CEPHALOPODS IN THE DIET OF CETACEANS AND SEALS

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Introduction

Undeniably, the study of food chains in the sea is of central importance to marine biology. Undeniably also, the study has barely begun. This is most evident when one considers the deep sea and, in particular, the midwater of the deep sea. Too often the listing of species in the diet of predators has been the main and often the only consequence of stomach content analysis. But far more can come from such work if a knowledge of the predators' biology is combined with a knowledge of the prey. To illustrate the breadth of information which such an approach can provide we shall consider the cephalopod part of the diet of marine mammals. The fish and crustacean fractions of the diets are susceptible to similar treatment.

The basic requirements for the study are a technique for identifying and quantifying the food organisms, a knowledge of the ecology of the predators, principally their geographic and depth distributions, growth parameters and numbers, and a knowledge of cephalopod biology principally their habitat, way of life, and muscularity.

Identification

Macerative and early digestive processes of marine toothed mammals are rapid with the result that very few complete fish or cephalopods are found in the stomachs of freshly killed or stranded animals. Cephalopods are particularly quick to disintegrate but their eye lenses and chitinous mandibles or "beaks" are very resistant to gastric juices and accumulate in the stomachs. The beaks in particular may accumulate in very large numbers before being vomited; in one sperm whale they represented 7855 cephalopods. A critical prerequisite to identifying the cephalopods in the diet has therefore been a study of beak variation and most genera of cephalopods can now be identified from their lower beaks (Clarke, 1980, 1985a). Similar efforts on otoliths have provided a basis for recognition of fish in diets (Fitch & Brownell, 1978).

Quantification

The relative numbers of cephalopod genera and sometimes species is derived directly from identification of lower beaks. The relative weights of the taxa can be estimated from curves relating the 'beak' size or "lower rostral lengths" with the total wet weights of the cephalopods. Because of the great diversity of squid form the estimates should be made from curves of the lowest taxa which have been identified i.e. for the particular species, genus or family concerned. Such relationships are not always known but curves for most families now permit rough estimates (Clarke, 1985a). Within families body form is less variable than between families so that use of even family curves has considerable advantages over using general curves for squids, cuttlefish or octopods etc. Dry weight would be better than wet weight but many of the species concerned are rare in collections so that it has not been possible to prepare curves based on dry weight. Calorific values of cephalopods vary considerably according to whether they are negatively-buoyant jet swimming and muscular like loliginids or neutrally buoyant like oily squids such as gonatids or gelatinous squids such as octopoteuthids. Calorific values have been measured for several muscular cephalopod species (Croxall & Prince, 1982) but this has not been done for the gelatinous species which are very important in the diet of many predators.

Where a mixture of fish and cephalopods are eaten it is difficult to establish the relative proportions because they are digested at different rates. In very large collections of samples it may be possible to compare all the intact animals to find the relative weights but this is rarely possible (Perrin et al. 1973). To find the relative numbers of fish and squid eaten the eye lenses can be helpful. Cephalopod eye lenses are formed in two parts, one often smaller than the other, which join together to form a sphere. The distinction between this and the complete sphere of a fish lens is very obvious and, as digestion proceeds, some cephalopod lenses fall into two parts and expose flat faces where they were formerly joined.

The time which beaks, otoliths and eye lenses are retained in stomachs can be estimated from calculations of the total amount of food required by marine mammals (e.g. Sergeant, 1969; Clarke, 1980). Ross (1979a) found that in two experiments captive Tursiops aduncus excreted or vomited 63% of otoliths within 24 hrs of being fed fish and at least 70% within 48 hrs. They also excreted or vomited (probably the latter) in two experiments at least 66% of beaks in 22 hrs and at least 72% of beaks in 17 hrs (no more were found) after being fed squids.

