Temporal variation of cephalopods in the diet of Cape fur seals in Namibia

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Cape fur seal (*Arctocephalus pusillus pusillus*) scats were sampled over a period of eight years (1994–2001) at Atlas and Wolf Bay seal colonies in order to assess the cephalopod component of the diet of these seals and cephalopod diversity off the coast of Namibia. The temporal variation within the cephalopod component was investigated. A low diversity of cephalopods, only six species, are preyed upon, with *Todarodes angolensis* being the most important component both in numbers and wet weight in all years. Its lowered weight contribution during winter coincided with a greater diversity of other cephalopod species in the diet, which showed higher proportional weight contribution relative to *Todarodes angolensis*. Scat sampling was found to be an unreliable method of providing estimates of total prey weight consumption by seals, but was considered an acceptable method for proportional comparisons, especially given the ease of scat collection over extended periods.

Key words: *Arctocephalus pusillus pusillus,* Benguela ecosystem, cephalopods, diet, scat samples.

INTRODUCTION

The Cape fur seal, *Arctocephalus pusillus pusillus,* is arguably the most abundant marine mammal species off the coasts of Namibia and South Africa (Wickens *et al.* 1991). The 25 breeding and nine non-breeding colonies of Cape fur seals currently recognized (Oosthuizen & David 1988; Balmelli & Wickens 1994) are distributed from Baia los Tigres on the southwestern coast of Angola to Algoa Bay on the southeast coast of South Africa. Some 65–70% of the total annual pup production takes place in breeding colonies situated on the Namibian coastline or associated islands (David 1987).

Cape fur seals are predators within the Benguela marine ecosystem along the west coast of southern Africa and the population, possibly in excess of 1.5 million animals (Anon. 1991; Balmelli & Wickens 1994), consumes a large absolute quantity of prey within these waters, some of which are commercially important (David 1987; Punt & Butterworth 1995). Studies on the diet of Cape fur seals have mainly focused on the teleost fish component (David 1987; Balmelli & Wickens

1994; Butterworth *et al.* 1995; Punt & Butterworth 1995; Punt & Leslie 1995; Punt *et al.* 1995) and less on the cephalopod component (Lipinski & David 1990; Punt *et al.* 1995). However, cephalopods are a vital source of food for numerous marine mammals and birds, particularly in the productive, cooler oceanic masses such as the Southern Ocean (Roper *et al.* 1985; Rodhouse 1990) and cool currents such as the Benguela on the west coast of southern Africa (Smale *et al.* 1993).

The accurate assessment of the composition of cephalopod fauna throughout different marine ecosystems has been impeded by a general lack of knowledge about the biology, systematics and distribution of these animals. All these factors are exacerbated by the inadequacy of conventional sampling methods such as the use of rectangular mid-water trawl (RMT) 1, 8 or 25 nets or Bongo nets (Rodhouse 1990; Rodhouse *et al.* 1992). The indigestible beaks (mandibles) of cephalopods allow retrieval of a large variety of cephalopod taxa from stomach contents or scats of predators such as cetaceans or pinnipeds. Species-specificity of beaks, particularly lower beaks, enables identification of the composition of cephalopod species in

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the diet of predators, providing indications as to cephalopod diversity and abundance within the foraging range of the predator (Clarke 1962, 1980, 1986; Klages 1996).

Working from pelagic stomach sample analyses, Lipinski & David (1990) provided evidence that cephalopods were relatively unimportant in the diet of Cape fur seals, particularly those feeding off the coast of Namibia. However, that study was irregular in terms of both the temporal and spatial scales. While it provided valuable initial information regarding cephalopod species composition within the diet, it could not describe annual or seasonal variation therein. Consequently, the inference that cephalopods are unimportant in the diet (Lipinski & David 1990) may only hold for the areas and/or time of year when the data were collected. Furthermore, while stomach sampling techniques may be effective means of assessing prey diversity and abundance (Klages 1996), inability to assess the retention time of certain prey elements within the stomach of the predator can result in overestimation of prey intake per unit time. This is particularly the case with cephalopods as the practically indigestible beaks may accumulate as a result of extended gut retention times (Staniland 2002).

The present study aims to augment that of Lipinski & David (1990), thereby enhancing our understanding of the availability and abundance of cephalopods within the northern Benguela ecosystem, and their importance to Cape fur seals. Data are utilized from an ongoing monitoring programme at a locality on the Namibian coast. Although certain biases are associated with the use of scats for diet analyses (Pierce & Boyle 1991), it remains far simpler, cheaper, and more humane than most stomach analyses, which are often destructive (Lipinski & David 1990), or at least highly disruptive (Rodhouse *et al.* 1992; Ferreira & Bester 1999).

MATERIALS AND METHODS

Study area

Cape fur seals haul out at a few sites along the arid Namibian coast, adjacent to their feeding grounds in the Benguela marine ecosystem. The Benguela is characterized by highly productive coastal upwelling centres (Shannon & Jarre-Teichmann 1999), the upwelling intensity of which vary spatially and temporally and is dependent on prevailing wind conditions, the angle of the coast-line and the depth and width of the continental shelf (Shannon 1989). The upwelling centre off the coastal town of Lüderitz, known to be the most intense in the world, divides the Benguela system in two and may form a barrier to the movement of marine species (Shannon 1989). Two large mainland Cape fur seal colonies exist adjacent to the Lüderitz Upwelling Centre, namely Atlas Bay (26°50′S; 15°08′E) and Wolf Bay (26°49′S; 15°07′E). These two colonies are in close proximity to each other (within two kilometres).

