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Patterns and trends in the diet of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic

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ABSTRACT

There is little previous information on feeding habits of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic. The present study analyzed stomach contents of pilot whales stranded in Portugal (n = 6), Galicia (northwest Spain) (n = 32), and Scotland (United Kingdom) (n = 10), from 1990 to 2011. These animals ranged from 213 to 555 cm in length (24 females, 19 males and 5 of unknown sex). The main prey identified were cephalopods of the families Octopodidae and Ommastrephidae, the former being numerically more important in Iberia (Portugal and Galicia) and the latter more important in Scotland, with Iberian whales also showing a more diverse diet. Multivariate analysis revealed evidence of geographical and seasonal variation in diet. Generalized Additive Modeling results indicated that more octopus (*Eledone cirrhosa*) were eaten in Iberia than in Scotland, more in the first half of the year, and more in larger whales. Numbers of ommastrephid squids in the stomach decreased over the study period and varied with season and whale length. This study confirms cephalopods as the main prey of pilot whales, as previously reported, although our results also suggest that, in the northeast Atlantic, ommastrephid squid are largely replaced as the main prey by octopods at lower latitudes.

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Key words: pilot whale, *Globicephala melas*, diet, northeast Atlantic, stomach content analysis.

The long-finned pilot whale (*Globicephala melas*), herein after referred to as pilot whale, is one of the largest odontocetes, with maximum length recorded as 625 cm (Bloch *et al.* 1993). The species is distributed throughout temperate and subarctic regions of the Northern and Southern Hemisphere, being absent from tropical waters (Reid *et al.* 2003). Although occupying mainly oceanic habitats (Bloch *et al.* 2003, Macleod *et al.* 2007, Azzellino *et al.* 2008, De Stephanis *et al.* 2008*a*), with most sightings recorded in waters over 2,000 m (Baird *et al.* 2002), pilot whales can range over the continental shelf and, in Galicia, the species has occasionally been observed during land-based sightings surveys (Pierce *et al.* 2010*a*).

Several studies have analyzed the stomach contents obtained from pilot whales stranded in different parts of the world (*e.g.*, Desportes and Mouritsen 1993, Gannon *et al.* 1997, Santos and Haimovici 2001, Pierrepont *et al.* 2005, Beatson *et al.* 2007, Beatson and O'Shea 2009, Spitz *et al.* 2011). In general, these studies have found cephalopods to be the main component of pilot whale diet, although fish may also be important (Overholtz and Waring 1991, Spitz *et al.* 2011). The only previous study for the NW Iberian Peninsula was by González *et al.* (1994), who described cephalopod remains in stomach contents of three individuals stranded in Galicia: material from these three samples has been included in the present analysis. There are no previous studies of the diet of this species in UK waters.

Due to the difficulty of carrying out direct observations in their natural habitat, obtaining information on the feeding ecology of cetaceans has traditionally involved the examination of stomach contents of dead animals (either from stranded or directly caught individuals). Although several indirect methods to obtain information on the feeding habits of marine mammals have been developed over the last two to three decades and include the use of fatty acid and stable isotope profiles of predator tissues, DNA analysis of prey remains in feces, *etc.* (for a recent review see Tollit *et al.* 2009), such techniques are most useful once some information on diet is already available, since they rely on the existence of a library of prey "signatures." Because of these limitations, examination of stomach contents remains the most widely used method to study cetacean diet.

Provided that possible biases in the samples available are kept in mind, *i.e.*, that the sample could show an overrepresentation of sick animals not able to feed properly, that prey hard structures are subject to differential digestion, *etc.* (see Pierce *et al.* 2004, Tollit *et al.* 2010 for discussions on the topic), strandings monitoring programs afford an excellent opportunity to study feeding habits and factors affecting cetacean diet. Stomach contents can often be extracted even from partially decomposed carcasses and important ancillary data such as location, date, sex, and body size can also be obtained together with cause of death in some cases. These data can be used then to investigate differences in diet between different population components. In addition, the use of all hard remains has been shown to increase the rate of prey detection, especially for those species which have small and/or fragile otoliths (for example, Brown and Pierce 1998).

As top predators, cetaceans play an important role in marine food webs and improved knowledge of their diet and the factors that can affect it (*e.g.*, season, year, ontogeny, *etc.*) are of considerable importance to help us determine their ecological role, to quantify the predator-prey relationships, and to evaluate the possible threats these predators could be facing (*e.g.*, prey depletion due to overfishing, changes in prey distribution, and availability due to other anthropogenic pressures such as climate change, Pierce *et al.* 2004). In the case of pilot whales their oceanic habitat and deep diving capabilities make direct observations of whale feeding a challenge, and as with many other odontocete species, information on diet and on basic life history has been obtained by the study of stranded individuals and those obtained by direct hunt, which is still carried out in the Faroe Islands (*e.g.*, Desportes and Mouritsen 1993).

The main goals of the present study are therefore: (1) to describe the feeding habits of pilot whales in the northeast Atlantic based on the analysis of the stomach contents obtained from animals stranded in three different geographical locations (Portugal, Scotland, and northwest Spain) and (2) to analyze the dietary variability in relation to area, year, season, length, and sex of the whales.

METHODS

Sample Collection

In our study area, three stranding monitoring programs are responsible for the examination of marine mammal carcasses and the collection of samples. Strandings are attended in all cases by experienced personnel, from the Sociedade Portuguesa de Vida Selvagem (SPVS) in northern Portugal, from the Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA) in Galicia (northwest Spain), and from the Scottish Agriculture College Veterinary Science Division (SAC) in Scotland. In all cases, when the condition of the animal permitted it, detailed necropsies were performed. Otherwise, basic measurements/information (*i.e.*, length, sex, decomposition state) and samples were collected (*i.e.*, teeth, blubber, and, when possible, stomach contents). Since not all animals were assessed for maturity status, we summarized the likely distribution of maturity stages based on body length, following Bloch *et al.* (1993).

