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Long-term variation in common dolphin diet in relation to prey abundance

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ABSTRACT: Understanding the effects of changes in prey abundance on predators is essential to predict responses of marine ecosystems to perturbation and ensure sustainable fishing. As abundant top predators feeding largely on commercially exploited fish, common dolphins *Delphinus delphis* are expected to be affected by fluctuations in fish abundance. Previous studies variously suggest that common dolphins show a preference for energy-rich species or that they are opportunistic predators. In the latter case, the intensity of predation on all prey species would be expected to vary in proportion to their abundances. If such relationships are seen for only a few prey species, and the importance of other species varies inversely with the abundance of these 'preferred' prey, this would indicate selective feeding. We suggest that studies on diet at the population level can provide insights into such individual-level foraging decisions. We analysed stomach contents from 514 stranded and by-caught common dolphins in Galicia (NW Spain), collected over 2 decades. The most important prey were sardine, blue whiting and hake. Using zero-inflated generalised additive models to deal with non-linear relationships and the high number of zeros in prey count data, we tested for evidence of 'preference' for the main prey species, as well as confirming the existence of ontogenetic, spatial and seasonal variation in diet. Relationships between diet and annual prey abundance do not conclusively confirm either opportunistic or selective predation, but there is more evidence for the former. Lack of evidence for selective predation on energy-rich sardine could be due to current low stock levels.

KEY WORDS: Diet selection · Sardine · Hake · Blue whiting · Feeding ecology · Zero-inflated models

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INTRODUCTION

Common dolphins *Delphinus delphis* are among the most abundant cetaceans in European waters. Based on the results of 2 large-scale internationally coordinated sighting surveys in 2005 and 2007 (SCANS II and CODA, respectively), Cañadas et al. (2009) estimated a population of 185 000 (95% CI = 99 200–345 700) in European Atlantic waters, including almost 20 000 individuals in the shelf waters of the Iberian Peninsula and the southern Bay of Biscay (SCANS-II block W). The species is the most abundant cetacean in Galician (NW Spain) waters, as reflected in stranding records and results from boat-

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based sighting surveys (López et al. 2002, 2004), although trends in abundance are unknown, and high fishery by-catch mortality recorded for small cetaceans in the area (López et al. 2002, 2003) may represent a significant threat.

Results from several studies on the diet of common dolphins in Europe (e.g. Collet 1981, Desportes 1985, Berrow & Rogan 1995, Silva 1999, Pusineri et al. 2007, Meynier et al. 2008) indicate that the main prey are small pelagic shoaling fish. Variation in diet between areas and seasons led several authors to suggest that the species feeds opportunistically, with the diet reflecting local prey abundance and availability (e.g. Evans 1994). More recently, it has been shown that common dolphins exhibit an apparent preference for fatty species with high calorific density (Meynier et al. 2008, Spitz et al. 2010a).

Linking predator diet with prey abundance requires access to prey abundance data at a meaningful scale. For individual predators, this scale is likely to be small, and measuring fish abundance at a local scale is generally difficult since fish are highly mobile (Torres et al. 2008). However, information on large-scale abundance of prey can provide insight into predator dietary choices at the population level, and several studies have compared fish abundance from fisheries surveys with predator diet, e.g. for Steller sea lions *Eumetopias jubatus* (Womble & Sigler 2006) and common murres *Uria aalge* (Buren et al. 2012). However, such approaches have not been used for common dolphins, and the hypothesis of opportunism has not actually been tested.

The diet selected by a predator is potentially a function of multiple and interacting covariates, including the abundances of different prey species. Relationships between predator diet and prey abundances can be viewed as multivariate functional responses (after Holling 1959), the forms of which can be predicted from optimal foraging theory. Thus, a predator will rank available prey types according to their energetic profitability (i.e. calorie content divided by handling time). Preferred prey species will be taken whenever encountered, leading to a positive relationship between prey abundance and their importance in stomach content samples, while less preferred prey species will be eaten only when preferred types are insufficiently abundant, resulting in a less clear relationship between dietary importance and abundance for such prey species, plus the expectation that their importance in the diet will decrease as the abundance of preferred prey increases. Physiological limits to the amount of prey consumed by an individual predator (e.g. satiation) may result in a threshold of prey abundance above which no increase in predation is seen. Finally, there are various scenarios — e.g. when a predator mis-identifies prey, is in a poor nutritional state, or has imperfect knowledge of prey distribution, abundance or energy density — under which the predator may be expected to show less discrimination and thus ultimately approximate to opportunistic prey selection, i.e. taking all prey species in proportion to their abundance (e.g. Emlen 1966, Estabrook & Dunham 1976, Hughes 1979). Although we have been referring to prey abundance here, strictly speaking, the appropriate measure is availability to the predator.

The relationships between the importance of a fish species in a predator's diet and the abundances of different fish in the sea may well be non-linear, so it is logical to use a generalised additive modelling (GAM) framework to quantify these relationships. The GAM framework potentially allows us to model diet selection as a function of the abundance of several prey species and, at least for pairs of prey species, to visualise (as 'smooth' surfaces) the interactions between effects of these putative explanatory variables.

A further issue relates to the statistical distribution of numbers of fish of each species found in the stomach contents: except in the case of the preferred prey of specialist feeders, very often the most frequent number of individuals of a given prey species in cetacean stomachs is zero. Sometimes prey numbers will fit a Poisson (P) or negative binomial (NB) distribution, but often the distributions are overdispersed. A fit to one of these familiar distributions might be achievable by transformation of the data, but this is not generally regarded as an appropriate way to treat count data (Zuur et al. 2012). Possible alternatives include use of quasi-Poisson models to correct for mild overdispersion or modelling presence–absence, although such an analysis clearly excludes much of the information available. A 2-stage modelling procedure is possible if the non-0 component of the data adequately fits a standard distribution (or at least its zero-truncated version). It is also probable that some 0s are 'false 0s', i.e. in the context of stomach contents, the prey species was eaten by the predator but its remains were not detected. Obviously, stomach contents consist mainly of the most recent meal and will not generally provide evidence of feeding over a long period, but even some components of the last meal may go undetected. This may arise if heads of large fish are not ingested, identifiable bones are damaged during ingestion, or material is rapidly digested and/or passed through the stomach (see reviews by Pierce & Boyle 1991, Tollit et al. 2010). This brings us into the realm of zero-inflated models, which were designed to model count data with many zero-values, based on the idea that these zeros comprise a mixture of true and false absences. Zero-inflated P and NB (ZIP and ZINB) GAM models have only recently been implemented in the R programming language and represent a possible solution for the analysis of the sort of dietary data typically available from stomach content analysis (Zuur et al. 2012).

Generally, information on fish abundance is available at regional and/or stock level and some caution is needed when deriving inferences about local abundance based on such data. For the main commercially fished species of Galician waters, annual abundance series exist, based on stock assessments by the International Council for the Exploration of the Sea (ICES) and, at least for sardine *Sardina pilchardus*, there is empirical evidence that local abundance, measured as research trawl catches, varies in proportion to stock size (Santos et al. 2013), permitting us to test ideas about the relationships between dolphin diet and fish abundance. The objectives of the present paper were thus as follows:

(1) to summarize the overall composition of common dolphin diet in Galician waters and to estimate the uncertainty around the estimated importance of different prey species;

(2) to determine if and how several putative explanatory variables (e.g. year, season, region, dolphin size and sex) contribute to dietary variability;

(3) to determine whether there has been significant interannual variation in the importance of the main prey in common dolphin diet, and whether this is related to large-scale trends in their abundance or the abundance of other main prey;

(4) to identify 'preferred' prey species and to determine whether diet–abundance relationships for these species are more consistent with opportunistic or selective predation;

(5) to demonstrate a preliminary application of zero-inflated models to cetacean dietary data.

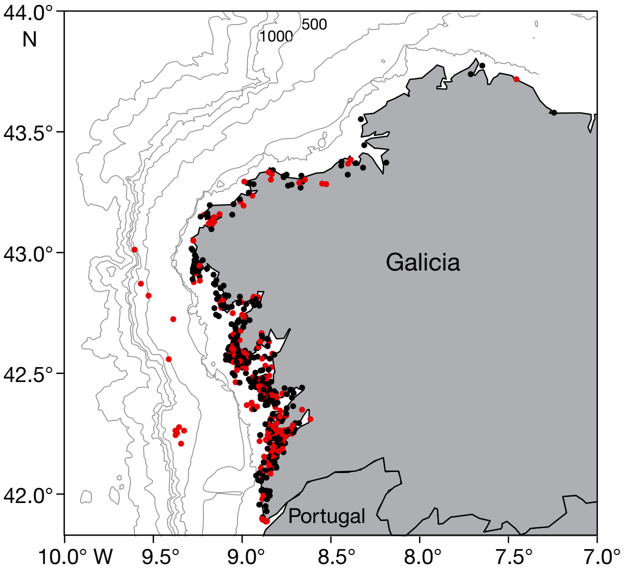

Fig. 1. *Delphinus delphis.* Galician (NW Spain) coastline, showing the locations of strandings and by-catches of common dolphins analysed in this study. Some jittering was applied to the locations to ensure that each point is visible. Animals which were confirmed by-catches or showed clear indications of having been by-caught are represented in red, while all the other animals are shown in black. Depth contours of 500 and 1000 m are indicated

MATERIALS AND METHODS

Collection of samples

Stomach contents of common dolphins were collected from animals stranded and by-caught in Galicia, NW Spain, between 1991 and 2008. These dolphins were identified and sampled by experienced personnel of the NGO Coordinadora para ó Estudio dos Mamíferos Mariños (CEMMA). When the condition of the carcass allowed it, a full necropsy was carried out to establish health status and cause of death, following the criteria of Kuiken (1994). Minimum information collected from the carcasses typically included body length and sex, together with samples of teeth (for age determination), gonads (for maturity status) and stomach contents. Although body weight, age and maturity data are available for some of the sampled animals, we used length as a proxy for size and age because length data were available for almost all animals.

