Chapter 1: General Introduction

1.1. INTRODUCTION

1.1.1. DESCRIPTION OF THE SPECIES UNDER STUDY

The Subantarctic fur seal (*Arctocephalus tropicalis*) and the Antarctic fur seal (*A. gazella*) were at first regarded as conspecifics and were both referred to as *A. gazella*. Later, they were separated into subspecies by King (1959a, 1959b) on the basis of cranial and dental characters, with *A. tropicalis gazella* denoted as the southern subspecies and *A. tropicalis tropicalis* as the northern subspecies. However, in a more recent review of the genus *Arctocephalus*, Repenning *et al.* (1971) distinguished between the two taxa at the species level.

External features, particularly pelage colour and flipper size, usually allow for distinction between adults of the two species (Condy 1978; Kerley 1985). The colour of the chest and face of *A. tropicalis* bulls is white to orange, the belly is brown to ginger and the rest of the body is dark grey to dark brown (Bester 1977). *Arctocephalus gazella* bulls have a silvery grey chest and neck with a slightly dark face and grey to dark brown body (Condy 1978). *Arctocephalus tropicalis* cows have a white to orange chest and face and their dorsal surface is grey to brown with a light brown to ginger belly, while *A. gazella* cows have a white to grey neck and chest, grey to brown dorsal surface and white to grey belly (Condy 1978). Further, *A. tropicalis* have short broad flippers compared to the long, slender appendages of *A. gazella* (Fig. 1 & 2). Also, the vocalizations of the two species differ (Condy 1978; St. Clair-Hill *et al.* 2001). Nevertheless, limited hybridisation between the two species does occur (Condy 1978; Kerley 1983; Hofmeyr *et al.* 1997).

Fig 1.1: *Arctocephalus tropicalis* bull at Marion Island.

Fig 1.2: *Arctocephalus gazella* bull at Marion Island.

1.1.2. GEOGRAPHICAL DISTRIBUTION

Most *A. gazella* breeding sites are to the south of the Antarctic Polar Front (APF). These include South Georgia (Bonner 1968), the South Orkney Islands (Laws 1973; Daneri & Coria 1992), the South Shetland Islands (Daneri & Carlini 1999), Bouvetøya (Kirkman *et al.* 2000) and Heard Island (Shaughessy 1993). *Arctocephalus tropicalis* typically breed to the north of the APF (Bester 1984; Hofmeyr *et al.* 1997) at Gough Island (Bester 1987), Amsterdam Island (Roux 1987), Tristan da Cunha (Bester 1980), St Paul Island (King 1983; Guinet *et al.* 1994) and the Prince Edward archipelago (Condy 1978; Kerley 1987). The two species breed sympatrically at three sites, each located just to the north of the APF, at Macquarie Island (Goldsworthy 1999), Îles Crozet (Guinet *et al.* 1994) and the Prince Edward Islands (Condy 1978). Recent estimates of population sizes and population trends over the entire range of the two species are shown in Tables 1.1 and 1.2, taken and updated from SCAR (2002).

1.1.3. EXPLOITATION

Both *A. tropicalis* and *A. gazella* were subjected to intense, uncontrolled harvesting from the 17th to 20th century. This resulted in severe reductions in the population numbers of each, and local extinctions at some breeding sites (Roux 1987; Shaughnessy & Fletcher 1987). Small populations of *A. tropicalis* survived at Gough Island (Bester 1987), Amsterdam Island (Roux 1987) and the Prince Edward archipelago (Kerley 1987). *Arctocephalus gazella* survived in severely reduced numbers at South Georgia (Bonner 1968). After the cessation of intensive exploitation, numbers of both species have increased often dramatically, and many islands have been re-colonised (Payne 1977; Bester 1987; Kerley 1987; Roux 1987; Guinet *et al.* 1994; Isaksen *et al.* 2000). The likely process of re-colonisation has been described by Wynen *et al.* (2000).

Table 1.1. Estimated sizes and trends of Antarctic fur seal (*Arctocephalus gazella*) populations.

Site	Pup numbers	Total population	Year of census	Mean annual rate of change	Reference
Macquarie Island	152^{a}		1999/00	increasing (1988/89 to 99/00)^{a}	Goldsworthy (pers. comm.)
	164^{a}		2001/02	increasing	Goldsworthy (pers. comm.)
Heard Island	1,012		2000/01	+ 20.1 % (1962/63 to 2000/01)	Goldsworthy (pers. comm.)
McDonald Island	100	300	1979/80	increasing	Johnstone (1982)
Îles Nuageuses (Îles Kerguelen)	5,000	?	2000	increasing	Lea (pers. comm.)
Courbet Peninsula (Îles Kerguelen)	1,500-1,700	? ?	2000	increasing	Lea (pers. comm.)
Ile de la Possession (Îles Crozet)	67	?	1992/93	+ 21.4% (1983 to 92)	Guinet *et al.* (1994)
Ile de la Possession (Îles Crozet)	234	?	1999/00	+ 16.9% (1992 to 1999)	Guinet (pers. comm.)
Marion Island	251^{b,c}	1,205^{d}	1994/95	+ 17% (1988/89 to 94/95)	Hofmeyr *et al.* (1997)
Prince Edward Island	400	2000^{i}	2001/02	Increasing + 16.2%	Bester *et al.* (submitted.)
Nyrøysa (Bouvetøya)	15,665	51,067	1998/99	+ 14%	Kirkman *et al.* (2000)
	15,692		2001/02	0 (1996/97 to 2001/02)	Norwegian Polar Institute - unpublished data
South Georgia		4,500,000 – 6,200,000^{f,g}	1999/00	+6% to 14% (1990/91 to 99/00)	Boyd (pers. comm.)
South Sandwich Islands	346		1997/98	stable	Boyd (pers. comm.)
South Orkney Islands	<1,000		1970/71	?	Laws (1973), Boyd (1993)
South Shetland Islands	10,057^{h}		2000/01	+ 0.9% (1995/96 to 01/02)	Goebel (pers. comm.)
Cape Shirreff (SSSI No32, S. Shetland Is.)	8,455		1999/00	+ 6%^{i} (1991/92 to 99/00)	Hucke-Gaete (pers. comm.), Vallejos *et al.* (press. Comm.)
	8,557	21,190	2001/02	4.6%^{i} (1992/93 to 2001/02)	Hucke-Gaete *et al.* (press. comm)

a - For populations of both *A. tropicalis* and *A. gazella*
b - Corrected for observer undercount
c - Corrected for precount mortality
d - Recalculated from population values in publication
e - Number of breeding females
f - Estimated from the number of breeding females
g - Standard deviation = 300,000
h - Standard error = 140
i - Calculated from pup counts

Table 1.2. Estimated sizes and trends of Subantarctic fur seal (*Arctocephalus tropicalis*) populations.

Site	Pup numbers	Total population	Year of census	Mean annual Rate of change	Reference
Macquarie Island	152[a]		1999/00	increasing (1988/89 to 99/00)[a]	Goldsworthy (pers. comm.)
Heard Island	1	13	2000/01	?	Goldsworthy (pers. comm.)
Ile Amsterdam	>9,638[b]		1992/93	+ 0.4% (1981/82 to 92/93)[e]	Guinet *et al.* (1994)
Ile Saint Paul	365		1992/93	+ 23.8% (1984/85 to 92/93)[e]	Guinet *et al.* (1994)
Ile de la Possession (Îles Crozet)	190		1990/91	+ 21.6% (1978-91)[e]	Guinet *et al.* (1994)
Ile de la Possession (Îles Crozet)	251		1999/00	+ 3.1% (1991-2000)[e]	Guinet (pers. comm.)
Marion Island	10,137[c,d]	55 000	1994/95	+ 1.8% (1988/89 to 94/95)	Hofmeyr *et al.* (1997)
Prince Edward Island	5,372[c,d] 15,000[f]	72 000	1988/89	+ 9.7% (1981/82 to 88/89) + 9.5% (1987/88 to 2000/01)	Wilkinson & Bester (1990) Bester (submitted)
Gough Island	>53,076[b,c,d]		1977/78	+ 14.9% (1955 to 1977/78)[e]	Bester (1987)
Tristan da Cunha	50	250	1993/94	Increasing	C. Glass (pers. comm.)
	?	700	1998/99	Increasing	C. Glass (pers. comm.)
Nightingale Island (Tristan da Cunha Group)	?	>500	1998/99	Increasing	C. Glass (pers. comm.)
Inaccessible Island (Tristan da Cunha Group)	>3	>200	1999/00	Increasing	P.G. Ryan (pers. comm.)

a - For populations of both *A. tropicalis* and *A. gazella*
b - Extrapolation based on a proportion of the total populated area
c - Corrected for observer undercount
d - Corrected for precount mortality
e - Recalculated from population values in publication
f – Extrapolated from peak adult male counts, and known adult male:pup ratios, in breeding colonies

1.2. THE FUR SEAL POPULATIONS OF MARION ISLAND

1.2.1. POPULATION SIZES AND TRENDS

Censuses of the *A. tropicalis* and *A. gazella* populations at Marion Island in 1994/95 yielded estimates of 50 000 and 1200 individuals of each species respectively (Hofmeyr *et al.* 1997). This meant that the *A. tropicalis* population had increased at a rate of 2.0% per annum since 1988/89, and *A. gazella* had increased at a rate of 17% over the same period (Hofmeyr *et al.* 1997). The latter species had possibly entered the rapid recolonisation phase of population growth by this stage, whereas the former appeared to be entering a maturity phase (Hofmeyr *et al.* 1997).

1.2.2. HABITAT PREFERENCES AND SEASONAL HAULOUT PATTERNS

On land there is some ecological separation between the two species, mainly as a result of different breeding habitat preferences (Condy 1978, Kerley1983) and the timing of the seasonal breeding haulout (Kerley 1983,1987). Generally, *A. tropicalis* prefer the exposed, irregular, west coast of the island, whereas *A. gazella* prefer sheltered beaches on the south and east coasts (Condy 1978; Kerley 1987; Hofmeyr *et al.* 1997). *Arctocephalus tropicalis* breed mostly among jumbled rocks, while *A. gazella* prefer pebble beaches or vegetated areas (Kerley 1984).

There is also some variation in the seasonal haulout pattern of the two species. *Arctocephalus gazella* adult females give birth over a shorter time period and, on average, ten days earlier than *A. tropicalis* at Marion Island where the median birth dates of the two species were found to be 6 and 17 December, respectively (Kerley 1983). In addition, *A. gazella* pups grow rapidly (Kerley 1984) and are weaned at about 112 days of age (in early March) at Marion Island. *Arctocephalus* *tropicalis* pups have a slower growth rate and more protracted lactation period. They are weaned at ±300 days of age (September-October) (Kerley 1984). Thus *A. gazella* adult females and underyearlings are absent from the island during winter, while *A. tropicalis* adult females and pups are present then (Kerley 1983, 1984). Adult male *A. tropicalis* are rarely present on the island during winter and are rarely seen in August, September and October, but their numbers increase rapidly after October to the breeding season peak between mid–December and early January (Kerley 1983). The haulout pattern of *A. gazella* adult males is similar but their breeding season peak is a little earlier in December. In contrast, the autumnal moulting peak of *A. gazella* males and females are a little later than that of *A. tropicalis* (Kerley 1983).

Genetic factors consistent with the climatic conditions typical of the historical home ranges of each species have been suggested to influence the timing of the terrestrial phases of the annual cycles of the two species (Kerley 1983, 1984). Although there is some temporal separation between the haulouts of *A. tropicalis* and *A. gazella* at Marion Island, there is extensive overlap (Kerley 1984). Adult males of both species are ashore while females of both species are in oestrus. Thus the temporal variation in the annual haulout cycle is not sufficient to prevent hybridisation (Kerley 1983, 1984).

1.2.3. PELAGIC MOVEMENT OF THE FUR SEALS

Seals using a single haulout site may forage in spatially distinct (horizontally, vertically or both) areas, depending on their species, sex and age (Pierce & Boyle 1991) and the time of the year (Green *et al.* 1997). Lactating *A. gazella* females forage relatively close to their natal island during lactation, as they are restricted by the need to periodically return to land to suckle their pups (Green *et al.* 1997), presumably the case at Marion Island too (Bester & Bartlett 1990).

Lactating *A. tropicalis* females at Marion Island spend a mean of approximately 25.5 and 7.0 days at sea per trip during winter and summer respectively (Kirkman *et al.* 2002), but comparable periods to lactating *A. gazella* females (5.2 days) at sea during summer foraging trips (Bester & Bartlett 1990; Kirkman *et al.* 2002).

Despite fidelity to their natal islands, *A. tropicalis* and *A. gazella* range widely, occasionally visiting the continents abutting on the southern ocean, and even the pack ice region (Bester 1989; Payne 1979; Bester & Odendaal 2000). Lactating *A. gazella* mothers have been recorded foraging at a distance of about 200 km from their natal island (Green *et al.* 1997; Lea *et al.* 2002) while *A. tropicalis* females from Amsterdam Island, from the first trip to the last trip, foraged at a distance of between 60 km to 130 km south of Amsterdam Island respectively (Georges *et al.* 2000[a]). At Macquarie Island, there was no obvious separation of foraging areas between *A. gazella* and *A. tropicalis* adult females, with individuals from both species travelling for about 2.5 hours before foraging commenced (Goldsworthy *et al.* 1997). Apart from foraging trip duration, nothing is known about the foraging areas of the two species at Marion Island (Bester 1989; Bester & Bartlet 1990), but their foraging behaviour is likely to be related to prey concentration and movement (Green 1997; Boyd *et al.* 1998).

1.3. RATIONALE AND OBJECTIVES OF THE STUDY

Fur seals often defecate soon after arrival on land, enabling the study of their diet through the identification of undigested prey parts in their faeces. Such studies permit investigation of their role in the marine ecosystem, and enable quantification of seal-fisheries biological interactions. The latter is in many instances of considerable economic, as well as ecological, significance

(Pierce & Boyle 1991). With this in mind, it is important to monitor the diets of the two fur seal species at Marion Island, particularly in view of their continued population increase (Hofmeyr *et al.* 1997), the advent of commercial fishing in the Prince Edward Islands Exclusive Economic Zone (PEIEEZ), and the overall decline in population numbers of elephant seals, *Mirounga leonina* (Condy 1978; Bester 1980; Bester & Wilkinson 1994; Pistorius *et al.* 1999) and rockhopper penguins (*Eudyptes chrysocome*) with which the fur seals share the island habitat.

The present study is a continuation of the long term Prince Edward Islands Pinniped Monitoring Programme, and expands upon a previous description (1989 to 1994) of the fish diet of the two species at Marion Island by Klages & Bester (1998).

The main objectives of this study are addressed in the following key questions, based on scat sampling:

- What are the main dietary items of the fur seals at Marion Island?
- Does the diet of fur seals vary according to season?
- Does the diet of fur seals vary interannually?
- How do the diets of the two fur seals species compare by composition, season and year?
- What prey biomass are estimably required to support the fur seal populations at the current population levels?

The chapters of this thesis were largely prepared as separate manuscripts. This has led to a certain amount of repetition, which is unavoidable.

Chapter 2. Study Area

2.1. GEOGRAPHICAL DESCRIPTION

Marion Island and Prince Edward Island together constitute the Prince Edward archipelago. The islands are located in the southern Indian Ocean, where they were formed some 1.2 million years ago in a series of volcanic events. They lie approximately 2180 km to the south east of Cape Town, 2300 km to the north of Antarctica (Chown & Hänel 1998) and 950 km to the west of the closest landmass, Îles Crozet (Fig 1.3).

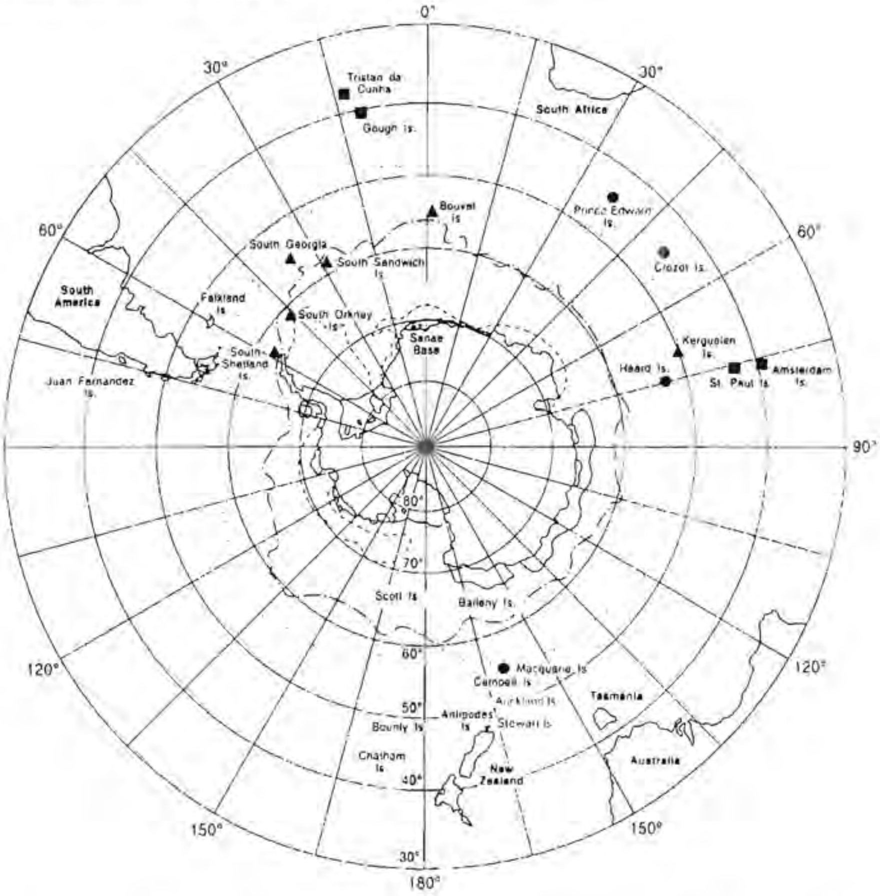

Fig. 1.3: Distribution of breeding haulout sites for *Arctocephalus tropicalis* (squares), *A. gazella* (triangles) and sites at which the two species breed sympatrically (circles). The mean positions of the A.P.F (….), the winter pack ice limit (_. _. _) and the summer pack ice limit (_ _ _) are indicated.

2.2. TOPOGRAPHICAL FEATURES

Marion Island has an area of about 290 km^2, and a relatively unindented coastline of approximately 72 km (Fig 1.4). The volcanic origin of the Prince Edward Islands, their isolation from other landmasses and the effect of the surrounding ocean on their climate and biota make the Prince Edward Islands truly oceanic by nature (Verwoed 1971; Crafford *et al.* 1986).

Marion Island has several distinct physiographic regions; a central highland, an island slope divided into relatively high and relatively low-lying areas and a coastal plain separated in places from the island slope by an escarpment (Crafford *et al.* 1986). Beaches of an extremely irregular nature characterise the exposed west coast of the island while most of the beaches on the leeward east coast are composed of small rounded rocks, stones and pebbles (Wilkinson *et al.* 1987). The leeward east coast beaches have a flat, regular appearance and seals can gain access to inland moulting areas along the drainage lines (Wilkinson 1992) while the western coastline is dominated by a rugged, jumbled rock type of beach with an irregular profile and limited stacking of rocks (Kerley 1984).

2.3. CLIMATE

Marion Island has a cool, extremely oceanic climate with the following outstanding features:

- predominantly strong westerly winds, regularly gale force, high relative humidity, with little annual or diurnal variation from 80%,

- relatively low mean temperature showing little diurnal and seasonal variation (mean air temperature of the coldest and warmest months are 3.2 ^{0}C and 7.3 ^{0}C respectively),

- high degree of cloudiness with only 20 - 33% of the possible amount of sunshine reaching the island surface (Schulze 1971), and

- abundant precipitation in the form of rain, snow or graupel (ice rain) with a mean annual precipitation of 2576 mm (Schulze 1971). Mean air and sea temperatures have been increasing steadily since 1949 when the first measurements were done (Smith 1992).

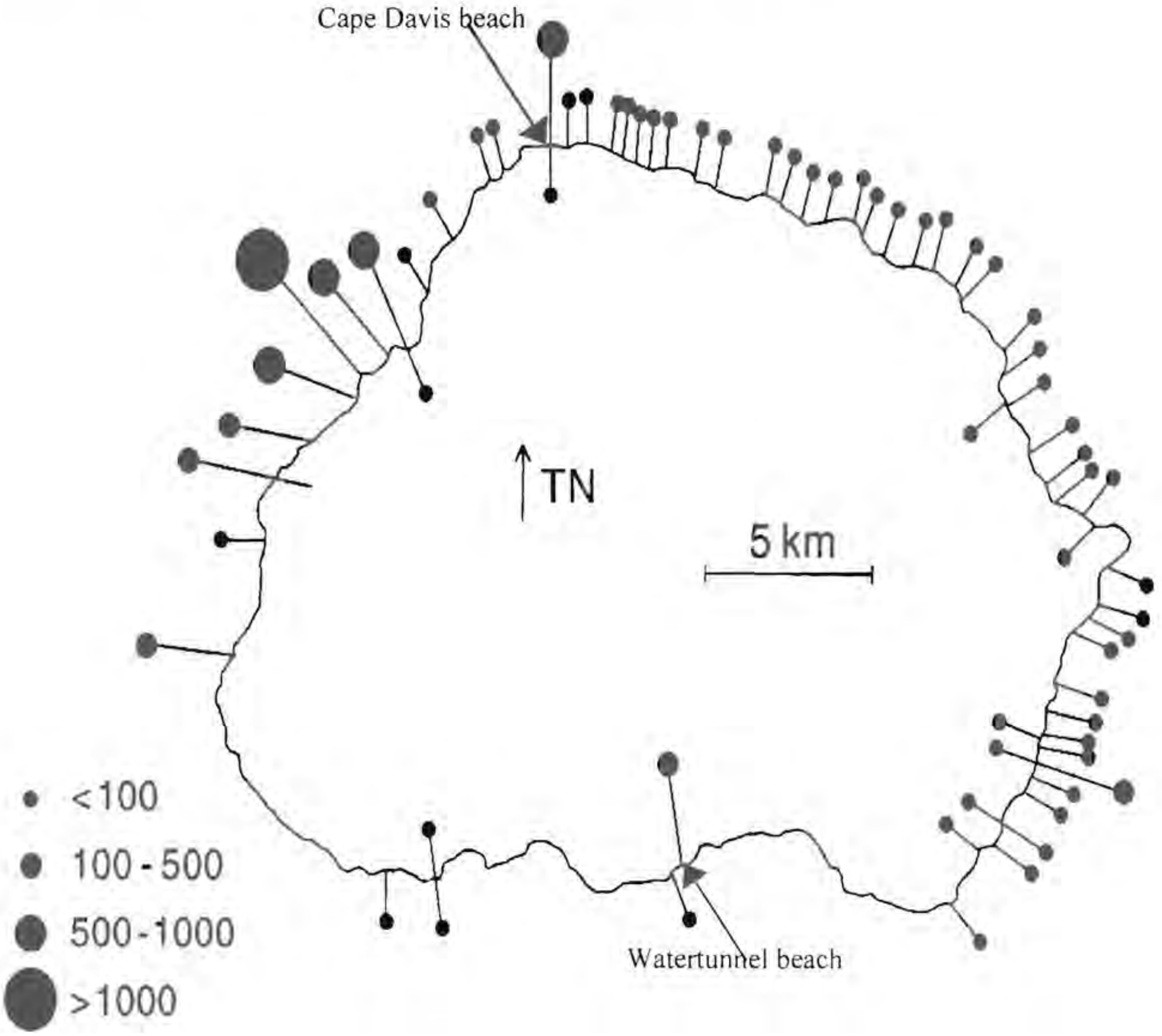

Fig 1.4. Distribution of *Arctocephalus tropicalis* (outside circle) and *A. gazella* (inside circle) pup production during the 1993/1994 breeding season at Marion Island. The size of the filled circle is proportional to the number of pups counted at each site.

Chapter 3. Materials and Methods

3.1. COLLECTION AND PREPARATION OF DATA

The diets of pinnipeds are difficult to quantify as they spend most of their time away from the land. Most studies of pinniped diet are based upon identification of hard prey remains in digestive tracts or faeces (Pierce *et al.* 1991). The majority of studies investigating the diets of *A. gazella* and *A. tropicalis* seals have been based on scat samples collected on land, although stomach contents have been obtained from shot animals (Condy 1981; Klages & Bester 1998; Croxall & Pilcher 1984; Bester & Laycock 1985) and by stomach flushing (Reid & Arnould 1996; Ferreirra & Bester 1998).

Only hard remains (mainly fish otoliths, cephalopod beaks and some crustaceans) are likely to be identifiable from scats, however, some hard parts are entirely digested and are reduced in size during the passage through the digestive tract (Pierce & Boyle 1991; Pierce *et al.* 1991; Klages & Bester 1998). Several authors have discussed the reliability of using otoliths to estimate dietary composition and prey sizes (Dellinger & Trillmich 1999; Reid 1995; North 1996; Klages & Bester 1998; Bowen 2000; Staniland 2002), consensus being that biases are introduced because of differential digestion of otoliths (Daneri & Carlini 1999; Staniland 2002) and passage rate of items in relation to their size (Staniland 2002). Most piscivorous marine mammals' stomach contents are partially or completely digested, posing problems for both identification of prey and quantification of diet. This results in biases when determining the total amount of fish in the diet, which depends on the rate of digestion. In addition, seals may not eat the heads of larger fish, and consequently, their otoliths and skull bones will therefore not be ingested (Pierce

& Boyle 1991).

Faecal analysis may not be an appropriate method for determining the diet of those seal species where a large proportion of fish otoliths ingested is completely or severely digested (North 1996). Furthermore, the use of faecal analysis to determine the diet of seals relies on the assumption that the solid remains pass into the faeces in the same proportions as they were consumed (Reid 1995) which is not the case (Gales & Cheal 1992; Staniland 2002). However, with proper caution, analysis of faecal samples can still provide some qualitative and quantitative information (Dellinger & Trillmich 1999).

Regression equations relating otolith length to fish length have been developed using otoliths from fresh fish. This leads to an underestimate of prey sizes as a result of partial digestion of otoliths. A correction factor must be applied to compensate for this partial digestion (Reid 1995; Bowen 2000; Staniland 2002). Otoliths of different species are eroded at different rates, thus number of fish ingested, and fish sizes derived by back calculation from the measurements of hard remains will require different correction factors. Food residues take several hours to pass out in faeces. Different types of prey are degraded at different rates, i.e. squid flesh are degraded more rapidly than fish flesh resulting in biases in the quantities of recognisable remains of different types of prey (Pierce & Boyle 1991). The identifiable items in the faecal analysis probably indicate prey items eaten 24 hours prior to fur seals coming ashore (Pierce & Boyles 1991) and therefore are a reflection of their diet in the vicinity of Marion Island.

In this study, the likelihood of otoliths being completely digested is high as suggested by Staniland (2002) for *A. gazella* at least. However, most scats contained otoliths and these could be identified, and faecal analysis is likely to be a reasonable technique for comparing the diet of the two fur seal species (Klages & Bester 1998). Biases associated with prey sizes and masses were minimised by discarding all the eroded otoliths.

Despite their spatial and some temporal segregation when ashore (Kerley 1983; Klages & Bester 1998), the current study shows a substantial overlap in the diet of both fur seals species at Marion Island. The total number of scats (471) collected was very similar to the 469 scats collected from 1989 to 1995 (Klages & Bester 1998). The number of otoliths identified (n = 14300), however, was much higher than that in the previous study (n = 13817) of the same species in the same study area and was likely the result of an increased effort in collecting and sorting of scat contents.