Monitoring of strandings along the Galician coast started in 1990. A mean of 183 animals stranded per year between 1990 and 2010. Of 232 long-finned pilot whales recorded over this period, detailed necropsies were carried out on 56 whales and stomach contents were obtained from 32 of them. In Scotland, the strandings monitoring network started in 1992 and registered a mean of 152 cetacean strandings per year, with a total of 149 pilot whales strandings up until June 2011. Of these, only the animals in a fresh state were sent for detailed necropsies (n = 24) and of the 24, stomach contents were recovered from 10 animals. A detailed monitoring program in the center and north of Portugal (with active search and detailed necropsies on stranded animals carried out whenever possible) began in 2000, registering *ca.* 160 strandings per year. A total of 17 pilot whales was recorded stranded in this area up to 2011, with stomach contents being recovered from seven out of the eight animals which were fully necropsied. One of these seven animals with nonempty stomachs had only milk in its stomach and further analysis therefore refers to six whales from Portugal. Thus, from 1990 to June 2011, a total of 48 nonempty stomachs were collected and analyzed (Fig. 1, Table 1).

All nonempty stomachs were either taken to the laboratory whole or dissected on the beach. Stomachs contents were preserved frozen or in 70% ethanol prior to further analysis. Prey remains consisted almost exclusively of cephalopod mandibles (beaks), which were preserved in 70% ethanol, as were crustacean and other mollusc remains. Some fish otoliths, bones, and eye lenses were also found and these remains were stored dry.

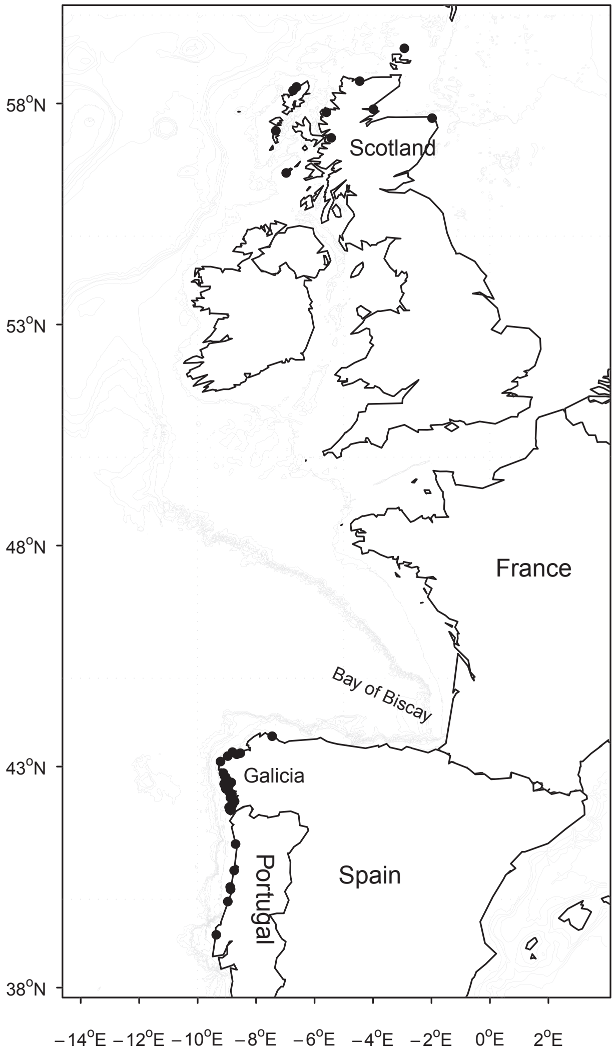

Figure 1. Map of the northeast Atlantic showing the location of the strandings of pilot whales (*Globicephala melas*) from which stomach contents were analyzed in this study (*n* = 48).

Sample Analysis

The cephalopod beaks, and fish otoliths and bones were identified using published guides (Clarke 1986, Harkonen 1986, Watt *et al.* 1997, Tuset *et al.* 2008) and reference collections of cephalopod beaks (provided by Malcolm Clarke from his extensive collection identified from the stomach of predators) and of fish otolith and bones from the northeast Atlantic held at the University of Aberdeen. In practice, very few fish otoliths were recovered and other fish remains (*e.g.*, vertebrae, other bones, and eye lenses) were therefore also used to identify the prey taken, when possible, and to

Table 1. Summary of composition of sampled pilot whales in each year period, by season (quarter), sex, area, and maturity. The second table summarizes the sample composition by area in relation to sex and maturity. Season: Q1, January–March; Q2, April–June; Q3, July–September; Q4, October–December. Sex: F, female; Ma, male; U, unknown. Location: PT, Portugal; GAL, Galicia; SCOT, Scotland; Maturity (inferred from length): I, immature; M, mature, U, unknown.

		Quarter				Sex			Area			Maturity		
Years	*n*	Q1	Q2	Q3	Q4	F	Ma	U	PT	GAL	SCOT	I	M	U
1990–1995	13	3	8	1	1	6	6	1	0	11	2	11	2	0
1996–2000	12	6	5	0	1	6	6	0	0	10	2	5	7	0
2001–2005	7	2	3	2	0	3	3	1	2	2	3	5	1	1
2006–2011	16	4	10	2	0	9	4	3	4	9	3	6	8	2
Total	48	15	26	5	2	24	19	5	6	32	10	27	18	3

		Sex			Maturity		
Location	*n*	F	Ma	U	I	M	U
PT	6	2	2	2	1	3	2
GAL	32	17	12	3	19	10	1
SCOT	10	5	5	0	5	5	0
Total	48	24	19	5	25	18	3

quantify the number of fish taken. Not all remains could be identified to species. Thus, the highest number of otoliths (18) was recovered from a whale stranded in Scotland but these otoliths could not be identified since they did not correspond to any of the many species available in the reference collection or in the published guides for the northeast Atlantic.

The minimum number of individual cephalopods of a taxon present in each stomach was estimated from the numbers of upper or lower beaks, whichever was higher. Likewise, the minimum number of fish of each taxon present in each stomach was estimated by counting sagittal otoliths and three of the jaw bones (premaxilla, dentary, maxilla), and using the most numerous. Each otolith, premaxilla, dentary, or maxilla was assumed to represent 0.5 fish, while each upper or lower beak represented one cephalopod. Crustacean and other mollusc remains were identified to the lowest possible taxon, although identification was usually difficult due to the poor state of preservation in which they were found.

