OCEANIC CEPHALOPOD DISTRIBUTION AND SPECIES DIVERSITY IN THE EASTERN NORTH ATLANTIC

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This work provides a baseline against which we might measure future changes to oceanic midwater cephalopod stability in the eastern North Atlantic It records a considerable sampling effort from 1959 to 1986 aimed at oceanic midwater cephalopods made by the author and colleagues in the eastern North Atlantic between approximately 10ºN to 70ºN and 0ºto 30ºW. From these samples the latitudinal distribution, the biodiversity and, to some extent, the relative rarity of the species present in the area is shown. Over 700 collections were made with a range of nets from small plankton nets to large commercial trawls of many designs. As an independent measure of the efficiency of our sampling, the species represented by lower beaks from the stomach contents of 241 sperm whales (*Physeter catodon*) caught or stranded at five different localities in the area are listed and discussed. In total, over 40,000 cephalopods of 82 oceanic midwater species and 16 shelf and slope species were identified and are included here. The number of midwater species caught by nets increases regularly from 11ºN to 32ºN and decreases from 32ºN to 60ºN. A sharp increase at 32ºN of about 10 species above the curve produced by the catches at other stations is very probably due to the use of lights on the nets at this position. This suggests that further use of lights at all stations might elevate the curve at each position commensurate with the numbers of species found by conventional nets. The number of midwater cephalopods caught by nets in each of the 32 families show that Cranchiidae are by far the most numerous (and speciose) followed by Pyroteuthidae and Enoploteuthidae at half the number. 18 families numbered less than 100 individuals. Families eaten by sperm whales showed that Histioteuthidae was by far the most numerous (22787) with Cranchiidae (3285), Octopoteuthidae (1710) and Cycloteuthidae (1360) following in importance. Architeuthidae was not caught by nets but was present in the whale diet (221). The scarcity and expense of net collections suggests that estimates of cephalopod distribution and relative numbers should rely more on analysis of the diet of predators than on net catches. The value of monitoring cephalopods in the deep ocean is discussed.

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INTRODUCTION

Net caught samples of pelagic species, particularly cephalopods, vary according to the size and speed of nets used to catch them. Nets with mouths up to 10 m^2 catch only paralarvae or young immatures of large species or adults of very small species. To try to sample the adults of the majority of species our only recourse is to use much larger nets, such as commercial midwater trawls or find evidence for them in the stomachs of large predators such as cetaceans or large fish. Fortunately, the chitinous beaks (jaws) of cephalopods are not digested. By their identification and their size it is possible to find the contribution of a species by number to the diet (CLARKE 1980, 1986b). Cephalopods are not sampled as well as fish and rarely represent more than a small proportion of the nekton caught in nets, e.g. 1:227 cephalopods to fish, in the Bay of Biscay (CLARKE & PASCOE 1985). That the rarity of cephalopods in nets is a reflection of their avoidance capacity rather than their low numbers is shown by their importance in diets of many cetacean, fish and bird species. Many squid species in the diets of oceanic predators are almost unknown from commercial catches of cephalopods which are mainly from the continental shelves.

Although many collections of midwater cephalopods from the oceanic eastern North Atlantic have been made, their aerial distribution has been rather neglected although distributions are sometimes given in general works without quoting many sources or accurate positions (GUERRA 1992; NESIS 1987). While these generalizations are often helpful, any future comparisons will require accurate information on the position of each collection. To take a fresh look at this, I have re-examined 24 collections which were made at particular localities by the author and colleagues over a period of 27 years from 1959-1986.

The accumulated collection effort described here greatly exceeds that of any other sampling of cephalopods in the region and, because of the diversity of samplers, it must provide a credible estimate of the horizontal distribution of the midwater species to 2000m. On the other hand, bottom sampling does not have a good coverage and the continental shelf is not included.

Over the years, taxonomy of oceanic cephalopods has been greatly improved (notably by NESIS 1987 and both Gilbert and Nancy Voss and their students and by several cooperative efforts instigated by the Cephalopod International Advisory Council (CIAC). Here, advantage has been taken of the taxonomic work of the last two decades to update some identifications since the publication of the original results of some of these collections.

The present work should give a good insight into latitudinal distribution, species diversity and the relative rarity of oceanic midwater cephalopods to relate to previous observations and stated beliefs. Positive records of squid species outside the distributions shown by the present sampling (but within the eastern North Atlantic) will be added in the discussion (e.g. as given in CLARKE 1966 and GONÇALVES 1991 and in more general terms by NESIS 1987). This will give a firmer basis for observing any changes to latitudinal distribution of single species (GUERRA et al. 2002).

The problems in using such data for monitoring biodiversity and change to midwater oceanic cephalopods and future alternatives for their study are discussed.

MATERIAL & METHODS

A variety of samplers from hand lines to nets of many descriptions from $1m^2$ to commercial trawls were used. Although the great majority of sampling was in midwater, a few bottom trawls were also used. At six localities, cephalopods from vertical series of opening-closing nets were examined and published to show vertical distribution and migration of the cephalopods concerned (CLARKE & LU 1974, 1975; LU & CLARKE 1975a & b). Two other series of hauls compared catches with or without lights attached to the mouth of the net (CLARKE & PASCOE 1985, 1998) and others were from localities where collection was intensive for other purposes such as physiological work or experimental fishing. They include series taken with a variety of nets over the abyssal plain, over the continental slope, island slopes and a collection from around Madeira and the Azores. Added to these are surface samples taken with hand lines and handnets from research ships and weather ships and by commercial trawls operated from trawlers fishing on Northern fishing grounds. Also included here are the cephalopods identified from lower beaks collected from the stomachs of sperm whales stranded or killed commercially at five localities.

A brief review of the sampling methods used at the time of these collections is given by CLARKE 1977 and greater details of the gear and methods used in the United Kingdom at the time are given by CLARKE (1969); BAKER et al. (1973); FOXTON (1969) and CLARKE & PASCOE (1985, 1998). The bulk of this sampling was carried out by cruises of RRS "DISCOVERY II', RRS "DISCOVERY", RRS "CHALLENGER", RRS "FREDERICK RUSSELL", and RS "SARSIA" in which the author took part. Surface squids were also taken by handlines and handnets wherever other work permitted it although this added only five more species.

In 1960-63 trawler skippers operating from Hull and Grimsby were asked to collect any cephalopods sampled by their commercial trawls (mainly bottom Granton trawls) on their traditional fishing grounds at Iceland, Faroe islands, Bear Island, Lofoten Islands and the Norwegian coast. Most samples probably came from less than 400m depth and only one species (*Todarodes sagittatus*) was caught (unpubl.).

In 1966-68 collections were made by enlisting the help of the crew of weatherships to catch cephalopods by handline, handnet and crossbow and observe surface squid. Several hundred were caught (unpubl.).

The cephalopods in the diet of 241 sperm whales (*Physeter catodon*), caught or stranded in the area, are included for comparison with net samples and to act as an indicator of our relative ability to catch cephalopods. These results depend partly on flesh remains but mainly on identification of lower beaks (jaws) of cephalopods retained in the whales' stomachs. Methods used in identifying beaks are given elsewhere (CLARKE 1986a & b).

Positions of the sampling are given in Fig. 1

RESULTS

General efforts and catches

Samples from 22 localities numbered sequentially from south to north are compared (Table 1, Figure 1).

1. At 11ºN 20ºW, 1617 cephalopods identified as 39 species were caught with 1m^2 ring nets (N113H) and rectangular midwater trawls (RMT8 combination net, BAKER et al 1973) fished to examine vertical migration down to 2000m over the abyssal plain in February 1968 and March 1972. 87 hauls, in all, were examined. (LU & CLARKE 1975b)

2. At 18ºN 25ºW 921 cephalopods identified as 40 species were caught with rectangular midwater trawls (in all, 53 hauls with RMT8 combination net and RMT25) fished to examine vertical migration down to 2000m over the abyssal plain in November 1968 and February 1972. (CLARKE & LU 1975)

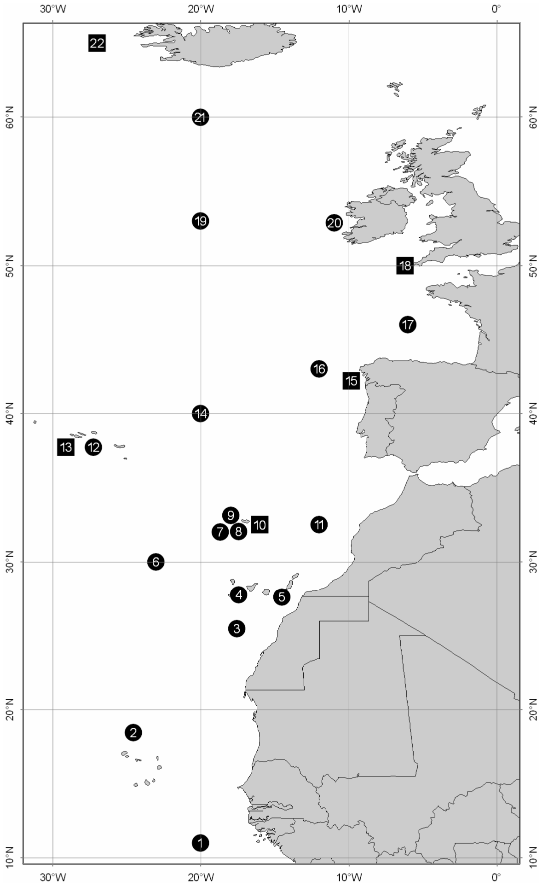

Fig. 1. Positions and number of the samples compared in the text and table 1. Circles - positions of net sampling. Squares - positions of whale samples.