One animal sampled had an occluded gut, and many thousands of fish otoliths had accumulated in the stomach. Data for this animal were excluded from the analysis, leaving a total of 514 animals. The composition of the sample set in terms of season, size class, sex, etc., is indicated in Table 1, while locations of strandings and by-catches are shown in Fig. 1.

Prey identification

Prey remains consisted mainly of fish (sagittal) otoliths, bones and lenses, and cephalopod mandibles (beaks). Few crustacean remains were present, and these could not always be further identified,

Table 1. *Delphinus delphis.* Summary of numbers of sampled dolphins in each year, by season (quarter), sex (F: female, M: male; Nd: not determined), size class (S: ≤150 cm, M: 151–190 cm, L: >190 cm, ND: not determined) and cause of death (C: recorded fishery by-catch, IN: evidence of by-catch, Ls: live stranded, Sh: shot, O: other or undiagnosed). Location was not determined in 1 case

Year	n	Quarter				Sex			Size				Cause of death				
		1	2	3	4	F	M	ND	S	M	L	ND	C	IN	Ls	Sh	O
1991	9	5			4	3	5	1	1	5	2	1		3	1		5
1992	17	2	3		12	4	12	1		11	3	3	1	4			12
1993	19	4	11	2	2	8	8	3	2	9	8		1	4	1		13
1994	23	8	7	1	7	5	16	2	1	15	7		1	5		1	16
1995	34	15	11	1	7	8	24	2	3	20	9	2	1	14			19
1996	47	16	13	10	8	15	27	5	2	13	16	16	2	8	1		36
1997	25	15	5	1	4	14	9	2		12	7	6	1	9			15
1998	60	24	26	8	2	18	39	3		19	23	18	1	17			42
1999	40	28	5	3	4	15	25		3	25	5	7	3	11	1[a]		25
2000	41	31	6	2	2	14	20	7	4	13	10	14		5			36
2001	28	11	5	11	1	14	13	1	2	7	12	7	1	12			15
2002	32	14	12	2	4	14	18		1	12	13	6	2	11			19
2003	48	9	24	7	8	22	26		6	19	12	11		21	1		26
2004	9	1		1	7	4	5		2	5	1	1		4			5
2005	15	11	1		3	5	10		1	8	5	1	2	8			5
2006	18	2	4	4	8	5	13			9	6	3	11	4			3
2007	29	6	5	15	3	6	22	1	2	10	16	1	13	8	1		7
2008	20	13	7			12	8		1	7	7	5	3	9			8
Total	514	215	145	68	86	186	300	28	31	219	162	102	43	157	6	1	307

[a] Live stranded but with indication of injuries caused by a bottlenose dolphin

due to the poor state of preservation. Fish otoliths and bones were identified using reference material and published guides (e.g. Härkönen 1986, Watt et al. 1997, Tuset et al. 2008). The number of fish was estimated from the number of otoliths or (for species with fragile otoliths, e.g. sardines) specific jaw bones (e.g. premaxilla, dentary), whichever number was higher. Fish sizes were estimated by measuring the otoliths, using callipers or a binocular microscope fitted with an eyepiece graticule. Calibration of the graticule was checked regularly using a slide micrometer. For stomachs in which a fish species was represented by >30 otoliths, a random sample of 30 to 60 otoliths was measured. Usually otolith length was measured, except for the otoliths of sardine and Gobiidae, for which width is the standard measurement (Härkönen 1986), and any identifiable otolith that was broken lengthways.

Fish length and weight were calculated from standard regressions (e.g. Härkönen 1986). For otoliths identifiable to genus, family or other grouping of species, regressions based on combined data from all of the species in the group were used. To reconstruct individual prey weight, each otolith was assumed to represent 0.5 fish. Thus, if both otoliths of an individual fish were present, the estimated weight of this fish would be the average of the weights estimated separately from the 2 otoliths. Since fish were not always represented by otoliths, not all otoliths were measured, and only measured otoliths were used to reconstruct weight, total overall weight for each prey taxon was adjusted based on the ratio of measured to unmeasured individuals. Note that the estimates are not corrected for otolith erosion, so fish lengths and weights are therefore likely to be underestimated. While possible solutions exist (e.g. measurement of only apparently uneroded otoliths, correction based on visual grading of otoliths into digestion categories), none are entirely satisfactory (see Tollit et al. 2010 for discussion).

Cephalopod beaks were also identified using reference material and guides (Clarke 1986, Pérez-Gándaras 1986). Standard measurements (rostral length for squid and hood length for octopods and sepiolids; Clarke 1986, Pérez-Gándaras 1986) were taken on either upper or lower beaks, using a binocular microscope fitted with an eyepiece graticule. Dorsal mantle length (DML) and body weight of the animals were estimated using standard regressions for lower beaks (Clarke 1986) or our own unpublished regressions for upper beaks. Complete pairs of cephalopod beaks were rarely present, and in all cases, DML and weight was estimated from either the upper or the lower beak. Cephalopod remains from 17 of the dolphins from 1992 and 1993 were previously identified by Dr. Angel González (IIM CSIC), and these partial results have been published (González et al. 1994). These beaks were re-examined, all fish material from the 17 stomach samples was identified, and all beaks and otoliths were measured.

The importance of individual prey species/taxa in each stomach was evaluated in terms of presence/absence, number and summed estimated weight. For overall diet, relative importance was estimated as (1) percentage frequency of occurrence, (2) proportion of the total number of prey and (3) proportion of total prey weight. For the latter 2 indices, the totals are those for all stomachs combined.

Traditionally, no explicit weighting is applied to such data when estimating overall diet, hence animals with larger amounts of food in the stomach contribute relatively more to the estimated overall diet. Alternative weightings are possible, including equal weighting of all animals or weighting according to body weight (and hence expected daily energy intake). The latter approach implies that dolphin size is taken into account when the data from the stomachs are added together to describe overall diet, i.e. bigger dolphins, regardless of number or weight of prey recovered from the stomach contents, contribute more to the overall diet (Pierce et al. 2007, Tollit et al. 2010). We explored the effect of these alternative weightings on the proportional contribution of the main prey species to total prey weight.

Confidence limits for diet composition

Approximate confidence limits for diet composition, taking into account sampling error, were derived by bootstrapping (sampling with replacement) using the package boot (Canty & Ripley 2011) in R 2.13.0 (R Development Core Team 2008). The process involves the addition of all prey weights from a sample to the overall diet each time a sample is selected. When *n* samples have been taken, weights for each prey category are expressed as percentages of the all-categories total and the results are stored. After 1000 runs, the median and 95% confidence limits are calculated separately for each category by sorting the 1000 importance measures for that category, and identifying the median, 26th and 975th value in the sorted sequence. This process was repeated 1000 times. Previous studies suggest that sampling error is generally the major component of quantifiable errors associated with diet estimation (Santos et al. 2001, Pierce et al. 2007).

Data exploration

For analysis of factors affecting dietary variation, response variables were the presence or numbers of each of the main prey taxa in individual stomachs. We chose numbers rather than weight because numbers are subject to fewer errors than (back-calculated) weight estimates (e.g. effects of otolith erosion, inherent variability in otolith size–fish size relationships, use of combined regressions for several prey species within a family). The following explanatory variables were considered: year, day of year, stranding location (latitude, longitude), dolphin length and dolphin sex. For response variables which showed interannual variation, we additionally investigated effects of annual prey abundance.

All data series were explored for e.g. outliers, collinearity and interactions following the protocol proposed by Zuur et al. (2010). Numbers of prey species in dolphin stomachs were characterised by a high number of zeros and a few extreme values (i.e. stomachs with high numbers of prey), indicating the possibility of zero-inflated (ZI) data, i.e. the occurrence of 'false' zeros in addition to the 'true' count data (Zuur et al. 2007, 2009, 2012).