Prey length and weight were estimated from beak and otolith dimensions using a compilation of published regressions (see Table S1). For cephalopods, since complete pairs of beaks were rarely present, weight and length were estimated using, in most cases, the lower beak measurements (rostral length for squid and hood length for octopus and sepiolids; Clarke 1986). For stomachs in which a cephalopod species was represented by more than 30 beaks, we measured a random sample of around 10% of the total number of beaks of that species (not less than 30 beaks). In fish, size estimates were mainly based on otolith length (Härkönen 1986) or width for any otolith broken lengthways. All measurements were taken with a binocular microscope, fitted with an eyepiece graticule, or with calipers. When identification to species level was not possible and remains were assigned to a group of species (*e.g.*, family or genus), the regression used to estimate fish size was based on a combination of data from all (relevant and available) species of that grouping (see Table S1). No correction was applied to the estimates of fish size obtained from otoliths to take account of potential gastric erosion. The measurement of only uneroded otoliths, which has been suggested as a possible solution to this problem, was not possible in our case since all fish material was found in a digested state with no flesh remaining.

Although all identifiable hard remains were used to estimate the numerical proportion of each prey taxa, only measurements of cephalopod beaks and fish otoliths were used to calculate original prey size. Therefore, because prey (generally fish) were sometimes represented only by other remains, *e.g.*, bones or eye-lenses, the proportion of fish (by weight) in the diet could be underestimated.

Analysis of Dietary Variation

Overall diet of pilot whales in each area was quantified using three standard indices (Hyslop 1980): (1) frequency of occurrence of each prey type (calculated as the number of stomachs where prey *i* was found divided by the total number of non-empty stomachs examined), (2) numerical proportion of each prey type *i* in relation to the total number of individual prey (calculated by adding all individuals of prey type *i* identified in all stomachs and dividing this total by the summed number of all individuals of all prey in all the stomachs), and (3) proportion of the total reconstructed prey weight represented by each prey type, calculated similarly to (2). For the latter two indices, the totals are those for all stomachs combined. This approach implies that no explicit weighting is applied to each sample (stomach) when estimating overall diet, so that animals with larger amounts of food in the stomach contribute relatively more to the estimated overall diet. Alternative weightings, for example equal weighting, are possible but this latter approach would assume that all whales, regardless of their size or the amount of food in their stomachs, contribute equally to the overall amount of food removed. For a discussion of the issue and the consequences of applying different weightings see Pierce *et al.* (2007) and Tollit *et al.* (2010).

To determine which explanatory variables may influence the stomach contents of pilot whales, the numerical importance of the main prey types in the diet was analyzed using a combination of multivariate exploration based on Redundancy Analysis (RDA) and univariate modeling using Generalized Additive Models (GAM), as implemented in Brodgar 2.7.2 (http://www.brodgar.com). The response variables were numbers of each type of prey present in individual stomach samples rather than estimated total weights since the latter are subject to additional errors. Specifically, not all individual prey were identified from cephalopod beaks or fish otoliths but only beaks and otoliths were measured to obtain prey sizes and weights, it was not possible to account for digestive size reduction of measured hard parts, and, finally, some weights were estimated using regression equations constructed using combined data from several prey species.

All data series were explored for outliers, collinearity, heterogeneity of variance and interactions between variables, and to visualize the relationships between response and explanatory variables, following the protocol proposed by Zuur *et al.* (2010). RDA was then used to visualize any patterns in the set of response variables (prey numbers) as well as any relationships between the set of response variables and the various explanatory variables. To avoid the results being unduly influenced by rare prey types, to deal with prey groups such as the genus *Histioteuthis* for which a substantial proportion of individuals could not be identified to species, and to use as much of the available stomach contents information as possible, prey categories were amalgamated, leaving the following groups: *Eledone cirrhosa*, *Octopus vulgaris*, *Chiroteuthis* spp., *Histioteuthis* spp., *Illex*/*Todaropsis*, *Todarodes sagitattus*, *Sepia* spp., *Teuthowenia megalops*, *Gonatus* spp., Sepiolidae, and fish. RDA employs permutation-based tests to identify statistically significant effects of explanatory variables. Here we used 9,999 permutations of the data (see Zuur *et al.* 2007). The explanatory variables considered were year, month, area of stranding (Portugal, Galicia, or Scotland, using Galicia as the reference value), sex (females used as the reference), and length. Because RDA assumes approximately linear relationships between response variables and explanatory variables, scores on axes 1 and 2 were plotted against continuous explanatory variables to check for evidence of serious nonlinearity.

Secondly, we used GAMs to analyze the effect of the explanatory variables on the numerical importance of the two most abundant prey categories (*Eledone cirrhosa* and *Illex*/*Todaropsis*). In addition, since exploratory analysis suggested a strong pattern in fish occurrence we also analyzed numerical importance of fish. Since the response variables were based on abundance (count data), a discrete probability distribution was applied. For the cephalopods we used a negative binomial error distribution with log link to account for overdispersion. Fish numbers adequately fitted a Poisson distribution. The explanatory variables were the same used for the RDA. We treated length, year, and month as continuous variables and their effects were thus included as smoothers. Although year and month are strictly speaking discrete variables, this approach has the advantage of providing a visualization of trends and the possibility of reducing degrees of freedom. For length and month, the complexity of smoothers was constrained by setting a maximum number of "knots" ($k = 4$). Since there is no reason to expect a simple relationship with year, no constraint was set for the year effect. Backwards selection was applied to identify the best models, with the optimum model being the one that presented the lowest Akaike Information Criterion (AIC, Akaike 1974) value, together with no obvious patterns in the residuals or highly influential data points ("hat" values) (see Zuur *et al.* 2007). If "final" models contained nonsignificant terms, the consequence of removing these was tested using an F-test; they were retained if they significantly improved the model fit.

