https://doi.org/10.24199/j.mmv.1983.44.09 30 June 1983

CEPHALOPOD BIOMASS – ESTIMATION FROM PREDATION

By M. R. Clarke

Marine Biological Association, Plymouth, England, U.K.

Abstract

North Atlantic deep sea cephalopods caught in research nets (mouth opening of 9 m^2) and large commercial trawls are compared with those eaten by Sperm Whales. It is shown that at three latitudes the nets and whales sample cephalopods very differently. Research nets are biased towards collecting small species and young specimens of several families, principally gonatids, cranchiids, enoploteuthids and onychoteuthids, while sperm whales are biased towards catching much larger cephalopods, particularly histioteuthids. Commercial trawls tend to bridge the gap in size of cephalopods selected by research nets and whales but where comparisons are possible they have a bias towards catching enoploteuthids. The contribution by numbers and weight of different cephalopod families to the cephalopod fraction of the diet of sperm whales throughout the world is reviewed.

A detailed study of Antarctic cephalopods in the diet of large predators including cetaceans, seals and birds indicates areas where more knowledge is required to make accurate estimates of the biomass of Antarctic cephalopods consumed. The value of direct studies of food webs for quantitative consideration of particular cephalopod taxa is demonstrated and discussed.

Introduction

Commercial catches of cephalopods have increased over several decades and an increasing number of species are now utilised for human consumption. The species concerned live in or move into inshore shallow seas at some stage of their life. We know that many other species live in the deep seas and are not caught commercially. Many of these may not be as highly nutritious as the inshore species and, up to the present, fishing techniques have not been adapted for their capture but their future exploitation cannot be ruled out. While this alone warrants their further investigation the fact that they are a principal food of many cetaceans, seals, fishes and birds shows that a proper understanding of oceanic ecology would be unobtainable without studying the cephalopod fraction by every means available.

The direct approach to understanding the importance of cephalopods in marine food webs is to examine stomachs of their common predators and to examine the stomachs of the cephalopods taken as prey. This approach has advantages: (1) the information provided is directly relevant to the food web, (2) effort is not wasted on ecologically 'unimportant' species (i.e. species which are both rare and small) and, (3) it is not necessary to know the sampling bias of predators (as opposed to research nets), since the total stock from which the cephalopods are being removed need not be calculated for many ecological purposes (large changes in stock, however, should be reflected by changes in the predators' diet). This direct approach also presents problems, but, because cephalopods are so poorly sampled by nets in the open ocean, it is the only approach at present which promises to provide answers to many of the questions of food web ecology.

The aim of this paper is to examine the difficulties and advantages of this direct approach and, in particular, to suggest ways of removing the barriers to a more quantitative study of cephalopods as important members of a food web.

Nets and Predators as Samplers

Even the largest nets, unless they are used on the bottom in less than 200 m of water, seldom catch cephalopods longer than half a metre. But such shallow water represents only a very small percentage of the sea's surface area and volume, and therefore does not harbour the full range of cephalopod species, especially the larger squids. Many of these are in the midwaters, that stretch down more than 2 000 m from the sea surface and across 70% of the earth's surface. Here we can sample only with midwater nets and hooks and lines. Such methods would lead us to suppose that in most regions cephalopods more than a half metre long are extremely rare. Can we believe this or should we doubt the efficiency of our methods?

If our methods are inefficient, how can we test them and how can we find a remedy?

To know if large cephalopods are common in the ocean is crucial to an understanding of the food webs and the biomass of the sea because, if they are, they will consume a significant fraction of other organisms and will themselves provide a large reservoir of food for fishes, whales, etc. The components of the web itself should answer the question 'Are large and poorly-known cephalopods important in the sea?'; the study of one large cephalopod predator should be enough to give an indication. The Sperm Whale is admirable for this purpose because: (1) it eats cephalopods primarily; (2) it is large and thus eats many large cephalopods; (3) it is abundant with a population estimated at one to two million individuals; (4) it is world ranging and has been killed commercially in many parts of the world. While this whale is an efficient sampler, gastric juices quickly dissolve and distort most of the cephalopod flesh. However, thousands of horny cephalopod mandibles or beaks remain undigested. An average of 2 000 and up to 8 000 cephalopods are represented in each Sperm Whale stomach. Most lower beaks can be identified to family, genus and often species and this provides our key for comparison with net hauls.

How do the data based on beaks from Sperm Whale stomachs compare with data from nets used in the deep sea? Precise scientific comparison is not possible because of differences in area, depth, time of fishing, etc. However, a broad comparison *is* possible and is valid because (1) the quantity of cephalopods caught by research nets does not vary enormously wherever they are used in the deep sea, (2) the number of lower beaks from Sperm Whales examined to date (>150 000) probably about equals the total number of net-caught deep sea cephalopods ever identified, and (3) the information from the two sources is so different that there is little possibility that differences are due only to chance or to difference in habitat sampled.

Comparisons have been made between beaks from various predators and net-caught cephalopods from many parts of the world but, as an example, we will consider North Atlantic data. Let us compare the cephalopods caught in almost 600 hauls made with the commonly used rectangular midwater trawl (Baker *et al.*, 1973; Clarke, 1977; Clarke & Lu, 1974, 1975; Lu & Clarke, 1975a & b) with those caught by 42 large commercial Engels and British Columbia trawls used over great depths (Clarke, 1977; Clarke & Lu, 1974), and the beaks from Sperm Whales caught commercially off Iceland, Spain and Madeira (Clarke, 1962; Clarke & MacLeod, 1974, 1976).

First we should consider the overall numbers collected in various ways. The only two complete stomach contents from the North Atlantic contained 2 136 and 3 776 lower beaks. The total number of cephalopods taken by over 400 research nets (mouth area = 9 m²) was 4 041 or about 10 per net. Thirty-four hauls with an Engel's midwater trawl (mouth area: 35 × 20 m ≃ 700 m²) used between 28-38°N, 8-20°W averaged 58 cephalopods per haul and 8 hauls with a British Columbia midwater trawl (mouth 15 × 15 m ≃ 230 m²) averaged 50 cephalopods per haul. To catch 3 000 cephalopods the 9 m² nets would have to be fished successfully for at least 50 days and the large trawls for more than 10 days. Secondly, we might ask if data derived from whales give the same information as that derived from nets or whether the biases in sampling give totally different results. Figure 1 compares the percentages of the most abundant families in the three sets of samples. Clearly the histioteuthids are dominant in the whale samples while the commercial trawls predominantly catch enoploteuthids at 30° & 40°N. Cranchiids are important in the 9 m² nets (21-28%) and in the whales caught in cold water off Iceland. Otherwise, the 9 m² net catches vary considerably with latitude taking mainly gonatids in high latitudes and several other families in lower latitudes.

