PYGMY SPERM WHALES *KOGIA BREVICEPS* IN THE NORTHEAST ATLANTIC: NEW INFORMATION ON STOMACH CONTENTS AND STRANDINGS

M. B. SANTOS

G. J. PIERCE

School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom E-mail: m.b.santos@abdn.ac.uk

A. LÓPEZ

Coordinadora para o Estudio dos Mamíferos Mariños, CEMMA, Apdo. 156-36380, Gondomar, Spain

R. J. Reid

SAC Veterinary Services, Drummondhill, Stratherrick Road, Inverness, IV2 4JZ, United Kingdom

V. RIDOUX

Laboratoire de Biologie et Environment Marins, Université de la Rochelle, Avenue de Lazaret, 17042 La Rochelle, France

E. Mente

School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ,United Kingdom

Abstract

Little is known about the feeding ecology of pygmy sperm whales (*Kogia breviceps*) in the Northeast Atlantic. Results are presented on the stomach contents of five whales stranded on the Galician coast (NW Spain) between 1995 and 2002 and seven whales stranded on the French Atlantic coast between 1984 and 2001. These results are compared with those obtained from the stomach contents of two pygmy sperm whales (a pregnant female and her calf) stranded on the Scottish (UK) coast in 1999, the first records of the species in Scotland. In 13 out of 14 cases, food remains consisted almost entirely of cephalopod beaks, although some crustacean and fish remains were also present. In all the Spanish specimens, the identified prey were oceanic species: the cephalopods *Histioteuthis reversa*, *H. bonnellii, Todarodes sagittatus*, the vipeffish *Chauliodus sloani*, and the giant mysid *Gnatophausia* sp. The same cephalopod species were found in the stomachs of the whales stranded in Scotland, although both whales had also consumed neritic cephalopod species such as *Rossia macrosoma* and other sepiolids. In the French specimens, almost all prey

identified were oceanic cephalopods (*H. reversa*, *Brachioteuthis riseii*, *T. sagittatus*, *Taonius pavo*, etc.), but remains of crustaceans and a neritic squid (*Loligo forbesi*) were also found. One whale from France had eaten mainly Henslow's swimming crab (*Polybius henslowi*). Results from the present study are consistent with those found by other authors in the Azores and the Canary Islands in that pygmy sperm whales appear to be mainly teuthophagous, with histioteuthid squids forming an important part of the diet. Strandings records suggest that occurrence of pygmy sperm whales in the NE Atlantic may be seasonal, with most strandings occurring in autumn and winter.

Key words: pygmy sperm whale, *Kogia breviceps*, cetaceans, diet, cephalopods, Northeast Atlantic.

The pygmy sperm whale *Kogia breviceps* (de Blainville 1838) is a small robust whale which has been recorded to reach a maximum length of 3.82 m (Eliason and Houck 1986). Originally placed in the family Physeteridae together with sperm whales (*Physeter macrocephalus*, L.), both pygmy sperm whale and dwarf sperm whale (*Kogia sima* Owen, 1866) species are now recognised as belonging to a separate family (Kogiidae) (Rice 1998).

Pygmy sperm whales are oceanic animals widely distributed in tropical and temperate waters of the Atlantic, Pacific, and Indian oceans (McAlpine 2002). In the eastern Atlantic, there are records of stranded specimens in Ireland (Berrow and Rogan 1997), the Netherlands (Fraser 1974), France (Duguy 1966, Duguy and Budker 1972), Spain (Penas Patiño and Piñeiro Seage 1989), and Portugal (Sequeira *et al.* 1992, 1996). In the present paper, we also present the first records of this species in Scotland (UK).

In common with other members of the superfamily Physeteroidea (Rice 1998), the pygmy sperm whale is thought to feed primarily on cephalopods, although fish and crustaceans have also been recorded in the diet. Information on stomach contents, which demonstrates this apparent preference for oceanic cephalopods, is available for South Africa (Ross 1979, Klages *et al.* 1989, Plön *et al.* 1999), Australia (Hale 1947), the Atlantic coasts of the United States and Canada (Raun *et al.* 1970, Candela 1987, McAlpine *et al.* 1997), the Caribbean (Cardona-Maldonado and Mignucci-Giannoni 1999), Brazil (Secchi *et al.* 1994), the Pacific coasts of the United States and Mexico (Scheffer and Slipp 1948, Eliason and Houck 1986, Vidal *et al.* 1987), the Azores (Martins *et al.* 1985), and the Canary Islands (Hernández-García and Martín 1996).

The aim of this paper is to provide new information on the diet of this species for the Northeast Atlantic, by presenting results from the analysis of the stomach contents of five specimens stranded in Galicia (NW Spain) between 1995 and 2002, two specimens stranded in Scotland (UK) in 1999 (which represent the first records of this species in Scotland) and seven specimens stranded in France between 1984 and 2001. The results presented here are also compared to those found by other authors for the Northeast Atlantic.

METHODS

Sample Collection

Strandings of pygmy sperm whales were attended and samples collected through the stranding networks operating in each area. All three strandings networks are well established and provide year-round coverage of the coast, funded through the national government in the case of Scotland (UK) and France and part-funded by the regional government in Galicia. The French and Galician networks also depend substantially on volunteer effort. In all cases, reporting of strandings by members of the public is an essential part of the process, and some seasonal and geographical bias in coverage is therefore inevitable. Nevertheless, strandings of relatively rare and unusual species such as the pygmy sperm whale are likely to attract particular attention and, therefore, to be reliability reported.

Stomach contents were collected from 5 out of 13 pygmy sperm whales stranded in Galicia (NW Spain) between 1983 and 2005 (see Fig. 1 and Table 1). The sample



Figure 1. Map showing strandings locations in Galicia (Spain), France, and Scotland (UK).

