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Variability in the diet of bottlenose dolphin, *Tursiops truncatus*, in Galician waters, north-western Spain, 1990–2005

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We describe the diet of bottlenose dolphins *Tursiops truncatus* in Galician waters, north-western Spain, based on 82 non-empty stomachs recovered and analysed from stranded animals between 1990 and 2005, quantifying interannual and seasonal variation in the diet, as well as dietary variation related to sex and size. The most important prey species (in terms of numerical importance and biomass) were blue whiting (*Micromesistius poutassou*) and hake (*Merluccius merluccius*), both of high commercial importance in Galician waters. Most blue whiting eaten by dolphins were mature fish but the estimated total consumption was relatively low (around 10%) compared to Spanish fishery landings of this species. In contrast, most hake eaten by dolphins were probably immature but the estimated total consumption is more than 20% of current annual fishery landings. The diet of by-caught animals, which made up around one third of the sample, was very similar to that in the overall sample. Although bottlenose dolphins are often seen close inshore, evidence from the diet suggests that they feed at the shelf edge. Evidence was found of ontogenetic dietary shifts and differences between diets of male and female dolphins. There were also clear changes in average diet over the 16-year study period, although there was no evidence that they were in response to changes in fish abundance. The amount of hake in the diet remained stable against a background of falling local abundance while the amount of blue whiting declined despite an increase in spawning stock size.

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) are widely distributed in inshore and offshore waters in the temperate and tropical zones of all oceans and peripheral seas (e.g. Pacific, Atlantic, Indian Oceans, Mediterranean, Black and Red Seas), sometimes entering rivers and estuaries (Wells & Scott, 1999). Of 19 marine mammal species recorded in Galician waters (16 cetaceans and 3 pinnipeds: Penas-Patiño & Piñeiro, 1989; Fernández de la Cigoña, 1990), bottlenose dolphins are the most frequently seen in coastal waters, where they inhabit the series of rías (inlets) along the western coastline (Fernández-Cordeiro et al., 1996; Aguilar, 1997; López et al., 2002). Based on opportunistic surveys from fishing boats, López et al. (2004) estimated that there were at least 660 bottlenose dolphins in Galician waters, occurring mainly in coastal waters off the south-west of Galicia, but also in offshore waters further north.

There has been a long history of interactions between bottlenose dolphins and fisheries. Pliny the Elder described dolphins herding large mullet schools toward the shore where fishermen would be waiting with nets ready. The same technique is still employed by the Imragen people of Mauritania (see Corkeron et al., 1990) and was probably also used by Australian Aborigines (Hall, 1984). Bottlenose dolphins have been recorded feeding on discarded fish from trawling boats and also apparently feeding on organisms stirred up by the trawl itself (Leatherwood, 1975). In Greek

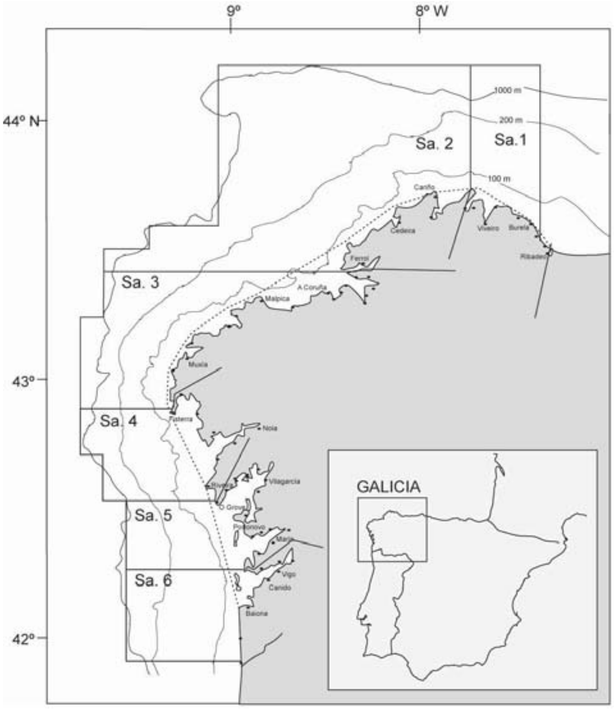

Figure 1. Map of the study area showing division of the Galician coastline into six (sub-) areas and locations of strandings (and by-catches) of bottlenose dolphins from which stomach contents were obtained.

waters, bottlenose dolphins remove fish from gill and trammel nets and damage nets, causing economic problems for the fishermen, as well as leading to both by-catch and direct killing of dolphins (Raitsos et al., 2003).

The Galician coast is characterized by high productivity and high biodiversity, including nearly 300 species of fish (Solórzano et al., 1988). There are 87 fishing ports on the Galician coast (Figure 1), used by more than 6000 fishing boats (data from the Galician Institute for Statistics). The total annual number of fishing trips by the (full-time) Galician fleet is estimated as being around 1.1 million. About 2900 commercial fishing boats (mainly small boats) operate in inshore waters, using traps, trawls, gill-nets and long-lines. Many of these boats target molluscs and crustaceans. Bottlenose dolphins are apparently by-caught in gill-nets in Galician waters and around 14% stranded bottlenose dolphins recorded in Galicia show evidence of by-catch mortality (López et al., 2002, 2003).

Diets of bottlenose dolphins have been studied in various parts of the world, including the northern Atlantic (Leatherwood et al., 1978; Desportes, 1985; Mead & Potter, 1990; Santos et al., 2001), the Gulf of Mexico (Gunter, 1942; Barros & Odell, 1990), South Africa (Ross, 1977; Cockcroft & Ross, 1990), Peru (van Waerebeek et al., 1990), eastern Australia (Corkeron et al., 1990), the Mediterranean (Voliani & Volpi, 1990; Relini et al., 1994; Miokovic et al., 1997; Blanco et al., 2001). Santos et al. (2001) found the gadid fish cod (*Gadus morhua*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) to be the main prey in stomach contents of ten bottlenose dolphins from Scotland (UK), although several other fish species, including salmon (*Salmo salar*), and some cephalopods were also found.

There is little published information on the diet of bottlenose dolphins on the Spanish Atlantic coast, although the incidence of by-catch suggests that dolphins eat species targeted by gill-net fishing. González et al. (1994) summarized information on cephalopods found in stomach contents of cetaceans stranded on the Galician coast (north-western Spain), recording the presence of squid of the family Ommastrephidae (one specimen of *Todarodes sagittatus* and three *Illex coindetii*) among the stomach contents of five individuals from a sample of 14 bottlenose dolphins.

