mirounga leonina*. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (eds) *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, pp 1-6
- Emami-Khoyi A, Hartley DA, Paterson AM et al (2016) Mitochondrial DNA structure and colony expansion dynamics of New Zealand fur seals (*Arctocephalus forsteri*) around Banks Peninsula. *NZ J Zool* 43:322-335. <https://doi.org/10.1080/03014223.2016.1179649>
- Ferreira SM, Bester MN (1999) Chemical immobilisation, physical restraint, and stomach lavaging of fur seals (*Arctocephalus* spp.) at Marion Island. *S Afr J Wildl Res* 29:55–61. <https://hdl.handle.net/10520/EJC117076>

Juvenile SES cephalopod diet

- Field IC, Bradshaw CJA, Burton HR, Hindell MA (2007) Differential resource allocation strategies in juvenile elephant seals in the highly seasonal Southern Ocean. *Mar Ecol Prog Ser* 331:281–290. <https://doi.org/10.3354/meps331281>
- Green K, Burton HR (1993) Comparison of the stomach contents of southern elephant seals, *Mirounga leonina*, at Macquarie and Heard islands. *Mar Mamm Sci* 9:10–22. <https://doi.org/10.1111/j.1748-7692.1993.tb00422.x>
- Harvey JT, Antonelis GA (1994) Biases associated with non-lethal methods of determining the diet of northern elephant seals. *Mar Mamm Sci* 10:178-187. <https://doi.org/10.1111/j.1748-7692.1994.tb00259.x>
- Hindell MA, McMahon CR, Bester MN et al (2016) Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere* 7(5):e01213. <https://doi.org/10.1002/ecs2.1213>
- Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Mar Mamm Sci* 13:114–132. <https://doi.org/10.1111/j.1748-7692.1997.tb00615.x>
- Jackson GD, Buxton NG, George MJA (1997) Beak length analysis of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) from the Falkland Islands region of the Patagonian shelf. *J Mar Biol Assoc UK* 77:1235-1238. <https://doi.org/10.1017/S0025315400038765>
- James BS, McIntyre T, Tosh CA et al (2012) Inter-population differences in diving behaviour of adult male southern elephant seals (*Mirounga leonina*). *Polar Biol* 35:1759-1766. <https://doi.org/10.1007/s00300-012-1214-3>
- King RA, Read DS, Traugott M, Symondson WOC (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. *Mol Ecol* 17:947-963. <https://doi.org/10.1111/j.1365-294X.2007.03613.x>

Juvenile SES cephalopod diet

- Klages NTW (1996) Cephalopods as prey. II. Seals. *Philos Trans R Soc B* 351:1045–1052. <https://doi.org/10.1098/rstb.1996.0092>
- Krockenberger MB, Bryden MM (1994) Rate of passage of digesta through the alimentary tract of southern elephant seals (*Mirounga leonina*) (Carnivora: Phocidae). *J Zool* 234:229-237. <https://doi.org/10.1111/j.1469-7998.1994.tb06071.x>
- Laws RM (1956) The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Falklands Isl Depend Surv Sci Rep* 13:1–88
- Lea M-A, Cherel Y, Guinet C, Nichols PD (2002) Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. *Mar Ecol Prog Ser* 245:281-297. <https://doi.org/10.3354/meps245281>
- Lübcker N, Reisinger RR, Oosthuizen WC et al (2017) Low trophic level diet of juvenile southern elephant seals *Mirounga leonina* from Marion Island: a stable isotope investigation using vibrissal regrowths. *Mar Ecol Prog Ser* 577:237-250. <https://doi.org/10.3354/meps12240>
- Martin C, Bentaleb I, Steelandt S, Guinet C (2011) Stable carbon and nitrogen isotope variations in canine dentine growth layers of Kerguelen southern elephant seals. *Mar Ecol Prog Ser* 439:295–305. <https://doi.org/10.3354/meps09331>
- Maschette D, Sumner M, Raymond B (2019) SOMap: Southern Ocean maps. Version 0.5.0 <https://github.com/AustralianAntarcticDivision/SOMap>
- Park Y-H, Durand I (2019) Altimetry-derived Antarctic Circumpolar Current fronts. SEANOE. <https://doi.org/10.17882/59800>
- Park Y-H, Park T, Kim T-W et al (2019) Observations of the Antarctic Circumpolar Current over the Udintsev Fracture Zone, the narrowest choke point in the Southern Ocean. *J Geophys Res Oceans* 124:4511-4528. <https://doi.org/10.1029/2019JC015024>