3. At 25ºN, 19º30'W a small collection of cephalopods made at Endeavour Bank in 1968 and 1969 (unpubl.).

4. Near to the Canary Islands. 144 cephalopods of 22 species from 16 hauls with British Columbia Midwater Trawls and Isaacs Kidd midwater trawls (IKMTs: FOXTON 1969) in August 1961 and 1976 (cephalopods unpublished).

5. Off the East of the southern tip of Fuerteventura, Canary Islands, 185 cephalopods of 18 species from a series of 76 hauls made with an opening/closing Isaacs Kidd Trawl and N113 (ring net with a mouth of 1m^2), at 0-1000m October 1965 for the purpose of studying the deep scattering layer (FOXTON 1969; CLARKE

Table 1 (continued)

Numbers caught of all the species at 22 of the positions compared here. N = many. Italics = species identified from beaks. Underlined = species represented by flesh in sperm whales stomachs. A few species names are not given or have been synonymised since the time of identification. See text for more detail.

Family	Species	Samples 1	2	3	4	5	6	7	8	9	10	11
Spirulidae	*Spirula spirula*			1	4	122	8	17	5	17		
Sepiidae	*Sepia officinalis*									N		
Sepiolidae	*Heteroteuthis dispar*	5			2	33		25	11			
	Rossia sp			28								1
	Sepiola sp			6								
	Sepietta oweniana									2		
Loliginidae	*Loligo forbesi*									N		
	Loligo vulgaris									N?		
Architeuthidae	*Architeuthis dux*										***37***	
Ancistrocheiridae	*Ancistrocheirus lesueurii*	2	2			3		1		8	***4***	1
Bathyteuthidae	*Bathyteuthis abyssicola*	73	11					4	1	1		
Brachioteuthidae	*Brachioteuthis riisei*	17	3			3	12			31		1
Chiroteuthidae	*Chiroteuthis* sp.		1		1	7	9	24				
	Valbyteuthis danae	10	17				30	4	2			
Chtenopterygidae	*Chtenopteryx sicula*	1	3		5	32	17	77	5			
Cranchiidae	*Cranchia scabra*	27	61		2	2	21	21				
	Leachia cyclura	140	19			11		6	5	30		
	Liocranchia reinhardti	490	118	1	59	7	2	182	2			
	Bathothauma lyromma	1	5			7	31	21	15			
	Helicocranchia pfefferi	25	5			1	107	121	9			
	Megalocranchia sp.				2	9		51	9		***31***	
	Sandalops melancholicus		2				1					
	Phasmatopsis cymoctypus									*1		
	Phasmatopsis oceanica		1					154				
	Teuthowenia megalops	17						3				
	Teuthowenia maculata											
	Galiteuthis armata	49	5									
	Belonella belone		21				23					
	Taonius pavo				1			156	1			1
Cycloteuthidae	*Discoteuthis lacinosa*							3	2			
	Discoteuthis discus									2		
	Cycloteuthis sirventi		6			1	2				***16***	
Enoploteuthidae	*Abralia redfieldi*	**3**						10				
	Abraliopsis pfefferi	4	6		8	341	73	376	9			1
	Abraliopsis affinis	44	5									
	Enoploteuthis leptura		2			38	6	10		2		
	Enoploteuthis anaspis									8		
Gonatidae	*Gonatus steenstrupi*											
Grimalditeuthidae	*Grimalditeuthis bonplandi*	4	3					4				
Histioteuthidae	*Histioteuthis arcturi*		4		1	36	12	206	1		***67***	
	Histioteuthis bonnellii	2									***1,886***	
	Histioteuthis corona		3				7			1		
	Histioteuthis celetaria							9				
	Histioteuthis meleagroteuthis		5			10		5	1			1
	Histioteuthis reversa	13	1						2	2		
Joubiniteuthidae	*Joubiniteuthis portieri*		1				6	13				
Lepidoteuthidae	*Lepidoteuthis grimaldii*	2					1	1			***28***	
Lycoteuthidae	*Lampadioteuthis megaleia*		1					1				
	Selenoteuthis scintillans					1	3					
Mastigoteuthidae	*Idioteuthis hjorti*		8		1	5	1	5				6
	Mastigoteuthis flammea					1		18	12			1
	Mastigoteuthis magna							130				
	Mastigoteuthis schmidti	158	22							19		
	Mastigoteuthis talismani	1										
	Mastigoteuthis glaukopis									8		
Neoteuthidae	*Neoteuthis theilei*	11	2		1		6		3	13		
Octopoteuthidae	*Taningia danae*	2					4	3	3		***11***	
	Octopoteuthis danae	1										
	Octopoteuthis sicula					1		7				
	Octopoteuthis rugosa											
	Octopoteuthis 'giant'											

Table 1 (continued)

Numbers caught of all the species at 22 of the positions compared here. N = many. Italics = species identified from beaks. Underlined = species represented by flesh in sperm whales stomachs. A few species names are not given or have been synonymised since the time of identification. See text for more detail.

		Samples										
Family	**Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Ommastrephidae	*Hyaloteuthis pelagica*					1						
	Ommastrephes bartramii				1	2	1	2	28	N		
	Sthenoteuthis pteropus				6			4	16	N		
	Todarodes sagittatus				2	7		15	15	N		6
	Todaropsis eblanae											
Onychoteuthidae	*Onychoteuthis banksii*	109	142			18	36	53	2			
	Ancistroteuthis lichtensteini				1							
	Chaunoteuthis mollis									2		1
	Onykia carribaea	29	5					2	1			
	Moroteuthis robsoni							44			***4***	
Pholidoteuthidae	*Tetronychoteuthis massyae*					14		1		2		
	Pholidoteuthis boschmai	8								2		
Pyroteuthidae	*Pterygioteuthis* sp.	10	9		26	227	49	195	45			2
	Pterygioteuthis giardi									21		
	Pterygioteuthis gemmata									174		
	Pyroteuthis margaritifera		27		1	9	33	105	11			1
Thysanoteuthidae	*Thysanoteuthis rhombus*					1	1	+	2	N		
Vampyroteuthidae	*Vampyroteuthis infernalis*	27	28		1		5	14	2			1
Alloposidae	*Haliphron atlanticus*	1						+		1	***18***	
Argonautida	*Argonauta argo*	25	29							1		
	Argonauta hians				1				5	1		
Bolitaenidae	*Eledonella pygmaea*							10	2			
	Japetella diaphana	103	81		17	28	43	153	11			3
	Bolitaena microcotyla									8		
Octopodidae	*species*		22			4						
	Bathypolypus sp.											
	Benthoctopus sp.											
	Eledone cirrhosa											
	Octopus vulgaris									N		
	Octopus macropus									6		
	Octopus defilippi									1		
	Scaergus unicirrhus	161								1		
	Pteroctopus tetracirrhus									8		
Ocythoidae	*Ocythoe tuberculata*							3				
Tremoctopodidae	*Tremoctopus violaceus*	11	74						6	4		
Vitreledonellidae	*Vitreledonella richardi*	23	21		1		2		9	5		
Opisthoteuthidae	*Opisthoteuthis agassizi*									1		1
Cirroteuthidae	*Grimpoteuthis plena*											
Totals		**1,609**	**781**	**36**	**144**	**982**	**552**	**2269**	**253**	**382**	**2,102**	**28**

Table 1 (continued)

Numbers caught of all the species at 22 of the positions compared here. N = many. Italics = species identified from beaks. Underlined = species represented by flesh in sperm whales stomachs. A few species names are not given or have been synonymised since the time of identification. See text for more detail.