The present work describes new results on the feeding habits of bottlenose dolphins in Galician waters as revealed by analysis of stomach contents of stranded and by-caught animals. We include full dietary data for the animals examined by González et al. (1994) and new data from animals collected over the last 16 years. We analyse variation in diet between sexes and between seasons and in relation to body size and cause of death. Finally, we examine evidence that dolphin diet tracks changes in fish abundance and discuss the potential for competition between dolphins and Galician fisheries.

MATERIALS AND METHODS

Sample collection and stomach contents analysis

From December 1990 to December 2005, 82 of the bottlenose dolphins examined by the Galician stranding network (CEMMA) had food remains in the stomach. Information on four specimens of squid, three octopuses and one unidentified cephalopod found amongst the contents of the stomachs of 5 out of 14 bottlenose dolphins collected during 1990–1993 was previously included in González et al. (1994). Fishery by-catches were identified from net and/or ropes attached to carcasses, net marks on the body, missing flukes or lobes from the tail, etc. When possible, the dolphins were measured (total length) and sexed. Gonads and teeth were removed to obtain data on maturity and age. However, since length data were more often available than maturity or age data, length is used as a proxy for age and maturity in the present study.

Stomach contents were sieved (0.355 mm mesh) and recognizable prey hard parts were transferred to 70% ethanol to clean and sterilize them. Prey animals that were largely undigested were stored frozen. Crustacean remains were not identified, due to their poor state of preservation. Fish otoliths and bones were dried while cephalopod mandibles (beaks) were retained in 70% ethanol. Otoliths, bones and beaks were identified using reference collections held at the University of Aberdeen and published guides (Clarke, 1986; Härkönen, 1986; Watt et al., 1997).

The numbers of fish and cephalopods present were estimated from the numbers of otoliths and beaks. Prey length and weight were estimated from linear measurements on otoliths, jawbones or beaks based on a compilation of published and unpublished regressions (e.g. Clarke, 1986; Härkönen, 1986; see Appendix 1). Complete pairs of cephalopod beaks were rarely present and, in all cases, length and weight was estimated from either the upper or lower beak (usually the latter since most published regressions estimate cephalopod length and weight from lower beak measurements). Each fish otolith was assumed to represent 0.5 fish. Thus, when both otoliths were present, the estimated fish weight is the average of the weights estimated from the two otoliths. Usually otolith length was measured, except for the otoliths of Clupeidae, Gobiidae and Zoarcidae for which width is the standard measurement (Härkönen, 1986), and any otoliths with broken tips. Standard measurements for cephalopod beaks are rostral length (squid) and hood length (octopus and sepiolids). For otoliths identifiable to one of a group of species, regressions based on combined data from all the species in the group were used. For stomachs in which one fish species was represented by >30 otoliths, a random sample of 30–60 otoliths was measured. No corrections were applied for possible otolith erosion.

Relative overall importance in the diet for each prey type was estimated using three standard indices: (a) percentage frequency of occurrence; (b) proportion of the total number of prey (summed across all stomachs); and (c) proportion of total prey weight (summed across all stomachs).

Analysis of dietary variation

We analysed variation in the numerical importance and total weight of each prey category in stomach contents of individual dolphins. Explanatory variables considered were: sex, body length-class, season, year (dividing the data into three time periods, 1990–1995, 1996–2000 and 2001–2005) and cause of death (by-catch or other). Animals were assigned to one of three length-classes (<260 cm, 260–280 cm and >280 cm), giving approximately the same number of dolphins in each group (Table 1).

Table 1. *Summary of the composition of the set of samples.*

		By half-decade			By sex			By length-class				By CoD	
Quarter	Sum	Y1	Y2	Y3	F	M	U	S	M	L	U	B	U
1	24	8	9	7	12	10	2	10	9	5	0	6	18
2	16	4	7	5	9	6	1	8	4	3	1	2	14
3	14	3	8	3	6	7	1	6	3	4	1	3	11
4	28	9	11	8	8	17	3	7	7	10	4	6	22
SUM	82	24	35	23	35	40	7	31	23	22	6	17	55

		By half-decade			By length-class				By CoD	
Sex	Sum	Y1	Y2	Y3	S	M	L	U	B	U
F	35	10	15	10	16	9	9	1	5	30
M	40	12	15	13	14	11	13	2	11	29
U	7	2	5	0	1	3	0	3	1	6
SUM	82	24	35	23	31	23	22	6	17	65

		By length-class				By CoD	
Half-decade	Sum	S	M	L	U	B	U
Y1	24	7	10	6	1	2	22
Y2	35	12	10	8	5	12	23
Y3	23	12	3	8	0	2	21
SUM	82	31	23	22	6	17	65

		By CoD	
L class	Sum	B	U
S	31	7	24
M	23	4	19
L	22	2	20
U	6	4	2
SUM	82	17	65

Half-decade periods were Y1, 1990–1995; Y2, 1996–2000; Y3, 2001–2005. Sex: F, female; M, male; U, unknown. Length class: S, small <260 cm; M, medium 260–280 cm; L, large >280 cm; U, unknown. CoD, Cause of death; B, by-catch; U, unknown and other.

Redundancy analysis (RDA) was used to visualize relationships between response variables (numbers or weights for prey categories present in the stomachs) and the set of explanatory variables. The response variables for RDA on prey number were the numbers present in each stomach for all prey categories present in more than 5% of the stomachs (13 fish taxa, three cephalopod taxa, one category for crustaceans and one category for other molluscs; see Table 2). For RDA on prey weights, response variables were the total weights of each prey category in each stomach, excluding crustaceans and other molluscs, for which no biomass estimates were available. All explanatory variables were nominal and were therefore each coded as a set of binomial dummy variables: thus season is recoded into three dummy variables, each representing one quarter of the year Q2, Q3 and Q4. Significance testing for explanatory variables was based on 9999 random permutations of reduced models. The RDA was carried out using Brodgar 2.5.1. (Highland Statistics Ltd).