ID	Area	Date	Place	Length (cm)	Sex	Comments
	Galicia	05/12/83	Meiras, Valdoviño	220	_	
KB701	Galicia	25/10/95	P. SanXurxo, Ferrol*	287	F	
KB702	Galicia	28/10/95	P. San Xurxo, Ferrol*	266	F	Lactating
	Galicia	28/10/95	P. San Xurxo, Ferrol	147	F	Live stranding
KB704	Galicia	03/10/97	P. Baldaio, Carballo*	324	F	Pregnant (the
						fetus was a
						male 125 cm
						long)
	Galicia	06/09/97	P. Area Grande, Vicedo	-	-	
	Galicia	10/01/99	Caión, Laracha	188	Μ	
KB705	Galicia	01/12/99	P. Esteiro, Mañón*	200	Μ	
	Galicia	16/02/01	C. Estay, Canido	196	F	
KB703	Galicia	27/01/02	P. Hermida, Ponteceso*	212	Μ	
	Galicia	11/01/03	P. Cobas, Ferrol	_	-	Skull with flesh
						still attached
	Galicia	25/11/04	P. Riás, Malpica	202	Μ	
	Galicia	20/01/05	P. Niñón, Ponteceso	217	F	
KB901	France	03/02/84	Saint Pierre d'Oleron*	185	F	
KB902	France	29/08/86	Bidart*	225	Μ	
KB904	France	30/12/89	Tarnos*	213	F	
KB903	France	11/12/90	Hendaye*	160	Μ	
KB905	France	08/03/93	Talmont Saint Hilaire*	275	Μ	
KB906	France	07/12/99	Cap Ferret*	200	Μ	
KB907	France	28/12/01	Montalivet*	211	Μ	
KB601	Scotland	18/10/99	Loch Ryan*	268	F	Pregnant
KB602	Scotland	18/10/99	Loch Ryan*	208	-	Calf

Table 1. Pygmy sperm whales stranded in Galicia (Spain), Scotland (UK), and France. Animals from which stomach contents were analyzed are marked with an *.

includes four females (three of which stranded in the same location within a period of a few days) and a male. One of the females was lactating and had marks of shark teeth in the skin. Stomach contents from two whales stranded in Scotland were also examined. These whales represent the first records of the species in Scotland. The whales, an adult female and her calf, stranded in Loch Ryan near Stranzaer (see Fig. 1) on 18 October 1999. The adult female was in the early stages of pregnancy with a male fetus 25 cm long. The calf originally stranded with its mother but it later refloated and was not rediscovered for 11 d. Due to the advanced state of decomposition its sex could not be determined (Table 1). Finally, the stomach contents of seven whales stranded on the French Atlantic coast were also collected and examined. The sample consisted of two females and five males. All stranding locations are shown in Figure 1.

Diet Analysis

Cephalopod beaks were identified using a published guide (Clarke 1986) and a reference collection originally provided by M. R. Clarke and now housed in the School of Biological Sciences, University of Aberdeen, UK. Standard measurements were taken of the lower beaks: rostral length (LRL) for decapods and hood length (LHL) for octopods (Clarke 1986), using a binocular microscope fitted with an eyepiece graticule. All undamaged lower beaks were measured except in the cases of specimens

KB701, KB704, and KB907, which contained large numbers of *H. reversa* beaks, of which random sub-samples of 200, 200, and 272 beaks, respectively, were measured. Mantle length (ML) and body weights of cephalopod prey were estimated from lower beak measurements, using regressions from Clarke (1986). The total number of individuals of each cephalopod species present in a stomach was estimated as the number of lower or upper beaks (whichever was higher).

Fish bones (two dentaries, probably from the same individual fish) were identified using reference material held at the University of La Rochelle, France. The presence of other remains (*e.g.*, eye lenses) was also noted. Crustacean remains were found, in almost all cases, to be in a very poor state of preservation and most could not be identified to species level.

The total weight represented by the beaks of each species in each stomach was estimated as (sum of weights represented by beaks measured)/(proportion of individuals measured). For the Sloane's viperfish (*Chauliodus sloani*), Debrot and Barros (1992) used a ratio of 1:8 to estimate fish length from mandible length. Applying a length-weight relationship from Merella *et al.* (1997), the dentaries found in this study (19.7 and 19.0 mm, respectively) would correspond to a fish weighing between 5.2 and 5.8 g. Note, however, that the reference specimen used for identification (originally identified by V. R., University of La Rochelle, France) had a weight of 34 g and a dentary measurement of 25.7 mm. In any case, this fish would make a very small contribution to the diet (<0.2% of the estimated reconstructed prey weight for that whale). For the crustacean remains regressions were applied only to the prey identified to species level, *Polybius henslowi*. Remains of *Gnatophausia* sp. were weighed directly.

Overall diet composition for each whale was calculated in terms of prey numbers and biomass by expressing the counts and summed weights, respectively, for each prey species as a proportion of the all-species totals.

RESULTS

Galician Whales

Food remains consisted almost entirely of cephalopod beaks, although some crustacean and fish remains were also found. No cephalopod or fish flesh was found. Numbers of beaks in the stomachs were 941 upper and 1,072 lower beaks (KB701), 233 upper and 231 lower beaks (KB702), 795 upper and 807 lower beaks (KB704), 53 upper and 56 lower beaks (KB705), and 12 upper and 22 lower beaks (KB703).

Fish eye lenses were found in four of the five whale stomachs and, in addition, two fish dentaries identified as belonging to the viperfish *Chauliodus sloani* Schneider 1801 were found in whale KB703. Crustacean remains were found in almost all Galician whales. In the case of whale KB701, these remains were identified as belonging to a giant mysid of the genus *Gnathophausia* sp. In the case of whale KB703, the body of a small parasitic isopod was identified. Further identification of the crustacean remains found in the other whales was not possible.

