1	Fish prey of sub-Antarctic fur seals Arctocephalus tropicalis at the
2	Tristan da Cunha Islands, South Atlantic Ocean
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14	
15	Abstract
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17	Some top predator populations in the South Atlantic and South Indian oceans are in decline,
18	presumably contingent upon reduced food availability, precipitated by climate change. This
19	phenomenon impacts on the positions of major ocean frontal zones which are hypothesised to act
20	as natural dispersal borders for fish in the Southern Ocean. We investigate this hypothesis by
21	establishing the vertebrate diet of sub-Antarctic fur seals, Arctocephalus tropicalis, at Tristan da
22	Cunha Island (37°15'S 12°25'W) and Gough Island (40°19'S, 9°57'W), South Atlantic Ocean. The
23	diet of these island populations, located on either side of the Subtropical Convergence, are
24	compared with published dietary information from populations further south on islands located
25	within the Polar Frontal Zone. To this end fur seal scats were collected and analysed for remains
26	of hard parts from prey in 2012-2013. The myctophid fish Gymnoscopelus piabilis,
27	Protomyctophum tenisoni and Symbolophorus barnardi predominated in the diet. Lampichthys
28	gemellarii, Myctophum aurolaternatum, S. barnardi and the Diaphus genus are recorded for the
29	first time in the diet of A. tropicalis. Sub-Antarctic fur seal populations clustered around the
30	Subtropical Convergence (~41°40'S), compared with those in the Polar Frontal Zone (~47°25' to

~50°47'), showed a considerable difference in the myctophid fish prey taken. The latitudinal
 differences in the fish diet of sub-Antarctic fur seals support suggestions that major frontal zones
 act as natural dispersal borders for fish in the Southern Ocean.

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35 Key words: *A. tropicalis*, climate change, diet, myctophid fish, frontal zones, foraging range 36

37 Introduction

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39 The Southern Ocean is undergoing substantial changes associated with anthropogenically driven 40 climate change (Turner et al. 2014). Southern Ocean ecosystems are under pressure from resource 41 exploitation and climate change, and information on the foraging behaviour of marine predators is 42 needed to identify regions that should be considered for protection (Hindell et al. 2020; Requena 43 et al. 2020). Sub-Antarctic fur seal populations (Hofmeyr et al. 2016) primarily occur at the Tristan 44 da Cunha Islands (South Atlantic Ocean) and at Amsterdam and Saint Paul Islands (South Indian 45 Ocean) which are clustered around the Subtropical Convergence (Deacon 1982; Beauplet et al. 46 2004; Requena et al. 2020), and the Prince Edward Islands and Îles Crozet (South Indian Ocean), together with Macquarie Island (South Pacific Ocean), which are located within the Polar Frontal 47 48 Zone, bound by the Subantarctic Front to the north and the Antarctic Polar Front to the south 49 (Koubbi 1993; Moore et al. 1999; Ansorge and Lutjeharms 2007).

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51 The Tristan da Cunha (TdC) islands (Fig. 1A) are home to more than 63% of the global population 52 of sub-Antarctic fur seals (Hofmeyr et al. 2016). The overwhelming majority breeds on Gough 53 Island (Bester et al. 2006), the southernmost and most isolated island in the archipelago at $40^{\circ}19$ 'S, 54 9°57'W (Fig. 1B). Much smaller numbers of seals breed at the three northern islands, centered on 55 37°04'S, 12°18'W (Fig. 1B): Tristan da Cunha (TdC), Inaccessible and Nightingale islands (Bester 56 et al. 2019). The northern islands of the Tristan da Cunha group and the southernmost Gough 57 Island (GI) belong to different oceanographic systems (Requena et al. 2020), separated by the 58 Subtropical Convergence Front. The northern islands lie in the warm temperate realm of the South 59 Central Atlantic Gyre, whereas GI is in the Subtropical Convergence Zone, with colder water all 60 year round (Requena et al. 2020).

62 Nothing is known about the fish diet of sub-Antarctic fur seals at the TdC islands, with the 63 exception of an earlier study based on stomach samples, which were skewed towards hard to digest prey items retained in stomachs. Cephalopods therefore appeared to dominate the diet, but the fur 64 65 seals also took bony fish (Bester and Laycock 1985). Opportunistic and pelagic foragers, sub-Antarctic fur seals are known to feed on a variety of myctophid and notothenid fish, cephalopods, 66 67 and small numbers of crustaceans throughout their range (Hofmeyr et al. 2016). They also kill and 68 feed on northern rockhopper penguins *Eudyptes moseleyi* at Amsterdam Island (Paulian 1964; 69 Tollu 1974) and the TdC northern islands (Bester et al. 2020), and perhaps at GI (Ryan and Kerr 70 2012).