For the most important prey categories (blue whiting, hake), factors affecting their numerical importance were further analysed using generalized additive models (GAMs). Since the two response variables appeared to have an approximately log-normal distribution, Gaussian GAMs were fitted to log-transformed data on numbers in each stomach contents using Brodgar 2.5.1. Explanatory variables considered were as for RDA except that: (a) categorical variables do not have to be recoded as binomial dummy variables as the software does this automatically; and (b) the explanatory variable year was replaced by two variables related to large-scale prey abundance, namely annual recruitment (in millions of fish) and annual spawning stock biomass (in tonnes) of the fish species in question, based on data from ICES (2005). For blue whiting, data are for the combined European stock. For hake, data refer to the 'southern' stock in ICES areas VIIIc and IXa. Spawning stock biomass (SSB) indices were divided by 10,000 to reduce the numbers to a similar scale to those of the other explanatory variables. Cross-validation was applied to estimate degrees of freedom for smoothing parameters. Models were optimized using forwards and backwards selection procedures, finally accepting the model with the

Table 2. *The main prey species of* Tursiops truncatus *stranded on the Galician coast. For animals diagnosed as fishery by-catches (N=17), importance in the diet for each prey category is shown as percentage frequency of occurrence (%F). For the whole sample set (N=82), dietary importance is shown as %F, % importance by number (%N), % importance by weight (%W) and 'index of relative importance' (IRI), calculated as (%N + %W) × %F and re-scaled to a maximum value of 100. Various sub-totals ('ALL…') for major prey groups are given. Although %N and %W (but not %F) sum to 100 when summed across all prey categories, they do not do so in this table since rows containing sub-totals are included and incompletely identified prey falling within each major prey group are not listed separately. Codes used elsewhere for analysis are given in column 1, for all prey categories occurring in more than 5% of stomachs. (Not shown: F4, unidentified Gadidae.)*

		By-catch	All dolphins			
Code	Species	%F	%F	%N	%W	IRI
	Clupeidae	11.7	4.9	0.3	0.2	0.0
	Argentina sp.	5.9	3.7	0.8	0.8	0.0
F5	*Conger conger*	5.9	7.3	0.3	6.8	0.3
	Macrorhamphosus scolopax	0.0	4.9	2.5	0.0	0.1
	Trachyrincus scabrus	0.0	1.2	0.0	-	-
F1	*Micromesistius poutassou*	82.3	75.6	72.9	48.3	45.8
F2	*Trisopterus* spp.	17.6	24.4	1.7	1.3	0.4
F3	*Gadiculus argenteus thori*	23.5	47.6	3.2	0.2	0.8
	ALL GADIDAE	**82.3**	87.8	77.3	50.1	55.9
F6	*Merluccius merluccius*	47.1	65.8	8.3	28.8	12.2
	Beryx decadactylus	0.0	1.2	0.1	0.2	0.0
F8	*Trachurus trachurus*	5.9	19.5	2.0	3.0	0.5
F9	*Mugil* sp.	5.9	12.2	0.7	6.0	0.4
F10	Sparidae	5.9	8.5	0.7	1.1	0.1
F11	Ammodytidae	0.0	7.3	0.9	0.3	0.0
F13	Gobiidae	5.9	11.0	0.7	0.0	0.0
	Aphanopus carbo	0.0	1.2	0.0	0.2	0.0
F12	*Scomber scombrus*	5.9	6.1	0.2	0.2	0.0
F7	*Atherina presbyter*	5.9	6.1	1.0	0.1	0.0
	Callionymus maculatus	0.0	1.2	0.0	0.0	0.0
	Zoarcidae	0.0	1.2	0.1	0.1	0.0
	ALL FISH	**100**	98.8	96.6	98.2	96.2
C1	Sepiolidae	5.9	6.1	0.1	0.0	0.0
	Todarodes sagittatus	11.8	4.9	0.1	0.3	0.0
C2	ALL OMMASTREPHIDAE	**41.2**	24.4	0.7	1.0	0.2
	Chiroteuthis sp.	5.9	3.7	0.1	0.0	0.0
C3	*Eledone cirrhosa*	11.8	9.8	0.2	0.5	0.0
	ALL CEPHALOPODS	**58.8**	39.0	1.5	1.8	07
O1	Crustacea	17.6	24.4	1.8	0.0	0.2
O2	Other Mollusca	5.9	7.3	0.1	0.0	0.0
	Polychaeta	5.9	2.4	0.0	0.0	0.0

lowest AIC provided that no serious outliers were detected and no serious patterns remained in residuals. Effects of adding interaction terms were also explored.

All other prey categories occurred too infrequently for the GAM approach to be useful and additional univariate analyses were carried out to determine factors affecting numerical response of those prey categories with frequency of occurrence above (approximately) 20%. The influence of time period, season, sex and dolphin length-class on prey numbers was tested using Kruskal–Wallis tests. The relationship between the number of prey present and dolphin length was also determined using Spearman rank-order correlations. Overall dietary diversity (as indicated by the number of different prey taxa found in each stomach) and total number of prey items (summed across all taxa) were also compared between sexes, seasons, time periods and dolphin body length-classes.

Overall size–frequency distributions were derived for the most common prey species. Median sizes for the main fish species were also calculated for each dolphin and analysed in relation to sex, season, time period, and body size (as for prey numbers).

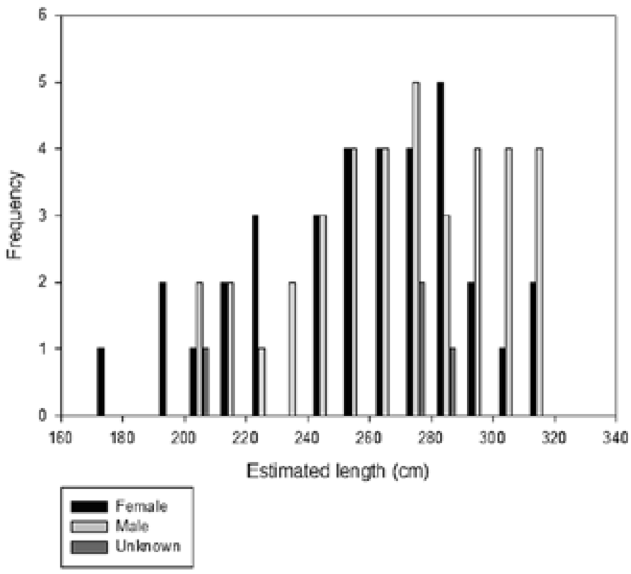

Figure 2. Size distribution of sampled dolphins. Sample sizes are: females = 34, males = 38, unknown sex = 4.

RESULTS

Composition of the sample of bottlenose dolphins

The dolphins examined comprised 35 females, 40 males and 7 animals for which sex could not be determined (due to poor state of preservation). The majority were stranded in quarters 1 (N=24) and 4 (N=28) of the year (Table 1). Length was measured or could be estimated for 76 individuals and ranged from 179 to 318 cm. Although males tended to be slightly larger (Figure 2), the difference in average body length was not statistically significant (Kruskal–Wallis test, P=0.2).