For four of the five whales, the cephalopod *H. reversa* Verrill 1880 was the most numerous prey consumed and comprised most of the estimated weight of prey items eaten while for the other individual (KB703) it only comprised 5% of the total weight (Table 2). For this whale, cephalopods of the family Histioteuthidae and another cephalopod species, *Lepidoteuthis grimaldi* Joubin 1895 comprised most of the estimated prey weight. Other cephalopod species found in the stomachs included *H. bonnellii* Férussac 1835, *Todarodes sagittatus* Lamarck 1798, and *Teuthowenia megalops*

= N%	r fish and	includes	
mportance	stated). For	86b) which	
iains and i	otherwise a	Clarke 198	
vother rem	aks unless	A" group (
er of beaks	l (lower be	the "type .	
pes, numb	e indicated	elonged to	
all prey tyl	cs found ar	cies but be	
licia. For a	bers of beal	ified to spe	
nded in Ga	pods, numl	ot be ident	
rhales strar	or cephaloj	ks could n	
y sperm w	ndicated. F	oteuthis bea	
five pygm	ight) are ii	Some Histi	lii.
omachs of	tage by we	ndicated. S	H. bonnel
d in the st	7 = percen	s found is i	oteuthis, and
ecies foun	er and %W	of remains	H. meleagro
. Prey sp	: by numbe	s, the type	H. corona,
Table 2.	percentage	crustacean	H. arcturi,

		KB	701 (287	cm)	KB	702 (266	cm)	KB	704 (324	cm)	KB	705 (200	cm)	KB	703 (212 -	(m)
Family	Species	Beaks	N%	AN %	Beaks	N%	M%	Beaks	N%	Μ%	Beaks	N%	Μ%	Beaks	N%	AN %
						Cephalopc	od prey									
Octopoteuthidae	Octopoteuthis sicula	I	I	I	I	I	I	7	0.25	0.84	I	I	I	I	I	I
Gonatidae	Gonatus sp.	ŝ	0.28	0.40	1	0.43	0.93	ŝ	0.37	0.55	I	I	I	I	I	I
Lepidoteuthidae	Lepidoteuthis grimaldii	I	I	I	I	I	I	I	I	I	I	I	I	-	4.17	40.67
Histioteuthidae	Histioteuthis reversa	997	92.74	64.50	194	82.55	63.91	724	89.60	53.09	49	87.5	82.62	ŝ	12.50	5.16
	H. bonnellii	16	1.49	14.65	9	2.53	19.89	4	0.87	9.38	I	I	I	I	I	I
	H. meleagrotenthis	I	I	I	I	I	I	I	I	I	I	I	I	1	4.17	4.82
	H. type A	13	1.21	1.62	1	0.43	0.38	37	4.58	18.58	I	I	I	9	25.00	30.23
Brachioteuthidae	Brachioteuthis riisei	-	0.09	0.01	2	0.83	0.14	I	I	I	I	I	I	I	I	I
Ommastrephidae	Todarodes sagittatus	17	1.58	16.81	1	0.43	2.60	8	0.99	11.14	I	I	I	I	I	I
	Unid. ommastrephids	I	I	I	1	0.43	0.48	I	I	I	4	7.14	11.96	I	I	I
Chiroteuthidae	Chiroteuthis veranyi	1	0.09	0.07	I	I	I	1	0.12	0.13	I	I	I	ŝ	12.50	4.96
	Chiroteuthis sp. (type 2)	ŝ	0.28	0.39	I	I	I	1	0.12	0.26	I	I	I	1	4.17	3.36
Pholidoteuthidae	Pholidoteuthis boschmai	1	0.09	0.33	I	I	I	ŝ	0.37	4.22	I	I	I	I	I	I
Mastigoteuthidae	Mastigoteuthis schmidti	I	I	I	1	0.43	0.05	1	0.12	0.09	I	I	I	ŝ	12.50	2.35

					Ta	ble 2. (Continue	.pg								
		KB70	1 (287 -	cm)	KB70)2 (266 c	m)	KB70	4 (324 c	m)	KB7()5 (200 -	cm)	KB703	(212 cr	(u
Family	Species	Beaks	N%	AM %	Beaks	N%	AN %	Beaks	N%	AM %	Beaks	N%	AN %	Beaks	N%	AN %
						Cephalo	pod prey									
Cranchiidae	Taonius pavo	1	0.09	0.04	%	1.28	0.59	~	0.37	0.16	e S	5.36	5.42	e S	12.50	5.42
	Galiteuthis armata	I	I	I	I	I	I	1	0.12	0.29	I	I	I	1	4.17	2.88
	Teuthowenia megalops	14	1.30	0.91	21	8.94	11.02	16	1.98	1.26	I	I	I	I	I	I
	Teuthowenia sp.	1	0.09	0.24	I	I	I	I	I	I	I	I	I	I	I	I
	(type 2)															
Alloposidae	Haliphron atlanticus	1	0.09	I	I	I	I	I	I	I	I	I	I	I	I	I
Broken beaks		ŝ	0.28	I	I	I	I	I	I	I	I	I	I	I	I	I
Upper beaks		941	I	I	233	0.85	I	795	I	I	53	I	I	12	I	I
Family	Species	Remains	N%	Μ%	Remains	N%	AN %	Remains	N%	AN %	Remains	N%	AN %	Remains	N%	AN %
					Fisł	n and cru	stacean	prey								
Chauliodontidae	Chauliodus sloani	Ι	I	I	I	I	I	I	I	I	I	I	I	bones	4.17	0.16
Unidentified	Unid. fish	1 eye lens	0.09	I	1 eye lens	0.43	I	1 eye lens	0.12	I	I	I	I			
Mysidacea	Gnatophausia sp.	2 bodies	0.19	0.04	I	I	I	I	I	I	I	I	I	I	I	I
Isopoda	Parasitic	I	I	I	I	I	I	I	I	I	I	I	I	1 body	4.17	I
Unidentified	Unid. Crustacean	I	I	I	1 caparace	0.43	I	I	I	I	I	I	I	I	I	I
TOTAL			100	100		100	100		100	100		100	100		100	100
																I

Prosch 1847. The number of prey taxa identified in the stomachs ranged from 9 (KB703) to 12 (KB701, KB704) (Table 2).