Importance of main prey in the diet: ZINB GAM and binomial GAM

GAMs were used to determine the relationships between dietary importance (numbers) of the main prey species (sardine, blue whiting *Micromesistius poutassou* and hake *Merluccius merluccius*) and the explanatory variables. Initial models, fitted using GAMs with P or NB distributions and log link, indicated that data were overdispersed. Since it is possible that some zeros in the data are 'false zeros' and that this could account for the overdispersion, we explored the suitability of ZI models. We fitted ZIP and ZINB GAMs, finding that overdispersion persisted in the former but not the latter (in which the dispersion parameter was <1) and that the latter also performed better according to a log-likelihood test. We therefore used ZINB GAMs. Models were fitted using the packages mgcv (Wood 2006) and VGAM (Yee 2011) in R 2.13.0 (R Development Core Team 2008). The traditional approach to deal with overdispersed data, i.e. converting response variables to presence/absence data, was also explored using binomial GAMs (with a logit function).

For all final models which showed significant interannual variation in diet, to determine whether this could be related to changes in annual prey abundance, models were re-run substituting year by variables reflecting the abundance for the relevant prey species — in practice, this is restricted to considering abundance of sardine, blue whiting and hake. For sardine and hake, we considered 2 measures of annual stock size commonly derived from stock assessments, namely the estimated number of new recruits (recruitment) and spawning stock biomass (SSB). Values of recruitment and SSB for the Iberian sardine stock and the southern hake stock were taken from advice published by ICES (ICES 2011a). For blue whiting, the currently assessed stock covers fish distributed from Gibraltar to Norway, and as such, overall abundance values cannot be assumed to be applicable to Galician waters where only a small portion of the stock is located. Instead, we used biomass and number indices obtained for the species by the northern Spanish shelf groundfish survey ('Demersales'). This survey has covered the north and northwestern shelf waters of the Iberian Peninsula in autumn annually since 1983 and, although not used in the assessment of the stock because it does not cover its whole distribution area, it can give an indication of year class strength at regional level. Due to the annual nature of the various fish abundance estimates, there are few unique values, and it is therefore not feasible to evaluate interactions between effects of the abundances of the 3 species.

In general, for an opportunistic predator or for the preferred prey of a selective predator, a positive relationship is expected between dietary importance and stock size of the prey species in question, possibly reaching an asymptote. A negative relationship between consumption of one prey species and abundance of another species is expected if the second species is preferred over the former. Other or more complex relationships might occur as an indirect consequence of relationships between the abundances of different prey species (i.e. interactions).

For all GAMs, a backwards selection procedure was used. At each step, the least important non-significant variable was dropped and the model was re-run. In all cases, relationships with continuous explanatory variables (i.e. everything except dolphin sex) were fitted using loess smoothers (with the maximum number of degrees of freedom restricted to 3 [k = 4] to avoid overfitting). If 'final' models contained non-significant terms, the consequence of removing these was tested using an *F*-test; such terms were retained if they significantly improved the model fit. Once 'final' models were obtained, residuals were checked for patterns, and the absence of highly influential data points was checked, based on 'hat' values. Possible interactions between effects of explanatory variables were also checked at this stage. All statistical analyses were carried out using R 2.13.0 (R Development Core Team 2008) and the statistical programmes Brodgar (Highland Statistics) and Minitab (Minitab).

RESULTS

Composition of the sample

Numbers of dolphin stomachs examined each year by each category are summarized in Table 1. The majority of samples came from the southern part of the study area (Fig. 1). Forty-three out of the 514 animals for which stomach contents were examined were recorded by-catches in fishing gear (mainly pair trawlers and trawls). A further 157 animals examined exhibited signs of by-catch, such as cuts (on flippers and/or abdomen), net marks, net remains on the carcasses, absence of the tailstock, or the presence of ropes in the tail, making death in fishing gear the origin of at least 38.9% of all samples. The remaining dolphins did not show clear signs of by-catch, although it was often not possible to exclude this as a cause of death because, in many cases, carcasses were found in an advanced stage of decomposition. In addition, 1 dolphin had been shot and 6 animals were live-stranded, including 1 that had marks consistent with an attack by a bottlenose dolphin *Tursiops truncatus*. Detailed pathological and histopathological analyses for a sub-sample of 45 animals collected during 2001 to 2003 revealed 21 by-catch mortalities and 16 deaths from pathological causes, the majority of the latter being parasitical or infectious pneumonia (CEMMA unpubl. data).

Of the 487 dolphins for which sex was known, 60% were males. Most strandings occurred in the first half of the year: 41.7% in the first quarter, 28.3% in the second quarter, 13.2% in the third quarter and 16.7% in the fourth quarter. Total length was available for 412 ind. and ranged between 122 and 240 cm. Dolphin length followed an approximately normal distribution with modal size at 180 cm (mean ± SD = 184.5 ± 22.1 cm).

General description of diet and estimates of prey consumption

Remains of at least 62 575 individual fish were recovered from the stomachs together with remains of 6258 cephalopods, 977 crustaceans and 35 polychaetes. We identified 26 fish taxa and 15 cephalopod taxa from these remains (Table 2). Crustacean remains were found in 30.5% of the stomachs and consisted mainly of parasitic isopods. Polychaete remains were found in 25 stomachs (4.9%). From the stomach of the individual that we removed from further analysis due to having an occluded gut, we identified remains of 629 blue whiting, 8 scads (*Trachurus* sp.), 1 hake and 1 garfish *Belone belone*.

Blue whiting and sardine were the most important prey categories by reconstructed weight, together making up almost 52% of the diet, while gadoids (mainly blue whiting) were the most numerous prey group. The next most important prey categories were *Atherina* sp., scads and hake, comprising 8, 7 and >5%, respectively, of the total reconstructed prey weight. Of the cephalopod prey, the common squid *Loligo* sp. (there are 2 species of this genus present in Galician waters with very similar mandibles, *L. vulgaris* and the less common *L. forbesii*) was the main prey by reconstructed weight, followed by ommastrephid squids. By number, bobtail squids (Sepiolidae) were the main cephalopod prey, but due to their small size they contributed relatively little to total prey mass. Remains of 2 species of octopus (common octopus *Octopus vulgaris* and lesser octopus *Eledone cirrhosa*) were also found in the stomachs.

The main consequence of correcting diet composition estimates, to take account of fish identified from hard parts other than otoliths, is the increased importance of sardine and mackerel in the diet and the consequent decrease of the importance of all other prey categories. Despite this, the general picture of diet composition changes relatively little (Table 2): the importance (by reconstructed weight) of sardine rose from 11.4 to 15.3%, and that of mackerel from 1.2 to 3.2%, while blue whiting importance decreased correspondingly from 40.9 to 33.5%.

In the previous paragraphs we have described the diet of the common dolphins assuming that each stomach contributes to the overall diet in proportion to the amount of food in it, i.e. animals with more food in the stomach have contributed more to the overall diet estimate. Results for the main prey species based on alternative weightings are shown in Table 3. When equal weighting was applied to each sample, the importance of sardine increased (from 11.4 to 17.8% of biomass). Gobies, *Trisopterus* spp. and cephalopods also increased, but the importance of blue whiting, the main prey, decreased to almost half of the previous value (from 41.1 to 24.2%). Results for the overall diet when each stomach was weighted according to estimated dolphin weight were similar to the unweighted results. In general, and for most prey categories, confidence limits for importance in the diet were relatively narrow. They were widest for blue whiting: for the estimated importance value of 41.1%, the 95% confidence limits were 35.4 to 46.5% (Table 3).

The estimated length of blue whiting eaten by dolphins ranged from 4 to 31 cm total length, with a mode at 17.5 cm and a mean ± SD at 16.3 ± 3.4 cm, while sardines ranged from 16 to 22.5 cm total length with a mode at 18.5 cm and mean at 18.3 ± 1.0 cm. Scads eaten by dolphins ranged from 3.5 to 37 cm with a mode at 12.5 cm and a mean at 14.2 ± 5.6 cm, while hake ranged from 3 to 61 cm with a mode at 15.0 cm and a mean at 18.2 ± 7.3 cm.

GAM results on dietary variation

In all cases, data exploration and model validation indicated that no important interactions between explanatory variables had been missed. In addition, no evident interactions were present between the abundances (measured either as recruitment or SSB) of the main prey species, justifying their use as individual variables in the models.

