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Cephalopods as prey. II. Seals

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SUMMARY

For 31 of the 33 extant species of pinnipeds it is either known or suspected that they include cephalopods in their diet. The two exceptions are the Baikal Seal and the Caspian Seal, which inhabit freshwater where cephalopods do not occur. The available evidence indicates that no species of seal specializes entirely on cephalopods and only few regularly eat appreciable quantities of this prey, although for several they appear to be seasonally important prey. For most pinnipeds only rudimentary prey identifications have been published. The most common taxa of cephalopods reported to be consumed by seals are members of the neritic Loliginidae, the oceanic Ommastrephidae, Onychoteuthidae and Gonatidae, as well as benthic octopods. Too few quantitative diet analyses on enough pinnipeds have been done to quantify the consumption of cephalopods by seals globally with any precision.

1. INTRODUCTION

There are 33 extant species of pinnipeds, comprising 14 species of fur seals and sea lions (Otariidae), 18 true seals in the family Phocidae and the walrus as the lone member of the Odobenidae. An additional species, the Caribbean Monk Seal *Monachus tropicalis* has been excluded from this review because it is very likely that it has become extinct in the mid-twentieth century (Le Boeuf *et al*. 1986). It is not known whether cephalopods were part of its diet. All except two seal species are marine. The Baikal Seal *Phoca sibirica* and the Caspian Seal *Phoca caspica* inhabit large hyposaline inland lakes where cephalopods are absent. The remaining 31 seals occur in all major oceans, from the polar regions to the tropics and from the coastal zone to the high seas. However, most populations are distributed along the continental fringes and around oceanic islands, and there are large areas in the tropical and subtropical regions of the world's oceans devoid of seals. Roughly 35 million seals populate the world's oceans today (Erickson & Hanson 1990; Riedman 1990), suggesting that their impact on prey stocks is not insignificant.

Not surprisingly we know most about the diet of those species of seals that are of considerable economic importance, either because they were, or still are, hunted for their pelts and meat or because they prey on commercially sought after prey and are thus in conflict with human fisheries. During the last decade or so we have also learnt a great deal about those seal species whose stocks are monitored as indicators of the health of the marine environment, such as the Antarctic species of pinnipeds. We know least about those species that are rare, threatened or endangered, because there are few ethically acceptable opportunities to sample these seals and to determine their diet.

Great strides have been made in our knowledge of cephalopods as food of marine mammalian predators (pinnipeds and cetaceans) since Clarke (1985*a*, 1986*a*) last reviewed this subject. In the older scientific literature this prey type was often identified only as 'squid' or 'octopus' because the expertise to identify them was lacking. Although Clarke (1962) had laid the foundation for a method that allows cephalopods to be identified from their beaks (mandibles), his work did not receive the attention it deserved until he provided the first comprehensive keys for the identification of cephalopods beaks (Clarke 1980, 1986*b*). These publications stimulated the assembly of reference collections in museums and marine mammal laboratories and the publication of regional beak keys for squids and octopods (e.g. Wolff 1984; Smale *et al*. 1993). Most of our recent insight into cephalopods as prey of seals has been derived employing this method. Pens and cuttlebones are much less often used for prey identification, although they too are species-specific in their shape (Roeleveld 1972). Soft parts (flesh) seldom last long enough after being swallowed by a predator to be of diagnostic value. In contrast, cephalopod beaks are resistant to digestion and accumulate in the predator's stomach until regurgitated periodically or passed through the gut. Special care is needed therefore in the analysis of food to separate fresh from accumulated items, otherwise the importance of cephalopods in the diet of a predator may be overestimated. In addition, differential digestion of the various components (fish, cephalopod, crustacean, etc.) of the prey may take place in the stomach, which may complicate the accurate assessment of the composition of the diet (or the relative importance of squid). Cephalopod beaks can also be used to estimate the size of the cephalopod using regressions that relate beak dimensions to mantle length and mass. This makes the analysis of accumulated beaks from seal stomachs most rewarding in that it sheds light on prey choice, size selection, diving depth and foraging locality of these warm-blooded predators.