Overall diet composition

Remains of 6839 individual prey items were recovered. Fish made up 98% of the diet by number, with most of the remainder of the diet comprising of cephalopods and crustaceans. Polychaetes and shell fragments from non-cephalopod molluscs were found occasionally. Remains of fish from at least 23 different families were recorded. Gadidae were the most important group, with blue whiting *Micromesistius poutassou* (73% of diet by number, 48% by weight) being the most important prey species. Hake *Merluccius merluccius* (8%, 29%) was the second most important species in terms of contribution to overall prey biomass (Table 2). Only three other prey categories contributed more than 5% of overall prey biomass, unidentified Gadidae (around 9%, based on a composite regression for Gadidae species), mullet *Mugil* sp. (6%) and conger eel *Conger* sp. (7%). Two deep-sea fish species, black scabbard fish (*Aphanopus carbo*) and roughsnout grenadier (*Trachyrincus scabrus*) were identified among the prey, each from one dolphin.

At least 12 species of cephalopods were identified from beaks. None comprised a major part of the diet although they were present in almost 40% of the stomachs analysed. The most frequently recorded cephalopods were squid of the family Ommastrephidae (24% frequency of occurrence). It is likely that all these beaks belonged to *Illex coindetii*, *Todaropsis eblanae* and/or *Todarodes sagittatus*, all of which were present, but a large proportion of the Ommastrephidae beaks could not be identified to species.

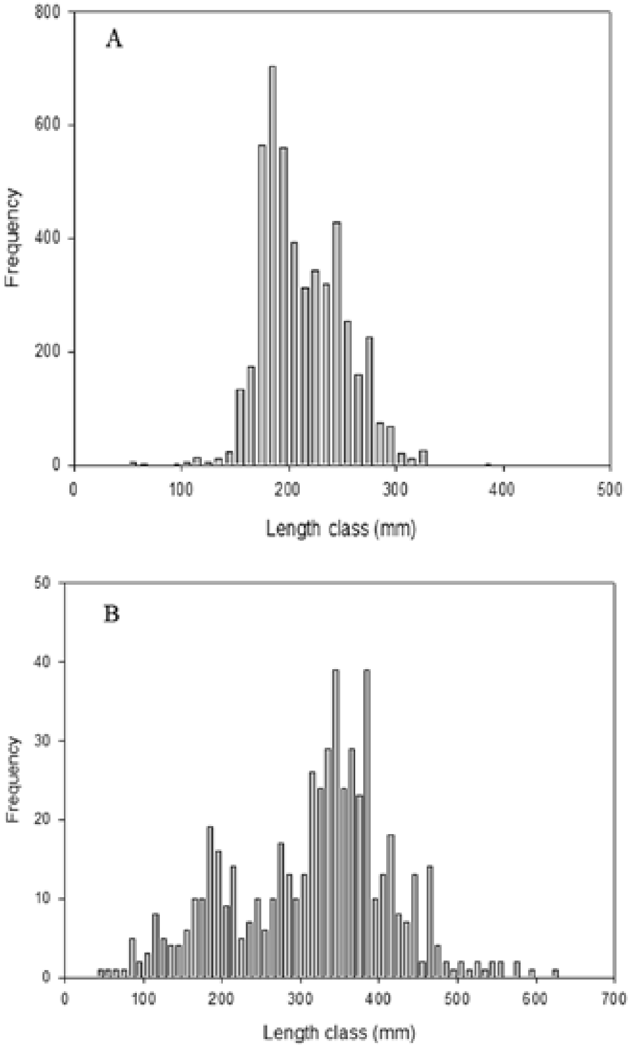

Figure 3. Distribution of estimated size (total length) of fish in stomachs of bottlenose dolphins: (A) blue whiting (reconstructed from measurements of 1552 out of 9665 otoliths present in the stomachs); (B) hake (reconstructed from measurements of 666 out of 1095 otoliths present in the stomachs).

The distribution of reconstructed lengths of blue whiting is right skewed with a major mode at 19 cm, although it appears that the distribution is a composite of at least three size modes, perhaps representing three age-classes (Figure 3A). Median sizes of blue whiting eaten by individual dolphins ranged from 62 mm to 274 mm. The distribution of reconstructed lengths of hake contains at least two modes, one around 19 cm and one around 35–40 cm although again there are probably additional size components present (Figure 3B). Median sizes of hake eaten by individual dolphins ranged from 146 mm to 409 mm.

Seventeen dolphins were known or diagnosed fishery by-catches. The diet composition of these animals was very similar to that recorded for the whole sample set, with blue whiting and hake the most frequently recorded (see Table 2) and numerous prey categories in the stomach contents.

Table 3. *Results of redundancy analysis for data on (a) prey numbers and (b) prey weight. The table gives values for F and associated probability (*P*) for each explanatory variable. Significant values are indicated by bold face. For each original nominal variable with N different possible values, N-1 binomial dummy variables were entered into the analysis. Thus there were three time periods and significant values for time periods 2 or 3 would imply a difference from time period 1. Unknowns are treated as missing values (except for the variable 'by-catch').*

Variable	(a) Prey numbers	(b) Prey weight
Time period 2	2.106 (**P=0.001**)	1.755 (**P=0.010**)
Time period 3	1.346 (P=0.145)	0.941 (P=0.526)
Season 2	1.165 (P=0.292)	0.781 (P=0.700)
Season 3	1.597 (P=0.098)	1.686 (P=0.085)
Season 4	0.985 (P=0.469)	1.196 (P=0.247)
Female	1.408 (P=0.083)	1.491 (P=0.050)
Length class 2	1.744 (**P=0.020**)	1.441 (P=0.092)
Length class 3	1.891 (**P=0.014**)	2.397 (**P=0.001**)
By-catch	0.747 (P=0.735)	1.068 (P=0.380)

Analysis of dietary variability

Redundancy analysis on data for prey numbers indicated significant effects of time period (1990–1995 differed from 1996–2000) and dolphin length-class (length-classes 2 and 3 differed from length-class 1; see Table 3). The RDA axis 1 relates most strongly to numbers of *Trisopterus*, *Mugil*, Sparidae, Ammodytidae and Ommastrephid squid in the stomach contents; the last of these prey categories being negatively correlated with the other four. It can also be seen that the explanatory variable most closely related to RDA axis 1 is Y2, i.e. the difference between the periods 1990–1995 and 1996–2000. The second RDA axis relates most strongly to numbers of blue whiting, silvery pout and *Atherina* sp., the latter being negatively correlated with the other two (see Figure 4A).

The RDA on prey biomass supports the above results, with significant effects of time-period and length-class being found (Table 3); the effect of sex is almost significant (P=0.05). In this analysis, RDA axis 1 relates most strongly to the weight of hake, *Mugil*, *Eledone*, Sepiolidae and Ommastrephidae in stomach contents, the latter two categories being negatively associated with the first three (Figure 4B).