		Samples											Total	
Family	**Species**	**12**	**13**	**14**	**15**	**16**	**17**	***18***	**19**	**20**	**21**	**22**	**nets**	**whales**
Spirulidae	*Spirula spirula*	1											175	0
Sepiidae	*Sepia officinalis*												0	0
Sepiolidae	*Heteroteuthis dispar*	26		1									103	0
	Rossia sp												29	0
	Sepiola sp									1			7	0
	Sepietta oweniana												2	0
Loliginidae	*Loligo forbesi*									6			6	0
	Loligo vulgaris												0	0
Architeuthidae	*Architeuthis dux*		***135***		***1***			***47***				***1***	0	221
Ancistrocheiridae	*Ancistrocheirus lesueurii*		***189***		***2***		2					***1***	19	196
Bathyteuthidae	*Bathyteuthis abyssicola*	2		5									97	0
Brachioteuthidae	*Brachioteuthis riisei*	1					9		64			***3***	141	3
Chiroteuthidae	*Chiroteuthis* sp.	9	***168***	1								***1***	52	169
	Valbyteuthis danae												63	0
Chtenopterygidae	*Chtenopteryx sicula*			2									142	0
Cranchiidae	*Cranchia scabra*												134	0
	Leachia cyclura	1		5									217	0
	Liocranchia reinhardti	4	***4***	14									879	4
	Bathothauma lyromma	1		1									82	0
	Helicocranchia pfefferi		***4***	2			1						271	4
	Megalocranchia sp.	1	***30***									***3***	72	64
	Sandalops melancholicus												3	0
	Phasmatopsis cymoctypus		***333***		***4***								0	337
	Phasmatopsis oceanica	2	984										157	984
	Teuthowenia megalops		***984***				31		195		54	***386***	300	1,370
	Teuthowenia maculata		522										0	522
	Galiteuthis armata	6		1			3	***1***					64	1
	Belonella belone												44	0
	Taonius pavo	2	***12***				17					***1***	178	13
Cycloteuthidae	*Discoteuthis lacinosa*	1	***1,291***										6	1,291
	Discoteuthis discus												2	0
	Cycloteuthis sirventi		***152***									***1***	9	169
Enoploteuthidae	*Abralia redfieldi*												13	0
	Abraliopsis pfefferi	1		13									832	0
	Abraliopsis affinis												49	0
	Enoploteuthis leptura												58	0
	Enoploteuthis anaspis												8	0
Gonatidae	*Gonatus steenstrupi*		***378***				13		93		207	***63***	313	441
Grimalditeuthidae	*Grimalditeuthis bonplandi*												11	0
Histioteuthidae	*Histioteuthis arcturi*		***1973***	4			4						268	2040
	Histioteuthis bonnellii		***18,087***		***47***		3	***49***		1		***174***	6	20,243
	Histioteuthis corona												11	0
	Histioteuthis celetaria		***426***										9	426
	Histioteuthis meleagroteuthis		***59***				1						23	59
	Histioteuthis reversa		***19***						3				21	19
Joubiniteuthidae	*Joubiniteuthis portieri*	2											22	0
Lepidoteuthidae	*Lepidoteuthis grimaldii*	1	***521***		***4***							***3***	5	556
Lycoteuthidae	*Lampadioteuthis megaleia*												2	0
	Selenoteuthis scintillans												4	0
Mastigoteuthidae	*Idioteuthis hjorti*												26	0
	Mastigoteuthis flammea	5	***85***	3			8						48	85
	Mastigoteuthis magna												130	0
	Mastigoteuthis schmidti								2		2		203	0
	Mastigoteuthis talismani												1	0
	Mastigoteuthis glaukopis												8	0
Neoteuthidae	*Neoteuthis theilei*												36	0
Octopoteuthidae	*Taningia danae*		***1,198***	2	***10***				1				15	1,219
	Octopoteuthis danae												1	0
	Octopoteuthis sicula	1											9	0
	Octopoteuthis rugosa		***371***									***5***	0	376
	Octopoteuthis 'giant'		***115***										0	115

Table 1 (continued)

Numbers caught of all the species at 22 of the positions compared here. N = many. Italics = species identified from beaks. Underlined = species represented by flesh in sperm whales stomachs. A few species names are not given or have been synonymised since the time of identification. See text for more detail.

		Samples											Total	
Family	**Species**	**12**	**13**	**14**	**15**	**16**	**17**	***18***	**19**	**20**	**21**	**22**	**nets**	**whales**
Ommastrephidae	*Hyaloteuthis pelagica*												1	0
	Ommastrephes bartramii		***6***			10							44	6
	Sthenoteuthis pteropus												26	0
	Todarodes sagittatus	1	***333***	3			2	***8***		12		***21***	63	362
	Todaropsis eblanae					2				2			4	0
Onychoteuthidae	*Onychoteuthis banksii*		***2***	32		5	1					***4***	398	6
	Ancistroteuthis lichtensteini												1	0
	Chaunoteuthis mollis												3	0
	Onykia carribaea												37	0
	Moroteuthis robsoni		***110***										44	114
Pholidoteuthidae	*Tetronychoteuthis massyae*												17	0
	Pholidoteuthis boschmai		***330***									***1***	10	331
Pyroteuthidae	*Pterygioteuthis* sp.	12		42									617	0
	Pterygioteuthis giardi												21	0
	Pterygioteuthis gemmata												174	0
	Pyroteuthis margaritifera	9											196	0
Thysanoteuthidae	*Thysanoteuthis rhombus*												4	0
Vampyroteuthidae	*Vampyroteuthis infernalis*		***5***	1									79	5
Order Octopoda													0	0
Alloposidae	*Haliphron atlanticus*		***305***		***2***				1			***11***	3	336
Argonautida	*Argonauta argo*												55	0
	Argonauta hians												7	0
Bolitaenidae	*Eledonella pygmaea*	2											14	0
	Japetella diaphana			4									443	0
	Bolitaena microcotyla												8	0
Octopodidae	*species*		***1***										26	1
	Bathypolypus sp.									3			3	0
	Benthoctopus sp.									1			1	0
	Eledone cirrhosa									1			1	0
	Octopus vulgaris												0	0
	Octopus macropus												6	0
	Octopus defilippi												1	0
	Scaergus unicirrhus												162	0
	Pteroctopus tetracirrhus												8	0
Ocythoidae	*Ocythoe tuberculata*												3	0
Tremoctopodidae	*Tremoctopus violaceus*												95	0
Vitreledonellidae	*Vitreledonella richardi*			6									67	0
Opisthoteuthidae	*Opisthoteuthis agassizi*												2	0
Cirroteuthidae	*Grimpoteuthis plena*	4					1						5	0
Totals		95	29,132	142	70	17	96	***105***	359	27	263	679	8,035	32,088

1969) and eight catches made at the same location with a commercial Engel's midwater trawl (mouth 34.4m x 19.8m) fished in November 1966 at 570-0m (unpubl.).

6. At 30ºN 23ºW, 618 cephalopods of 29 species caught with 80 net hauls including two series of combination rectangular midwater trawls (RMT 8+1) fished to examine vertical migration down to 2000m over the abyssal plain used in April 1972 together with collections made with Isaacs Kidd Midwater trawls (IKMT) and British Columbia Midwater trawls (BCMT) in various months April to November 1961-62 at the same position (CLARKE & LU 1974)

7. At 32º30'N 17º15'W, 1258 cephalopods of 55 species caught in 57 net hauls made in October 1986 with RMT50s near Madeira at a fishing depth from 700 to 1200m, according to the ship's course, over a sounding of 2500m during comparisons designed to test the effectiveness of headline lights to enhance catches of cephalopods (CLARKE & PASCOE 1998).

8. At stations all round but mainly to the North, East and South of Madeira in May-July 1962 (9 hauls) and in Sept-Oct 1975 (57 hauls). 225 cephalopods of 33 species sampled with handlines and handnets, with 9 IKMT fished to a maximum of 1225m, 7 RMT8 hauls fished between 150m and 2800m depth., 11 RMT8 + RMT 7 fished, one above the other, to between 200 and 1500m depth) and 10 RMT90 hauls fished to 100-1030m (CLARKE unpubl.).

9. At Madeira, cephalopods listed for Madeira (CLARKE & LU 1995) which includes eight shelf species and three species not sampled by research gear but regularly appearing in the Funchal market. Seven species caught commercially inshore (CLARKE & LU 1995) and two observed (one caught) from a submersible (GONÇALVES & MARTINS 1992)

10. At Madeira, 2136 lower beaks from one sperm whale's stomach contents collected August 1959 (CLARKE 1962 adjusted by CLARKE & MACLEOD 1974).