But what of the size of cephalopods sampled? Figure 2 shows the mantle length of the largest squid by family caught in the 9 m² research nets and the minimum and range of mantle lengths of squids found intact in stomachs of sperm whales caught throughout the world. Except for the cranchiids and histioteuthids the ranges do not overlap. In

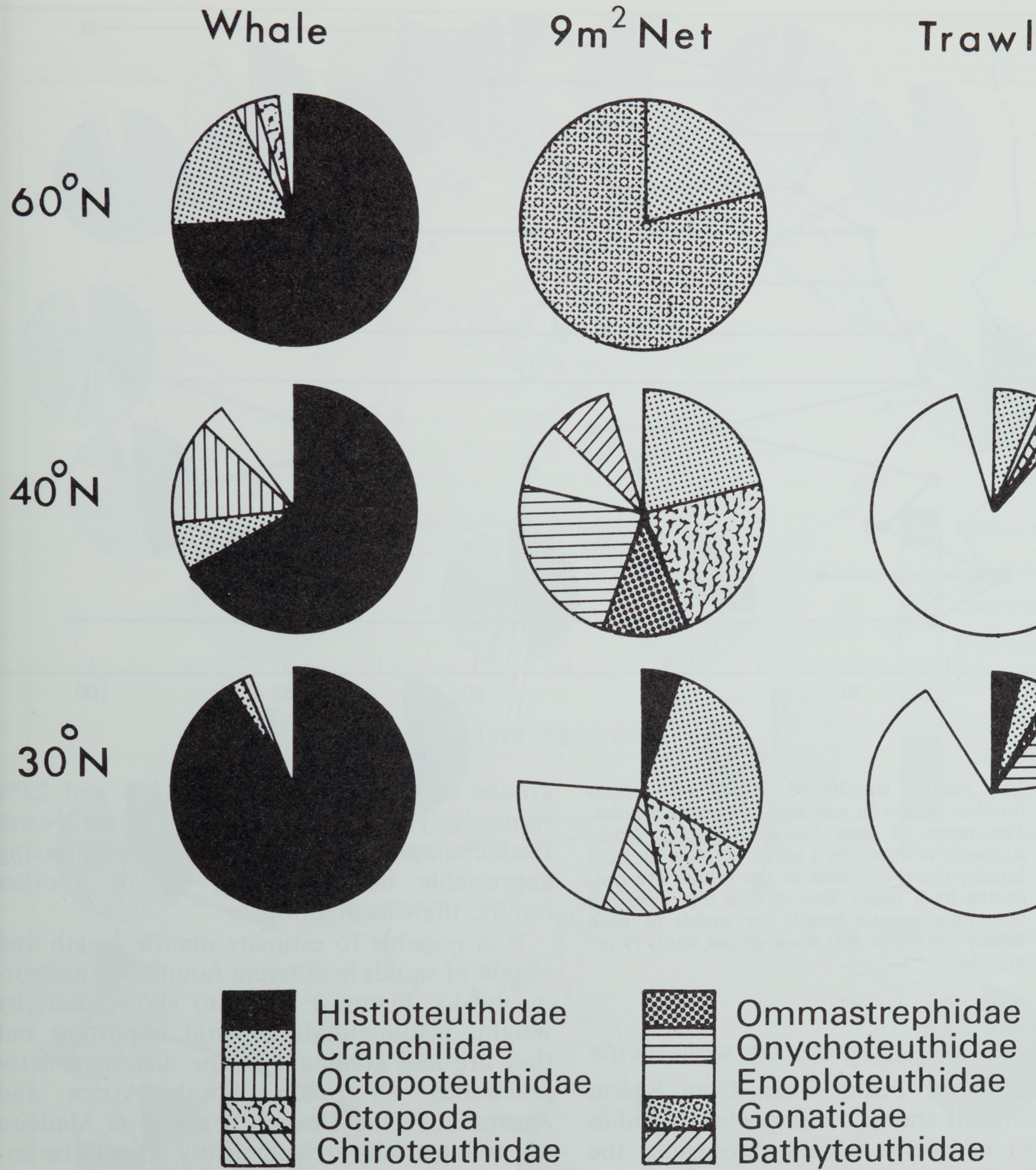

Figure 1. The families of oceanic cephalopods (mainly squid) caught by Sperm Whales, research nets (9 m² mouth opening) and commercial trawls in three areas of the North Atlantic. The whales eat histioteuthids, cranchiids and octopoteuthids primarily. Nets catch squids mostly from other families.

fact, some squid *beaks* from whale stomachs are more than 10 cm long and exceed the maximum *mantle length* of squids from all but two of the families from nets! Squids from commercial trawls often are larger than those from 9 m² nets and a few ommastrephids from these also exceed the minimum length of those from sperm whales.

Thus, comparisons between families show that research trawls, commercial trawls and whales all provide different and complementary views of cephalopod abundance, size and distribution.