Scat collections

In most months from January 1994 to September 2001, either or both of these colonies were searched once a month for scat samples, by field technicians of the Namibian Ministry of Fisheries and Marine Resources (NMFMR). Samples were collected at random throughout the colonies, until a plastic bag was filled with scats; depending on the sizes of scats, it could take approximately 15–40 scats to do this. Scats from the two colonies were pooled due to their proximity to each other. The scats were subsequently washed under running water, the rinsed material passed through nested stainless steel laboratory test sieves, and the remaining material dried in an oven overnight. Cephalopod beaks were removed from the dried material and stored, either dry or in 70% ethanol, for further analysis.

Analysis

All beaks stored dry were placed in 70% ethanol to re-hydrate for at least 76 hours prior to identification to prevent biases in identification (Clarke 1986). Cephalopod lower beaks show species-specific characteristics and the Port Elizabeth Museum reference collection, as well as several publications (Clarke 1986; Lipinski & David 1990; Lipinski *et al.* 1992; Villanueva & Sanchez 1993; Smale *et al.* 1993; Ogden *et al.* 1998; Bianchi *et al.* 1999) were consulted in the identification process. Once identified, the lower rostral length (LRL) of the lower beaks of certain species and the dorsal hood and crest lengths of the lower beaks of other species, were measured to the closest 0.05 mm with vernier callipers (large beaks) or a graticule on a light microscope, (Clarke 1986; Tollit & Thompson 1996). Species-specific regressions were used to calculate dorsal mantle length (DML) and wet weight (hereafter simply referred to as weight) from the LRL of lower beaks for certain species, and the dorsal hood or crest length of lower beaks

for other species (Clarke 1962, 1980, 1986). The differences in calculation of DML and weight between species are a result of differing beak morphology (Clarke 1986). Numbers of upper and lower beaks were counted to determine total abundance of cephalopods; however, due to lower beaks' species-specific characters being more unambiguous than upper beak characters only the lower beaks were used for weight and DML calculation. Frequency of occurrence as presented in this paper can be expressed as the percentage of times each cephalopod species appeared within bags containing beaks (*n* = 80). The numerical abundance can be defined simply as the number of individual cephalopods of one species identified (by means of lower beaks) within all bags collected within the respective time periods used in analyses. The percentage weight contribution of each species to the diet during each of the respective time frames was calculated as follows: the total estimated weight (from lower beaks) of all specimens of one species, taken as a percentage of the total estimated weight for all specimens of all species within that relevant time frame. The percentage numerical abundance was similarly calculated as the number of lower beaks of one species as a percentage of the total number of lower beaks of all species within a time period.

Once DML and weight were calculated for each specimen, variation within and between species was investigated using three temporal scales, namely seasonal, annual and the entire study period. Seasons were categorized into four three-month periods within the year; 1 December to 28 February (summer), 1 March to 31 May (autumn), 1 June to 31 August (winter) and 1 September to 30 November (spring). The mean weight of each species per season and per year was calculated.

RESULTS

A total of 1817 upper and 1253 lower cephalopod beaks were retrieved from scats collected at Wolf and Atlas bays over 93 months. Among the bags containing beaks (*n* = 80), the mean number of lower beaks per bag was 16 (range 1–158). Some 224 fragments of upper and lower beaks were retrieved that could not be identified, nor reassembled to determine how many beaks were represented.

From the lower beaks, six species of cephalopod from five different families were identified (Table 1). Among the bags containing beaks, the

number of species identified per bag ranged from one to five (mean = 2 ± 1.095).

The percentage frequency of occurrence of each cephalopod species found within bag samples, absolute and proportional numerical abundance, estimated weight and percentage weight contribution, are shown for each year of study in Table 1. The percentage weight and number contributions of each species as a mean over the entire study period are shown in Fig. 1. The family Ommastrephidae dominated the seals' diet in terms of numerical abundance (78%) and estimated weight (80%) over the study period, with *Todarodes angolensis* dominating in each year, both numerically and in weight. The mean weight of ommastrephids was relatively small compared in particular to *Octopus magnificus* (Fig. 2a). The largest cephalopod specimen in the diet of the seals was a *T. angolensis* (DML = 265 mm; weight = 473 g), the heaviest was *O. magnificus* (DML = 127 mm; weight = 787 g), and the smallest specimen *Argonauta argo* (DML = 6.2 mm; weight = 1.2 g). The importance of *O. magnificus* during the years that it was present was substantial (Table 1; *e.g.* in 1998 it contributed 20% and in 1995, 13% of total weight consumed) but over all the years it was less important (2%; Fig. 1a). *Sepia australis, Lycoteuthis lorigera* and *A. argo,* together constituted only 18% of the diet over the study period (Fig. 1a), despite *L. lorigera* contributing as much as 28% to the weight consumed in 1997 (Table 1).

Fig. 3 shows the dominance of *T. angolensis* in terms of weight in all seasons (all years combined), followed in particular by *S. australis* in spring and *T. eblanae* in autumn and winter. Certain species dominated the diet during a particular season of one year but were unimportant in other years. For example, during the summer of 1996/1997 the only cephalopod found in scats was *S. australis* while during the winter of 2001 *A. argo* constituted 45% of the diet, the next highest being 23% in the autumn of 1997.

DISCUSSION

Assumptions and biases related to cephalopod beak remains in scats

Scat or faecal analysis remains a favoured method of assessing pinniped diets because of the ease of collection, the relative abundance of samples and the non-disruptive nature of collection (Naya *et al.* 2002). Scat sampling does, however, include some potential biases and these should be taken

Table 1. Percentage frequency of occurrence (% FO), as well as absolute numerical abundance (No.) and weight of cephalopods within scat 'bags' containing cephalopod beaks ($n = 80$) collected from the Atlas and Wolf bays *Arctocephalus pusillus pusillus* colonies between 1994 and 2001. The percentage numerical and weight contribution of each species per year is included in brackets next to each absolute numerical and weight value, respectively. The number of bags collected each year is denoted by *n*.