11. North of the Canary Islands above and on the continental slope at 32-33ºN, 11-13ºW, 29 cephalopods caught in 15 hauls of Bottom trawls and RMT nets in August 1976 (unpubl.).

12. At 37º-38ºN 25º-28ºW round the Azores islands, 95 cephalopods of 23 species caught with 35 combination RMT8+1 nets and 10 RMT25 hauls fished in October and November 1970 (unpubl.).

13. Near 39ºN 28ºW, 28,738 lower beaks of 31 species from 17 sperm whales caught off Pico and Flores Islands in the Azores in 1981-84 (CLARKE et al. 1993)

14. At 40ºN, 20ºW, 942 cephalopods of 12 species caught by a vertical series of 35 RMT hauls October and November 1970 (LU & CLARKE 1975a)

15. From a sperm whale caught at 41º32'N, 9º48'W, 70 lower beaks belonging to 7 species were taken from the stomach at Vigo, Spain in June 1966 (CLARKE & MACLEOD 1974).

16. Near Galicia Bank, at 43ºN 12ºW. 17 cephalopods of 3 species caught at the surface by handline and handnets. RRS 'Discovery II' in Mar-Apr. 1959 (unpubl.).

17. Bay of Biscay, 46-47ºN, 5-8ºW. 96 cephalopods of 14 species collected over several years mainly in May -June using RMTs and Boris trawls (a commercial midwater trawl used by Plymouth fishermen) (unpubl. data).

18. Near 50ºN, 10ºW, 110 lower beaks belonging to 6 species were taken from one stranded sperm whale's stomach collected at Penzance, England in February, 1990 (CLARKE & PASCOE 1997).

19. At 53ºN, 20ºW, 358 cephalopods of 7 species caught by a vertical series of 34 RMT hauls in May and June 1971 (LU & CLARKE 1975a)

20. At 49-59ºN, 9-11ºW, 27 cephalopods of 8 species caught with 8 hauls of a Granton trawl (a standard U.K. commercial trawl) fished on the continental slope west of Great Britain in January1974 by the RS "Cirolana" (unpubl.).

21. At 60ºN, 20ºW, 264 cephalopods of 3 species caught by an RMT series of 34 RMT hauls in April and May 1971 (LU & CLARKE 1975a).

22. Collected from 221 sperm whales caught at 63-67ºN, 24-30ºW, to the West of Iceland, 675 lower beaks belonging to 22 species in 1977-1978 (MARTIN & CLARKE 1986).

Extensive collections were made by the following means and are not included in Table 1 and Figure 1 because they resulted in sampling only one or two species.

23. In 1960-63 trawler skippers operating from Hull and Grimsby were asked to collect any cephalopods sampled by their commercial trawls (mainly bottom Granton trawls) on their traditional fishing grounds at Iceland, Faroes islands, Bear island, Lofoten islands and the Norwegian coast. Most samples probably came from less than 400m depth (unpubl.).

24. In 1966-68 collections were made by enlisting the help of people on weatherships to catch by handline, handnet and crossbow and observe surface squid. Several hundred were caught unpubl.).

Latitudinal Distribution

Figure 1 shows the positions from where the collections came (except for 23 and 14 above) and Table 1 shows the cephalopods collected from those positions (collection 9 which is a list of species in the Madeira area duplicates some from other collections). This includes some bottom and shelf-living species which were not adequately sampled to show their horizontal distribution and they are excluded from Table 2 which only deals with midwater oceanic species. As distribution of oceanic midwater species in the eastern North Atlantic is mainly dependant on physical factors predominantly dependent on latitude, it would seem justified to interpolate between latitudes where a species is sampled, to describe its general distribution (III in Table 2) Where published evidence indicates extension of their distribution beyond the latitudes shown here, "EE" is inserted to show extension. Thus, from table 2 the latitudinal extension of each species in the eastern North Atlantic is shown. The five positions at which whales provided lower beak identifications (10, 13, 15, 18 and 22) are treated differently from the net samples. Where an adjacent position shows the presence of the species from a net (PP) the sample of that species in the whale is also labelled PP. Where it is present in the whale but not in adjacent net stations, the number of beaks of the species in the whale is shown.

The collections of the Hull and Grimsby fishermen, are not shown in table 2 because, although a total of more than 1500 squids were collected from the fishing grounds at Iceland, Faroes, Bear Island and the Norwegian coast north to 70ºN they all proved to be one species, *Todarodes sagittatus* and all but three were females.

From the weatherships, cephalopods were collected from station KILO, at 45ºN 16W, JULIET, at 52ºN 20ºW, INDIA, 59ºN 19W and ALPHA, at 62ºN 33ºW and these are also excluded from table 2 because only two species were caught (*Todarodes sagittatus, Ommastrephes bartrami.*)

All together, well over 40,000 cephalopod individuals have been identified as 99 species including 79 oceanic midwater species and 15 continental slope and shelf species.

No samples were taken on the continental shelves, but hauls were done on the continental slope at 32-33ºN and 49-59ºN which caught *Sepiola* sp., *Loligo forbesi* and *Todaropsis eblanae* as well as *Eledone cirrhosa.* The species *Sepia officinalis*, *Loligo forbesi*, *L. vulgaris* at Madeira and *L. forbesi* at the Azores are regularly caught commercially at the islands but are generally continental shelf species.

Although nearly all specimens were identified to species, the present work depends on many identifications made long ago, before the publication of major revisions and condensations (e.g. NESIS 1987). Consequently, some specimens are presently unavailable and proved impossible to check from notes. Genera proving difficult were, *Sepiola*, *Chiroteuthis*, *Megalocranchia*, *Mastigoteuthis* and *Pterygioteuthis.*

Table 2 (continued)

Summary of the latitudinal distribution of midwater cephalopods in net catches and collections of lower beaks from sperm whale stomachs described here. Underlined = species represented by flesh in whales' stomachs. PP = species present. III = interpolated presence. EE = extrapolated presence