Despite this and other biases inherent to the method (Dellinger & Trillmich 1988; Klages & Bester 1998), scat analysis provides the least intrusive method of investigating the diets of the fur seals (Pierce *et al.* 1991), and is the method of choice for this study. Typically, scat analysis involves four fundamental procedures:

3.1.1. COLLECTIONS

Scats were collected at colonies known to be occupied almost exclusively by either species, namely Watertunnel Beach (*A. gazella*) and Cape Davis Beach (*A. tropicalis*) from 1996 to 2000 during each visit to these sites. Only fresh scats (still moist and dark in colour) were collected. Neither age nor sex group of the seals frequenting the beaches was determined at the time of sampling, as the seasonal haulout pattern of both fur seals species at Marion Island is well known (Condy 1978; Kerley 1983; Hofmeyr *et al.* 1997; Klages & Bester 1998). Each scat was placed separately in a plastic bag, labelled as to site and date of collection, and returned to the laboratory for subsequent cleaning and sorting. In some years, scats that consisted exclusively of crustacean remains were deposited, and samples of these were collected.

3.1.2. SORTING

In the laboratory, scat samples were washed through a 0.5 mm sieve under running water to collect the undigested remains (mainly otoliths and some crustaceans and squid beaks). The fish otoliths (sagitta only used for identification of the fish species), cephalopods (squid lower beaks) and crustacean carapaces were preserved in 70% ethanol and were then stored in vials for further identification and measurement. All the prey remains (otoliths, beaks and carapaces) were then sorted to species level when possible, under a Zeiss dissecting microscope following Klages & Bester (1998).

3.1.3. MEASURING AND IDENTIFICATION

The diameters of otolith specimens in good condition were measured using a Zeiss dissecting microscope fitted with graticules. Eroded otoliths were simply identified to genus level and then counted. If the extent of erosion prevented identification at any taxonomic level, they were classed as being too eroded to identify (Goldsworthy *et al.* 1997). Otoliths were identified using identification manuals (Australian National Antarctic Research Manual 1990; Hecht 1987, 1995) and by comparison with the reference specimen collection obtained from the Port Elizabeth Museum at Bayworld (Klages & Bester 1998).

3.2. STATISTICAL ANALYSIS

All otolith measurements were used for calculating fish standard length, mass and determining percentage prey composition of the fish diets of the fur seals. Prey length and masses were estimated from otolith diameters of pristine specimens, using standard regression equations published in Adams & Klages (1987), Hecht (1987), Williams & McEldowney (1990), Reid (1996) and Cherel *et al.* (1997). Prey mass was not reconstituted for *Gymnoscopelus nicholsi* as the regression equation could not be located For comparison of samples, number of otoliths (frequency), number of samples (equivalent to number of scats) in which given otoliths occurred (occurrence), and the number of samples in which otoliths from a given species was dominant, that is, most abundant (dominant), were used. Percentages were calculated by relating these values to yearly or overall totals of otoliths or to the total number of scats (percentage frequency, percentage occurrence, percentage dominance) (Dellinger & Trillmich 1999).

The year was divided into three seasons, namely early summer (October to January which coincided with the breeding season haulout and pupping season), late summer (February to May which coincided with the post breeding season moulting and lactation period) and winter (June to September when most seals are at sea on a regular basis Kerley 1983; Bester & Bartlet 1990) to check for any possible variation in the diet among seasons. In addition, grouping of the months into these seasons was required as scat collection was irregular with no scats being collected during some months in some years. The computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick 1994) was used to analyse prey abundances in the diets. SIMPER (similarity percentages) was also used to determine percentage contributions of each prey species in the diet of the two fur seal species. Sigma Plot was used to generate scatter plots for showing similarity in seasons between and within species and histograms for showing any monthly variation between species. Multivariate techniques that included ANOSIM (Analysis of Similarities) were used to test the significance of differences among seasons within species and between species, while MDS (non-metric Multi-Dimensional Scaling) was used to show the similarity and dissimilarity of prey abundances among seasons. Fourth root transformation was done to enable even the rare species to be indicated or taken into consideration in the diet analysis. Analysis of variance (ANOVA) was used to detect any significant differences in the sizes of the prey species between the diets of the two fur seal species.

As far as possible, squid lower beaks were identified to species level but those that were unidentifiable were simply recorded as unidentified squid beaks and were treated similar to the unidentifiable otoliths. Completely broken otoliths and squid upper beaks were regarded as unidentifiable and then discarded.

Chapter 4: The diet of the Antarctic fur seal (*Arctocephalus gazella*) at Marion Island

4.1. INTRODUCTION

The study of the diet of seals is fundamental to the assessment of their role as predators in the southern ocean marine ecosystem. Such studies may also provide information about potential competition for food resources among predator species and between these and commercial fisheries (Daneri & Carlini 1999). In the Southern Ocean, fish constitute an important food resource of apex predators such as birds, seals and whales (Daneri *et al*. 1999). However, of the two fur seal species breeding at Marion Island, the Antarctic fur seal (*A. gazella*) is the only eared seal (family Otariidae) that occur characteristically on islands south of the Antarctic Polar Front (APF) (Daneri *et al.* 1999), where it is a specialist feeder on krill (*Euphausia superba*) (Reid & Arnould 1996). The current population at Marion Island has increased from a rate of 11.3% between 1981/82-1988/89 (335 seals) (Wilkinson & Bester 1990) to 17% for 1988/89-1994/95 (1,205 seals) (Hofmeyr *et al*. 1997). However, at Marion Island the population numbers of this fur seal are low during winter and spring but increase to reach peaks in December and March when they are breeding and moulting respectively (Kerley 1983).

The feeding ecology of *A. gazella* has been studied at numerous sites throughout its range, namely South Georgia (Bonner 1968; North *et al.* 1983; Reid 1995; Reid & Arnould 1996), Heard Island (Green *et al*. 1991, 1997), South Shetland Islands (Daneri *et al.* 1999), South Orkney Islands (Daneri & Coria 1992), Macquarie Island (Goldsworthy *et al.* 1997), Îles Kerguelen (Cherel *et al.* 1997) and Bouvetøya (Klages *et al.* 1999; Kirkman *et al.* 2000). Krill and various fish species seem to constitute the bulk of the diet, the relative proportions of the different prey species varying between the sexes, geographic location, and seasons (Daneri & Coria 1992; Casaux *et al.* 1998; Daneri & Carlini 1999). Most studies of the diet of *A. gazella* have been based on analysis of scat samples, although stomach contents have been obtained from shot animals and by stomach flushing (Kirkman *et al.* 2000).

Few papers have been published on the diet of this species at Marion Island (Condy 1981; Klages & Bester 1998). Investigation of the foraging ecology (Bester & Bartlett 1990) and the diet of the Antarctic fur seal at Marion Island have recently been intensified (this study; Kirkman *et al.* (submitted); MRI unpublished data). Information on the diet of the Antarctic fur seal from other islands such as South Georgia (North *et al.* 1983; Reid 1995; Reid & Arnould 1996) and Bouvetøya (Kirkman *et al.* 2000) indicates that krill (*Euphausia superba)* is the main prey whereas at the other islands where *E. superba* does not occur, fish predominated in the diet of the fur seals (Goldsworthy *et al.* 1997; Casaux *et al.* 1998; Klages & Bester 1998).

This chapter is aimed at investigating the diet of *A. gazella,* the variation in prey species taken according to season and amongst the years, and to compare it with the situation at other islands where this predator species occur.

4.2. RESULTS

A total of 258 faecal samples containing identifiable food remains were collected from April 1996 to April 2000 on the southern side of the island at Watertunnel Stream where an exclusively *A. gazella* breeding colony is found. The number of scats collected differed considerably between months and years (Table 4.1).

Table 4.1: Number of *A. gazella* scats collected at the Watertunnel Stream breeding colony on Marion Island by month and year.

Months	1996	1997	1998	1999	2000	Total
Jan		9	11	10	6	36
Feb		8	7	1	5	21
Mar		7	10	22	4	43
Apr		5	7	9	11	32
May	10	12	14	9		45
Jun	13		6			19
Jul	8	4	1			13
Aug		11		2		13
Sep	1	11		6		18
Oct		4		4		8
Nov			2			2
Dec	6			2		8
Total	38	71	58	65	26	258

The number of scats collected was highest in 1997 (n=71 scats), followed by 1999 (n=65 scats) and 1998 (n=58 scats). The lowest number of scats collected was 38 and 26 for 1996 and 2000 respectively, as scats were collected only from May to December in 1996 and January to April in 2000 (Table 4.1).

4.2.1. OTOLITHS RECOVERED

Of 7390 otoliths isolated from scats, only 24 otoliths were unidentifiable, the remainder was allocated to at least family, and most were identified as to species. The highest number of otoliths was collected in 1997 and 1999 (NA=2362 and NA=2008), followed by 1998 and 2000 with NA=1399 and NA=832 respectively. The lowest number of otoliths (NA=789) was collected in 1996. Only 5 squid beaks were identified in the scats.

Table 4.2: Percentage numerical abundance (%NA) and frequency of occurrence (FO) of prey species appearing in scat samples of *A. gazella*.

Prey items	Fish	Crustacean	Cephalopod	Total
FO	249	7	3	259
NA	7390	7	5	7402
%FO	96.1	2.7	1.2	100
%NA	99.7	0.2	0.1	100

4.2.2. DIET COMPOSITION

Percentage numerical abundance (%NA) of food items in faecal samples of Antarctic fur seals at Marion Island showed that fish remains predominated in the diet of this species, occurring in 96.1 % of samples containing food items (Table 4.2). Cephalopods and crustaceans occurred in only 1.2 % and 2.7 % of the samples respectively. Fish species were present in 249 scats (n = 258) while cephalopods and crustaceans were only present in three and seven scats respectively (Table 4.2). Crustaceans at most occurred in scats from September, October and December. Besides fish species, crustaceans and cephalopods, scats of Antarctic fur seals on occasion contained penguin feathers and Antarctic fur seals were on occasions observed pursuing and killing king penguins, macaroni penguins and rockhopper penguins.

Fish, cephalopod and crustacean species identified from the scat samples are shown in Table 4.3, together with their numerical abundance and frequency of occurrence. Twenty-five different prey species were identified (Table 4.3) of which 21 were fish species, 1 was crustacean and 3 were cephalopods. The main species of cephalopod identified was *Brachioteuthis* spp., *Octopus magnificus* and the rest were only identified to taxon (squid) while the only crustacean prey species was the swimming prawn (*Nauticaris marionis*).

Fish from 7 different families were identified, Myctophidae being the most dominant, contributing more than seven prey species in individual scats and accounting for 97.2% NA of prey species in the scats of Antarctic fur seals. Notothenididae contributed 1.9% of the NA of prey species, followed by all other families (Paralepididae, Microstomatidae, Gempylidae and Notosudidae) in small quantities, contributing only 0.3%, 0.09%, 0.01% and 0.2% respectively (Table 4.3).

Otoliths that could be identified only as *Electrona* spp. (NA=85), *Gymnoscopelus* spp. (NA=194), and *Notothenia* spp. (NA=4) together formed 3.83% of the total number of otoliths obtained. The remaining 24 otoliths (accounting for 0.32%) could not be identified. The myctophids comprised mainly of *Electrona carlsbergi, E. subaspera, Gymnoscopelus bolini, G. fraseri, G. nicholsi, G. piabilis* and *Protomyctophum choriodon*, together forming 89.8% of the myctophid fish prey (Table 4.3). The most abundant and frequently occurring prey species identified was *G. piabilis*, contributing 2519 of 7390 otoliths obtained from the scats. *Gymnoscopelus piabilis* was by far the most numerous prey species and contributed 34.09% of NA, and occurred in 159 of 249 scats containing fish, contributing 63.86 % FO.

Electrona carlsbergi was the second most dominant species with a NA of 13.4% and FO of 94 (37.8%), followed by *G. fraseri* with a NA of 937 (12.7%) and FO of 102 (41%). Although *E. carlsbergi* is the more dominant prey species (in terms of numerical abundance) than *G. fraseri*, it occurred less frequently in the scat samples than *G. fraseri*, both prey species making a substantial contribution to the diet of this fur seal. Predation of these fish species was common during the whole study. In addition, the prey species *E. subaspera, G. bolini, G. nicholsi, Krefftichthyes anderssoni* and *P. choriodon* contributed more than 4% of the NA leading to an overall contribution of 29.6% NA (Table 4.3).

Table 4.3: Frequency of occurrence (FO) and numerical abundance (NA) of prey species identified from otoliths (n=7390) found in the scats (n=258) sampled from *A. gazella* at Marion Island.

Prey species	FO	NA	%FO	%NA
Myctophidae				
Electrona antarctica	4	13	1.61	0.18
E. carlsbergi	94	993	37.75	13.44
E. subaspera	55	667	22.09	9.03
Electrona sp.	20	85	8.03	1.15
Gymnoscopelus bolini	50	328	20.08	4.44
G. fraseri	102	937	40.96	12.68
G. nicholsi	34	322	13.65	4.36
G. piabilis	159	2519	63.86	34.09
Gymnoscopelus sp.	54	194	21.69	2.63
Krefftichthyes anderssoni	32	551	12.85	7.46
Metelectrona ventralis	32	200	12.85	2.71
Protomyctophum tenisoni	5	15	2.01	0.20
P. bolini	7	37	2.81	0.50
P. choriodon	49	319	19.68	4.32
Protomyctophum sp.				
Nototheniidae				
Gabionotothern marionensis	12	76	4.82	1.03
Dissostichus eleginoides	3	15	1.20	0.20
Lepidonotothern larsen	1	43	0.40	0.58
Notothenia sp.	3	4	1.20	0.05
Paranotothenia magellanica	4	18	1.61	0.24
Paralepididae				
Magnisudis prionosa	2	8	0.80	0.11
Gempylidae				
Paradiplospinus gracillis	1	1	0.40	0.01
Microstomatidae				
Nansenia antarctica	1	7	0.40	0.09
Notosudidae				
Scopelosaurus ahlstromi	2	14	0.80	0.19
Scopelareus sp				
Unidentified otoliths	12	24	4.82	0.32
Crustacean	7	7	2.7	0.2
Cephalopod	3	5	1.2	0.1

4.2.3. SEASONAL VARIATION

When the data was partitioned into two seasons (summer and winter), there was a highly significant difference between them (ANOSIM; $P< 0.001$). When the data was divided into three seasons (early summer, winter and late summer; Chapter 3), there was significant differences between early summer and winter ($P< 0.03$) and between early summer and late summer ($P< 0.001$) as well as between late summer and winter ($P< 0.002$) (c.f. Fig. 4.1).

Gymnoscopelus piabilis predominated in the diet of *A. gazella* from January to June; the utilisation of this species subsequently decreased from August to November and reached the lowest levels (zero) in December (Table 4.4). The other three major prey species (*E. subaspera, E. carlsbergi,* and *G. fraseri*) rarely appeared towards the end of the year, from June to September. Their NA decreased from 0.91 to zero over the last months (October to December) (Fig. 4.2). *Gymnoscopelus fraseri* was utilised heavily in late summer, very few were taken in winter and none in early summer. The next most utilized prey species was *E. carlsbergi* with the highest NA over the first five months; *E. subaspera* followed with the majority being taken in the first five months of the year (January to May), subsequently decreasing from June to September. No *E. subaspera* appeared in the scats from October to December (Table 4.4). *Krefftichthys anderssoni* and *G. nicholsi* were less abundant as compared to the other four major prey species (Fig. 4.2). All six major prey species were present in the scats during April, decreasing (NA) to very low numbers towards the end of the year, some being absent at that time.

During August, September and December, minor fish species (*Dissostichus eleginoides, G. marionensis, Lepidonotothen larsen, G. bolini*) and cephalopods (*Brachioteuthis* spp.) appeared in the diet. The only crustacean (*N. marionis*) was taken in september, October and December of one year only.

Table 4.4: Mean numerical abundance (NA) of major fish prey species identified in the scats of *A. gazella* averaged on a monthly basis over 5 years period (sample size represented on table 4.3)

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Months	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. nicholsi*	*G. piabilis*	*K. anderssoni*
Jan	5.50	3.00	7.00	0.00	108.50	6.25
Feb	3.13	2.75	18.00	9.38	51.88	5.25
Mar	2.50	5.08	4.08	3.08	36.08	26.50
Apr	51.25	30.00	77.50	26.00	57.50	26.50
May	20.20	4.95	12.30	4.05	22.55	0.15
Jun	6.58	6.50	3.58	0.42	16.58	0.00
Jul	1.05	21.71	0.14	0.67	0.86	0.05
Aug	7.56	8.56	2.13	0.19	8.31	0.00
Sep	1.56	1.81	0.33	0.08	0.56	0.00
Oct	0.05	0.00	0.00	0.00	4.85	0.00
Nov	0.91	0.00	0.36	0.00	6.46	0.00
Dec	0.00	0.00	0.00	0.00	0.00	2.21

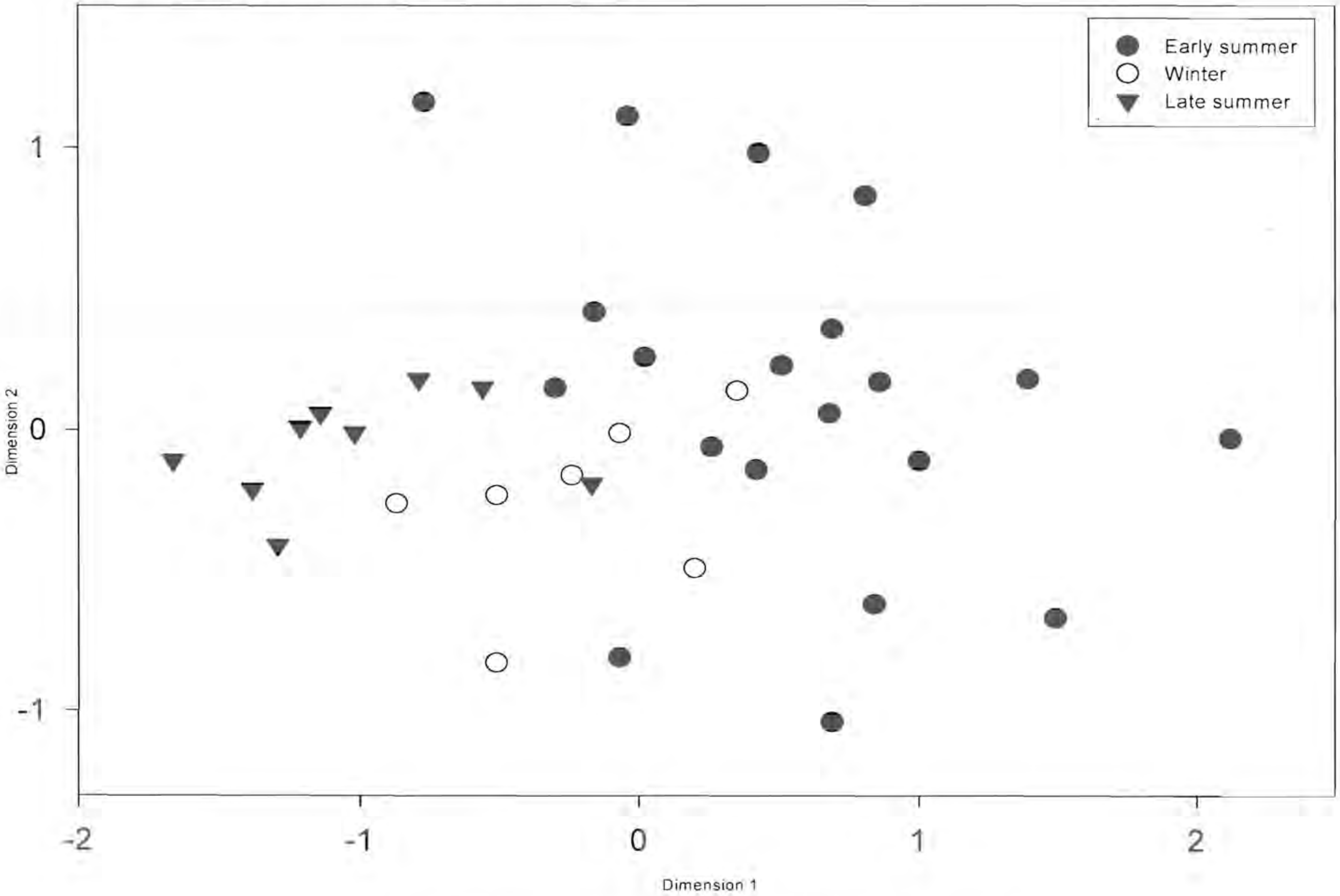

Fig. 4.1. Seasonal variation of prey species eaten by *A. gazella*

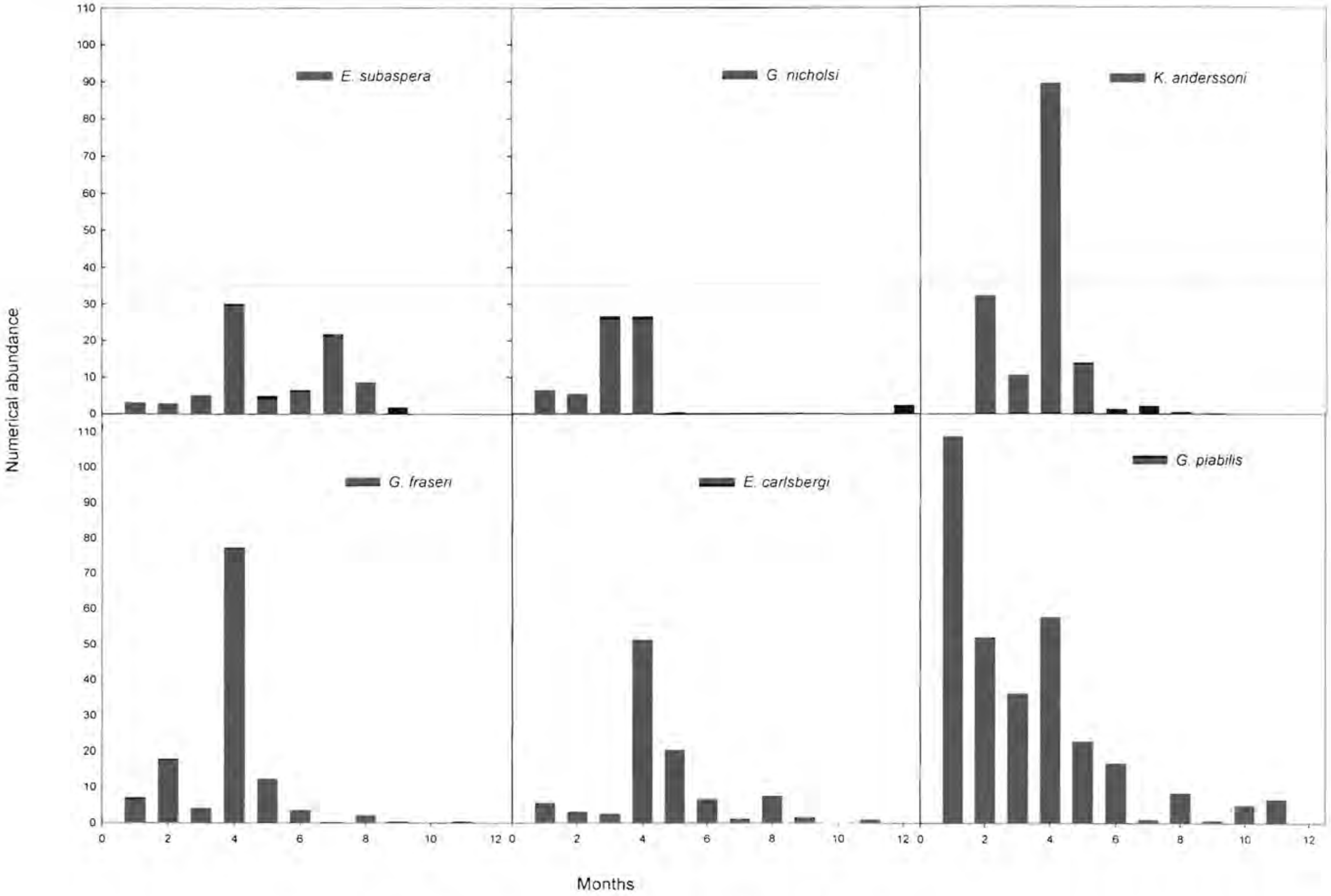

Fig. 4.2. Mean numerical abundance of prey species eaten by *A. gazella*.

4.2.4. INTER-ANNUAL VARIATION

Cephalopods only appeared in the scats of *A. gazella* in 1998 and 1999 with a low mean NA of 0.14 and 0.01 respectively. Crustaceans began to appear in the scats in 1999 with a mean NA of 0.167 while fish appeared in large quantities in the scats in all the years. Few *Notothenia* spp. were observed in the scats with a few species occurring in some years, i.e *D. eleginoides* (1997 and 1998), *P. magellanica* and *L. larsen* (1999), while *G. marionensis* appeared sporadically in the diet from 1996 to 2000. Unlike notothens, myctophids dominated the diet throughout the study. *Gymnoscopelus piabilis* was by far the most dominant species in every year from 1996 to 2000, followed by *G. fraseri*. The remaining major species that occurred most frequently in the scats throughout all the years were *E. carlsbergi, E. subaspera, G. bolini, K. anderssoni, M. ventralis* and *P. choriodon* (Table 4.5).

4.2.5. SIZE CLASSES OF FISH CONSUMED

The size class distributions of fish eaten were mostly bimodal for every prey species except for *G. fraseri* and *G. piabilis* (Fig. 4.3). Of the major nine prey species eaten *G. piabilis* was most favoured although it was not the largest prey taken. The modal size of *G. piabilis* ranged from 115 mm to 165 mm with the most preferred size classes being from 125 mm - 135 mm, and a mean standard length (SL) of 115.1 mm. *Gymnoscopelus piabilis* showed a normal size class distribution. Few very large species were eaten; *P. magellanica* ranged from 193.27 mm to 371.55 mm with a mean size of 250.09 mm and was one of the largest prey species taken by *A. gazella*, followed by very few *D. eleginodes* with a mean SL of 242.51 mm and size classes ranging from 140.41 mm to 319.08 mm.

For *E. carlsbergi*, the most preferred size classes ranged from 60 mm - 80 mm with a mean SL of 77.54 mm, while in *E. subaspera*, the sizes ranged from 65 mm - 100 mm with a mean SL of 93.32 mm. *Krefftichthyes anderssoni*, one of the most preferred species, had the smallest size classes ranging from 20 mm - 50 mm (Fig. 4.3) with a mean SL of 42. 47 mm (Table 4.6).

4.2.6. FISH MASSES

Arctocephalus gazella took fish ranging from 0.1 g to 50 g in mass, the heaviest being *G. piabilis*. One of the heavier prey species, *G. piabilis* was the most favoured species ranging from 5 g to 50 g with the most preferred masses between 25 g to 40 g with a mean mass of 21.25 g. The next heaviest consumed prey species was *G. nicholsi* with masses ranging from 3.02 g to 49.65 g with a mean mass of 15.6 g. *Electrona carlsbergi* and *E. subaspera* ranging from 2 g to 10 g and 4 g to 20 g respectively (Table 4. 6) were largely eaten. The smallest prey species consumed was *K. anderssoni* with the majority of fish mass ranging from 0.4 g to 0.8 g and 1 g to 1.4 g (Fig. 4.4).

