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Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species

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Published information on the diet of Cuvier's beaked whales *Ziphius cavirostris* (Odontoceti: Ziphiidae) is reviewed and new information on the stomach contents of three animals: two stranded in Galicia (north-west Spain) in February 1990 at A Lanzada, and in February 1995 at Portonovo; and the third stranded in February 1999 in North Uist (Scotland), is presented. The whale stranded in 1990 was a male; the other two were adult females. All animals were >5 m long.

The limited published information on the diet of this species indicates that it feeds primarily on oceanic cephalopods although some authors also found remains of oceanic fish and crustaceans.

Food remains from the three new samples consisted entirely of cephalopod beaks. The Scottish sample set is the largest recorded to date for this species. The prey identified consisted of oceanic cephalopods, mainly squid (Cephalopoda: Teuthoidea). The most frequently occurring species were the squid *Teuthowenia megalops*, *Mastigoteuthis schmidti* and *Taonius pavo* (for the Galician whale stranded in 1990), *Teuthowenia megalops* and *Histioteuthis reversa* (for the second Galician whale) and *T. megalops*, *Gonatus* sp. and *Taonius pavo* (for the Scottish whale). Other prey included the squid *Histioteuthis bonnellii*, *Histioteuthis arcturi* and *Todarodes sagittatus* as well as *Vampiroteuthis infernalis* (Cephalopoda: Vampyromorpha), *Stauroteuthis syrtensis* and *Japetella diaphana* (Cephalopoda: Octopoda). The squid eaten (estimated from the measurement of the lower beaks) included juvenile and mature individuals of the most important species (*Teuthowenia megalops*, *Gonatus* sp.).

The range of species found in the diet of *Z. cavirostris* is greater than that reported for sperm whales and bottlenosed whales in the north-east Atlantic.

INTRODUCTION

Little information exists on the ecology, behaviour, population structure and numbers of beaked whales (Ziphiidae) in the north-east Atlantic or elsewhere in the world. *Ziphius cavirostris* (Cuvier, 1823), one of the best known species, was discovered only in 1804, when a partial cranium was collected from a beach in France.

Ziphius cavirostris has a cosmopolitan distribution in all oceans except the Arctic and Antarctic waters (Moore, 1963; Mitchell, 1975). In the North Atlantic it has been reported as far north as the North Sea in the east and Cape Cod in the west (Mitchell, 1975). Although sightings of this species are more common than those of most other beaked whales, they are still relatively rare and most of the information available on the distribution, biology and ecology of the species comes from strandings (Heyning, 1989; Waerebeek et al., 1997) and, in the past, from catches in the Japanese 'smaller whale' fishery (Omura et al., 1955; Nishiwaki & Oguro, 1972).

Maximum lengths for this species have been recorded as 23 feet (7 m) for both males and females, with an average adult size of $\sim$6 m (Omura et al., 1955; Nishiwaki & Oguro, 1972; Heyning, 1989). Very few data exist on reproductive parameters. Mead (1984) estimated an average size at birth of 2.7 m by measuring the largest foetus and the smallest calf found.

Most sightings of this species consist of single animals or pairs and in few cases larger groups have been recorded (e.g. Marini et al., 1996). Generally, reported strandings are of single animals although a few mass strandings have also taken place (e.g. 13 whales stranded on the Greek Ionian coast in May 1996, (Lefkaditou & Poulopoulos, 1998)).

Like all beaked whales, *Z. cavirostris* is thought to feed primarily on oceanic cephalopods (e.g. Clarke, 1986a), although data from the Japanese fishery reported that fish were the most abundant prey in animals taken in waters deeper than 1000 m (Nishiwaki & Oguro, 1972). Crustacean remains have also been reported in the diet of this species (Debrot & Barros, 1994). The duration of dives has been reported to be at least 30–40 min (Miyazaki & Wada, 1978).

Strandings of this species in the north-east Atlantic are relatively numerous (e.g. in the UK and Ireland: Harmer, 1927; Stephen, 1932; Fraser, 1934, 1946, 1953, 1974; Cabot, 1966; Sheldrick, 1989; Sheldrick et al., 1994; Berrow & Rogan, 1997; in Spain: e.g. Casinos & Vericad,

1976; Grau et al., 1980, 1986; García-Castrillo & Cendrero, 1987; García-Castrillo et al., 1991; González et al., 1994; Kitchener & Herman, 1995), but there is very little information on its feeding ecology for this area. In the rest of the world, despite the abundance of material potentially available from strandings and fisheries, only a limited number of stomach contents have been analysed.