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This study aims to (a) provide preliminary information on the fish diet of sub-Antarctic fur seals from scats collected at the TdC islands, including GI, and (b) using published accounts, comment on the latitudinal variation in the diet of the species. Relatively small sample sizes, spread over two years and various seasons (see methods and results below), prevented us from exploring any detailed spatio-temporal variation in prey taken, and by inference, preferred foraging areas. Here we simply list the species of fish prey taken by the sub-Antarctic fur seals from TdC and GI for comparison, as well as with other conspecific populations, in a latitudinal context.

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80 Methods

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Hard parts from prey found in scat samples of marine predators are the best possible approach to
study diet in a non-invasive and relatively easy way, despite the biases (Dellinger and Trillmich
1988; Arim and Naya 2003; Casper et al. 2004).

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Scats were collected opportunistically (2012-2013) from two southeast coast beaches (Tumbledown and Seal beaches) on GI, as well as from the only colony of sub-Antarctic fur seals on TdC at Seal Bay on the south coast. Scat collections were broadly assigned to seasons that were delineated based on the seasonal cycle of the fur seals; 1) breeding and pupping season in late spring-early summer (October to January), 2) post-breeding moult and lactation in late summermid autumn (February to May), and 3) late lactation in winter (June to September) following Bester
(1981), Kerley (1983), Bester and Bartlett (1990) and Luque et al. (2007).

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Of all scats collected, only those scats containing fish prey hard parts (sagittal otoliths) were included for comparison. Otoliths too eroded to be identified were excluded from analyses. Scats were individually processed (see Makhado et al. 2013) and the percentage frequency of occurrence (%FO) of fish hard parts was expressed as the number of times each species appeared within all scats containing otoliths, while percentage numerical abundance (%NA) was the number of otoliths of each fish species present in all scats.

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101 A seasonal comparison of prey species taken (this study) and the calculation of the percentage 102 mass of prey species (see Makhado et al. 2013) was not possible due to the small sample sizes, 103 and the strong bias against large prey (Arim and Naya 2003) which may be taken seasonally. Such 104 a change in diet from small to large prey is associated with a large increment in the incidence of 105 empty scats in pinnipeds (Naya et al. 2002), which therefore introduces a bias against larger prey 106 species occurring in scats. Also, less than the minimum number (n = 94) of scats were collected 107 which would allow existing differences (over time and between areas) to be statistically detected, 108 nor the minimum number (n = 59) of scats necessary to identify principal prey remains occurring 109 in >5% of scats (Trites and Joy 2005). Although the latter do not represent a general rule for all 110 pinniped dietary studies, it was decided to do a basic comparison of prey taken by sub-Antarctic 111 fur seals at TdC island and GI. The most important prey was nominally identified as those with 112 %NA > 10.0% following Reisinger et al. (2018).

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114 **Results**

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A total of 49 scats were collected at TdC in late spring-early summer and winter, while 34 scats were collected at GI in late spring-early summer, late summer-mid autumn and in winter. Of the 49 scats collected from TdC, 10 contained no otoliths, and of the 34 scats collected from GI, 19 contained no otoliths. A total of 749 and 493 identifiable otoliths were removed from scats collected at TdC and GI respectively during the whole study period (Table 1). These were identified to species (n = 13) and to genera only (n = 4), with a further six unknown genera appearing in the scat samples.

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Three species predominated namely *G. piabilis*, *P. tenisoni* and *S. barnardi*. Symbolophorus sp.
mostly occurring in scats from GI (Table 1). Symbolophorus barnardi were found in 46.7% and
43.6% of the scats containing otoliths at GI and TdC respectively (Table 1). *Gymnoscopelus piabilis* (31.2%) and *P. tenisoni* (39.1%) showed the highest %NA in fur seal scats from TdC, *G. piabilis* being also abundant at GI (41.0%) (Table 1).
Of the minor prey species in this study, *Diaphus* sp., *Gymnoscopelus bolini*, *Lampichthys*

procerus, Metelectrona ventralis, Myctophum aurolaternatum, Scopelosaurus ahlstromi and Symbolophorus boops only occurred in scats from GI, whereas G. fraseri, L. gemellarii and Protomyctophum sp. only were only present in scats from TdC. Electrona carlsbergi and G. nicholsi featured at both GI and TdC.