RESULTS

Composition of the Sample of Pilot Whales

Of the 48 pilot whales for which stomach contents were obtained, 6 had stranded along the coast of northern Portugal, 32 in Galicia (northwest Spain), and 10 in Scotland (Table 1). The final set of samples comprised stomach contents from 24 females, 19 males, and 5 individuals for which sex could not be determined due to the poor state of preservation of the carcasses. Most of the whales in the sample had stranded in the first half of the year (1st and 2nd quarters). The length of the animals ranged between 213 and 555 cm (Fig. 2). Following the length-based criteria of Bloch *et al.* (1993) most of the sample set comprised immature individuals (Table 1).

Diet Composition

Remains of 2,347 individual prey items were recovered from the stomachs. Pilot whale diet consisted mainly of cephalopods (98.9% by number), but also included fish, crustaceans, and other molluscs (0.9%, 0.1%, and <0.1% by number, respectively) (Table 2).

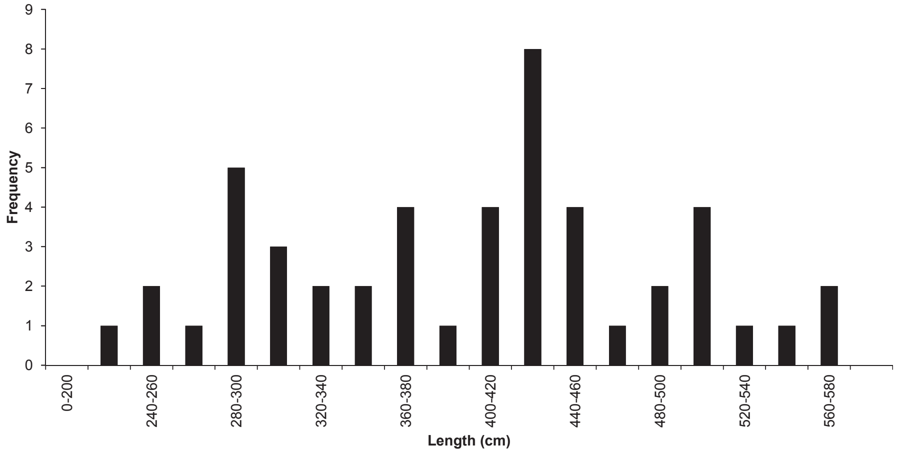

Figure 2. Size distribution of pilot whales (*Globicephala melas*) stranded in northern Portugal, Galicia (northwest Spain) and Scotland with nonempty stomachs analyzed in this study (n = 48).

Overall, remains of 2,322 individual cephalopods belonging to at least 18 species of 12 families were found, corresponding to a total reconstituted mass of *ca.* 694 kg. In terms of numerical importance, Octopodidae were the most abundant group in Iberian samples (58.2% in Portugal and 72.3% in Galicia), with *Eledone cirrhosa* being the most abundant species (Table 2, Fig. 3). In terms of biomass, Octopodidae were by far the most important prey group for the whales stranded in Galicia (representing more than 78% of the reconstructed weight of all prey), with *E. cirrhosa* again being the most important prey species (58.6% by weight) (Table 2). The family Ommastrephidae was the most abundant prey group taken by the pilot whales stranded in Scotland (36.6% by number), contributing more than 80% to the reconstructed prey weight. It was also the most important group by weight in the diet of whales stranded in Portugal, although not the most numerous. The ommastrephid squid *Todarodes sagitattus* was the main prey species by weight in both Scotland and Portugal (80.6% and 53% by weight, respectively), although it only represented one-third of the prey numbers in Scotland and half that amount in Portugal, reflecting the relative large size of the individual squid (*e.g.*, those in samples from Scotland ranged from 21 to 54 cm dorsal mantle length) (Table 2). Fish remains appeared in a total of 12 stomachs across the three areas, almost always representing very small numbers of fish (one or two), the exception being a Scottish sample that contained 18 otoliths. Although identification of the eroded fish remains was difficult, fish belonging to the family Gadidae were identified in Scotland and fish of the Gadidae, Merluccidae, and Carangidae in Galicia. Crustacean remains were found in three stomachs, generally in a poor state of preservation, and only remains of the swimming crab *Polybius henslowii* could be identified to species level in the stomach of one of the Galician whales.

Dietary Variation

RDA on the 11 response variables indicated that, overall, 17% of dietary variation was captured in the RDA axes, with axes 1 and 2 explaining 6.0% and 4.7% of variance, respectively. The first RDA axis was most strongly related to numbers of

Table 2. Prey species identified from the stomach contents of *Globicephala melas* stranded in Portugal (PT, *n* = 6), Galicia (GAL, *n* = 32), Scotland (SCOT, *n* = 10) and for the whole sample set. Dietary importance is shown as % frequency of occurrence (%F), % importance by number (%N), and % importance by weight (%W).