The aim of this paper is to give an overview of the present knowledge of the feeding ecology of this species and to provide new dietary information for the north-east Atlantic by presenting results from the analysis of the stomach contents of three specimens: one stranded in Scotland and two in Galicia (north-west Spain). This represents the largest collection of cephalopod beaks from stomachs of Cuvier's beaked whales examined so far.

HISTORICAL DATA

European waters

Desportes (1985) identified prey remains from stomach contents of eight specimens stranded on the Atlantic and Mediterranean coasts of France. The five non-empty stomachs contained cephalopods of the families Histioteuthidae, Enoploteuthidae, Gonatidae, Octopoteuthidae, Brachioteuthidae and Chiroteuthidae. No food remains were recorded in the stomach of an animal stranded in Galicia (north-west Spain) in 1991 (González et al., 1994).

Hernández García (1995) analysed the stomach contents of two whales stranded in the Canary Islands. Remains of cephalopods (including *Histioteuthis* sp.) were recovered from the stomach of the first whale, while remains of fish (four specimens) and cephalopods (including *Histioteuthis* sp. and *Pholidoteuthis adami* Voss, 1956) were found in the stomach of the second whale.

In the Mediterranean, Podestà & Meotti (1991) analysed 73 upper and 78 lower beaks collected from the stomach of a female stranded on the west coast of Italy. The cephalopods identified were *Histioteuthis bonnellii* (Férussac, 1835), *Histioteuthis* sp., *Ancistroteuthis lichtensteinii* (Férussac, 1835), *Eledone* sp. and Cranchiidae. Carlini et al. (1992) analysed 233 lower beaks from the stomach of another female stranded on the west coast of Italy and identified eight cephalopod species: *Histioteuthis bonnellii*, *H. reversa* (Verrill, 1880), *Todarodes sagittatus* (Lamarck, 1798), *Ommastrephes bartramii* (LeSueur, 1821), *Ancistroteuthis lichtensteinii*, *Octopoteuthis sicula* (Rüppell, 1844), *Chiroteuthis veranyi* (Férussac, 1835) and *Heteroteuthis dispar* (Rüppell, 1844). Stomach contents from seven whales out of 17 animals stranded on the Greek Ionian coast were analysed by Lefkaditou & Poulopoulos (1998). The authors identified two species, *Octopoteuthis sicula* and *Histioteuthis bonnellii*, from remains of 33 lower and 33 upper beaks. Blanco & Raga (2000) identified ten cephalopod species in the diet of a male and a female stranded on the Spanish Mediterranean coast. The species identified from 526 lower beaks were: *Todarodes sagittatus*, *Octopoteuthis sicula*, *Histioteuthis bonnellii*, *H. reversa*, *Chiroteuthis veranyi*, *Galiteuthis armata* (Joubin, 1898), *Chtenopteryx sicula* (Vérany, 1851), *Ancistrocheirus lesueurii* (Orbigny, 1842), *Heteroteuthis dispar* and *Ancistroteuthis lichtensteinii*.

Other northern hemisphere records

Kenyon (1961) found remains of 1304 squid and two shrimps in a female *Ziphius cavirostris* shot in Alaska. Some of the squid were identified as *Gonatus* sp. by the author. Fiscus (1997) later identified a subset of 1042 beaks from the original set of cephalopod remains collected by Kenyon. He found that the families Gonatidae and Cranchiidae were the most abundant in the sample, although beaks of *Histioteuthis dofleini* (Pfeffer, 1912), *Chiroteuthis* sp., *Vampyroteuthis infernalis* (Chun, 1903) and the octopod *Japetella* sp. were also present. Foster & Hare (1990) analysed food remains found in the stomach of an immature female stranded in the same area and recorded crustacean remains and 458 lower and 547 cephalopod upper beaks. Three cephalopod families were identified from this sample: Gonatidae (*Gonatus* sp.), Cranchiidae (*Taonius* sp.) and Chiroteuthidae (*Chiroteuthis* sp.).

In the Netherlands Antilles (West Indies), Debrot & Barros (1994) reported crustacean and squid remains in the stomach of a whale stranded in 1991. The cephalopods were not identified, the crustacean remains were found to belong to *Gnathophausia* cf. *ingens* (Dohrn, 1870).