Year:	1994 ($n = 8$)			1995 ($n = 12$)			1996 ($n = 9$)			1997 ($n = 11$)		
Family and species	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g) (%)
Ommastrephidae												
Todarodes angolensis	58	47 (67)	746 (72)	75	83 (53)	1555 (56)	58	42 (88)	667 (83)	67	34 (31)	1259 (46)
Todaropsis eblanae	42	13 (19)	153 (15)	50	25 (16)	483 (17)	17	2 (4)	47 (6)	25	5 (5)	204 (8)
Octopodidae												
Octopus magnificus	0	0 (0)	0 (0)	8	18 (12)	371 (13)	0	0 (0)	0 (0)	8	2 (2)	146 (5)
Sepiidae												
Sepia australis	8	5 (7)	73 (7)	50	23 (15)	303 (11)	25	3 (6)	76 (10)	67	12 (11)	188 (7)
Argonautidae												
Argonauta argo	17	3 (4)	30 (3)	8	1 (<1)	8 (<1)	8	1 (2)	10 (1)	50	8 (7)	156 (6)
Lycoteuthidae												
Lycoteuthis lorigera	8	2 (3)	28 (3)	17	7 (4)	88 (3)	0	0 (0)	0 (0)	17	49 (44)	749 (28)

	1998 ($n = 11$)			1999 ($n = 9$)			2000 ($n = 11$)			2001 ($n = 9$)		
	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g) (%)	%FO	No. (%)	Weight (g)(%)
Ommastrephidae												
Todarodes angolensis	58	189 (76)	4357 (65)	75	76 (83)	1463 (80)	75	149 (71)	2381 (71)	78	202 (64)	3112 (59)
Todaropsis eblanae	25	7 (3)	223 (3)	17	11 (12)	284 (16)	50	30 (14)	493 (15)	89	88 (28)	1734 (33)
Octopodidae												
Octopus magnificus	17	2 (<1)	1369 (20)	0	0 (0)	0 (0)	0	0 (0)	0 (0)	0	0 (0)	0 (0)
Sepiidae												
Sepia australis	33	34 (14)	456 (7)	8	2 (2)	18 (1)	25	9 (4)	150 (4)	11	1 (<1)	5 (<1)
Argonautidae												
Argonauta argo	50	16 (7)	372 (5)	8	3 (3)	47 (3)	50	9 (4)	160 (5)	44	23 (8)	413 (8)
Lycoteuthidae												
Lycoteuthis lorigera	0	0 (0)	0 (0)	0	0 (0)	0 (0)	17	16 (8)	166 (5)	11	1 (<1)	9 (<1)

a

A. argo
5% (1.16 - 167.55)

L. lorigera
6% (4.69 - 29.16)

T. eblanae
14% (4.19 - 101.41)

O. magnificus
2% (7.88 - 786.57)

S. australis
7% (5.17 - 34.05)

T. angolensis
66% (1.05 - 472.65)

b

A. argo
5% (1 - 19)

L. lorigera
4% (1 - 44)

T. eblanae
15% (1 - 19)

O. magnificus
8% (1 - 18)

S. australis
5% (1 - 26)

T. angolensis
63% (1 - 128)
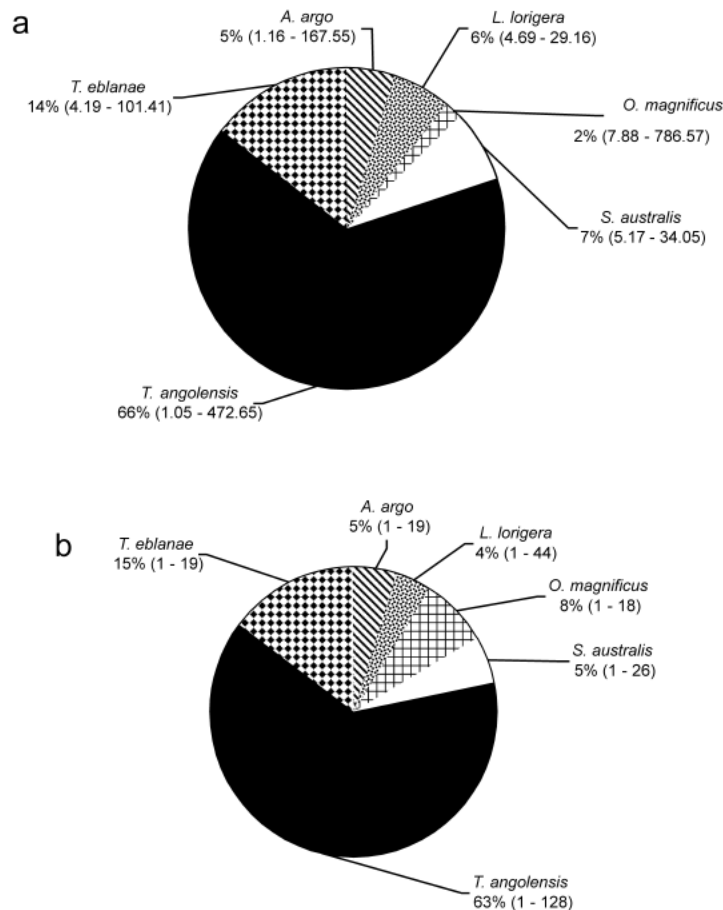
Fig. 1. (a) Percentage weight contribution and (b) the percentage numerical abundance of each cephalopod species for all years combined (1994–2001). The range (over the entire study period) of (a) the estimated mass and (b) numbers of lower beaks of each species found in samples are included in brackets beside each percentage value.

into account when interpreting results.

The diet of different age and sex classes is known to vary in a number of pinnipeds including the Cape fur seal (Lipinski & David 1990). Castley *et al.* (1991) found that there were differences in prey eaten by male and female Cape fur seals along the southeast coast of South Africa. In the present study, it was impossible to quantify differences between sex–age classes since the identity of individuals that deposited the sampled scats was not known. It is probable that the samples largely represented animals undertaking short foraging trips, as those foraging further from the colony for extended times will undoubtedly defecate at sea (Naya *et al.* 2002). Thus, prey occurring closer to the haul-out site of the seals are expected to be better represented in the scats. As the present study focused on a breeding seal colony, the bulk

of movement is that of lactating females that presumably do not venture too far from the colony as they need to return at regular intervals (mean = 2.9 days) to tend to their young (David & Rand 1986).