Family	Sample No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
	° North	**11**	**18**	**25**	**28**	**28**	**30**	**32**	**32**	**32**	**32**	**32**	**38**	**38**	**40**	**42**	**43**	**46**	**50**	**53**	**49**	**60**	**65**
Spirulidae	*Spirula spirula*			PP	PP	PP	PP	PP	PP	PP		III	PP										
Sepiolidae	*Heteroteuthis dispar*	PP	III	III	PP	PP	III	PP	PP	III		III	PP		PP								
Architeuthidae	*Architeuthis dux*						E	E	E	E	37	E	E	135	E	1	E	E	47	E	E	E	1
Ancistrocheiridae	*Ancistrocheirus lesueurii*	PP	PP	III	III	PP	III	PP	III	PP	PP	PP	III	189	III	2	III	PP					1
Bathyteuthidae	*Bathyteuthis abyssicola*	PP	PP	III	III	III	III	PP	PP	PP		III	PP		PP	E	E	E	E				
Brachioteuthidae	*Brachioteuthis riisei*	PP	PP	III	III	PP	PP	III	III	PP		PP	PP		III		III	PP	III	PP			3
Chiroteuthidae	*Chiroteuthis veranyi*		PP	III	PP	PP	PP	PP	III	III		III	PP	PP	PP								1
	Valbyteuthis danae	PP	PP	III	III	III	PP	PP	PP														
Chtenopterygidae	*Chtenopteryx sicula*	PP	PP	III	PP	PP	PP	PP	PP	III		III	III		PP								
Cranchiidae	*Cranchia scabra*	PP	PP	III	PP	PP	PP	PP															
	Leachia cyclura	PP	PP	III	III	PP	III	PP	PP	PP		III	PP		PP								
	Liocranchia reinhardti	PP	PP	PP	PP	PP	PP	PP	PP	III		III	PP	PP	PP		E	E					
	Bathothauma lyromma	PP	PP	III	III	PP	PP	PP	PP	III		III	PP		PP								
	Helicocranchia pfefferi	PP	PP	III	III	PP	PP	PP	PP	III		III	III	PP	PP		III	PP					
	Megalocranchia sp.				PP	PP	III	PP	PP	III		III	PP	PP									3
	Sandalops melancholicus		PP	III	III	III	PP																
	Phasmatopsis cymoctypus									PP	E	E	E	333		4							
	Phasmatopsis oceanica		PP	III	III	III	III	PP	III	III		III	PP	PP									
	Teuthowenia megalops	PP	PP	III	III	III	III	PP	III	III		III	III	984	III		III	PP	III	PP	III	PP	PP
	Teuthowenia maculata													522									
	Galiteuthis armata	PP	PP	III	III	III	III	III	III	III		III	PP		PP		III	PP	PP				
	Belonella belone		PP	III	III	III	PP																
	Taonius pavo				PP	III	III	PP	PP	III		PP	PP	PP	III		III	PP					1
Cycloteuthidae	*Discoteuthis lacinosa*							PP	PP	III		III	PP	PP									
	Discoteuthis discus									PP													
	Cycloteuthis sirventi		PP	III	III	PP	PP				16			152									1
Enoploteuthidae	*Abralia redfieldi*	PP	PP	III	III	III	III	PP															
	Abraliopsis atlantica	PP	PP	III	PP	PP	PP	PP	PP	III		PP	PP		PP								
	Abraliopsis hoylei	PP	PP																				
	Enoploteuthis leptura	E	PP	III	III	PP	PP	PP	III	PP													
	Enoploteuthis anaspis									PP													
Gonatidae	*Gonatus steenstrupi*													378				PP	III	PP	III	PP	PP
Grimalditeuthidae	*Grimalditeuthis bonplandi*	PP	PP	III	III	III	III	PP															
Histioteuthidae	*Histioteuthis arcturi*		PP	III	PP	PP	PP	PP	PP	III	67	III	III	PP	PP		III	PP					
	Histioteuthis bonnellii	PP	PP	III	III	III	III	III	III	III	1886	III	III	18087	III	47	III	PP	PP	III	PP		174
	Histioteuthis corona		PP	III	III	III	PP	III	III	PP													
	Histioteuthis celetaria							PP						426									
	Histioteuthis meleagroteuthis	E	PP	III	III	PP	III	PP	PP	III		PP	III	59	III		III	PP					
	Histioteuthis reversa	PP	PP	III	III	III	III	III	PP	PP		III	III	19	III		III	III	III	PP			
Joubiniteuthidae	*Joubiniteuthis portieri*		PP	III	III	III	PP	PP	III	III		III	PP										
Lepidoteuthidae	*Lepidoteuthis grimaldii*	PP	III	III	III	III	PP	PP	III	III	28	III	PP	PP		4							3
Lycoteuthidae	*Lampadioteuthis megaleia*		PP	III	III	III	III	PP															
	Selenoteuthis scintillans					PP	PP																
Mastigoteuthidae	*Idioteuthis hjorti*		PP	III	PP	PP	PP	PP	III	III		PP											
	Mastigoteuthis flammea					PP	III	PP	PP	III		PP	PP	PP	PP		III	PP					
	Mastigoteuthis magna							PP															
	Mastigoteuthis schmidti	PP	PP	III	III	III	III	III	III	PP		III	III	19	III		III	III	III	PP	III	PP	
	Mastigoteuthis talismani	PP	E	E	E	E	E	E		E		E	E		E		E	E					
	Mastigoteuthis glaukopis									PP		E	E	E	E	E	E	E					
Neoteuthidae	*Neoteuthis theilei*	PP	PP	III	PP	III	PP	III	PP	PP													
Octopoteuthidae	*Taningia danae*	PP	III	III	III	III	PP	PP	PP	III	11	III	III	PP	PP	PP	III	III	III	PP			
	Octopoteuthis danae	PP	E	E	E	E	E	E	E														
	Octopoteuthis sicula					PP	III	PP	III	III		III	PP		E	E	E	E	E				
	Octopoteuthis rugosa													371									5
	Octopoteuthis 'giant'													115									
Ommastrephidae	*Hyaloteuthis pelagica*					PP																	
	Ommastrephes bartramii	E	E	E	PP	PP	PP	PP	PP	PP		PP	III	6	III	III	PP	PP	PP	E	E	E	
	Sthenoteuthis pteropus	E	E	E	PP	III	III	PP	PP	PP		E											
	Todarodes sagittatus	E	E	E	PP	PP	III	PP	PP	PP		PP	PP	PP	PP		III	PP	PP	III	PP	E	21

Table 2 (continued)

Summary of the latitudinal distribution of midwater cephalopods in net catches and collections of lower beaks from sperm whale stomachs described here. Underlined = species represented by flesh in whales' stomachs. PP = species present. III = interpolated presence. EE = extrapolated presence

Family	**Sample No.**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
	° North	**11**	**18**	**25**	**28**	**28**	**30**	**32**	**32**	**32**	**32**	**32**	**38**	**38**	**40**	**42**	**43**	**46**	**50**	**53**	**49**	**60**	**65**
Onychoteuthidae	*Onychoteuthis banksii*	PP	PP	III	III	PP	PP	PP	PP	III		III	III	PP	PP		PP	PP	E	E	E	E	4
	Ancistroteuthis lichtensteini			E	PP																		
	Chaunoteuthis mollis									PP		PP											
	Onykia carribaea	PP	PP	III	III	III	III	PP	PP														
	Moroteuthis robsoni							PP			4			110									
Pholidoteuthidae	*Tetronychoteuthis massyae*					PP	III	PP	III	PP													
	Pholidoteuthis boschmai	PP	III	III	III	III	III	III	III	PP				330									1
Pyroteuthidae	*Pterygioteuthis sp.*	PP	PP	III	PP	PP	PP	PP	PP	III		PP	PP		PP								
	Pterygioteuthis giardi									PP													
	Pterygioteuthis gemmata									PP													
	Pyroteuthis margaritifera		PP	III	PP	PP	PP	PP	PP	III		PP	PP										
Thysanoteuthidae	*Thysanoteuthis rhombus*					PP	PP	PP	PP	PP													
Vampyroteuthidae	*Vampyroteuthis infernalis*	PP	PP	III	PP	III	PP	PP	PP	III		PP	III	PP	PP								
Alloposidae	*Haliphron atlanticus*	PP	III	III	III	III	III	PP	III	PP	18	III	III	305	III	2	III	III	III	PP			11
Argonautida	*Argonauta argo*	PP	PP	III	III	III	III	III	III	PP		E	E										
	Argonauta hians				PP	III	III	III	PP	PP													
Bolitaenidae	*Eledonella pygmaea*							PP	PP	III		III	PP										
	Japetella diaphana	PP	PP	III	PP	PP	PP	PP	PP	III		PP	III		PP								
	Bolitaena microcotyla									PP													
Ocythoidae	*Ocythoe tuberculata*							PP	E	E		E	E										
Tremoctopodidae	*Tremoctopus violaceus*	PP	PP	III	III	III	III	III	PP	PP		E	E										
Vitreledonellidae	*Vitreledonella richardi*	PP	PP	III	PP	III	PP	III	PP	PP		III	III		PP								

Distributions, of all the midwater species found here, will now be discussed with respect to previously published distributions (CLARKE 1966; NESIS 1987)

Oceanic Midwater species

Spirulidae

Spirula spirula (Linnaeus, 1801) was caught from South of the Canary Islands at Endeavour Bank to near the Azores.

Sepiolidae

Heteroteuthis dispar (Ruppell, 1845) was caught from 11º-40ºN. It has been recorded from about 50ºN to the Equator (Guinea) (NESIS 1987).

Architeuthidae

Architeuthis dux Steenstrup, 1857, extends from 30ºN to 75ºN in the North Atlantic according to strandings (CLARKE 1966). It is only known from stomachs of whales in this collection. Its absence south of 32ºN is not certain.

Ancistrocheiridae

Ancistrocheirus lesueuri (d'Orbigny, 1839) occurs mainly as paralarvae in the nets and the adults are from sperm whales' stomachs. The young have often been called *Thelidioteuthis alessandrini.* They were caught from 11ºN to 46-47ºN.

Bathyteuthidae

Bathyteuthis abysycola Hoyle, 1885 was caught from 11º-40ºN. It has been recorded to 50ºN (CLARKE 1966).

Brachioteuthidae

Brachioteuthis reesei (Steenstrup, 1882) was caught from 11º-53ºN. It has been recorded to 65ºN (CLARKE 1966).

Chiroteuthidae

Chiroteuthis veranyi (Ferrussac, 1835) was caught from 18º to 40ºN. It has been reported from the Bay of Biscay to south of the Equator (NESIS 1987). A few of these may have been *C. joubini*.

Valbyteuthis danae Joubin, 1931 was caught from 11º-32ºN. Although this was identified as *V. danae* Joubin, 1931, NESIS (1987) regarded the species to be of the Pacific and not of the North Atlantic.

Cthenopterygidae

Cthenopteryx siculus (Verany, 1851) was caught from 11º-40ºN. It has previously been recorded from the Bay of Biscay (CLARKE 1966).

