

Fish in the diet of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia during winter and spring

A.W. NORTH

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

Abstract: The occurrence of fish in the diet of the Antarctic fur seal (*Arctocephalus gazella*) at Bird Island, South Georgia was investigated by analysis of fish otoliths in scats (faeces) collected during late May to early November 1983. Of the 55 scats examined, 49 contained fish remains, and 45 contained fish otoliths. Ten fish species were represented by 415 otoliths, and 33 otoliths were too digested to be identified unequivocally. Fish size was estimated from otolith size based on published allometric equations. Four coastal notothenioid fishes dominated the fish component of the diet: *Champscephalus gunnari* and *Gobionotothen gibberifrons* each comprised about 40% of the total fish mass; *Chaeocephalus aceratus* was ranked third by mass and the smaller *Lepidonotothen larseni* occurred in one quarter of the scats but was of lower importance in terms of mass. The length-frequency distribution of *C. gunnari* landed by the commercial fishery in October 1982 to June 1983 is similar to that which comprised the bulk of the diet in the present study. Compared with recent studies on the fish component of the diet in the literature, the dominance of *C. gunnari* is generally similar, however, there was a greater proportion of *G. gibberifrons* during the 1983 winter and spring than reported for recent winters.

Received 26 October 1995, accepted 4 January 1996

Key words: *Arctocephalus*, *Champscephalus*, diet, fish, seal, South Georgia

Introduction

The diet of seals is difficult to quantify because they spend much of their time at sea. Analysis of seal scats (faeces) deposited ashore currently provides the least intrusive method to investigate their diet (see Croxall 1993). Seals have rapid digestion rates, and so when their scats are sampled the remains they contain probably only represent fish eaten during the last 24 h (Prime 1979). Care needs to be exercised in extrapolating from prey remains in the scat of predators to their diet. In particular, small specimens and species with small thin otoliths are likely to be under-represented because of differential digestion of the otoliths (da Silva & Neilson 1985, Jobling & Briebly 1986, Dellinger & Trillmich 1988, Croxall 1993 p. 282–285). However, Antarctic fish generally have moderately large otoliths (North *et al.* 1984, Hecht 1987, Williams & McEldowney 1990). These otoliths are partly digested by passage through Antarctic fur seals but many can nevertheless be identified and, after correction for digestion, used to give an estimate of fish size (North *et al.* 1983, Green *et al.* 1989, Reid 1995, Reid & Arnould 1996).

The South Georgia population of Antarctic fur seals has grown rapidly since the 1930s (Bonner 1968, Payne 1977) and in the late 1980s was still increasing at a rate of around 10% per year (Boyd 1993). In 1990/91, it comprised about 1 550 000 individuals and produced 96% of all Antarctic fur seal pups (Boyd 1993). The diet of fur seals at Bird Island, South Georgia contains Antarctic krill *Euphausia superba*, mackerel icefish *Champscephalus gunnari* and other fish and squid (Bonner 1968, Payne 1977, North *et al.* 1983,

Croxall & Pilcher 1984, Doidge & Croxall 1985, Boyd *et al.* 1991, Reid 1995, Reid & Arnould in press). The dominance of krill and icefish remains in the scats of Antarctic fur seals over much of the year indicates that they are likely to consume a large amount of these species annually (Doidge & Croxall 1985, Croxall *et al.* 1985, Laws 1985, Croxall *et al.* 1988, Reid 1995, Reid & Arnould 1996).

To assess the interactions between commercial fisheries and seals quantitative data is required on the fisheries, fish and seal populations and the diet of the seals (Harwood & Croxall 1988). At South Georgia in 1982/83, the fishery reported its biggest ever icefish catch of 128 000 t, and the estimated stock biomass of *C. gunnari* was around 250 000 t (CCAMLR 1990a, 1990b, 1992, 1994a, Kock 1992, fig. 70). Since 1990 the reported catches of *C. gunnari*, and their estimated stock biomass, have been less than 40 000 t (Kock 1992, CCAMLR 1994b). This decline of the *C. gunnari* population may have reduced their availability to the seals. Based on the winter diet of fur seals in 1992 and 1993, Reid (1995) has estimated that during recent winters the seals could have consumed more than four times the estimated biomass of the icefish stock. The seals also feed on the icefish in summer (Reid & Arnould 1996). Despite the pilot study by North *et al.* (1983) there are very few quantitative data on the diet of the seals prior to 1990. However, a fairly extensive set of scat samples collected between May and November 1983 was not completely analysed. This paper reports on the fish component of the seal diet based on these samples and compares the results with the more recent diet reported in the

literature. The aim was to determine if there has been any change in the fish species composition of the diet between 1983 and 1992/93.