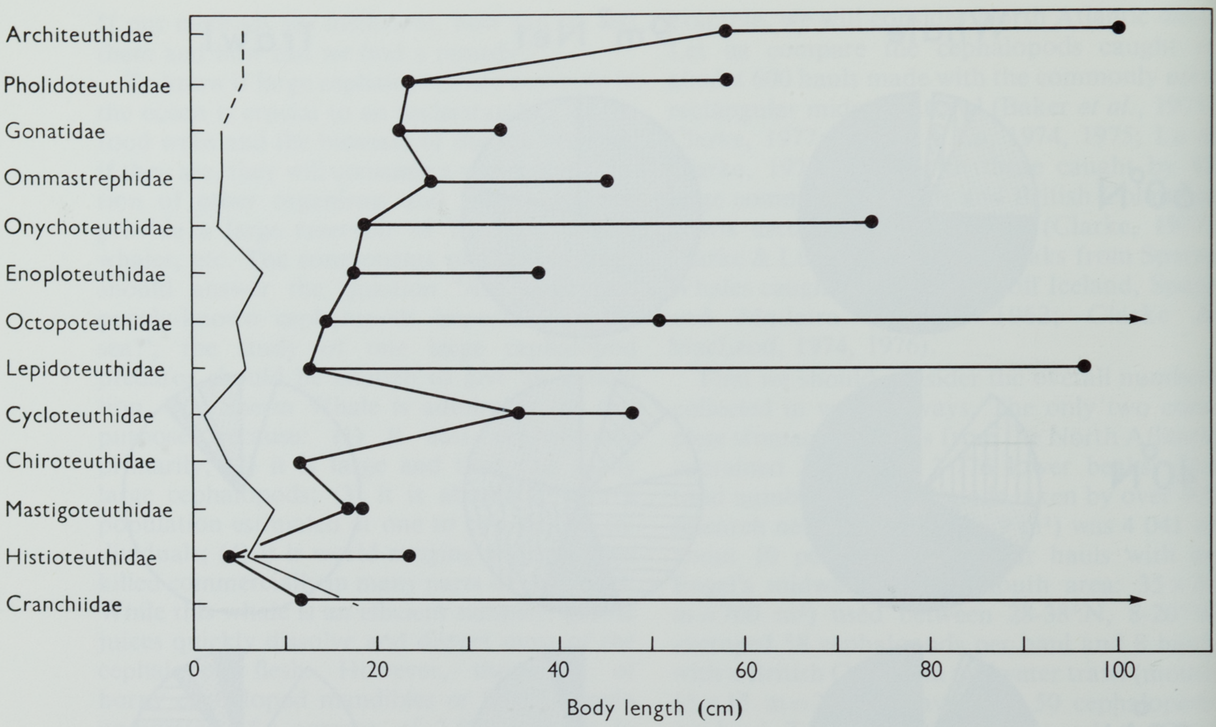

Figure 2. The mantle lengths of squids of various families caught in nets and by Sperm Whales. The range of sizes found in Sperm Whale stomachs is shown by a horizontal line for each family; the lower ends of the ranges are connected by a heavy line. A thin line joins the maximum mantle length for squids of each family caught in 600 research net hauls (9 m² mouth).

A CONSIDERATION OF THE OCEANS WORLDWIDE

An analysis of beaks taken from Sperm Whale stomachs shows the important families in the diet of sperm whales throughout the world (Fig. 3, top). In temperate regions and Iceland, histioteuthids are very dominant (30-91%) except in the North Pacific where they form a small (<8%) part of the diet. In most temperate regions, except the North Atlantic and North Pacific, the octopoteuthids also are well represented (10-33%). Whales in the North Pacific have large proportions of gonatids (32-69%; also common in high latitude Atlantic nets), onychoteuthids (3-24%) and cranchiids (26-33%). From the beaks (Fig. 3) the onychoteuthids and cranchiids are the main groups in the Antarctic with 53% and 23% respectively. Finally, Peru and some North Pacific samples differ from all the rest by having appreciable numbers (16-17%) of another family, the Chiroteuthidae.

It is possible to estimate mantle length and weight of squids in different families by measuring beaks. Figure 3 (bottom) shows that, by weight, histioteuthids are still important but they are less dominant in the diet than octopoteuthids off Spain, South Africa and Australia. In the Tasman Sea and off Madeira the architeuthids are sufficiently large to be important in the diet (19% and 40% respectively) while various families particularly the ommastrephids, enoploteuthids and pholidoteuthids are moderately important by weight in some regions of the southern temperate seas. In the Antarctic, a gigantic cranchiid growing to over 10 m total length and, except for a few larval specimens, only once caught by a net, forms the bulk (76%) of the sperm whale's food. Second to this are the onychoteuthids (21%) which also comprise most of the food by weight in the eastern North Pacific. The weights