Types of Cephalopod

The families of cephalopods can be grouped according to several structural features and ways of life which have relevance to their use as food by predators. A knowledge of these should aid marine mammal workers interested in diet, methods of capture and distribution (table 1). For example, the size to which squids are thought to grow and their rarity in net hauls and predators' stomachs are valuable with respect to diet. The buoyancy is relevant to the calorific value and food type as well as to the swimming speed of the prey. Muscular, negatively buoyant squids are fast swimming and have calorific values which are greater than the slow swimming, ammoniacal neutrally buoyant squids (Clarke et al., 1979). The fast swimming gonatids become neutrally buoyant by having much low density oil in their livers and are therefore in a special dietary category. Whether or not cephalopods have photophores is relevant to the vision of the predator and the depth and time of feeding (day or night). Absorption maxima of the retinal pigments of some deep diving, squid eating cetaceans (McFarland, 1971) match the emission spectra of cephalopod photophores (Herring, 1983). Particular families of cephalopods have particular habitats. Some are neritic only living on or over the continental shelves while others are only found in oceanic water.

Table 1 Cephalopod families with some details of their biology

Cephalopod Family	No. of Genera	Size	Rarety		Buoyancy		Luminous	Habitat
			Nets	Predators	Neutral	Neg.		
Architeuthidae	1	L	R	F	A			O MB
Thysanoteuthidae	1	L	VR	VR		√		O M
Ommastrephidae	11	M-L	C	C		√	(√)	O-N MB
Onychoteuthidae	6	S-L	R	C		√	(√)	O MB
Pholidoteuthidae	2	M	VR	R-F		√		O M
Psychroteuthidae	1	M	VR	F				O M
Brachioteuthidae	1	S	F	R				O M
Gonatidae	4	S-M	C	C	O		(√)	O M-B
Enoploteuthidae	8	S-M	C	C	A	√	√	O M
Lycoteuthidae	5	S-M	R	F	A**		√	O-N M
Octopoteuthidae	2	S-L	F	C	A		√	O M
Lepidoteuthidae	1	L	VR	R-F	A			O M
Histioteuthidae	1	S-M	C	C	A		√	O M
Neoteuthidae	2	S-M	VR	R		√		O M
Bathyteuthidae	1	S	C	R*	A		√	O M
Ctenopterygidae	1	S	F	R		√	√	O M
Cycloteuthidae	2	M	R	R-F	A		√	O M
Mastigoteuthidae	1	S	F	R	A		√	O M
Chiroteuthidae	3	S	F	R	A		(√)	O M
Joubiniteuthidae	1	S	VR	O	A			O M
Batoteuthidae	1	S	VR	O	A		√	O M
Grimalditeuthidae	1	S	VR	O	A		√	O M
Cranchiidae	13	S-L	C	C	A		√	O M
Pickfordiateuthidae	1	S	VR	O		√		O M
Loliginidae	6	S-M	C	C		√	(√)	N M-B
Sepiolidae	7	S	C	R*		√	√	N B
Sepiidae	2	S-M	C	C	V			N B
Sepiadariidae	2		R	VR	V			N B
Spirulidae	1	S	F	R*	V		√	O M
Vampyroteuthidae	1	S	F	F	S		√	O M
Octopodidae	9	S-L	C	C		√		N B
Cirroteuthidae	2	M	R	O	S			O B
Stauroteuthidae	2	M	R	O	S			O B
Opistoteuthidae	1	S-M	R	O	S			O B
Tremoctopodidae	1	M	R	VR		√		O M
Ocythoidae	1	S-M	R	O		√		O M
Argonautidae	1	S	R	R		√		O M
Vitreledonellidae	1	S	R	O	S			O M
Bolitaenidae	3	S	C	R*	S		√	O M
Alloposidae	1	M	R	F	S			O M