Methods

Fur seal scats were collected between 31 May to 3 November 1983 from beaches close to the British Antarctic Survey (BAS) research station at Freshwater Bay, Bird Island, South Georgia (54°00'S, 38°03'W). Five to twelve scats were collected each month which gave a total of 55 scats. Samples collected during May to September were stored frozen at -20°C. Scats were soaked in detergent and disinfectant solution for 1–2 days, then gently sieved (0.5 mm mesh) under running freshwater, and all retained material was dried and thoroughly examined at ×6 magnification under a binocular microscope. Fish otoliths were measured using an eyepiece graticule and their outline drawn with the aid of a drawing tube. They were stored dry in labelled envelopes together with fish bones and teeth and squid beaks.

At the BAS laboratory in Cambridge, sagittal otoliths were identified by comparison with a reference collection. Fish species names are according to DeWitt *et al.* (1990). Otoliths of juvenile *Lepidonotothen larseni* are similar to those of a group of closely related species, although those of the adults are more distinct. In the samples the larger otoliths from this group were all identified as *L. larseni* and it was assumed that all otoliths in this group were probably of this species (see note in Table I). To predict fish size from otolith size previous studies have used one or several overall correction factors to compensate for the reduction in otolith length by digestion (North *et al.* 1983, Reid 1995). In the present study, each otolith was individually assessed to obtain the best estimate of reduction in otolith length by digestion. This subjective assessment was based on comparisons between

otoliths from scat samples with undigested otoliths in the BAS collection. Reduction in otolith length by digestion was assessed on a scale from 10% reduction (the least digested), in increments of about 2.5% reduction, to 20% reduction and more than 20% reduction. Otoliths apparently reduced by more than 20% in length were classed as unidentified teleost fish. Fish length and mass were estimated from otolith length, corrected for digestion (Table II). For comparability with Reid (1995), fish size was based on the relationships given in Hecht (1987), Williams & McEldowney (1990), North *et al.* (1983), Olsson & North (in press), and for *Gymnoscopelus fraseri* total mass (TM) was estimated from total length using the equation:

$$\log_{10} TM = -0.691 + 0.0153 \cdot TL$$

$$(r^2 = 0.86, n = 117,$$

$$\text{ranges: TL} = 68\text{--}101 \text{ mm, TM} = 2.1\text{--}7.0 \text{ g}$$

$$\text{(BAS unpublished data).}$$

Each fish has a pair of sagittal otoliths, and so, the fish mass estimated from the otoliths representing each species was divided by two. The otolith collection at BAS has been improved over the last decade, and so some otoliths that could not be identified by North *et al.* (1983) were re-examined. Squid lower beaks were identified by Dr P.G.K. Rodhouse (BAS) and their lower rostral length was used to estimate mantle length (see Clarke 1986, Rodhouse *et al.* 1987, 1992).

Data were analysed using the MINITAB statistical package (Ryan *et al.* 1985).

Results

Of the total of 55 scats collected between 31 May to 3 November, 45 contained a total of 448 fish otoliths. In addition, four scats contained fish remains (bones, teeth, scales) but no otoliths and one of these contained many bones

Table I. Number of otoliths (*n*) and % of total number (%), frequency of occurrence (FO) and % frequency of occurrence (%FO), estimated total mass (M) (corrected for otolith digestion) and % by mass (%M) for fish represented in the 45 scats containing otoliths that were collected during May to November 1983 at Bird Island, South Georgia.