	PT			GAL			SCOT			Total		
Prey species	%F	% N	%W	%F	% N	%W	%F	% N	%W	%F	% N	%W
Cephalopods	100	99.6	100	100	99.5	99.9	100	78.9	99.5	100	98.9	99.9
Sepiidae	33.3	2.9	0.4	28.1	2.5	0.2	0.0	0.0	0.0	22.9	2.4	0.2
Sepia sp.	33.3	2.9	0.4	28.1	2.5	0.2	0.0	0.0	0.0	22.9	2.4	0.2
Sepiolidae	0.0	0.0	0.0	9.4	0.4	0.0	0.0	0.0	0.0	6.3	0.3	0.0
Rossia sp.	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.1	0.0
Sepiola atlanticus	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.1	0.0
Gonatidae	16.7	1.8	0.1	9.4	0.5	0.2	40.0	15.5	3.3	16.7	1.1	0.3
Gonatus sp.	16.7	1.8	0.1	9.4	0.5	0.2	40.0	15.5	3.3	16.7	1.1	0.3
Lepidoteuthidae	0.0	0.0	0.0	3.1	0.1	0.4	0.0	0.0	0.0	2.1	0.0	0.3
Lepidoteuthis rimaldii	0.0	0.0	0.0	3.1	0.1	0.4	0.0	0.0	0.0	2.1	0.0	0.3
Histioteuthidae	33.3	4.3	0.5	9.4	1.2	0.3	20.0	14.1	6.9	14.6	1.9	0.7
Histioteuthis reversa	16.7	3.6	0.3	3.1	1.0	0.2	10.0	1.4	0.1	6.3	1.3	0.2
Histioteuthis Type A	33.3	0.7	0.3	6.3	0.1	0.1	10.0	12.7	6.8	10.4	0.6	0.4
Brachioteuthidae	0.0	0.0	0.0	3.1	0.1	0.0	10.0	1.4	0.0	4.2	0.1	0.0
Brachioteuthis riisei	0.0	0.0	0.0	3.1	0.1	0.0	10.0	1.4	0.0	4.2	0.1	0.0
Ommastrephidae	50.0	24.3	57.6	84.4	18.3	19.8	60.0	36.6	83.5	75.0	19.6	28.9
Illex /Todaropsis	50.0	8.6	4.6	65.6	16.5	14.4	0.0	0.0	0.0	50.0	15.1	12.1
Todarodes sagitattus	33.3	15.7	53.0	25.0	1.2	5.3	40.0	32.4	80.6	29.2	3.9	16.5
Chiroteuthidae	50.0	7.1	1.4	18.8	0.7	0.1	0.0	0.0	0.0	18.8	1.4	0.3
Chiroteuthis veranii	33.3	3.2	0.3	12.5	0.3	0.1	0.0	0.0	0.0	12.5	0.6	0.1
Chiroteuthis Type II	33.3	3.9	1.1	3.1	0.1	0.0	0.0	0.0	0.0	6.3	0.6	0.2
Mastigoteuthidae	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Mastigoteuthis schmidti	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Cranchiidae	33.3	0.7	0.1	15.6	3.3	0.3	10.0	1.4	0.5	16.7	2.9	0.3

(Continued)

Table 2. (Continued)

	PT			GAL			SCOT			Total		
Prey species	%F	% N	%W	%F	% N	%W	%F	% N	%W	%F	% N	%W
Taonius pavo	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Teuthowenia megalops	33.3	0.7	0.1	15.6	3.2	0.3	10.0	1.4	0.5	16.7	2.9	0.3
Alloposidae	0.0	0.0	0.0	3.1	0.1	0.2	0.0	0.0	0.0	2.1	0.0	0.1
Haliphron atlanticus	0.0	0.0	0.0	3.1	0.1	0.2	0.0	0.0	0.0	2.1	0.0	0.1
Octopodidae	66.7	58.2	40.0	81.3	72.3	78.3	20.0	7.0	5.3	66.7	68.7	68.7
Eledone cirrhosa	66.7	51.4	38.6	78.1	64.3	58.6	20.0	7.0	5.3	64.6	61.1	52.8
Octopus vulgaris	50.0	6.8	1.4	37.5	8.0	19.7	0.0	0.0	0.0	31.3	7.6	15.9
Unidentified Cephalopoda	16.7	0.4	0.0	9.4	0.3	0.0	20.0	2.8	0.0	12.5	0.3	0.0
Fish	16.7	0.4	0.0	21.9	0.4	0.1	40.0	18.3	0.5	25.0	0.9	0.1
Gadidae	0.0	0.0	0.0	3.1	0.1	0.0	10.0	2.8	0.5	4.2	0.1	0.0
Micromesistius poutassou	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Merlucciidae	0.0	0.0	0.0	3.1	0.1	0.1	0.0	0.0	0.0	2.1	0.0	0.1
Merlucius merlucius	0.0	0.0	0.0	3.1	0.1	0.1	0.0	0.0	0.0	2.1	0.0	0.1
Carangidae	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Trachurus sp.	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Unidentified fish[a]	16.7	0.4	0.0	12.5	0.2	0.0	30.0	15.5	0.0	16.7	0.7	0.0
Crustacea	0.0	0.0	0.0	6.3	0.1	0.0	10.0	1.4	0.0	6.3	0.1	0.0
Polybius henslowii	0.0	0.0	0.0	3.1	0.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Unidentified Crustacea	0.0	0.0	0.0	3.1	0.1	0.0	10.0	1.4	0.0	2.1	0.1	0.0
Mollusc	0.0	0.0	0.0	0.0	0.0	0.0	10.0	1.4	0.0	2.1	0.0	0.0

[a] Weight could not be estimated.

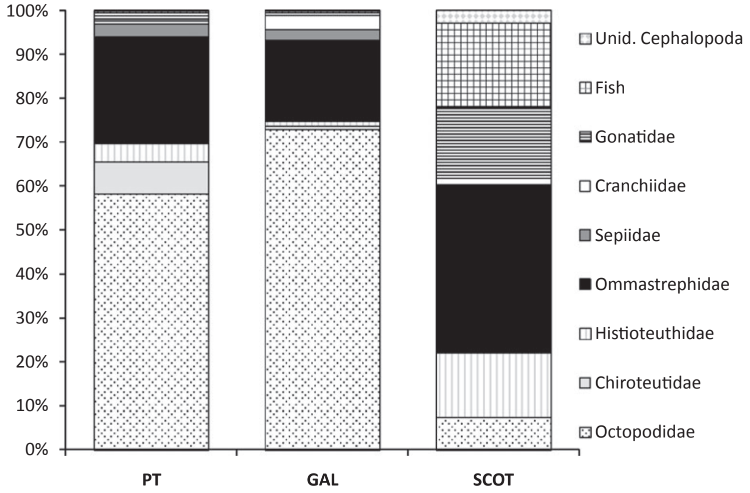

Figure 3. Numerical importance of the main prey families identified from the stomachs of the pilot whales analyzed in this study (PT: Portugal; GAL: Galicia; SCOT: Scotland). Unid. Cephalopoda: unidentified cephalopods.