Numbers of prey in stomach contents

Sardine

Results from the final ZINB GAMs for numbers of sardine in the stomachs ($n = 511$, once 2 outliers and 1 animal for which stranding location was not available were removed) showed a weakly significant interannual pattern ($p < 0.05$). Sardine numbers decreased up to the end of the 1990s, then increased until around 2002 to 2003 and subsequently steadily decreased. Numbers of sardine in the stomachs were not significantly affected by latitude of stranding or day of year. Repeating the analysis on the subset of dolphins for which estimated lengths were available reduced the sample size to 411 individuals (after 1 outlier was removed). A significant effect of year ($p < 0.05$) remained, and effects of day of year and dolphin size were also significant ($p < 0.01$ and $p < 0.05$, respectively), with bigger dolphins taking more sar-

Table 2. *Delphinus delphis.* Overall importance of prey species identified from Galician common dolphins (N = 514). The first estimate (%F) indicates the percentage of stomachs containing each prey category. The estimates for total number of individuals are based on (N_1) otoliths and beaks only and (N_2) all prey remains. Measurements on otoliths and beaks were used to derive the first estimate of total prey weight (W_1, g), while the second estimate (W_2, g) is adjusted to take account of fish and cephalopods identified from other remains. All 4 latter estimates are also expressed as percentages. (–) Remains found did not permit estimation of number and/or weight of prey

Prey species	% F	N_1	N_2	%N_1	%N_2	W_1	W_2	%W_1	%W_2
Fish	**98.6**	**58997**	**62575**	**90.4**	**89.6**	**787172**	**982922**	**92.5**	**93.9**
Sardine *Sardina pilchardus*	45.1	2040	3364	3.1	4.8	97117	160148	11.4	15.3
Anchovy *Engraulis encrasicolus*	5.8	196	205	0.3	0.3	14	14	0.0	0
All clupeoids	48.2	2238	4126	3.4	5.9	97208	189680	11.4	18.1
Argentine (*Argentina* sp.)	13.6	862	877	1.3	1.3	24609	25037	2.9	2.4
Lanternfish (Myctophidae)	6.6	1691	1756	2.6	2.5	1836	1907	0.2	0.2
Pearlsides	0.2	518	518	0.8	0.7	282	282	0.0	0.0
Barracudinas (Paralepididae)	0.2	3	3	0.0	0.0	–	–	–	–
Whiting *Merlangius merlangus*	0.2	2	3	0.0	0.0	25	38	0.0	0.0
Blue whiting *Micromesistius poutassou*	48.8	18362	18519	28.1	26.5	348027	351003	40.9	33.5
Trisopterus spp. (*T. esmarkii*, *T. minutus*, *T. luscus*)	33.9	2582	2618	4.0	3.7	32633	33088	3.8	3.2
Silvery pout *Gadiculus argenteus thori*	26.8	5746	5773	8.8	8.3	13179	13241	1.5	1.3
Rocklings	1.2	24	25	0.0	0.0	504	525	0.1	0.1
Phycidae	0.2	–	1	–	0.0	–	–	–	–
All Gadidae	72.2	26909	27198	41.3	38.9	396050	400151	46.6	38.2
Hake *Merluccius merluccius*	25.9	702	751	1.1	1.1	48667	52064	5.7	5.7
Snipefish *Macroramphosus scolopax*	1.9	–	179	–	0.3	–	–	–	–
Garfish *Belone belone*	2.5	4	35	0.0	0.1	647	5661	0.1	0.5
Scad (*Trachurus* sp.)	37.2	1690	1795	2.6	2.6	60443	64198	7.1	6.1
Sparidae	13	792	836	1.2	1.2	27183	28546	3.2	2.7
Mugilidae	0.2	2	2	0.0	0.0	178	178	0.0	0.0
Labridae	2.3	7	16	0.0	0.0	180	411	0.0	0.0
Sandeel (*Ammodytes* spp.)	21.2	1962	2001	3.0	2.9	23860	24334	2.8	2.3
Dragonet (Callyonymidae)	3.3	75	86	0.1	0.1	642	736	0.1	0.1
Gobiidae	44.9	16041	16148	24.6	23.1	20820	20959	2.4	2.0
Mackerel *Scomber scombrus*	20.4	97	319	0.1	0.5	10302	33879	1.2	3.2
Atherina sp.	21.2	5030	5057	7.7	7.2	68998	69369	8.1	6.6
Scaldfish (*Arnoglossus* sp.)	2.3	68	132	0.1	0.2	482	935	0.1	0.1
All Bothidae	3.5	116	182	0.2	0.3	1481	2324	0.2	0.3
Sole *Solea solea*	1.4	37	39	0.1	0.1	2061	2173	0.2	0.2
Other flatfish	4.7	62	69	0.1	0.1	1698	1890	0.2	0.2
Unidentified fish	23.5	65	374	0.3	0.5	–	–	–	–
Cephalopoda	**70.6**	**6234**	**6258**	**9.6**	**9.0**	**63584**	**64147**	**7.5**	**6.1**
Cuttlefish (*Sepia* spp.)	2.7	61	62	0.1	0.1	306	311	0.0	0.0
Sepiolid (*Sepiola atlantica*)	7.4	217	217	0.3	0.3	312	311	0.0	0.0
Sepiolid (*Sepietta oweniana*)	2.5	36	36	0.1	0.1	193	193	0.0	0.0
All Sepiolidae	43.6	2860	2860	4.4	4.1	6478	6471	0.8	0.6
Squid (*Loligo* sp.)	20.4	524	526	0.8	0.8	27160	27264	3.2	2.6
Squid (*Alloteuthis* sp.)	40.7	2140	2141	3.3	3.1	10542	10547	1.2	1.0
Squid (*Illex coindetti*)	1.4	15	15	0.0	0.0	1225	1225	0.1	0.1
Squid (*Todaropsis eblanae*)	0.8	5	5	0.0	0.0	274	274	0.0	0.0
Squid (*Todarodes sagittatus*)	0.2	1	1	0.0	0.0	883	883	0.1	0.1
All Ommastrephidae	24.3	505	510	0.8	0.7	12413	12536	1.5	1.2
Squid (*Gonatus steenstrupi*)	1.4	24	26	0.0	0.0	2593	*2809*	0.3	*0.3*
Squid (*Histioteuthis reversa*)	0.2	1	1	0.0	0.0	28	28	0.0	0.0
All Histioteuthidae	0.4	3	3	0.0	0.0	155	155	0.0	0.0
Squid (*Chiroteuthis* sp.)	2.1	57	57	0.1	0.1	1437	1437	0.2	0.1
Squid (*Mastigoteuthis* sp.)	0.2	1	1	0.0	0.0	90	90	0.0	0.0
Squid (*Teuthowenia megalops*)	0.6	8	8	0.0	0.0	366	366	0.0	0.0
Octopus (*Octopus vulgaris*)	3.5	27	27	0.0	0.0	875	875	0.1	0.1
Octopus (*Eledone cirrhosa*)	2.9	19	19	0.0	0.0	1150	1150	0.1	0.1
Unidentified Cephalopoda	2.9	2	18	0.0	0.0	–	–	–	–
Crustacea	**30.5**	**–**	**977**	**–**	**1.4**	**–**	**–**	**–**	**–**
Polychaeta	**4.9**	**–**	**35**	**–**	**0.1**	**–**	**–**	**–**	**–**

Table 3. Importance (% reconstructed weight) of the main prey species in the diet of common dolphin in Galicia after applying different sample weighting. Figures in brackets are 95 % confidence intervals

Prey species	No weighting	Equal weighting	Weighting according to dolphin weight
Sardine *Sardina pilchardus*	11.4 [9.2–14.3]	17.8 [15.2–20.3]	10.6 [8.1–13.7]
Blue whiting *Micromesistius poutassou*	41.1 [35.4–46.5]	24.2 [21.4–27.4]	44.4 [38.1–50.2]
Trisopterus spp. (*T. esmarkii*, *T. minutus*, *T. luscus*)	3.8 [2.7–5.2]	6 [4. 7–7.4]	3.1. [2.2–4.2]
Silvery pout *Gadiculus argenteus thori*	1.6 [1.1–2.0]	1.2 [0.8–1.8]	1.6 [1.1–2.2]
Other Gadidae	0.3 [0.1–0.5]	0.1 [0.3–1.5]	0.3 [0.1–0.4]
Hake *Merluccius merluccius*	5.7 [4.2–7.3]	4.9 [3.7–6.1]	5.9 [4.4–7.5]
Scad (*Trachurus* sp.)	7.1 [4.9–10.0]	7.1 [5.6–8.9]	8.1 [5.4–11.3]
Sparidae	3.2 [2.1–4.4]	2.94 [2.0–4.0]	3.3 [2.0–4.9]
Gobiidae	2.5 [1.6–3.7]	4.4 [3.3–5.79]	1.8 [1.2–2.6]
Mackerel *Scomber scombrus*	1.2 [0.8–1.8]	1.7 [1.0–2.5]	1.3 [0.8–2.0]
Atherina sp.	8.1 [5.6–11.0]	7.4 [5.7–9.3]	6.7 [4.4–9.2]
Other fish	6.6 [3.9–9.8]	5.7 [4.4–7.18]	5.9 [3.5–9.1]
Squid (*Loligo* sp.)	3.2 [2.1–4.6]	4.7 [3.3–6.0]	3 [1.9–4.3]
Squid (*Alloteuthis subulata*)	1.2 [0.9–1.6]	3.4 [2.6–4.4]	1 [0.8–1.4]
Other Cephalopoda	3 [2.3–3.9]	6.4 [5.1–7.8]	3.1 [2.3–4.1]

dine and fewer sardines being eaten in the summer months (Fig. 2a–c).