Taxa	<i>n</i>	%	FO	%FO	M (g)	%M
<i>Champscephalus gunnari</i>	201	44.9	25	55.6	12704.3	39.8
<i>Lepidonotothen larseni</i> *	91	20.3	12	26.7	1506.0	4.7
<i>Gobionotothen gibberifrons</i>	55	12.3	11	24.4	11946.7	37.4
Unidentified teleost fish**	32	7.1	20	44.4	—	—
<i>Pseudochaenichthys georgianus</i>	26	5.8	4	8.9	1648.1	5.2
<i>Electrona antarctica</i>	22	4.9	5	11.1	144.1	0.5
<i>Chaenocephalus aceratus</i>	7	1.6	4	8.9	2855.1	9.0
<i>Muraenolepis microps</i>	4	0.9	2	4.4	1091.7	3.4
<i>Protomyctophum choriodon</i>	4	0.9	1	2.2	9.5	0.03
<i>Protomyctophum bolini</i>	3	0.7	1	2.2	3.1	0.01
<i>Krefflichthys anderssoni</i>	2	0.5	1	2.2	0.3	< 0.01
Channichthyidae sp.***	1	0.2	1	2.2	—	—
Total	448				31909	

* Mainly *L. larseni* but may include a very small proportion of *Lepidonotothen nudifrons*, *Gobionotothen marionensis* (= *Notothenia angustifrons*) and *Patagonotothen guntheri*; ** Too digested and eroded to be accurately identified but probably comprises in order of importance: *L. larseni*, *G. gibberifrons* and *M. microps*; *** Very digested.

Table II. Number of identified otoliths (*n*), mean estimated percent digested (%) ± standard deviation (sd) in the 45 scats containing otoliths that were collected during May to November 1983 at Bird Island, South Georgia.

Taxa	<i>n</i>	% ± sd
<i>Champscephalus gunnari</i>	201	16.1 ± 2.3
<i>Lepidonotothen larseni</i>	91	16.0 ± 1.6
<i>Gobionotothen gibberifrons</i>	55	17.2 ± 1.7
Myctophidae	31	16.3 ± 2.1
<i>Pseudochaenichthys georgianus</i>	26	18.7 ± 1.5
<i>Chaenocephalus aceratus</i>	7	17.9 ± 1.7
<i>Muraenolepis microps</i>	4	20.0 ± 0.0

probably from several fish. Ten fish species were represented by 415 otoliths (Table I); the remainder were so digested as to make identification uncertain. The range of estimated reduction in length of identified otoliths by digestion was between 10 to 20%, with mean values for each taxon between 16–20% (Table II).

The identified otoliths indicate that *C. gunnari* predominated by number and percent frequency of occurrence in the diet (Table I, Fig. 1). There were two peaks in the size-frequency distribution of *C. gunnari* at 125–175 mm total length (TL) and 225–325 mm TL, and the latter peak contributed most of the mass of this species to the diet (Fig. 2). *C. gunnari* and the humphead notothen *Gobionotothen gibberifrons* each comprised about 40% of the total fish mass. *G. gibberifrons* between 300–550 mm TL represented much of the mass, and the largest peak in numbers was around 375 mm TL (Fig. 3). The largest fish in the diet were *G. gibberifrons* and the blackfin icefish *Chaenocephalus*

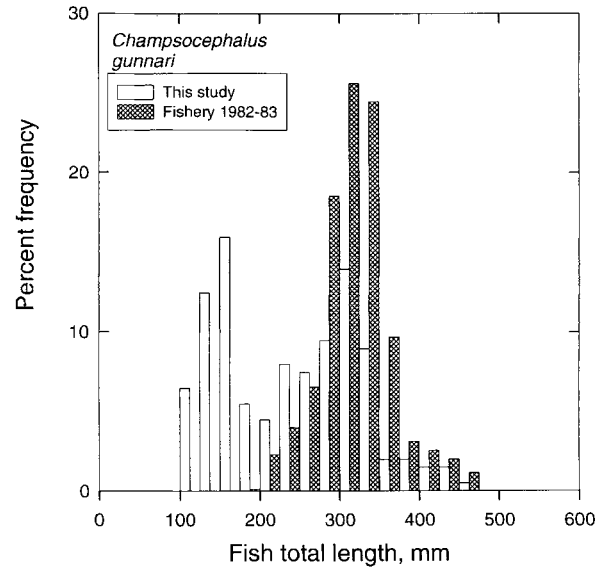


Fig. 2. Length frequency of *Champscephalus gunnari* in the diet of Antarctic fur seals at Bird Island, South Georgia during May to November 1983 and in the fishery at South Georgia during October 1982 to June 1983 (fishery data from Kock & Köster 1989).