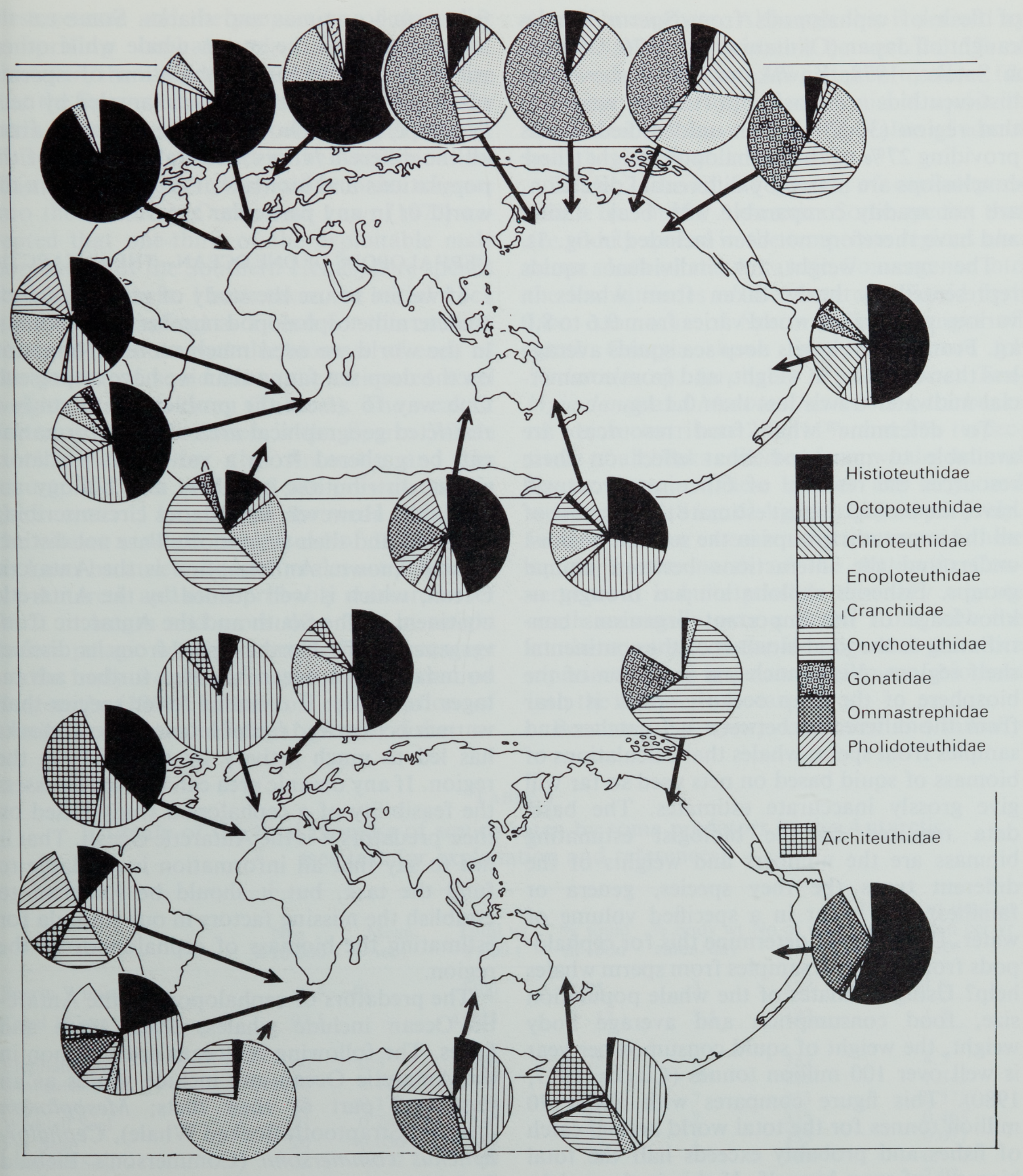

Figure 3. Squid families in the diet of Sperm Whales caught in various regions of the world. Top, Composition based on the number of lower beaks. Bottom, Composition by weight estimated from the numbers and sizes of beaks. Data for Kurile islands, Aleutian islands and Gulf of Alaska from Tarasevich, 1963, 1968. Other data from papers by Clarke and colleagues.

of flesh of cephalopods from Sperm Whales caught off Japan (Okutani *et al.*, 1976; Okutani & Satake, 1978; Kawakami, 1980) show that histioteuthids are most important by weight in that region (30-38%) with unidentified squids providing 27% of the cephalopod weight (these conclusions are biased by differential digestion, are not readily comparable with beak studies and have therefore not been included in fig. 3).

The mean weight for individual squids represented by beaks taken from whales in various parts of the world varies from 0.6 to 8.0 kg. From research nets deep sea squids average less than 0.002 kg in weight, and from commercial midwater trawls less than 0.1 kg.

To determine what food resources are available to man and what effect on these resources the removal of other resources will have, the biologist must estimate the biomass of all the important groups in the sea and he must understand the interactions between animal groups. Fisheries exploitation has brought us knowledge of the important organisms contributing to the total biomass of the continental shelf regions. Very much less is known of the biosphere of the deep oceans, and it is clear from the differences between net catches and samples from sperm whales that calculations of biomass of squid based on nets used so far will give grossly inaccurate estimates. The basic data required by the biologist estimating biomass are the numbers and weights of the different types (be they species, genera or families) that occur in a specified volume of water. If we cannot determine this for cephalopods from nets, can samples from sperm whales help? Using estimates of the whale population size, food consumption and average body weight, the weight of squid consumed per year is well over 100 million tonnes (Clarke, 1977, 1980). This figure compares with about 70 million tonnes for the total world annual catch of fishes and probably exceeds half the total biomass of man himself. If this is the weight consumed by sperm whales, what is the total weight of squids in the world? We can only guess.

Many oceanic animals eat squids including toothed whales, dolphins and porpoises, seals, birds such as albatrosses and penguins and fishes such as tunas and sharks. Some eat the same species as the sperm whale while others eat a very different combination of species, often quite different from that sampled by nets. We hope to somehow sum the estimates from all the different 'views' to obtain an idea of the populations and biomass of cephalopods in the world or in any particular area.

CEPHALOPODS OF ONE OCEAN – THE ANTARCTIC

If we are to use the study of predators' food to determine cephalopod numbers and biomass in the world we need much more information on the deep sea fauna than we have at present. One way to assess the problem is to study a restricted geographical area where information can be gathered from a variety of predators whose distribution, numbers and biology are available. However, boundaries circumscribing sea areas and their faunas often are not distinct or well known. An exception is the Antarctic Ocean, which is well defined by the Antarctic continent to the South and the Antarctic Convergence to the North. Apart from its distinct boundaries this ocean has two further advantages for study: it contains fewer species than warmer oceans and recent interest in krill stocks has led to much activity by ecologists in the region. If any oceanic area can be used to assess the feasibility of a cephalopod study based on their predators it is the Antarctic Ocean. That is not to say that all information is available to fulfil the task, but it should be sufficient to establish the missing factors in our formula for estimating the biomass of cephalopods of the region.

The predators of cephalopods in the Antarctic Ocean include whales, seals, birds and fishes. The following cetaceans are common in the Antarctic Ocean and include squids as an important part of their diets; *Mesoplodon layardii* (Straptooth Beaked Whale), *Cephalorhynchus commersonii* (Commerson's Piebald Dolphin) and *Lissodelphis peronii* (Southern Rightwhale Dolphin). Others eating some cephalopods are *Lagenorhynchus australis* (Blackchin Dolphin), *Hyperoodon planiformis* (Southern Bottlenose Whale), *Berardius arnuxii* (Southern Fourtooth Whale) and *Orcinus orca* (Killer Whale). The numbers and biomass of these cetacea and the proportion of their diet comprising cephalopods is not known. However, there is little doubt because of its size that the Sperm Whale (*Physeter catodon*) is the main odontocete predator of squids (Table 1). This whale eats few fishes in the Antarctic—less than 5% of the diet. Only adult males migrate into the Antarctic Ocean and Laws (1977) accepted that one-third of the exploitable male population of the Southern Hemisphere spends the summer there. I have taken the initial stock (i.e. before whaling) as a basis for this calculation and have derived the biomass of each of the genera of squid from the estimated total weight of squids eaten (Table 2). The weakest factor in the calculation is the Sperm Whale stock estimate for the Antarctic and the assumption that one-third are present only in the summer. I have taken the mean weight of the whales as 40 tonnes instead of 30 t as used by Laws because only adult males are present in the Antarctic and most probably measured over 38 ft in length and more than 30 t in weight before pelagic whaling started. The percentage of the body weight eaten per day is based on Sergeant's (1969) figures of consumption of smaller cetaceans of high protein fishes or squids in captivity. Although this is derived by extrapolation it is probably between 2-3.5% of body weight per day. 3% is taken to allow for the large proportion of ammoniacal squids in the diet which have a calorific value of about half that of muscular squids.