Table 4.5: Numerical abundances (NA) of prey species obtained from the scats of *A. gazella* averaged per year

Year	*D. eleginoides*	*E. carlsbergi*	*E. subaspera*	*G. bolini*	*G. fraseri*	*G. marionensis*	*G. piabilis*	*K. anderssoni*	*L. larsen*	*N. marionis*	*P. choriodon*	*P. magellanica*	Cephalopod
1996	0.00	2.61	14.01	0.12	1.86	1.58	10.26	0.03	0.02	0.00	0.03	0.00	0.00
1997	0.15	6.69	3.89	3.88	14.93	0.57	45.68	0.09	0.00	0.00	1.37	0.11	0.00
1998	0.35	4.82	5.08	1.67	6.89	1.87	23.03	1.96	0.00	0.00	0.63	0.00	0.14
1999	0.00	8.31	3.49	8.72	4.01	0.92	21.30	15.41	0.56	0.17	6.57	0.05	0.03
2000	0.00	5.94	3.35	2.27	3.71	0.50	35.73	6.58	0.00	0.00	4.19	0.00	0.00

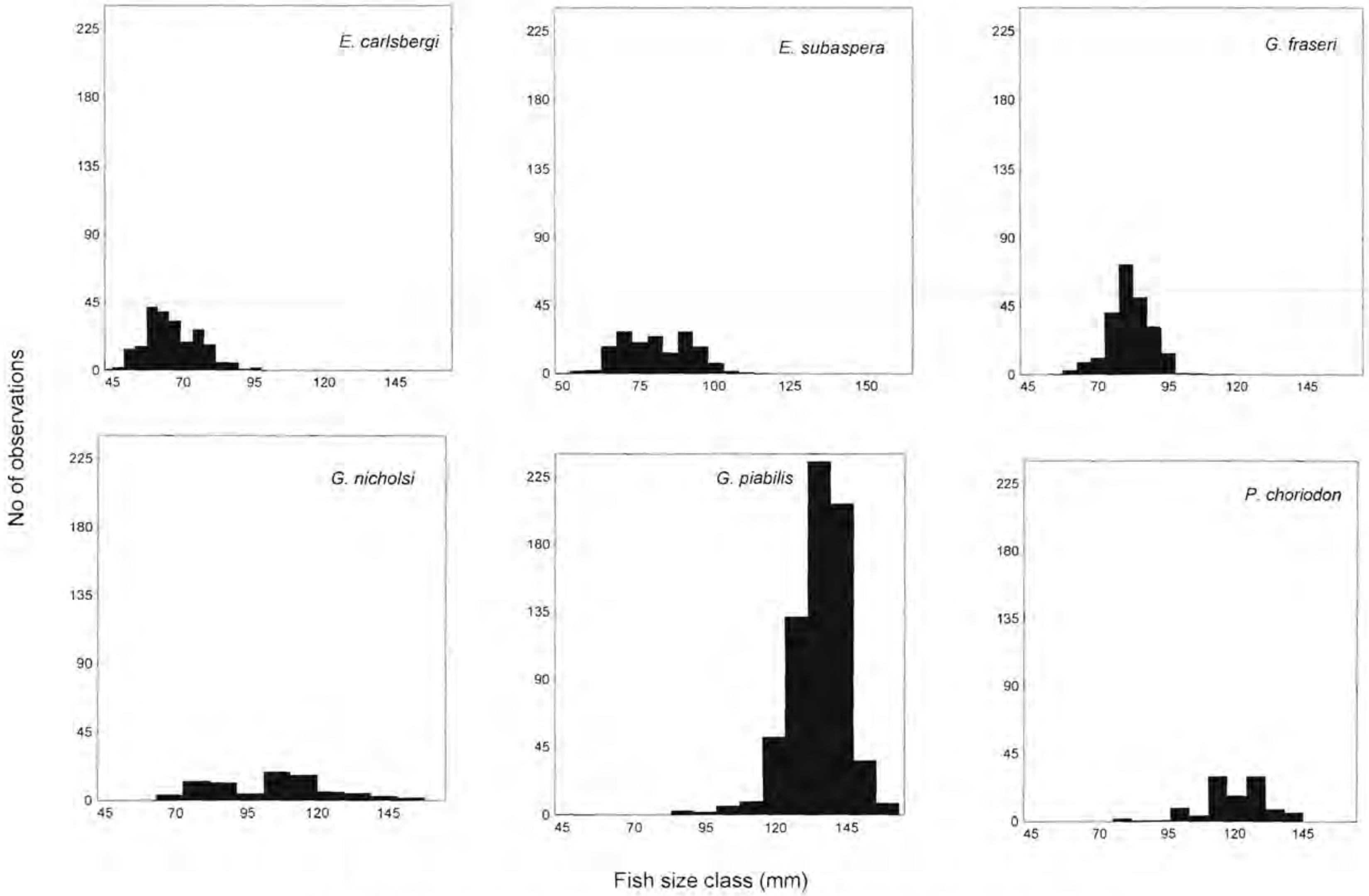

Fig. 4.3. Reconstituted size classes of fish species eaten by *A. gazella*.

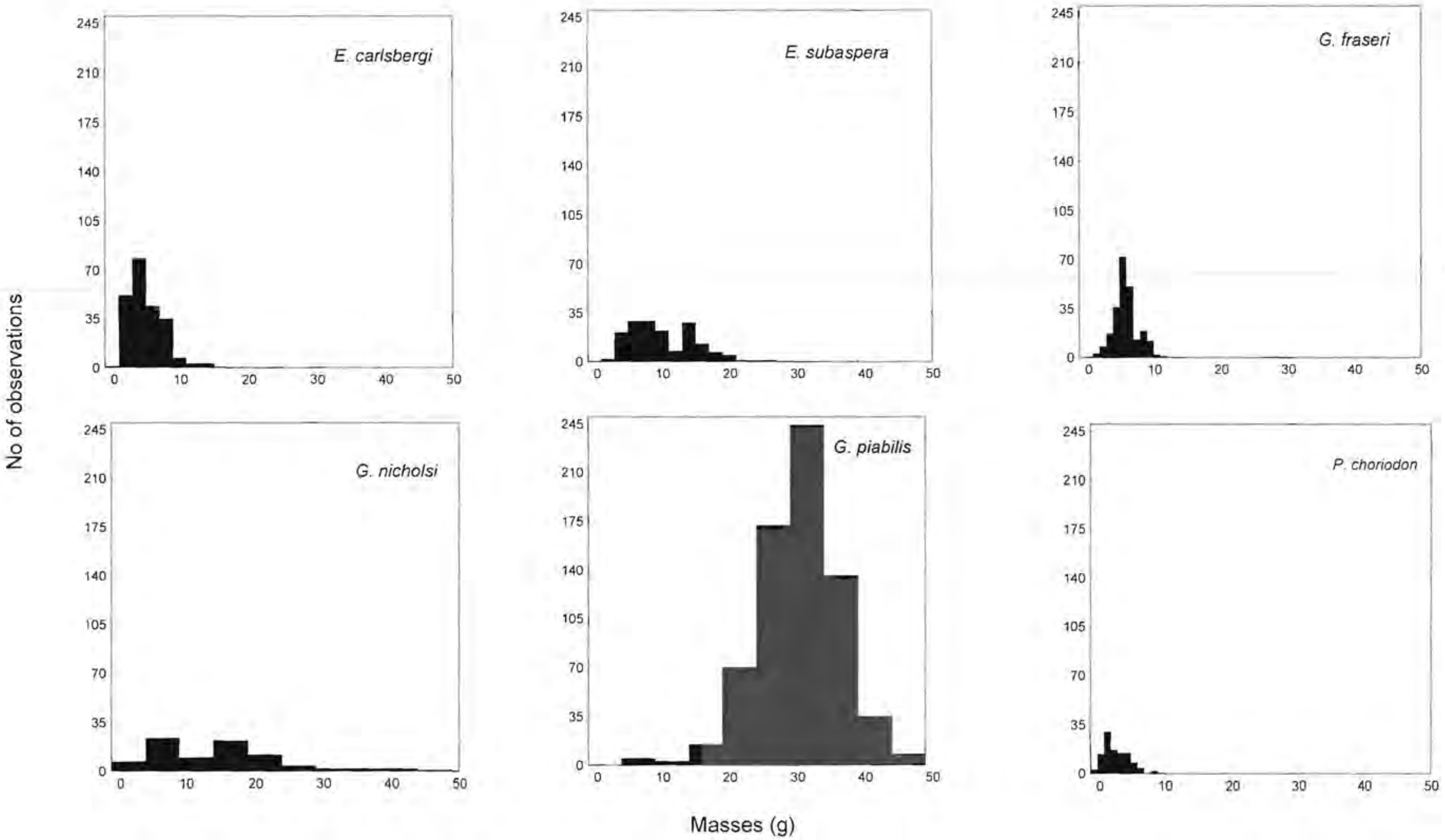

Fig. 4.4. Reconstituted mass of fish species eaten by *A. gazella.*

Table 4.6: Summary of standard lengths and mass of fish consumed by *A. gazella* at Marion Island.

	Standard length (mm)			Mass (g)		
Prey species	Average	S.D	Range	Average	S.D	Range
Dissostichus eleginoides	242.51	74.42	140.41-319.08	225.20	166.25	32.03-438.28
Electrona antarctica	79.38	17.11	55.61-103.56	7.66	4.6254	2.26-15.34
Electrona carlsbergi	68.86	10.03	43.61-100.20	5.991	2.4707	1.63-15.91
Electrona subaspera	82.883	11.4572	58.62-111.24	11.221	4.8769	3.48-26.89
Metelectrona ventralis	99.70	7.62	66.66-100.20	8.97	2.3996	5.22-15.91
Gymnoscopelus bolini	118.95	22.444	82.09-196.82			
Gymnoscopelus nicholsi	115.92	26.618	60.24-109.30	21.2	12.55	2.41-15.29
Gymnoscopelus fraseri	84.096	7.4535	60.24-165.23	6.9551	1.8639	2.41-15.29
Gymnoscopelus piabilis	137.05	9.48632	85.33-165.23	31.168	6.1637	7.158-54.57
Krefftichthys anderssoni	42.468	5.78185	21.71-57.31	0.7974	0.3166	0.08-2.01
Protomyctophum bolini	43.13	0.00	0.00	1.10	0.00	0.00
Protomyctophum choriodon	78.77	12.83	33.76-103.39	3.76	1.9015	0.47-9.68
Protomyctophum tenisoni	79.36	3.13	74.74-83.36	7.609	0.9138	6.29-8.82
Lepidonotothern larsen	124.34	4.41	119.53-128.19	0.89	0.0562	0.83-0.94
Paranotothenia magellanica	250.09	60.65	193.27	399.01	335.8	158.10-1123.30
Gabionotothern marionensis	99.489	26.2305	64.63-145.96	9.9442	9.1684	65.74-159.69

4.3. DISCUSSION

Based on the census results and behaviour of the fur seals, mostly lactating females deposited the scats at Watertunnel Stream from December to April/May, thereafter subadults and non-breeding adults hauled out on the beaches (Kerley 1983) and were responsible for depositing scats. The total number of scats (n=258) collected in this study was higher than those collected between 1989 and 1995 (n=224) which undoubtedly contributed to the higher number of fish species (n=7390 versus n=6750) identified (Klages & Bester 1998), and was the likely result of increased effort in collecting scats.

4.3.1. DIET COMPOSITION

Krill (*Euphausia superba*) is the most dominant prey species in the diet of this fur seal species at South Georgia (North *et al.* 1983; Doidge & Croxall 1985; Boyd *et al.* 1991; Reid 1995; Reid & Arnould 1996). By contrast, the diet of this species at Marion Island is predominated by fish, as was the case at Macquarie Island (Goldsworthy *et al.* 1997), Heard Island (Green *et al.* 1997) and Îles Kerguelen (Cherel *et al.* 1997). No krill was identified in the scats of *A. gazella* at Marion Island, *N. marionis* being the only crustacean found in the scats. Only few crustaceans and cephalopods were identified, and it is possible that crustaceans might even have been taken incidentally or secondarily, as amphipods were recorded as a prey for myctophid species (Hulley 1990). Cephalopod beaks are likely to accumulate in the stomachs of marine predators (Reid 1995; Klages & Bester 1998) or to have been ejected by vomiting (Kirkman *et al.* 2000) and may not appear in scats on a regular basis. The central tenet of scat analysis, that the solid prey remains pass into the faeces in the same proportions as they were consumed, may therefore not hold for squid beaks, more especially if they are of large size (> 10mm diameter) (Klages & Bester 1998). Therefore, scat analysis may be an unsuitable method to fully determine the contribution of cephalopods to the diet of these fur seal species resident on Marion Island (Klages & Bester 1998; this study).

The majority of fish prey taken around Marion Island were mesopelagic myctophids (*Electrona* spp., *Gymnoscopelus* spp., *Protomyctophum* spp. and *Kreffftichthys* spp.) which are characteristic of deep, offshelf water and can constitute the deep scattering layers, usually at 200 m to 500 m, the exception being *G. nicholsi* that can also be found near the bottom of the shelf (Green *et al.* 1997).

Gymnoscopelus piabilis was by far the most abundant prey species in the diet. It continually appeared in the diet of this seal species as well as in the diet of the co-occurring *A. tropicalis* at Marion Island (Klages & Bester 1998) and Macquarie Island (Goldsworthy *et al.* 1997). Together with *E. carlsbergi* and *G. fraseri, G. piabilis* were numerically the most important prey species in the diet of *A. gazella* at Marion Island. By contrast, Reid & Arnould (1996) reported that *P. choriodon* was numerically the most abundant fish taxon in the diet of *A. gazella* at South Georgia, followed by *Champsocephalus gunnari*, which never appeared in the diet of *A. gazella* at Marion Island. The low presence, or absence, of the latter two prey species in the diet might be related to the overwhelming abundance of the other major prey species around Marion Island. *Champsocephalus gunnari* is an epipelagic predator that is attracted to the sea surface by the presence of potential prey such as myctophids and crustaceans (Nel *et al.* 2002) and, therefore, could potentially have been taken incidentally by *A. gazella.* This might suggest that this prey species, dominant in the area around the islands of the Scotia Sea including the Antarctic Peninsula, Îles Kergeulen, Heard Island, and Bouvet Island (Hulley 1990), are less abundant at Marion Island.

The lack or rare occurrence of *D. eleginoides* and *C. gunnari* in the diet of *A. gazella* might suggest that the seals are feeding offshore as these species are found closer inshore (Klages & Bester 1998; Goldsworthy *et al.* 1997; Green 1997). Furthermore, at localities where the shelf is narrow (Macquarie Island, Marion Island), myctophids dominated the diet, but in the area where it is wide (Heard Island, Îles Kerguelen) demersal and benthic fish (*Champsocephalus gunnari*, notothenids, skates) become more important and abundant in the diet (Klages & Bester 1998).

4.3.2. SEASONAL VARIATION

Fish species were preferably consumed in all seasons over all other prey components. Highly seasonal patterns of consumption of fish species, particularly the myctophids, have been documented for Antarctic fur seals at Heard Island (Green *et al.* 1989), South Georgia (Reid & Arnould 1996) and Marion Island (Klages & Bester 1998) and are similar to the present study. Therefore it appears that seasonal variation in the consumption of different fish species relates to their relative abundances or availability with respect to the season, within the range and dive depth distribution of foraging fur seals (Lea *et al.* 2002) while the take of cephalopods showed no seasonal variation. This is in line with studies at other sites such as Heard Island, South Georgia and Marion Island where cephalopods had contributed negligibly to the diet of *A. gazella* (Green *et al.* 1989; Reid 1995; Reid & Arnould 1996; Cherel *et al.* 1997; Klages & Bester 1998), and seemed to be taken opportunistically by this fur seal (Kirkman *et al.* 2000).

Comparison between the early summer and winter diet showed that most species decreased drastically in scats in winter. *Electrona carlsbergi, E. subaspera, G. fraseri, G. nicholsi, G. piabilis* and *K. anderssoni* dominated in early summer rather than in winter. This might have resulted from both increasing number of scats, which could have contained the species, being washed away by heavy rainfall and changes in high tides, waves and swells during winter months when storms become more frequent (Lutjeharms 1990; Hänel & Chown 1998) and the seasonal change in haulout of the fur seal species at Marion Island. Very low numbers of both sexes and various age classes of this fur seal species are present in winter (Kerley 1983; Hofmeyr *et al.* 1997). In addition, high production of prey species is determined by the stability of water; therefore, the scarcity in abundance of prey species in winter might have been influenced by the instability in the marine environment (Lutjeharms 1990). Moreover, the sympatrically occurring *A. tropicalis* females with their extended lactating period made significantly longer feeding trips in winter (Kirkman *et al.* 2002), which could suggest that suitable prey had to be obtained further away from the island (Green 1997; Kirkman *et al.* 2002; Lea *et al.* 2002) and could have been voided at sea (Staniland 2002).

4.3.3 INTER-ANNUAL DIFFERENCES

The observed trend that *G. piabilis*, followed by *G. fraseri*, were the major prey species eaten in all years by *A. gazella* was similar to the trend in the diet of this species at Marion Island from 1989 to 1994 (Klages & Bester 1998). The other prey species (*E. carlsbergi, E. subaspera, G. nicholsi, L. larsen, P. magellanica* and *K. anderssoni*) contributed less or were completely absent in some years at Marion Island which might relate to fluctuation in the abundance due to environmental factors (Lutjeharms 1990) and might also be the results of less effort in collecting scats samples in some years which have led to fewer number of species. The presence of crustaceans (*N. marionis*) during the breeding season of *A. gazella* only in 1999 and 2000 suggests that lactating females fed in areas where *N. marionis*, were more available and abundant.

4.3.4 FISH SIZE AND MASS CLASSES CONSUMED

The estimated size and mass classes of the fish species consumed by *A. gazella* in this study ranged from 2.71 cm and 0.08 g (*K. anderssoni)* to 37.16 cm (*P. magellanica*) and 438.28 g (*D. eleginoides*). This was similar to the sizes and masses (1.9 cm and 0.2 g for *P. tensioni* to 22.4 cm and 208 g for *Notothenia squamifrons*) of the prey species formerly taken by the Marion Island population (Klages & Bester 1998), although they were generally smaller and lighter in the previous study. Similarly, at Harmony Point, Nelson Island, South Shetland Islands, Casaux *et al.* (1998) showed that although prey of *A. gazella* was generally larger (4.0 cm to 39.8 cm for *E. antarctica* and *Cryodraco antarcticus* respectively), the estimated fish size classes were more similar to this study.

By contrast to Marion Island, where *A. gazella* feed on prey species of varying sizes, from the smallest (*K. anderssoni)* to the largest (*Paranotothenia magellanica* and *G. piabilis*). *A. gazella* at South Georgia (Reid & Arnould 1996) and Heard Island (Green *et al.* 1997), fed on prey species of very large size (*C. gunnari*), which co-dominantly occurred with *K. anderssoni* at Heard Island (Green *et al.* 1997). At Marion Island, *C. gunnari* was never taken despite its presence around the island (Klages & Bester 1998), while at Heard Island (Green *et al.* 1991), South Georgia (Reid 1995; Reid & Arnould 1996; North 1996) and the South Shetland Islands

(Casaux *et al.* 1998) *C. gunnari* predominated in the diet of *A. gazella*. *Champsocephalus gunnari* is found in relatively shallow water during the day (approximately 150–300 m) and become more pelagic at night (Gon & Heemstra 1990), when *A. gazella* fur seals forage exclusively (Boyd *et al.* 1998). It would therefore seem that very few *C. gunnari* are present around Marion Island, as at least some have been taken by the co-occurring *A. tropicalis* (Klages & Bester 1998; this study).

4.3.5. PREDATION ON PENGUINS

Three of four species of penguin breeding at Marion Island; king penguins (*Aptenodytes patagonicus*), macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*) are taken by *A. gazella* while gentoo penguin (*Pygoscelis papua*) were never seen to be attacked or fed upon by *A. gazella* (this study). Only adult males were the major predators of penguins, including the large king penguins which they also take on land (Hofmeyr & Bester 1993; unpublished data).

Chapter 5: The diet of the Subantarctic fur seal (*Arctocephalus tropicalis*) at Marion Island

5.1. INTRODUCTION

The study of the diet of seals is fundamental to the assessment of their role as predators in the southern ocean marine ecosystem. Such studies may also provide information about potential competition for food resources among predator species and between these and commercial fisheries (Daneri & Carlini 1999). The Subantarctic fur seal, *Arctocephalus tropicalis*, breed on islands north of the Antarctic Polar Front at Gough Island (Bester 1980), Tristan da Cuhna (Bester 1980), Amsterdam Island (Paulian 1964), St Paul Island (Segonzac 1972), Îles Crozet (Jouventin *et al.* 1982), Macquarie Island (Shaughnessy & Fletcher 1987) and Marion and Prince Edward islands (Condy 1978).

The largest population of *A. tropicalis* resides at Gough Island with approximately 200 000 individuals in 1977 and increasing (Bester 1980, 1990), followed by the Amsterdam Island (Guinet *et al.* 1994) and Marion Island (Kerley 1984) populations. The *A. tropicalis* population at Prince Edward Island in the 1981-82 austral summer was estimated at 14 761 individuals while at Marion Island total estimates yielded 19 857 seals (Kerley 1983a). Hofmeyr *et al.* (1997) estimated 49 523 seals during 1994/95 at Marion Island where the population appeared to be entering the maturity phase of population growth, while the 72 000 strong Prince Edward Island population in 2001 appeared to have remained in the rapid recolonisation phase (Bester *et al.* submitted). Knowledge of the diet of *A. tropicalis* is fundamental to our understanding of their feeding behaviour (Klages & Bester 1998) and any potential interaction with commercial fisheries (Reid 1995). Although fish and cephalopod are the staple diet of many southern ocean vertebrates (Klages & Bester 1998), relatively little was known about the diet of this fur seal species until fairly recently when it was considered a fairly generalist feeder on squid (Bester & Laycock 1985), nototheniid fish and krill (Condy 1981).

The feeding ecology of *A. tropicalis* has been studied at a few sites throughout its range, namely at Macquarie Island (Goldsworthy *et al.* 1997), Gough Island (Bester & Laycock 1985) and Marion Island (Klages & Bester 1998). Cephalopod and various fish species seem to constitute the bulk of the diet (Bester & Laycock 1985; Klages & Bester 1998). At Amsterdam Island, a breeding colony site in the Southern Indian Ocean, they are feeding on seasonally abundant rockhopper penguins, *Eudyptes chrysocome,* squid and fish (e.g. snoek, *Thyrsites atun*) (Tollu 1974). Most studies of the diet of *A. tropicalis* have been based on the analysis of scat samples, although stomach contents have been obtained from shot animals (Bester & Laycock 1985) and by stomach flushing (Ferreira & Bester 1999).

Investigation of the diet (Condy 1981) and foraging ecology (Bester & Bartlett 1990) of the Subantarctic fur seals at Marion Island have recently been intensified (Klages & Bester 1998; Kirkman *et al.* 2002). This chapter continues to investigate the diet of *A. tropicalis* at Marion Island, assess if there is any variation in prey species taken according to season and amongst years, and compares it with the current situation at other islands where this species occur.

5.2. RESULTS

A total number of 213 faecal samples containing identifiable food remains were collected from April 1996 to April 2000 on the western side of Marion island at Cape Davis where an exclusively *A. tropicalis* breeding colony is found. The number of scats collected differed considerably between months and years (Table 5.1).

Table 5.1: Number of *A. tropicalis* scats collected at the Cape Davis breeding colony on Marion Island by month and year.

Months	1996	1997	1998	1999	2000	Total
Jan				2	9	11
Feb		8		1	6	15
Mar		6		11	4	21
Apr			15	8	14	37
May			27	3		30
Jun	11					11
Jul	8		6			14
Aug			4			4
Sep	9		9	13		31
Oct	5		7	1		13
Nov	6			7		13
Dec	7			6		13
Total	46	14	68	52	33	213

The highest number of scats was collected in 1998 (n=68 scats), followed by 1999 (n=52) and

1996 (n=46). The lowest number of otoliths was collected in 1997 (n=14) due to the irregular collection of scats during the same year (Table 5.1). Scats collected in 2000 were also low (n=33) as scats were collected only up to April 2000 (Table 5.1).

5.2.1. OTOLITHS RECOVERED

A total of 6910 otoliths were recovered from the faecal samples, the number of otoliths collected varying amongst the years. The highest number of otoliths collected was in 1998 and 1999 (NA = 2779 and NA = 1651 respectively), followed by 1996 and 2000 (NA = 1310 and NA = 1170 respectively). The lowest number of otoliths (NA = 158) was collected in 1997. Fish remains were by far the most numerous prey items appearing in the scats of *A. tropicalis* (Table 5.2).

Table 5.2: Percentage numerical abundance (%NA) and frequency of occurrence (FO) of prey species appearing in scat samples of *A. tropicalis*.

Prey items	Fish	Crustacean	Cephalopod	Total
FO	209	0	3	213
%FO	98.6	0	1.4	100
NA	6910	0	6	6916
%NA	99.91	0	0.09	100

Of the 6910 otoliths recovered, only 29 otoliths were unidentifiable and the rest were identified to at least family and genus level.

5.2.2. DIET COMPOSITION

Fish constituted the most important dietary items, representing 99,91% of all the prey items eaten by *A. tropicalis*, while cephalopods contributed only 0.09% (Table 5.2). Of all collected scats (n = 212), 209 scats contained fish and only 3 scats contained cephalopod items (Table 5.2). Nineteen different prey species were identified, the dominant prey species being fish (18 out of 19) and one species of cephalopod (*Brachioteuthis* spp.). Otoliths from mesopelagic fish (Myctophidae) were the most dominant, contributing more than seven species in most scats and 99.19% numerical abundance (NA) of prey species in the diet of *A. tropicalis*. The other five fish families were uncommon, contributing a very small percentage (Table 5.3).

Nototheniddae contributed 0.04 % of the NA of prey species, followed by all other families (Channichthyidae, Paralepididae, Microstomatidae and Notosudidae) in small quantities, contributing only 0.01 %, 0.04 %, 0.01 % and 0.27 % respectively (Table 5.3).

Thirteen species of myctophids were identified in the scats (Table 5.3). *Gymnoscopelus piabilis* was by far the most numerous prey species, accounting for 24.5 % of NA. Some 1694 of 6910 otoliths obtained from the scats belonged to this prey species, and it occurred in 141 of 209 scats containing fish (FO = 67.46 %). *Gymnoscopelus fraseri* was the second most dominant prey species with 18.8 % NA (n = 1297) and 60.8 % FO (n = 127), followed by *E. carlsbergi* with 13.02 % NA (n = 937) and 45.9 % FO (n = 96) while *K. anderssoni* was also favoured at 11.02 % NA (n = 762) and 16.3 % FO (n = 34).

Table 5.3: Frequency of occurrence (FO) and numerical abundance (NA) of prey species

identified from otoliths (n = 6910) found in the scats (n = 213) sampled from *A. tropicalis* at Marion Island

Prey species	FO	%FO	NO	%NO
Channichthyidae				
Champsocephalus gunnari	1	0.48	1	0.01
Paralepididae				
M. prionosa	3	1.44	3	0.04
Myctophidae				
Electrona antarctica	3	1.44	30	0.43
E. carlsbergi	96	45.93	900	13.02
E. subaspera	44	21.05	403	5.83
Electrona sp.	15	7.18	24	0.35
Gymnoscopelus bolini	45	21.53	490	7.09
G. fraseri	127	60.77	1297	18.77
G. nicholsi	35	16.75	92	1.33
G. piabilis	141	67.46	1694	24.52
Gymnoscopelus sp.	55	26.32	145	2.10
Krefftichthyes anderssoni	34	16.27	762	11.03
Metelectrona ventralis	43	20.57	587	8.49
Protomyctophum bolini	8	3.83	101	1.46
P. choriodon	29	13.88	272	3.94
P. tenisoni	6	2.87	51	0.74
Protomyctophum sp.	4	1.91	6	0.09
Nototheniidae				
Dissostichus eleginoides	1	0.48	2	0.03
Gabionotothern marionensis	1	0.48	1	0.01
Microstomatidae				
Nansenia antarctica	1	0.48	1	0.01
Notosudidae				
Scopelareus ahlstromi	7	3.35	18	0.26
Scopelareus sp	1	0.48	1	0.01
Cephalopod	3	1.4	6	0.09
Unidentified otoliths	10	4.78	29	0.42

Electr

ona subaspera, G. bolini, G. nicholsi, M. ventralis and *P. choriodon* contributed more than 1.3 % NA which lead to an overall contribution of 26.6 % of NA in the scats. The remainder were minor prey species and rarely occurred in the diet of *A. tropicalis* (Table 5.3).