In northern California, Mitchell & Houck (1967) found 'more than one litre of squid beaks' in the stomach of a female stranded in the area, but did not identify the food remains. In southern Texas, part of the stomach contents of a female was analysed by Fertl et al. (1997), who identified the species *Loligo pealei* (LeSueur, 1821) from a sample of three upper and one lower beak.

The presence of a fishery for *Z. cavirostris* in the waters off Japan has provided more information on this species than is generally available elsewhere. Nevertheless, the first available record simply tells us that an immature female was caught on a tuna long line baited with saury pike *Scomberesox saurus saurus* (Walbaum, 1792) (Omura et al., 1955). Nishiwaki & Oguro (1972) reported that the diet consisted mainly of deep-sea fish or squid. Deep-sea fish predominated in animals taken from waters deeper than 1000 m, whereas squid were the most abundant prey found in animals taken in shallower waters. They suggested that this could be interpreted as evidence that *Z. cavirostris* was somewhat opportunistic in its feeding habits.

Southern hemisphere

The stomach of a male stranded in New Zealand contained 74 upper and 77 lower beaks, identified as cephalopods of the families Onychoteuthidae, Brachioteuthidae, Pholidoteuthidae, Histioteuthidae and Cranchiidae (Fordyce et al., 1979).

Ross (1984) provided information on the stomach contents recovered from two males stranded in South Africa. One stomach contained nine lower beaks, the second contained a total of 84 upper and 101 lower beaks, together with otoliths of *Antimora* sp. (a deep-sea fish of the family Moridae) and crustacean remains. The cephalopods identified belonged to eight families: Cranchiidae (*Taonius*, *Pyrgopsis*, *Galiteuthis*, *Mesonychoteuthis*, *Phasmatopsis*), Histioteuthidae, Octopoteuthidae, Chiroteuthidae, Onychoteuthidae (*Moroteuthis*), Lycoteuthidae (*Lycoteuhtis*), Gonatidae (*Gonatus*) and Ommastrephidae.

From the above review it is clear that the available information on the feeding habits of *Z. cavirostris* is

sketchy, based largely on the total or partial analysis of single stomach contents. Results from these studies indicate that *Z. cavirostris* feeds mainly on oceanic, mesopelagic or deep-water benthic fish and cephalopods. This feeding niche is consistent with *Z. cavirostris* being an offshore, deep-diving species (Heyning, 1989), which also explains the scarcity of sightings of this species near the coast, except in areas with a narrow continental shelf (Reeves, 1990).

MATERIALS AND METHODS

Sample collection

Two *Ziphius cavirostris* stranded on 2 February 1990 at A Lanzada (Galicia, Spain) and on 16 February 1995 at Portonovo (also Galicia, Spain) were identified and sampled by one of the authors (A.L.) and collaborators from 'Coordinadora para o Estudio dos Mamíferos Mariños' (CEMMA), a voluntary organization which runs the strandings network in Galicia. The first was a male, the second a female, both 510 cm long. The third sampled whale stranded on 27 February 1999 in North Uist (Outer Hebrides, Scotland). This was a female of 586 cm total length. Samples were collected by one of the authors (J.H.) and other staff at the National Museums of Scotland, Edinburgh. The stranding locations are indicated in Figure 1.

Diet analysis

Cephalopod beaks were identified using published guides (Clarke, 1980, 1986b) and a reference collection of