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137 Discussion

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139 The lanternfish Symbolophorus barnardi, Lampichthys gemellarii, Myctophum aurolaternatum 140 and the Diaphus genus (Myctophidae) consumed by sub-Antarctic fur seals from TdC and GI 141 (Table 1) has not previously been recorded in their diet anywhere The closely related L. procerus 142 are taken in small numbers at GI, Amsterdam Island (Beauplet et al. 2004) and at Marion Island 143 (de Bruyn et al. 2009; Reisinger et al. 2018) while *M. phengodes* was one of four major prey 144 species of sub-Antarctic fur seals at Amsterdam Island (Beauplet et al. 2004). The Symbolophorus 145 genus has previously been recorded in diets of sub-Antarctic fur seals at Amsterdam Island, 146 although not identified to species level (Beauplet et al. 2004). Very few S. boops were recorded at 147 GI, and elsewhere only in small numbers from Marion Island (Reisinger et al. 2018). Many 148 Symbolophorus sp. otoliths were, however, severely digested or broken, making their identification 149 challenging. Hence the species S. boops and S. barnardi might have had a much larger contribution 150 to the diet of the fur seals at GI.

Eight of the myctophid species, *G. bolini*, *G. fraseri*, *L. gemellarii*, *L. procerus*, *M. ventralis*, *M. aurolaternatum*, *S. ahlstromi* and *S. boops*, were present exclusively at either TdC or GI. This is likely an artefact of the small sample sizes and seasonal effects. These islands are situated only 380 km apart, a distance regularly covered by SAFS at Amsterdam and Marion islands (Beauplet et al. 2004; de Bruyn et al. 2009) and at the TdC islands (MNB unpubl. data). Furthermore, the foraging ranges of the TdC and GI fur seal populations overlap (Requena et al. 2020; MNB, unpubl. data).

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160 Considering only the prey species that could be identified to species level, although many could 161 not, the most important prev of sub-Antarctic fur seals at both GI and TdC combined, nominally 162 identified as those with %NA > 10.0%, was G. piabilis (35.9%), followed by P. tenisoni (27.86%) 163 and finally S. barnardi (10.79%). This is in contrast to Amsterdam Island where Symbolophorus 164 sp. (22.6% compared to 25.35% for all Symbolophorus spp. combined at GI), outstripped three other major species (Beauplet et al. 2004). None of the aforementioned three major species 165 166 occurred in scats on the TdC islands, nor at any other sub-Antarctic island in the Southern Ocean 167 (e.g., Robinson et al. 2002; Luque et al. 2007; Makhado et al. 2013; Reisinger et al. 2018).

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169 Similar to the present study, G. piabilis was, on average, the most important prey (24.49% to 170 26.2%) at Marion Island in some years (Makhado et al. 2006; Reisinger et al. 2018), and second only to G. fraseri (both species > 25%) at Îles Crozet (Luque et al. 2007). The second most 171 172 important species *P. tenisoni* (this study), occasionally featured strongly at Marion Island (17.0%, 173 Reisinger et al. 2018). Other minor species ($\leq 10\%$ NA) taken at TdC islands (Table 1) such as 174 G. fraseri invariably were present in seal scats from Marion Island at between 11.21-16.9% 175 (Klages and Bester 1998; Makhado et al. 2013; Reisinger et al. 2018), and as high as 33.13% in 176 some winters (de Bruyn et al. 2009). Gymnoscopelus nicholsi and Electrona carlsbergi may be 177 important (between 10.0% and 22.0%) at Marion Island in some years (de Bruyn et al. 2009; 178 Reisinger et al. 2018), while G. bolini may outstrip (~28%) all of the abovementioned species in 179 other years (de Bruyn et al. 2009). The staple diet of sub-Antarctic fur seals at Macquarie Island, 180 E. subaspera at 94.0% NA (Robinson et al. 2002), is also found at Marion Island usually in small 181 numbers (Klages and Bester 1998; de Bruyn et al. 2009; Makhado et al. 2013; Reisinger et al.