Octopus vulgaris while axis 2 was related to the occurrence of fish, sepiolids, *Chiroteuthis* spp. and *Teuthowenia megalops*. Numbers of fish were negatively related to numbers of most cephalopod groups except *O. vulgaris* and *Gonatus* sp. Statistical tests for conditional effects indicated effects of region (Scotland differed from Galicia) and year ($P = 0.037$ in both cases). Examination of biplots also suggested a possible relationship between numbers of fish and body length. Retrospective exploration of relationships between RDA axis scores and continuous explanatory variables suggested possible nonlinear relationships between the axis 1 score and both month and length. The existence of nonlinear relationships between response and explanatory variables would violate the assumptions of RDA and may have prevented detection of effects of month and length. Since the multivariate dietary patterns were weak, no further analysis was carried out using RDA.

Results from the GAMs indicated that the numbers of *Eledone cirrhosa* (N_E) in pilot whale stomachs were significantly related to area ($P < 0.0001$), whale length ($P < 0.0001$), month of stranding ($P = 0.0078$), and year ($P = 0.0443$). The model explained 71.4% of deviance. There was a wide range of hat values with four values exceeding 0.8 although none exceeded 1.0. Smoothers illustrated in Figure 4A suggest that the numerical importance of *E. cirrhosa* in the diet increased with whale length (reaching an asymptote around 350 cm) and increased during the first half of the year (although wide confidence limits, especially in the second half of the year obscured any further trend). There was also a significant effect of region, with fewer *E. cirrhosa* in the stomachs of the pilot whales stranded in Scotland than in whales stranded in Spain or Portugal ($P < 0.0001$ in both cases). Numbers of *E. cirrhosa* found were highest in 1995, 2001, and 2011.

The final model for the numerical abundance of the ommastrephid group *Illex/Todaropsis* in pilot whale stomach contents (chosen on the basis of lowest AIC and absence of patterns in residuals or influential data points) explained 50.7% of

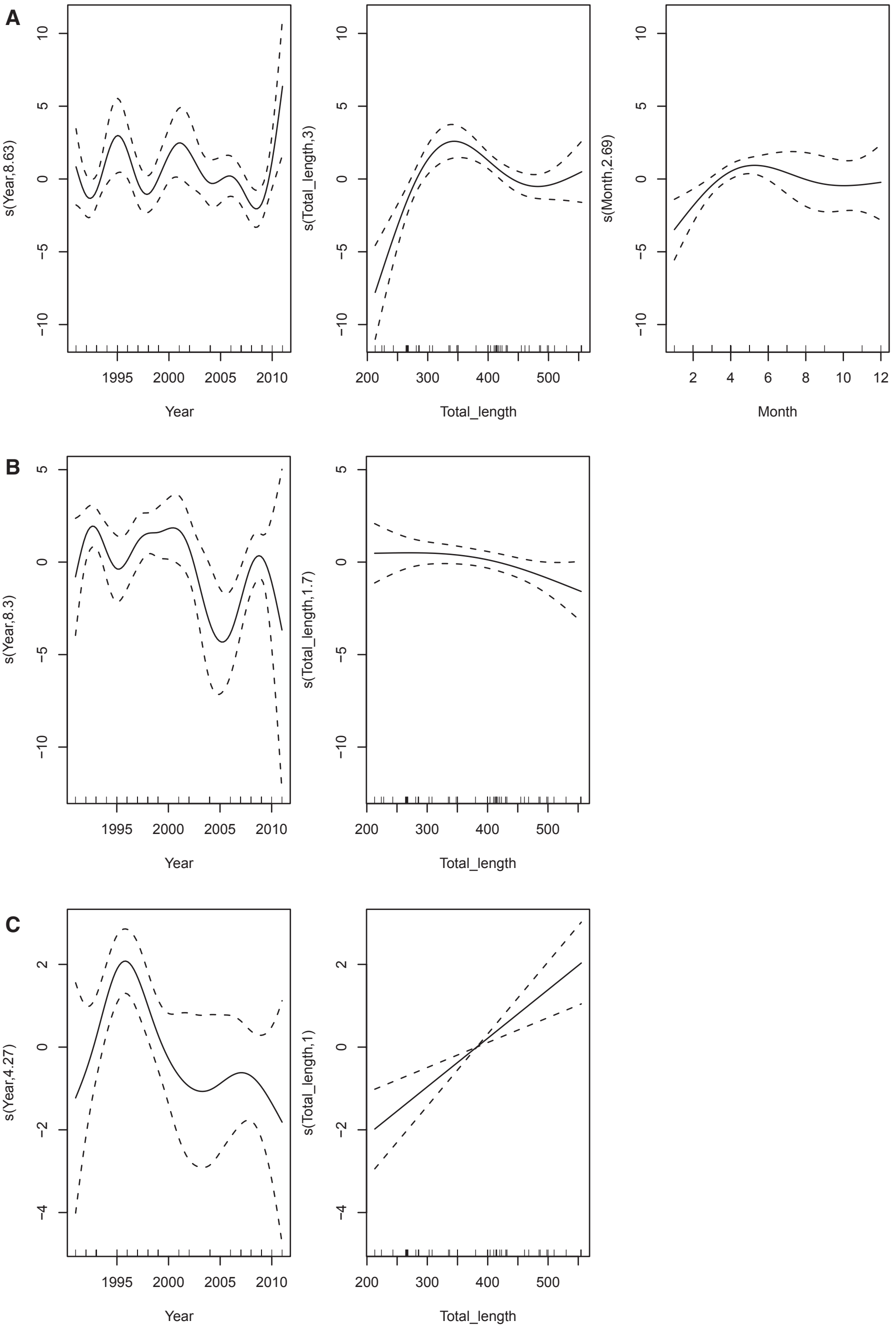

Figure 4. Relationships between numerical importance of *Eledone*, *Illex/Todaropsis* and fish in the stomachs of pilot whales and explanatory variables as visualized by fitting GAMs. (A) Smoothers for the effect of year, pilot whale length (cm), and month on *Eledone* numerical importance. (B) Smoothers for the effect of year and pilot whale length on *Illex/Todaropsis* numerical importance. (C) Smoothers for the effect of year and pilot whale length on numerical importance of fish. Dotted lines are 95% confidence intervals.

deviance and included a significant effect of year ($P = 0.0065$) and a nonsignificant effect of pilot whale length ($P = 0.0611$), which, nevertheless, significantly improved overall goodness of fit (F test, $P < 0.05$). Smoothers illustrated in Figure 4B suggest that the numerical importance of these ommastrephids in the diet decreased with increasing pilot whale length. Numbers eaten were lowest in 2005.