The estimated sizes of the *H. reversa* eaten ranged from 5 to 65 mm ML (KB701), from 35 to 55 mm ML (KB702), from 15 to 55 mm (KB704, KB705), and from 45 to 65 mm (KB703) (Fig. 3A). In all five whales, the modal size of *H. reversa* eaten was around 45 mm (Fig. 3A).

French Whales

Food remains consisted entirely of cephalopod beaks with the exception of KB901, in which carapaces of 29 Henslow's swimming crab (*Polybius henslowi*) were found, together with the remains of three unidentified shrimp and the gladius of a squid. No fish remains were found. Numbers of beaks in the stomachs were 10 upper and 13 lower beaks (KB902), 9 upper and 18 lower beaks (KB903), 16 upper and 32 lower beaks (KB904), 1 lower beak (KB905), 97 upper and 99 lower beaks (KB906), and 437 upper and 458 lower beaks (KB907).

The squid *H. reversa* was the most common prey in five out of six stomachs, although the stomach of whale KB901 was almost entirely filled with crustacean remains (Table 3).

Estimated sizes of *H. reversa* ranged from 15 to 35 mm ML with a mode at 25 mm (KB902), from 25 to 55 mm with a mode at 55 mm (KB903), from 25 to 55 mm with a mode at 35 mm (KB904, KB906), and from 15 to 65 mm with a mode at 35 mm (KB907) (Fig. 3B).

Scottish Whales

The results for the whales stranded in Scotland were similar, with most of the remains consisting of cephalopod beaks and no fish or cephalopod flesh found. Numbers of beaks in the stomachs were 139 upper and 109 lower beaks (KB601) and 115 upper and 104 lower beaks (KB602). Fish eye lenses were found in both whales, but crustacean remains were found only in the stomach of the calf (KB602).

Squid of the family Histioteuthidae were again the main prey. However, while the mature female had eaten mainly *H. bonnellii*, the calf had taken mainly *H. reversa*. Ten prey taxa were identified in the stomachs of both individuals (Table 4).

Estimated sizes for *H. reversa* eaten varied between 15–45 mm ML with two modes at 25 and 45 mm (KB601) and 5–45 mm with a mode at 15 mm (KB602) (Fig. 3C).

DISCUSSION

Of the 22 pygmy sperm whale standings reported in this study (Fig. 1), 20 were found in the first and last quarter of the year. This could reflect the seasonal (autumn and winter) appearance of the species in more temperate waters of the Northeast Atlantic (Fig. 2). In Galicia most strandings take place between October and December in areas of the coast that are predominantly orientated to the north (Fig. 1), with a high percentage of the animals in good condition (approximately one-third were "fresh"). In two cases (KB704 and KB702) the animals showed signs of having recently been attacked by killer whales and sharks, respectively. These attacks may have forced the animals into coastal waters where they then stranded. In the case of whale KB702, two types of shark bites were found: old and already healed wounds on the tail and flippers, and a fresh bite on the snout. It was not possible to determine

		Kł	3901 (18	35 cm)	KB	902 (2:	25 cm)	KE	3903 (16	(0 cm)	KF	904 (2)	[3 cm)	KB	05 (2.	75 cm)	KB	906 (20() cm)	KB9(07 (211	cm)
Family	Species	R	N%	AN %	В	N%	M %	В	N%	Μ%	В	N%	AN %	В	N%	AN %	В	N%	AN %	В	N%	AN %
								Ŭ	sphalopo	d prey												
Loliginidae	Loligo vulgaris	Ι	I	I	Ι	I	I	I	I	I	I	I	I	I	I	I	-	1.00	3.79	I	I	I
Chtenopterygidae	Chtenopteryx sicula	I	I	I	I	I	I	I	I	I	I	I	I	I	I	Ι	I	Ι	Ι		0.22	0.11
Gonatidae	Gonatus steenstrupi	I	I	I	I	I	I	1	5.56	12.77	I	I	I	I	I	I	I	I	I	-	0.22	0.86
Histioteuthidae	Histioteuthis reversa	I	I	I	13	100	100	15	83.33	72.56	26	81.25	59.02	1	100	100	35 8	5.00 (54.60	407 8	38.67	80.12
	H. meleagroteuthis	I	I	Ι	I	I	I	I	I	I	I	I	I	T	I	I	I	I	I	-	0.22	0.77
	H. corona	I	I	I	Ι	I	I	I	I	I	I	I	I	I	I	I	I	I	I	13	2.83	6.68
Brachioteuthidae	Brachioteuthis riisei	I	I	I	I	I	I	-	5.56	1.20	I	I	I	I	I	I	I	I	I	I	I	I
Ommastrephidae	Todarodes sagittatus	I	I	I	I	I	I	1	5.56	13.47	9	18.75	40.98	I	I	I	~	2.00	27.05	7	0.44	1.24
	Unid.	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	Ś	5.00	4.56	I	I	I
Chiroteuthidae	ommastrephids Chiroteuthis veranyi	I	I	I	I	I	I	I	I	I	I	I	I	Т	I	I	I	I	I	4	0.87	0.49
	Chiroteuthis sp.	I	I	I	I	I	I	I	I	I	I	I	I	I	I	Ι	I	I	I	~	1.53	3.39
Mastigoteuthidae	(type 2) Mastigotenthis	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	~	1.53	1.57
Cranchiidae	Taonius pavo	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	6	1.96	1.59
	Galiteuthis armata	I	Ι	Ι	I	I	I	I	I	I	I	I	Ι	I	I	I	I	Ι	I	0	0.44	1.93
	Teuthowenia	I	I	Ι	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	4	0.87	1.25
Becken hooks	megalops																					
Unner heaks					101			0										1 00		437		
Unidentified	Unid. squid	1	3.03	I	, I	T	I	<u> </u>	I	I	16	I	I	Т	I	I	-	1.00	I	P	I	I
Family	Species	R	N%	AN %		N%	AN %		N%	M%		N%	AN %	-	N%	AN %		N%	AN %		N%	Μ%
								C	rustacea	n prey												
Unidentified	Unid. shrimp	\tilde{s}	9.09	Ι	I	I	I	I	I	I	I	I	I	Ι	I	I	I	I	I	I	I	I
Portunidae	Polybius benslowii	29*	87.88	100	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
TOTAL			100	100		100	100		100	100		100	100		100	100		100	100		100	100
*Caparaces.																						