Otoliths that could be identified only to genus level, i.e *Electrona* (NA = 24), *Gymnoscopelus* (NA = 145), *Protomyctophum* (NA = 6) and *Scopelareus* (NA = 1) together formed 2.55 % NA. Unidentified prey species in the scats were few (n =29) and contributed 0.4% NA.

5.2.3. SEASONAL VARIATION

Scat collections were too irregular over the years (Table 5.1) to permit an investigation of monthly changes in their composition, but differences became evident when three different seasons (early summer, late summer and winter), were compared. When the data was partitioned into two seasons (summer and winter), there was a significant difference (ANOSIM; $P< 0.019$) between them. When the data was divided into three seasons (late summer, early summer and winter), there was a significant difference between winter and early summer ($P< 0.004$), and no significant difference ($P> 0.96$) between late summer and winter and a significance difference ($P< 0.004$) between early summer and late summer (c.f. Fig 5.1).

Diet composition showed clear seasonal differences when all the major fish prey species were compared. *Gymnoscopelus piabilis* was the most dominant prey species in all the seasons. The majority of *G. piabilis* primarily appeared in the scats during the first five months of the year (January to May), with the highest mean NA (54.5) in January, decreasing steadily over the last six months (June to December) (Table 5.4). *Gymnoscopelus fraseri* was also utilised in all the seasons, declining to a low %NA towards the end of the year, at a time when *Electrona carlsbergi* and *E. subaspera* rarely appeared in scats (Table 5.4).

Krefftichthyes anderssoni contributed substantially to the diet of these fur seals although it was not consistently taken. *Krefftichthyes anderssoni* was primarily utilised in January and October, being absent or rare at other times of the year (Fig 5.2). The remaining species (*M. ventralis* and *G. bolini*) occurred in the diet of *A. tropicalis* only during some months.

5.2.4. INTER-ANNUAL VARIATION

The major myctophid fish prey, *G. piabilis, G. fraseri* and *E. carlsbergi* occurred frequently and in large numbers in scats in all the years. *Gymnoscopelus piabilis* was the most dominant prey species in 1998 and 2000 with a mean NA of 43.2 and 18.9 respectively, decreasing to a low mean NA of 4.97 and 6.67 in 1996 and 1997 respectively. *Gymnoscopelus fraseri* was the second most preferred prey species in 1996 and 1997 respectively, decreased in 1998 and 1999 but picked up again in 2000 when it was the third most preferred prey.

Electrona carlsbergi also predominated in the diet of *A. tropicalis* in 1998 and in 2000 when it was the second most preferred prey species (mean NA of 15.3 and 21.2 respectively). But it was the third preferred prey species, at its lowest presence in 1996, 1997 and 1999 (mean NA of 3.3, 3.4 and 1.5 respectively). Other prey species contributed heavily to the diet and dominated in some years while some rarely occurring in other years, e.g. *E. subaspera, K. anderssoni, M. ventralis* and *P. choriodon* (Table 5.5).

Cephalopods first appeared in the diet during 1999 and 2000 in very low numbers, and constituted one of the minor prey species, while crustaceans were never isolated from the scats.

5.2.5. SIZE CLASSES OF FISH CONSUMED

The size class distribution of most of the prey species varied considerably. *Electrona subaspera* ranged between 50 mm to 130 mm, with a mean standard length (SL) of 83.6 mm, but the majorities were from 70 mm to 100 mm. The modal size of *E. subaspera* was from 60 mm - 105 mm and for *P. choriodon* the modal size was from 90 mm - 150 mm. For both prey species, the size distribution is skewed slightly towards mature fish. For the rest of the major prey species (*E. carlsbergi, G. fraseri, G. piabilis* and *K. anderssoni*), the size distribution of fish taken was unimodal and normally distributed.

Table 5.4: Mean numerical abundance (NA) of major fish prey species identified in the scats of *A. tropicalis* averaged on a monthly basis over a five year period (sample size represented in Table 5.3).

Months	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*M. ventralis*	*P. choriodon*
Jan	10.5	0.5	6.0	54.5	0.5	3.0
Feb	17.8	14.5	18.5	17.5	0.8	2.3
Mar	6.1	0.7	12.4	10.2	31.8	0.2
Apr	5.8	4.4	15.4	23.8	5.5	3.0
May	31.2	11.0	10.8	29.2	15.5	1.8
Jun	4.8	7.2	17.2	1.3	5.3	1.3
Jul	8.4	2.2	8.0	2.7	0.2	3.4
Aug	16.5	1.4	0.5	1.9	0.0	0.0
Sep	2.0	2.0	14.6	15.3	1.4	0.1
Oct	0.0	0.1	2.5	3.5	0.0	0.0
Nov	0.0	0.0	0.3	2.7	0.0	4.0
Dec	0.0	0.0	2.4	4.3	0.0	2.0

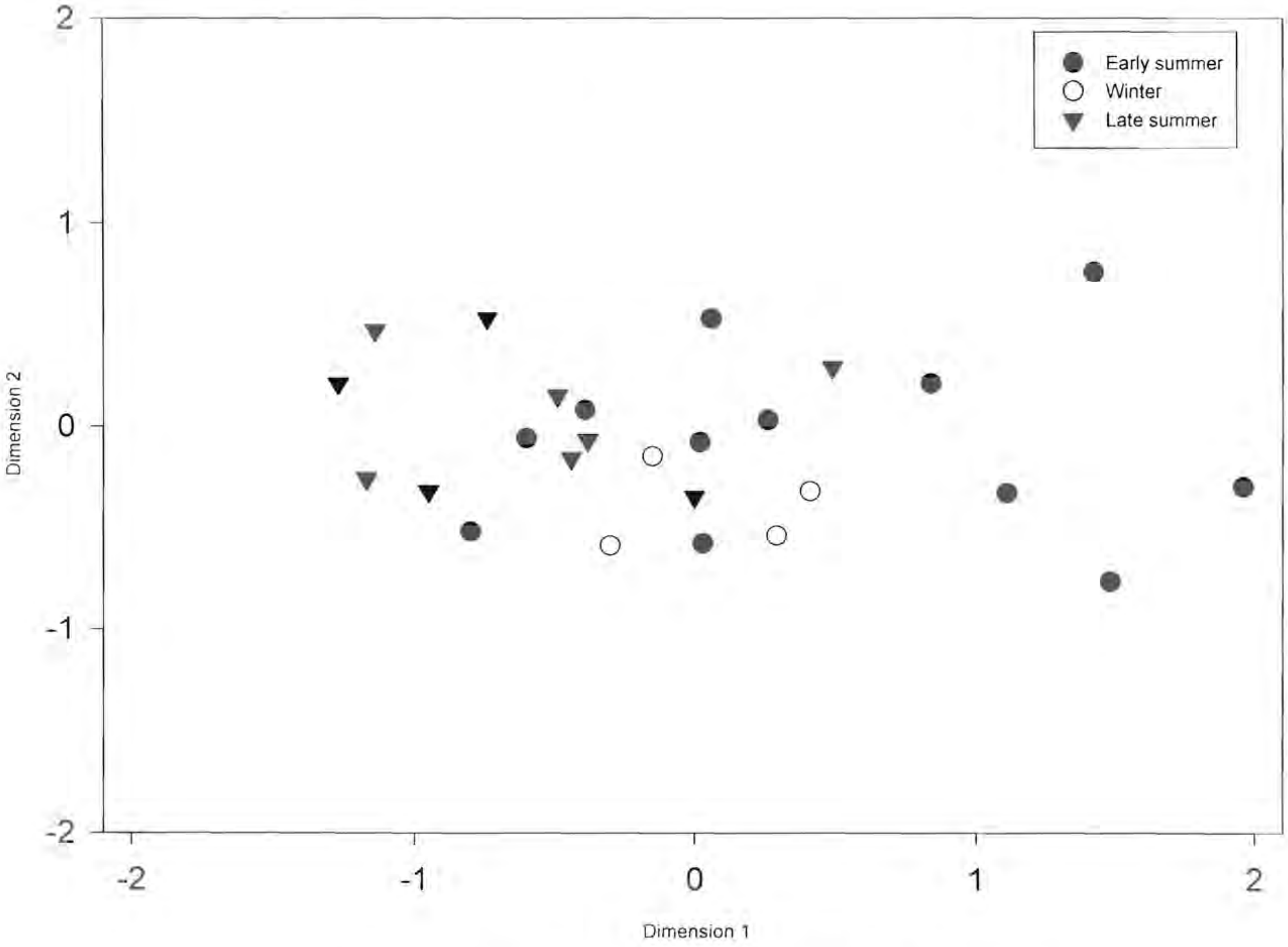

Fig. 5.1: Seasonal variation of prey species eaten by *A. tropicalis*.

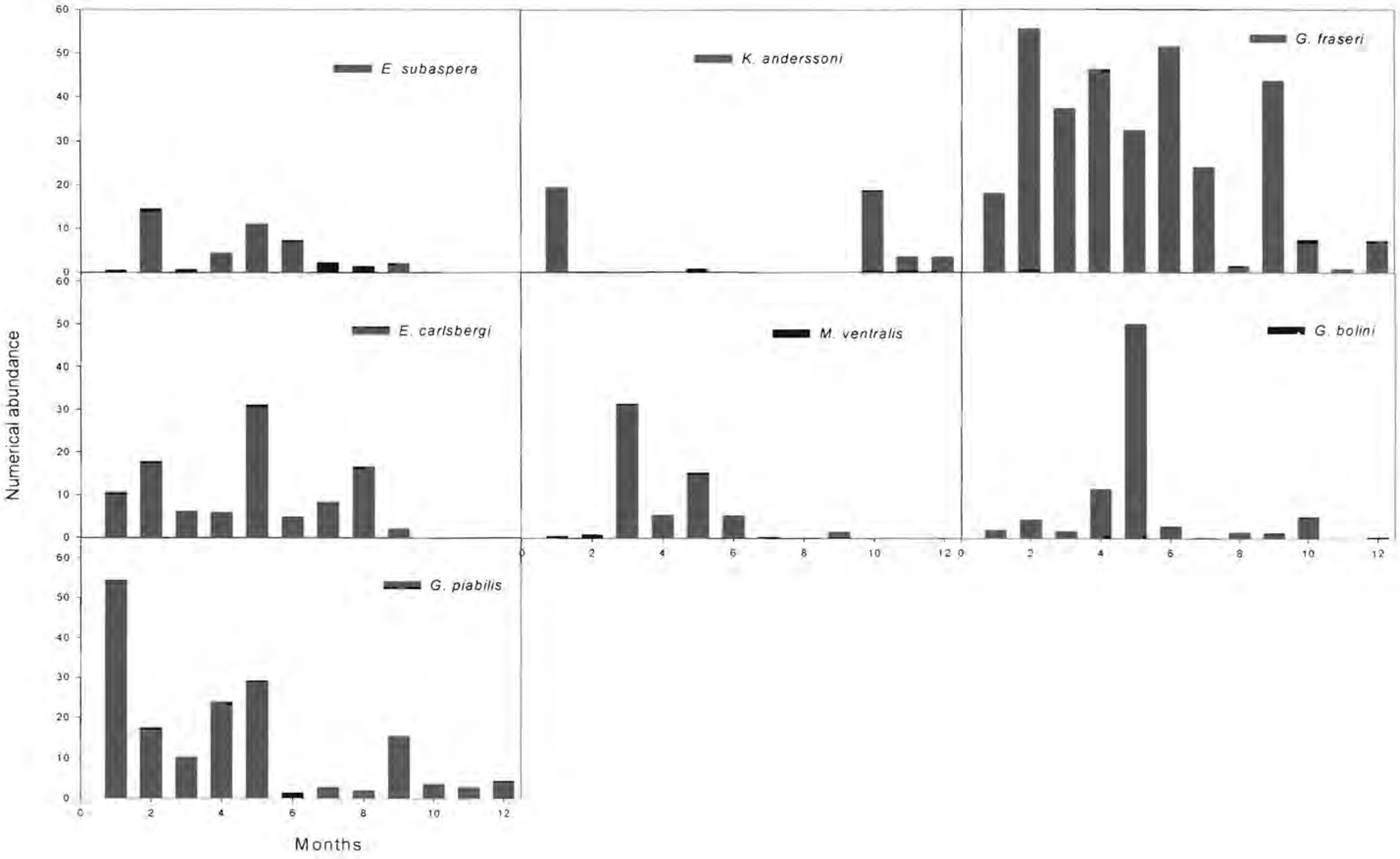

Fig. 5.2. Mean numerical abundance of major prey species eaten by *A. tropicalis*.

Table 5.5: Numerical abundances (NA) of prey species obtained from the scats of *A. tropicalis* averaged per year

Year	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*K. anderssoni*	*M. ventralis*	*P. choriodon*
1996	3.28	2.08	11.41	4.97	1.01	0.91	1.40
1997	3.42	0.17	13.67	6.67	0.00	0.75	3.50
1998	15.32	4.84	8.87	18.19	8.12	6.13	1.78
1999	1.55	1.10	6.20	8.46	2.14	9.49	1.60
2000	21.21	12.38	14.50	43.25	9.83	6.81	1.60

Compared to *E. subaspera*, the majority of *E. carlsbergi* utilised were smaller from 55 mm to 75 mm with a mean SL of 67.5 mm (Fig 5.3). The most preferred size of *M. ventralis* ranged from 70 mm to 90 mm. *Gymnoscopelus piabilis* was the most preferred *Gymnoscopelus* species and the majority were adults in the size range from 125 mm to 155 mm, with a mean SL of 136.84 mm (Table 5.6).

The majority of *K. anderssoni* utilised were between 43 mm and 53 mm in length, while those between 25 mm and 40 mm were eaten in very low numbers. *Gymnoscopelus fraseri* (n = 280) were most preferred in the size classes of 70 mm to 100 mm. Very few larger *G. fraseri* prey (100 mm to 130 mm, n = 20) were taken (Fig 5.3).

5.2.6. FISH MASSES

Dissostichus eleginoides, the heavier prey species, contributed the highest mass (198.55 g) to the diet of *A. tropicalis*. Only two *D. eleginoides* appeared in the scats. *Gymnoscopelus piabilis* was the second heaviest prey species taken by *A. tropicalis* with approximate mass ranging from 7.33 g – 50.97 g, followed by *E. subaspera* and *E. carlsbergi* with approximate mass between 1.86 g and 45 g. The majority of other major prey species eaten ranged from 0.14 g - 20 g with few prey species >20 g taken. The majority of *G. piabilis* eaten ranged from 20 g - 40 g (Table 5.6) while the most favoured size classes of *E. subaspera* ranged from 5 g - 20 g (NA = 44) and a few from 20 g - 45 g. *Kreffichthyes anderssoni* had the lowest mass ranging from 0.2 g – 1.8 g but contributed less by mass to the diet although it was taken in large numbers. *Electrona carlsbergi* individuals taken ranged between 5 g and 10 g while *G. fraseri*, also a major prey species in the scats of *A. tropicalis*, ranged from 5 g - 10 g (Fig 5.4).

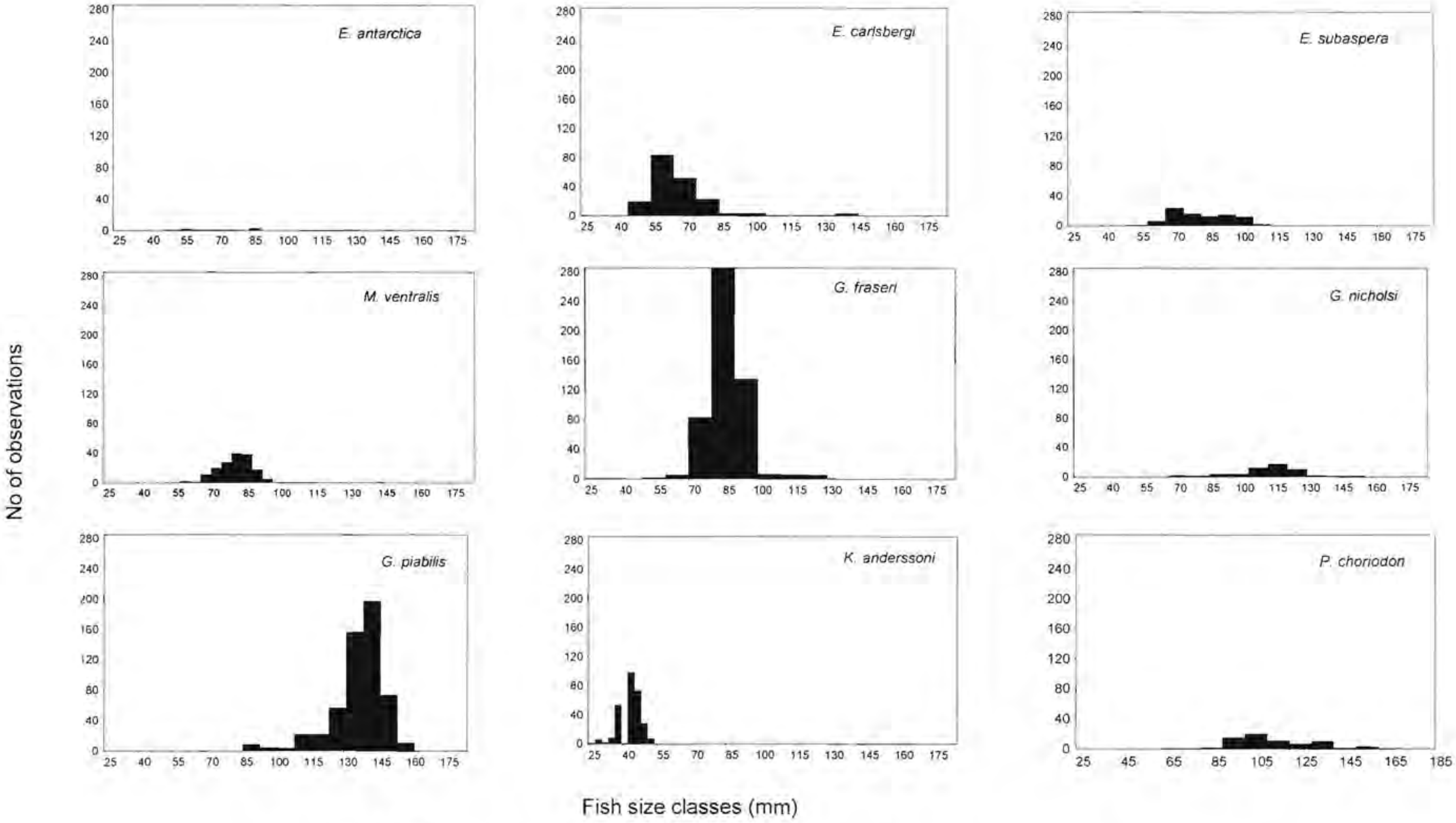

Fig. 5.3: Reconstituted size classes of fish species eaten by *A. tropicalis*.

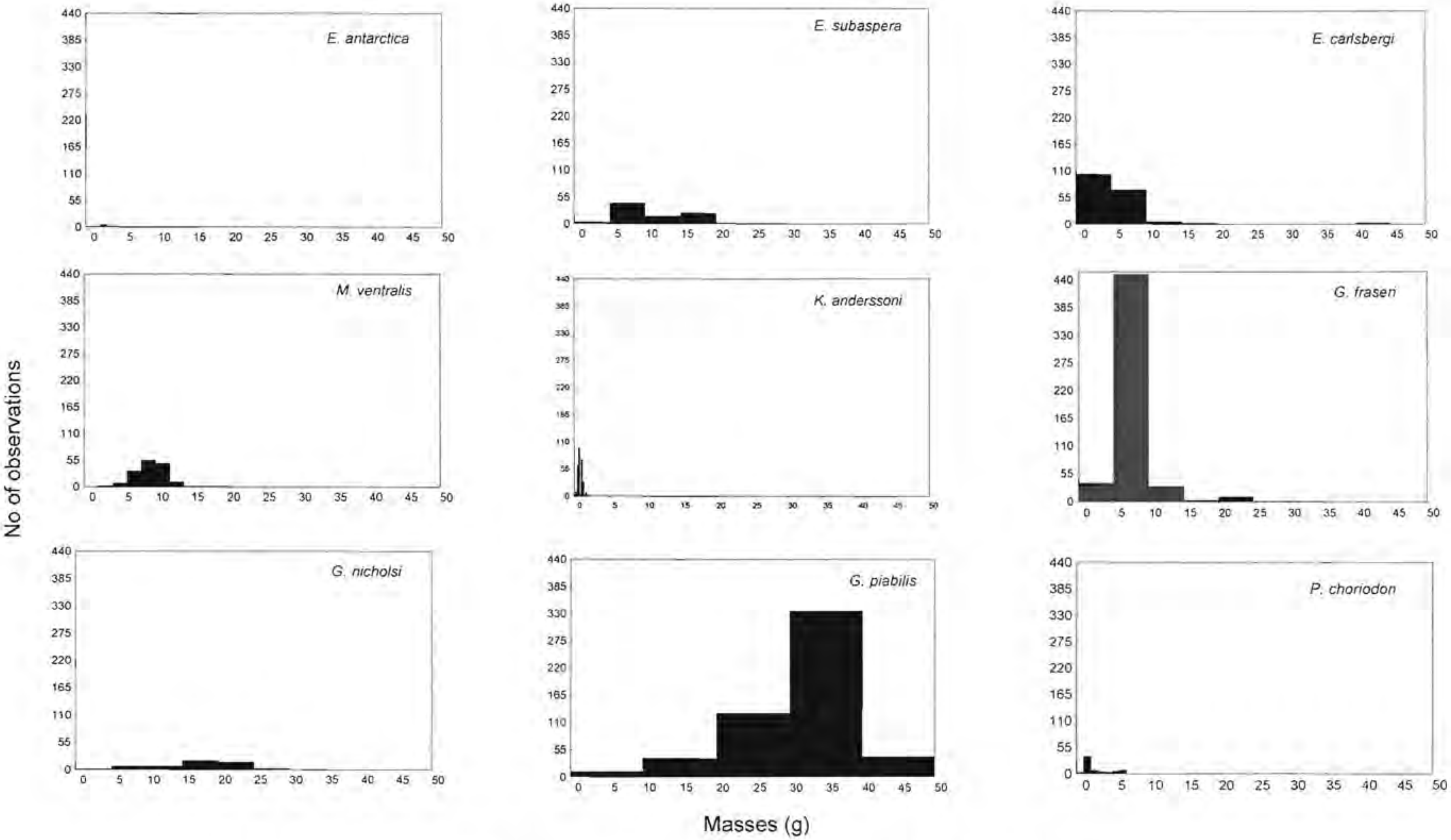

Fig. 5.4: Reconstituted masses of fish species eaten by *A. tropicalis*.

Table 5.6: Summary of standard lengths and masses of fish species consumed by *A. tropicalis* at Marion Island.

		Standard Length (mm)			Mass (g)		
Prey species	N	Average	S.D	Range	Average	S.D	Range
Champsocephalus gunnari	1						
Dissostichus eleginoides	2	248.89	0	0	198.55	0	0
Electrona antarctica	30	64.46	14.46	59.30-99.87	4.14	3.57	1.46-13.72
E. carlsbergi	900	67.50	14.63	45.71-146.30	6.08	5.62	1.86-44.84
E. subaspera	403	83.62	13.92	51.87-128.79	11.89	6.62	2.36-42.90
Metelectrona ventralis	587	81.67	6.93	58.28-102.29	9.25	2.08	3.61-16.84
Gymnoscopelus bolini	490	114.03	18.49	56.27-182.48			
G. fraseri	1297	86.37	9.02	30.04-132.80	7.64	2.85	0.28-27.98
G. nicholsi	92	112.76	16.02	68.21502495	17.65	7.32	340-47.27
G. piabilis	1694	136.84	11.84	85.98-161.60	31.26	7.17	7.33-50.97
Krefftichthys anderssoni	762	43.67	4.63	25.27-53.75	0.85	0.28	0.14-1.63
Magnisudis prionosa	3.00						
Nansenia antarctica	1.00						
Protomyctophum bolini	101	31.39	2.95	24.54-36.16	0.45	0.12	0.22-0.67
P. choriodon	272	69.21	17.35	43.04-112.68	3.00	2.84	0.70-14.50
P. tenisoni	51	75.24	8.02	63.38-93.17	6.65	2.27	3.78-12.44
Gabionotothern marionensis	1						
S. ahlstromi	29						

5.3. DISCUSSION

Census results and the haulout pattern of the fur seals (Kerley 1983) indicate that mostly lactating females deposited the scats at Cape Davis throughout the year. After the breeding season (December/January), subadults and non-breeding adults also hauled out onto the beaches (Kerley 1983), contributing to the scats in the study area. The total number of scats (n = 212) collected in the present study was much lower than those collected between 1989 and 1995 (n = 245) (Klages & Bester 1998), with a resultant lower number of fish otoliths isolated (n = 6910 versus n = 7067) (Klages & Bester 1998). This was the likely result of irregular collecting of scats in the present study.

5.3.1. DIET COMPOSITION

The diet of *A. tropicalis* has been studied at a number of different localities, namely Gough Island (Bester & Laycock 1985), Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997) and Marion Island (Rand 1956; Condy 1981; Klages & Bester 1998). At Gough Island, the diet of *A. tropicalis* was predominated by cephalopods, however, small quantities of fish also appeared in the stomach samples (Bester & Laycock 1985). In contrast, Condy (1981) found that the diet of *A. tropicalis* at Marion Island was constituted of about 50% cephalopods, 45% fish and 5% euphausiids. In the current study, however, fish species predominated the diet of this fur seal with only small numbers of cephalopods (%NA=0.09) obtained from the scats.

A predominance of fish in the diet of *A. tropicalis* at both Macquarie Island and Marion Island was also reported by Klages & Bester (1998) and Goldsworthy *et al.* (1997). Both studies showed that cephalopods were minor prey items as it had contributed little to the scats. The disparity in the diet of *A. tropicalis* amongst the different populations in all probability relates to the type of sampling; stomach contents at Gough Island (Bester & Laycock 1985), scats and stomach contents at Marion Island (Condy 1981) and scats only at Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997) and in later studies at Marion Island (Klages & Bester 1998; this study).

The lower number of prey components such as cephalopods might have been due to the likelihood of beaks accumulating in the stomachs of marine predators (Reid 1995, Klages & Bester 1998) or have been ejected by vomiting (Kirkman *et al.* 2000). The central tenet of scat analysis, that the solid prey remains pass into the faeces in the same proportions as they were consumed, may therefore not hold for squid beaks, more especially if they are of large size (> 10mm diameter) (Klages & Bester 1998). Therefore, scat analysis may be an unsuitable method to fully determine the contribution of cephalopods to the diet of fur seals resident on Marion Island (Klages & Bester 1998).

Based on the scats analysis, myctophid fish predominated in the diet of *A. tropicalis* at Marion Island as it did in the former study (Klages & Bester 1998) and at Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997). Amongst the myctophids, fish from the genus *Gymnoscopelus* spp. were also the most common species in the waters around Marion Island (Hulley 1990).

Pelagic myctophids which predominated the diet (*Electrona* spp., *Gymnoscopelus* spp., *Krefftichthys* spp. and *Protomyctophum* spp.) are characteristic of deep, offshelf water and can constitute the deep scattering layers, usually at 200 m to 500 m, the exception being *G. nicholsi* that can also be found near the bottom of the shelf (Green *et al.* 1997). The diel diving pattern and changes in dive parameters of *A. tropicalis* throughout the night, suggest that the fur seals follow the nycethemeral migrations of their main prey (Georges *et al.* 2000a).