Of the 2 stock size variables (sardine SSB and recruitment) tested in the ZINB models in place of year, only sardine recruitment was significantly related to the number of sardines in dolphin stomachs. The final model for the whole data set included only the effect of sardine recruitment ($p < 0.05$). For the subsample of data with dolphin length, the final model included significant effects of sardine recruitment ($p < 0.05$), day of year ($p < 0.01$) and dolphin length ($p < 0.05$). Fewer sardines were eaten in years of poor sardine recruitment (Fig. 2d). Bigger dolphins took more sardines, and sardine numbers in dolphin stomachs decreased in the summer months.

Blue whiting

For blue whiting numbers in the stomachs, the final ZINB GAMs ($n = 512$, once 1 outlier and 1 animal for which stranding location was not available were removed) showed significant interannual and seasonal patterns ($p < 0.001$ in both cases), with blue whiting importance in the stomachs decreasing markedly until 2000 and then increasing again, and being highest in the summer months. When dolphin length was taken into account ($n = 411$), blue whiting importance continued to show significant effects of year and day of year ($p < 0.001$ in both cases) but also of dolphin size ($p < 0.001$), with more blue whiting appearing in the stomachs of bigger dolphins (Fig. 3a–c).

When fish abundance indices were included among candidate explanatory variables in the ZINB GAMs, numbers of blue whiting in dolphin stomachs were significantly related to trawl survey numerical abundance ($p < 0.05$) and day of year ($p < 0.001$), with dolphin eating more blue whiting in years when more fish were taken in the trawls, and in the summer months. However, no significant relationship was found with the survey biomass index. Once dolphin estimated length was included in the models, blue whiting numbers in stomachs were found to be significantly negatively related to the survey biomass index ($p < 0.01$; Fig. 3d), day of year and dolphin length ($p < 0.001$ for both). More blue whiting were taken in the summer months and by bigger dolphins. No significant relationship was found with the numerical survey abundance index.

Hake

The ZINB model for hake numbers was unstable. A square root transformation was applied to hake numbers in the stomachs to reduce the data dispersion. The final ZINB GAMs model for the transformed hake numbers in common dolphin stomachs showed significant interannual and seasonal variation ($p < 0.001$ and $p < 0.05$, respectively, Fig. 4) with increasing importance of this species in the stomachs from 1998 onwards.

When year was substituted in the models by the 2 stock variables (recruitment and SSB) tested, both hake recruitment ($p < 0.01$) and hake SSB ($p < 0.05$)

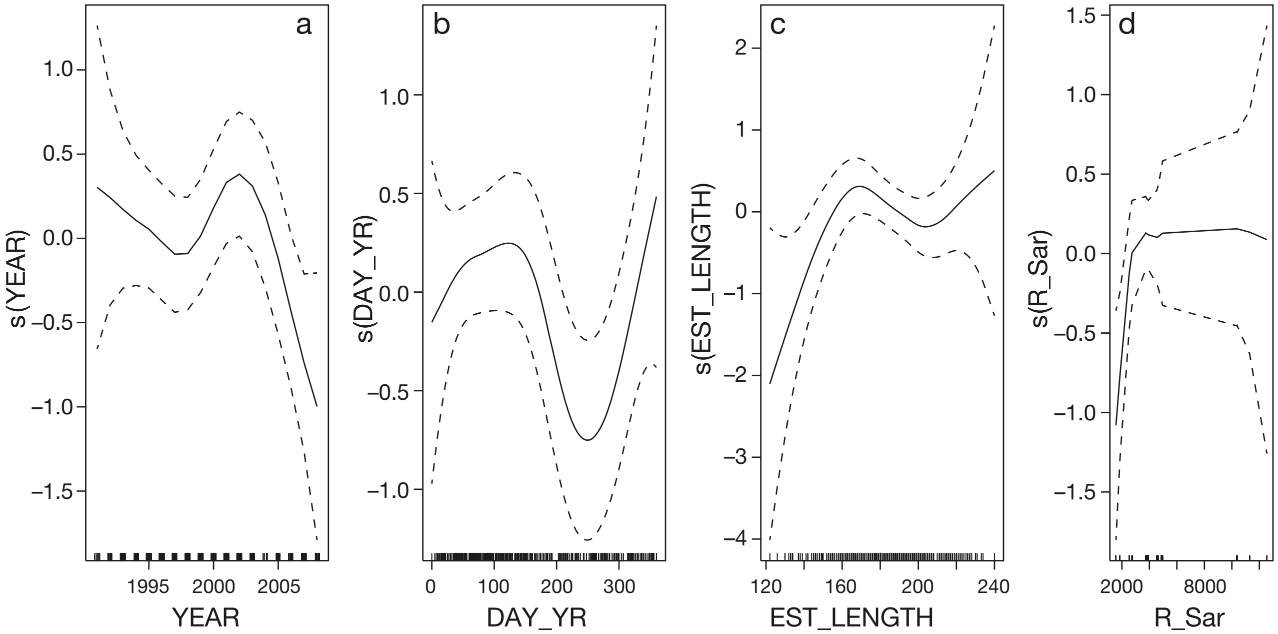

Fig. 2. *Sardina pilchardus.* Final zero-inflated negative binomial generalised additive models (hereafter ZINB GAMs) of sardine numbers in common dolphin stomachs in relation to explanatory variables for the sample set that included only dolphins for which length was available: smoothers for significant effects of (a) Year of stranding, (b) Day of Year (DAY_YR) of stranding and (c) Estimated length of dolphin (EST_LENGTH); (d) smoother for significant effects of Recruitment of the Iberian sardine stock (R_Sar) (when it was inserted in place of Year in the previous model). For all smoothers, an upward trend implies an increasing positive (or decreasingly negative) effect of the explanatory variable, provided that confidence limits (dashed) are not so wide that a zero trend is plausible. Thus in (a), there is a negative trend over time in recent years but trends prior to around 2002 are not significant

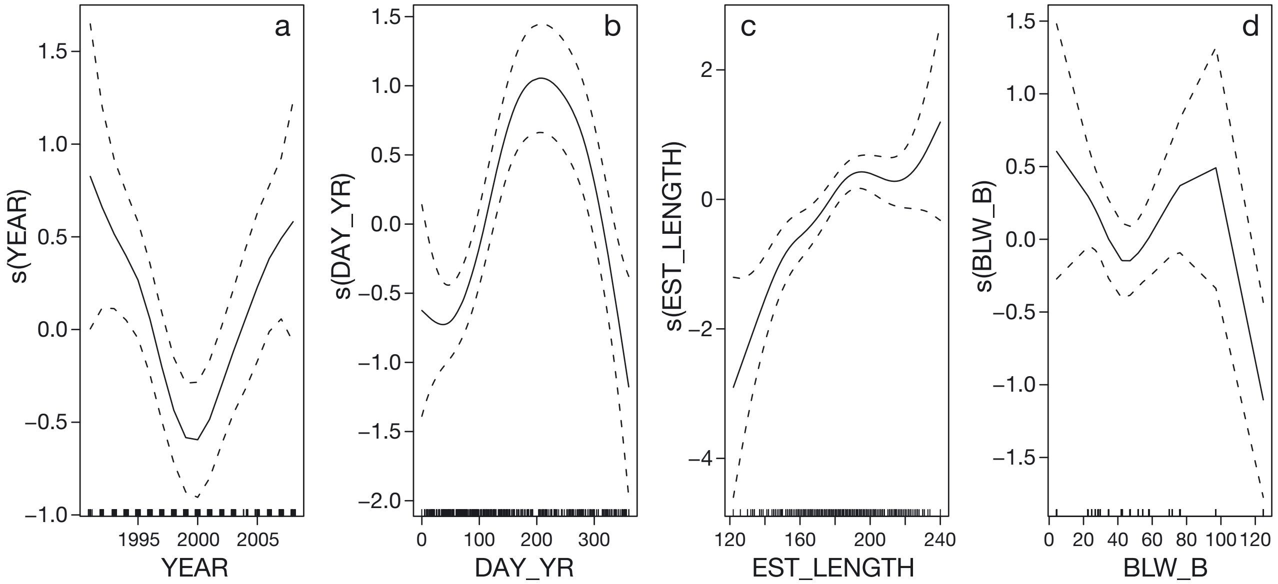

Fig. 3. *Micromesistius poutassou.* Final ZINB GAMs of blue whiting numbers in common dolphin stomachs in relation to explanatory variables: smoothers for significant effects of (a) Year of stranding, (b) Day of Year (DAY_YR) of stranding and (c) Estimated length of dolphin (EST_LENGTH) for the sample set that included only dolphins for which length was available; (d) smoother for significant effects of blue whiting index of Biomass obtained by the Spanish demersal trawl survey (BLW_B) (when it was inserted in place of Year in the previous model)

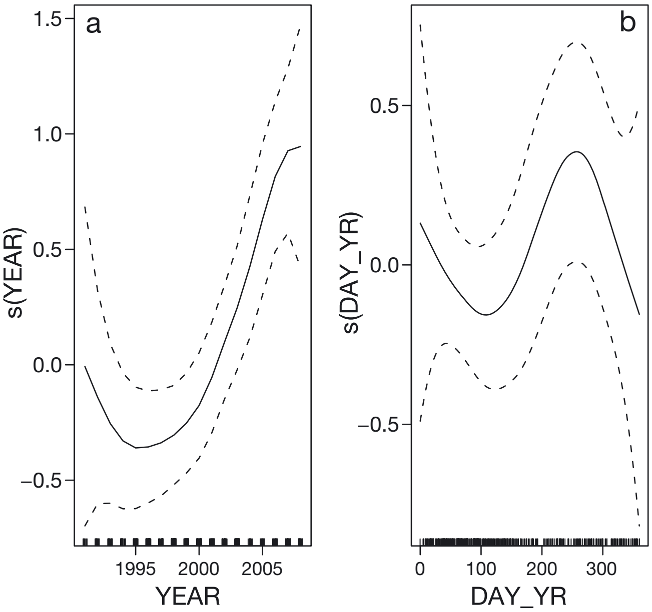

Fig. 4. *Merluccius merluccius.* Final ZINB GAMs for hake numbers in dolphin stomachs in relation to explanatory variables: smoother for significant effects of (a) Year of stranding and (b) Day of Year (DAY_YR) for the whole sample set

were significantly positively related to importance of hake in dolphin stomachs.