Table 2 shows the genera of cephalopods which live in the Antarctic. Some species that are widely spread in the temperate regions also occur south of the Antarctic Convergence into the low latitudes of the Antarctic. Squid flesh from stomachs of Sperm Whales caught off South Georgia shows that this is true for *Todarodes* sp. (probably *T. filippovae*) *Taningia danae* and *Moroteuthis robsoni*, the beaks of which contribute 2%, 11% and 7% respectively of all beaks collected from whales around South Georgia. These species are large and weigh up to 3.8 kg, 61 kg and 3 kg respectively. In view of the extensive distribution of these squids to the north of the Antarctic Convergence it is quite possible that they migrate south seasonally over a broad front with the southern retreat of the ice edge and therefore represent a very large annual input of biomass into the Antarctic Ocean.

Because of the very large size and initially

TABLE 1

Estimate of the total biomass of squids eaten by some predators in the Antarctic (see text for explanation and references)

	Nos ×10 000	Mean wt t	Total wt 1 000 t	% squid in food	% body wt eaten/day	No of days of yr	Estimated total wt squid eaten per yr ×10⁶
Sperm Whale	8.5	40	3400	95	3	122	11.8
Total Baleen Whales	97.5	–	43125	1?	3.5	122	1.8
Elephant Seal	60	0.5	300	75	6	333	4.5
Crabeater Seal	1500	0.193	2868	2	7	335	1.345
Ross Seal	22	0.173	38	64	7	335	0.571
Weddell Seal	73	0.246	180	11	7	335	0.463
Fur Seal	20	0.050	10	33	7	335	0.077
Leopard Seal	22	0.272	60	8	7	335	0.112
Total Seals							7.07
Wandering Albatross	7	0.009	0.630	80	7	365	0.013
Grey-headed Albatross	38.5	0.0036	1.39	49	7	365	0.017
Black-browed Albatross	1200	0.0035	42	21	7	365	0.225
Total Albatrosses	1263	–	44.45	?30	7	365	0.34
All birds	35000	0.0024	850	24	7	365	13.54
Total estimate							34.21

TABLE 2

The percentage contribution by weight (underlined) of particular genera of cephalopods to the diet of different predators estimated from the number and sizes of beaks. These percentages, together with the estimates of total biomass of cephalopods consumed by each predator (Table 1) were used to calculate the biomass (in 10^6 t and not underlined) for each genus. For explanations of totals (a), (b), and (c) and for references see text.

	Kondakovia		Moroteuthis		Mesonychoteuthis		Ommastrephid		Gonatus		Other squids		Octopods	
Sperm Whale	18	2.1	4	0.47	77	9.09	+				1	0.1		
Baleen Whales	50	0.90	50	0.90										
Elephant Seal	7	0.27	10	0.39					15	0.59	8	0.31	60	2.34
Ross Seal	63	0.36	4	0.02							34	0.19		
Weddell Seal			49	0.23					1		25	0.12	26	0.12
Fur Seal	48	0.40	18	0.15			32	0.27			2	0.02		
Leopard Seal	42	0.05	57	0.07							1			
Wandering Albatross	81	0.01	2						1		16		1	
Grey-Headed Albatross	4						91	0.02			5			
Black-Browed Albatross	1						76	0.17	1		27	0.05	1	
Totals (a)		4.09		2.23		9.09		0.46		0.59		0.79		2.46
(b)		7.14		3.89		15.86		0.80		1.03		1.38		4.29
(c)		9.68		5.28		9.09		1.09		1.40		1.87		5.82

large populations of baleen whales that include Blue, Fin, Sei, Humpback and Minke Whales (Table 1) even if squids contributed as little as 1% to the diet, an appreciable biomass of squids would be involved. This contribution probably is higher for Sei and Minke Whales which are known to take squid in considerable quantities elsewhere in the world but is not known for Blue, Fin and Humpback Whales. We have very little information on the species of cephalopods eaten by baleen whales but *Moroteuthis knipovitchi* has been collected from Fin and Blue whale stomachs (Clarke, 1980 & unpublished). *Mesonychoteuthis hamiltoni* probably lives very deep, as the only capture of a near-adult specimen was at 2 000 m (Clarke, in preparation); there is no evidence at present that it is found at the relatively shallow depths where baleen whales eat krill. Therefore. I have not included *Mesonychoteuthis* in the diet of baleen whales and in the absence of better data have assumed that *Kondakovia* and *Moroteuthis* each contribute 50% of the squids eaten (Table 2).

The food requirements of seals (Table 1) are based upon the stocks and mean weights given by Laws (1977) whose work is based largely on the work of Øritsland (1977). The diet of Elephant Seals at sea is not well known as they fast when onshore but Laws concluded that they probably eat fishes in inshore waters and cephalopods offshore. However, some cephalopod remains were obtained for analysis from Elephant Seals caught at Signy Island (Clarke & MacLeod, 1982); the estimate of 75% cephalopods in the diet must remain a guess at present. All the seals eat some cephalopods and of the six species, the Elephant and Ross Seals very probably consume the greatest percentage of cephalopods. Because the Crabeater Seals have by far the largest stock (over 14 million), even if cephalopods contribute only 2% to the diet, this represents a substantial biomass of over 1 million tonnes. The percentages of the cephalopod species (Table 2) eaten by Elephant Seals, Weddell Seals, Fur Seals, one Leopard Seal and one Ross Seal are based upon analyses in press or preparation (Clarke & MacLeod, 1982a & b). It is unfortunate that information is not available for Crabeater Seals.