MARINE MAMMAL SCIENCE, VOL. 22, NO. 3, 2006

Family		Mature fe	male (KB601, 2	68 cm)	Calf (K	CB602, 208 cm	
4 TTTTT 1	Species	Beaks	N%	AN %	Beaks	N%	AN %
		Ceph	alopod prey				
Sepiolidae	Rossia macrosoma	I	I	I	1	0.78	2.08
	Unid. sepiolids	11	7.89	0.43	62	56.25	22.39
Octopoteuthidae	Octopotenthis sicula	1	0.66	0.74	I	I	I
Gonatidae	Gonatus sp.	8	5.26	6.58	1	0.78	2.37
Histioteuthidae	Histioteuthis reversa	39	25.66	10.68	27	21.09	43.49
	H. bonnellii	15	9.87	53.50	I	I	Ι
	H. type A	ŝ	1.97	0.61	ŝ	2.34	2.35
Brachioteuthidae	Brachioteuthis riisei	~	1.97	0.08	1	0.78	0.39
Ommastrephidae	Todarodes sagittatus	2	1.32	11.51	1	0.78	14.37
	Unid. ommastrephids	5	3.29	5.35	I	I	Ι
Chiroteuthidae	Chiroteuthis sp. (type 2)	10	6.58	5.23	1	0.78	0.33
Cranchiidae	Teuthowenia megalops	10	6.58	2.61	Ś	3.91	12.24
	Teuthowenia sp. (type 2)	2	1.32	2.68	Ι	I	Ι
Octopodidae	Unid. octopod	I	I	I	1^*	0.78	I
Broken beaks		1	0.66	I	2	1.56	I
Upper beaks		139	26.31	I	115	0.78	Ι
Family	Species	Remains	N%	AN %	Remains	N%	AN %
		Fish and	crustacean prey				
Unidentified	Unid. fish	1 eye lens	0.66	I	1 eye lens	0.78	I
Unidentified	Unid. crustacean	I	I	I	11 caparaces	8.59	I
TOTAL			100	100		100	100

SANTOS ET AL.: PYGMY SPERM WHALES

609



Figure 2. Seasonal distribution of stranding records for pygmy sperm whale in Galicia (NW Spain), France, and Scotland (UK).

which species of shark was involved in the attack. However, the available data (including for other areas outside the Northeast Atlantic) do not provide clear evidence of migration or seasonal movements (McAlpine 2002). The pygmy sperm whale has not been recorded previously from Scotland. The appearance of new cetacean species in the Scottish strandings record in recent years has been interpreted as indicating a shift in community composition, perhaps related to global warming (see MacLeod *et al.* 2005).

The majority of the pygmy sperm whale stomachs analyzed in the present study contained mainly oceanic cephalopod remains and very little else, with the exception of the St. Pierre whale, whose stomach was almost entirely filled with crustacean remains (*H. reversa*), the most common prey is an oceanic squid with a recorded maximum size of 186 mm DML. It has been found from the surface to more than 1,000 m depth (Voss *et al.* 1998), being more abundant in areas of higher productivity (*e.g.*, near the continental slope). The congeneric *H. bonnellii* is also an oceanic species, which has been found in a wide range of depths (100–2,000 m, Voss *et al.* 1998). It has been recorded to reach 330 mm DML. Both species seem to move closer to the surface at night and remaining in deeper waters during the day. Both *H. reversa* and *H. bonnellii* have been found in the diet of several predators in the area, sometimes in large numbers *e.g.*, in Cuvier's beaked whale (*Ziphius cavirostris*), northern bottlenose whale (*Hyperoodon ampullatus*), sperm whale, blue shark (*Prionace glauca*), striped dolphin (*Stenella coeruleoalba*), and common dolphin (*Delphinus delphis*) (Clarke and Stevens 1974; Macnaughton *et al.* 1998; Santos *et al.* 1999, 2001*a*,*b*, 2002, 2004).

The other prey remains identified included Sloane's viperfish (*Chauliodus sloani*), a meso-bathypelagic species believed to occupy deep waters up to 1,000 m. It is considered to be quite common in deep oceanic waters, although it may migrate to near the surface at night (especially smaller fish) (Whitehead *et al.* 1989). The crustacean remains identified from the Galician whale stomachs belonged to the genus



(B)



(C)



Figure 3. Frequency distribution of estimated size (DML = dorsal mantle length) of *Histioteuthis reversa* taken by pygmy sperm whales in (A) Galician, (B) France, and (C) Scotland.

Gnatophausia, a group of bathypelagic giant mysids with a circumglobal distribution between 30° N and 30° S. The most common species in the genus, *G. ingens*, has been recorded to reach 35 cm in length and to live in waters ranging from 400 to 800 m depth (Barnes 1974, Sanders and Childress 1990). *G. ingens* has been previously reported in the stomachs of odontocetes (Ross 1984, Debrot and Barros 1994, Dolar *et al.* 2003). Henslow's swimming crab (*Polybius henslowii*), recorded in one of the French samples, has been described as a benthic species with pelagic phases, which has been recorded moving into coastal waters in large groups (Munilla 1997). Its distribution extends in the Atlantic from the British Islands to Morocco and it is also found in the Mediterranean.