Cephalopod beaks vary in size and the recovery rates of beaks in scats are negatively related to their size (Staniland 2002). Larger squid beaks have lower recovery rates, because they are regurgitated or retained in the gut for longer, thereby facilitating fragmentation and rendering them unidentifiable in the scats (Staniland 2002). In addition, the awkward shapes of cephalopod beaks increase their retention time (Staniland 2002). Small beaks (from small specimens of larger species such as *T. angolensis* or from small species such as *Inioteuthis* spp.) may also be under-represented as such beaks could be completely digested in the gut. However, beaks
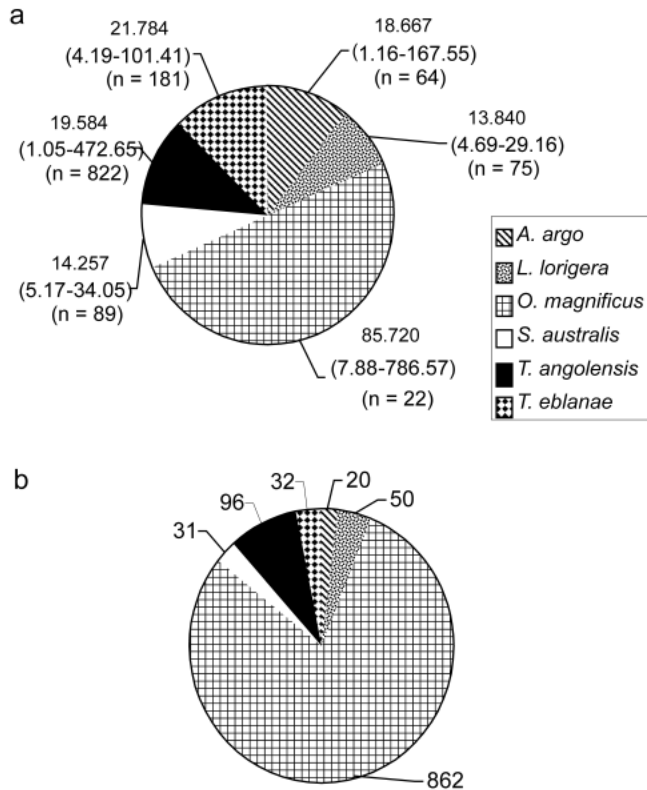
Fig. 2. (a) Relative mean weight (g) and in brackets the range of weights followed by sample size of the six cephalopod species consumed by Cape fur seals at Atlas and Wolf bays from 1994 to 2001 compared to (b) the published mean weight (g) of these species in the diets of seals (Clarke 1986; Lipinski & David 1990; Lipinski *et al.* 1992; Arkhipkin & Laptikhovsky 2000).

recovered do not show reduction in size during digestion (Harvey 1989) and the cephalopods' size can be accurately reconstructed. The retention of larger beaks for longer periods in the stomach results in either an overestimation of cephalopods fed upon during stomach sampling (Staniland 2002), or an underestimate when doing scat sampling (Daneri *et al.* 1999). In captive feeding trials involving Antarctic fur seals (*Arctocephalus gazella*), a mean of only 33% of squid beaks originally fed were recovered. The recovery of beaks varied from 0 to 90% between individuals (Staniland 2002). Captive feeding trials on Cape fur seals showed that the recovery of squid beaks (*Loligo reynaudi*) was 52.4% (*n* = 124; Millar 1996).

From the above an underestimate of consumed cephalopods is likely and the present study therefore concentrated on comparative analyses (*e.g.* seasonal or annual percentage changes in prey composition). Inconsistent sampling in the present study has further necessitated the use of relative

comparisons. Prey numeric proportions are also affected in several ways and Bowen (2000) recommends the use of prey-number correction factors. Based on Cape fur seal captive feeding trials, a correction factor of 1.91 for the squid *L. reynaudi* was determined (Millar 1996). Correction factors for all seal prey do not exist, but from Millar's (1996) study, it seems that beak numbers found in scats should be approximately doubled to obtain the true number of beaks.