182 2018) but has not been recorded at the TdC islands (this study) and Amsterdam Island (Beauplet183 et al. 2004).

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185 Clearly, geographical position of island breeding colony sites has an impact on the diet of sub-186 Antarctic fur seals in the Southern Ocean. Metelectrona ventralis, for example, is distributed from 36°S to 51°S latitude (Smale et al. 1995) and taken by SAFS at both temperate (this study) and 187 188 sub-Antarctic islands (e.g. Klages & Bester 1998; Luque et al. 2007). On the other hand, the most 189 species rich myctophid genus, *Diaphus*, include pseudoceanic warm-water species as well as cool 190 temperate, oceanic species, which are generally found north of 38°S off South Africa (Prosch et 191 al. 1989; Hulley and Lutjeharms 1995). Myctophum aurolaternatum frequents the warm Agulhas 192 current and Lampichthys gemellarii are found in tropical and subtropical waters off the southern 193 African coast (Smale et al. 1995). Lampichthys procerus is found in the region of, or slightly to 194 the north of the Subtropical Convergence (Hulley 1981). Scopelosaurus ahlstromi too is found in 195 tropical and subtropical waters circum-globally while Symbolophorus barnardi is a subtropical 196 species (Hulley 1981). Symbolophorus sp., found in the diet of SAFS at Amsterdam Island 197 (Beauplet et al. 2004) and the TdC islands, do not appear at more southerly islands due to its 198 distribution not extending beyond ~30°S (Smale et al. 1995).

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200 The Subtropical Convergence acts as a northern border for many myctophid distributions (Smale 201 et al. 1995). TdC, GI and Amsterdam Island are all closely associated with the Subtropical 202 Convergence (Beauplet et al. 2004; Requena et al. 2020) and it is therefore expected that diets of 203 sub-Antarctic fur seals would be more similar at these localities. With the exception of S. boops, a 204 semi-subantarctic species that is known to occur in colder waters south of the Subtropical 205 Convergence and north of the Subantarctic Front (Hulley 1981), the abovementioned warm-water 206 and cool-temperate species are not found at sub-Antarctic islands. Therefore, major frontal zones 207 such as the Subantarctic Front possibly act as natural dispersal borders for fish in the Southern 208 Ocean (Andrew et al. 1995; Smale et al. 1995; this study).

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Studies of the diet of top predators that act as sentinel species which can indicate an ecosystem response to changing environmental conditions (Hazen et al. 2019), need to factor in their foraging

212 range. Scopelosaurus sp., predominantly warm temperate ocean species, were unexpectedly also

213 identified as prev of sub-Antarctic fur seals at Marion Island (Reisinger et al. 2018) and Île de la 214 Possession, Îles Crozet (Luque et al. 2007), in particular, which lie well south of the Subtropical 215 Convergence. Scopelosaurus ahlstromi specifically are only found north of the Subtropical 216 Convergence (Smale et al. 1995) but appeared in scats at Marion Island (Reisinger et al. 2018). 217 This would result from the foraging range of sub-Antarctic fur seals from GI (Requena et al. 2020) 218 and Marion Island (de Bruyn et al. 2009; Wege et al. 2019) that includes areas to the north of the 219 Subtropical Convergence. Small-scale foraging areas of sub-Antarctic fur seals from Marion 220 Island during winter were even located to the north of 38°S latitude (Wege et al. 2019).

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223 Conclusions

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225 In general, the sub-Antarctic fur seal populations of the TdC islands, clustered around the 226 Subtropical Convergence, show diets broadly similar to the more southern populations at Îles 227 Crozet, Macquarie Island and Marion Island which all lie within the Polar Frontal Zone. The 228 myctophids Gymnoscopelus, Electrona and Protomyctophum are found in scats collected at all 229 islands with breeding populations of sub-Antarctic fur seals, affirming the importance of 230 myctophids in the diet of sub-Antarctic fur seals. The differences that exist relates to the 231 taxonomical composition of myctophid fish at the species level. The different fish prey species 232 distribution, as well as their presence in the diet of sub-Antarctic fur seals would indicate a higher 233 dependency on the latitudinal rather than on the longitudinal position of the islands (Andrew et al. 234 1995; Robinson et al. 2002; this study).