The final (Poisson) model for numerical importance of fish (selected using the same criteria mentioned in the previous paragraph) included effects of sex (females ate more fish than males, $P = 0.0057$), year (most fish taken around 1996, $P = 0.0138$), and length (increased predation on fish in larger individuals, $P < 0.0001$) (Fig. 4C).

DISCUSSION

Diet Composition

Remains of at least 22 prey species belonging to 16 families were identified from the stomach contents in our study and, with the exception of three species of fish and one crustacean, all remaining prey types were cephalopods. This apparent preference for cephalopods as prey is consistent with most previous studies of the diet of pilot whales carried out in other areas, which described the diet of this species as consisting mainly of squid. In the Faroe Islands, analysis of stomach contents from 391 animals killed for human consumption showed the main prey species to be the oceanic squids *Todarodes sagittatus* and *Gonatus* sp. (Desportes and Mouritsen 1993). In the western Atlantic, the main prey of 30 whales accidentally captured off the northeastern United States consisted of the neritic squid *Loligo pealei*, followed by oceanic squids of the families Ommastrephidae and Histioteuthidae (Gannon *et al.* 1997). In Brazil, the stomachs of fives whales stranded from 1985 to 1998 contained remains of squid of the oceanic families Lycoteuthidae, Histioteuthidae, and Cranchiidae (Santos and Haimovici 2001). Cephalopods were also found as the main prey category in pilot whales stranded in France (Pierrepont *et al.* 2005), New Zealand (Beatson *et al.* 2007, Beatson and O'Shea 2009), and the Bay of Biscay (Spitz *et al.* 2011).

The number of cephalopod species (18) identified from Galicia (our biggest sample set with 32 stomachs analyzed) is quite high, particularly when compared with the numbers identified from other studies with bigger sample sizes, although our samples were collected over an extended time period (almost 20 yr). Desportes and Mouritsen (1993) identified 13 cephalopod taxa in 391 stomachs contents obtained from the carcasses of pilot whales landed in the Faroe Islands as part of their annual hunt.

Diet Variability

We found evidence of geographical, seasonal, and ontogenetic variation in the diet of the pilot whales examined. Scottish whales had consumed a higher number of squids (oceanic species in all cases) when compared with the Iberian whales (northern Portugal and Galicia), for which the lesser octopus (*Eledone cirrhosa*), constituted the most numerous prey in the diet. *E. cirrhosa* is a benthic species found over a wide range of water depths. Although mainly recorded between 50 and 300 m (Belcari *et al.* 2002, Hastie *et al.* 2009), it has also been found in waters up to 800 m depth (Belcari *et al.* 2002, Pierce *et al.* 2010*b* and references therein). Other prey found in the stomachs included the common octopus, *Octopus vulgaris*, another benthic species but with a more restricted depth distribution, having been recorded from the coast to

200 m depth (Hastie *et al.* 2009, Pierce *et al.* 2010*b* and references therein). It is worth noting that in northwest Iberia, long-finned pilot whales are occasionally sighted from the coast (in Galicia they are the fifth most frequently sighted species from land-based surveys; Pierce *et al.* 2010*a*), although most sightings in the area have taken place in waters off the shelf or on the shelf break.

The prevalence of octopus in the diet of long-finned pilot whales is also reported in a recent study based on analysis of 11 stomachs of pilot whales stranded in the Bay of Biscay (Spitz *et al.* 2011). The authors found benthic octopods to be the main prey in the stomachs analyzed (21.1% of prey biomass), followed by oceanic squids, such as *Todarodes sagitattus* and *Histioteuthis reversa* (17.2% and 10.7% of prey biomass, respectively). Cuttlefish (*Sepia sp.*) have also been recorded in the diet of long-finned pilot whales, being the most numerous prey in stomachs of two pilot whales that stranded on the French Atlantic coast, with *E. cirrhosa* representing only 14.3% of the total number of prey (Pierrepont *et al.* 2005). The second most important prey family identified in our study is the squid family Ommastrephidae. Of the species present in the diet, *Todarodes sagitattus* has an oceanic distribution, while *Illex coindettii* and *Todaropsis eblanae* are also recorded in shelf waters (Guerra 1992).

Long-finned pilot whales are widely distributed in the cold temperate waters of the northeast Atlantic but little is known on its population structure and movements in the area. Fullard *et al.* (2000) analyzed microsatellite DNA of whales from the East coast of the United States, West Greenland, the Faroe Islands, and the United Kingdom and the authors reported that their results did not support a simple isolation-by-distance model of population differentiation. The authors explained the pattern found in their samples as possible if population differentiation occurs in areas of different sea surface temperature. Smaller-scale studies based on genetic and stable isotope results, together with photoidentification studies carried out in the Strait of Gibraltar, suggest that at least some pilot whales are resident all year round and show a complex social structure constituted by several clans containing several pods each (De Stephanis *et al* 2008*b*). No information exists for other areas of the Northeast Atlantic. Desportes and Mouritsen (1993) noted that all prey species found in the stomach contents of pilot whales killed off the Faroes were common species in the area, but the authors also suggested that pilot whales showed a preference for the oceanic ommastrephid squid, *Todarodes sagitattus*, when this species was available in high numbers, information that these authors obtained from fishery data since this cephalopod species is also exploited commercially. As a mainly teuthophagous species, long-finned pilot whale is clearly in some respects a specialist feeder. However, the wide range of prey species recorded in the diet by several authors and the geographical differences in the main prey taken by the pilot whales would suggest a more generalist feeding behavior, with whales feeding on the most abundant cephalopod species in each area with several authors suggesting that it is the abundance and movements of prey that drives pilot whale abundance and movements. In addition to this suggestion being made for pilot whales and *T. sagittatus* off the Faroe Islands (Desportes and Mouritsen 1993, Zachariassen 1993, Jákupsstovu 2002), pilot whales have also been reported to be associated with *Illex illecebrosus* off Newfoundland (Mercer 1975) and *Loligo pealei* and *Scomber scombrus* off the United States (Payne and Heinemann 1993).