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2. THE CEPHALOPOD PREY OF SEALS

Walrus Odobenus rosmarus

Walrus are primarily benthic feeders on banks and coastal margins of the Arctic in depths of less than 100 m. Their main food is clams (Fay 1981). Other prey taken occasionally includes cephalopods, but they only constitute a minor prey of this species. Fay *et al.* (1984) summarize the available information and provide a list of cephalopod species taken by walrus. These consist of *Octopus californicus*, *Octopus* sp. and *Benthoctopus* sp.

Northern Fur Seal Callorhinus ursinus

The diet and foraging ecology of the Northern Fur Seal throughout its range in the eastern Pacific and Bering Sea is well established (Kajimura 1985; Perez & Bigg 1986; Antonelis *et al.* 1990; Sinclair *et al.* 1994). Small schooling fishes and neritic squids are the principal prey species over the continental shelf; they are replaced by oceanic squids further offshore. About 10 species of squid have been reported from their diet. *Loligo opalescens*, *Onychoteuthis* sp., *Berryteuthis magister* and *Gonatopsis borealis* are reported to be the most dominant. Studies in Japanese waters (Wada 1971; Yoshida *et al.* 1980) have added *Todarodes pacificus*, *Watasenia scintillans* and unspecified Enoploteuthidae to this list.

Guadalupe Fur Seal Arctocephalus townsendi

Very little is known about the diet of this endangered species, which is restricted to the Pacific coast of Baja California. Apparently they eat cephalopods and lanternfish (Reeves *et al.* 1992).

Juan Fernandez Fur Seal Arctocephalus philippii

No detailed study of the stomach contents of this species, which lives off the coast of Chile, has been completed. The stomachs of stranded animals contained beaks of *Dosidicus gigas*, *Onychoteuthis banksi*, *Todarodes filippovae*, *Octopoteuthis* sp. and *Tremoctopus violaceus* (Torres 1987).

Galapágos Fur Seal Arctocephalus galapagoensis

Clarke & Trillmich (1980) detailed the cephalopod part of the diet of this fur seal in the tropical Pacific. *Onychoteuthis banksi* was the most frequently occurring species in the regurgitations from seven adults. Beaks from ommastrephids and from two other species, one possibly a *Mastigoteuthis* sp., occurred in smaller numbers.

South American Fur Seal Arctocephalus australis

The diet of this species is poorly documented. Reijnders *et al.* (1993) provide a list of broad prey classes which includes cephalopods but details are not given.

Cape and Australian Fur Seal Arctocephalus pusillus

Because they are thought by many to compete with commercial fisheries, the diet of this species is well known, both in southern Africa and in southern Australian waters where the two subspecies occur. David (1987) published a comprehensive account of the diet of *Arctocephalus pusillus* from the western South African and Namibian coasts. The cephalopod component is detailed in Lipinski & David (1990). Twenty different cephalopods were identified; six species or species groups were considered to be numerically significant: *Loligo vulgaris*, *Sepia* spp., *Octopus* sp., *Todaropsis eblanae*, *Todarodes angolensis* and *Ocythoe tuberculata*. Along the south and east coasts of South Africa, *Loligo vulgaris*, *Lycoteuthis diadema*, *Octopus vulgaris* and *O. magnificus* are of foremost importance in the diet of this seal (N. Klages, unpublished). Operational conflicts between seals and Eastern Cape fishermen jigging for *Loligo vulgaris* are a common problem (personal observation). As in southern Africa, fish dominates the diet of the Australian Fur Seal in Tasmanian waters (Gales & Pemberton 1994), however, 11 species of cephalopods were identified (Gales *et al.* 1993), with *Nototodarus gouldi* predominant, followed by *Sepioteuthis australis* and *Sepia apama*.

New Zealand Fur Seal Arctocephalus forsteri

New Zealand Fur Seals feed mainly on fish and cephalopods, though they are known to take penguins in the southern part of their range (Green *et al.* 1990). Stomach contents of 64 fur seals collected from South Island contained 53% by mass of squid (*Nototodarus* sp.) and unspecified octopods (Street 1964).