Cranchiidae

Cranchia scabra Leach, 1817 was caught from 11ºN-32ºN.
Leachia cyclura Lesueur, 1821 was caught from 11º-40ºN.
Liocranchia reinhardti (Steenstrup, 1856) was caught at 11-40N but had been caught in the Bay of Biscay previously (CLARKE 1966).
Bathothauma lyromma Chun, 1906 was caught from 11º-40ºN.
Helicocranchia pfefferi Massy, 1907 was caught from 11ºN to the Bay of Biscay. It has been taken to 50ºN (CLARKE 1966)
Megalocranchia oceanica (Voss, 1960) was caught from 18º-38ºN. NESIS (1987) grouped all the North Atlantic specimens of *Megalocranchia* and *Carynoteuthis* in *M. oceanica* . The young include two forms (the same species), one with bright cerulean coloured photophores under its digestive organ and the other with brilliant green photophores (unpubl. observation).
Sandalops melancholicus Chun, 1906 caught at 18ºN and 30ºN. Redescribed as *Uranoteuthis bilucifer* by LU & CLARKE (1974) and synonymised by NESIS (1987).
Phasmatopsis cymoctypus de Rochbrune, 1884 was found at 32ºN and 38ºN. Flesh of this species was found in whales' stomachs at the Azores and beaks were found at Vigo, at 42ºN
Teuthowenia megalops (Prosch, 1849) caught from 11º-60ºN. The beaks attributable to this species from whales off Iceland fall into three groups, possibly three species. Previous records extend to 70ºN (as *Taonius megalops* in CLARKE 1966).
Teuthowenia maculata (Leach, 1817). VOSS (1985) considered this a southern species. A considerable number of beaks, thought to be this species, were collected from whales at the Azores but their identity must remain in doubt at present.
Galiteuthis armata Joubin, 1898 was collected between 11º-50ºN with a gap from Endeavour Bank to just North of the Canaries. Previous records (as *Taonidium pfefferi*) take it to 60ºN (CLARKE 1966).
Belonella belone (Chun, 1906) has been caught at 18ºN and 30ºN. It was not recognised as distinct from *Taonius pavo* in the early collections and specimens are not available to check.
Taonius pavo (Lesueur, 1821) was caught between 28ºN and the Bay of Biscay at 47ºN. Its characteristic beaks were found in whales at Madeira and Iceland. A few of those referred to this species may have been the previous species. This collection extends the range of the species in this region (CLARKE 1966).

Cycloteuthidae

Discoteuthis lacinosa Young & Roper, 1969 was caught at 32ºN and 38ºN. The genus has been recorded from 3ºN to 33ºN (YOUNG & ROPER 1969). Beaks of the species were found in whales at the Azores.
Discoteuthis discus Young & Roper, 1969 was caught at Madeira.
Cycloteuthis sirventi Joubin, 1919 was caught at 18-30ºN. Beaks of the species were collected from whales at Madeira and the Azores and just one at Iceland. The type came from 30º45'N. It has also been recorded from 37ºN to 8ºS (YOUNG & ROPER 1969).

Enoploteuthidae

Abralia redfieldi Voss, 1955 was caught at 11ºN and 32ºN. Previously this was mainly recorded from the Western Atlantic (YOUNG et al. 1998). Its relationship with specimens of *A. veranyi* recorded from the area is not clear (GUERRA 1992).
Abraliopsis atlantica Nesis 1982 specimens probably belonging to this species were caught at 11º-40ºN. Previously called *A. pfefferi* by LU & CLARKE (1975a & b; CLARKE & LU 1974, 1975) NESIS (1987) reviewed the genus and grouped the North Atlantic specimens in this species and *A. hoylei pfefferi* Joubin 1896. YOUNG et al. (1998) kept *A. pfefferi* and *A. atlantica.* Material is not

available to check the specific identity of these and the last species against Nesis's criteria.

Abraliopsis hoylei (Joubin 1896). Specimens possibly referable to this species were caught at 11º-18ºN.

Enoploteuthis leptura (Leach, 1817) was caught from 18º-32ºN. The type came from west Africa at 1ºN 7ºE.

Enoploteuthis anapsis Roper, 1964 was caught off Madeira. Previously collected at 32ºN 16ºW (YOUNG et al. 1998).

Gonatidae

Gonatus steenstrupi Kristensen, 1981 was caught from 46º-60ºN and beaks occurred in whales' stomachs in the Azores and west of Iceland. The northern boundary between this and *G. fabricii* has not been clearly established.

Grimalditeuthidae

Grimalditeuthis bonplandi (Verany, 1837) was caught from 11º-32ºN.

Histioteuthidae

Histioteuthis arcturi (Robson, 1948) was caught from 18º-46ºN and was numerous in whales' stomachs at Madeira and the Azores. VOSS et al. (1998) did not record this further North than 35ºN in the eastern North Atlantic.

Histioteuthis bonnellii (Ferussac, 1834) was caught at 11ºN, the Bay of Biscay and by commercial bottom trawl at 49-59ºN. Although only 7 were caught over the whole region, large numbers were eaten by whales from Madeira to Iceland. The absence between 20ºN and 37ºN noted by VOSS et al. (1998) is not supported here since 20 specimens were identified from sperm whales in Madeira at 32ºN.

Histioteuthis corona N. Voss & G.Voss, 1962 was caught from 18º-32ºN.

Histioteuthis celetaria G. Voss, 1960 was only caught at 32ºN but its beaks were found in whale stomachs at the Azores.

Histioteuthis meleagroteuthis (Chun, 1910) was caught from 18º-46ºN. Its beaks were collected from whales at the Azores. It was previously recorded from further south beyond the Equator to 44ºN (VOSS et al. 1998).

Histioteuthis reversa (Verrill, 1880) was caught at 11º-53ºN. It had previously been recorded from south of the Equator to 59ºN (VOSS et al. 1998).

Joubiniteuthidae

Joubiniteuthis portieri (Joubin, 1912) was caught between 18ºN and the 38ºN.

Lepidoteuthidae

Lepidoteuthis grimaldii Joubin, 1895 was caught from 11ºN to the Azores and beaks from adults came from whales from Madeira to Iceland.

Lycoteuthidae

Lampadioteuthis megaleia Berry, 1916 was caught 18º-32ºN. YOUNG (1964) recorded it near the Azores.

Selenoteuthis scintillans Voss, 1958 was caught at 28º-30ºN.

Mastigoteuthidae

Idioteuthis hjorti Chun, 1913 was caught from 18º-46ºN. Previously known from the western North Atlantic.

Mastigoteuthis flammea. The specific identity of some specimens of this species could not be checked. Specimens thought to be this species were caught from 28º-46ºN. NESIS (1987) doubted the species was in the North Atlantic.

Mastigoteuthis magna Joubin, 1913 was only caught at 32ºN. The type specimen came from near 32ºN 42W.

Mastigoteuthis schmidti Degner, 1925 was caught from 11º-60ºN

Mastigoteuthis talismani (Fischer & Joubin, 1906) was only caught at 11ºN. The type was caught at 34ºN, 36ºW. NESIS (1987) recorded it from near the Azores.

Mastigoteuthis glaukopis Chun, 1908 was only caught near Madeira. Joubin (1933) recorded it from the Bay of Biscay but the relationship of the north Atlantic specimens to the type from the Indian Ocean is uncertain.

Neoteuthidae

Neoteuthis thielei Naef, 1921 was caught from 11º-32ºN.

Octopoteuthidae

Taningia danae Joubin, 1931 was caught from 11ºN-53ºN. This was important in whale food from Madeira to Vigo but did not occur in whales examined in Iceland.
Octopoteuthis danae Joubin, 1931 was only caught at 11ºN. The type was collected at 33ºN, 68ºW so it is surprising we did not catch it further North in the eastern North Atlantic. NESIS (1987) considered it a sub-tropical species.
Octopoteuthis sicula (Ruppell, 1844) was caught from 28ºN to the Azores. Some other records from the Equator to 50ºN may have been due to misidentifications (CLARKE 1966).
Octopoteuthis rugosa Clarke, 1980. Beaks of this species were common in sperm whale stomachs at the Azores and a few were present in stomachs at Iceland. NESIS (1987) listed this from Mauritania in the North Atlantic.
Octopoteuthis 'giant'. Beaks of this very large species, were collected from whales at the Azores. One complete specimen was collected by commercial bottom trawl at 59º30'N, 17º00"W. (unpubl.).