The three main prey categories for pilot whales identified in our study are also among the most important cephalopod species marketed in Spain and Portugal, with mean annual landings in Galicia alone of 1,423 tons and 2,800 tons, for *Eledone cirrhosa* and *Octopus vulgaris* respectively and 3,154 tons of ommastrephids, between

1997 and 2010 (http://www.pescadegalicia.com). Little is known on the abundance of noncommercial cephalopods since many of these species live in oceanic open waters and therefore they are rarely found in research surveys which tend to cover mainly fish resources in shelf waters. Because of this lack of data, the assumption that pilot whales feed on the most abundant prey species, so that diet differences would be due to the local availability of potential prey, is difficult to prove since there is no contemporary information on the local abundance of many of the prey species (and sizes) identified in the diet.

Besides the variation in pilot whale feeding habits in relation to geographical area, evidence of ontogenetic changes in diet was detected in our samples. Larger whales ingested a higher number of *E. cirrhosa*, this relationship reaching an asymptote at around 350 cm whale length, *i.e.*, before the animals normally reach sexual maturity (Bloch *et al.* 1993), and also more fish. There was also a nonsignificant tendency for larger whales to eat fewer ommastrephid squids of the genera *Illex/Todaropsis*. Smaller whales, in contrast, showed a more varied diet. Juvenile whales could be limited in their ability to capture prey, either due to inexperience or physiological limitations. Thus they may not be able to swim as fast as adults, perhaps an issue for the capture of fast swimming prey species or may lack the capacity to carry out deep and/or long dives needed to reach and search the seafloor for benthic octopus, at least in deeper waters. Variation in the diet of individuals of different reproductive status, length and age has been previously described for this species (Desportes and Mouritsen 1993), as well as for other odontocetes such as bottlenose dolphin (Blanco *et al.* 2001, Santos *et al.* 2007), common dolphin, *Delphinus delphis*, (Silva 1999), and harbor porpoise, *Phocoena phocoena* (Santos *et al.* 2004). Desportes and Mouritsen (1993) found that although cephalopods represented the main prey of Faroese pilot whales, calves measuring less than 300 cm ate smaller cephalopods and that the consumption of shrimp and fish also varied between groups of whales of different length and reproductive status.

Our results suggest that the consumption of several prey categories fluctuates significantly year to year. Few data are available to indicate abundance of the main prey categories, although fishery statistical data from ICES subarea IX (west of the Iberian Peninsula) suggest that ommastrephid (virtually all of which will be *Illex coindetii* and *Todaropsis eblanae*, Pierce *et al.* 2010*b*) abundance has fluctuated widely. Landings in the early 1990s were low, as little as 250 tons in 1993, before rising to a peak of almost 3,000 tons in 1997 before declining again reach slightly over 300 tons in 2007. A similar trend was seen in Bay of Biscay waters (ICES 2000, 2011). Our dietary data are clearly inadequate to test whether diet has tracked prey abundance, but there was evidence of a decline in the numerical importance of *Illex* and *Todaropsis* in pilot whale diet during approximately 2000 to 2005.

The higher importance of octopus in the diet of pilot whales found in the present study (and by Spitz *et al.* 2011) compared to most previous studies probably reflects a latitudinal trend, with squids (mainly ommastrephids) dominating the diet at higher latitudes while octopods are more important at lower latitudes. These differences could relate to differences in prey availability, but there are no relevant abundance estimates for these cephalopod groups and this hypothesis is not presently testable.

Improving our knowledge of the factors affecting the diet of deep divers such as pilot whales could help us to understand the trophic links within these systems and also the relationships between oceanic and shelf waters that this predator seems to be able to exploit simultaneously. It would be interesting to understand why the whales appear to take mostly prey species of relatively low energy density. Few data exist on the calorific values of oceanic cephalopods although some figures are available for neritic species. For example, Spitz *et al.* (2011) gave values of 4.7 kJ/g for *E. cirrhosa* and 4.4 kJ/g for squid of the family Ommastrephidae (only *Illex coindetti* and *Todaropsis eblanae* were analyzed). These values are similar to those for fish of the family Gadidae but are quite low when compared with the energetic content of some other fish such as clupeids and some myctophids. In principle, diet selection is expected to reflect a trade-off between calorific content of the prey and the energetic cost of capturing them, suggesting that prey species such as *Eledone cirrhosa* may be particularly abundant and/or easy to capture. However, it is also true that not all biases can be accounted for when inferring the diet of a species by the analysis of the stomach contents of stranded individuals, *e.g.*, complete digestion of certain prey, lack of information from animals with empty stomachs, and, ultimately, the combination of the information obtained from several methods (stomach contents analysis, stable isotopes, fatty acids, *etc.*) probably represents the best approach to improve our knowledge on the feeding ecology of these species.

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SUPPORTING INFORMATION

The following supporting information is available for this article online: http://onlinelibrary.wiley.com/doi/10.1111/mms.12015/suppinfo.

Table S1. Regression equations used to estimate fish and cephalopod sizes: L, total length (mm) for fish and dorsal mantle length (mm) for cephalopods; W, total weight (g); OL, otolith length (mm); OW, otolith width (m); LHL, lower hood length; LRL, lower rostral length (mm); UHL, upper hood length; URL, upper rostral length. Sources are as follows: Cl, Clarke (1986); Co, Coull *et al*. (1989); GP, Graham Pierce (unpublished data); Ha, Harkönen (1986); Sa, Santos *et al*. (2002); AG, Angel González (unpublished data); S, Santos *et al*. (2007); *, combined data from more than one species.