Antarctic Fur Seal Arctocephalus gazella

There are detailed papers available on the diet of *Arctocephalus gazella* from most localities in the Southern Ocean where they are plentiful. In general, south of the Antarctic Convergence, Antarctic Fur Seals take almost exclusively krill *Euphausia superba* during the breeding season; squid is only a minor dietary component (Bonner 1968; Doidge & Croxall 1985). Daneri & Coria (1992) retrieved squid beaks from 34% of scats collected at the South Orkney Islands but these were not identified further. At South Georgia, Doidge & Croxall (1985) reported four squid taxa: *Kondakovia longimana*, *Moroteuthis knipovitchi*, *Galiteuthis glacialis* and an unidentified ommastrephid (possibly *Martialia hyadesi*). At Heard Island, where *E. superba* is scarce, fish is the main constituent of their diet, with remains of this food type occurring throughout the year in more than 90% of the samples investigated by Green *et al.* (1989, 1991). Unspecified squids and octopods occurred in 3.4% and 0.2% respectively of the samples. At sub-Antarctic Marion Island, otoliths from myctophid fish dominated the scats analysed by Bester & Klages (unpublished). Squid beaks were rare in these sample types and were limited to the remains of young Onychoteuthidae, possibly *Moroteuthis ingens*.

Sub-Antarctic Fur Seal Arctocephalus tropicalis

At Gough Island, *Arctocephalus tropicalis* takes the ommastrephid *Todarodes* sp. (52.5% by frequency of occurrence), Histioteuthidae (25.2%), Onychoteuthidae (19.9%), Cranchiidae (2.1%) and Octopoteuthidae (0.3%) (Bester & Laycock 1985). At

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Amsterdam Island in the Indian Ocean, Paulian (1964) noted the importance of squid in their diet. Bester & Klages (unpublished) investigated scats of this species at Marion Island and found an almost complete overlap in the fish component of the diet of this species with that of the Antarctic Fur Seal. Beaks of *Moroteuthis* sp., *Alluroteuthis antarcticus* and *Martialia hyadesi* were found in small numbers in scats and in samples obtained with stomach lavage.

Steller Sea Lion Eumetopias jubatus

Squid (Gonatidae) and *Octopus* sp. have been reported in the diet of this north Pacific species (Pitcher 1981). Perlov (1975) listed Octopoda and *Gonatus magister*, as well as the polar cod *Theragra chalcogramma*, as the chief food items in the 138 stomachs that he examined.

Californian and Galapágos Sea Lion Zalophus californianus

The diet of this abundant pinniped is well known in the coastal waters off California, where seasonal and annual variability have been investigated (Antonelis *et al.* 1984; Aurioles *et al.* 1984; Lowry *et al.* 1991), but the feeding habits of the Galapágos population are not nearly as well documented (Trillmich & Dellinger 1991). Off the American west coast *Loligo opalescens* occurred in 46.7% of the 195 scats analysed by Antonelis *et al.* (1984) and attained a frequency of occurrence of 29.1% in 1085 scats sampled from 1981–1986 by Lowry *et al.* (1991). *Octopus rubescens*, *O. bimaculatus*, *Onychoteuthis borealijaponicus*, *Abraliopsis* spp. and *Gonatus* spp. were also identified, suggesting that cephalopods are pursued by this seal on the sea bed, in inshore waters and on the continental slope. Consistent with the seasonal onshore movement of *L. opalescens*, Lowry *et al.* (1991) found that this prey increased in autumn and winter in the diet of Californian Sea Lions, thus exhibiting a pronounced dietary and behavioural flexibility in response to the movements and availability of prey.

South American Sea Lion Otaria byronia

This species occurs on both the Atlantic and Pacific shores of South America, including the Falkland Islands. They forage mainly in shallow water of less than 300 m, often in multi-species assemblages on a variety of marine organisms, but mainly on demersal and mesopelagic fish (Reeves *et al.* 1992). Squid and Octopoda are apparently also taken (Riedman 1990; Reijnders *et al.* 1993), but specific details are lacking for this seal which inhabits regions where major fisheries for cephalopods are located.