Gymnoscopelus piabilis occurred frequently and is the most abundant prey species in the diet of *A. tropicalis*, possibly because it has a high calorific value, and therefore is presumably very rewarding. Goldsworthy *et al.* (1997) also reported *Gymnoscopelus* spp. as the major prey species in the diet of *A. tropicalis* at Macquarie Island. *Dissostichus eleginoides*, though absent in the previous study at Marion Island (Klages & Bester 1998), might have been taken opportunistically as only two were identified in the present study. Similarly, few specimens of *C. gunnari* appeared in the diet of *A. tropicalis* at Marion Island (Klages & Bester 1998; this study), and might have also been rarely available as they are usually found at depths of 150 m to 250 m (Everson *et al.* 1999). *Arctocephalus tropicalis* females only dive to depths of between 10 m to 20 m in summer which correspond to the oceanic mixed layer (Georges *et al.* 2000a), and may take *C. gunnari* on the occasion that it is attracted to the sea surface by the presence of potential prey such as myctophids and crustaceans (Nel *et al.* 2002). However, in winter they increased their diving depth pattern to between 20 m to 50 m (Georges *et al.* 2000a). In addition, males of *A. tropicalis* on occasion dive to 500 m (Georges *et al.* 2001) and this age/sex class in *A. tropicalis* may therefore be the source of scats containing *D. eleginoides* and *C. gunnari*. Interestingly, *C. gunnari* never appeared in scats of co-occcuring *A. gazella* at Marion Island (Klages & Bester 1998; this study), and presumably is not one of the most favoured prey species as it is large and have a low calorific value (Green *et al.* 1997).

5.3.2. SEASONAL VARIATIONS

Fish species dominated the diet of *A. tropicalis* in all the seasons at Marion Island. *Gymnoscopelus piabilis* and *G. fraseri* are generally the most favoured prey species overall, in particular in the summer diet of *A. tropicalis* despite the absence of *G. piabilis* in the diet during January. Goldsworthy *et al.* (1997) also found that *G. piabilis* predominated the summer diet of *A. tropicalis* at Macquarie Island. *Electrona carlsbergi* and *E. subaspera* predominated the winter diet of *A. tropicalis* at Marion Island as it did in the previous study (Klages & Bester 1998).

Most prey species decreased to very low numbers in scats in early summer as well as in winter, but were more abundant in late summer. This seems to coincide with the seasonal haulout pattern of fur seals at Marion Island where lactating females and breeding males haul out at the breeding sites in numbers and lactating female have already begun with their foraging trips during the late summer. In addition, the scarcity of prey species in scats during winter might have resulted from both more scats being washed away by heavy rainfall and also changes in high tides, waves and swells during winter months when storms become more frequent (Lutjeharms 1990). Lactating females have substantially longer foraging trips during winter (Kirkman *et al.* 2002), which lead to a low number of scats deposited on the beaches. Pup mortality which exceeds 10 % in the first 6 weeks of life (Bester 1987; Kerley 1987, Georges & Guinet 2000) also takes its toll, decreasing the number of lactating females regularly visiting the study area (Bester & Bartlett 1990). Relatively low numbers of both sexes and various age classes of this fur seal species are present in winter (Kerley 1983; Hofmeyr *et al.* 1997). In addition, high production of prey species is determined by the stability of water; therefore, the scarcity in abundance of prey species in winter might have been influenced by the instability in the marine environment (Lutjeharms 1990), such a change in their distribution and abundance probably forced lactating females to forage at greater distances from the island in winter (Georges & Guinet 2000; Georges *et al.* 2000b; Kirkman *et al.* 2002), and voiding dietary prey remains at sea (Staniland 2002).

5.3.3. INTER-ANNUAL DIFFERENCES

The variation in prey species taken over the years were similar, although they differ according to frequency of occurrence and in relative contribution to prey composition. This might have been because the same species are not equally abundant in the foraging zone around Marion Island. However, the higher number of the major prey species retrieved in 2000 as compared to other years may have been the result of an increased effort in collecting scats. The fact that major prey such as *G. piabilis*, *G. fraseri* and *E. carlsbergi* occurred more frequently and in larger numbers in scats during 2000 and 1998, compared to 1996 and 1997, may reflect variation in prey availability between the years. Environmental factors such as El Niño may also affect the prey abundance at these latitudes (Guinet *et al.* 1994) and cause differences amongst the years. Furthermore, changes in oceanic conditions or circulation also may seem to be responsible for the fluctuations in prey abundance from year to year (Lutjeharms 1990).

5.3.4. FISH SIZE AND MASS CLASSES CONSUMED

The range of fish size and mass classes of prey selected by *A. tropicalis*, from 24.54 mm and 0.22 g (*P. bolini*) to 182.48 mm and 161.60 mm (*G. bolini* and *G. piabilis* respectively) and 24.54 g (*G. piabilis*) was narrower than in the previous studies ((26 mm and 0.2 g for *P. tenisoni* to 230 mm for *Paradiplospinus gracillis*) and 49.8 g (*G. piabilis*)) at Marion Island (Klages & Bester 1998). This might have been because few otoliths of prey species that are larger in size and mass have been eaten by *A. tropicalis* in the previous years, and they have contributed heavily to the size and mass of prey.

Gymnoscopelus piabilis appeared to be the most rewarding prey for *A. tropicalis* as it was the largest with a high calorific value (Green *et al.* 1997). The majority of *G. piabilis* taken were adults as they mostly matured at 99 mm (Hulley 1990) and were taken in the range from 85 mm to 165 mm. This suggests that *A. tropicalis* might be feeding in shallow water as well as in deeper layers, which might be related to a possible vertical segregation of prey size classes in the water column. The smaller sized prey can probably be found in shallow water while larger sized prey might be found in both shallow and deeper layers (Green *et al.* 1997). *Gymnoscopelus fraseri* taken ranged from juvenile to adult fish. Other prey species, *P. choriodon* and *P. tensioni*, were all adults as the majority mature at 77 mm and 45 mm respectively (Hulley 1990).

5.3.5. PREDATION ON PENGUINS

Arctocephalus tropicalis on Marion and Gough Islands were never recorded to supplement their diet with penguins (Condy 1981; Bester & Laycock 1985; this study), although they occasionally kill or injure rockhopper penguins *Eudyptes chrysocome* at Gough Island (Bester 1977). At Amsterdam Island, however, rockhopper penguins were taken at sea (Paulian 1964) and penguin remains were reported in the scats of a mixed population of *A. gazella* and *A. tropicalis* at Macquarie Island (Green *et al.* 1990).

Chapter 6: Comparison of the diet of Antarctic fur seals (*Arctocephalus gazella*) and Subantarctic fur seals (*A. tropicalis*) at Marion Island

6.1. INTRODUCTION

Seals are important top predators in most marine ecosystems, especially in the southern ocean (Laws 1977; North *et al.* 1983). Therefore, the study of the diet of seals is fundamental to the assessment of their role as predators in the southern ocean marine ecosystem. Such studies may also provide information about potential competition for food resources among predator species and between these and commercial fisheries (Croxall 1993; Daneri & Carlini 1999). However, it is difficult to obtain appropriate data for assessing the diet quantitatively (North *et al.* 1983), and accurate quantitative data are required for the assessment of the role of marine mammals in food chains (Staniland 2002). The analysis of pinniped scats has been used to quantify their diet using prey remains to identify species and to estimate the number and sizes of prey consumed (North *et al.* 1983), despite the problem associated with the method (Brown & Pierce 1998).

Two species of otariid, the Subantarctic fur seal *Arctocephalus tropicalis* and the Antarctic fur seal *A. gazella* breed on Marion Island (Condy 1978; Klages & Bester 1998). Although these species were considered to be conspecific (King 1983), they are now treated as distinct species. Each species occupied its own breeding sites on the island (Watertunnel Stream for *A. gazella* and Cape Davis for *A. tropicalis*) although some hybridisation occurs in colonies (Kerley 1984) where they overlap. The timing of the pupping season is similar in both *A. gazella* and *A. tropicalis* (Kerley 1983, 1987; Bester & Bartlet 1990; Goldsworthy *et al.* 1997), however, the duration of lactation is very different. *Arctocephalus gazella* adult females give birth over a shorter time period and, on average, ten days earlier than *A. tropicalis* at Marion Island where the median birth dates of the two species were found to be 6 and 17 December respectively (Kerley 1983). In addition, *A. gazella* pups grow rapidly (Kerley 1984) and are weaned at about 112 days (approximately four months of age, in early March) at Marion Island. *Arctocephalus tropicalis* pups have a slower growth rate and more protracted lactation period. They are weaned at ±300 days of age (approximately 8 to 10 months, in September) (Kerley 1984). The foraging strategies of the two species have been studied at various sites, including a few studies on the diet of the two fur seals where they occur sympatrically, e.g. Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997) and Marion Island (Klages & Bester 1998).

Identifying and measuring fish otoliths recovered from faeces (Brown & Pierce 1998) has been the main method for assessing fish in diets of seals from around Marion Island (Klages & Bester 1998), although stomach contents have also been investigated (Croxall & Pilcher 1984; Bester & Laycock 1985; Pierce & Boyle 1991; Klages & Bester 1998), and is associated with several important sources of error. Nevertheless, analysis of faeces probably represents the single best method available to assess the diet of seals (Brown & Pierce 1998) and is the method of choice for the present study. The present study aims to compare and assess the diet of the two fur seals species breeding sympatrically at Marion Island. This includes investigating possible interspecies differences and examining seasonal and annual variations in the diets of the two fur seal species.

6.3. RESULTS

A total of 471 scats were collected from May 1996 to April 2000 on the breeding colonies known to be occupied exclusively by either species of fur seals, namely, Watertunnel Stream for *A. gazella* and Cape Davis for *A. tropicalis*. Most scats were collected between January and April in each year for *A. gazella*, which coincided with the annual haulout (Table 6.1). For *A. tropicalis* the number of scats found per month was more erratic (Table 6.1). The number of scats collected varied between months and years (Table 6.1), the highest numbers collected for both species being in 1998 (n=126), followed by 1999 (n=117). In 2000 the lowest number of scats (n=59) were encountered.

6.3.1. DIET COMPOSITION

A total of 14300 otoliths were recovered from the 471 scat samples of the two species of fur seal of which 53 were unidentifiable; the remainder were identified to at least family and genus level. Only 7 crustaceans and 11 cephalopods were retrieved from the scats of the fur seals. Fish remains in the form of otoliths occurred in almost every scat. Otoliths were found in 458 scats, accounting for a FO of 96.1 % for all scat samples while crustaceans and cephalopods were minor components of the diet occurring in only 7 scats (FO = 2.7 %) and 3 scats (FO = 1.2 %) respectively (Table 6.1).

Fish (n = 7150) were the main dietary items taken by the fur seals, contributing 99.87 % NA while crustaceans and cephalopods contributed only 0.05 % and 0.08 % NA (Table 6.2).

Table 6.1: Number of scats collected from *Arctocephalus gazella* (A.g) and *A. tropicalis* (A.t) at Marion Island.

Months	1996		1997		1998		1999		2000		Totals	
	A.g	A.t	A.g	A.t	A.g	A.t	A.g	A.t	A.g	A.t	A.g	A.t
Jan			9		11		10	2	6	9	36	11
Feb			8	8	7		1	1	5	6	21	15
Mar			7	6	10		22	11	4	4	43	21
Apr			5		7	15	9	8	11	14	32	37
May	10		12		14	27	9	3			45	30
Jun	13	11			6						19	11
Jul	8	8	4		1	6					13	14
Aug			11			4	2				13	4
Sep	1	9	11			9	6	13			18	31
Oct		5	4			7	4	1			8	13
Nov		6			2			7			2	13
Dec	6	7					2	6			8	13
Sums	38	46	71	14	58	68	65	52	26	33	258	213

Table 6.2: Percentage numerical abundance (% NA) and frequency of occurrence (FO) of prey species appearing in scat samples of *A. gazella* and *A. tropicalis* at Marion Island.

Prey items	Fish	Crustacean	Cephalopod	Total
FO	458	7	6	471
%NA	99.87	0.05	0.08	100

6.3.2. INTERSPECIFIC COMPARISONS

Twenty-one species of fish were identified from sagittal otoliths (Table 6.3) in the scats of both fur seals species combined. *Arctocephalus gazella* has a slightly more diverse diet (20 versus 18 taxa), but the two predators still shared 17 out of 21 taxa. These shared prey species contributed more than 99 % of the numerical abundance (NA) of fish prey. Otoliths of the mesopelagic fish family Myctophidae (lantern fish) were by far the most numerous (98.1 % NA) hard prey components identified in the scats of the fur seals, with up to eight different species making up an individual scat. Fish from other families were rare contributing 1.9 % of numerical abundance to the diet of *A. tropicalis* and *A. gazella* (Table 6.3).

No significant difference was found between the diets of the two fur seal species as prey species lists and numerical compositions of the scats from both showed much similarity (two-way nested analysis: $p > 0.5$; $p = 45.5$ %). For both *A. gazella* and *A. tropicalis*, otoliths from the genera *Gymnoscopelus* (NA = 8032) and *Electrona* (NA = 3903) were most numerous (Table 6.3). Diets of both species of fur seals were dominated by *G. piabilis* (NA = 34 % and 24 %), *G. fraseri* (NA = 12.7 % and 18.8 %) and *E. carlsbergi* (NA = 13.4 % and 13.2 %) for *A. gazella* and *A. tropicalis* respectively. Minor differences in their diets were that *Champsocephalus gunnari* was utilised by *A. tropicalis* only while *Lepidonotothen larseni, Paradiplospinus gracillis* and *Paranotothenia magellanica* were eaten by *A. gazella* only.

6.3.3. TEMPORAL DIFFERENCES IN DIET

6.3.3.1. Monthly variations

When the diet of the two species was considered on a monthly basis, no significant difference was found between the two fur seals species (two-way nested analysis: $p > 0.5$; $p = 45.5$ %). This is despite the highly significant difference between months for the combined diet of both fur seals species (two-way nested analysis: $p < 0.5$; $p = 0.2$ %). There was an enormous temporal fluctuation in the frequency of occurrence of the major prey genera (*Electrona* spp., *Gymnoscopelus* spp. and *Protomyctophum* spp.*)* and other items (representing all those genera that appeared only once), between January and December (Fig 6.1). Otoliths from *Electrona* spp. declined steadily in % NA from 57.08 % in January to 0.05 % in October, while otoliths from *Gymnoscopelus* spp. occurred frequently in all the months, varying from 34.8 % to 75.6 %. Fish from the genus *Protomyctophum* spp. and other genera occurred in very low numbers although a slight increase was observed from October to November and September to October for *Protomyctophum* spp. and other genera respectively (Fig. 6.1).

Table 6.3: Frequency of occurrence (FO) and numerical abundance (NA) of fish species identified in the scats sampled from both fur seals species at Marion Island.

	Overall (n = 458)				*A. gazella* (n = 249)				*A. tropicalis* (n = 209)			
Prey species	FO	NA	%FO	%NA	FO	NA	%FO	%NA	FO	NA	%FO	%NA
Channichthyidae												
C. gunnari	1	1	0.21	0.01					1	1	0.48	0.01
Myctophidae												
E. antarctica	7	43	1.49	0.30	4	13	1.61	0.18	3	30	1.44	0.43
E. carlsbergi	190	1893	40.34	13.24	94	993	37.75	13.44	96	900	45.93	13.02
E. subaspera	101	1070	21.44	7.48	55	667	22.09	9.03	44	403	21.05	5.83
Electrona spp.	35	109	7.43	0.76	20	85	8.03	1.15	15	24	7.18	0.35
G. bolini	95	818	20.17	5.72	50	328	20.08	4.44	45	490	21.53	7.09
G. fraseri	226	2234	47.98	15.62	102	937	40.96	12.68	127	1297	60.77	18.77
G. nicholsi	68	414	14.44	2.90	34	322	13.65	4.36	35	92	16.75	1.33
G. piabilis	300	4213	63.69	29.46	159	2519	63.86	34.09	141	1694	67.46	24.52
Gymnoscopelus spp.	109	339	23.14	2.37	54	194	21.69	2.63	55	145	26.32	2.10
K. anderssoni	66	1313	14.01	9.18	32	551	12.85	7.46	34	762	16.27	11.03
M. ventralis	37	787	7.86	5.50	32	200	12.85	2.71	43	587	20.57	8.49
P. tenisoni	11	66	2.34	0.46	5	15	2.01	0.20	6	51	2.87	0.74
P. bolini	14	138	2.97	0.97	7	37	2.81	0.50	8	101	3.83	1.46
P. choriodon	78	591	16.56	4.13	49	319	19.68	4.32	29	272	13.88	3.94
Promyctophum spp.	4	6	0.85	0.04					4	6	1.91	0.09
Nototheniidae												
G. marionensis	13	77	2.76	0.54	12	76	4.82	1.03	1	1	0.48	0.01
D. eleginoides	4	17	0.85	0.12	3	15	1.20	0.20	1	2	0.48	0.03
L. larsen	1	45	0.21	0.31	1	43	0.40	0.58				
Notothenia spp.	3	4	0.64	0.03	3	4	1.20	0.05				
P. magellanica	4	18	0.85	0.13	4	18	1.61	0.24				
Paralepididae												
M. prionosa	5	11	1.06	0.08	2	8	0.80	0.11	3	3	1.44	0.04
Gempylidae												
P. gracillis	1	1	0.21	0.01	1	1	0.40	0.01				
Microstomatidae												
N. antarctica	2	8	0.42	0.06	1	7	0.40	0.09	1	1	0.48	0.01
Notosudidae												
S. ahlstromi	9	32	1.91	0.22	2	14	0.80	0.19	7	18	3.35	0.26
Scopelareus spp.	1	1	0.21	0.01					1	1	0.48	0.01
Unidentified otoliths	20	51	4.25	0.36	12	24	4.82	0.32	10	29	4.78	0.42

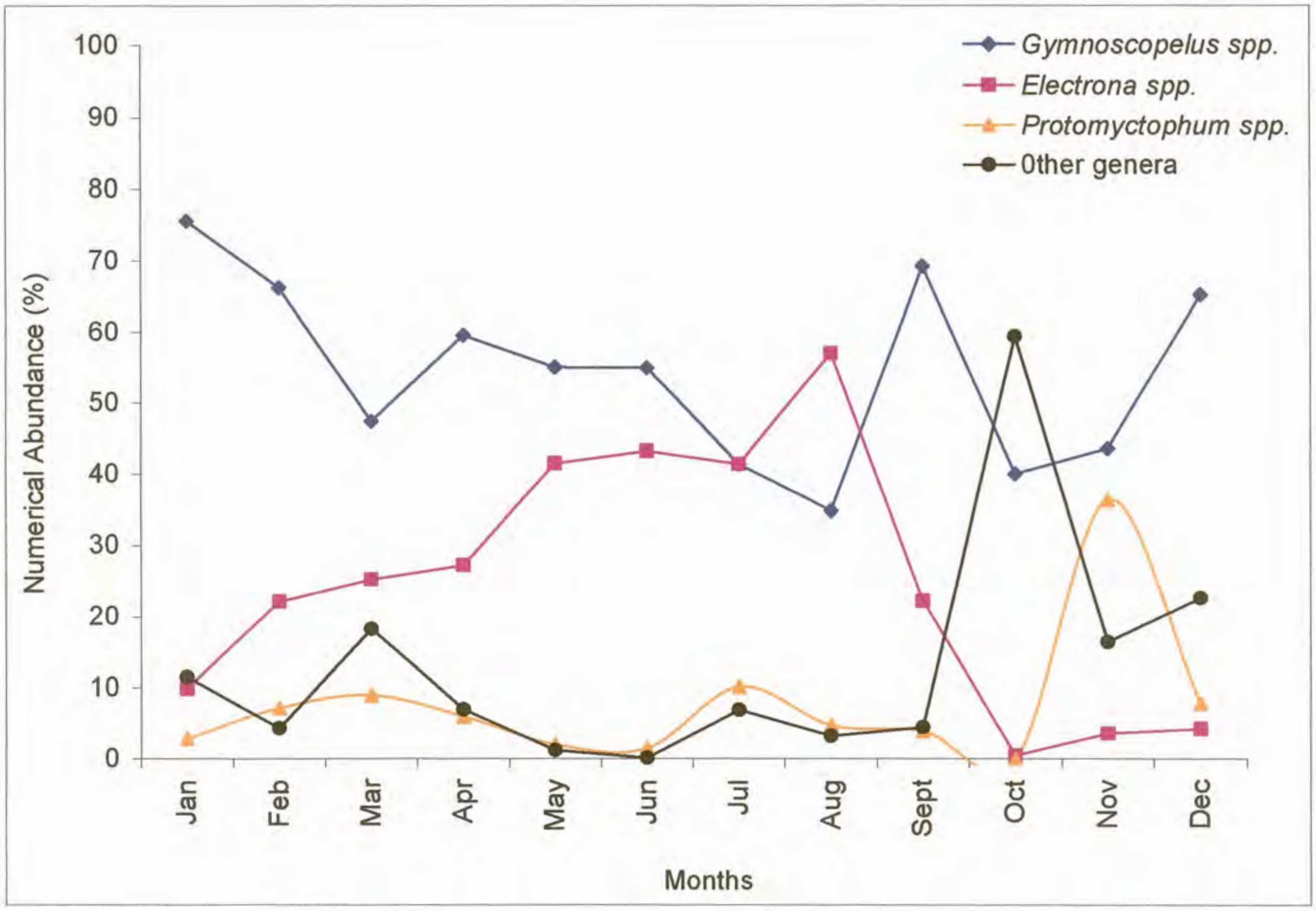

Fig. 6.1: Temporal changes in the numerical abundance of the most common fish genera taken by *A. gazella* and *A. tropicalis* at Marion Island.

Within *A. tropicalis*, the mean numerical abundance of *E. carlsbergi* was much higher in January, February, May and August (10.5, 17.83, 31.20 and 16.5 respectively), but declined significantly between October and December to 0.03, 0.05 and 0.04 respectively (Table 6.4). *Electrona subaspera* were utilised more in February, May and June with average numerical abundances of 14.5, 11 and 7.17 respectively (Fig. 6.2) but decreased to a low from October to

December. *Gymnoscopelus piabilis* and *G. fraseri* dominated the diet throughout the year, with the lowest prey consumption between June and August for *G. piabilis*, and August and November for *G. fraseri*. The latter two prey species were equally consumed during September and February (Table 6.4).

In *A. gazella*, *E. subaspera* were utilised more in April and July (mean numerical abundances of 30 and 21.71 respectively) while *E. carlsbergi* were preferred more in April and May (mean numerical abundances of 51.25 and 20.20 respectively). The mean numerical abundance of *E. subaspera* then declined to zero between September and December with a similar trend in *E. carlsbergi* over the same period (Fig. 6.3). *Gymnoscopelus piabilis* were eaten throughout the year with the lowest numerical abundance in August followed by a slight increase in October and November and then a decline to zero in December. Subsequently, the mean numerical abundance of *G. piabilis* was higher (108.5) in January, decreased steadily to 0.86 in July, and fluctuated between August and November with very low averages (0.56 - 8.31) (Table 6.5).

6.3.3.2. Inter-seasonal variations

A significant difference (ANOSIM; $P< 0.001$) existed between the late summer, winter and early summer diets of both fur seals species (averaged across all species groups) in prey utilization (c.f. 6.4).

Table 6.4: Mean numerical abundances (NA) of major prey species identified in the scats of *A. tropicalis* on a monthly basis at Marion Island.

Months	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*M. ventralis*	*P. choriodon*
Jan	10.5	0.5	6.0	54.5	0.5	3.0
Feb	17.8	14.5	18.5	17.5	0.8	2.3
Mar	6.1	0.7	12.4	10.2	31.8	0.2
Apr	5.8	4.4	15.4	23.8	5.5	3.0
May	31.2	11.0	10.8	29.2	15.5	1.8
Jun	4.8	7.2	17.2	1.3	5.3	1.3
Jul	8.4	2.2	8.0	2.7	0.2	3.4
Aug	16.5	1.4	0.5	1.9	0.0	0.0
Sep	2.0	2.0	14.6	15.3	1.4	0.1
Oct	0.0	0.1	2.5	3.5	0.0	0.0
Nov	0.0	0.0	0.3	2.7	0.0	4.0
Dec	0.0	0.0	2.4	4.3	0.0	2.0

Table 6.5: Mean numerical abundance (NA) of prey species identified in the scats of *A. gazella* on a monthly basis at Marion Island.

Months	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*M. ventralis*	*P. choriodon*
Jan	5.5	3.0	7.0	108.5	7.5	2.3
Feb	3.1	2.8	18.0	51.9	3.9	1.1
Mar	2.5	5.1	4.1	36.1	0.5	13.1
Apr	51.3	30.0	77.5	57.5	25.5	14.3
May	20.2	5.0	12.3	22.6	2.5	2.0
Jun	6.6	6.5	3.6	16.6	0.4	0.2
Jul	1.0	21.7	0.1	0.9	0.1	0.3
Aug	7.6	8.6	2.1	8.3	0.1	2.1
Sep	1.6	1.8	0.3	0.6	0.0	0.2
Oct	0.1	0.0	0.0	4.9	0.0	0.0
Nov	0.9	0.0	0.4	6.5	0.0	0.0
Dec	0.0	0.0	0.0	0.0	0.0	0.0

Both fur seal species are feeding on the same prey in different proportions in the three seasons (Fig 6.4). All seven most common prey species, that together contributed approximately 96 % of NA in the diet of *A. gazella* and 92.7 % of NA in the diet of *A. tropicalis*, appeared in all three seasons. Comparing the summer (early summer and late summer combined) diets of both fur seals species, *A. tropicalis* preyed more on *G. fraseri* (13.81 %), *K. anderssoni* (26.38 %) and *M. ventralis* (10.34 %) while the *A. gazella* summer diet was dominated by *G. piabilis* (50 % NA). No major difference existed in the utilisation of prey species during winter for both fur seal species although there were some little variations in the relative consumption of some prey. Both fur seal species utilised other prey species in more or less similar proportions (Table 6.6).

There were seasonal variations in the utilization of some of the prey species. The utilization of *E. carlsbergi, E. subaspera, G. bolini* and *G. fraseri* by both *A. tropicalis* and *A. gazella* were higher in winter than in early and late summer. During the winter season, *A. tropicalis* predominantly fed on *E. subaspera* (7.45 %), *G. fraseri* (22.17 %) and *G. piabilis* (26.56 %) whereas there was a 50 % decrease in consumption of *G. piabilis* to 23.39 % by *A. gazella*, with a concomitant increase in other major prey species (Table 6. 6). *Krefftichthys anderssoni* seemed to be utilized more in summer by both *A. tropicalis* and *A. gazella* (NA of 26.38 % and 14.88 % respectively). There was a seasonal fluctuation in the utilisation of *G. piabilis* by *A. tropicalis* as well as *A. gazella*. The utilisation of this prey species was considerably more in winter (Table 6.6). For *A. gazella* the utilisation of *G. piabilis* was more in summer with approximately 50 % of what had been eaten in summer being taken in winter (Table 6.6).

Table 6.6: Seasonal trend in percentage numerical abundances (% NA) of the major prey species in the diet of both *A. tropicalis* and *A. gazella* at Marion Island.