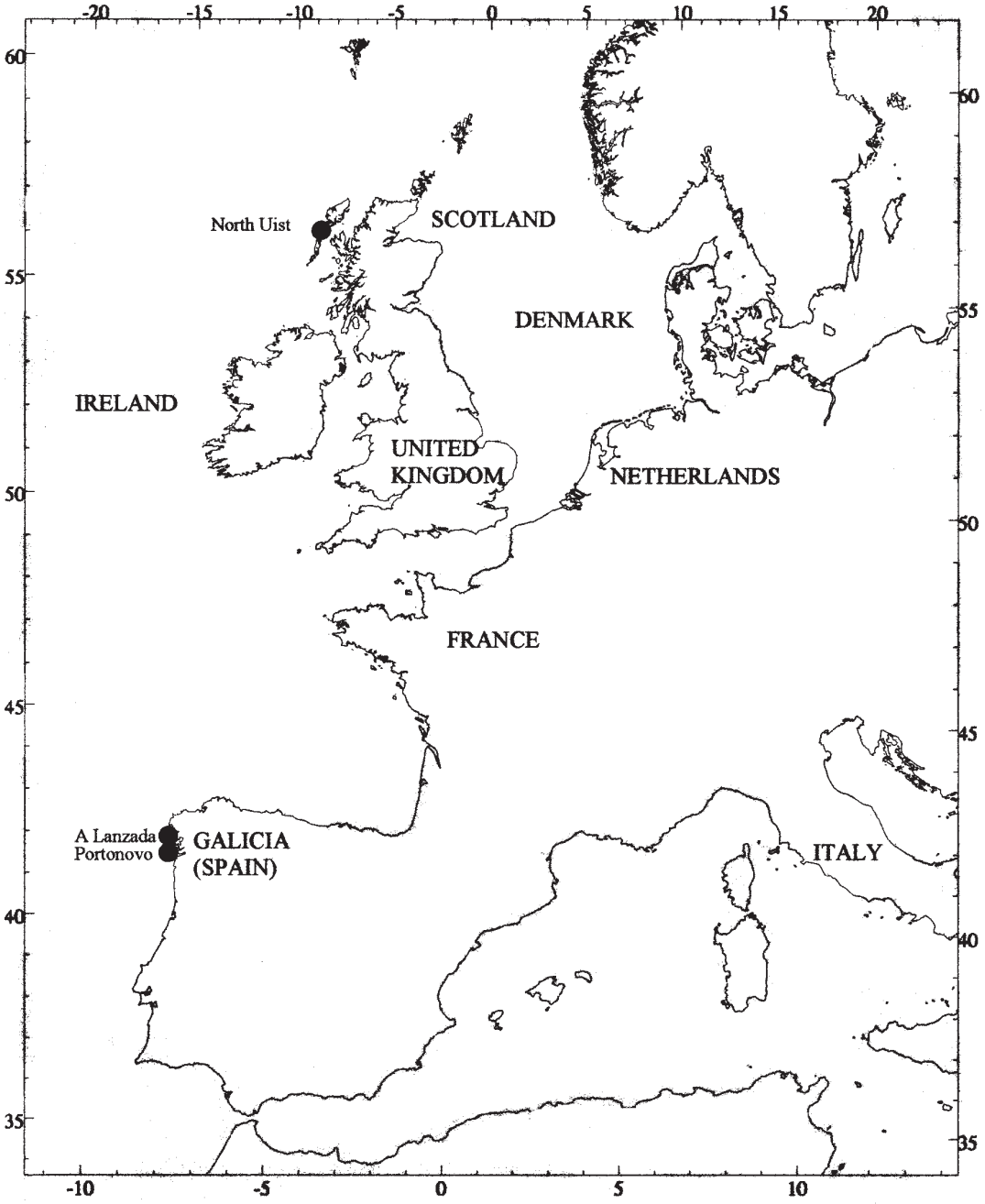

Figure 1. North-east Atlantic and North Sea showing the locations of *Ziphius cavirostris* strandings in the present study.

Table 1. *Prey species found in stomachs of beaked whales stranded at A Lanzada and at Portonovo (Galicia, north-west Spain) and at North Uist (Scotland).*