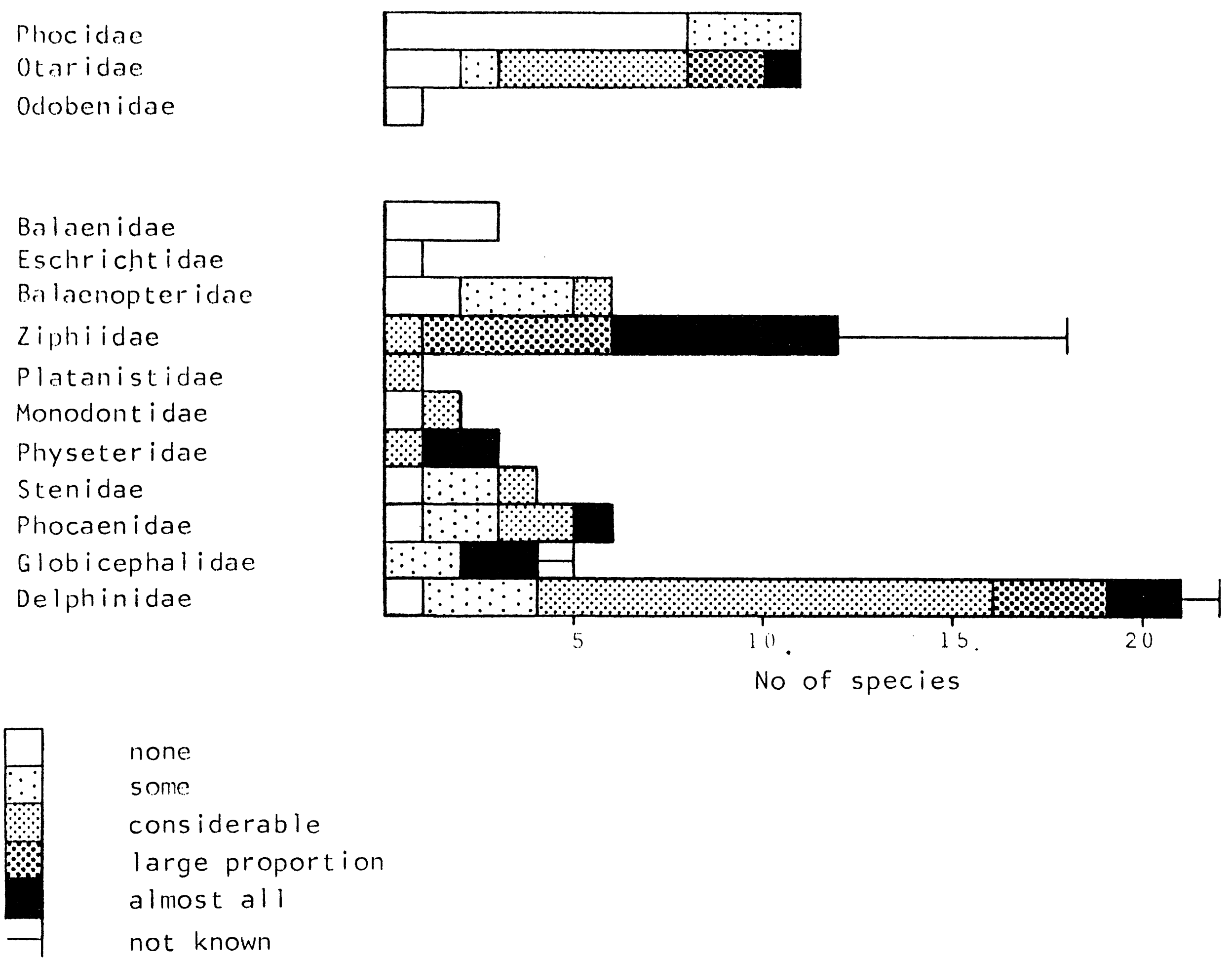
Size: Total L approximately = S 150 mm, M 700 mm, L 700 mm. Rarety in nets, VR = very rare, R = rare, F = often present in range, C = common, O = not known, *probably less rare than at present thought. ** Ross 1979a thesis. Buoyancy, Neutral, A = Ammoniacal, O = Oil, V = Vacuum, S = Sulphate replacement. Luminosity: √ = all genera luminous, (√) = some luminous species. Habitat: N neritic, O oceanic, B bottom, M midwater.

A few semi-oceanic species notably in the Ommastrephidae migrate on to the shelf in pre-spawning migrations. Some cephalopods only live clear of the bottom except when spawning while others live on or very close to the bottom all or most of the time.