	A. tropicalis		*A. gazella*	
Prey species	Summer	Winter	Summer	Winter
E. antarctica	0.89	0.12	0.10	0.23
E. carlsbergi	6.59	17.45	2.96	20.37
E. subaspera	3.47	7.45	3.20	12.88
G. bolini	4.14	9.12	4.41	4.43
G. fraseri	13.81	22.17	7.95	15.78
G. nicholsi	0.74	1.74	3.77	4.73
G. piabilis	21.49	26.56	49.83	23.39
K. anderssoni	26.38	0.42	14.88	2.45
M. ventralis	10.34	7.21	1.21	3.67
P. bolini	2.02	1.08	1.14	0.07
P. choriodon	5.63	2.76	5.89	3.24
P. tenisoni	0.32	1.03	0.07	0.29

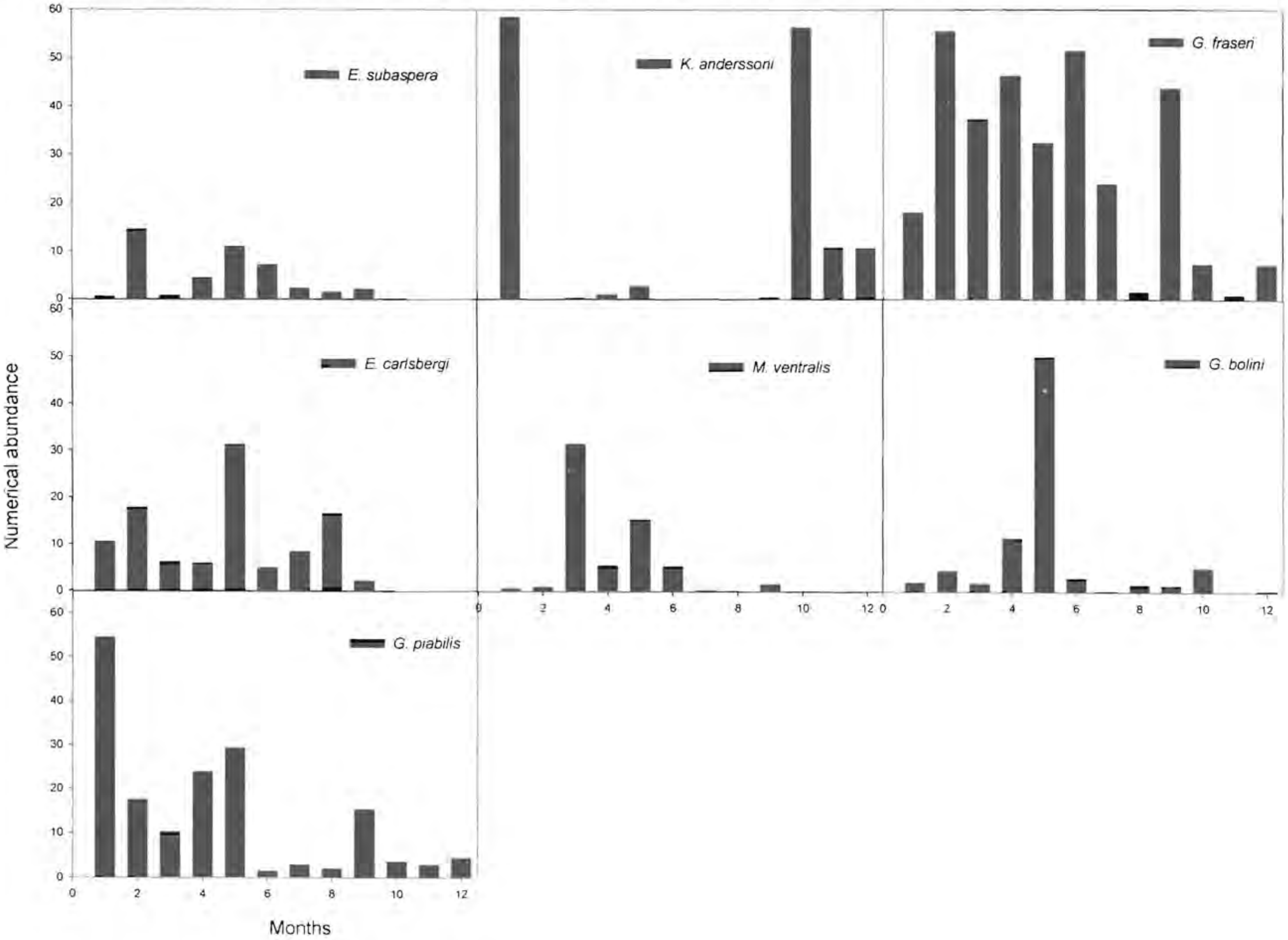

Fig. 6.2: Mean numerical abundance of major prey species eaten by *A. tropicalis*.

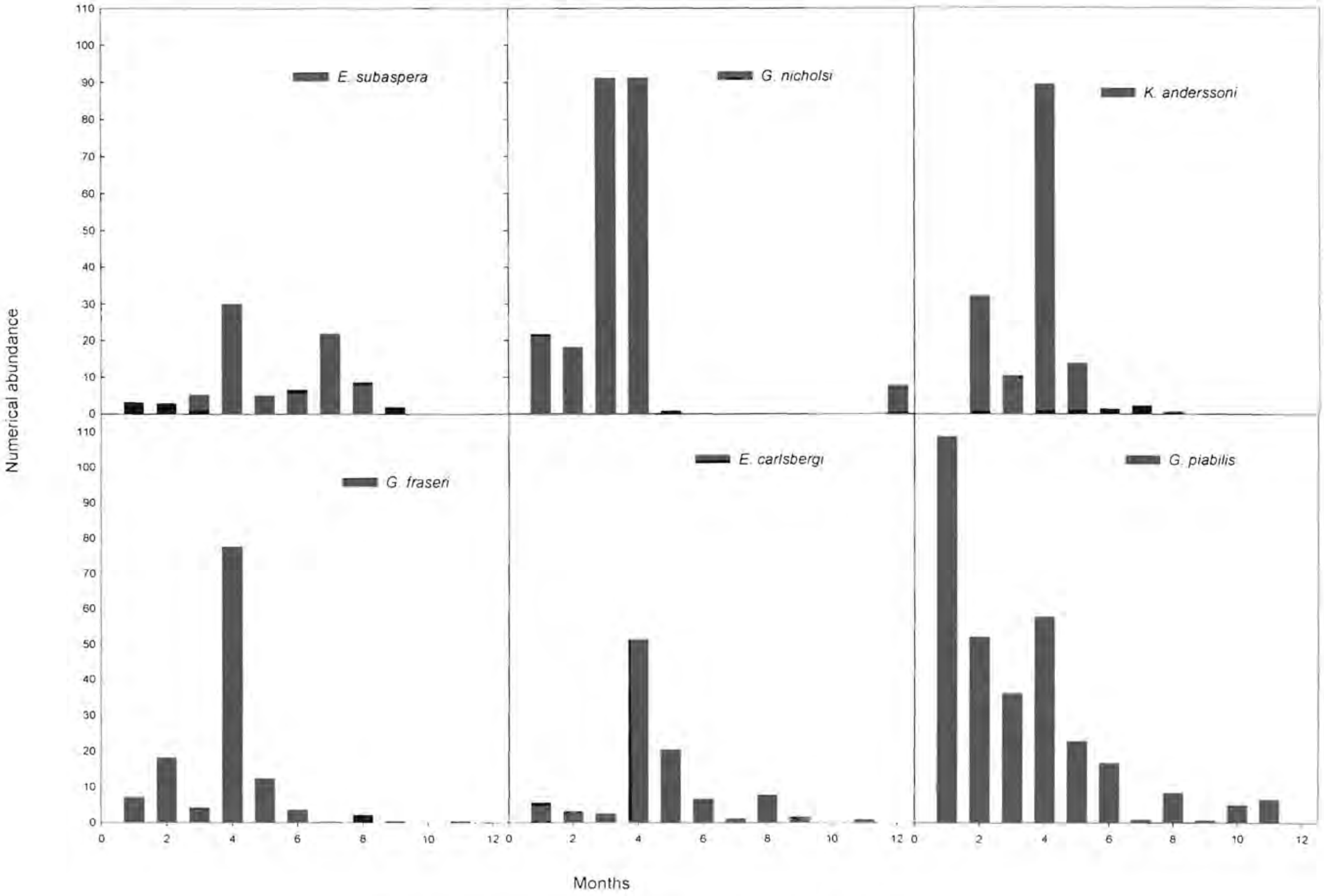

Fig. 6.3. Mean numerical abundance of prey species eaten by *A. gazella*.

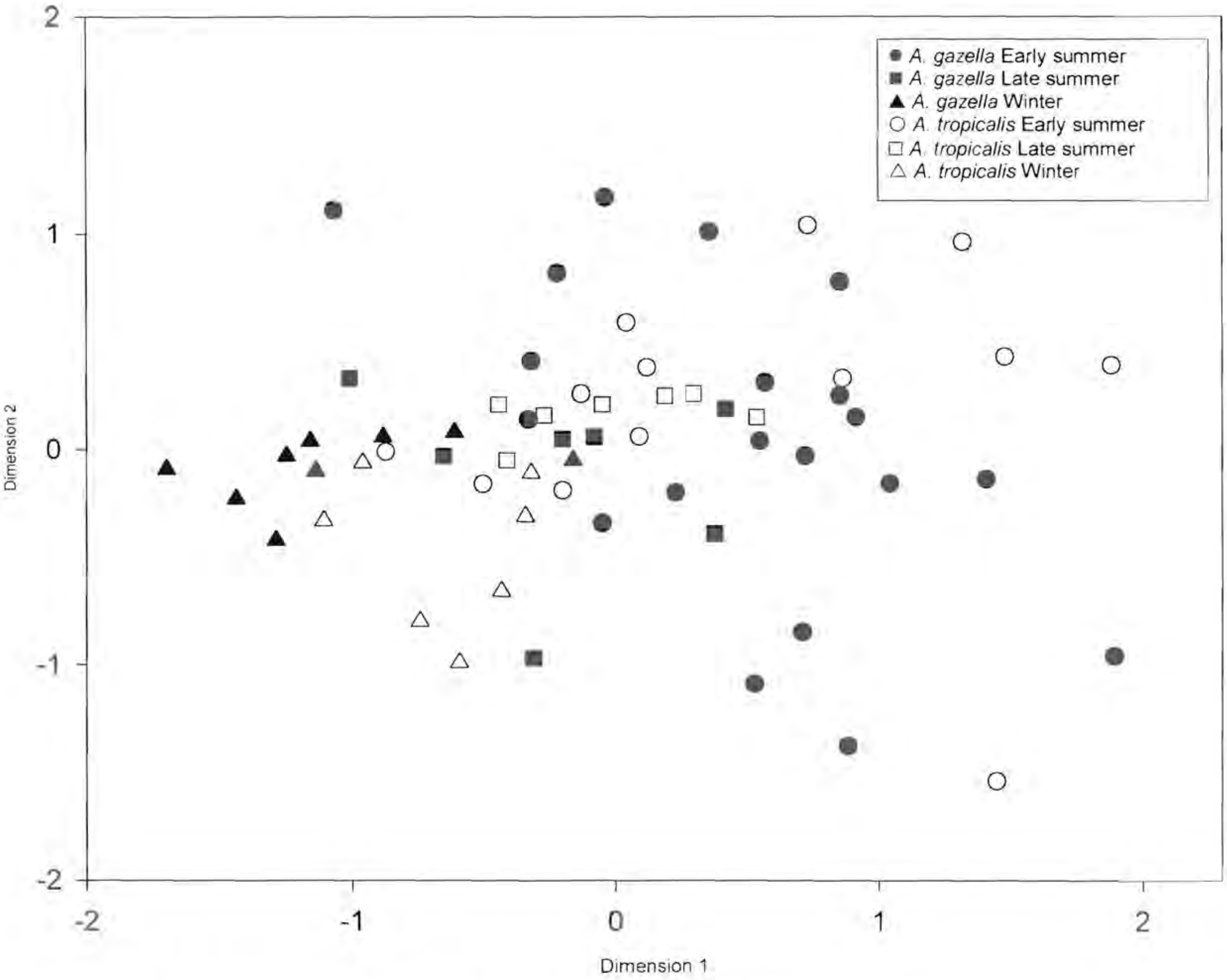

Fig. 6.4 Seasonal variation in prey species eaten by *A. gazella* and *A. tropicalis* at Marion Island.

6.3.3.4. Inter-annual variations

The number of otoliths collected was highest in 1998/99, followed by 1999/2000 and 1996/97, and lowest in 1997/98. Statistically, there is no significant difference ($p > 0.05$; $p = 96.3$ %; ANOSIM, two way nested analysis) in the diet of the two fur seals species between the years.

There was great variability in the diet amongst years. Both fur seal species preyed on a total of 21 different species of fish during each year for the period 1998 - 2000, while during 1996 and 1997, the number ranged from 13 to 17 species (Fig 6.5). In *A. tropicalis,* the proportion of *E. carlsbergi* in the diet remained more or less the same between the years, ranging from 0.05 to 0.32. In *A. gazella* some months produced no *E. carlsbergi* in the diet, while in other months, the proportions ranged from 0.01 to 0.35. *Gymnoscopelus piabilis* predominated in the diet of both species in all the years, despite being absent in some months for *A. gazella* (May 1998 and September 1999). Whenever there was a decrease in the major prey, minor prey species such as *C. gunnari, D. eleginoides* and *E. antarctica* began to appear (Table 6.7)

The utilisation of *G. piabilis* was the most in 1996, decreasing yearly from 37.8 % in March-April 1996/97 to 20.2 % in March-April 1998/1999 but increased again to 32.96 % in March-April 1999/00 (Table 6.8). For *A. tropicalis* the utilisation rate of *G. fraseri* was most in 1996/1997 (% NA = 31.85) but decreased steadily each year to 9.6 % in 1997/98, 1998/99 and 1999/00 (Table 6.8 & Fig. 6.5).

Table 6.7: Proportional annual variations of major prey species taken by both fur seals species at Marion Island (some months were omitted due to lack of samples collected during those months).

			A. tropicalis				
Prey species	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*M. ventralis*	*P. choriodon*	*K. anderssoni*
Jun-96	0.12	0.18	0.43	0.05	0.13	0.03	0.00
Jul-96	0.32	0.11	0.34	0.02	0.00	0.18	0.00
Dec-96	0.01	0.01	0.32	0.63	0.00	0.01	0.01
Feb-97	0.10	0.00	0.46	0.09	0.01	0.20	0.00
Mar-97	0.12	0.01	0.41	0.39	0.04	0.00	0.00
Apr-98	0.08	0.05	0.19	0.36	0.02	0.07	0.00
May-98	0.23	0.08	0.08	0.22	0.13	0.01	0.00
Mar-99	0.04	0.01	0.19	0.06	0.62	0.00	0.00
Apr-99	0.02	0.07	0.29	0.43	0.06	0.00	0.00
Sep-99	0.05	0.09	0.20	0.48	0.07	0.00	0.01
Jan-00	0.08	0.00	0.08	0.41	0.00	0.02	0.16
Feb-00	0.26	0.23	0.21	0.26	0.01	0.00	0.00
Mar-00	0.24	0.00	0.03	0.30	0.38	0.02	0.01
Apr-00	0.10	0.08	0.19	0.26	0.13	0.01	0.01

Table 6. 8: Overall percentage numerical abundances of prey species taken annually by both fur seals species at Marion Island.

			A. gazella				
Prey species	*E. carlsbergi*	*E. subaspera*	*G. fraseri*	*G. piabilis*	*M. ventralis*	*P. choriodon*	*K. anderssoni*
Jun-96	0.10	0.13	0.09	0.54	0.01	0.00	0.00
Jul-96	0.11	0.17	0.34	0.29	0.00	0.00	0.00
Dec-96	0.00	0.00	0.08	0.91	0.00	0.00	0.01
Feb-97	0.06	0.00	0.25	0.66	0.00	0.02	0.00
Mar-97	0.01	0.00	0.02	0.80	0.00	0.01	0.00
Apr-98	0.27	0.15	0.09	0.08	0.09	0.07	0.00
May-98	0.29	0.12	0.00	0.00	0.00	0.00	0.00
Mar-99	0.01	0.00	0.01	0.20	0.00	0.22	0.48
Apr-99	0.36	0.21	0.02	0.15	0.06	0.00	0.15
Sep-99	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan-00	0.09	0.03	0.05	0.57	0.00	0.04	0.09
Feb-00	0.05	0.03	0.19	0.52	0.00	0.02	0.08
Mar-00	0.11	0.08	0.03	0.63	0.00	0.06	0.03
Apr-00	0.08	0.06	0.02	0.28	0.10	0.08	0.10

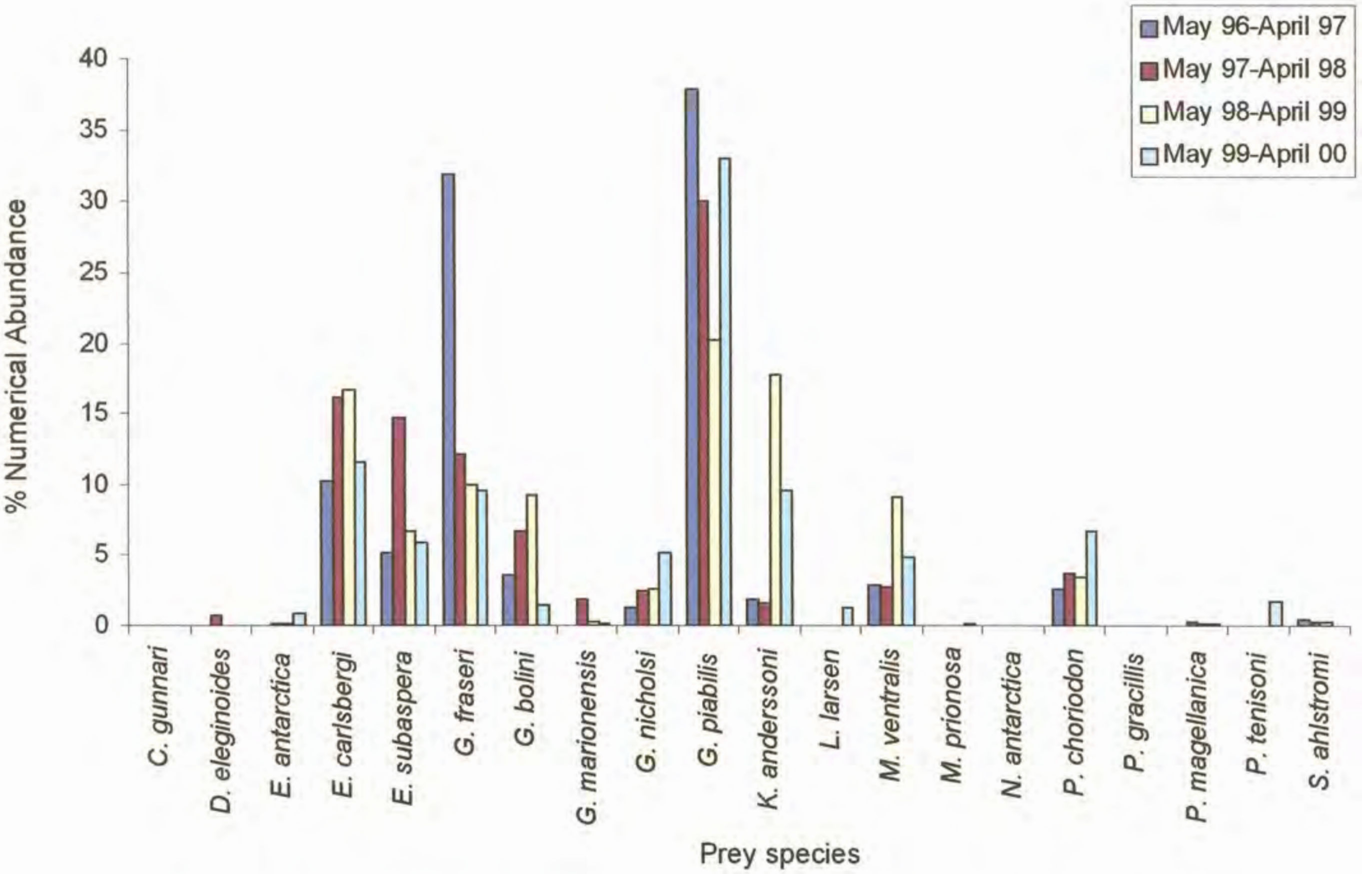

Fig. 6.5: Annual variation of prey species (% NA) eaten by both fur seals species combined at Marion Island.

6.3.4. PREY SIZE AND MASS

The two fur seals species fed on fish prey over a wide size range but more or less of the same size. The length and the weight of fish consumed were similar (Table 6.9), the fur seals feeding on both small species (*K. anderssoni* and *P. bolini*) (Fig. 6.6) as well as larger prey species (*G. nicholsi, G. piabilis* and *P. choriodon*). *Arctocephalus gazella* in particular preyed on species with a very wide size range such as *D. eleginoides*. The mean size of *G. piabilis* eaten by *A. gazella* was similar to that eaten by *A. tropicalis,* both preferring size classes larger than the median (125 mm - 145 mm) (Fig. 6.6). ANOVA showed a highly significant difference in the size frequency distribution of *P. choriodon* taken by the two fur seals (Table 6.10). *Arctocephalus gazella* selected significantly larger individuals of *P. choriodon* than *A. tropicalis*, both feeding on adult fish (Fig. 6.6). There were also significant differences in the consumption of *G. fraseri*, *G. nicholsi* and *K.anderssoni*, *A. tropicalis* taking on average larger fish on all counts (Table 6.10; Fig. 6.6).

Dissostichus eleginoides, was the largest fish taken in low numbers by the both fur seals species, at a mean SL of 242.5 mm and mean mass ranging from 32.02 g to 438.28 g. *Gymnoscopelus piabilis* was the next largest while the smallest prey species were *K. anderssoni* and *P. bolini* with a mean SL of 42.468 mm and 43.133 mm and a mass of 0.797 g and 1.104 g respectively (Fig. 6.7). Most prey weighed between 0.1 g and 10 g (Fig. 6.7). Overall, the median fish lengths and mass estimated from the scats were 88.54 mm and 106.23 mm SL, and masses of 7.96 g and 10.84 g for *A. tropicalis* and *A. gazella* respectively.

There was no significant difference in the mass of prey species eaten, except for *G. fraseri* and *P. choriodon* (Table 6.11), as both fur seals preyed on adult fish of more or less the same mass.

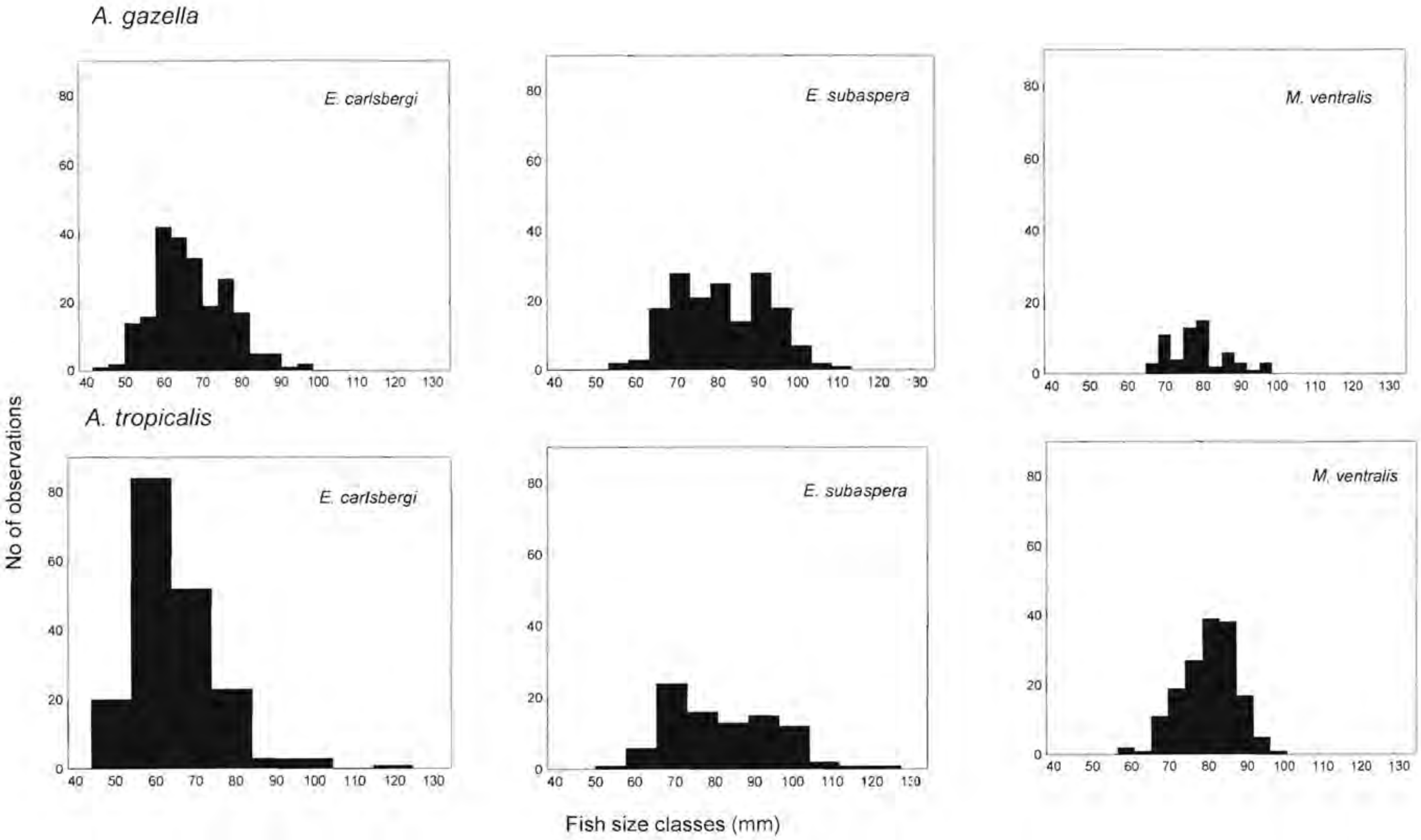

Fig. 6.6: Reconstituted size classes of fish species eaten by both fur seals species.

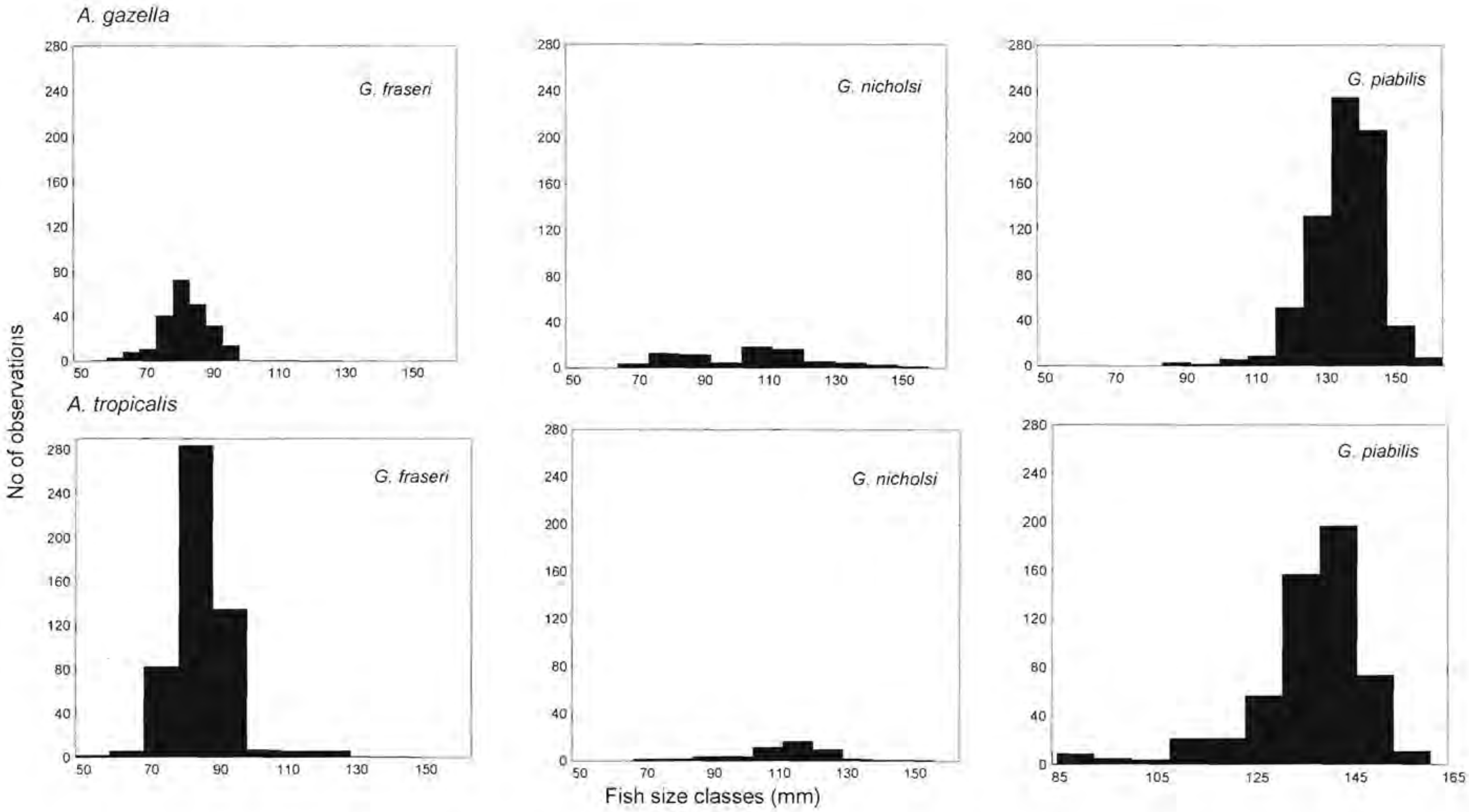

Fig. 6.6: Reconstituted size classes of fish species eaten by both fur seals species-continued.