Australian Sea Lion Neophoca cinerea

Beaks from octopus and *Sepia apama* were found among the stomach contents of fresh strandings of Australian Sea Lions worked by Gales & Cheale (1992). One beak from *Sepioteuthis australis* was also recovered. Scats collected from free-ranging animals by the same authors also contained octopus and cuttlefish remains.

Hooker's Sea Lion Phocarctos hookeri

Also known as the New Zealand Sea Lion, Hooker's Sea Lions appear to have a catholic diet, ranging from fish, crustaceans and cephalopods to warm-blooded animals, but a detailed list of prey species has not been published (Reeves *et al.* 1992). Each year several hundred Hooker's Sea Lions are taken incidentally with fishing gear near their breeding grounds on the Auckland Islands by a commercial squid fishery for *Nototodarus* sp. (Reijnders *et al.* 1993), suggesting that this squid species is seasonally targeted on its spawning grounds by the seals.

Harbour Seal Phoca vitulina

This species is widely distributed in temperate and sub-Arctic regions in the northern hemisphere. As Harbour Seals have such a wide range and occupy a correspondingly diverse number of habitats, their diet includes an extremely large variety of organisms. This includes pelagic and benthic fishes, cephalopods and crustaceans (Reeves *et al.* 1992). Small schooling fishes often feature strongly in their diet (Härkönen 1987; Payne & Selzer 1989; Pierce et al. 1991*a*; Thompson *et al.* 1991). Squid and octopus beaks have been found in stomach contents at the Aleutian and Pribilof Islands (Lowry & Frost 1981), the Gulf of Alaska (Pitcher 1980), British Columbia (Spalding 1965), the southern Californian coast (Reeves *et al.* 1992) and in Scottish waters (Bonner 1972), but specific details are not given in these publications. Payne & Selzer (1989) reported *Illex illecebrosus* and *Loligo pealei* in the diet of Harbour Seals from the American east coast.

Spotted Seal Phoca largha

Fish are the major food source of this seal in the Bering Sea, but crustaceans and octopods are also consumed on occasion. Crustaceans appear to be most important to young seals, while *Octopus* spp. are most frequently eaten by adults (Lowry & Frost 1981).

Ringed Seal Phoca hispida

Ringed Seals are the most abundant and widely distributed phocids in the northern hemisphere. Lowry *et al.* (1980*a*) investigated the variability in the diet at eight locations along the Alaskan coast and Gjertz & Lydersen (1986) reported on the diet in Svalbard. Neither their publications nor the Soviet literature reviewed by Lowry *et al.* (1980*a*) reported cephalopods in the diet of this seal. Possibly based on unpublished evidence, Dunn (1979) attributed a minimum annual consumption of 30000 tonnes of squids combined to Ringed and Ribbon Seals in the eastern Bering Sea. It may therefore be suspected that Ringed Seals do eat cephalopods.

Harp Seal Phoca groenlandica

Fish and crustaceans, especially amphipods and euphausiids, are considered the main prey items consumed by Harp Seals in the Canadian Arctic, in the Barents Sea and north west Atlantic (Sergeant 1973; Lydersen *et al.* 1991; Beck *et al.* 1993; Nilssen *et al.*

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1995). Remains of *Gonatus fabricii* and octopods, including *Bathypolipus arcticus* and *Eledone cirrhosa*, were identified in stomach samples by Lydersen *et al.* (1991), where they constituted 1% by volume.

Ribbon Seal Phoca fasciata

Ribbon Seals are known to prey on gadid and clupeid fishes, but all major diet studies have been based on animals collected during the spring period of reduced feeding so they are not very representative of the general feeding habits of this seal. Nevertheless, octopod beaks found in samples on a few occasions by Shustov (1965) and Frost & Lowry (1980) confirmed that this prey type is taken.

Bearded Seal Erignatus barbatus

Bearded Seals occur in shelf areas of the Arctic and sub-Arctic, where they feed on benthic prey such as bivalve molluscs, crabs and demersal fish (Lowry *et al.* 1980*b*; Finlay & Evans 1983). In a recent study by Antonelis *et al.* (1994), unspecified octopods comprised 4% of the diet by frequency of occurrence.