For the two most frequently occurring (and numerically important) prey categories, blue whiting and hake, factors affecting their numerical importance in the diet were modelled using Gaussian GAMs fitted to log-transformed data on prey numbers. The explanatory variable year was replaced by two variables related to large-scale prey abundance, namely annual recruitment (in millions of fish) and annual spawning stock biomass (in tonnes) of the species in question. The optimal model for numerical importance of blue whiting (N_{bw}) explained 33.8% of deviance (AIC=161.92) and was as follows:

$$\mathrm{Log}(N_{bw}) \sim s(\mathrm{length},\ df=2.37)+SSB_{bw}+\ \mathrm{as.factor(sex)}$$

where SSB_{bw} is annual spawning stock biomass for blue whiting. Smoothers for both length (P=0.0005) and SSB_{bw} (P=0.033) were statistically significant. However, while including sex as a factor improved the model, its effect was not statistically significant (P=0.287). The shapes of the smoothers (see Figure 5) indicate that the importance of blue whiting in the stomachs increased with dolphin length (up to around 280 cm body length) but decreased at higher blue whiting SSB.

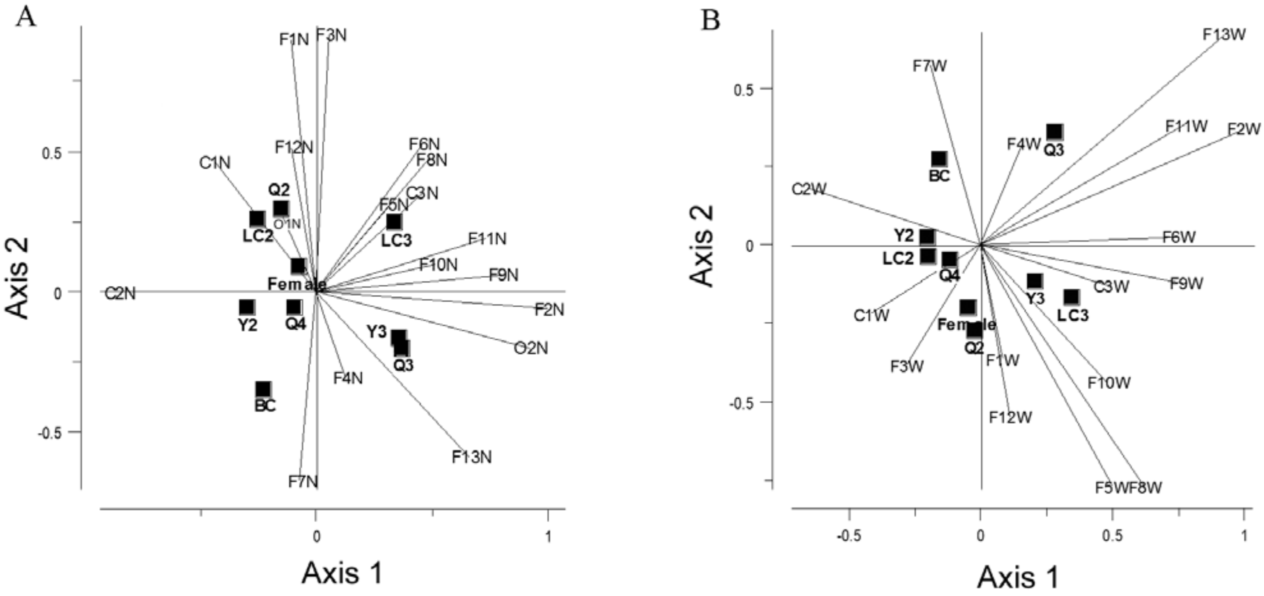

Figure 4. Redundancy analysis results for factors affecting diet of bottlenose dolphins: bi-plots showing explanatory variables (which appear as squares) and response variables (which appear as vectors): (A) based on prey numbers and (B) based on prey weight. Explanatory variables were: time periods, Y2 (1996–2000), Y3 (2001–2005); dolphin length-classes, LC2 (260–280 cm), LC3 (>280 cm); seasons, Q2, Q3, Q4; sex, Female; by-catch, BC. For categorical variables, effects are expressed relative to a reference value, e.g. the effect of variable Y2 refers to the difference between periods Y2 and Y1. Response variable codes are as in Table 2, with the addition of 'N' to denote prey numbers or 'W' to denote prey weight.

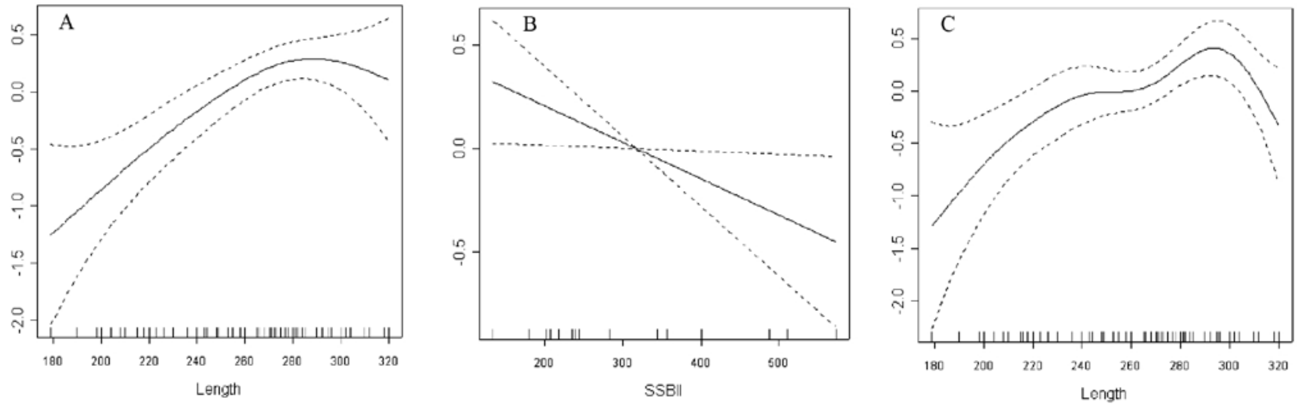

Figure 5. Relationships between numerical importance of blue whiting and hake and explanatory variables as visualized by fitting GAMs. (A) Smoother for the effect of dolphin length on blue whiting numerical importance; (B) linear effect of blue whiting SSB on blue whiting numerical importance; (C) smoother for the effect of dolphin length on hake numerical importance.