Prey presence in stomach contents

Sardine

Results from the binomial GAMs for sardine presence in common dolphin stomachs showed significant effects of year, latitude and day of year, although the deviance explained was small (6.05%, see Table 4). Sardines appeared in fewest stomachs in the summer months and at medium latitudes (Fig. 5). Inclusion of dolphin sex as an additional explanatory variable did not improve the overall fit (as demonstrated by results of an *F*-test to compare models with and without this term). Final models for the subset of samples with dolphin length data (n = 411) indicated no significant effect of year on sardine presence in the stomachs.

Inclusion of either sardine recruitment or sardine SSB as an explanatory variable instead of year in the binomial GAM for the full data set resulted in new

Table 4. *Sardina pilchardus, Micromesistius poutassou* and *Merluccius merluccius.* Results of the GAMs for presence/absence of sardine, blue whiting and hake found in the stomachs of common dolphins stranded and by-caught in Galicia (NW Spain) from 1991 to 2008. The basic data set comprises all dolphins for which location data were available, and results are also presented for the subset of dolphins for which length was available. SSB: spawning stock biomass; % Dev: percentage of deviance explained by the model. Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns: not significant

Species Data set	Variable	Significance level	N	% Dev
Sardine				
All dolphins	Year	*	511	6.1
	Latitude	*		
	Day of Year	**		
	Sardine recruitment	*	511	5.9
	Latitude	*		
	Day of Year	**		
	Sardine SSB	**	511	6.3
	Latitude	**		
	Day of Year	**		
Dolphins with length data	Sardine recruitment	*	411	9.4
	Latitude	*		
	Day of Year	**		
	Dolphin length	*		
	Sardine SSB	*	411	9.8
	Latitude	*		
	Day of Year	***		
	Dolphin length	*		
Blue whiting				
All dolphins	Year	**	512	12.4
	Latitude	***		
	Day of Year	***		
Dolphins with length data	Year	**	411	18.6
	Latitude	***		
	Day of Year	***		
	Dolphin length	***		
Hake				
All dolphins	Year	***	486	10.2
	Latitude	*		
	Day of Year	**		
	Sex	ns		
	Hake recruitment	***	486	9.7
	Latitude	**		
	Day of Year	**		
	Sex	ns		
	Hake SSB	***	486	10.8
	Latitude	*		
	Day of Year	***		
	Sex	ns		
Dolphins with length data	Year	***	412	13.7
	Latitude	*		
	Day of Year	**		
	Dolphin length	**		
	Hake recruitment	***	412	12.3
	Latitude	*		
	Day of Year	**		
	Dolphin length	*		
	Hake SSB	**	412	12.6
	Latitude	*		
	Day of Year	**		
	Dolphin length	**		

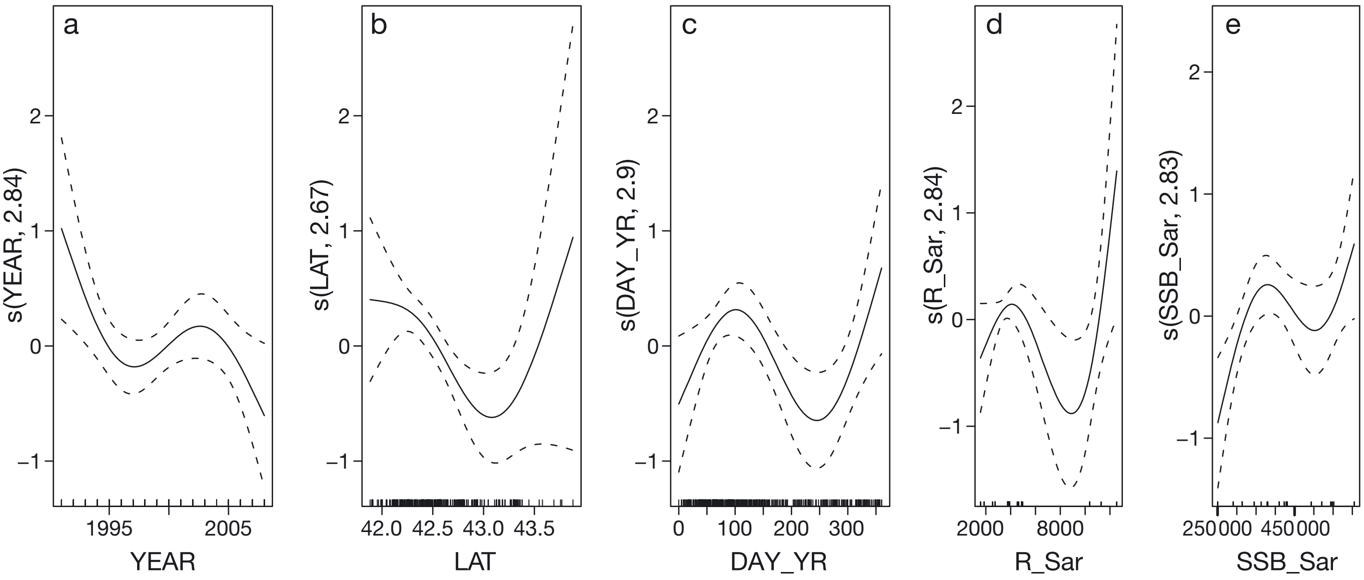

Fig. 5. *Sardina pilchardus.* Final binomial GAM of sardine presence/absence in common dolphin stomachs in relation to explanatory variables: smoothers for significant effects of (a) Year, (b) Latitude of stranding (LAT), (c) Day of Year (DAY_YR); and smoothers for significant effects of 2 abundance indices: (e) Recruitment and (f) Spawning stock biomass (SSB), when each was inserted into the previous model in place of Year

best models for sardine presence in the stomachs that included a weak positive effect of sardine recruitment ($p < 0.05$) or a stronger positive effect of sardine SSB ($p < 0.01$), respectively, although the shape of the relationships was not linear. There were also negative effects of latitude ($p < 0.01$) and day of year ($p < 0.01$) in both cases. The seasonal pattern observed in sardine presence in the stomachs showed an increase in March and April, a decrease in summer and again an increase at the end of the year. In both models, all variables together explained less than 6.5% of the deviance. Repeating this analysis for the subset of samples for which dolphin length was known, the new final models included positive effects of sardine abundance ($p < 0.01$ in both cases, Fig. 5d–e), latitude, day of year and dolphin length on sardine presence in dolphin stomachs (Table 4). Sardines were found more frequently in medium-sized dolphins.

Blue whiting

The final binomial GAM for presence of blue whiting also showed significant effects of year ($p < 0.01$), latitude and day of year ($p < 0.001$ in both cases), and explained 12.4% of the deviance. There was a linear increase over time in the number of dolphins recorded with blue whiting in their stomachs, with this prey also being more frequently found at medium latitudes and in the summer months (Table 4). When the sample set was reduced to include only those dolphins for which information on length was available, dolphin length also appeared as significant in the final model in addition to year, latitude and day of year. Deviance explained by the final model was 18.7%. Results indicate a linear increase in blue whiting presence in stomachs with increasing dolphin length (Fig. 6).

In the full binomial GAM for blue whiting presence, substituting year by one of the survey indices (numerical abundance or biomass) resulted in new models in which only day of year and latitude were significant, with neither survey index having any significant effect. As was the case for the full data set, blue whiting presence in stomachs of dolphins for which length data were available was not significantly related to either of the survey indices.