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236 Climate change and the continual southward movement of the Antarctic Polar Frontal Zone 237 (Deacon 1982; Ansorge et al. 1999), could have consequences for foraging strategies of top 238 predators in the Southern Ocean. Climate change here includes a robust warming at the sub-239 Antarctic and mid-latitude islands, most pronounced in austral summer (Richard et al. 2012). 240 Populations at different islands are expected to have different response times to change depending 241 on their proximity to the changing fronts. Colonies of sub-Antarctic fur seals at islands associated 242 with the Subtropical Convergence could possibly reveal the effects of warming waters and 243 southward movements of prey earlier than those island populations further south. This is consistent with observed or forecasted declines in abundance of other top predators in the Southern Ocean at
the northern extent of their distributional ranges (e.g., Cristofari et al. 2018; Weimerskirch et al.
2018; Jones et al. 2020) likely attributed to distributional range shifts as a response to rapid climate
change by these species. Studying various predator populations throughout the Southern Ocean
will give a more accurate representation of diet composition and dependence of predators on
particular prey species, as it focuses on a broader ecological scale.

250 Author Contributions

MNB and PJNdB conceived and designed research, MNB wrote the manuscript, modelled on a
chapter in the M.Sc. dissertation of LJS. MNB and PJNdB conducted field work, and supervised
LJS who analysed data. TG provided logistic support and permitted the research. All authors
read and approved the manuscript.

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256

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266

267 Compliance with ethical standards

- 269 <u>Conflict of interest</u>: The authors declare that they have no conflict of interests.
- 270

<u>Ethical approval</u>: Field procedures were approved by the TdC Conservation Department and the
 Animal Ethics Committee of the University of Pretoria.

273 **References**

274

275	Andrew TG. Hecht T, Heemstra PC, Lutjeharms JRE (1995) Fishes of the Tristan da Cunha group
276	and Gough Island, South Atlantic Ocean. Icht Bull JLB Smith Inst Icht 63:1-41

Ansorge IJ, Lutjeharms JRE (2007) The cetacean environment off Southern Africa. In: Best PB
(ed) Whales and dolphins of the Southern African subregion. Cambridge University Press,
Cape Town, pp 5-13

Ansorge IJ, Froneman PW, Pakhomov EA, et al (1999) Physical-biological coupling in the waters
surrounding the Prince Edward Islands (Southern Ocean). Polar Biol 21:135-145

- Arim M, Naya DE (2003) Pinniped diets inferred from scats: analysis of biases in prey occurrence.
 Can J Zool 81:67–73
- Beauplet G, Dubroca L, Guinet 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. Mar Ecol Prog Ser 273:211–225
- 287
- Bester MN (1981) Seasonal changes in the population composition of the fur seal *Arctocephalus tropicalis* at Gough Island. S Afr J Wildl Res 11:49–55
- 290
- Bester MN, Bartlett PA (1990) Attendance behaviour of Antarctic and Subantarctic fur seal
 females at Marion Island. Antarct Sci 2:309–312
- 293
- Bester MN, Dilley BJ, Davies D, Glass T (2020) Sub-Antarctic fur seals depredate northern
 rockhopper penguins at Nightingale Island, Tristan da Cunha. Polar Biol 43(7):925-927
- Bester MN, Laycock PA (1985) Cephalopod prey of the Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient

299	cycles and food webs. Proceedings of the 4th SCAR symposium on Antarctic Biology.
300	Springer-Verlag. Berlin, pp 551–554
301	
302	Bester MN, Wege M, Glass T (2019) Increase of sub-Antarctic fur seals at the Tristan da Cunha
303	Islands. Polar Biol 42:231-235
304	
305	Bester MN, Wilson JW, Burle M-H, Hofmeyr GJG (2006) Population trend of Subantarctic fur
306	seals at Gough Island. S Afr J Wildl Res 36(2):191-194
307	
308	Casper RM, Gales NJ, Hindell MA, Robinson SM (2006) Diet estimation based on an integrated
309	mixed prey feeding experiment using Arctocephalus seals. J Exp Mar Ecol 328:228-239
310	
311	Cristofari R, Liu X, Bonadonna F, et al (2018) Climate-driven range shifts of the king penguin in
312	a fragmented ecosystem. Nat Clim Change 8:245–251
313	
314	Deacon GER (1982) Physical and biological zonation in the Southern Ocean. Deep Sea Res 29:1-
315	15
316	
317	de Bruyn PJN, Tosh CA, Oosthuizen WC, et al (2009) Bathymetry and frontal system interactions
318	influence seasonal foraging movements of lactating Subantarctic fur seals from Marion
319	Island. Mar Ecol Prog Ser 394:263–76
320	
321	Dellinger T, Trillmich F (1988) Estimating diet composition from scat analysis in otariid seals
322	(Otariidae): is it reliable? Can J Zool 66:1865–1870
323	
324	Hazen EL, Abrahms B, Brodie S, et al (2019) Marine top predators as climate and ecosystem
325	sentinels. Front Ecol Evol 17:565-574
326	
327	Hindell MA, Reisinger RR, Ropert-Coudert Y, et al (2020) Tracking of marine predators to protect
328	Southern Ocean ecosystems. Nature 580:87–92
329	