Populations of birds and their food have been described by Mougin & Prévost (1980) and Prévost (1981). There are discrepancies in the figures they quote but some can be used for this discussion. The total number of the 46 species of birds in the Antarctic is estimated at 350×10^6 with a biomass of 0.85×10^6 t. These authors conclude that the birds eat 4.7×10^6 t of food per month, which is 56.4×10^6t per year, or over 66 times their biomass. (This may not be excessive as a recent detailed study shows that 1×10^7 Macaroni Penguins are estimated to eat 28-45 times their body weight during the 116 days of their breeding season at South Georgia (Croxall & Prince, in press)). Cephalopods are estimated to comprise 24% of the food; this represents a biomass of 13.54×10^6 t. Penguins consume 82% of the total cephalopods eaten by birds according to these authors. The cephalopods eaten by albatrosses represent only about 3% of the weight eaten by all birds. However, in the light of recent quantitative data especially relating to Macaroni Penguin diet, Black-browed Albatross populations and King Penguin populations the importance of birds as predators of cephalopods may have been exaggerated by Prévost (J. P. Croxall, personal communication). The species of cephalopods eaten by penguins have not been identified although they have been for three species of albatross (Table 2) (from Clarke, Croxall *et al.*, 1981; Clarke & Prince, 1981).

The weights of the different species of cephalopods (Table 2) in the diets of the predators has been calculated by multiplying their percentage by weight in the diet (see Clarke, 1980 for Sperm Whales; Clarke & MacLeod, 1982a & b for seals and Clarke *et al.*, 1981 for albatrosses) by the weight consumed by the predators (Table 1). The total weight of each cephalopod species eaten by the predators examined is shown in totals (a) of Table 2. If the predators whose cephalopod diets have not been identified ate the same species in much the same proportions the total weight of each cephalopod would be as in total (b). However, we know this not to be true; *Mesonychoteuthis hamiltoni* is eaten only by the Sperm Whale in substantial quantities and probably lives outside the depth range for most seals and birds. Thus its total should not be expanded to take account of the consumption by other predators and totals (c) in which this species is included only for Sperm Whales may give a closer estimate of the true totals consumed. Similarly, however, other genera in Table 2 may prove more or less important than shown in totals (c) when more is known of diets of predators of which the cephalopod proportion has not yet been analysed.

From the data given here combined with that of Laws (1977) the total consumption before whaling of *Kondakovia*, *Moroteuthis*, *Mesonychoteuthis* and octopods probably was about 35 million tonnes. The effect of whaling on the biomass of krill and, indirectly, on the stocks of other predators of krill, has been much discussed (Sayed, 1981). The direct effect on cephalopod populations has been less than for krill but assuming a drop in Antarctic Sperm Whale population to about a half and a very large reduction in the baleen whale stock it would seem that perhaps 7 million additional tonnes of cephalopods are now available as food for predators, other than whales, in the Antarctic.

If we accept that our estimates of cephalopod consumption are to some degree accurate for the predators concerned we might ask what figures should be added to 35 million tonnes for predators not considered, such as other odontocetes and fishes and what 'standing' stock of cephalopods is necessary to allow such a predation.

To sum up, it seems likely that most of the predation on cephalopods is carried out by Sperm Whales, baleen whales, Elephant Seals, Crabeater Seals and penguins (the Adelie is by far the most numerous penguin).

Of these we know too little about the population of Sperm Whales involved, too little about the percentage of cephalopods in the diets of all their predators (except the Sperm Whales) and too little about the cephalopod species eaten by baleen whales, Crabeater Seals and Adelie Penguins. This study clearly indicates that the study of biomass of cephalopods from predators' diets must first include the most numerous and the largest predators of an area. The strategy of such a study in the future should be to (a) define realistic biogeographical limits for the study; (b) find which large and abundant predators eat cephalopods; (c) estimate biomass of these predators and the biomass they require for food; (d) find the percentage of cephalopods in the diet; and (e) determine the cephalopod species in the diet and their relative proportions by weight. While all these requirements present difficulties, those associated with (d) are often under-emphasised. Where fishes, cephalopods and crustaceans, which are digested at different rates, co-occur, quantitative results obtained by estimating weights from hard parts such as fish otoliths, squid beaks, and crustacean carapaces should be more accurate than merely weighing the flesh remains of each group left in the stomach after partial digestion.

CONSIDERATION OF SPECIES

Although general taxonomic problems and other difficulties associated with identifying beaks make it difficult to identify some cephalopods to species from their beaks (e.g., in Architeuthidae, Cranchiidae) this does not apply to all species. Indeed, where species have very characteristic beaks, are very well known because of large collections, or are from monotypic genera, considerable confidence can be attached to their identification. Table 3 summarises data on the species whose beaks from predators' stomachs have been studied in detail and, together with the flesh remains, can be used with confidence to assess the distribution and relative importance in the diets of predators. Further records of flesh of these species from Sperm Whales caught off Japan (Okutani *et al.*, 1976) and New Zealand (Gaskin & Cawthorn, 1967) have been added.

The species may be grouped into the Antarctic species *Mesonychoteuthis hamiltoni*, *Gonatus antarcticus*, *Moroteuthis knipovitchi*, *Kondakovia longimana* (which possibly may have a close relative in the Arctic seas according to Clarke & MacLeod, 1976) and the species living in temperate and tropical seas. Of the latter *Taningia danae* is very widespread and, almost everywhere, is very important in the diet of Sperm Whales. Similarly widespread species are *Octopoteuthis rugosa*, *Ancistrocheirus lesueuri* and *Lepidoteuthis grimaldii*. Other species such as *Moroteuthis robsoni* and *Histioteuthis miranda* are widespread in the Southern hemisphere but do not appear to extend into the Northern hemisphere. *Moroteuthis robusta* and *Gonatus fabricii* have close relatives in the Southern hemisphere but are themselves limited to the Northern hemisphere. In a few species (* in Table 3) specimens caught in nets indicate that the ranges are greater than shown in Table 3. The maximum sizes and the length of life of the species are indicated in Table 3 by estimates from beak size based upon size relationships and beak growth previously published (Clarke, 1980).