Prey		A Lanzada				Portonovo				North Uist			
Family	Species	LB	N	% N	% wt	LB	N	% N	% wt	LB	N	% N	% wt
Sepiolidae	*Heteroteuthis dispar*	–	–	–	–	–	–	–	–	2	2	0.02	–
Chtenopterygidae	*Chtenopteryx sicula*	–	–	–	–	–	–	–	–	14	14	0.17	0.05
Octopoteuthidae	*Octopoteuthis sicula*	11	11	1.59	2.85	4	4	0.59	1.80	55	55	0.65	1.74
Onychoteuthidae	*Moroteuthis* sp.	–	–	–	–	–	–	–	–	17	17	0.20	1.75
Cycloteuthidae	*Cycloteuthis sirventi*	1	1	0.14	0.70	–	–	–	–	3	3	0.04	0.35
	Discoteuthis sp.	3	3	0.43	–	–	–	–	–	–	–	–	–
Gonatidae	*Gonatus* sp.	32	32	4.61	8.96	24	24	3.56	5.80	942	942	11.18	26.28
Histioteuthidae	*Histioteuthis reversa*	21	21	3.03	1.22	186	186	27.63	15.80	365	365	4.33	2.22
	H. corona	–	–	–	–	–	–	–	–	127	127	1.51	5.30
	H. arcturi	3	3	0.43	0.49	6	6	0.89	1.69	–	–	–	–
	H. bonnellii	3	3	0.43	2.08	–	–	–	–	37	37	0.44	2.94
	H. meleagroteuthis	1	1	0.14	0.12	2	2	0.30	0.41	31	31	0.37	0.84
	Histioteuthis type A	–	–	–	–	1	1	0.15	0.38	244	244	2.90	1.42
Bathyteuthidae	*Bathyteuthis abyssicola*	–	–	–	–	–	–	–	–	1	1	0.01	–
Brachioteuthidae	*Brachioteuthis riisei*	–	–	–	–	2	2	0.30	0.03	25	25	0.30	0.02
Ommastrephidae	*Todarodes sagittatus*	7	7	1.01	13.89	7	7	1.04	12.27	24	24	0.28	5.69
Chiroteuthidae	*Chiroteuthis veranyi*	23	23	3.31	1.29	17	17	2.53	1.11	199	199	2.36	1.91
	Chiroteuthis sp. (type 2)	6	6	0.86	0.80	9	9	1.34	1.67	21	21	0.25	0.29
Pholidoteuthidae	*Pholidoteuthis boschmai*	9	9	1.30	19.51	1	1	0.15	2.73	17	17	0.20	4.28
Mastigoteuthidae	*Mastigoteuthis schmidti*	132	132	19.02	11.20	35	35	5.20	4.12	804	804	9.54	8.13
	Mastigoteuthis sp. (type 2)	–	–	–	–	2	2	0.30	0.84	–	–	–	–
Cranchiidae	*Liocranchia reinhardtii*	–	–	–	–	–	–	–	–	3	3	0.04	–
	Taonius pavo	119	119	17.15	9.67	33	33	4.90	3.67	908	908	10.78	9.42
	Megalocranchia sp.	–	–	–	–	–	–	–	–	21	21	0.25	0.80
	Galiteuthis armata	–	–	–	–	–	–	–	–	804	804	9.54	7.23
	Teuthowenia megalops	246	246	35.45	24.79	329	329	48.89	47.32	1873	1873	22.23	13.90
	Teuthowenia sp. (type 2)	16	16	2.31	2.43	–	–	–	–	225	225	2.67	5.44
Vampyroteuthidae	*Vampiroteuthis infernalis*	–	–	–	–	2	2	0.30	0.36	–	–	–	–
Cirroteuthidae	Unidentified	–	–	–	–	–	–	–	–	1	1	0.01	–
Stauroteuthidae	*Stauroteuthis syrtensis*	1	1	0.14	–	1	1	0.15	–	–	–	–	–
Bolitaenidae	*Japetella diaphana*	–	–	–	–	–	–	–	–	2	2	0.02	–
Unidentified	Unidentified octopod	–	–	–	–	–	–	–	–	3	3	0.04	–
	Unidentified cephalopod	–	–	–	–	4	4	0.59	–	11	11	0.13	–
Broken beaks		25	25	3.61	–	8	8	1.19	–	79	79	0.94	–
Upper beaks		693	35	5.04	–	525	–	–	–	8423	1568	18.60	–
TOTAL			694	100	100		673	100	100		8426	100	100

Number of lower beaks (LB), number of individual squid (N) and percentages (%N=percentage by number and %wt=percentage by weight) in the sample for each prey species. Some *Histioteuthis* beaks could not be identified to species but belonged to the 'type A' group (Clarke, 1986b) which includes *H. arcturi*, *H. corona*, *H. meleagroteuthis* and *H. bonnellii*.

identified oceanic cephalopod beaks. Standard measurements were taken on the lower beaks: rostral length (LRL) for decapods and hood length (LHL) for octopods (Clarke, 1980, 1986b), using either callipers or a binocular microscope fitted with an eyepiece graticule. All undamaged lower beaks were measured except for species represented by more than 300 beaks, for which random sub-samples of 200–250 beaks were measured. Mantle length (ML) and body weight of cephalopods were estimated from lower beak measurements, using regression equations from Clarke (1986b).

The total number of specimens of each cephalopod species present in a stomach was estimated as the number of lower or upper beaks (whichever was higher). The total weight of each species in each stomach was estimated as: sum of weights represented by beaks measured/proportion of specimens for which beaks were measured.