Juvenile SES cephalopod diet

- Piatkowski U, Vergani DF, Stanganelli ZB (2002) Changes in the cephalopod diet of southern elephant seal females at King George Island, during El Niño-La Niña events. *J Mar Biol Assoc UK* 82:913-916. <https://doi.org/10.1017/S0025315402006343>
- Pretorius LE (2020) Effect of sex and ontogeny on the trophic ecology of Southern Ocean fur seals. MSc Dissertation, University of Pretoria, Pretoria
- Reed JZ, Tollit DJ, Thompson PM, Amos W (1997) Molecular scatology: the use of molecular genetic analysis to assign species, sex and individual identity to seal faeces. *Mol Ecol* 6:225–234. <https://doi.org/10.1046/j.1365-294X.1997.00175.x>
- Reisinger R, Raymond B, Hindell M et al (2021) Habitat model forecasts suggest potential redistribution of marine predators in the southern Indian Ocean. *Div Dist* 28:142–159. <https://doi.org/10.1111/ddi.13447>
- Rodhouse PG, Arnbom T, Fedak MA, Yeatman J, Murray AWA (1992) Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can J Zool* 70:1007–1015. <https://doi.org/10.1139/z92-14>
- Ryan PG, Bester MN. 2008. Pelagic predators. In: Chown SL, Froneman PW (eds) *The Prince Edward Islands: land-sea interactions in a changing ecosystem*. Sun Media, Stellenbosch, pp 121–164
- Slip DJ (1995) The diet of southern elephant seals (*Mirounga leonina*) from Heard Island. *Can J Zool* 73:1519–1528. <https://doi.org/10.1139/z95-18>
- Tollit DJ, Steward MJ, Thompson PM et al (1997) Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Can J Fish Aquat Sci* 54:105-119. <https://doi.org/10.1139/f96-264>
- Tosh CA, de Bruyn PJN, Steyn J et al (2015) The importance of seasonal sea surface height anomalies for foraging juvenile southern elephant seals. *Mar Biol* 162:2131–2140. <https://doi.org/10.1007/s00227-015-2743-4>

Juvenile SES cephalopod diet

Tosh CA, Steyn J, Bornemann H et al (2012) Marine habitats of juvenile southern elephant seals from Marion Island. *Aquat Biol* 17:71–79. <https://doi.org/10.3354/ab00463>

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Phil Trans R Soc B* 362:2351–2365. <http://doi.org/10.1098/rstb.2006.1953>

Van den Hoff J (2004) Comparative study of the cephalopod prey of Patagonian toothfish (*Dissostichus eleginoides*) and southern elephant seals (*Mirounga leonina*) near Macquarie Island. *Polar Biol* 27:604–612. <https://doi.org/10.1007/s00300-004-0628-y>

Van den Hoff J, Burton H, Davies R (2003) Diet of male southern elephant seals (*Mirounga leonina* L.) hauled out at Vincennes Bay, East Antarctica. *Polar Biol* 26:27–31. <https://doi.org/10.1007/s00300-002-0447-y>

Walters A, Lea M–A, van den Hoff J et al (2014) Spatially explicit estimates of prey consumption reveal a new krill predator in the Southern Ocean. *PLoS One* 9:e86452. <https://doi.org/10.1371/journal.pone.0086452>

Wilkinson IS, Bester MN (1990) Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *J Zool Lond* 222:591–600. <https://doi.org/10.1111/j.1469-7998.1990.tb06016.x>

Xavier JC, Cherel Y, Medeiros R et al (2018) Conventional and molecular analysis of the diet of gentoo penguins: contributions to assess scats for non-invasive penguin diet monitoring. *Polar Biol* 41:2275–2287. <https://doi.org/10.1007/s00300-018-2364-8>

Xavier JC, Cherel Y (2021) *Cephalopod Beak Guide for the Southern Ocean: an update on taxonomy*. British Antarctic Survey, Cambridge, UK