Marine Mammal Predators

While we know little about the food of many cetaceans and seals it is possible to make very rough preliminary estimates of the amount of squid in the diet from the literature (Clarke, 1983; 1985b). In figure 1 the percentage of predator species in each family eating various amounts of cephalopod are shown. From this it will be seen that a few balaen whales do eat squid while cetaceans eating most squids are members of the Ziphiidae and Physeteridae.

Fig. 1. Number of species in each marine mammal family having particular proportions of cephalopods in the diet



Certain features of the cetaceans can be correlated with the inclusion of cephalopods in the diet (Clarke, 1985b). Predominantly fish eating odontocetes have more teeth than those mainly eating cephalopods. Also odontocetes which eat neritic squid and more fish have wider and possibly shorter mouths and swim faster than those eating oceanic squid and fewer fish.

The marine mammals in which the cephalopod diet has been analysed from beaks are Physeter macrocephalus (see Clarke, 1980, Clarke & MacLeod, 1982), the cetaceans shown in table 2 and the Elephant seal, Ross seal, Weddell seal, Fur seal, Leopard seal and Galapagos fur seal (Clarke, 1983; Clarke & Trillmich, 1980).

Cephalopods in the diet

The data collected so far shows that the cephalopod families of greatest importance in the diet of the cetaceans other than the sperm whale (table 2) are the oceanic Ommastrephidae, Onychoteuthidae, Histioteuthidae, Cranchiidae and the neritic Loliginidae and Sepiidae but some of these are only important to one of the species examined. The families of greatest importance in the diet of the antarctic seals examined so far are the Octopoda, Onychoteuthidae, Ommastrephidae, Cranchiidae and Gonatidae (Clarke, 1983). The Galapagos fur seal apparently eats predominantly Onychoteuthidae and Ommastrephidae (Clarke & Trillmich, 1980).

The sperm whale has been studied in greatest detail (figure 2). In temperate regions and Iceland, histioteuthids are very dominant (30-91%) by number 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%). In the Antarctic the onychoteuthids (53%) and cranchiids (23%) are the most numerous. Peru and some North Pacific samples differ from all the rest by having appreciable numbers (16-17%) of another family, the Chiroteuthidae.

Estimates of the weights of the families represented by beaks (figure 2, bottom) shows that histioteuthids are less important 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 in 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 of flesh of cephalopods from sperm whales caught off Japan show that hisitoteuthids are most important by weight in that region (30-38%) with unidentified squids providing 27% of the cephalopod weight (these conclusions are biassed by differential digestion and are not comparable with beak studies).

Table 2. Cephalopods in the diet of cetaceans % No. by species *Unidentified octopods

1. Stenella attenuata (spotted) (Perrin et al., 1973)
2. Stenella longirostris (Perrin et al., 1973)
3. Globicephalus melaena, Faeroes (Moore, pers. comm.)
4. G. melaena, France (Collet, pers. comm.)
5. G. melaena, Tierra del Fuego (Goodall, pers. comm.)
6. Globicephalus macrorhynchus, South Africa (Roeleveld, pers. comm.)
7. G. macrorhynchus, Indonesia (Hembree, pers. comm.)
8. Tursiops truncatus, South Africa (Roeleveld, pers. comm.)
9. T. truncatus, Canada (Mercer, 1973)
10. Ziphius cavirostris, New Zealand (Fordyce et al.,
11. Kogia breviceps (Ross, 1979b)
12. Kogia simus (Ross, 1979b)
13. Grampus griseus, English Channel (unpublished)
14. Lagenorhynchus cruciger, S.E. of South Africa (unp
15. Cephalorhynchus commersoni, Tierra del Fuego (Good
16. Hyperoodon ampullatus, Denmark (Clarke & Kristense
17. Hyperoodon planifrons, Tierra del Fuego (Goodall,
18. Mesoplodon carlhubbsi, Califo[illegible] (Mead et al., 19