Hooded Seal Cystophora cristata

Hooded Seals live over the deep waters of the North Atlantic near the outer edge of the pack ice. Although these seals are hunted in large numbers no detailed study on the diet of this species appears to have been published. They are said to feed on redfish, halibut, capelin, cod, crustaceans, octopus and squid (Reeves *et al.* 1992).

Grey Seal Halichoerus grypus

Grey Seals inhabit the North Atlantic Ocean in three populations. Cephalopods have not been recorded in the diet of the Baltic stock of Grey Seals, presumably because of the depauperate cephalopod fauna of that ocean. The western and eastern populations of Grey Seals eat schooling fish species, squids and octopods, and even seabirds occasionally (Rae 1973). However, there is no strong evidence that cephalopods are of more than incidental importance in their diet (Bowen *et al.*1993; Prime & Hammond 1990; Hammond *et al.* 1994). An exception are the data presented by Pierce *et al.* (1991*b*) from Scottish waters, where the octopus *Eledone cirrhosa* constituted nearly a quarter of the diet by mass, but this result may be biased because it was not adjusted for differential digestion.

Crabeater Seal Lobodon carcinophagus

Most numerous of all species of pinnipeds, Crabeater Seals eat krill almost exclusively. For squid, Øritsland (1977) calculated an overall proportional frequency of occurrence of 2%, but Green & Williams (1986) failed to find any cephalopod remains in scats.

Ross Seal Ommatophoca rossii

Remains of fish and squid formed the bulk of the stomach contents of Ross Seals analysed by Skinner & Klages (1994) that were taken in the Antarctic pack ice zone. The squid component was dominated by *Psychroteuthis glacialis*. Additional squid beaks identified in this material were the cranchiid *Galiteuthis glacialis*, *Chiroteuthis* sp., *Alluroteuthis antarcticus* and *Kondakovia longimana*. Prey sizes derived from beak measurements ranged from an *Alluroteuthis antarcticus* with a mantle length of 61 mm (estimated mass of 25 g) to a *Kondakovia longimana* with 412 mm mantle length (897 g).

Leopard Seal Hydrurga leptonyx

This powerful Antarctic seal has a catholic diet ranging from krill and fish to warm-blooded animals (Øritsland 1977). Squid remains have been found in the stomach of this species comprising on average 6% by frequency of occurrence (Laws 1984). Diet samples identified by Clarke (1985*b*) contained *Moroteuthis knipovitchi* and *Kondakovia longimana*. The contents of one stomach contained a large beak of *K. longimana* estimated to have come from a squid with a mantle length of 407 mm (N. Klages, unpublished).

Weddell Seal Leptonychotes weddellii

Cephalopods feature prominently in the diet everywhere in the Antarctic where stomach contents of these expert divers have been investigated. At the South Shetland Islands, *Moroteuthis knipovitchi*, *Kondakovia longimana*, *Psychroteuthis glacialis*, *Alluroteuthis antarcticus*, *Brachioteuthis* sp. and *Gonatus antarcticus* were identified (Clarke & MacLeod 1982*b*). In another set of samples from this locality, Lipinski & Woyciechowski (1981) identified the octopods *Megaeledone senoi*, *Pareledone turqueti* and *Parledone charcoti* in the diet of Weddell Seals. Plötz (1986) and Plötz *et al.* (1991) identified *Megaeledone senoi*, *Parledone charcoti* and *Psychroteuthis glacialis* in the diet in the Weddell Sea, but these represented only 3.6% of total prey items. However, the considerable mass contribution of this prey component suggested that cephalopods, in terms of biomass, may exceed even the most abundant fish species found in the diet. Green & Burton (1987) compared Weddell Seal diet at three Antarctic localities. Although they did not identify the species of cephalopods they emphasized the importance of this prey type in the diet of this seal.