330	Hofmeyr GJG, de Bruyn PJN, Wege M, Bester MN (2016) A conservation assessment of
331	Arctocephalus tropicalis. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-
332	Mostert HT (eds) The Red List of Mammals of South Africa, Swaziland and Lesotho. South
333	African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, pp 1-
334	6
335	
336	Hulley PA, Lutjeharms JRE (1995) The south-western limit for the warm-water, mesopelagic
337	ichthyofauna of the Indo-West Pacific: lanternfish (Myctophidae) as a case study. S Afr J
338	mar Sci 15:185-205
339	
340	Hulley PA (1981) Results of the research cruises of FRV 'Walther Herwig' to South America.
341	LVIII. Family Myctophidae. Arch Fisch Wiss 31:1–300
342	
343	Jones CW, Risi MM, Bester MN (2020) Local extinction imminent for southern elephant seals
344	Mirounga leonina at their northernmost breeding site, Gough Island - South Atlantic
345	Ocean. Polar Biol 43:893–897
346	
347	Kerley GIH (1983) Comparison of seasonal haulout patterns of fur seals Arctocephalus tropicalis
348	and A. gazella at the Prince Edward Islands Southern Ocean. S Afr J Zool 18:388–392
349	
350	Klages NTW, Bester MN (1998) Fish prey of fur seals Arctocephalus spp. at Subantarctic Marion
351	Island. Mar Biol 131:559–566
352	
353	Koubbi P (1993) Influence of the frontal zones on ichthyoplankton and mesopelagic fish
354	assemblages in the Crozet Basin (Indian sector of the Southern Ocean). Polar Biol 13:557-
355	564
356	
357	Luque SP, Arnould JPY, Miller EH, et al (2007) Foraging behaviour of sympatric Antarctic and
358	Subantarctic fur seals: does their contrasting duration of lactation make a difference? Mar
359	Biol 52:213–224
360	

Makhado AB, Bester MN, Somhlaba S, Crawford RJM (2013) The diet of the subantarctic fur seal
Arctocephalus tropicalis at Marion Island. Polar Biol 36:1607-1617
Moore JK, Abbott MR, Richman JG (1999) Location and dynamics of the Antarctic Polar Front
from satellite sea surface temperature data. J Geophys Res 104:3059-3073
Naya DE, Arim M, Vargas R (2002) Diet of South American fur seals (Arctocephalus australis)
in Isla de Lobos, Uruguay. Mar Mamm Sci 18:734–745
Paulian P (1964) Contribution á l'étude de l'otarie de l'Ile Amsterdam. Mammalia 28:3-146
Prosch RM, Hulley PA, Cruickshank RA (1989) Mesopelagic fish and some other forage species.
In: Payne AIL, Crawford RJM (eds) Oceans of life off Southern Africa. Vlaeberg
Publishers. Cape Town, pp. 130-135
Reisinger RR, Landman M, Mgibantaka N, et al (2018) Diet of sympatric Antarctic and
Subantarctic fur seals (Arctocephalus spp.) at sub-Antarctic Marion Island: overlap and
temporal variation. Polar Res 37:1, 1451142
Requena S, Oppel S, Bond AL, et al (2020) Marine hotspots of activity for threatened pelagic
megafauna in a large oceanic jurisdiction. Animal Cons 23(5): 585-596
Richard Y, Rouault M, Pohl B, et al (2012) Temperature changes in the mid- and high-latitudes of
the Southern Hemisphere. Int J Climatol https://doi.org/10.1002/joc.3563
Robinson SA, Goldsworthy SD, van den Hoff J, Hindell MA (2002) The foraging ecology of two
sympatric fur seal species, Arctocephalus gazella and Arctocephalus tropicalis, at
Macquarie Island during the austral summer. Mar Freshw Res 53:1071–1082
Ryan PG, Kerr J (2012) Is fur seal predation driving the decrease in northern rockhopper penguins
Eudyptes moseleyi at Gough Island? Mar Ornithol 40:69–71