Ommastrephidae

Hyaloteuthis pelagica (Bose, 1802) was only caught at 28ºN.
Ommastrephes bartramii (Lesueur, 1821) was caught from 28ºN-43ºN with nets. Flesh was found in a whales' stomach in the Azores but this was exceptional. The species is known from the Bay of Biscay and from strandings around Great Britain from Cornwall and to about 79ºN (as *O. caroli* and *O. pteropus,* see CLARKE 1966). It was caught from weather ships at 45º and 52ºN and photographed with baited cameras at 40ºN 20ºW (CLARKE 1966).
Sthenoteuthis pteropus (Steenstrup, 1855) was caught from 28º-32ºN. It has been recorded north to 35ºN (ZUYEV et al. 2002). Although this has been recorded from strandings around Britain all were probably misidentifications of *Ommastrephes bartrami*.
Todarodes sagittatus (Lamark, 1799) was caught from 28º to 49-59ºN. It was caught at all weather stations North to 62ºN and by commercial trawlers to along the Norwegian coast to 75ºN in the Arctic Ocean. All cephalopods caught by trawlers were *Todarodes sagittatus* and all but three were females close to or in spawning condition. The males were lacking skin and had probably mated.

Onychoteuthidae

Onychoteuthis banksii (Leach, 1817) was caught from 11º-47ºN. This has been recorded previously further North to 72ºN (CLARKE 1966).
Ancistroteuthis lichtensteini (Ferussac & d'Orbigny, 1839) was only caught at 28ºN. This is mainly a Mediterranean species but other 'strays' into the Atlantic are known (CLARKE 1966) and one from 20ºN 22ºW was identical to the typical Mediterranean form (KUBODERA et al. 1998).
Chaunoteuthis mollis Appellof, 1890 was only caught at 32º-33ºN. These may be spent females of *Onychoteuthis* (CLARKE 1992a) or some may be even *Moroteuthis* species.
Onykia carriboea (Lesueur, 1821) was caught from 11º N to Madeira at 32ºN. A previously recorded specimen outside this range, in the Bay of Biscay was very probably a misidentification (CLARKE 1966).
Moroteuthis robsoni Adam, 1962 was caught at 32ºN. Beaks of this species were found in whales' stomachs from Madeira to Iceland. These specimens were the first from the eastern North Atlantic although they have been recorded in the Gulf of Mexico (KUBODERA et al. 1998).

Pholidoteuthidae

Tetronychoteuthis dussumieri (d'Orbigny, 1839) was caught from 28º-32ºN. This may be a species of *Pholidoteuthis* (CLARKE 1992b).
Pholidoteuthis boschmai Adam, 1950 paralarvae were caught from 11ºN to Madeira at 32ºN. Flesh of adults was collected from whales at the Azores at 38ºN and just one beak from Iceland.

Pyroteuthidae

Pterygioteuthis spp. were caught from 11º-40ºN.
Pterygioteuthis giardi Pfeffer, 1912 and *Pterygioteuthis gemmata* Chun 1908 were both identified at 32ºN but not all the specimens could be checked for the present work.
Pyroteuthis margaritifera (Ruppell, 1894) was caught from 18ºN to the Azores. This extends the

southern limit of the species in the North Atlantic (CLARKE 1966).

Thysanoteuthidae

Thysanoteuthis rhombus Troschel, 1857 was caught from 28º-32ºN. Adults are recorded from Madeira.

Vampyroteuthidae

Vampyroteuthis infernalis Chun, 1903 was caught from 11º-40ºN.

Alloposidae

Haliphron atlanticus Steenstrup, 1861 was caught at 11º-53ºN. Beaks of adults occurred in whale stomachs from 32ºN to Iceland. Examples are often found floating dead at the sea surface close to the Azores islands, some possibly after being vomited by predators including sperm whales (personal observations and GONÇALVES 1991).

Argonautidae

Argonauta argo Linneus, 1758 was caught at 11º-32º N. This was confirmed in the Azores by GONÇALVES (1991).
Argonauta hians Solander, 1786 was caught from 28-32ºN.

Bolitaenidae

Eledonella pygmaea Verrill, 1884 was caught between 32ºN and the Azores at 38ºN.
Japetella diaphana Hoyle, 1885 was caught from 11º-40ºN.
Bolitaena microcotyla Steenstrup, 1856 was only caught at 32ºN.

Ocythoidae

Ocythoe tuberculata Rafinesque, 1814 was only caught at 32ºN. It was confirmed by GONÇALVES (1991) at the Azores.

Tremoctopidae

Tremoctopus violaceus violaceus delle Chiaje, 1830 was caught from 11º-32ºN but it has also been confirmed at the Azores (GONÇALVES 1991).

Vitreledonellidae

Vitreledonella richardi Joubin, 1918 was caught from 11º-40ºN.

Oceanic midwater species previously reported from the region but not caught in the present sampling.

Ornithoteuthis antillarum Adam, 1957 has been reported south of 20ºN. (see DUNNING 1998).

Illex illecebrosus has been recorded off Iceland and south to 60ºN but ROPER et al. (1998) considers these to be either misidentifications or are only occasional visitors to the East Atlantic.

Illex coindetii seems to be limited to the shelf and was not caught in this sampling.

Shelf and slope species.

These species were not adequately sampled with the gear used to show distribution, and are therefore not included in Table 2.

Sepia officinalis Linnaeus, 1758 was only caught at Madeira but is known to extend from Scotland and southern Norway to the Cape Verde islands at about 10ºN on the continental and island shelves (KHROMOV et al. 1998).

Rossia sp. was caught on Endeavour Bank and at 32º N on the African slope.

Sepiola sp. was caught on Endeavour Bank and on the shelf to the west of Great Britain.

Sepietta oweniana (d'Orbigny, 1839) recorded at Madeira. Also known from Norway to the West African shelf (NESIS 1987).

Loligo forbesi (Steenstrup, 1856) was collected at Madeira but is known from central Norway to about 20ºN on the continental shelf, at the Azores archipelago and the Canary Islands. Rare to the South of the Bay of Biscay (NESIS 1987).

Loligo vulgaris (Lamarck, 1798) is known from the Faroe Islands to Senegal, West Africa (NESIS 1987). It occurs in Madeiran waters (CLARKE & LU 1995) where there is a small fishery of the species but it is not recorded from the Azores.

Todaropsis eblanae (Ball, 1841) was caught on Galicia Bank at 43ºN and on the Continental slope, west of Great Britain. This is a slope and shelf species and has not been sampled effectively in the present work. It is known to extend from the North of Scotland to South of the Equator (CLARKE 1966).

Bathypolypus sp., *Benthoctopus* sp. and *Eledone cirrhosa* were only caught on the continental slope to the west of Great Britain at 49º-59ºN. Wider bottom sampling would have shown the first two extended from the Arctic to the Mediterranean and the Equator respectively and *Eledone* from Iceland to Morocco (NESIS 1987).

Octopus vulgaris Lamarck, 1798, was collected at Madeira. This species extends from the English Channel south to beyond the Equator (MANGOLD 1998). It was confirmed at the Azores by GONÇALVES (1991) who also recorded *O. salutii* Verany, 1837 at the Azores for the first time.

Octopus macropus Risso, 1826 was collected at Madeira. It is found mainly near islands and was reconfirmed at the Azores by GONÇALVES (1991)

Octopus defilippi Verany, 1851 was collected at Madeira but was only found as a macrotritopus larva. It extends south to beyond the Equator and Madeira is probably it's most northerly record (MANGOLD 1998).

Scaergus unicirrhus (delle Chiaje, 1830) was caught from 11º-32ºN GONÇALVES (1991) recorded the species from the Azores. It is known to extend from the Bay of Biscay South to beyond the Equator (NESIS 1987).

Pteroctopus tetracirrhus (della Chiaje, 1890) was captured at Madeira by DSRV JOHNSON SEALINK I (GONÇALVES & MARTINS 1992) and further specimens were later found (CLARK & LU 1995) This is a slope species extending to south of the Equator. It was recorded by JOUBIN (1900) at the Azores from one individual.

Opisthoteuthis agassizi Verrill, 1883 was collected at 32ºN near Madeira and on the African continental slope. This is broadly spread on slopes in the region (NESIS 1987).

Grimpoteuthis plena (Verrill, 1895). One specimen was collected at 47º53'N, 9º3'W on a longline at 1750m. The closely related species *G.umbellata* (Fisher, 1883) was recorded at the Azores (GONÇALVES 1991)

Biodiversity by latitude

The numbers of species collected by nets for the various latitudinal positions (Fig. 1) are extracted from table 2 and are shown in Fig. 2 by assuming the interpolated and extrapolated positions for the species are correct. Fig 2 also includes species only collected by handnets and handlines at the sea surface and species from commercial trawlers; these were almost all ommastrephids of the species *Ommastrephes bartrami*, *Sthenoteuthis pteropus* and *Todarodes sagittatus*.