Overall diet composition was calculated by summing the weights of all prey from each sample and expressing the weight of each species as a proportion of that total.

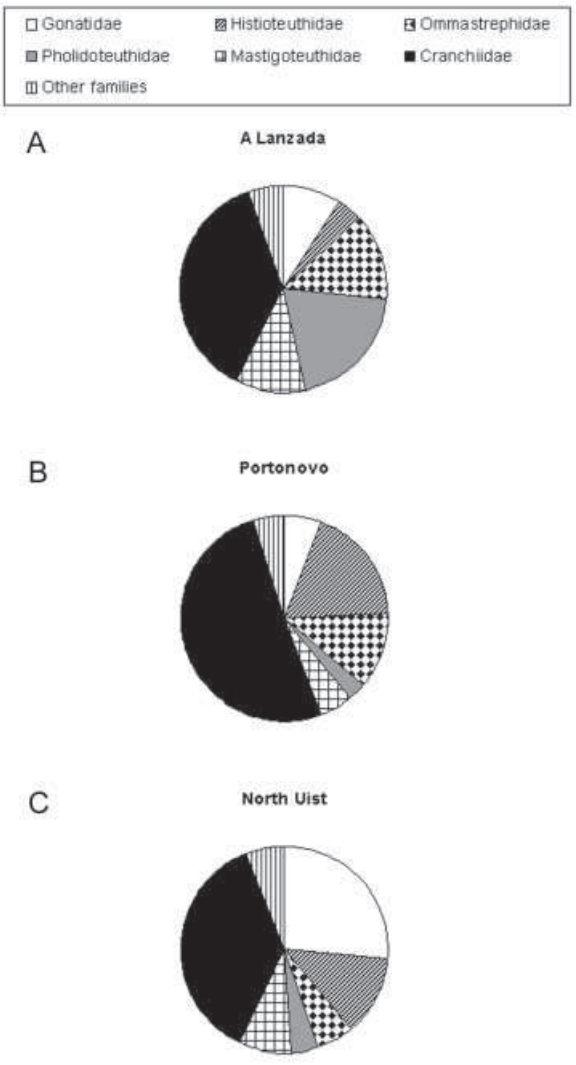

Figure 2. Percentage by weight of the main squid families identified in the diet of: A, (A) Lanzada; (B) Portonovo; and (C) North Uist *Ziphius cavirostris*.

RESULTS

For the three specimens of *Z. cavirostris*, food remains consisted entirely of cephalopod beaks. Numbers of beaks found were: 693 upper and 659 lower beaks from the whale stranded at A Lanzada; 525 upper and 673 lower beaks from the whale stranded at Portonovo; and 8423 upper and 6858 lower beaks from the animal stranded in North Uist. No cephalopod flesh or fish remains were found.

Both whales stranded in Galicia had plastic remains in their stomachs, while the stomach of the whale stranded in Scotland also contained remains of at least six plastic bags or refuse sacks, one of which was tightly screwed up and apparently jammed in the entrance to the stomach.

Fifteen cephalopod species were identified from the whale stranded in A Lanzada, 14 species from the animal stranded in Portonovo and 23 species were identified from the whale stranded in North Uist (Table 1).

The most common prey species for the A Lanzada whale, both by number and by percentage weight, was *Teuthowenia megalops* (Prosch, 1847); *Mastigoteuthis schmidti* (Degner, 1925) and *Taonius pavo* (LeSueur, 1821) were also common. The estimated MLs of *Teuthowenia megalops* ranged from 145 to 335 mm, with a mode of 205 mm (Figure 3A).

For the Portonovo whale, the most common prey species, both by number and by percentage weight, were *Teuthowenia megalops* and *Histioteuthis reversa*. The estimated