Cephalopod diversity in the diet

The six cephalopod species encountered in this study, of the 65 known to inhabit the waters off Namibia (Villanueva & Sanchez 1993), were the most significant species encountered by Lipinski & David (1990) in the southern Namibian region, although they reported a total of 20 species over the entire range of *A. p. pusillus*. The spatially restricted sampling of the present study may account for the lower diversity relative to the 1990
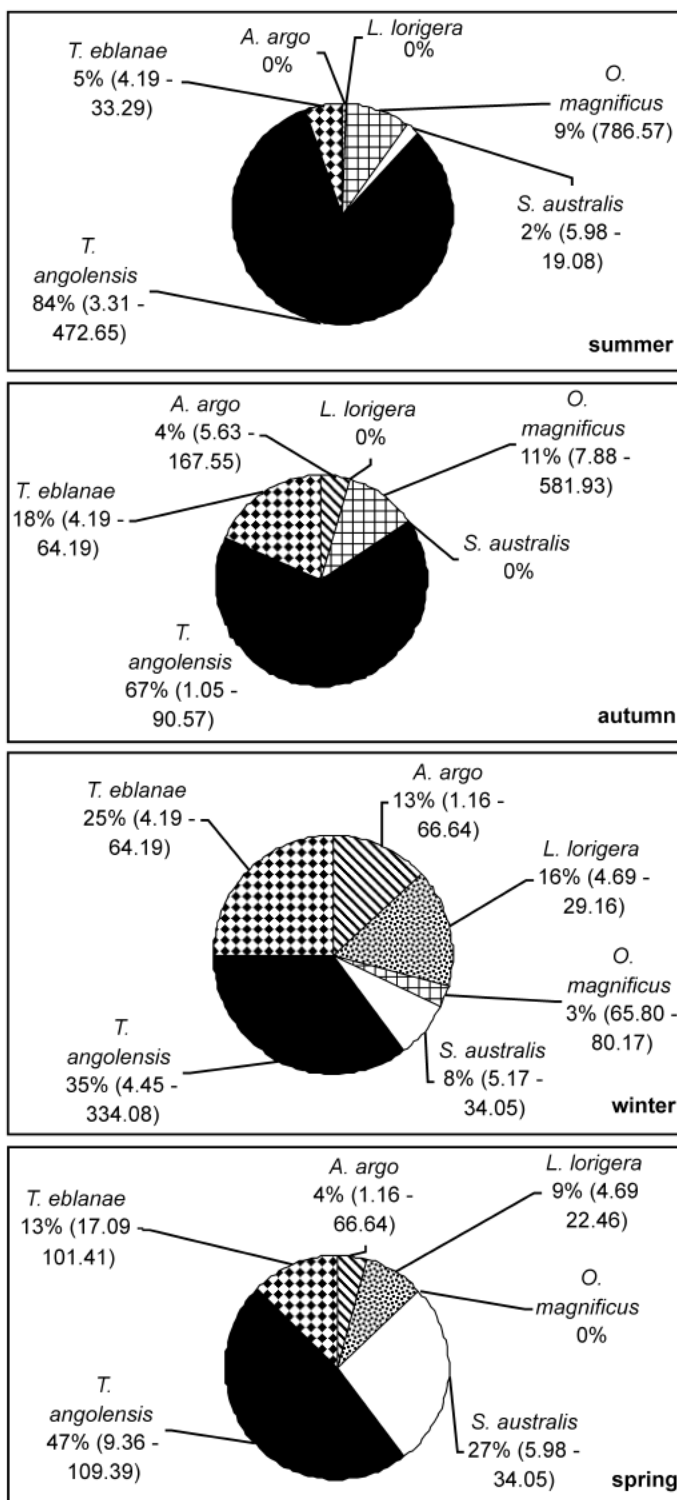
Fig. 3. Percentage weight of cephalopods consumed by Cape fur seals during each season over the eight study years combined. The ranges of weights (g) are shown in brackets.

study, but potential biases associated with digestion may also contribute. The most notable species not found in the present study was *Ocythoe tuberculata,* which Lipinski & David (1990) found to be important, representing 44.29% of the weight of the cephalopod component of the pup diet in particular. The spatially restricted sampling of the present study would explain to some extent the lower diversity although the species encountered in this study undoubtedly constitute the most important cephalopod prey. *O. tuberculata* may have been absent in the diet, misidentified by the authors, or its absence in this study may be an artifact of the scat sampling method. However, other small species, notably *A. argo,* were encountered, which suggests that *O. tuberculata* were not eaten as it was rare (see Lipinski & David 1990).

The prey taken suggests that *A. p. pusillus* forages intensively on the continental shelf and frequently near or on the bottom. Demersal cephalopod species such as *T. angolensis* and *T. eblanae* dominate in the cephalopod component of the seal diet, and *S. australis* is also important at certain times. All of these species ascend in the water column at night (Augustyn & Smale 1989; Bianchi *et al.* 1999), when they are most likely taken, as most dives of *A. p. pusillus* are shallow (<50 m) and occur during the night; only some shallow dives occur in the day, and limited deep diving could occur at any hour (Kooyman & Gentry 1986). *Octopus magnificus* is a benthic cephalopod inhabiting depths of 0 to 200 m over the continental shelf, with a tendency to move to shallower benthic areas during summer (Bianchi *et al.* 1999). *Lycoteuthis lorigera* is another bottom-dwelling species occurring on the slope of the shelf at depths of around 500 m (Roeleveld *et al.* 1992) and is presumably either caught when fur seals infrequently descend to greater depths to forage (Kooyman & Gentry 1986), or as the cephalopod ascends in the water column. There is one epipelagic species, namely *A. argo* (Bianchi *et al.* 1999), which is presumably caught closer to the surface and not necessarily in the neritic zone. However, these species constitute a low and irregular proportion of the seals' cephalopod diet. The mean of two species per bag sampled suggests that seals either do not encounter a large diversity of cephalopods on their foraging excursions or alternatively target only these few species. In addition, as seals hunt to a maximum depth of 200 m but concentrate their feeding in the

upper 50 m of the water column (David 1987), they may not always encounter a large array of cephalopods. The greater diversity of cephalopods within the diet of, for example, southern elephant seals (*Mirounga leonina*), may partly be ascribed to this seals' deeper diving capabilities (*e.g.* Jonker & Bester 1994) and the corresponding greater diversity of cephalopods at greater depths (Rodhouse *et al.* 1992).

Total weight and size of cephalopod prey

The total weight of approximately 25 kg of cephalopods reconstituted from 80 bag samples over a period of eight years is extraordinarily low compared to the 224 kg of cephalopods estimated from 384 stomachs of adult and pup *A. p. pusillus* (Lipinski & David 1990) and a derived total cephalopod consumption of 72 000 tons per annum off the Namibian coast by *A. p. pusillus* (David 1987). This discrepancy could be explained by the likelihood that cephalopod beaks, especially the large ones (>10 mm), accumulate in the stomachs of marine predators (Reid 1995; Klages & Bester 1998), become fragmented (Staniland 2002) or have been ejected by vomiting (Rand 1959; Fea & Harcourt 1997; 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, therefore does not hold for squid beaks (Klages & Bester 1998) as was confirmed for *A. gazella* (Staniland 2002).