Hake

Final binomial GAMs for hake presence in dolphin stomachs also showed significant effects of year, latitude and day of year. Although dolphin sex was not significant in the final model, it significantly improved the overall model fit (*F*-test, $p < 0.05$, Table 4). The deviance explained by the final model was 10.6%. There was an increase in the number of stomachs with hake over the time series, as well as greater presence at higher latitudes and in the summer months. Inclusion of dolphin length reduced the sam-

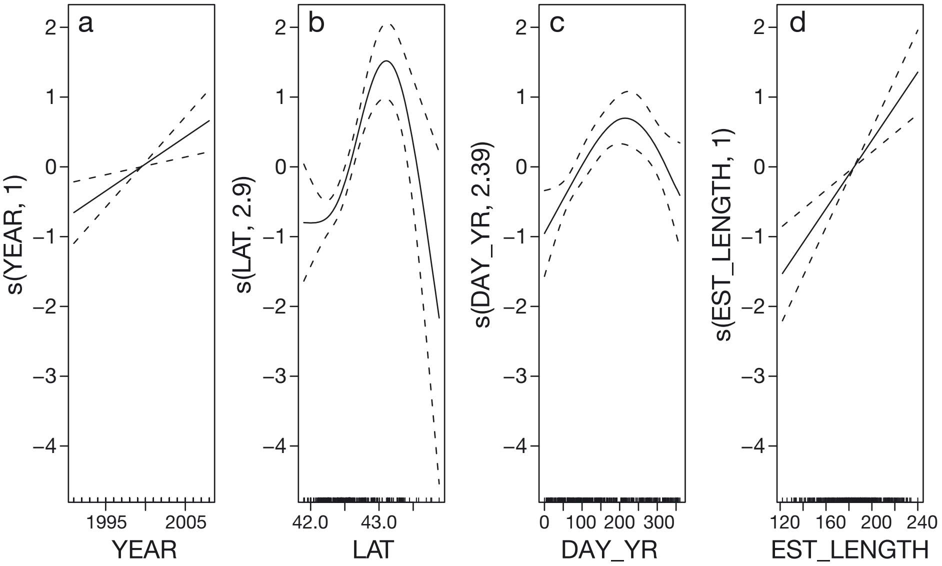

Fig. 6. *Micromesistius poutassou.* Final binomial GAM of blue whiting presence/absence in common dolphin stomachs in relation to explanatory variables: smoothers for significant effects of (a) Year, (b) Latitude of stranding (LAT), (c) Day of Year (DAY_YR) and (d) Estimated length of dolphin (EST_LENGTH)

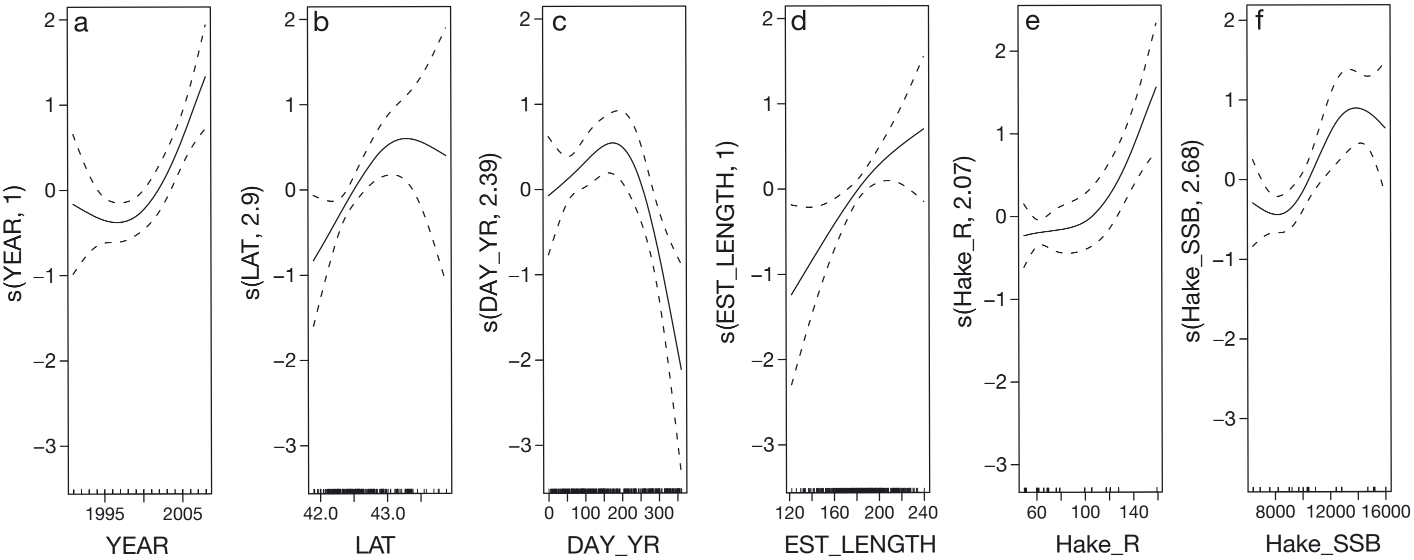

Fig. 7. *Merluccius merluccius.* Final binomial GAM of hake presence/absence in common dolphin stomachs in relation to explanatory variables: smoothers for significant effects of (a) Year, (b) Latitude of stranding (LAT), (c) Day of Year (DAY_YR) and (d) Estimated length of dolphin (EST_LENGTH); and smoothers for significant effects of 2 abundance indices: (e) Recruitment and (f) Spawning stock biomass (SSB), when each was inserted into the previous model in place of Year

ple set and produced new models in which year, latitude, day of year and dolphin length all showed significant effects on hake presence in dolphin stomachs (Table 4). The new model explained a slightly higher percentage of deviance (13.7%) and indicated that hake were more frequently found in the stomachs of bigger dolphins (Fig. 7).

For the binomial GAMs, when year was replaced by hake recruitment or SSB, both variables showed strong positive significant effects on the presence of hake in dolphin stomachs ($p < 0.001$ in both cases). Final models also included effects of latitude and day of year. Again, dolphin sex, although not significant, remained in the final models because it significantly

Table 5. *Sardina pilchardus, Micromesistius poutassou* and *Merluccius merluccius.* Results of the ZINB GAMs for numbers of sardine, blue whiting and hake found in the stomachs of common dolphins stranded and by-caught in Galicia (NW Spain) from 1991 to 2008 in relation to main prey stock size. The shading indicates significant trends which are consistent with (green), equivocal (yellow) or contradictory (red) to the hypothesis that the species eaten is a 'preferred' prey, '+' indicates a positive effect while '–' indicates the opposite. Sar_R: sardine recruitment, Sar_SSB: sardine spawning stock biomass, BLW_N: blue whiting abundance, BLW_B : blue whiting biomass, Hake_R: hake recruitment, Hake_SSB: hake spawning stock biomass. Significance levels (*p < 0.05, **p < 0.01, ***p < 0.001) refer to the effect of stock size on numbers of main prey in the stomachs; if both indices (recruitment/abundance and SSB/biomass) have the same significant effect, only 1 value is provided for simplicity

Species Data set	Variable	Sar_R	Sar_SSB	Significance level	BLW_N	BLW_B	Significance level	Hake_R	Hake_SSB	Significance level	N
Sardine											
All dolphins	Stock size	🟩 +		*							510
Dolphins with length data	Stock size Day of Year Dolphin length	🟩 +		*							410
Blue whiting											
All dolphins	Stock size Day of Year				🟥 –		*		🟨 ∿	*	510
Dolphins with length data	Stock size Day of Year Dolphin length					🟥 –	**				410
Hake											
All dolphins	Stock size Day of Year	🟥 –	🟨 ∩	***	🟥 –		***	🟩 +	🟩 +	*	510
Dolphins with length data	Stock size Day of Year Dolphin length	🟥 –	🟨 ∩	***	🟥 –		*	🟩 +		***	410

improved the overall model fit (*F*-test, $p < 0.05$, Table 4). For the subset of samples with dolphin length data available, both hake recruitment ($p < 0.001$) and hake SSB ($p < 0.01$) were significantly positively related to hake presence in dolphin stomachs (Fig. 7), with final models also including significant effects of latitude, day of year and dolphin length in both cases. The deviance explained by these models was slightly reduced (12.3 and 12.6%, respectively, Table 4).

Prey selection

Here we recap results on dietary importance of sardine, blue whiting and hake in relation to their abundance in the sea and briefly describe results of models for each species which included the abundance of other species as predictors. Results are summarized in Tables 5 & 6 and may be compared with predictions previously described.

Sardine

Results of the ZINB GAMs models for sardine numbers indicate that common dolphin consumption of sardine was significantly (positively) related to sardine recruitment ($p < 0.05$) but not related to hake recruitment or hake SSB, or either of the blue whiting survey indices tested or indeed sardine SSB. For the reduced model, the one in which only animals with length data available were included, similar results were obtained (Table 5).

Results from the binomial GAMs for sardine presence/absence in dolphin stomachs showed that sardine presence was significantly (positively) related to sardine recruitment and sardine SSB. In contrast to results of the ZINB model of sardine numbers, sardine presence was negatively related to hake recruitment (Table 6). No significant relationship was found between sardine presence/absence in the stomachs and hake SSB or the survey indices of blue whiting abundance or biomass. Results for the reduced data set (only dolphins for which length was available) were similar.