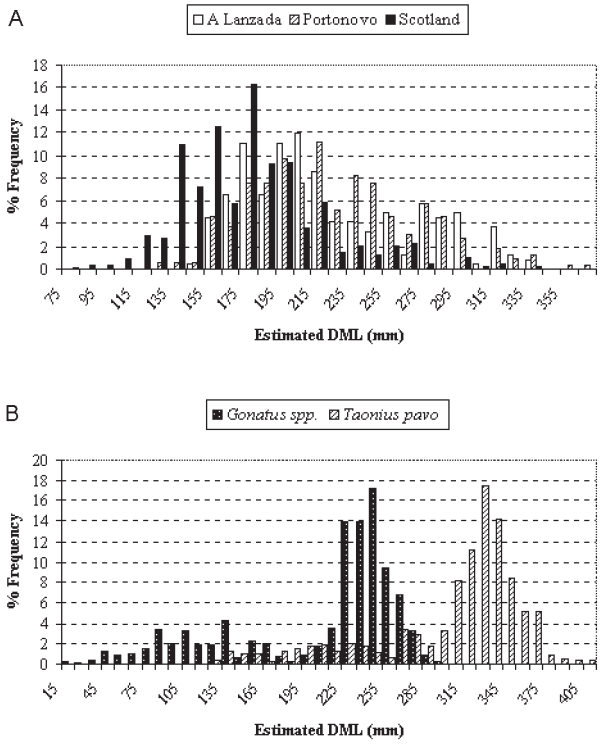

Figure 3. Frequency distribution of estimated size (DML=dorsal mantle length) of: (A) *Teuthowenia megalops* eaten by the Galician and Scottish beaked whales; and (B) *Gonatus* spp. and *Taonius pavo* taken by the Scottish whale. Sample sizes for *Teuthowenia megalops* were $n_{A\ Lanzada}=246$ beaks, $n_{Portonovo}=329$, and $n_{Scotland}=1873$. Sample size for *Gonatus* spp. was $n_{Scotland}=942$ beaks and sample size for *Taonius pavo* was $n_{Scotland}=908$ beaks.

MLs of *T. megalops* ranged from 125 to 365 mm, with a mode of 195 mm (Figure 3A). *Histioteuthis reversa* ranged in size from 45 to 65 mm ML.

For the North Uist whale, the most common prey species were *Teuthowenia megalops*, *Gonatus* sp., and *Taonius pavo*. Estimated MLs for *Gonatus* sp. varied between 15 and 295 mm, with most of the animals being between 225 and 265 mm (Figure 3B). *Teuthowenia megalops* ranged in size from 75 to 335 mm ML, with a single mode at 175 mm (Figure 3A). *Taonius* sp. ranged in size from 125 to 405 mm ML, with a mode of 325 mm (Figure 3B).

DISCUSSION

The limited published information on the diet of *Ziphius cavirostris* indicates that this species feeds primarily on oceanic cephalopods, whereas some authors also found remains of oceanic fish and crustaceans.

Although the sample size for this study was small, with only three animals sampled, the collection of 15,281 beaks from the Scottish whale (representing up to 8426 individual cephalopods) represents the highest number ever recorded for a single *Z. cavirostris*. Pooling the information from the three stomachs, some conclusions can be drawn. All animals had been eating a wide variety of cephalopods, mainly oceanic species such as *Teuthowenia megalops*, *Gonatus* sp., *Mastigoteuthis schmidti*, *Histioteuthis reversa* and *Taonius pavo*.

Teuthowenia megalops, which reaches 380 mm ML, is found from the surface to 1500 m depth. In the Atlantic, its northern limit is at 65–66°N, between Greenland and Iceland (Nixon, 1983; Voss, 1985). *Teuthowenia megalops* larvae migrate to the surface after hatching in deep waters. In later stages of development, the distribution spreads vertically in the water column and the squid appears to undertake a day–night migration, with the animals occurring closer to the surface during the day and in deeper waters during the night (Lu & Clarke, 1975). Nixon (1983) and Voss (1985) summarized the published information on the life cycle of *T. megalops*. Males reach maturity at between 182 to 244 mm ML while females reach maturity at 300 mm ML. The ML estimated for the majority of *T. megalops* beaks in the stomachs varied between 75 and 365 mm (Figure 3A), thus potentially including animals at all life stages from juvenile to adult.

Gonatus fabricii (Lichtenstein, 1818) is another oceanic species, probably the most abundant squid in Arctic and subarctic waters of the North Atlantic (Kristensen, 1983). Juvenile squid (ML up to 50 mm) are found in the surface layers. At a length of 50–70 mm *G. fabricii* disappears from the surface (Bjørke, 1995). Squid between 80 and 250 mm have been caught at depths of 200–550 m with deep pelagic and bottom trawls (Wiborg et al., 1984). In western Greenland, the males probably mature at a ML of ~200 mm and an estimated age of two years. Females mature at ~2–3 years of age and at MLs >200 mm (Kristensen, 1983). The ML estimated for the majority of *Gonatus* sp. in the Scottish beaked whale stomach varied between 225 and 265 mm (Figure 3B), which corresponds with the size of mature, including spawning, animals (Kristensen, 1983), although smaller squid were also found.