The mean weights of cephalopods consumed in this study (Fig. 2a) compared to published mean weights of the particular species (Fig. 2b) also showed that specimens found in this study are considerably smaller with the possible exception of *A. argo.* Only a few large specimens, notably *T. angolensis,* were found but it is clear from such comparisons that scat sampling is not suitable for estimation of total weight consumed.

Between-species variation in numbers and reconstituted weight

The dominance of the two ommastrephid species, *T. eblanae* and in particular *T. angolensis,* may be attributed to the greater number of these cephalopod species within these waters and/or a preference for these species by seals. Ommastrephids regularly appear at the surface at night (Clarke 1966) where *A. p. pusillus* forages (Kooyman & Gentry 1986; David 1987). They may even be

taken incidentally with myctophid fish (Goldsworthy *et al.* 1997; Dellinger & Trillmich 1999), which form an important component of the *A. p. pusillus* diet (David 1987; Balmelli & Wickens 1994; Mecenero & Roux 2002). Myctophids inhabit the deep scattering layer, usually at 200 m to 500 m and migrate to the surface during the night (Green *et al.* 1997).

Annual variation in the cephalopod component of the diet

Argonauta argo and *S. australis* showed marked fluctuations in the number and weight consumed between years. The fluctuations in *A. argo* consumption could conceivably be a result of the bulk of this epipelagic species periodically moving out of the *A. p. pusillus* foraging range. The years of greater abundance of *S. australis* in the seals' diet could be an artefact of secondary ingestion by seals, as Cape hake (*Merluccius capensis*), which feed on large quantities of *S. australis* (Lipinski *et al.* 1992), may be consumed in higher numbers during such years by the seals. Although the consumption of *O. magnificus* and *L. lorigera* varied considerably between years, they were not taken at all during some years, confirming their lesser role in the Cape fur seals' diet. *Todarodes angolensis* and *T. eblanae* were consistently taken by seals over the eight-year period, which emphasized their importance as prey for these seals.

Seasonal variation in the cephalopod component of the diet

Fluctuations in the consumption of the most important species in the diet, *T. angolensis* (the highest in summer at 84% and the lowest in winter at 35%) dictate to some degree the relative contribution of other species throughout the seasons in terms of weight. The consumption of *T. angolensis* is roughly inversely proportional to that of *T. eblanae* (low during summer at 5%, increasing through autumn to a high of 25% during winter). The sharp seasonal decline in *T. eblanae* could be the result of a sudden influx of *S. australis* during spring (27%). *Sepia australis* disappears almost completely from the seals' diet during summer and autumn, with a low presence in winter (8%) followed by a peak during late spring and early summer which coincided with a peak in abundance of the species in trawl samples taken off the west coast of South Africa and southern Namibia (Lipinski *et al.* 1992).

During the seasons of highest relative weight

contribution of *T. angolensis, O. magnificus* shows its greatest proportional contribution of 9% during summer and 11% during autumn, possibly as a result of its tendency to move to shallower water during the summer season, making it more vulnerable to seal predation. During summer in particular, *O. magnificus* is proportionately the second most important source of cephalopod food, indicating that seals feed on this species when the opportunity best presents itself. *Lycoteuthis lorigera* shows a presence in the seals diet only during winter (16%) and spring (9%), probably due to the seals making more frequent deep foraging dives in an attempt to augment their diet, or foraging further afield as may be deduced from the extended duration of foraging trips of Cape fur seal mothers, as pups approach weaning age (David & Rand 1986). The observation that *A. argo,* an epipelagic species, is most abundant in the diet during winter (13%), and absent during summer could again be due to the seals foraging over a wider area in winter (David & Rand 1986) and perhaps being less selective of which species they target. The absence of *A. argo* in the diet during summer is probably better explained by the seals focusing their foraging efforts on other, perhaps larger species, rather than the absence of *A. argo* in foraging areas during this time. The greater diversity of cephalopod species being taken during winter also suggests that seals are possibly foraging further afield and being more opportunistic in their feeding habits.

Finally, it should be kept in mind that due to the natural fluctuations in life stages of the cephalopod prey, larger specimens may be available during certain seasons, conceivably associated with a peak in spawning, so that large cohorts of single age classes are present at any one time, and in this way the relative weight contribution of a particular species to the diet may fluctuate without the seal feeding on fewer of those species.

Other factors

Irregular occurrences of certain species dominating the seals' diet during a certain season of one year and then not again during other years may be the result of a variety of factors. Meteorological events such as ENSO (El Niño southern oscillation event) can cause a shift in species ranges (*e.g.* Gammelsrød *et al.* 1998) and thus abundance of seal prey in areas where seals usually feed (Arntz *et al.* 1991), or an unusually high abundance of a certain cephalopod species may be due to its

fish prey items being more abundant. Environmental factors such as wind speed and direction, precipitation, temperature, oxygen content and water turbidity, for example, could conceivably influence both the distribution of cephalopods in the water column and therefore the hunting efficiency of seals. Many other predators also depend on cephalopods for nutrition, and fall prey to seals, for example the Cape hake feeds intensively on *S. australis* (Lipinski *et al.* 1992; Augustyn *et al.* 1995), but is in turn widely fed upon by *A. p. pusillus,* thereby increasing the chances of secondary prey ingestion. The overall relative importance of cephalopods within the diet of seals will remain unknown until such time as data of the fish component of the diet become available.

CONCLUSION

It cannot be accurately estimated whether *A. p. pusillus* consume a substantial quantity of cephalopods off the coast of southern Namibia, given the constraints of estimating total weight taken through the use of scat sampling techniques. Scat sampling indicated that the diversity of cephalopods fed upon by *A. p. pusillus* was low and dominated by the family Ommastrephidae. *Todarodes angolensis* alone provided almost 70% of the total weight consumed throughout the study period. The importance of other species fluctuates in accordance with season and the abundance of *T. angolensis* determines the proportional contribution of other cephalopods in the diet of the seals. Most species showed a constant presence and little variation between years over the eight years of study. Although scat sampling is unreliable for estimating total weight consumed, it provides a cheap, easy and non-disruptive method of assessing proportional changes in consumption of prey over time.