aceratus, with maximum sizes of 540 mm and 534 mm TL, respectively (Table III). Only a few *C. aceratus* were found in scats but because of their large size the species was ranked third by mass in the diet. The nototheniid *L. larseni* occurred in moderate numbers and in about one quarter of the scats, although it was of minor importance in terms of mass because of its small size (75–200 mm TL) (Fig. 3). Other fish, which

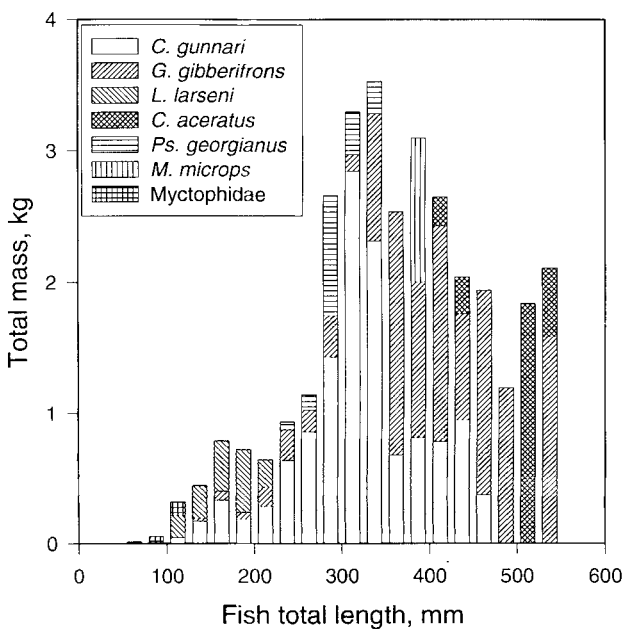


Fig. 1. Total mass of each fish taxa within each length-class in the diet of Antarctic fur seals at Bird Island, South Georgia during May to November 1983.

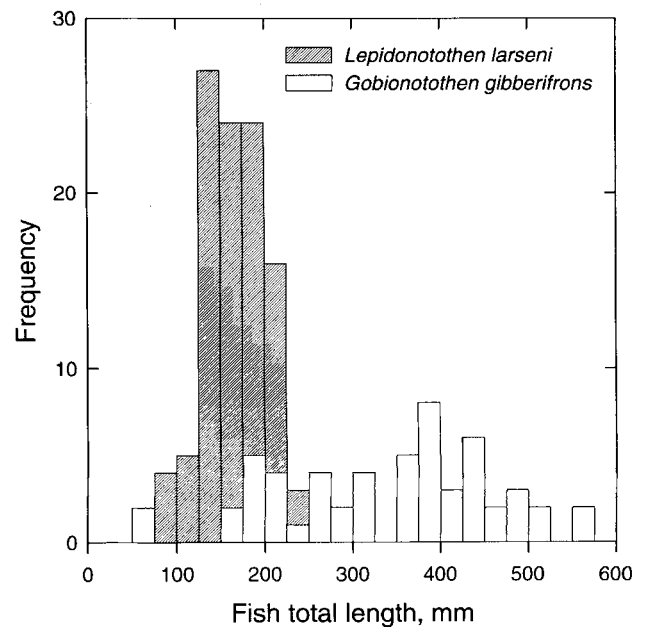


Fig. 3. Length frequency of *Lepidonotothen larseni* and *Gobionotothen gibberifrons* in the diet of Antarctic fur seals at Bird Island, South Georgia during May to November 1983.

Table III. Summary of fish total length (TL, mm) estimated from otolith length (corrected for otolith digestion) for fish represented in 45 fur seal scats during May to November 1983 at Bird Island, South Georgia.

Taxa	n	mean	median	sd	min	max
<i>Champscephalus gunnari</i>	201	238	238	86	100	460
<i>Lepidotothen larseni</i>	91	147	149	33	78	220
<i>Gobionotothen gibberifrons</i>	55	316	345	117	59	540
<i>Pseudochaenichthys georgianus</i>	26	288	289	24	241	348
<i>Electrona antarctica</i>	22	98	101	10	77	110
<i>Chaenocephalus aceratus</i>	7	493	511	45	414	534
<i>Muraenolepis microps</i>	4	383	383	7	375	391
<i>Protomyctophum choriodon</i>	4	71	73	5	65	75
<i>Protomyctophum bolini</i>	3	48	40	16	37	67
<i>Krefflichthys anderssoni</i>	2	—	—	—	33	33
Total	415	226	199	107	33	540

contributed 3–5% by mass, were the South Georgia icefish *Pseudochaenichthys georgianus* and the eel-cod *Muraenolepis microps*. Four species of lantern fishes (Myctophidae) made a very small contribution to the diet. Two lantern fish species represented the smallest fish of 33–37 mm TL.