Cephalopod Family	1	2	3	4	5	6	7	8	9	10	11	12	[illegible]	[illegible]	15
Nos. of beaks	7596	266	353	52	106	64	13	140	82	94	407	1436	[illegible]	[illegible]	[illegible]
(No. samples of cephalopods)	(94)	(12)	(2)	(6)	(4)	(1)	(1)	(2)	(1)		(13)	(10)	[illegible]	[illegible]	[illegible]
Architeuthidae															
Thysanoteuthidae															
Ommastrephidae	41.6	[illegible]	96.3	21.2					96.3		1.7	4.3	[illegible]		
Onychoteuthidae	45.0	[illegible]			16.1					8.5	2.7	0.1		[illegible]	
Pholidoteuthidae										1.1					
Psychroteuthidae											0.2				
Brachioteuthidae				9.6	8.5					1.1					
Gonatidae															
Enoploteuthidae	10.4	[illegible]	3.7			15.6								[illegible]	
Lycoteuthidae								83.8			5.6	0.1			
Octopoteuthidae	<0.1						30.8				19.1	16.3			
Lepidoteuthidae											8.8	0.2			
Histioteuthidae	<0.1			9.6	30.2		7.7			7.4					
Neoteuthidae					0.9						38.0	5.9			
Bathyteuthidae															
Ctenopterygidae															
Cycloteuthidae															
Mastigoteuthidae					4.7										
Chiroteuthidae	<0.1	0.8					7.7				4.7	0.6			
Joubiniteuthidae															
Batoteuthidae															
Grimalditeuthidae															
Cranchiidae	<0.1			26.9	7.5		30.8			81.9	13.1	2.0			
Pickfordiateuthidae															
Loliginidae				21.2	31.1	84.4		16.2			0.7	0.3	4.9		97.5
Sepiolidae				1.9											
Sepiidae				1.9							2.5	69.5	29.3		
Sepiodariidae															
Spirulidae															
Vampyroteuthidae											0.2	<0.1			
Octopodidae	(0.4)*			7.7	0.9				(3.7)*		2.7	0.4	39.0		2.5
Alloposidae															
Unidentified	2.4	1.1					23.1							11.0	
Total	99.9	100.0	100.0	100.0	99.8	100.0	100.1	100.0	100.0	100.0	100.0	99.8	100.1	100.0	100.1

The estimated mean weights of squids eaten by sperm whales in Iceland was 1.5 kg, in Spain 8.0 kg, in Madeira 1.6 kg, in Brazil 0.6 kg, in both Donkergat and Durban (S. Africa) 0.6 kg, in the Antarctic 7.2 kg, offWestern Australia 2.3 kg, in the Tasman Sea 3.6 kg, off Peru 1.3 kg and off Western Canada 1.2 kg.

Migration

The presence of flesh, even just the buccal muscles around the beaks, shows that a cephalopod was ingested within a few miles of the point at which the predator was killed or stranded. Such samples indicate the distribution of the cephalopod species concerned and should always be carefully collected. When the distribution is known it is often possible to use the beaks to find whether any predators examined recently migrated from an area distant from the place in which it was collected. In this way it was shown (Clarke, 1980) that some of the sperm whales caught off South Africa had recently moved from the Antarctic since they had beaks of Antarctic species in their stomachs and, conversely, some whales killed in the Antarctic were shown to have previously migrated from temperate seas further north. Other migrations have also been shown for sperm whales in this way and the proportion of the population which have recently migrated can be shown for different seasons.

Shorter movements can also be shown if, for example, stranded cetaceans in the English Channel contain beaks of oceanic species.

Biomass calculations

The total biomass of a species of cephalopod eaten by a well-investigated predator can be estimated providing we know the percentage by weight that it represents of the food, the weight of food required by the predator, the total population of the predator and the mean weight of the predator (Clarke, 1980 for sperm whales). If this were done for as many predators as possible it might be possible to assess the biomass of one particular cephalopod species or of all cephalopods much more accurately than from net samples. This is more likely to meet with success in an enclosed well defined area such as the Mediterranean sea than in very large areas (Clarke, 1983).