The pygmy sperm whales that stranded in Galicia, France, and Scotland had eaten a similar range of prey species (e.g., predominantly oceanic cephalopods, Ross 1979, Martins et al. 1985, Klages et al. 1989, McAlpine et al. 1997) that have been reported elsewhere. The main prey group taken by the whales in the present study (family Histioteuthidae) was also recorded by authors analyzing the stomach contents of K. breviceps further south in the Atlantic, in the Azores (a male pygmy sperm whale stranded on Faial island in 1984, Martins et al. 1985) and the Canary islands (two pygmy sperm whales stranded in 1993, Hernández-García 1995). Five previously reported stranded whales in European waters (one in the Netherlands and four in France) were reported as having mainly cephalopod beaks in their stomachs together with fish and crustacean remains (in the case of the Dutch whale, a beak "apparently" belonging to the cuttlefish Sepia officinalis and remains of several green crabs Carcinus maenas). However, in all cases, other cephalopod beaks were not identified (Allen 1941, Duguy 1966). Desportes (1985) identified the prey remains found in the stomachs of two female pygmy sperm whales stranded in France. One of the stomachs contained cephalopods and the remains of eight blue whiting (Micromesistius poutassou), while the other contained cephalopods and the remains of 37 decapod crustaceans. The author listed the families Ommastrephidae, Loliginidae, Sepiolidae, Octopodidae, Histioteuthidae, and Chiroteuthidae, but did not give an indication of the relative importance of each family in the diet.

Although the dominance of histioteuthid squid in most reports suggests a rather specialised diet, *Kogia breviceps* also seems to feed on a wide variety of other species. In the present study at least 22 species of cephalopods belonging to 15 families were recorded in the 14 stomachs examined, while up to 55 cephalopod species and 22 other prey species (fish, crustacean, molluscs, and other invertebrates) were found in the 42 stomachs examined by Plön *et al.* (1999). Other authors also have reported a varied diet for this species (*e.g.*, 11 prey taxa) even when sample sizes were small (*e.g.*, McAlpine *et al.* 1997). Given the relatively small sample size in the present study, although the more common prey species are likely to have been recorded, it is also probable the full range of prey species was not detected.

The distribution and ecology of the majority of the species in the diet suggest that pygmy sperm whales generally feed in deep shelf and slope waters. Clarke (2003) suggested that *Kogia* could dive between 500 and 1,000 m because its shares the same prey species as the (great) sperm whale. However, the fact that many prey species migrate to the surface at night makes it difficult to estimate the depth at which whales are feeding. Some authors believe the pygmy sperm whale takes its prey at or near the bottom because of the presence in benthic fishes and crabs (*e.g.*, Gaskin 1982) and also because of its "small underslung lower jaw and anterio-ventrally flattened snout" (Caldwell and Caldwell 1989).

In the present study, the stomachs of all five Galician pygmy sperm whales sampled, including the lactating and pregnant females, and almost all French whales sampled,

contained only the remains of oceanic prey. However, the Scottish whales had also eaten a few neritic cephalopod species (*e.g.*, sepiolids), which would indicate feeding in more coastal waters prior to stranding, perhaps related to the presence of the calf with the pregnant female. Only remains of neritic species (Henslow's swimming crab) were identified in the stomach of one of the French whales. This is not the first time that neritic species have been recorded in the diet of pygmy sperm whales, although they usually comprise a minority of the prey remains. Hale (1947) found neritic cephalopods (*Sepioteuthis australis*) in the stomach of a suckling calf from the south Australian coast while the stomach of the mother contained only remains of shrimps (*Penaeus* and *Hymenodora*). Although the author did not identify the shrimp to species the majority of *Penaeus* species are neritic, while *Hymenodora* is a pelagic genus.

Ross (1979) found that neritic cephalopods such as loliginids, sepiids, and octopodids represented up to 25% of all the cephalopods found in the stomachs of 13 whales stranded in South Africa. Candela (1987) found loliginids in a third of the 53 stomachs analyzed from Kogia breviceps stranded in Florida and Georgia, although the author also noted that the remains of neritic species accounted for only 1.5% of all the beaks. Plön et al. (1999) also found neritic species in the stomach contents of pygmy sperm whales stranded in South Africa. The authors grouped the samples into (1) immature whales of both sexes and females that were lactating and/or pregnant and/or accompanied by a calf, and (2) sexually mature males and females (neither lactating, pregnant or accompanied by a calf). Animals from the first group had a significantly higher proportion of inshore cephalopods (cuttlefish *Sepia* spp.) in their diet. Inshore cephalopods were also found in the other group (b), but in a much smaller proportion (less than 2% of the total prey number). Ross (1984) also found a higher proportion of oceanic food items in the diet of eight adult whales from South Africa when compared with the stomach contents of seven immature whales, calves and accompanying adult females. The author suggested that this was an indication that juvenile and immature whales were living closer to the coast than adults, probably inhabiting the outer part of the continental shelf and the upper part of the slope.

Results from the present study also allow us to consider the likelihood of competition for food between pygmy sperm whales and its larger relative, the sperm whale (*Physeter macrocephalus*) in the Northeast Atlantic. The stomach contents of pygmy sperm whales from three different parts of the Northeast Atlantic suggest that, although there are differences in diet composition, the diet is dominated by squid of the genus *Histioteuthis*. (Great) sperm whales stranded on North Sea coasts had normally fed most recently on the Arctic squid *Gonatus fabricii* (Santos *et al.* 1999) whereas animals stranded in Ireland, including the only record of the stomach contents of a sperm whale calf, had fed mainly on *Histioteuthis* spp. (Santos *et al.* 2006, in press). It is interesting to note that the size of *Histioteuthis* eaten by the pygmy sperm whales was generally smaller than the modal size (65 mm ML) taken by an adult sperm whale, but very similar to the size range (25–55 mm ML with a mode at 45 mm) taken by a sperm whale calf. Thus, there may be competition between adult pygmy sperm whales and juvenile sperm whales in areas where the two species overlap.

ACKNOWLEDGMENTS

The analysis described in this paper was supported by CEC Contract ERB 4001 GT93 3630. Stomach contents from the whales stranded in Scotland were collected during necropsies

carried out by SAC Veterinary Services as part of the UK Department of the Environment, Food and Rural Affairs Cetacean Stranding Project. In Galicia, the network is run by volunteers with some funding from the regional government. In France, the coordination of the National Stranding Scheme is funded by the Ministère de l'Ecologie et du Développement Durable, and numerous volunteers contribute data and samples. Jianjun Wang supplied the map used in Figure 1. We also thank Nélio Barros, an anonymous referee and the associate editor for useful comments on the original manuscript.