Squid beaks were present in only two scats, suggesting that squid was of little importance in the diet. A scat from June contained four squid lower beaks representing *Martialia hyadesi* of 158–183 mm mantle length (mean 174.6 mm \pm 11.3 mm), one squid upper beak and 63 otoliths from *C. gunnari*. One scat from October contained a single squid upper beak and otoliths from *C. gunnari*, *L. larseni* and *P. georgianus*.

The otoliths reported by North *et al.* (1983) contained a further two lantern fish species. Otoliths denoted as species A by North *et al.* (1983) were those of the myctophid *Protomyctophum choriodon*, representing fish of 95.6–110 mm TL with a combined mass of 48 g. Six of the ten otoliths formerly identified as *Gymnoscopelus nicholsi* are probably those of *G. fraseri*. The revised length range of the *G. nicholsi* is 133–197 mm TL with a combined mass of 58 g. A size of 70–94 mm TL and a combined mass of 14 g is predicted for the *G. fraseri*.

Discussion

Faecal analysis may not be an appropriate method for determining the diet of some seal species where a large proportion of fish otoliths ingested is completely or severely digested (see Jobling & Breiby 1986, Reid 1995). In the present study, however, most scats contained otoliths and the majority (92.6%) of otoliths was less than 20% digested and could be identified, indicating that faecal analysis is a reasonable technique for assessing the diet of Antarctic fur seals (Reid 1995). Of the total number of otoliths recovered, the 33 otoliths (7.4%) that could not be confidently identified appeared to be dominated by well digested otoliths from *L. larseni* (Table I). This species is relatively small compared

with *C. gunnari* and *G. gibberifrons*. Therefore, although the unidentified otoliths may indicate a small underestimate in the mass of *L. larseni* in the diet they are unlikely to represent a substantial error in the overall contribution of fish by mass to the diet. Given that *C. gunnari* and *G. gibberifrons* each represented at least four times the mass of any of the other species in the diet it is reasonable to conclude that they dominated the fish component of the fur seal diet during the winter and spring of 1983.

Four studies have investigated fish otoliths in the scats of Antarctic fur seals at Bird Island. The pilot study by North *et al.* (1983) was during February–March 1983 (summer) on eight scats from immature bulls. The present study and the investigation by Reid (1995), during the 1992 and 1993 winters (May to September), both covered the non breeding period when most seals ashore were males (Duck 1990, Reid 1995). Reid & Arnould (1996) reported the diet of lactating females during summer (January–March) in four (1991–1994) breeding seasons. The results from these four studies are briefly compared.

The re-examination of the otoliths previously reported by North *et al.* (1983), adds two species of lanternfish to the diet, reduces the importance of *P. choriodon* (= species A) by mass, and increases the predominance of *C. gunnari* in terms of mass. By number, the same three fish species, *C. gunnari*, *G. gibberifrons* and *L. larseni* dominated the fish component of the male diet in summer, spring and winter (North *et al.* 1983, Reid 1995, this study). *C. gunnari* and *G. gibberifrons* were co-dominant by mass in the present study and each comprised about 40% of the fish mass. During the 1992 and 1993 winters, *C. gunnari* comprised 40–50% of the fish component of the diet, and *G. gibberifrons* only comprised one half to one third the mass of *C. gunnari* (Reid 1995). Therefore, the proportion of *C. gunnari* in the fish component of the diet of males was similar during 1983 and 1992/93, whereas that of *G. gibberifrons* was lower during 1992/93. This is unexpected because between 1982/83 and 1992/93 the stock biomass of *C. gunnari* has declined from 250 000 to < 40 000 t, and the biomass of *G. gibberifrons* has increased from about 12 000 t to between 25 000 and 30 000 t (Kock 1992, CCAMLR 1994b). *G. gibberifrons* contributed < 1% by mass to the diet of females, which was also dominated by *C. gunnari*, with *P. choriodon* ranked second in terms of numbers of otoliths but *L. larseni* ranked second by mass (Reid & Arnould 1996). Together these four studies indicate that *C. gunnari* comprises the bulk of the mass of fish in the diet of these fur seals.