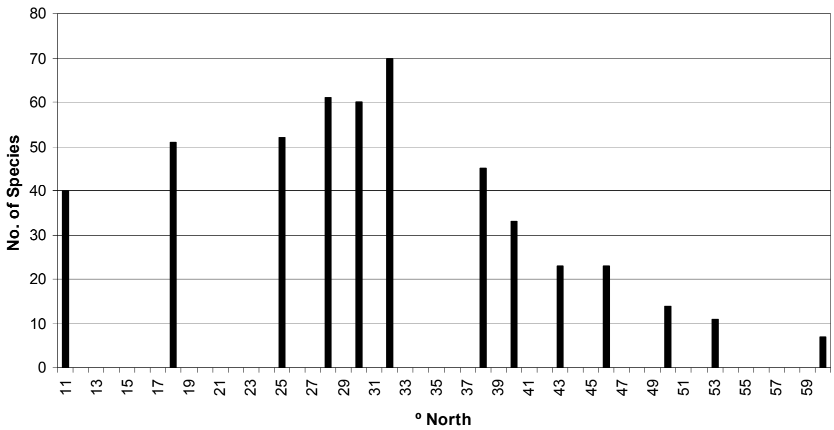

Fig. 2. Number of species at each position derived from Table 2. Including interpolated and extrapolated positions.

Figure 2 shows that the number of species appears to increase from 11º N to 32ºN and then to decrease to 60ºN. The sampling at positions 11º, 18º, 30º, 40º, 53º and 60º North were all done with the same methods and similar effort. The extra sampling included here (Tables 1 and Fig. 2) support the acceptance of the curve produced by these "standard" methods even though they were with different efforts and methods.

The peak at 32º seems to lie off the curve made by the other positions but this is largely the result of the introduction of lights on the headlines of RMT50 nets which noticeably increased the number of species caught (CLARKE & PASCOE 1997). This series caught 14 species not sampled by the other nets at the same latitude. It is, therefore, probable that introduction of lights on nets at other latitudes would cause a similar elevation of the number of species caught but the increase is likely to be commensurate with the number caught without lights so that the shape of the curve would remain much the same.

Relative numbers

Because of the large number of hauls and the diversity of sampling methods, the number of individuals of each midwater species caught by the nets in this work (Table1) might be expected to give some picture of their relative numerical importance in the eastern North Atlantic. The five species most numerous in net capture are *Liocranchia reinhardti* (879)*, Abraliopsis pfefferi* (832), *Pterygioteuthis* spp. (812), *Japetella diaphana* (443) and *Onychoteuthis banksi* (398). Table 3 shows the relative numbers of individuals in each family. The families containing the above five species also rank at the top with the Cranchiidae having 2401 individuals, Pyroteuthidae 1008, Enoploteuthidae 960, Onychoteuthidae 483 and Bolitaenidae 465.

However, this picture would probably differ if a different mixture of net sizes and designs were used; larger nets and faster trawling speeds sampling more of the large species and smaller nets (with smaller meshes) and slower trawling speeds sampling more of the smaller species.

Cephalopods from Sperm whale stomachs

The sperm whales, considered here, sampled the same biosphere as we did with nets and lines but the analysis of beaks gives a completely different picture of what was present. The five most numerous species in the diet (Tables 1 & 3) are *Histioteuthis bonnellii* (20243) of which the nets only caught 6, *H.arcturi* (2040) of which the nets only caught 268, *Teuthowenia megalops* (1370) of which the nets caught 300, *Discoteuthis laciniosa* (1291) of which the nets caught only 6 and *Taningia danae* (1219) of which the nets only caught 15. *Architeuthis dux* was not caught at all by nets but was represented by 221 beaks.

Table 3
The number of specimens of each family caught in nets and identified from beaks in whales' stomachs.

	In nets	**In sperm whales**
Cranchiidae	2,401	3,285
Pyroteuthidae	1,008	0
Enoploteuthidae	960	0
Onychoteuthidae	483	120
Bolitaenidae	465	0
Mastigoteuthidae	416	85
Histioteuthidae	349	22,787
Gonatidae	313	441
Spirulidae	175	0
Chtenopterygidae	142	0
Brachioteuthidae	141	3
Ommastrephidae	134	368
Chiroteuthidae	115	169
Sepiolidae	103	0
Bathyteuthidae	97	0
Tremoctopodidae	95	0
Vampyroteuthidae	79	5
Vitreledonellidae	67	0
Argonautida	62	0
Neoteuthidae	36	0
Pholidoteuthidae	27	331
Octopoteuthidae	25	1,710
Joubiniteuthidae	22	0
Ancistrocheiridae	19	196
Cycloteuthidae	17	1,360
Grimalditeuthidae	11	0
Lycoteuthidae	6	0
Lepidoteuthidae	5	556
Thysanoteuthidae	4	0
Alloposidae	3	336
Ocythoidae	3	0
Architeuthidae	0	221

Most beaks representing all the species eaten by whales are of a size and advanced pigmentation to indicate they are from reproducing or nearly adult cephalopods.

Species too large to be regularly caught in nets as adults are *Architeuthis dux, Cycloteuthis sirventi, Octopoteuthis rugosa* and *Haliphron atlanticus, Megalocranchia* sp., *Phasmatopsis cymoctypus, Teuthoweni megalops* and *T. maculata, Gonatus steenstrupii, Histioteuthis bonnellii, Histioteuthis arcturi, H.celetaria, H.meleagroteuthis, H.reversa, Taningia danae, Octopoteuthis* 'Giant', *Todarodes sagittatus* and *Moroteuthis robsoni*.

The biomass necessary to feed the whales in the region is not inconsiderable and cephalopods are required in such numbers by the whales that we might ask why they do not occur more frequently as juveniles and paralarvae in the nets. If the young of these species live with the adults in deep canyons or close to rough bottoms inaccessible to large and small trawls, that may be the explanation of our poor sampling of the species found in sperm whales.

When the whales have recently eaten a cephalopod before being killed or stranded, there is often flesh attached to the beaks. This may be anything from a complete animal to a buccal mass around the beak and shows that feeding had taken place recently, close to the site of capture. In Table 1 and 2 species with flesh are underlined. At Madeira 6 out of 10 species were represented by flesh and, of the remainder, only one was outside the range of the species as indicated by nets. At the Azores 10 out of 31 species were represented by flesh and only six were outside the range. The ranges shown by the net catches of *Phasmotopsis cymoctypus* and *Pholidoteuthis boschmai* were extended by the sperm whale samples. *Architeuthis dux, Teuthowenia maculata* and *Octopoteuthis rugosa* were not collected by nets.

DISCUSSION

Because of the overall amount of sampling and the latitudinal extent, this collection provides a good coverage of the midwater, oceanic cephalopods of the eastern North Atlantic.

Treatment of the data to show overall latitudinal spread might hide details where a species may be, for instance, in a northern and southern but not in a central water mass. However, if such an influence is present, one would expect it to be evident in several species and this is not obvious from the present collection. Detailed sampling to show such detail, if it exists, would be very costly and of a geographical and time scale unlikely to attract funds.

One of the main reasons for studying distribution is the hope that future changes might be recognized. To show changes in midwater cephalopods we require a baseline of distribution and relative numbers of the species.

Sampling with many nets has given us broad distributions. By using flesh from predators' stomachs we can extend these and if there is no flesh, numerous beaks in the stomachs can also be used to indicate the likely presence of species in the locality (e.g. with *Histioteuthis bonnellii* and *Teuthowenia megalops* off Iceland).

To obtain relative numbers which reflect compositions of cephalopod populations in the sea is not possible with nets whatever the effort, because of net selection. Neither can this be done by predators which select in a different way.

Comparison of future collections with the present data will be difficult because of the expense of repeating general collection, the difficulty in selecting a standard method of collection (to go for small or large, more numerous or rare species) rules out monitoring over any sizeable area with nets. Sampling with a standard method in one particular place, might show changes in the relative numbers of the commonest species but would require a faith, planning, dedication and financial backing which would almost certainly (to judge from previous experience) not be maintained over the many years necessary.

A more viable alternative would be to accept the limitations in selection and look for changes in the diets of predators. Any one predator species in an area and season is probably more standard in its selection of food than are nets which reflect small deviations in methodology. If the predator is commercially fished it can be easily and cheaply sampled and, as long as the fishery continues, monitoring can continue. The sampling of a number of teuthophagous predators in one place would broaden the size and depth range covered.

Selection of the best area for such comparative studies of oceanic change must be oceanic islands, such as those on the Mid Atlantic Ridge. Madeira at 32ºN has the most species. Previous work on cephalopods in the diets of predators gives a better baseline for study in the Azores. By careful selection of predators sampling can be made over a big depth range from the sea surface (birds) to midwater (tuna, sharks and swordfish) and the sea bottom (orange roughy). Although sperm whales and other cetaceans are not caught commercially, as in the past, they do strand and, their special top place in the foodchain, makes the study of their diet particularly important for showing changes over time.

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