Northern Elephant Seal Mirounga angustirostris

Elephant seals make very long foraging excursions during which they dive almost continuously to depths of several hundred metres (Le Boeuf *et al.* 1986; Steward & DeLong 1993). Condit & Le Boeuf (1984) published information on the stomach contents of 27 specimens of this species collected opportunistically over 30 years. *Onychoteuthis borealijaponicus* and *Gonatopsis borealis* were the most frequently identified squid species on a list comprising 12 species. The most comprehensive data on diet were obtained by Antonelis *et al.* (1987) using stomach lavage on 59 seals. They identified 13 species of squid and two species of octopods in their samples. *Octopoteuthis deletron*, *Gonatopsis borealis*, *Histioteuthis dofleini* and *H. heteropsis* were present in at least 20% of stomachs lavaged. Sinclair (1994) found that *Loligo opalescens* was the most dominant cephalopod in diet samples taken from juvenile seals in Californian waters.

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Table 1. *Biological characteristics of cephalopod prey consumed by pinnipeds*

(+ = present in diet; ? = not known; blank = absent.)

	type consumed			where consumed			
seal species	muscular	oily	ammoniacal	inshore	offshore	benthic	pelagic
Walrus	+					+	
Northern Fur Seal	+	+		+	+	+	+
Guadelupe Fur Seal	?	?	?	?	?	?	?
Juan Fernandez Fur Seal	+				+		+
Galapagos Fur Seal	+				+		+
South American Fur Seal	?	?	?	?	?	?	?
Cape and Australian Fur Seal	+			+	+	+	+
New Zealand Fur Seal	+				+	+	+
Antarctic Fur Seal	+		+		+		+
Subantarctic Fur Seal	+				+		+
Steller Sea Lion	+	+				+	+
Californian Sea Lion	+	+		+	+	+	+
South American Sea Lion	+					+	+
Australian Sea Lion	+			+		+	+
Hooker's Sea Lion	?	?	?	?	?	?	?
Harbour Seal	+			+		+	+
Spotted Seal	+			+		+	
Ringed Seal	?	?	?	?	?	?	?
Harp Seal	+	+		+	+	+	+
Ribbon Seal	+	?	?	?	?	+	?
Bearded Seal	+					+	
Hooded Seal	+	?			+	+	+
Gray Seal	+	?				+	?
Crabeater Seal	?				+		+
Ross Seal	+		+	+	+		+
Leopard Seal	+				+		+
Weddell Seal	+	+		+	+	+	+
Northern Elephant Seal	+	+	+	+	+	+	+
Southern Elephant Seal	+	+	+	+	+	+	+
Mediterranean Monk Seal	+					+	
Hawaiian Monk Seal	+					+	

Southern Elephant Seal Mirounga leonina

This species is capable of sustained and deep dives (Hindell *et al.* 1991) and cephalopods are reported to be a major part of the diet of this large seal. Clarke & MacLeod (1982*a*) provided the first information on the species and sizes consumed by Southern Elephant Seals at the South Orkney Islands. They listed *Gonatus antarcticus*, *Moroteuthis knipovitchi* and octopods as the most numerous species in their sample from 11 seals. Rodhouse *et al.*(1992) published a comprehensive analysis based on 51 animals stomach-lavaged at South Georgia. In all, 16 species of cephalopods from 13 families were found, including the octopods *Pareledone charcoti* and *P. polymorpha*. *Psychroteuthis glacialis* was identified as the most numerous squid, while *Moroteuthis knipovitchi* contributed most in terms of estimated biomass. Green & Burton (1993) compared the stomach contents of Southern Elephant Seals from Macquarie and Heard Islands, where other major breeding populations of this seal are located. A combined total of 17 cephalopod taxa was identified at both localities, but there were significant differences in diet composition between islands and between seasons. Stomach contents at Macquarie Island were dominated numerically by *Histioteuthis eltaninae* and at Heard Island by *Moroteuthis knipovitchi*. Southern Elephant Seals are conceivably the major consumers of cephalopods among pinnipeds. For the South Georgia population Boyd *et al.* (1994) estimated an annual consumption of squid of 2.28×10^6 t.