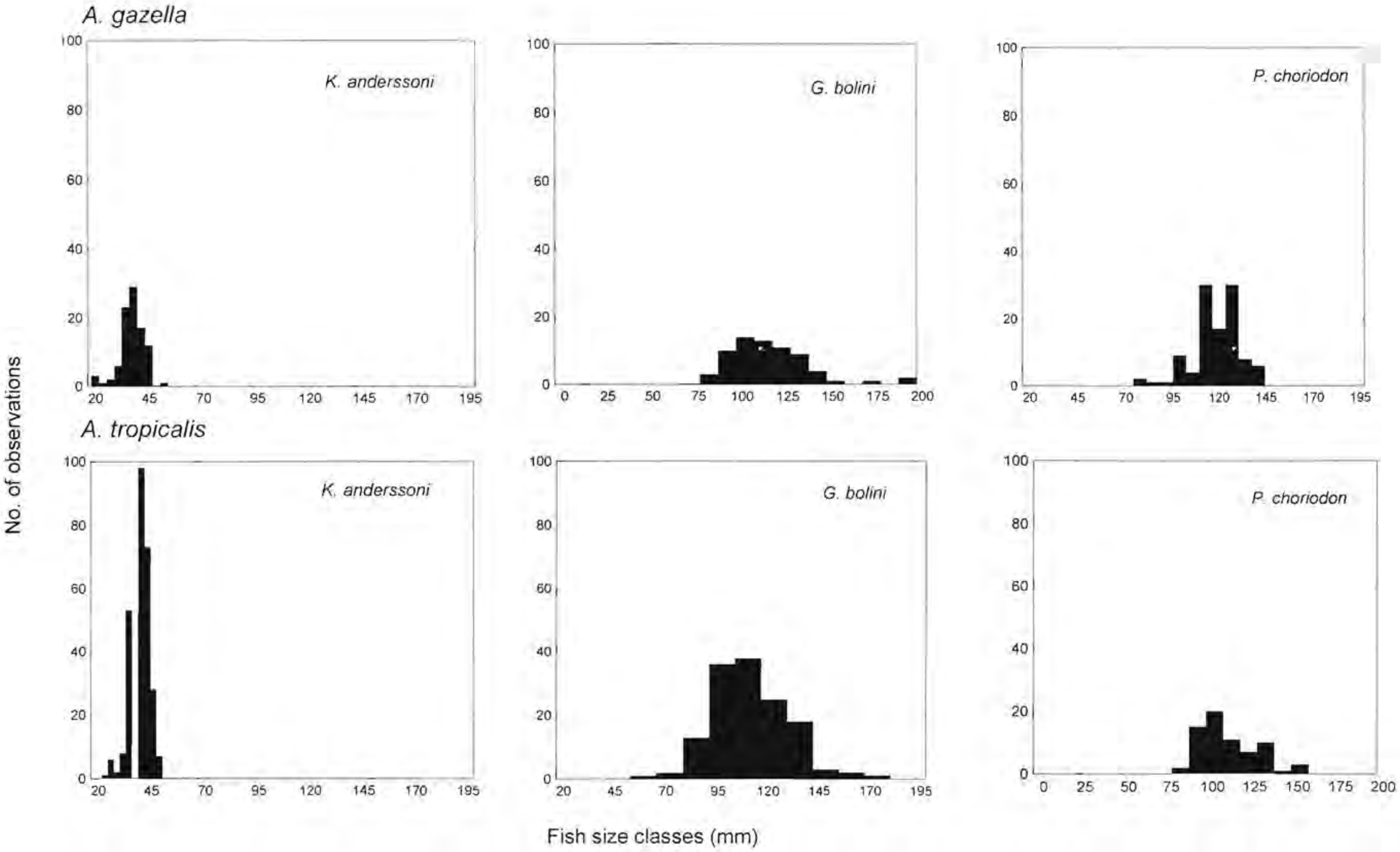

Fig. 6.6: Reconstituted size classes of fish species eaten by both fur seals species-continued.

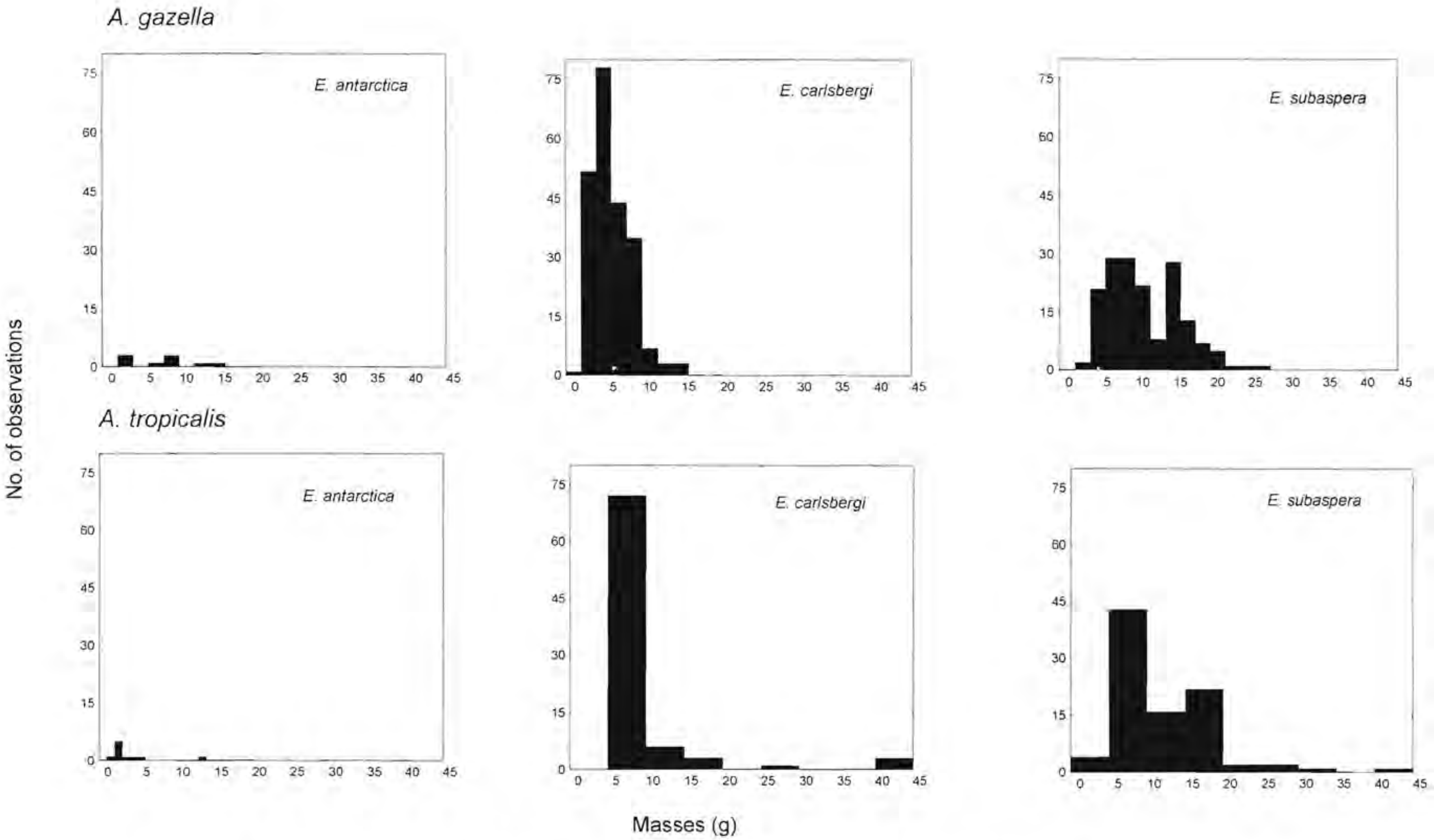

Fig. 6.7: Reconstituted masses of fish prey eaten by both fur seals species.

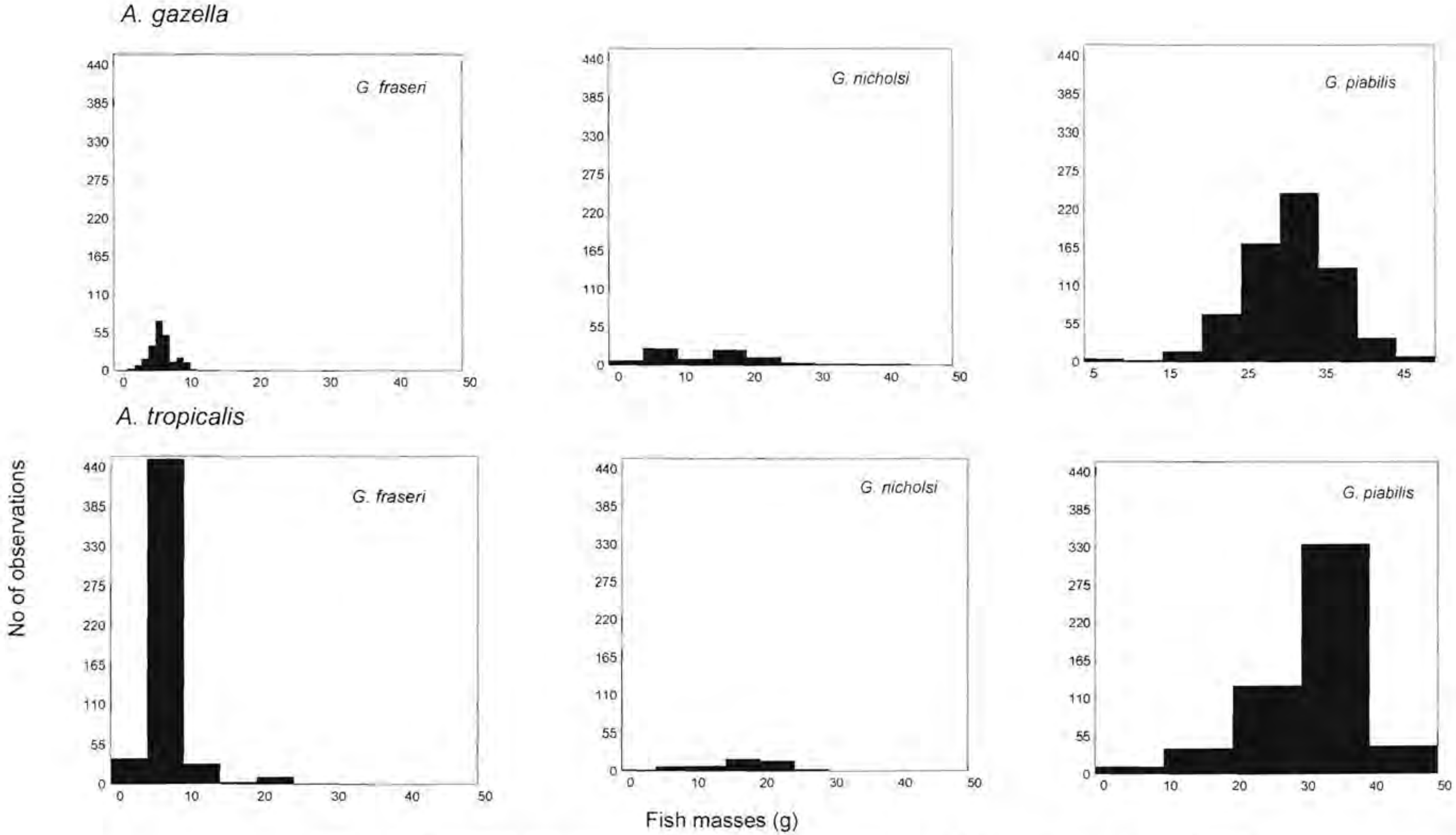

Fig. 6.7: Reconstituted masses of fish prey eaten by both fur seals species-continued.

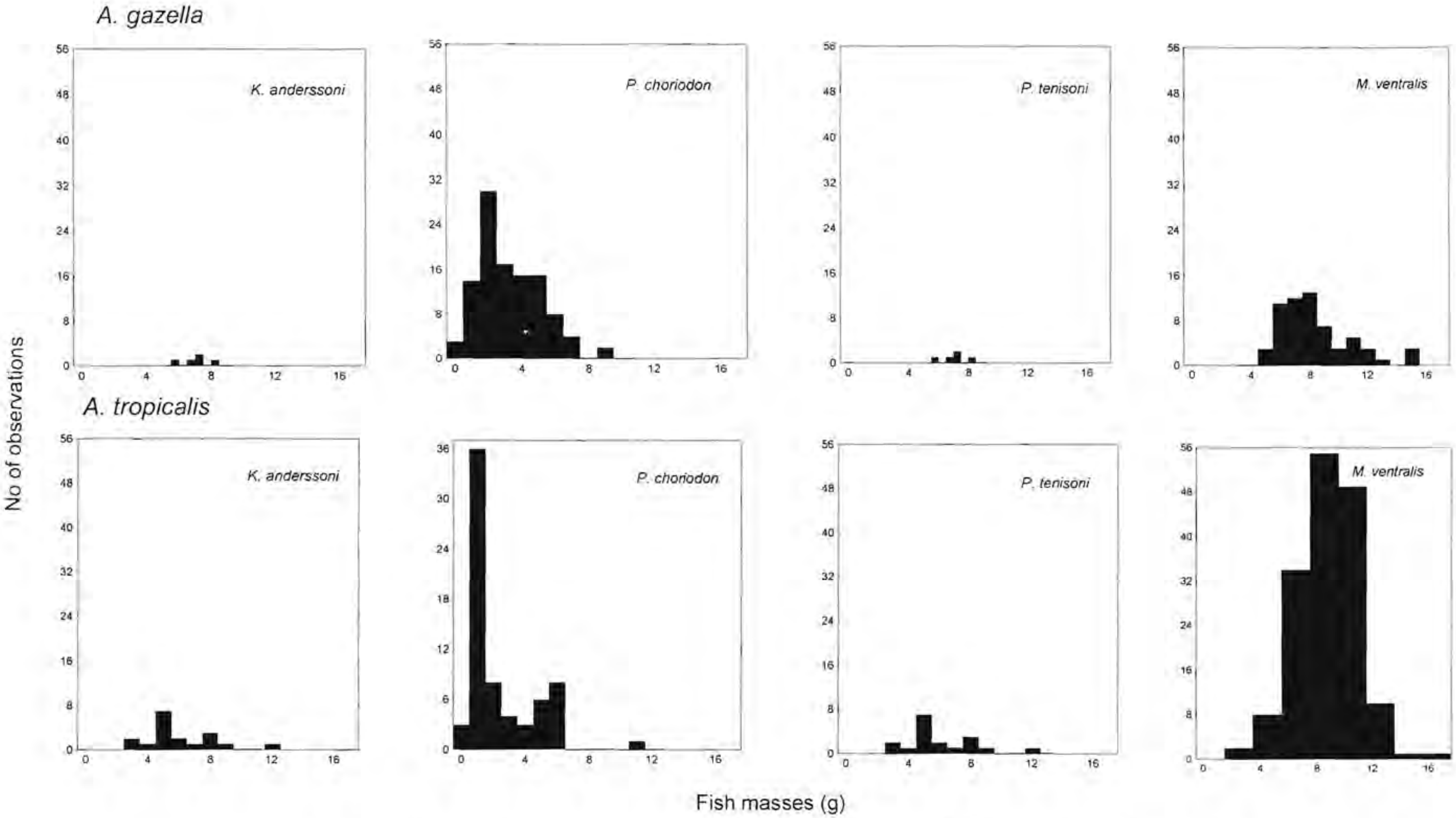

Fig. 6.7: Reconstituted masses of fish prey eaten by both fur seals species-continued.

Table 6.9: Summary of standard length and mass of fish consumed by *A. gazella* and *A. tropicalis* resident on Marion Island.

	A. gazella							*A. tropicalis*						
	Standard Length (mm)				Mass (g)			Standard Length (mm)				Mass (g)		
Prey species	N	Mean	S.D	Range	Mean	S.D	Range	N	Mean	S.D	Range	Mean	S.D	Range
Champsocephalus gunnari								1						
Dissostichus eleginoides	15	242.51	74.42	140.41-319.08	225.20	166.25	32.03-438.28	2	248.89	0.00	0	198.55	0.00	0
Electrona antarctica	13	79.38	17.11	55.61-103.56	7.66	4.63	2.26-15.34	30	64.46	14.46	59.30-99.87	4.14	3.57	1.46-13.72
E. carlsbergi	993	68.86	10.03	43.61-100.20	5.99	2.47	1.63-15.91	900	67.50	14.63	45.71-146.30	6.08	5.62	1.86-44.84
E. subaspera	667	82.88	11.46	58.62-111.24	11.22	4.88	3.48-26.89	403	83.62	13.92	51.87-128.79	11.89	6.62	2.36-42.90
Metelectrona ventralis	200	99.70	7.62	66.66-100.20	8.97	2.40	5.22-15.91	587	81.67	6.93	58.28-102.29	9.25	2.08	3.61-16.84
Gymnoscopelus bolini	328	118.95	22.44	82.09-196.82				490	114.03	18.49	56.27-182.48			
G. fraseri	937	84.10	7.45	60.24-165.23	6.96	1.86	2.41-15.29	1297	86.37	9.02	30.04-132.80	7.64	2.85	0.28-27.98
Gabionotothern marionensis	76	99.49	26.23	64.63-145.96	9.94	9.17	65.74-159.69	1						
G. nicholsi	322	115.92	26.62	60.24-109.30	21.20	12.55	2.41-15.29	92	112.76	16.02	68.22-157.22	17.65	7.32	3.40-47.27
G. piabilis	2519	137.05	9.49	85.33-165.23	31.17	6.16	7.158-54.57	1694	136.84	11.84	85.98-161.60	31.26	7.17	7.33-50.97
Krefftichthys anderssoni	551	42.47	5.78	21.71-57.31	0.80	0.32	0.08-2.01	762	43.67	4.63	25.27-53.75	0.85	0.28	0.14-1.63
Lepidonotothern larsen	43	124.34	4.41	119.53-128.19	0.89	0.06	0.83-0.94							
Magnisudis prionosa	8							3.00						
Nansenia antarctica	7							1.00						
Protomyctophum bolini	37	43.13	0.00	0.00	1.10	0.00	0.00	101	31.39	2.95	24.54-36.16	0.45	0.12	0.22-0.67
P. choriodon	319	78.77	12.83	33.76-103.39	3.76	1.90	0.47-9.68	272	69.21	17.35	43.04-112.68	3.00	2.84	0.70-14.50
P. tenisoni	15	79.36	3.13	74.74-83.36	7.61	0.91	6.29-8.82	51	75.24	8.02	63.38-93.17	6.65	2.27	3.78-12.44
Paradiplospinus gracilis	1													
Paranotothernia magellanica	18	250.09	60.65	193.27-371.55	399.01	335.80	158.10-1123.30							
S. ahlstromi	14							29						

Table 6.10: Simple classification ANOVA showing the significance of observed differences in the sizes of fish eaten by *A. tropicalis* and *A. gazella*.

	A. gazella		*A. tropicalis*				
Prey species	N	Mean	N	Mean	F	d.f	P
E. antarctica	9	79,4	10	64,5	4,24	1,7	0,055
E. carlsbergi	223	68,9	189	67,5	1,24	4,10	0,266
E. subaspera	167	82,9	91	83,6	0,21	1,256	0,648
G. bolini	68	119,0	139	114,0	2,80	1,205	0,096
G. fraseri	235	84,1	530	86,4	11,46	1,763	0,001
G. nicholsi	86	106,1	55	112,8	3,98	1,139	0,048
G. piabilis	690	137,1	558	136,8	0,12	1,1246	0,726
K. anderssoni	94	42,5	276	43,8	5,88	1,365	0,016
M. ventralis	61	80,6	160	81,7	0,92	1,219	0,340
P. choriodon	108	122,7	69	113,1	17,6	1,175	0,000
P. tenisoni	5	79,4	18	75,2	1,24	1,21	0,279

Table 6.11: Simple classification ANOVA showing the significance of observed differences in the mass of fish (g) eaten by *A. tropicalis* and *A. gazella*.

	A. gazella		*A. tropicalis*				
Prey species	N	Mean	N	Mean	F	d.f	p
E. antarctica	9	7,65	10	4,14	3,48	1,17	0,079
E. carlsbergi	223	5,96	189	6,08	0,08	1,41	0,779
E. subaspera	167	11,2	91	11,9	0,85	1,26	0,359
G. fraseri	235	6,92	530	7,64	12,6	1,76	0,000
G. nicholsi	86	15,6	55	17,7	1,87	1,14	0,173
G. piabilis	690	31,2	558	31,4	0,27	1,12	0,604
K. anderssoni	94	0,80	276	0,85	2,70	1,37	0,101
M. ventralis	61	8,97	160	9,25	0,72	1,22	0,398
P. choriodon	108	3,79	69	2,80	10,3	1,18	0,001
P. tenisoni	5	7,60	18	6,65	0,83	1,21	0,374

6.4. DISCUSSION

Several authors have discussed the reliability of using otoliths to estimate dietary composition and prey sizes (Dellinger & Trillmich 1999; Reid 1995; North 1996; Klages & Bester 1998; Bowen 2000; Staniland 2002), consensus being that biases are introduced because of differential digestion of otoliths (Daneri & Carlini 1999; Staniland 2002) and passage rate of items in relation to their size (Staniland 2002). Most piscivorous marine mammals' stomach contents are partially or completely digested, posing problems for both identification of prey and quantification of diet. This results in biases when determining the total amount of fish in the diet, which depends on the rate of digestion. In addition, seals may not eat the heads of larger fish, and consequently, their otoliths and skull bones will therefore not be ingested (Pierce & Boyle 1991).

Faecal analysis may not be an appropriate method for determining the diet of those seal species where a large proportion of fish otoliths ingested is completely or severely digested (North 1996). Furthermore, the use of faecal analysis to determine the diet of seals relies on the assumption that the solid remains pass into the faeces in the same proportions as they were consumed (Reid 1995) which is not the case (Gales & Cheal 1992; Staniland 2002). However, with proper caution, analysis of faecal samples can still provide some qualitative and quantitative information (Dellinger & Trillmich 1999).

Regression equations relating otolith length to fish length have been developed using otoliths from fresh fish. This leads to an underestimate of prey sizes as a result of partial digestion of otoliths. A correction factor must be applied to compensate for this partial digestion (Reid 1995; Bowen 2000; Staniland 2002). Otoliths of different species are eroded at different rates, thus number of fish ingested, and fish sizes derived by back calculation from the measurements of hard remains will require different correction factors. Food residues take several hours to pass out in faeces. Different types of prey are degraded at different rates, i.e. squid flesh are degraded more rapidly than fish flesh resulting in biases in the quantities of recognisable remains of different types of prey (Pierce & Boyle 1991). The identifiable items in the faecal analysis probably indicate prey items eaten 24 hours prior to fur seals coming ashore (Pierce & Boyles 1991) and therefore are a reflection of their diet in the vicinity of Marion Island.

In this study, the likelihood of otoliths being completely digested is high as suggested by Staniland (2002) for *A. gazella* at least. However, most scats contained otoliths and these could be identified, and faecal analysis is likely to be a reasonable technique for comparing the diet of the two fur seal species (Klages & Bester 1998). Biases associated with prey sizes and masses were minimised by discarding all the eroded otoliths.

Despite their spatial and some temporal segregation when ashore (Kerley 1983; Klages & Bester 1998), the current study shows a substantial overlap in the diet of both fur seals species at Marion Island. The total number of scats (471) collected was very similar to the 469 scats collected from 1989 to 1995 (Klages & Bester 1998). The number of otoliths identified (n = 14300), however, was much higher than that in the previous study (n = 13817) of the same species in the same study area and was likely the result of an increased effort in collecting and sorting of scat contents.

6.4.1. DIET COMPOSITION

At Marion Island (Klages & Bester 1998; this study), myctophid fish predominated in the diet. The most important myctophid fish species eaten by both *A. gazella* and *A. tropicalis* include *E. carlsbergi, E. subaspera, G. fraseri, G. nicholsi, G. piabilis, P. choriodon* and *K. anderssoni*. Klages & Bester (1998) and Goldsworthy *et al.* (1997) reported that similar prey species dominated the diet of both fur seals species at Marion Island and Macquarie Island respectively. However, crustaceans were also taken by *A. gazella* for a few months in summer, while at Bouvetøya (Kirkman *et al.* 2000), South Georgia (Reid & Arnould 1996) and the South Shetland Islands (Casaux *et al.* 1998) krill dominated the diet of Antarctic fur seals, fish species being taken in winter (Reid 1995). There was no major variation in the diet of the two fur seals species at Marion Island as they predominately fed on the same fish prey, although in different quantities.

The relatively low abundance of squid in the diet of fur seals at Marion Island is similar to that found for *A. gazella* in the Scortia Arc (Daneri *et al.* 1999) but contrasts that found for *A. tropicalis* at Gough Island (Bester and Laycock 1985). The disparity in the diet of both *A. tropicalis* and *A. gazella* amongst the different populations in all probability also relates to the type of sampling; stomach contents at Gough Island (Bester & Laycock 1985), scats and stomach contents at Marion Island (Condy 1981) and scats only at Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997), the Scortia Arc (Daneri *et al.* 1999) and in later studies at Marion Island (Klages & Bester 1998; this study).

6.4.2. INTERSPECIFIC DIFFERENCES

No major differences between the diet of *A. gazella* and *A. tropicalis* were found in this study. Similarly, Green *et al.* (1997) and Klages & Bester (1998) found that at Macquarie Island and Marion Island both fur seals species fed predominantly on similar prey in similar proportions and both followed the same temporal pattern of resource use (Klages & Bester 1998). Evidently, *A. gazella* now occupies the same dietary niche as *A. tropicalis*, although recolonisation of *A. gazella* at Marion Island gained momentum much later here and at other breeding localities where they occur in sympatry (Bester 1984; Hofmeyr *et al.* 1997; Wynen *et al.* 2000).

Cephalopods are taken in low number by both fur seals species and crustaceans were taken by *A. gazella* only (this study). This contrasts the situation in the South Atlantic where krill were abundant in the diet of *A. gazella* (Reid 1995; Daneri & Carlini 1999; Kirkman *et al.* 2000) while *N. marionis* was the only crustaceans identified in the scats of *A. gazella* at Marion Island. The low occurrence of crustaceans and cephalopods in the diet of fur seals at Marion Island suggests that their utilisation is either minimal or that crustaceans might have been taken incidentally or secondarily, as amphipods were recorded as prey for myctophids species (Hulley 1990). In addition, cephalopod beaks, especially the large ones (> 10mm), are likely to accumulate in the stomachs of marine predators (Reid 1995; Klages & Bester 1998), become fragmented (Staniland 2002) or are ejected by vomiting (Kirkman *et al.* 2000) and therefore may not appear in scats on a regular basis. The central tenet of scat analysis, that the solid prey remains pass into the faeces in the same proportions as they were consumed, may therefore not hold for squid beaks (Klages & Bester 1998) as was confirmed for *A. gazella* (Staniland 2002).