Discussion

It has been shown that useful information can be obtained on the distribution, relative importance and biology of many cephalopod taxa by analysis of the diet of their predators. The biomass of species of cephalopods eaten by well-investigated predators can be estimated, but we are a long way from being able to estimate the total biomass of cephalopods consumed in any particular oceanic region. If this is our aim we must define the biogeographical limits of the region, determine what interchange of fauna there is between regions, find which predators are the principal consumers of cephalopods, determine populations and biomasses of predators, and then study the numbers and weights of the species of cephalopods in the diets of the predators. Although some of these investigations inevitably will be carried out simultaneously or rest on previous work done with different aims, the more these tasks are done out of order the more time will be wasted on predators or cephalopods of minor importance. As we have seen for the Antarctic, potentially large cephalopod consumers like penguins, several odontocetes, Crabeater Seals and fishes require investigation as these species may greatly affect our estimates of cephalopod biomass.

We do not know the total biomass of cephalopods required to sustain the biomass consumed by predators. From the fishing experience of man we might expect this to be many times the biomass consumed (equivalent in fisheries to the catch removed). However, this parallel may be misleading. Sperm Whales prey upon short-lived squids, most of which are probably in their last year of life or even in pro-

TABLE 3

Percentages by weight (to nearest 1%) of squid species which live in area calculated from the number and size of beaks collected from Sperm Whales, other odontocetes (C), Seals (S), Albatrosses (A) and fish (F). Based on data from Clarke (1980) or references cited.

+ indicates that species is known to live in area from presence of flesh but either contributes <0.5% to diet or its % contribution is not known.

W = weight M.L. = Mantle Length Estimated from beaks except M. = measured

	Iceland	Denmark (Clarke & Kristensen)	Spain	Biscay (Clarke & Stevens)	Azores (R. Clarke)	Madeira		Brazil (Clarke *et al.*, 1980)	30°S 33°W		South Africa	South Georgia	Antarctic	W. Australia	Tasman Sea (Clarke & MacLeod, 1982)	New Zealand (Gaskin & Cawthorn)	Chile & Peru	W. Canada	Japan (Okutani *et al.*)	Maximum size		Length of life
									W	E										M.L.	W Kg	Yrs
*Todarodes sagittatus**	+	2C							1	11		+, +A, 91A,32S		18							3.8	2
Dosidicus gigas																	32					
*Moroteuthis ingens**																+				40	1.5	
Moroteuthis robsoni									14	5		+,2A	+	3	2							2
Moroteuthis robusta																		62	+			
Moroteuthis knipovitchi												+, +A, 18S	4,48S							40	1.0	
Kondakovia longimana	3?											+,81A, 4A,48S	18, +S							85	33.0	2
Berryteuthis magister																		18	+			
Gonatus fabricii	+	84C		7F																		
Gonatus antarcticus												+,1A	+, +S								0.07	
Pholidoteuthis boschmai					+				19	1		+A		12	4	+				60	5.7	
Ancistrocheirus lesueuri			+		+	+	5	+	11	15		1A		2	1		3		+	37	3.0	2
Octopoteuthis rugosa				4F(?)					6	12				1	1				+	24	0.6	
Taningia danae			83			14	22	+	13	22		+,6A		37	42				+	120	61.0	
Lepidoteuthis grimaldii			2		+	4		+	3	1		1A		4	1	+			+	100	11.0	
*Cycloteuthis akimushkini**								+	1	2				1	+					58	2.1	1
Histioteuthis bonnellii	60		6	2F	+	36																
Histioteuthis b. corpuscula								+	2	6		+A		+	+					7	0.2	
*Histioteuthis dofleini**						2		+										1	+	15(M)	0.5	
Histioteuthis miranda									4	8				4	1					22	0.8	
*Histioteuthis atlantica**									+	+					1	+				7	0.2	
Mesonychoteuthis hamiltoni												+, +A	77							150.0		
*Alloposus mollis**			2			1			+	+		1A								1.0M		
*Vampyroteuthis infernalis**									+	+										10M	2.0	

* *Todarodes sagittatus* Net caught specimens also show this to live throughout the Atlantic and Mediterranean
Moroteuthis ingens The type was from Patagonia, South America
If *Cycloteuthis sirventi* proves to be the same species the range will include the North Atlantic.
Alloposus mollis It is not certain whether Pacific specimens from nets are the same species
Vampyroteuthis infernalis Widespread between 40°N and 40°S
Histioteuthis dofleini also caught in nets in South Pacific (Voss, 1969)
H. atlantica also caught in nets off Chile (Voss, 1969)

cess of dying during spawning when they are consumed (Clarke, 1980). Providing enough squid survive to spawn enough eggs to replace the stock taken by Sperm Whales (assuming they are by far the most important predator), a stable relationship between the whales and the squid populations could be maintained, even if the whale ate a very large proportion of the squids living in their final year. Since physical conditions vary little from year to year in the deep ocean, the primary influence to change squid populations may well be changes in predation. As the population of a long-lived animal such as a Sperm Whale might be expected to change rather slowly (unless commercial fisheries reduced the stock dramatically) the population of squid might also be relatively stable. However, such an equilibrium, where the population of a short lived species eaten in its final year is controlled by one predator, would be very prone to a dramatic readjustment if commercial exploitation removed the predator. This could well be the case for some deep sea cephalopods such as *Kondakovia longimana, Taningia danae* and *Ancistrocheirus lesueuri* which may have dramatically increased in biomass as a result of removal of the predator by whaling. We do not yet know what other predators might replace the whale in eating the squids but large bottom fishes might well take advantage of large increases in spawning populations of squids on the continental slope where many of these species probably spawn.

Acknowledgements

The Author would like to thank the many collectors of stomach contents who made their collections available, Dr J. P. Croxall of British Antarctic Survey for helpful discussions, the organisers and funding authorities who made his participation in the 1981 Melbourne/Queenscliffe meeting possible, the reviewers for their comments and Mrs Sylvia Marriott for typing the manuscript.