Histioteuthis reversa and *Taonius pavo* are also oceanic species living from the surface to 1800 and 2000 m depth, respectively (Voss, 1969, 1980; Guerra, 1992). Few data exist on the size at maturity for either species, but maximum sizes have been recorded as 185 mm and 750 mm respectively (Guerra, 1992; Voss et al., 1998). The estimated sizes of the squid found in the beaked whale stomachs were around half these maximum values.

In the north-east Atlantic, only Desportes (1985) identifies stomach contents of *Z. cavirostris*, but gives no information on the relative importance of the various squid families. The families Histioteuthidae, Gonatidae, Octopoteuthidae, Brachioteuthidae and Chiroteuthidae, recorded by Desportes, were also found in this study. Only one family, Enoploteuthidae, was reported by Desportes but not represented in this study.

Comparing the diet of *Z. cavirostris* with that of other whales in the study area, one of the predators similar in terms of its niche, although much larger, is the sperm whale (*Physeter macrocephalus* L.). A smaller species, closer to *Z. cavirostris* in size, is the northern bottlenose whale (*Hyperoodon ampullatus* Forster, 1770). Several studies have been carried out on the diet of sperm whales in the north-east Atlantic, where it was found to be dominated by *Gonatus* sp. (probably *G. fabricii*), although other species such as *Teuthowenia megalops*, *Histioteuthis bonnellii* and *Todarodes sagittatus* were also found (Santos et al., 1999). Studies on the diet of northern bottlenosed whales (Clarke & Kristensen, 1980; Lick & Piatkowski, 1998; Santos et al., 2001) found mainly *Gonatus* sp. in the stomachs of animals stranded in the Faroes, Jutland, the western Baltic Sea, Scotland, the Netherlands and Denmark. Thus, the stomach contents of the *Z. cavirostris* from Scotland in this study show similarities to those of sperm whales and northern bottlenose whales and suggest that these three predators exploit the same locally abundant resources.

The *Z. cavirostris* stranded in Galicia had not eaten many *Gonatus* sp., which is likely to be due to the fact that of the two species of *Gonatus* in the north-east Atlantic, only *G. steenstrupii* (less common than *G. fabricii*) is present in this area, where it reaches the limit of its distribution (Guerra, 1992).

In contrast with the sperm whales, the *Z. cavirostris* from Scotland had eaten a wider size range of *Gonatus* sp., including both adult and juvenile squid. For northern bottlenose whales, the reported size range of *Gonatus* sp. in the different stomach analysed (Clarke & Kristensen, 1980; Lick & Piatkowski, 1998; Santos et al., 2001) was also wider than found in sperm whales, but corresponded to post-juvenile *Gonatus* sp., squid which had already abandoned surface layers and moved to deeper waters (Santos et al., 2001). This could indicate that the *Z. cavirostris* had been feeding closer to the surface (where juvenile *Gonatus* sp. are found) than is normally the case for either sperm or northern bottlenose whales. However, in most cephalopod species there is a degree of cannibalism (e.g. Sauer & Lipinski, 1991; Rocha et al., 1994; Santos & Haimovici, 1997; Quetglas et al., 1999) and the small *Gonatus* sp. could have been originally ingested by larger ones and/or by some other prey of the beaked whale (i.e. they could be secondary prey).

The estimated weight represented by most beaks in the stomachs (taking into consideration that unidentified beaks did not contribute to the total weight, so the figure is an underestimation) was slightly over 793 kg for the North Uist whale, 101 kg for the A Lanzada whale and 72 kg for the Portonovo whale. There are at present no data on food consumption/requirements by beaked whales. However, a sperm whale of 11.73 m length (double the length of the Scottish beaked whale and perhaps as much as eight times heavier) would have an average daily food intake equivalent to 557–649 kg of squid (see Santos et al., 1999 for an explanation of the calculations). It seems likely that the 793 kg of cephalopods represented by beaks in the Scottish beaked whale represented several days' feeding. Cephalopod beaks tend to become entrapped in the folds of the stomach lining and may accumulate until they are regurgitated. It may be that the plastic bags found in the stomach were preventing evacuation of the stomach.

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