393	Smale JM, Watson G, Hecht T (1995) Otolith atlas of Southern African marine fishes. Ichth
394	Monographs No1. JLB Smith Inst Ichth, Grahamstown, South Africa
395	
396	Tollu B (1974) L'Otarie de l'Ile Amsterdam, Arctocephalus tropicalis (Gray 1872). Thèse de
397	Doctorat de Troisième Cycle, Direction des Laboratoires Scientifiques, TAAF, Paris,
398	France
399	
400	Trites AW, Joy R (2005) Dietary analysis from fecal samples: how many scats are enough? J
401	Mamm 86:704–712
402	
403	Turner J, Barrand N, Bracegirdle T, Convey P, et al (2014) Antarctic climate change and the
404	environment: an update. Polar Rec 50(3):237-259
405	
406	Wege M, de Bruyn PJN, Hindell MA, et al (2019) Preferred, small-scale foraging areas of two
407	Southern Ocean fur seal species are not determined by habitat characteristics. BMC Ecol
408	19:36. https://doi.org/10.1186/s12898-019-0252-x
409	
410	Weimerskirch H, Le Bouard F, Ryan PG, Bost CA (2018) Massive decline of the world's largest

411 king penguin colony at Ile aux Cochons, Crozet. Antarct Sci 30:236–42

412 **Table 1:** Number of fish prey species otoliths (Num), the percentage frequency of occurrence 413 (%FO) and percentage numerical abundance (%NA) of each prey species collected in scats from 414 Gough Island (n = 15) and Tristan da Cunha (n = 39) in 2012-2013. Numbers in brackets are the 415 number of scats in which otoliths of each species were found. The most prevalent prey species in 416 the diet, nominally identified as those with %NA > 10.0% following Reisinger et al. (2018), at 417 one island (*), and at both islands (**), are indicated.

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Prey Species	Gough Island			Tristan da Cunha		
	Num	%FO	%NA	Num	%FO	%NA
Diaphus sp.	5 (1)	6.67	1.01	0 (0)	0.0	0.0
Electrona carlsbergi	49 (6)	40.00	9.94	3 (3)	7.69	0.40
Gymnoscopelus bolini	3 (1)	6.67	0.61	0 (0)	0.0	0.0
Gymnoscopelus fraseri	0 (0)	0.0	0.0	2 (2)	5.13	0.27
Gymnoscopelus nicholsi	9 (3)	20.0	1.83	55 (7)	17.95	7.34
Gymnoscopelus piabilis**	202 (12)	80.0	40.97	234 (8)	20.51	31.24
Gymnoscopelus sp.	1 (1)	6.67	0.20	31 (6)	15.38	4.14
Lampichthys gemellarii	0 (0)	0.0	0.0	3 (1)	2.56	0.40
Lampichthys procerus	1 (1)	6.67	0.20	0 (0)	0.0	0.0
Metelectrona ventralis	36 (9)	60.0	7.30	0 (0)	0.0	0.0
Myctophum aurolaternatum	3 (1)	6.67	0.61	0 (0)	0.0	0.0
Protomyctophum sp.	0 (0)	0.0	0.0	3 (3)	7.69	0.40
Protomyctophum tenisoni**	53 (10)	66.67	10.75	293 (8)	20.51	39.12
Scopelosaurus ahlstromi	3 (3)	20.0	0.61	0 (0)	0.0	0.0
Symbolophorus barnardi**	65 (7)	46.67	13.18	69 (17)	43.59	9.21
Symbolophorus boops	6 (2)	13.33	1.22	0 (0)	0.0	0.0
Symbolophorus sp.*	54 (4)	26.67	10.95	4(1)	2.56	0.53
Unidentified spp.	3 (1)	6.67	0.61	52 (25)	64.10	6.94
Total	493			749		

422 Fig. 1 A Position of the TdC islands in the South Atlantic Ocean. B The positions of the four
423 constituent islands of the TdC. The approximate position of the Subtropical Front is indicated on
424 both maps.



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