Mediterranean Monk Seal Monachus monachus

The diet of this endangered species is poorly known. Regarded as inshore feeders, unspecified *Octopus* is reported to be consumed by this seal (Kenyon 1981).

Hawaiian Monk Seal Monachus schauinslandi

No quantitative study of the diet of this species has been published. King & Harrison (1961) report cephalopods in the diet but do not give details. Kenyon (1981) provides a list of prey species for this seal but does not state from how many and what type of samples (scats, regurgitations, carcass, etc.) this was derived. Unspecified octopods feature last on this list.

3. DISCUSSION

The modal body length of all species of pinnipeds, males and females ($n = 66$), is 240 cm, ranging from 120 cm for a female Galapágos Fur Seal to 5 m for a male Southern Elephant. By comparison, squids of interest to fisheries – and this selection is already biased towards the larger sizes – attain a modal mantle length

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of 30 cm (range 3.5–400 cm, $n = 87$) (Roper *et al.* 1984). With a difference in length of an order of magnitude, squids would appear to be a suitable prey for seals. Many cephalopods are also relatively easily caught once they are detected by a seal because they are incapable of sustaining prolonged high-speed swimming when pursued. As this review has shown, all species of pinnipeds include cephalopods in their diet, with the possible exception of the Ringed Seal for which no definitive record was found in the scientific literature that they consume this type of prey. However, given our well-founded knowledge of the distribution and habitat of Ringed Seals in polar waters of the northern hemisphere, they ought to encounter octopods and gonatids and it must be suspected that they take them, at least on occasion. For four other species (Ribbon Seal, Hooker's Sea Lion, Guadalupe Fur Seal and South American Fur Seal) the information is so meagre that no meaningful qualitative assessment can be made of how important cephalopods are to them.

For most pinnipeds only rudimentary prey identifications have been published. Members of the Ommastrephidae, Loliginidae, Onychoteuthidae, Gonatidae and muscular benthic octopods are the most common taxa of cephalopods reported to be consumed by seals. This is as much a reflection of the habitat of most seal species of the world as it is a consequence of their diving capabilities. At least 14 of the 31 marine species of seals can be classified as entirely coastal in their distribution where representatives of the squid families listed above are most common. Calorific densities of fish are generally higher, often much higher, than that of cephalopods (Clarke 1986*a*). Ammoniacal squid are particularly low in calories and this may explain why they are so seldom consumed (table 1).

Although cephalopods can comprise a large proportion of the diet in some seals, no seal is a specialist cephalopod feeder, not even the elephant seals, which possess diving capabilities matching those of the great whales. Only these two can be classified as regular squid eaters. Spending a large part of their foraging efforts in offshore waters at depth, they consume muscular, oily and ammoniacal squid as well as octopods. Given its foraging habitat at the oceanic edge of the pack ice in the Arctic over deep water, future research may show that the Hooded Seal will also fall into this group. Presently its diet begs further study. There is some evidence that cephalopods may be important for seals on a seasonal basis. For example, Californian Sea Lions have been reported to take advantage of the seasonal nearshore movements of spawning *Loligo opalescens* each year in autumn and winter (Lowry *et al.* 1991). Conflicts between commercial fishermen operating on squid spawning grounds and seals can also be regarded as evidence for the temporal importance of cephalopods as food for seals.

An assessment of the exact proportion of cephalopods in the diet of pinnipeds is complicated by methodological problems of analysing seal diets quantitatively. Scats are evidently not an appropriate source to gauge the quantity of squids consumed (Gales & Cheale 1992) and even full stomach samples from freshly dead carcasses (Bigg & Fawcett 1985), or animals subjected to stomach lavage (Harvey & Antonelis 1994), may be biased. Too few quantitative diet analyses on enough pinnipeds have been done to quantify the consumption of cephalopods by seals globally with any precision. However, the publications reviewed in this article indicate that it must be much less than fish and crustaceans. More often than not cephalopods are only an occasional prey item. Moreover, for Crabeater Seals, which number at least 11 million individuals (Erickson & Hanson 1990), cephalopods play no role in their diet.

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