LITERATURE CITED

- ALLEN, G. M. 1941. Pygmy sperm whale in the Atlantic. Publications of the Field Museum of Natural History (Zoology) 27:17–36.
- BARNES, R. D. 1974. Invertebrate zoology. 3rd edition. W.B. Saunders Company, London, UK.
- BERROW, S. D., AND E. ROGAN. 1997. Review of cetaceans stranded on the Irish coast, 1901–95. Mammal Review 27:51–76.
- CALDWELL, D. K., AND M. C. CALDWELL. 1989. Pygmy sperm whale Kogia breviceps (de Blainville, 1838): Dwarf sperm whale Kogia simus Owen, 1866. Pages 349–430 in S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 4. River dolphins and the larger toothed whales. Academic Press, London, UK.
- CANDELA, S. M. 1987. Cephalopod prey of pygmy and dwarf sperm whales (*Kogia breviceps* and dwarf *K. simus*) stranded in Florida and Georgia. Page 9 *in* Abstracts of the 7th Biennial Conference on the Biology of Marine Mammals, Miami, Florida, 5–9 December 1987.
- CARDONA-MALDONADO, M. A., AND A. A. MIGNUCCI-GIANNONI. 1999. Pygmy and dwarf sperm whales in Puerto Rico and the Virgin Islands, with a review of *Kogia* in the Caribbean. Caribbean Journal of Science 35:29–37.
- CLARKE, M. R., ed. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, UK.
- CLARKE, M. R. 2003. Production and control of sound by the small sperm whales, *Kogia* breviceps and *K. sima* and their implications for other Cetacea. Journal of the Marine Biological Association of the United Kingdom 83:241–263.
- CLARKE, M. R., AND J. D. STEVENS. 1974. Cephalopods, blue sharks and migration. Journal of the Marine Biological Association of the United Kingdom 54:949–957.
- DEBROT, A. O., AND N. B. BARROS. 1992. Notes on a Gervais' beaked whale, *Mesoplodon europeaus*, and a dwarf sperm whale, *Kogia simus*, stranded in Curaço, Netherlands Antilles. Marine Mammal Science 8:172–178.
- DEBROT, A. O., AND N. B. BARROS. 1994. Additional cetaceans records for the Leeward Dutch Antilles. Marine Mammal Science 10:359–368.
- DESPORTES, G. 1985. La nutrition des Odontocetes en Atlantique Nord-Est (cotes Francaises - iles Feroe). Ph.D. thesis, Université de Poitiers, Poitiers, France. 190 pp.
- DOLAR, M. L. L., W. A. WALKER, G. L. KOOYMAN AND W. F. PERRIN. 2003. Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu sea. Marine Mammal Science 19:1–20.
- DUGUY, R. 1966. Quelques Donées nouvelles sur un Cétacé rare sur les Côtes d'Europe: Le Cahalot à tête courte, *Kogia breviceps* (Blainville 1838). Mammalia 30:259–269.
- DUGUY, R., AND P. BUDKER. 1972. Rapport annuel sur les cétacés et pinnipèdes trouvés sur les côtes de France I. Année 1971. Mammalia 36:517–520.
- ELIASON, J. J., AND W. J. HOUCK. 1986. Notes on the biology of a gravid pygmy sperm whale (*Kogia breviceps*) from California. Cetology 51:1–5.
- FRASER, F. C. 1974. Report on Cetacea stranded on the British coasts from 1948 to 1966. No. 14. British Museum (Natural History). 65 pp.
- GASKIN, D. E. 1982. The ecology of whales and dolphins. Heinemann, London, UK.
- HALE, H. M. 1947. The pigmy sperm whale (*Kogia breviceps*, Blainville) on South Australian coasts. Records of the South Australian Museum 8:531–546.