References

Baker, A. de C., Clarke, M. R., & Harris, M. J., 1973. The N.I.O. combination net (RMT 1 + 8) and further developments of rectangular midwater trawls. *J. mar. biol. Ass. U.K.* 53: 167-184.

Betesheva, E. I. & Akimushkin, I. I., 1955. Food of the sperm whale (*Physeter catodon*) in the Kurile Islands region. *Trudy Inst. Okeanol.* 18: 86-94. (In Russian).

Clarke, M. R., 1962. Stomach contents of a sperm whale caught off Madeira in 1959. *Norsk Hvalfangsttid.* 51: 173-191.

Clarke, M. R., 1977. Beaks, nets and numbers. *Symp. zool. Soc. Lond.* (38): 89-126.

Clarke, M. R., 1980. Cephalopods 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., Croxall, J. P., & Prince, P. A., 1981. Cephalopod remains in regurgitations of the wandering albatross *Diomedea exulans* L. at South Georgia. *Br. Antarct. Surv. Bull.* (54): 9-21.

Clarke, M. R. & Kristensen, T. K., 1980. Cephalopod beaks from the stomachs of two northern bottlenosed whales (*Hyperoodon ampullatus*). *J. mar. biol. Ass. U.K.* 60: 151-156.

Clarke, M. R. & Lu, C. C., 1974. Vertical distribution of cephalopods at 30°N 23°W in the North Atlantic. *J. mar. biol. Ass. U.K.* 54: 969-984.

Clarke, M. R. & Lu, C. C., 1975. Vertical distribution of cephalopods at 18°N 25°W in the North Atlantic. *J. mar. biol. Ass. U.K.* 55: 165-182.

Clarke, M. R. & Macleod, N., 1974. Cephalopod remains from a sperm whale caught off Vigo, Spain. *J. mar. biol. Ass. U.K.* 54: 959-968.

Clarke, M. R. & Macleod, N., 1976. Cephalopod remains from sperm whales caught off Iceland. *J. mar. biol. Ass. U.K.* 56: 733-750.

Clarke, M. R. & Macleod, N., 1982a. Cephalopods in the diet of elephant seals at Signy Island, Antarctic. *Br. Antarct. Surv. Bull.*, in press.

Clarke, M. R. & Macleod, N., 1982b. Cephalopod remains in the stomachs of eight Weddell seals. *Br. Antarct. Surv. Bull.*, in press.

Clarke, M. R. & Macleod, N., 1982c. Cephalopod remains from the stomachs of sperm whales caught in the Tasman Sea. *Mem. natn. Mus. Vict.* 43: 25-42.

Clarke, M. R., Macleod, N., Castello, H. P., & Pinedo, M. C., 1980. Cephalopod remains from the stomach of a sperm whale stranded at Rio Grande do Sul in Brazil. *Mar. Biol.* 59: 235-239.

Clarke, M. R. & Prince, P. A., 1981. Cephalopod remains in regurgitations of black-browed and grey-headed albatrosses at South Georgia. *Br. Antarct. Surv. Bull.* (54): 1-7.

Clarke, M. R. & Stevens, J. D., 1974. Cephalopods, blue sharks and migration. *J. mar. biol. Ass. U.K.* 54: 949-957.

Clarke, R., 1956. Sperm whales of the Azores. *Discovery Rep.* 28: 237-298.

Gaskin, D. E. & Cawthorn, M. W., 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait region of New Zealand. *N.Z. Jl. mar. Freshwat. Res.* 1: 156-179.

Kawakami, T., 1980. A review of sperm whale food. *Sci. Rep. Whales Res. Inst.* (32): 199-218.

Laws, R. M., 1977. Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond.* B. 279, 81-96.

Lu, C. C. & Clarke, M. R., 1975a. Vertical distribution of cephalopods at 40°N, 53°N and 60°N at 20°W in the North Atlantic. *J. mar. biol. Ass. U.K.* 55: 143-163.

Lu, C. C. & Clarke, M. R., 1975b. Vertical distribution of cephalopods at 11°N 20°W in the North Atlantic. *J. mar. biol. Ass. U.K.* 55: 369-389.

Mougin, J-L. & Prévost, J., 1980. Evolution annuelle des effectifs et des biomasses des oiseaux antarctiques. *Rev. Ecol. (Terre Vie).* 34: 101-133.

Okutani, T. & Sataka, Y., 1978. Squids in the diet of 38 sperm whales caught in the Pacific off northern Honshu, Japan, February 1977. *Bull. Tokai reg. Fish. Res. Lab.* 93: 13-27.

OKUTANI, T., SATAKE, Y., OHSUMI, S., & KAWAKAMI, T., 1976. Squids eaten by sperm whales caught off Joban District, Japan, during January-February. *Bull. Tokai reg. Fish. Res. Lab.* 87: 67-113.

ØRITSLAND, T., 1977. *Food consumption of seals in the antarctic pack ice.* In: *Adaptations within antarctic ecosystems.* Third Symposium of Antarctic Biology (ed. G. A. Llano), Scientific Committee for Antarctic Research.

PRÉVOST, J., 1981. Population, biomass and energy requirements of Antarctic birds. pp. 125-137 in *Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS)* Vol. 11: Selected Contributions to the Woods Hole Conference on Living Resources of the Southern Ocean 1976. Editor, Sayed Z. El-Sayed. Publ. SCAR and SCOR.

SAYED, Z. EL. SAYED (Editor), 1981. Selected Contributions to the Woods Hole Conference on Living Resources of the Southern Ocean 1976. SCAR & SCOR.

SERGEANT, D. E., 1969. Feeding rates of Cetacea. *Fisk Dir. Skr.* (Ser. Harunders) 15: 246-258.

TARASEVICH, M. N., 1963. Data on sperm whale diet in the northern part of Kurile waters. *Trudy Inst. Okeanol.* 71: 195-206.

TARASEVICH, M. N., 1968. The diet of sperm whales in the North Pacific ocean. *Zool Zh.* 47: 595-601.

VOSS, N. A., 1969. A monograph of the cephalopods of the North Atlantic. The family Histioteuthidae. *Bull. mar. Sci.* 19: 713-867.