Table 4. *Results of univariate one-factor analyses on numbers of prey items in stomachs. For each prey species and each explanatory variable, the probability associated with the Kruskal–Wallis test for equal medians is reported, along with an indication of the direction of any significant difference. The correlation coefficient and associated probability for the relationships between number of prey eaten and dolphin body length are also given. Finally, results for analysis of total numbers of prey (summed across all taxa) and prey diversity (number of taxa) are also given. Significant differences are highlighted using bold face. Abbreviations for factor levels are as in Table 1.*

Species	Time period (N=82)	Season (N=82)	Sex (N=75)	Length class (N=76)	Body length (N=76)
Blue whiting	**0.008 T1>T2>T3**	0.766	0.404	**0.000 L>M>S**	R=0.369, **_P_=0.001**
Silvery pout	**0.011 T3>T1>T2**	0.442	0.136	0.096	R=0.153, *P*=0.187
Trisopterus	**0.022 T1>T3>T2**	0.821	0.199	0.326	R=0.161, *P*=0.164
Hake	0.071	0.504	0.281	0.124	R=0.226, *P*=0.051
Scad	**0.029 T1>T3>T2**	0.385	0.994	0.062	R=0.258, **_P_=0.013**
Ommastrephids	**0.034 T2>T1>T3**	0.614	0.537	0.052	R=0.072, *P*=0.534
Crustaceans	0.177	0.186	0.367	0.181	R= −0.092, *P*=0.429
All taxa	0.220	0.766	0.404	**0.000 M>L>S**	R=0.432, **_P_=0.000**
No. of taxa	**0.032 T3>T1>T2**	0.703	0.278	0.347	R=0.158, *P*=0.164

Table 5. *Results of univariate analyses on median size of fish in stomachs. For blue whiting and hake, average sizes are analysed in relation to season and sex (Kruskal–Wallis tests) and body size (Kruskal–Wallis tests and correlation coefficients). Significant trends and differences are highlighted using bold face. Abbreviations for factor levels are as in Table 1.*

Analysis	Blue whiting	Hake
Compare time periods	*P*=0.326 (N=61)	0.380 (N=54)
Compare seasons	*P*=0.998 (N=61)	0.159 (N=54)
Compare sexes	*P*=0.295 (N=54)	**0.033 M>F** (N=48)
Compare size-classes	*P*=0.840 (N=55)	0.077 (N=49)
Correlation with size	R=0.071, *P*=0.071 (N=55)	**R=0.404, _P_=0.004** (N=49)

The optimal model for numerical importance of hake (Nh) explained 31.1% of deviance (AIC=115.07) and was as follows:

$$\mathrm{Log}(N_h) \sim s(\mathrm{length},\ df=4.84) + \mathrm{as.factor(season)} + \mathrm{as.factor(sex)} + \mathrm{as.factor(sex)} \times \mathrm{length}$$

As for blue whiting, the number of hake in stomach contents tended to be greater in bigger dolphins (see Figure 5C) and the effect of dolphin body length was significant (*P*=0.0137). The importance of hake in the stomachs was lower in the third and fourth quarters of the year than in quarter 1 (*P*=0.041, *P*=0.021, respectively) and females tended to eat more hake than males (*P*=0.018). There was also a significant interaction between effects of length and sex.

Results of additional univariate analyses of factors affecting the numerical importance of individual prey categories are summarized in Table 4. The numerical importance of blue whiting, silvery pout, *Trisopterus* sp., scad and Ommastrephidae differed significantly between time periods. Blue whiting numerical importance was also related to dolphin body length with small dolphins eating fewest of these fish. There were positive correlations between estimated dolphin body length and the numbers of blue whiting and scad in the stomach contents. There was no significant variation in the numbers of the main prey types in relation to season or sex. The total number of prey (summed across all taxa) varied significantly in relation to dolphin body size, reflected in a significant overall positive correlation between dolphin body length and number of prey in the stomach. The number of different prey taxa in the stomach was related to time period but unrelated to season, sex or body size (Table 4).

Analysis of factors affecting the median length of prey eaten by dolphins was carried out only for the two most numerous prey species, blue whiting and hake. Median blue whiting length in stomach contents was not related to time period, season, sex or body length-class and was not correlated with dolphin body length. Male dolphins ate bigger hake than did females but no relationship was found between median hake size in the stomach and season, sex or size-class (Table 5). However, there was a significant correlation between dolphin length and average hake length.

DISCUSSION

The dominance of the Gadiformes (Gadidae and Merluccidae) in the diet of bottlenose dolphins from Galicia is consistent with results from two previous studies on this species in the north-east Atlantic, on the Atlantic coast of France (Desportes, 1985) and on the Scottish (UK) coast (Santos et al., 2001). However, the identity of the important gadiform species in the diet differs between areas. Neither hake nor blue whiting is common in the Moray Firth in Scotland (see Hopkins, 1986, for a historical overview of Moray Firth fisheries) whereas both are important fishery species in Galicia. Hake was also the dominant species in the diet of bottlenose dolphins in the Mediterranean (Blanco et al., 2001). This consistent pattern does not extend to the diet of bottlenose dolphins in other parts of the world. Thus, anchoveta (*Engraulis ringens*), Patagonian squid (*Loligo gahi*) and Pacific sardine (*Sardinops sagax*) were found to be the most frequent prey of *Tursiops* off Peru (van Waerebeek et al., 1990).

The wide variety of species recorded in the stomach contents in the present study (e.g. including at least 12 species of cephalopods) is also consistent with results on bottlenose dolphins from other areas (Gunter, 1942; Ross, 1977; Leatherwood et al., 1978; Corkeron, 1989; Barros & Odell, 1990; Cockcroft & Ross, 1990; Corkeron et al., 1990; Mead & Potter, 1990; van Waerebeek et al., 1990; Voliani & Volpi, 1990; Relini et al., 1994; Miokovic et al., 1997; Blanco et al., 2001). This diversity of prey has generally been interpreted as indicating opportunistic feeding, an interpretation that is rarely justified: in the absence of information on individual dolphin's encounter rates with different prey species, it is impossible to rule out some degree of selective feeding.

The most frequently recorded prey species in the present study (blue whiting, hake, silvery pout, scad) are amongst the most abundant fish species in Galician waters. Galician waters are an important nursery ground for blue whiting, hake, and scad (*Trachurus trachurus* L., 1758), all of which are subjects of directed fisheries and of considerable commercial value. Silvery pout is also amongst the most numerous species in shelf waters (Fariña et al., 1985).