The size-frequency distribution of *C. gunnari* in the present study and that of the large catch reported by the fishery at South Georgia during the period from October 1982 to June 1983 (Kock & Köster 1989) are shown together in Fig. 2. The seals took many fish less than 200 mm TL, but *C. gunnari* larger than this contributed most to the mass of the diet and to the catch of the fishery (Fig. 1). Reid (1995) made a similar comparison between the size of *C. gunnari* from a

groundfish survey in early 1991 (Everson *et al.* 1992) and those taken by the seals in the 1992 and 1993 winters. The *C. gunnari* taken by the seals and the survey were of a similar size-range and both included many fish larger than 200 mm TL. Potential competition between the seals and the fishery is likely because they both take the larger *C. gunnari*.

In conclusion, the fish component of the fur seal diet at South Georgia is dominated by *C. gunnari*, and there is no evidence for a reduction of this species in the diet between 1983 and 1992/1993. However, between 1982/83 and 1995 the population of fur seals at South Georgia has increased fourfold and there are presently in the region of 3 000 000 individuals (Boyd 1993, I.L. Boyd, personal communication 1995). Recent estimates of the stock of *C. gunnari* at the island have been low (Everson *et al.* 1994, CCAMLR 1994a). If the seal population continues to grow it is likely to have a major influence on local prey populations and the potential to compete with any fishery for *C. gunnari*. To clarify the interactions between the higher predators and the fisheries at South Georgia further studies are required on the foraging distribution, behaviour and diet of the seals, and the abundance and distribution of their potential prey.

Acknowledgements

I gratefully thank: John Croxall for his help throughout the work, Malcolm Liddle for collecting scat samples, Paul Rodhouse for identification of squid beaks and for providing relationships to predict squid length, Keith Reid for valuable information, suggestions and discussion, and Andrew Clarke, Inigo Everson, Ian Boyd, Kenneth Green and Graham Pierce for useful comments on the manuscript.