Fish dominated the diet of the fur seals here and at Macquarie Island (Green *et al.* 1990; Goldsworthy *et al.* 1997; Klages & Bester 1998). Myctophidae and to a lesser extent some Nototheniidae, Paralepididae, Gempylidae and Microstomatidae are the most commonly represented in the diet of fur seals at Marion Island. These fish inhabit the deep scattering layer usually at 200 m to 500 m, and migrate to the surface during the night, where they are consumed by both fur seals species (Goldsworthy *et al.* 1997), which explains why fur seals are nocturnal foragers (Goldsworthy *et al.* 1997; Dellinger & Trillmich 1999).

The two fur seals species feed predominately on pelagic myctophids of two genera, *Electrona* and *Gymnoscopelus*, though there were a number of *Protomyctophum* spp. and *Krefftichthys* spp. Almost all these genera are characteristic of deep, off shelf water and inhabit the deep scattering layers (Green *et al.* 1997). The sole exception is *G. nicholsi*, which can also be found near the bottom of the shelf. Unlike the fur seal population at Macquarie Island where pelagic ice fish, *C. gunnari* dominated the diet of *A. gazella*, none has been identified for this species at Marion Island although it was taken by *A. tropicalis* there. Three other fish species, *Lepidonotothen larseni, Paranotothernia gracillis* and *P. magellanica,* were eaten by *A. gazella* only, as were crustaceans. The low presence of the latter three fish prey in the diet might be related to their low abundant or an overwhelming abundance of the major prey species around Marion Island.

A fairly clear picture has now emerged these diet studies depending on the localities where these fur seals are breeding. At the localities where the shelf is narrow (Macquarie, Marion Island), myctophids dominated the diet, but in the area where it is wide (Heard Island, Îles Kerguelen) demersal and benthic fish (*Champsocephalus gunnari,* notothenids, skates) become more important and abundant in the diet (Klages & Bester 1998). However, where krill is abundant (South Georgia, South Orkneys) fur seals preferably consume this prey species together with its fish predators (*C. gunnari*, *L. larsen*) (Daneri and Coria 1993; Reid 1995; Ried & Arnould 1996).

6.4.3. SEASONAL CHANGES

The results showed strong seasonal trends in the diet, with *E. carlsbergi*, *E. subaspera*, *M. ventralis* and *G. fraseri* being the most dominant prey species consumed by both fur seals species in winter (Klages & Bester 1990; this study) with *G. piabilis* showing the opposite trend. Green *et al*. (1990) and Klages & Bester (1998) also noted a greater proportion of *Gymnoscopelus* spp. in the summer diet of both fur seals species with a smaller proportion of *Electrona* spp. similar to the present study, and in the diet of king penguins (Adams & Klages 1987). This might be because *Gymnoscopelus* species are seasonally abundant within the foraging range of these predators, which will conceivably target the most abundant prey species.

For both fur seals species at Marion Island, *G. nicholsi* was much less important as compared to *A. gazella* at the South Orkney Islands (Daneri & Coria 1992) during the summer-autumn season. Unlike at Macquarie Island (Goldsworthy *et al*. 1997), but similar to Heard Island (Green *et al*. 1997), *K. anderssoni* dominated the summer diet of both fur seals species at Marion Island (this study). As *K. anderssoni* is especially rich in oil, it is possible that fur seals, especially lactating females which require high energy intake to produce milk for their pups, will target this energy rich prey species as do *A. gazella* at Heard Island (Green *et al*. 1997). Predation on fish with high oil content was also reported by William (1989) for Adélie penguins *Pygoscelis* *adeliae* which target *Pleuragramma antarcticum*, an oil rich fish species, once their chicks are hatched. By contrast, *C. gunnari* has a low fat content (Green *et al.* 1997) and the least likely to appear (this study). Very few *C. gunnari* are eaten by *A. tropicalis* at Marion Island, and none by *A. gazella* perhaps as a result of it being less rewarding prey (this study).

6.4.4. SIZE AND MASS OF PREY SPECIES

There were no major differences in the size and mass distribution of the prey species eaten by both fur seal species, which target prey species of varying size and mass classes. The size range of 43.07 mm to 193.27 mm for *A. gazella* and 28.83 mm to 151.93 mm for *A. tropicalis* overlapped considerably. The largest fish species recovered in the present study was *D. eleginoides* with the longest measuring 319.08 mm. Klages & Bester (1998) also reported that *D. eleginoides* was the largest prey species taken at Marion Island.

The mean sizes and masses of *G. piabilis* eaten at Marion Island were 137.1 mm and 31.2 g for *A. gazella* and 136. 8 mm and 32.4 g for *A. tropicalis* respectively and are considerably larger and heavier than those taken by *A. gazella* at Ile de Croy, Kerguelen (mean sizes and masses of 103 mm and 14 g respectively - Cherel *et al.* 1997). The reason for size differences of prey species eaten by the fur seals at the different localities is unclear and requires a greater understanding of the distribution and the physiological condition of the prey (Green *et al.* 1989).

Fur seal diets showed a lot of similarities with that of king penguins at Marion Island suggesting that these two predators might be major competitors (Klages & Bester 1998). However, the nocturnal diving of fur seals allows them to feed on vertical migrators that occur in shallow depths at night. This foraging strategy complements that of the other major predator of myctophid fish, the king penguin, *Aptenodytes patagonicus,* which feeds mainly during daylight hours, at deeper depths, and on truly oceanic species of lantern fishes (*Krefftichthys anderssoni* and *Electrona carlsbergi*) (Cherel *et al.* 1997). Klages & Bester (1998) suggested that fur seal fish diets show many striking similarities with that of the king penguins at Marion Island, suggesting that these two warm blooded predators could be major competitors for food.

Chapter 7: Estimation of prey biomass

7.1. INTRODUCTION

Knowing the amount of living matter is very important in assessing energy fluxes within the ecosystem (Trites & Pauly 1998). However, the most important factor needed to estimate the amount of food eaten by marine mammals occupying the top trophic level of the world's ocean is biomass (Trites & Pauly 1998). Therefore, quantitative accounts of the trophic relationships and the food consumption of the major groups of predators are needed in order to obtain the knowledge that is necessary for understanding the functioning of the Antarctic marine ecosystem and management of its renewable resources (Kock 1985).

Considerable interest has been focused in the past on the population sizes of the southern ocean pinnipeds (Gilbert & Erickson 1977), and their population biomass and annual food consumption (Laws 1977). The estimation of food consumption requires the following components: population size and structure (includes number of animals in each age- and reproductive class, provided that estimates of age-specific survival and fecundity rates are also available Harwood & Croxall 1988), daily energy requirements for each sex-age class, calorific values of various types of prey in the diet, and dietary composition for each age-sex class (Pierce & Boyle 1991). This chapter will attempt to estimate the biomass of prey species, mainly fish and squid, consumed by the two fur seal species (*A. tropicalis* and *A. gazella)* at Marion Island during the 1994/95 summer, when the last population estimates were made (Hofmeyr *et al.* 1997).

7.2. METHODS

7.2.1. POPULATION STRUCTURE AND SIZE

Hofmeyr *et al.* (1997) recorded pup production values for Marion Island of 10261 *A. tropicalis* and 251 *A. gazella* in the 1994/95 summer (Hofmeyr *et al.* 1997). A negligible rate of growth from 1987/88 and 1988/89 (Bester & Wilkinson 1990) to 1995 was also recorded, and it is therefore assumed that pup production has remained reasonably constant from 1996 to 2000. Population and biomass estimates are then based on the pup production and mass data (Goldsworthy *et al.* 1997).

Values from 1994/95 were used to represent the population size at Marion Island over the study period. From the pup production totals, I can assume that the number of pregnant females present in the population were 10261 individuals for *A. tropicalis* and 251 individuals for *A. gazella* following Kirkman *et al.* (2000). Assuming a similar population structure at Marion Island during 1994/95 to that at South Georgia in the early 1970s (Payne 1979), the total foraging population size was estimated by multiplying the number of births by 4.26 (derived from Payne 1979), which yields estimates of 43712 *A. tropicalis* and 1069 *A. gazella* older than pups. Assuming a pregnancy rate of 86% (Payne 1977), the total number of adult females is estimated to be 11931 *A. tropicalis* (10261 pregnant females and 1669 non-pregnant females) and 292 *A. gazella* (251 pregnant females and 41 non-pregnant females).

Assuming the same ratio of adult males to adult females as in the Payne (1979) study at South Georgia, the number of adult males is estimated at 3561 for *A. tropicalis* and 87 for *A. gazella*.

This yields an estimated total of 15492 adults of *A. tropicalis* and 379 for *A. gazella*. Of the remaining animals, 28220 and 690 were subadults of *A. tropicalis* and *A. gazella* respectively. Of these 19754 and 483 were males, and the rest (8466 and 207 individuals) were females of *A. tropicalis* and *A. gazella* respectively, using the same proportions as in Payne (1979).

7.2.2. DAILY ENERGY REQUIREMENTS

No detailed direct measurements of the growth and body masses of *A.gazella* and *A. tropicalis* have been done at Marion Island. Data published by Doidge & Croxall (1985) on *A. gazella* were therefore used, with the assumption that the body masses of *A. gazella* at Marion Island in 1994/95 are the same as those of the South Georgia population in 1994/96 (McCafferty *et al.* 1998). I therefore used a mean mass of 125 kg and 38 kg for adult and subadult males respectively and 32 kg and 16 kg for adult and subadult females respectively. Kerley (1987) calculated the average mass of *A. tropicalis* adult males and adult females to be 88.3 kg and 34.1 kg respectively at Marion Island.

The mass of *A. tropicalis* subadult females was obtained using the Gompertz equation:

$y = (ab^{r^{t}})$,

with a = 39.86, b = 0.131 and r = 0.75 (Trites & Pauly 1998)

The sub-adult male mass was obtained using the Logistic equation:

$y = a/(1+br^{t})$,

with a = 112.74, b = 15.01, r = 0.67 and t = age of animals in years (Bester & Van Jaarsveld 1994).

Arctocephalus tropicalis pups are weaned at between 10 - 11 months. Therefore, all immatures older than a year were regarded as subadults. Females were categorized as subadults from the age of 1 to 3 years (Trites & Pauly 1998) while males were regarded as subadults from the age of 1 to 6 years (Trites & Pauly 1998). Using the Gompertz equation for the body masses of each age-sex class, weights of 8.70 kg, 12.71 kg and 16.91 kg were obtained for subadult females, with an overall mean of 12.77 kg. Subadult males body mass for ages 1 to 6 years were then obtained using the Logistic equation, which yielded masses of 10.20 kg, 14.57 kg, 20.44 kg, 28.01 kg, 37.25 kg and 47.81 kg respectively, with an overall mean of 26.38 kg.

Daily energy requirements (kj) were estimated by substituting the average masses (in grams) of each sex-age class in an allometric equation describing the Field Metabolic Rate (FMRs) of eutherian mammals (Nagy 1994):

Daily energy requirements = 5.27 x body mass$^{0.723}$ kj/day

where kj = kilojoules and g = grams.

The estimated daily energy requirements as an average of each sex-age class were multiplied by the estimated number of individuals in each category to obtain the total daily energy requirements of each sex-age class. This was then multiplied by 365 days to obtain the annual total energy requirements of each sex-age class.

7.2.3. CALORIFIC VALUE

The following estimated calorific value for the various prey species taken from Doidge & Croxall (1985) were used namely:

Squid 3.47 kj g^{-1} and fish other than myctophids 3.97 kj g^{-1}. The calorific value of myctophids was assumed to be 7.00 kj g^{-1} (Cherel & Ridoux 1992; Guinet *et al.* 1996).

7.2.4. DIETARY COMPOSITION

Estimation of dietary composition was described in Chapters 4 and 5 for *A. gazella* and *A. tropicalis* respectively. Prey consumption was estimated using the following equation taken from Doidge & Croxall (1985):

$$PC = \Sigma_{xy}(P_{xy} \times EC_x \times ER_x / A)$$

where PC = biomass of prey consumed, P_{xy} = proportion of the yth prey species in the diet of the xth sex age class, EC_y = energy content per unit mass of the yth prey species, ER_x = energy requirement of the xth sex age class, and A = assimilation efficiency of the energy. Assimilation efficiency was taken as 0.93 for fish and 0.85 for squid (Miller 1978).

7.3. RESULTS

7.3.1. ENERGY REQUIREMENTS AND FOOD CONSUMPTION

The energy requirements and prey items consumed by each age-sex class of both fur seal species are shown in Table 7.1. Myctophids were taken as the dominant prey species when calculating the energy content while other fish species were clearly of less importance in the diet. The total annual fish consumption by *A. tropicalis* and *A. gazella* were 5.86×10^{12} g and 2.47×10^{11} respectively (Table 7.1). The total annual squid consumption was far less, at 4.35×10^{9} for *A.*

tropicalis and 6.77×10^{9} for *A. gazella* (Table 7.1). While fish were more heavily consumed than squid by both fur seals species, squid formed a mere 0.074 % of the prey biomass consumed by *A. tropicalis*, but considerably less than that consumed by *A. gazella*.

Table 7.1: Annual energy requirements (kj) and prey consumption (g) of various age-sex classes of sympatric populations of *A. gazella* and *A. tropicalis* breeding at Marion Island.

Energy requirements	Adult male	Adult female	Subadult male	Subadult female	Total
A. gazella	$8,10 \times 10^{8}$	1.02×10^{10}	1.9×10^{10}	3.15×10^{10}	7.86×10^{10}
A. tropicalis	2.58×10^{12}	4.34×10^{11}	5.98×10^{11}	1.5×10^{11}	3.76×10^{12}
Prey consumption					
Fish					
A. gazella	$5,85 \times 10^{9}$	7.3×10^{10}	1.37×10^{11}	3.15×10^{10}	2.47×10^{11}
A. tropicalis	1.94×10^{11}	3.27×10^{10}	4.49×10^{12}	1.14×10^{12}	5.86×10^{12}
Squid					
A. gazella	$1,3 \times 10^{9}$	$1,65 \times 10^{9}$	$3,11 \times 10^{9}$	$7,12 \times 10^{8}$	6.77×10^{9}
A. tropicalis	$9,48 \times 10^{6}$	$1,59 \times 10^{9}$	$2,19 \times 10^{9}$	$5,57 \times 10^{8}$	4.35×10^{9}

7.3.2. ESTIMATED BIOMASS

The estimated biomass, in metric tons, of the prey items consumed by the different age-sex classes of both fur seals species at Marion Island over the entire year, as well as the total biomass consumed, are shown in Table 7.2. Averaged over the whole study period of 5 years, the total biomass of fish species consumed by *A. tropicalis* and *A. gazella* were 1.9 x 10^5t and 1.1 x 10^4t respectively. Much less squid was consumed with *A. gazella* consuming a far larger amount (459.78 t) than *A. tropicalis* (367.79 t).

Table 7.2: Estimated annual biomass (in metric tons) of prey items consumed by various sex-age classes of *A. gazella* and *A. tropicalis* populations at Marion Island.

Sex-age class	Species	Fish	Squid	Total
Adult male	*A. tropicalis*	3959.6	6.69	3966.29
Adult male	*A. gazella*	119.6	4.98	124.58
Adult female	*A. tropicalis*	66680.3	132.6	66812.9
Adult female	*A. gazella*	1497.7	137.7	1635.4
Subadult male	*A. tropicalis*	91700.8	182.3	91883.1
Subadult male	*A. gazella*	2804.9	257.9	3062.8
Subdult female	*A. tropicalis*	23277.7	46.2	23323.9
Subadult female	*A. gazella*	6432.2	59.2	6491.4
Total	*A. tropicalis*	185618.4	367.79	185986.19
Total	*A. gazella*	10854.4	459.78	11314.18

7.4. DISCUSSION

Naturally, many errors are associated with the estimation of prey consumption of fur seals. Estimates of population size, age structures, mean masses and biomass are all based on several assumptions (Kirkman *et al.* 2000). Should any one of these be out, the final values will be affected.

Although the costs of growth and reproduction were incorporated when calculating the field metabolic rates (FMRs) using allometrically derived FMRs for estimating daily energy requirements, is likely to underestimate the true energy requirements. This is because the majority of females were expending energy on reproduction, which includes foraging for the young and lactation during periods of 11 months and 4 months for *A. tropicalis* and *A. gazella* respectively. Young pinnipeds are known to have extremely high rates of metabolism, relative to other growing mammals (Thompson *et al.* 1987; Kirkman *et al.* 2000), and most of the males involved in breeding activities fast for breeding, therefore many would have expended large amounts of energy when trying to maintain their territories at breeding colony sites (Doidge & Croxall 1985). Adult males are therefore likely to feed intensively during the post-breeding pelagic phase to regain condition.

Most of the food taken by the fur seals is probably consumed at distance from the island during winter. Greater sections of the populations concerned appear to be pelagic then (Condy 1981) and lactating females of *A. tropicalis* have substantially longer foraging trips during winter (Kirkman *et al.* 2002). These factors all lead to a low number of scats being deposited on the beaches. Pup mortality which exceeds 10 % in the first 6 weeks of life (Bester 1987; Kerley 1987, Georges & Guinet 2000) also takes its toll, decreasing the number of lactating females regularly visiting the study area (Bester & Bartlett 1990). Relatively low numbers of both sexes and various age classes of this fur seal species are present in winter (Kerley 1983; Hofmeyr *et al.* 1997). However, in summer the seals hauled out for breeding and resting, then go for fasting (Condy 1981), although lactating females make regular feeding trips to the sea (Bester & Bartlet 1990; Kirkman *et al.* 2002). It is therefore clear that food taken by these fur seals varies according to their age-sex classes, to the time of the year, and their distance from their pelagic feeding grounds (Condy 1981), all of which cannot be accounted for in the present study.

The present study suggests that adult females of both fur seal species consume much higher biomass as compared to other sex age classes (Table 7.2), followed by subadults of both age-sex classes. Males conceivably account for less biomass because they do not feed during the breeding period and they tend to spend a lot of energy during defence of their harems. The calculated total biomass (185986.19 tons/year and 11314.18 tons/year for *A. tropicalis* and *A. gazella* respectively) gives an approximate estimate of food consumed by the Marion Island population. The 72 000 strong *A. tropicalis* and 2000 strong *A. gazella* populations of the neighbouring Prince Edward Island (Bester *et al. submitted*), conceivably consumes another 306346.21 tons and 21167.78 tons respectively.

The consumption of total biomass of prey species was higher for *A. tropicalis* as compared to *A. gazella* owing to the higher population size of *A. tropicalis* at Marion Island. Due to the lack of data on the productivity of marine resources around Marion Island, it is impossible to determine the impact of the growing fur seal populations on available food resources to these top predators feeding in the Prince Edward Islands Exclusive Economic Zone. Despite these deficiencies it is clear that seals have an important impact on fish and squid stocks in the Prince Edward Islands area.

Chapter 8: Conclusions and Summary

8.1. CONCLUSIONS

The two species of fur seal (*A. tropicalis* and *A. gazella*) preyed on similar prey in similar proportions, with their diet dominated by fish species of the myctophid family, in particular *G. piabilis, E. carlsbergi, E. subaspera, G. fraseri, G. piabilis, K. anderssoni, M. ventralis* and *P. choriodon*. All other prey species, including cephalopods and crustaceans, were regarded as minor. Fish in the families Myctophidae and Nototheniidae, Paralepididae, Gempylidae and Microstomatidae are part of the deep scattering layer, which migrate to the surface during the night (Dellinger & Trillmich 1999). Therefore, the presence of these prey species in the diet imply that the fur seals are nocturnal foragers that feed on vertically migrating shoaling fish and cephalopods in open water, as has been determined for other populations (Dellinger & Trillmich 1999; Goldsworthy *et al.* 1997).

Continued increase in the populations of *A. tropicalis* and *A. gazella* suggests that food resources are not limiting factors at Marion Island despite the fact that they appear to occupy the same feeding niche. No significant differences were found between the diets of the two fur seal species on a monthly basis. Within *A. tropicalis*, the mean numerical abundance of *E. carlsbergi* and *E. subaspera* was highest in January, February, May and August, but declined significantly from October to December. *Gymnoscopelus piabilis* and *G. fraseri* dominated the diet throughout the year, with the lowest prey consumption between June and August for *G. piabilis*, and August and November for *G. fraseri*. The latter two prey species were equally consumed during September and February.

A highly significant difference in prey utilisation existed between the late summer, winter and early summer diets of both fur seals species. The clear seasonal differences might be linked to the annual behavioural cycle of fur seals, with a haulout in early summer (October to January for the breeding and pupping season haulout), another in the late summer (February to May) for the post-breeding season moulting and lactation period, while during the winter (June to September) most seals are at sea (Kerley 1983; Bester & Bartlett 1990) possibly feeding further offshore (Kirkman *et al.* 2002)

Despite the overwhelming overlap in the diet, small differences were found; *A. tropicalis* preyed more on *G. fraseri* (13.81 % NA), *K. anderssoni* (26.38 % NA) and *M. ventralis* (10.34 %) in summer while the *A. gazella* summer diet was dominated by *G. piabilis* (50 % NA). No major difference existed in the utilisation of prey species during winter. Minor differences observed in their diets were that *C. gunnari* was utilised by *A. tropicalis* only while *L. larseni*, *P. gracillis* and *P. magellanica* were eaten by *A. gazella* only.

The two fur seals species fed on fish prey over a wide but similar size range. The length and the mass of fish consumed indicated that most were adult. *Arctocephalus gazella* selected significantly larger individuals of *P. choriodon* than *A. tropicalis*. There were also significant differences in the sizes of *G. fraseri*, *G. nicholsi* and *K.anderssoni* consumed, *A. tropicalis* taking on average larger fish on all counts.

8.2. SUMMARY

The diets of the Subantarctic fur seal (*A. tropicalis*) and Antarctic fur seal (*A. gazella*) were investigated at Marion Island from 1996-2000. Scats were examined and the extent of possible dietary overlap determined. Overall, no significant differences existed between their diets. The *A. gazella* diet is comprised of fish, crustaceans and cephalopods while fish and cephalopods were the only two taxa identified in the diet of *A. tropicalis*. Twenty-one species of fish were identified from sagittal otoliths in the scats with *A. gazella* having a slightly more diverse diet than *A. tropicalis* (20 versus 18 taxa), the two predators sharing 17 out of 21 taxa. The shared prey species contributed more than 99 % of the numerical abundance (NA) of fish prey. Otoliths of the mesopelagic Myctophidae (lantern fish) were by far the most numerous (98.1 % NA) hard prey components identified in the scats of the fur seals, with up to eight different prey species making up an individual scat. Fish from other families were rarely taken by *A. tropicalis* and *A. gazella*.

Three myctophid species namely *E. carlsbergi, G. fraseri* and *G. piabilis* accounted for 60 % NA of prey items in the diets. Minor differences in their diets were that *C. gunnari* was utilised by *A. tropicalis* only while *L. larseni, P. gracillis* and *P. magellanica* were eaten by *A. gazella*. There were distinct seasonal variations in the utilization of some prey species. The utilization of *E. carlsbergi, E. subaspera, G. bolini* and *G. fraseri* by both *A. tropicalis* and *A. gazella* were higher in winter than in the early and late summer. During the winter season, *A. tropicalis* predominantly fed on *E. subaspera* (7.45 %), *G. fraseri* (22.17 %) and *G. piabilis* (26.56 %) whereas there was a 50 % decrease in the consumption of *G. piabilis* (23.39 %) by *A. gazella*, with a concomitant increase in other major prey species. *Krefftichthys anderssoni* seemed to be utilized more in summer by *A. tropicalis* and *A. gazella* (NA of 26.38 % and 14.88 % respectively).

The two fur seals fed on fish of more or less the same size over a wide size range. The length and the mass of fish consumed were similar, the fur seals feeding on both small species (*K. anderssoni* and *P. bolini*) as well as larger prey species (*G. nicholsi, G. piabilis* and *P. choriodon). Arctocephalus gazella* in particular preyed on large species such as *D. eleginoides*. All prey species appearing in the diet of *A. tropicalis* and *A. gazella*, except *E. antarctica, G. fraseri, G. nicholsi, K. anderssoni*, and *P. choriodon*, yielded non significant differences in size. *Arctocephalus gazella* ate significantly larger *E. antarctica* and *P. choriodon* while *A. tropicalis* took larger sized *G. fraseri, G. nicholsi* and *K. anderssoni*.

The estimated biomass, in metric tons, of the prey items consumed by the different age-sex classes of *A. tropicalis* and *A. gazella* at Marion Island over an entire year, as well as the total biomass consumed, averaged over the whole study period of 5 years, were 1.9 x 10^5t and 1.1 x 10^4t respectively. Much less squid was consumed with *A. gazella* consuming a far larger amount (459.78 t) than *A. tropicalis* (367.79 t). The calculated total biomass (185986.19 tons/year and 11314.18 tons/year for *A. tropicalis* and *A. gazella* respectively) gives an approximate estimate of food consumed by the Marion Island population. The 72 000 strong *A. tropicalis* and 2000 strong *A. gazella* populations of the neighbouring Prince Edward Island, conceivably consumes 306346.21 tons and 21167.78 tons respectively. Continued population increase suggests that the prey populations are adequate around Marion and the Prince Edward Islands to sustain such growth at least in the short term.

8.3. FUTURE STUDIES

Both Antarctic and Subantarctic fur seals have similar biology, except in their lactation, which lasts 4 and 10 months, respectively. Adult females are mature at 4 years of age, breed once a year until ~20 years old, giving birth to a single pup they care for by alterning foraging trips at sea where they feed, and visits ashore where they suckle their pup. Existing knowledge on the foraging ecology in these fur seals breeding sympatrically at Marion Island is poor. In the present study, foraging ecology has been investigated by analyzing diet from scat analyses by retrieving the remaining hard parts that are specific of prey. When rearing their young, both Antarctic and Subantarctic lactating fur seals forage at sea to feed mostly on myctophid fish and secondly on squid (Goldsworthy *et al.* 1997; Klages & Bester 1998; this study). Myctophid fish are considered to be potential targets for the fisheries industry with which fur seals may interact and compete.

Knowledge of the foraging ecology of marine predators has been revolutionized over the last decades by the use of miniaturized satellite-linked platform transmitter terminals (PTTs) and electronic time-depth recorders (TDRs). These devices, directly fixed to the animals allow precise determination of their at-sea distribution and their foraging behaviour. The regularity with which fur seals alternate foraging trips at sea and visits ashore makes them accessible for using these new methods. To date, the foraging behaviour of sympatric fur seals has only been described for Macquarie Island and Amsterdam Island. At Marion Island, lactating females of both species spend about 5 -7 days at sea in mid-summer (Bester & Bartlett 1990). Subantarctic fur seals breeding on Marion Island appears also to forage at night, but there is no obvious insights on the foraging areas, nor on the whole foraging ecology in Antarctic fur seals here.

The duration of the maternal foraging trips determines directly the pattern of maternal absence-presence with the pup, i.e. the pup provisioning pattern. This results in the growth of the pup, whose body mass at weaning seems to be an important factor for its future survivorship, and thus for population dynamics. At Marion Island, lactating fur seals spend a short time ashore with their pups (~2 days Bester & Bartlett 1990), so that they have to rapidly transfer large amounts of energy by the way of milk. Unfortunately, to date, the quality and quantity of milk delivered by the mother to her pup have never been, i.e. there is a gap in our knowledge of the way in which fur seals transfer their resources to their pups. The alternation of trips at sea and visits ashore induces high energy expenditure for the mother, and fasting adaptations for the young. In Antarctic fur seals, pups are suckled during a short 4-month period while Subantarctic fur seals are weaned within 10-11 months. This should have energetic implications both for the mother and the pup, with specific differences in the costs of rearing a pup. Furthermore, Antarctic fur seals have a relatively short time to respond to pup requirements, and changes in environmental (trophic) conditions may have more pronounced effects on the reproductive success than on Subantarctic fur seals.

In summary, there is an obvious gap in our understanding of the way marine top predators such as fur seals exploit the marine environment, particularly when sympatry may induce ecological segregation, and how environmental conditions and eventual interspecific interactions do affect their foraging and consecutive reproductive performances. Furthermore, studying fur seal foraging ecology may offer information on marine resources, their distribution, abundance, and changes in availability, to be considered for effective conservation and management.