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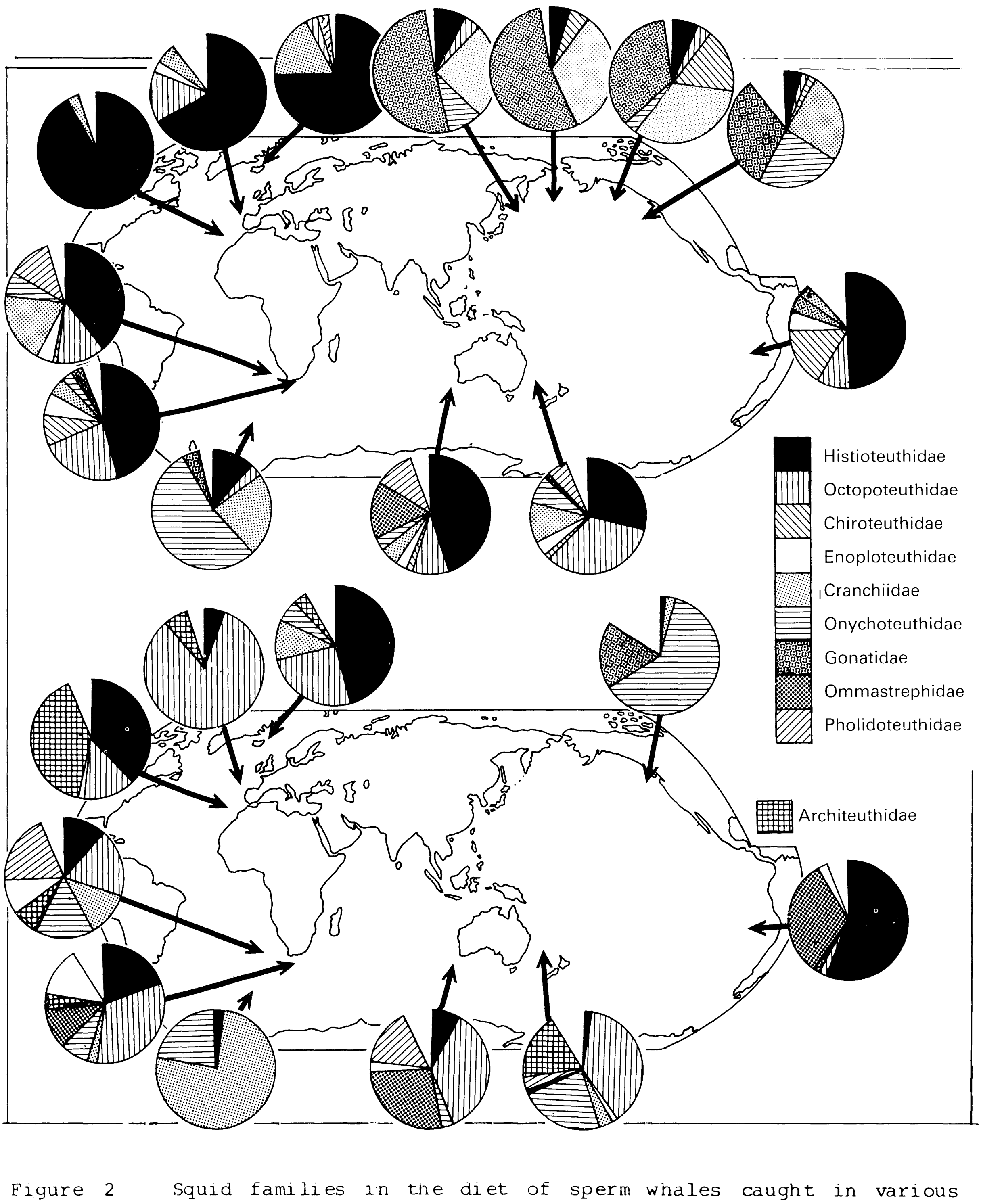

Figure 2 Squid families in the diet of sperm whales caught in various regions of the world. Top, Composition based on the number of lower beaks. Bottom, Composition by weight estimated from the numbers and sizes of beaks. Data for Kurile islands, Aleutian islands and Gulf of Alaska from Tarasevich, 1963, 1960. Other data from papers by Clarke & colleagues (see Clarke, 1985b)

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