Blue whiting is an oceanic species generally found in the area between the continental shelf and the continental slope (Robles, 1970), its distribution extending from the Mediterranean to northern Norway (Schmidt, 1909). Juvenile blue whiting (with a length between 7 and 14 cm) are pelagic and live in the upper 30 m of the water column beyond the continental slope (Raitt, 1968). At a length of around 16 cm blue whiting adopts a demersal lifestyle (Bas & Morales, 1966), which coincides with the first cycle of sexual maturity. In north-western Spain, the fish probably mature at a length of 20–21 cm and aged 2 y (Robles, 1970). Cendrero (1967) recorded maturity as being reached at 21–24 cm length and 2–3 y of age in North Spain.

Most of the blue whiting eaten by the bottlenose dolphins in Galician waters were estimated to be over 16 cm in length and some were as much as 30 cm in length (Figure 3A). Due to otolith erosion in the stomach, these sizes may be underestimated. Thus bottlenose dolphins start taking blue whiting after it has adopted a demersal lifestyle and prey on both immature and mature fish. Furthermore, given that the majority of blue whiting eaten are bigger than the legal minimum landing size (18 cm), the dolphins are potentially competing with fisheries. The dolphins presumably travel to shelf edge waters to feed on this species. The presence of two deep-sea fish species (black scabbard fish, *Aphanopus carbo* and roughsnout grenadier, *Trachyrincus scabrus*) in the stomach contents (albeit of single individuals) also suggests feeding in offshore waters.

The European hake generally live on the lower continental shelf at depths of 165 to 550 m (Wheeler, 1992). Its distribution in the Atlantic extends from northern Norway to Morocco, and it also occurs in the Mediterranean (Hickling, 1927). There are thought to be two stocks, the northern and the southern stocks, and it is the latter which occurs off Galicia—which is one of the most important nursery areas (Pereiro et al., 1980). Cárdenas & Fernández (1985) found that hake mature at a length of 50–55 cm in northern Spain. Hake is one of the most economically important species in Galician demersal fisheries (Fernández et al., 1978) but Spanish landings have dwindled steadily from a peak of 16,700 tonnes in 1984 to less than 5000 tonnes annually since 1998, parallel with declines in the stock, the abundance of which is presently well below safe limits (ICES, 2005). Most of the hake eaten by the bottlenose dolphins were thus probably immature, although mainly above the minimum legal landing size taken by the fishery (Figure 3B).

The diet of the by-caught animals looked very similar to that of the sample as a whole. Although some prey species were absent from the stomachs of by-caught animals this is likely to simply be a consequence of the smaller sample size. One problem with this comparison is that by-catches may go undiagnosed, so that the present figure of around one third of the animals examined being by-catch mortalities may be an underestimate. However, the results provide no evidence that by-caught animals are in any way atypical. Since the main prey of bottlenose dolphins in Galicia, blue whiting and hake, are important fishery resources, the occurrence of by-catches of dolphins in fishing gear is not surprising. It is clear that dolphins and fishermen are exploiting the same resources. Indeed, dolphins are perceived as competitors by fishermen and have been actively persecuted in the past (Fernández-Cordeiro et al., 1996).

Most fishing for hake and blue whiting takes place on the continental slope rather than on the shelf and this is presumably where the by-catch mortality is occurring. The evidence from diet and by-catch suggests that dolphins resident in the rías (coastal inlets) make regular foraging trips offshore. Almost all sightings of bottlenose dolphins in the south of Galicia are near to the coast (Aguilar, 1997; López et al., 2004). However, in the north of Galicia, sightings surveys have also recorded the species in deeper water (>200 m) and it is possible that there is also an offshore population (López et al., 2004).

Analysis of dietary variation indicated ontogenetic shifts in diet, with larger animals taking more and bigger fish of certain species, notably hake. This is likely to reflect increasing experience, improved diving and prey-catching abilities and increased stomach capacity. Blanco et al. (2001) found that adult bottlenose dolphins had eaten bigger hake (and a wider size range) than juveniles, in a sample of 16 animals stranded on the Spanish Mediterranean coast.

Male dolphins ate bigger (but fewer) hake than females, which could indicate that the sexes feed in different areas. López (2003) suggested that there is both age-related and sex-related segregation in Galician bottlenose dolphins.

Both multivariate and univariate analyses highlighted shifts in diet composition over the 16-y period of the study. In particular, the importance of blue whiting in the diet seems to have declined, even though overall abundance of this stock has increased over the same period (ICES, 2005). While this negative relationship is counterintuitive, it could indicate that blue whiting abundance in Galician waters has not followed overall stock trends. It is of interest to note that the numerical importance of hake in the diet has not declined significantly over time despite a drop in abundance of the southern hake stock of more than 50% over the study period (ICES, 2005). Following optimal diet selection theory (e.g. Pulliam, 1974), this could indicate that hake is a preferred prey species.

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Appendix 1. *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); DL, dentary length (mm, from symphysis to the tip of the outer fork); LHL, lower hood length; LRL, lower rostral length (mm); UHL, upper hood length; URL, upper rostral length. Sources are as follows: Be, Bedford et al. (1986); Bra, Brown & Pierce (1997); Brb, Brown & Pierce (1998); Brc, Brown et al. (2001); Cl, Clarke (1986); Co, Coull et al. (1989); Do, Dorel (1986); F, fishbase.org (2005); GH, Gema Hernández (unpublished data); GP, Graham Pierce (unpublished data); Ha, Harkönen (1986); IEO, Instituto Español de Oceanografía (unpublished data); JH, John Hislop (unpublished data); Le, data from Leopold et al. (2001); Ma, Martins et al. (1989); Me, Merella et al. (1997); Pe, Pereda & Villamor (1991); Sa, Santos et al. (2001); *, combined data from more than one species. A number in brackets after the abbreviation for source indicates that the regression refers to a particular month of the year.*