REFERENCES

ANONYMOUS 1991. Report on the Benguela Ecology Programme workshop on seal-fishery biological interactions. *Rep. Benguela Ecol. Prog. S. Afr.* 22: 25.

ARKHIPKIN, A.I. & LAPTIKHOVSKY, V.V. 2000. Age and growth of the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) on the north-west African shelf. *J. mar. Biol. Assoc. UK* 80: 747–748.

ARNTZ, W., PEARCY, W.G. & TRILLMICH, F. 1991. Biological consequences of the 1982–83 El Niño in the Eastern Pacific. In: F. Trillmich & K.A. Ono (Eds), Pinnipeds and El Niño: responses to environmental stress (pp. 22–42). Springer-Verlag, Berlin.

AUGUSTYN, C.J., LIPINSKI, M.R. & ROELEVELD, M.A.C. 1995. Distribution and abundance of Sepioidea off South Africa. *S. Afr. J. mar. Sci.* 16: 69–83.

BALMELLI, M. & WICKENS, P.A. 1994. Estimates of daily ration for the South African (Cape) fur seal. *S. Afr. J. mar. Sci.* 14: 151–157.

BIANCHI, G., KARPENTER, K.E., ROUX, J-P., MOLLOY, F.J., BOYER, D. & BOYER, H.J. 1999. Field guide to the living marine resources of Namibia. FAO, Rome.

BOWEN, W.D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. *Can. J. Fish. Aquat. Sci.* 57: 898–905.

BUTTERWORTH, D.S., PUNT, A.E., OOSTHUIZEN, W.H. & WICKENS, P.A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus. S. Afr. J. mar. Sci.* 16: 100–112.

CASTLEY, J.G., COCKCROFT, V.G. & KERLEY, G.I.H. 1991. A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south-east coast of South Africa. *S. Afr. J. mar. Sci.* 11: 573–577.

CLARKE, M.R. 1962. The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. *Bull. British Mus. Nat. Hist. Zool.* 8: 421–480.

CLARKE, M.R. 1966. A review of the systematics and ecology of oceanic squids. *Adv. mar. Biol.* 4: 91–300.

CLARKE, M.R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep.* 37: 1–324.

CLARKE, M.R. 1986. A handbook for the identification of cephalopod beaks. Clarendon, Oxford.

DANERI, G.A., PIATKOWSKI, U., CORIA, N.R. & CARLINI, A.R. 1999. Predation on cephalopods by Antarctic fur seals, *Arctocephalus gazella,* at two localities of the Scotia Arc, Antarctica. *Polar Biol.* 21: 59–63.

DAVID, J.H.M. 1987. Diet of the South African fur seal (1974–1985) and an assessment of the competition with fisheries in southern Africa. *S. Afr. J. mar. Sci.* 5: 693–713.

DAVID, J.H.M. & RAND, R.W. 1986. Attendance behaviour of South African fur seals. In: R.L. Gentry & G.L Kooyman (Eds), Fur seals: maternal strategies on land and at sea (pp. 126–141). Princeton University Press, Princeton, New Jersey.

DELLINGER, T. & TRILLMICH, F. 1999. Fish prey of the sympatric Galápagos fur seals and sea lions: seasonal variation and niche separation. *Can. J. Zool.* 77: 1204–1216.

FEA, N. & HARCOURT, R. 1997. Assessing the use of faecal and regurgitate analysis as a means of determining fur seal diet. In: M.A. Hindell & C. Kemper (Eds), Marine mammal research in the southern hemisphere: status, ecology and medicine (pp. 151–163). Surrey Beatty and Sons, Chipping Norton, Sydney.

FERREIRA, S.M. & BESTER, M.N. 1999. Chemical immobilisation, physical restraint, and stomach lavaging of fur seals (*Arctocephalus* spp.) at Marion Island. *S. Afr. J. Wildl. Res.* 29: 55–61.

GAMMELSRØD, T., BARTHOLOMAE, C.H., BOYER, D.C., FILIPE, V.L.L. & O'TOOLE, M.J. 1998. Intrusion of warm surface water along the Angolan-Namibian coast in February–March 1995: the 1995 Benguela *Niño. S. Afr. J. mar. Sci.* 19: 41–56.

GOLDSWORTHY, S.D., HINDELL, M.A. & CROWLEY, H.M. 1997. Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* at Macquarie Island. In: M.A. Hindell & C. Kemper (Eds), Marine mammal research in the southern hemisphere: status, ecology and medicine (pp. 151–163). Surrey Beatty and Sons, Chipping Norton, Sydney.

GREEN, K., WILLIAMS, R. & BURTON, H.R. 1997. Foraging ecology of Antarctic fur seals *Arctocephalus gazella* around Heard Island. In: M.A. Hindell & C. Kemper (Eds), Marine mammal research in the southern hemisphere: status, ecology and medicine (pp. 105–113). Surrey Beatty and Sons, Chipping Norton, Sydney.

HARVEY, J.T. 1989. Assessment of errors associated with harbor seal (*Phoca vitulina*) faecal sampling. *J. Zool., Lond.* 219: 101–111.

JONKER, F.C. & BESTER, M.N. 1994. The diving behaviour of southern elephant seal, *Mirounga leonina,* cows from Marion Island. *S. Afr. J. Antarct. Res.* 24: 75–93.

KIRKMAN, S.P., WILSON, W., KLAGES, N.T.W., BESTER, M.N. & ISAKSEN, K. 2000. Diet and estimated food consumption of Antarctic fur seals at Bouvetøya during summer. *Polar Biol.* 23: 745–752.