- HERNÁNDEZ-GARCÍA, V. 1995. Contribución al conocimiento bioecológico de la familia Ommastrephidae Steenstrup, 1857 en el Atlántico Centro-Oriental. Ph.D. thesis, Universidad de las Palmas de Gran Canaria, Las Palmas, Spain. 307 pp.
- HERNÁNDEZ-GARCÍA, V. AND V. MARTIN. 1996. Food habits of the pygmy sperm whale Kogia breviceps (de Blainville, 1838) stranded in the Canary Islands. Page 202 in Abstracts of the 2nd Symposium Fauna and Flora of the Atlantic Islands. Las Palmas de Gran Canaria, Spain, 12–16 February 1996.
- KLAGES, N., V. G. COCKCROFT AND P. B. BEST. 1989. Stomach contents of pygmy Kogia breviceps and dwarf Kogia simus sperm whales stranded on South African beaches. Page 35 in Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals, Monterrey, California, 7–8 December 1989.
- MACLEOD, C. D., S. M. BANNON, G. J. PIERCE, C. SCHWEDER, J. A. LEARMONTH, J. S. HERMAN AND R. J. REID. 2005. Climate change and the cetacean community of northwest Scotland. Biological Conservation 124:477–483.
- MACNAUGHTON, R., E. ROGAN, V. HERNÁNDEZ-GARCÍA AND C. LORDAN. 1998. The importance of cephalopods in the diet of the blue shark (*Prionace glauca*) south and west of Ireland. International Council for the Exploration of the Sea CM/M:07.
- MCALPINE, D. F. 2002. Pygmy and dwarf sperm whales (*Kogia breviceps* and *Kogia sima*). Pages 1007–1009 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. Academic Press, San Diego, CA.
- MCALPINE, D. F., L. D. MURISON AND E. P. HOBERG. 1997. New records for the pygmy sperm whale, *Kogia breviceps* (Physeteridae) from Atlantic Canada with notes on diet and parasites. Marine Mammal Science 13:701–704.
- MARTINS, H. R., M. R. CLARKE, F. REINER AND R. S. SANTOS. 1985. A pygmy sperm whale, *Kogia breviceps* (Blainville, 1838) (Cetacea: Odontoceti) stranded on Faial island, Azores, with notes on cephalopod beaks in stomach. Ciencias Biológicas 6:63–69.
- MERELLA, P., A. QUETGLAS, F. ALEMANY AND A. CARBONELL. 1997. Length-weight relationship of fishes and cephalopods from the Balearic Islands (western Mediterranean). Naga ICLARM Q. 20(3/4):66–68.
- MUNILLA, I. 1997. Henslow's swimming crab (*Polybius henslowii*) as an important food for yellow-legged gulls (*Larus cachinnans*) in NW Spain. ICES Journal of Marine Science 54:631–634.
- PENAS PATIÑO, X. M., AND A. PIÑEIRO SEAGE. 1989. Cetáceos, focas e tartarugas das costas ibéricas. Consellería de Pesca (Xunta de Galicia), Santiago de Compostela, Spain.
- PLÖN, S., R. T. F. BERNARD, N. T. K. KLAGES AND V. G. COCKCROFT. 1999. Stomach content analysis of pygmy and dwarf sperm whales and its ecological implications: Is there niche partitioning? European Research on Cetaceans 13:336–339.
- RAUN, G. G., H. D. HOESE AND F. MOSELELY. 1970. Pygmy sperm whales, genus *Kogia*, on the Texas coast. Texas Journal of Science 21:269–274.
- RICE, D. W. 1998. Marine mammals of the world-systematics and distribution. Special Publication No. 4. The Society of Marine Mammalogy, Lawrence, KS.
- ROSS, G. J. B. 1979. Records of pygmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons. Annals of the Cape Provincial Museums (Natural History) 11:259–327.
- ROSS, G. J. B. 1984. The smaller cetaceans of the south east coast of southern Africa. Annals of the Cape Provincial Museums (Natural History) 15:173–410.
- SANDERS, N. K., AND J. J. CHILDRESS. 1990. Adaptations to the deep-sea oxygen minimum layer: Oxygen binding by the hemocyanin of he bathypelagic mysid, *Gnathophausia ingens* Dohrn. Biological Bulletin 178:286–294.
- SANTOS, M. B., G. J. PIERCE, P. R. BOYLE, R. J. REID, H. M. ROSS, I. A. P. PATTERSON, C. C. KINZE, S. TOUGAARD, R. LICK, U. PIATKOWSKI AND V. HERNÁNDEZ-GARCÍA. 1999. Stomach contents of sperm whales (*Physeter macrocephalus*) stranded in the North Sea 1990-1996. Marine Ecology Progress Series 183:281–294.
- SANTOS, M. B., G. J. PIERCE, J. HERMAN, A. LÓPEZ, A. GUERRA, E. MENTE AND M. R. CLARKE. 2001a. Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): A review

with new information on the diet of this species. Journal of the Marine Biological Association of the United Kingdom 81:687-694.

- SANTOS, M. B., G. J. PIERCE, C. SMEENK, M. J. ADDINK, C. C. KINZE, S. TOUGAARD AND J. HERMAN. 2001b. Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. Journal of the Marine Biological Association of the United Kingdom 81:143–150.
- SANTOS, M. B., G. J. PIERCE, M. GARCIA HARTMANN, C. SMEENK, M. J. ADDINK, T. KUIKEN, R. J. REID, I. A. P. PATTERSON, C. LORDAN, E. ROGAN AND E. MENTE. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the NE Atlantic. Journal of the Marine Biological Association of the United Kingdom 82:501–507.
- SANTOS, M. B., G. J. PIERCE, A. LÓPEZ, J. A. MARTÍNEZ, M. T. FERNÁNDEZ, E. IENO, E. MENTE, C. PORTEIRO, P. CARRERA AND M. MEIXIDE. 2004. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. International Journal for the Exploration of the Sea CM/Q:09.
- SANTOS, M. B., S. BERROW AND G. J. PIERCE. In press. Stomach contents of a sperm whale *Physeter macrocephalus* calf in Co Clare (Ireland).
- SCHEFFER, V. B., AND J. W. SLIPP. 1948. The whales and dolphins of Washington State with a key to the cetaceans of the west coast of North America. American Midland Naturalist 39:257–337.
- SECCHI, E. R., M. B. CAMPOLIM AND L. M. MÖLLER. 1994. Notas sobre o encalhe de dois cachalotes pigmeus *Kogia breviceps* na costa do Rio Grande do Sul, Brasil. Pages 244–262 *in* Actas, 4 Reunión de Trabajo de Especialistas en mamíferos Acuáticos de América del Sur. 12–15 November 1990, Valdivia, Chile.
- SEQUEIRA, M., A. INÁCIO AND F. REINER. 1992. Arrojamentos de Mamíferos Marinhos na Costa Portuguesa entre 1978 e 1988. Estudos de Biología e Conservação da Natureza 7. Serviço Nacional de Parques, Reservas e Conservação da Natureza, Lisboa, Portugal.
- SEQUEIRA, M., A. INÁCIO, M. A. SILVA AND F. REINER. 1996. Arrojamentos de Mamíferos Marinhos na Costa Continental Portuguesa entre 1989–1994. Estudos de Biología e Conservação da Natureza 19. Serviço Nacional de Parques, Reservas e Conservação da Natureza, Lisboa, Portugal.
- VIDAL, O., L. T. FINDLEY, P. J. TURK AND R. E. BOYER. 1987. Recent records of pygmy sperm whales in the Gulf of California, Mexico. Marine Mammal Science 3:354–356.
- VOSS, N. A., K. N. NESIS AND P. G. RODHOUSE. 1998. The cephalopod family Histioteuthidae (Oegopsida): systematics, biology, and biogeography. Smithsonian Contributions to Zoology 586:293–372.
- WHITEHEAD, P. J. P., M.-L. BAUCHOT, J.-C. HUREAU, J. NIELSEN AND E. TORTONESE (eds.). 1989. Fishes of the North-eastern Atlantic and the Mediterranean. UNESCO, Paris, France.

Received: 4 February 2005 Accepted: 22 November 2005