FISH species	Estimated prey length mm	Source	Estimated prey weight g	Source
Sardine *Sardina pilchardus*	$L= -125.370+OW\times43.403$	IEO	$W=0.008080\times(L/10)^{3.009493}$	IEO
Argentine *Argentina* sp.	$L=10.466+OL\times40.030$	Ha	$W=0.559200\times OL^{3.173}$	Ha
	$L=51.240+OL\times41.945$	GP	$W=0.005300\times(L/10)^{3.053400}$	Co
Conger *Conger conger*	$L=OL\times150$ (see note 1)	Ha	$W=0.0002\times(L/10)^{3.509}$	Do
Snipefish *Macrorhamphosus scolopax*	See note 2		$W=0.004\times(L/10)^{3.15}$	Me
Roundsnout grenadier *Trachyrincus scabrus*	No regression available		No regression available	
Blue whiting *Micromesistius poutassou*	$L= -2.140+OL\times22.090$	JH	$W=0.006727\times OL^{3.89200}$	Ha
	$L= -17.800+OW\times70.770$	JH	$W=0.019350\times(L/10)^{3.34372}$	Ha
Haddock *Melanogrammus aeglefinus*/ Saithe *Pollachius virens*/Pollack *P. pollachius*	$L= -116.490+OL\times38.857$	Bra*	$W=0.01798\times(L/10)^{2.82680}$	Bra*
	$L= -204.540+OW\times125.360$	JH*		
Trisopterus spp. *T. esmarkii*, *T. minutus*, *T. luscus*	$L= -37.340+OL\times27.447$	Sa*	$W=0.003467\times OL^{4.60000}$	Sa*
	$L= -39.600+OW\times61.683$	Hi*	$W=0.002796\times(L/10)^{3.40400}$	Ha*
T. minutus/*T. luscus*	$L= -109.1000\times OL\times36.13900$	Ha*	$W=0.000790\times OL^{5.38000}$	Ha*
Silvery pout *Gadiculus argenteus thori*	$L=19.449000\times OL^{1.05300}$	Ha	$W=0.021289\times OL^{3.78500}$	Ha
Forkbeard *Phycis blennoides*	$L=1.555\times OL^{1.28500}$	Pe	$W=0.001980\times OL^{4.63400}$	Pe
Unidentified Gadidae	$L= -61.590+OL\times33.304$	Brb*	$W=0.016042\times(L/10)^{2.87419}$	Brb*
	$L= -54.350+OW\times76.582$	Brb*		
Hake *Merluccius merluccius*	$L= -0.630+OL\times23.884$	Ha	$W=0.009740\times(L/10)^{2.91300}$	Be
	$L= -68.180+OW\times76.276$	GP		
Beryx decadactylus	See note 3		$W=0.0139\times(L/10)^{3}$	F
Scad *Trachurus trachurus*	$L= -27.020+OL\times34.939$	Brb	$W=0.003400\times(L/10)^{3.29430}$	Co
	$L= -26.110+OW\times79.010$	Brb		
Mugilidae	$L= -137.540+OL\times63.621$	Le*	$W=0.046400\times OL^{4.39530}$	Le*
Sandeel *Ammodytes* spp.	$L=8.776+OL\times51.906$	Ha	$W=0.612150\times OL^{2.71000}$	Ha
Gobiidae	$L= -6.460+OW\times41.770$	Ha	$W=0.232809\times OW^{4.17000}$	Ha
Black scabbard-fish *Aphanopus carbo*	See note 4		$W=0.0004\times(L/10)^{3.27}$	Ma
Mackerel *Scomber scombrus*	$L= -20.410+OL\times87.590$	Ha	$W=0.002709\times(L/10)^{3.29000}$	Co(4)
	$L=33.3+DL\times19.7$	GH	$W=0.002738\times(L/10)^{3.29000}$	Co(3)
Sand smelt *Atherina presbyter*	$L=67.420+OL\times15.132$	GP	$W=0.006304\times(L/10)^{3.01000}$	GP
Dragonet *Callionymus maculatus*	$L=6.4+DL\times29.8$	GH	$W=0.022000\times(L/10)^{2.59070}$	Co
Zoarces viviparus	$L= -23.75+OW\times179.30$	Ha	$W=12.58\times OW^{4.43200}$	Ha
3-bearded rockling *Gaidropsarus vulgaris*	$L= -74.6+OL\times92.29$	GP	$W=0.0108\times(L/10)^{2.95900}$	F
Unidentified flatfish	$L= -25.950+OL\times53.274$	Brb*	$W=0.009923\times(L/10)^{3.03595}$	Brb*
CEPHALOPOD species				
Cuttlefish *Sepia* spp.	$L= -2.140+LHL\times21.890$	Cl*	$W=0.123690\times LHL^{4.06000}$	Cl*
Sepiolid *Stoloteuthis leucoptera*	$L=18.540+LHL\times1.650$	Cl*	$W=2.651170\times LHL^{0.54500}$	Cl*
Unidentified Sepiolidae	$L=18.540+LHL\times1.650$	Cl*	$W=2.651170\times LHL^{0.54500}$	Cl*
			$W=0.645454\times UHL^{0.35000}$	Cl*
Squid *Loligo* sp.	$L= -42.220+LRL\times84.274$	Cl*	$W=6.195360\times LRL^{3.24200}$	Sa*
Squid *Alloteuthis subulata*	$L= -30.990+LRL\times113.970$	Cl	$W=7.389060\times LRL^{2.75000}$	Cl
Squid *Histioteusthis arcturi*	$L= -13.602+LRL\times22.210$	Cl	$W=4.923403\times LRL^{2.31000}$	Cl
Squid *Histioteusthis reversa*	$L= -13.602+LRL\times22.210$	Cl	$W=4.923403\times LRL^{2.31000}$	Cl
Squid *Todaropsis eblanae*	$L= -10.320+LRL\times35.040$	Cl	$W=1.803990\times LRL^{3.17000}$	Cl
Squid *Illex coindetii*/*Todaropsis eblanae*			$W=2.415730\times LRL^{2.82000}$	Cl*
Squid *Todarodes sagittatus*	$L= -11.300+LRL\times41.360$	Cl	$W=2.188030\times LRL^{2.83000}$	Cl
Unidentified Ommastrephidae			$W=1.075333\times URL^{3.15300}$	Brc*
			$W=2.337310\times LRL^{2.82000}$	Brb*
Squid *Chiroteuthis* sp.	$L=11.400+LRL\times24.460$	Cl	$W=0.785840\times LRL^{2.70000}$	Cl
Squid *Taonius pavo*	$L= -12.300+LRL\times61.430$	Cl	$W=2.164600\times LRL^{2.19000}$	Cl
Octopus *Eledone cirrhosa*	$L=3.380+LHL\times26.570$	Cl	$W=5.365600\times LHL^{2.85000}$	Cl
			$W=8.250720\times UHL^{2.33740}$	Brb

Notes: (1) No regression was available for conger eel (*Conger conger*) but length was estimated based on Härkönen's (1986) observation that the otolith length to fish length ratio was approximately 1:150. (2) No otoliths were found for snipefish (*Macrorhamphosus scolopax*), which was identified from its large dorsal spine. As an approximation, all individuals were assumed to be 15 cm long: this is the largest size recorded for the species in Galicia and Cantabria (Sánchez et al., 1995). (3) No regressions were available for *Beryx decadactylus* but comparison with reference material suggested that otoliths came from fish of around 25 cm length. (4) The length of a black scabbard fish (*Aphanopus carbo*) (84 cm) was estimated from its dentaries.