KLAGES, N.T.W. 1996. Cephalopods as prey. II. Seals. *Phil. Trans. R. Soc. Lond.* B 351: 1045–1052.

KLAGES, N.T.W. & BESTER, M.N. 1998. Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Mar. Biol.* 131: 559–566.

KOOYMAN, G.L. & GENTRY, R.L. 1986. Diving behavior of South African fur seals. In: R.L. Gentry & G.L. Kooyman (Eds), Fur seals: maternal strategies on land and at sea. University Press, Princeton, New Jersey.

LIPINSKI, M.R. & DAVID, J.H.M. 1990. Cephalopods in the diet of the South African fur seal (*Arctocephalus pusillus pusillus*). *J. Zool., Lond.* 221: 359–374.

LIPINSKI, M.R., PAYNE, A.I.L. & ROSE, B. 1992. The importance of cephalopods as prey for hake and other groundfish in South African waters. *S. Afr. J. mar. Sci.* 12: 651–662.

MECENERO, S. & ROUX, J-P. 2002. Spatial and temporal variability in the diet of a top predator in the Northern Benguela. In: Small pelagic fishes and climate change programme. GLOBEC Report No. 16: 62–64.

MILLAR, D. 1996. Diet composition estimates for *Arctocephalus pusillus pusillus* from prey remains in the faeces: an experimental evaluation. B.Sc. (Hons) report, University of Cape Town.

NAYA, D.E., ARIM, M. & VARGAS, R. 2002. Diet of South American fur seals (*Arctocephalus australis*) in Isla de Lobos, Uruguay. *Mar. Mamm. Sci.* 18: 734–745.

OGDEN, R.S., ALLCOCK, A.L., WATTS, P.C. & THORPE, J.P. 1998. The role of beak shape in octopodid taxonomy. *S. Afr. J. mar. Sci.* 20: 29–36.

OOSTHUIZEN, W.H. & DAVID, J.H.M. 1988. Non-breeding colonies of the South African (Cape) fur seal *Arctocephalus pusillus pusillus* in southern Africa. *Investl. Rep. Sea Fish. Res. Inst. S. Afr.* 132: 1–17.

PIERCE, G.J. & BOYLE, P.R. 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanogr. mar. Biol. Ann. Rev.* 29: 409–486.

PUNT, A.E. & BUTTERWORTH, D.S. 1995. The effects of future consumption by the Cape fur seal on catches and the catch rates of Cape hakes. 4. Modelling the biological interaction between the Cape fur seal *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus. S. Afr. J. mar. Sci.* 16: 113–127.

PUNT, A.E. & LESLIE, R.W. 1995. The effects of future consumption by the Cape fur seal on catches and the catch rates of Cape hakes. 1. Feeding and diet of the Cape hakes *Merluccius capensis* and *M. paradoxus. S. Afr. J. mar. Sci.* 16: 37–55.

PUNT, A.E., DAVID, J.H.M. & LESLIE, R.W. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 2. Feeding and diet of the Cape fur seal *Arctocephalus pusillus pusillus. S. Afr. J. mar. Sci.* 16: 85–99.

RAND, R.W. 1959. The Cape fur seals (*Arctocephalus pusillus*): distribution, abundance and feeding habits off the southwestern coast of the Cape Province. *Investl. Rep. Div. Fish. S. Afr.* 34: 1–75.

REID, K. 1995. The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarct. Sci.* 7: 241–249.

RODHOUSE, P.G. 1990. Cephalopod fauna of the Scotia Sea at South Georgia: potential for commercial exploitation and possible consequences. In: K.R. Kerry & G. Hempel (Eds), Antarctic ecosystems: ecological change and conservation (pp. 289–298). Springer-Verlag, Berlin.

RODHOUSE, P.G., ARNBOM, T.R., FEDAK, M.A., YEATMAN, J. & MURRAY, W.A. 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can. J. Zool.* 70: 1007–1015.

ROELEVELD, M.A.C, LIPINSKI, M.R., AUGUSTYN, C.J. & STEWART, B.A. 1992. The distribution and abundance of cephalopods on the continental-slope

of the eastern south-Atlantic. *S. Afr. J. mar. Sci.* 12: 739–752.

ROPER, C.F., SWEENEY, M. & CLARKE, M.R. 1985. Cephalopods. In: W. Fischer & J.C. Hureau (Eds), FAO species identification sheets for fishery purposes: Southern Ocean (Fishing Areas 48, 58 and 88), Vol. 1: 118. FAO, Rome.

SHANNON, L.V. 1989. The physical environment. In: A.I.L. Payne & R.J.M. Crawford (Eds), Oceans of life off southern Africa (pp. 12–27). Vlaeberg Publishers, Cape Town.

SHANNON, L.J. & JARRE-TEICHMANN, A. 1999. A model of trophic flows in the northern Benguela upwelling system during the 1980s. *S. Afr. J. mar. Sci.* 21: 349–366.

SMALE, M.J., CLARKE, M.R., KLAGES, N.T.W. & COMPAGNO-ROELEVELD, M.A.C. 1993. Octopod beak identification – resolution at a regional level

(Cephalopoda: Octopoda, southern Africa). *S. Afr. J. mar. Sci.* 13: 269–293.

STANILAND, I.J. 2002. Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trails. *Mar. Mamm. Sci.* 18: 223–243.

TOLLIT, D.J. & THOMPSON, P.M. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Can. J. Zool.* 74: 1110–1121.

VILLANUEVA, R. & SANCHEZ, P. 1993. Cephalopods of the Benguela current off Namibia: new additions and considerations of the genus *Lycoteuthis. J. Nat. Hist.* 27: 15–46.

WICKENS, P.A., DAVID, J.H.M., SHELTON, P.A. & FIELD, J.G. 1991. Trends in harvests and pup numbers of the South African fur seal: implications for management. *S. Afr. J. mar. Sci.* 11: 307–326.