References

- BONNER, W.N. 1968. The fur seal of South Georgia. *British Antarctic Survey Scientific Reports*, No. 56, 81 pp.
- BOYD, I.L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science*, 5, 17–24.
- BOYD, I.L., LUNN, N.J., & BARTON, T. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology*, 60, 577–592.
- CCAMLR. 1990a. *Commission for the Conservation of Antarctic Marine Living Resources: Statistical Bulletin, Volume 1 (1970–1979)*. Hobart: CCAMLR, 61 pp.
- CCAMLR. 1990b. *Commission for the Conservation of Antarctic Marine Living Resources: Statistical Bulletin, Volume 2 (1980–1989)*. Hobart: CCAMLR, 109 pp.
- CCAMLR. 1992. *Commission for the Conservation of Antarctic Marine Living Resources: Statistical Bulletin, Volume 4 (1982–1991)*. Hobart: CCAMLR, 133 pp.
- CCAMLR. 1994a. *Commission for the Conservation of Antarctic Marine Living Resources: Statistical Bulletin, Volume 6 (1984–1993)*. Hobart: CCAMLR, 112 pp.
- CCAMLR. 1994b. *Commission for the Conservation of Antarctic Marine Living Resources: Report of the thirteenth meeting of the scientific committee*. Hobart: CCAMLR, 94 pp.
- CLARKE, M.R. 1986. *A handbook for the identification of cephalopod beaks*. Oxford: Clarendon Press, 273 pp.
- CROXALL, J.P. 1993. Diet. In LAWS, R.M., ed. *Antarctic Seals: research methods and techniques*. Cambridge: Cambridge University Press, 268–290.
- CROXALL, J.P. & PILCHER, M.N. 1984. Characteristics of krill *Euphausia superba* eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. *British Antarctic Survey Bulletin*, No. 63, 117–125.
- CROXALL, J.P., PRINCE, P.A. & RICKETTS, C. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., eds. *Antarctic Nutrient Cycles and Food Webs*. Berlin: Springer Verlag, 516–533.
- CROXALL, J.P., McCANN, T.S., PRINCE, P.A. & ROTHERY, P. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. In SAHRHAGE, D., ed. *Antarctic Ocean and Resources Variability*. Berlin: Springer-Verlag, 261–285.
- DA SILVA, J. & NEILSON, J.D. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 1439–1442.
- DELLINGER, T. & TRILLMICH, F. 1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? *Canadian Journal of Zoology*, 66, 1865–1870.
- DEWITT, H.H., HEEMSTRA, P.C. & GON, O. 1990. Nototheniidae Notothenis. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 279–331.
- DOIDGE, D.W. & CROXALL, J.P. 1985. Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. In SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., eds. *Antarctic Nutrient Cycles and Food Webs*. Berlin: Springer Verlag, 543–550.
- DUCK, C.D. 1990. Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South Georgia. *Journal of Zoology, London*, 222, 103–116.
- EVERSON, I., PARKES, G., KOCK, K.-H., CABELL, S., CIELNIASZEK, Z. & SZLAKOWSKI, J. 1992. Fish stock assessment survey in subarea 48.3. *Scientific Committee for the Conservation of Antarctic Marine Living Resources. Selected Scientific Papers 1991*, WG-FSA-91/14. Hobart: CCAMLR, 25–68.
- EVERSON, I., PARKES, G., KOCK, K.-H., GOSS, C., CIELNIASZEK, D., SZLAKOWSKI, J., DALY, H., ALLCOCK, L. & PILLING, G. 1994. Fish stock assessment survey in subarea 48.3. *Scientific Committee for the Conservation of Antarctic Marine Living Resources, WG-FSA-94/18*. Hobart: CCAMLR. [Unpublished.]
- GREEN, K., BURTON, H.R. & WILLIAMS, R. 1989. The diet of Antarctic fur seals *Arctocephalus gazella* (Peters) during the breeding season at Heard Island. *Antarctic Science*, 1, 317–324.
- HARWOOD, J. & CROXALL, J.P. 1988. The assessment of competition between seals and the commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Science*, 4, 13–33.
- HECHT, T. 1987. A guide to the otoliths of Southern Ocean fishes. *South African Journal of Antarctic Research*, 17, 1–87.
- JOBLING, M. & BRIEBY, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia*, 71, 265–274.
- KOCK, K.-H. 1992. *Antarctic fish and fisheries*. Cambridge: Cambridge University Press, 359 pp.
- KOCK, K.-H. & KÖSTER, F.-W. 1989. The state of exploited fish stocks in the Atlantic Sector of the Southern Ocean. *Mitteilungen aus dem Institut für Seefischerei der Bundesforschungsanstalt für Fischerei, Hamburg*, No. 46, 73 pp.
- LAWS, R.M. 1985. The ecology of the Southern Ocean. *American Scientist*, 73, 26–40.
- NORTH, A.W., CROXALL, J.P. & DOIDGE, D.W. 1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *British Antarctic Survey Bulletin*, No. 61, 27–37.

- NORTH, A.W., BURCHETT, M.S., GILBERT, C.J. & WHITE, M.G. 1984. Identification of fish from the Southern Ocean by means of otoliths. *British Antarctic Survey Bulletin*, No. 62, 83–94.
- OLSSON, C.O. & NORTH, A.W. In press. Diet of the King Penguin (*Aptenodytes patagonicus*) during three summers at South Georgia. *Ibis*.
- PAYNE, M.R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London*, B279, 67–79.
- PAYNE, M.R. 1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology, London*, 187, 1–20.
- PRIME, J.H. 1979. Observations on the digestion of some gadoid fish otoliths by a young common seal. *International Council for the Exploration of the Sea, Report No. CM 1979/N:14*. Copenhagen: ICES, 6 pp.
- REID, K. 1995. The diet of Antarctic fur seals *Arctocephalus gazella* during winter at South Georgia. *Antarctic Science*, 7, 241–249.
- REID, K. & ARNOULD, J.P.Y. 1996. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology*, 16, 105–114.
- RODHOUSE, P.G., CLARKE, M.R. & MURRAY, A.W.A. 1987. Cephalopod prey of the wandering albatross *Diomedea exulans*. *Marine Biology*, 96, 1–10.
- RODHOUSE, P.G., WHITE, M.G. & JONES, M.R.R. 1992. Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Marine Biology*, 114, 415–421.
- RYAN, B.F., JOINER, B.L. & RYAN, T.A. 1985. *Minitab Handbook*. Boston: PWS-Kent Publishing Company, 379 pp.
- WILLIAMS, R. & McELDOWNEY, A. 1990. A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. *ANARE Research Notes*, 75, 173 pp.