Hake

Hake numbers in dolphin stomachs were weakly but significantly positively related to both hake recruitment and hake SSB ($p < 0.05$, in both cases) but also strongly negatively related to sardine

Table 6. *Sardina pilchardus, Micromesistius poutassou* and *Merluccius merluccius.* Results of the binomial GAMs for presence/absence of sardine, blue whiting and hake found in the stomachs of common dolphins stranded and by-caught in Galicia (NW Spain) from 1991 to 2008 in relation to main prey stock sizes. The shading indicates significant trends which are consistent with (green), equivocal (yellow) or contradictory (red) to the hypothesis that the species eaten is a 'preferred' prey, '+' indicates a positive effect while '–' indicates the opposite. Abbreviations as in Table 5. Significance levels (*p < 0.05, **p < 0.01, ***p < 0.001) refer to the effect of stock size on numbers of main prey in the stomachs; if both indices (recruitment/abundance and SSB/biomass) have the same significant effect, only 1 value is provided for simplicity

Species Data set	Variable	Sar_R	Sar_SSB	Significance level	BLW_N	BLW_B	Significance level	Hake_R	Hake_SSB	Significance level	N
Sardine											
All dolphins	Stock size	🟩 +	🟩 +	*, **				🟥 –		***	513
Dolphins with length data	Stock size Day of Year Dolphin length	🟩 	🟩 	*				🟥 –		**	412
Blue whiting											
All dolphins	Stock size Latitude Day of Year	🟥 –		**					🟨 +	–	513
Dolphins with length data	Stock size Latitude Day of Year Dolphin length	🟥 –		**							412
Hake											
All dolphins	Stock size Day of Year	🟥 –	🟨 +	***		🟥 –	*	🟩 +	🟩 +	***	513
Dolphins with length data	Stock size Day of Year Dolphin length	🟥 –	🟨 +	***		🟥 –	*	🟩 +	🟩 +	***	412

recruitment and to sardine SSB (p < 0.001, in both cases, Table 5). Numbers of hake in the stomachs decreased with increased sardine recruitment, although the relationship with sardine SSB was more complex, increasing up to a certain sardine SSB and then decreasing sharply. Hake numbers were also significantly related to the blue whiting survey index of numerical abundance, with lower hake numbers in the stomachs when abundance of blue whiting was higher (p < 0.001). Similar results were obtained for the reduced data set, although hake SSB showed no significant effect on hake presence in the stomachs of dolphins for which data on length were available.

Results from the binomial GAMs indicated that again, the presence of hake in dolphin stomachs was strongly significantly (positively) related to hake recruitment and hake SSB. Presence of hake was also negatively related to sardine recruitment and broadly positively related to sardine SSB (p < 0.001 in both cases, Table 6) and weakly negatively related (p < 0.05) to the survey index of blue whiting biomass. In the case of sardine SSB, as it increased, there was an initial decrease in the presence of hake in stomachs followed by an increase and a further decrease. Models for the reduced dataset showed similar results.

Blue whiting

The numbers of blue whiting in dolphin stomachs showed no apparent relationship with the index of blue whiting biomass and a weakly significant (p < 0.05) negative relationship with the index of blue whiting numerical abundance from the same survey. Blue whiting numbers were (weakly) significantly related to hake SSB (p < 0.05, Table 5) but not to sardine abundance or hake recruitment. The relationship between blue whiting numbers in the stomachs and hake SSB was complex, initially increasing, then decreasing and subsequently further increasing at higher levels of hake SSB.

Repeating the analysis for the reduced data set (only dolphins with available length data) gave somewhat different results, with blue whiting numbers in dolphin stomachs appearing significantly related to the survey index of blue whiting biomass (p < 0.01) but not to sardine abundance or hake abundance. The relationship with the index of blue whiting biomass was negative at low levels of blue whiting biomass but became positive at intermediate levels.

Blue whiting presence in dolphin stomachs was not related to either the biomass or numerical abundance survey indices for blue whiting. It was significantly negatively related to sardine recruitment (p < 0.01) and weakly positively related to hake SSB ($p < 0.05$; Table 6). After re-running the binomial models with the reduced dataset, blue whiting presence in dolphin stomachs was only significantly ($p < 0.01$, negatively) related to sardine recruitment.

Under the hypothesis of opportunistic predation, we would have expected, for the 3 species analysed, to see sardine, blue whiting and hake presence and numbers in the stomachs to be proportional to their respective abundances in the sea and potentially negatively related to the abundances of other prey species (since prey are expected to be taken in proportion to relative abundance). If sardine were preferred, presence and numbers of sardine should increase as sardine abundance increases, while presence and numbers of the other species should probably decrease as sardine abundance increases.

Considering just the significant trends, the importance of sardine in the diet increased with sardine abundance, and the importance of hake in the diet increased with hake abundance, trends consistent with both opportunistic foraging and preference for both of these species. The negative relationships between dietary importance of both species and recruitment (but not SSB) of the other species are consistent with opportunistic foraging and with each species being less preferred than the other. The importance of blue whiting decreased with increased sardine and hake recruitments, again consistent with opportunistic foraging or blue whiting being a less preferred species.

DISCUSSION

There are several reasons for wanting to be able to describe and predict the diet of marine top predators, including to build realistic ecosystem models (ones which do not assume a constant diet), to quantify possible impacts of marine mammals on fisheries and to understand the likely impact of overfishing on the predator population. Ecosystem models can integrate all of this information and evaluate resource overlap between predators and fisheries in an area to study potential impacts on predators of increases (or decreases) in exploitation of commercially important prey (see Lassalle et al. 2012). Information is also required to relate availability of preferred prey with individual predator fitness, reproductive performance and finally population dynamics. However, it is rarely possible to determine diet by direct observation of individual predators in the field, and long-term data sets of stomach content data offer a possible alternative.

Caution is advised when inferring the diet of a population based on the analysis of the stomach contents of stranded animals, since it is subject to various possible biases, some of which are more amenable to solutions than others. Thus, strandings comprise only those carcasses which reach the coast and are likely to include individuals which had not recently been feeding normally due to ill health. In the present study, however, the substantial proportion of by-caught animals means that we were not primarily sampling sick animals which might be expected to show atypical feeding behaviour. Some authors have pointed out that dietary information derived from the examination of stomach contents of by-caught animals could also be biased towards the target species of the fishery, although this has rarely, if ever, been demonstrated as a source of bias (see, for example, reviews by Pierce & Boyle 1991, Tollit et al. 2010). Because by-catch diagnosis depends on carcass condition, and many of the dolphins from our sample that were categorized as 'other cause of death' were found in an advanced stage of decomposition, we cannot exclude the possibility that by-catch could have also been a cause of death for part of this group. Because of this we did not describe diet by cause of death categories. A less widely acknowledged bias arises because, in principle, the composition of the sample in terms of size, age, maturity and sex reflects the animals which die rather than the living population *per se*, although the age structure of the living population can be inferred from the age composition of sampled dead animals using life table methodology (Read et al. 2012). However, to some extent such biases in the resulting picture of interannual changes in diet can be accounted for during data analysis by factoring in differences between seasons and regions, and effects of e.g. dolphin size, age, maturity and sex on diet, as we have done here. In addition, while absolute values of prey importance are subject to bias (e.g. due to digestive erosion of fish otoliths), the patterns and trends in diet detected should be robust to any consistent sources of biases.

Sardines have been reported to be the main prey of common dolphins in Portuguese waters (Silva 1999), and research in the Bay of Biscay suggests that common dolphins show a preference for fatty fish (Meynier et al. 2008, Spitz et al. 2010a). Thus, the high importance of sardines in the diet of common dolphins in Galicia is not a surprising result. Overall, however, sardines were still considerably less important than the much less energy-rich blue whiting in our sample. Of more interest is how the importance of sardine in the diet has varied over time, particularly in comparison to other important prey species such as blue whiting and hake, and whether the emergent 'functional responses' are consistent with it being a preferred prey species.

Over the last 20 yr, the Iberian sardine stock (covering the area extending from the Gulf of Cadiz in the south to the border between Spain and Portugal in the inner Bay of Biscay) has shown marked fluctuations in abundance. The stock was estimated to have reached an all time low at the end of the 1990s, which triggered the adoption of important regulatory measures in both Spain and Portugal (ICES 2011b), the impact of which was felt particularly in Galician fisheries (Carrera & Porteiro 2003). Two good recruitments in 2000 and 2004 halted the downward trend in the stock and allowed recovery of the biomass, although not to the levels of the previous decades. The lack of further good recruitments since 2004 has again led to a decline in biomass of the stock, which is now estimated to be below the level at the end of the 1990s.

Similar data are available for one other important prey species, hake. The SSB of the southern stock (comprising fish living in Portuguese and south Galician waters) has shown a continuous increase since 1998 (before which the stock had been decreasing since the mid-1980s), with good recruitments taking place since 2005. Formal stock assessments are also available for blue whiting, but not specific to the Iberian Peninsula: blue whiting in the NE Atlantic are considered as a single stock for assessment purposes, and therefore abundance figures include fish found from Portuguese waters to northern Norway (ICES Areas I–IX, XII, XIV). Therefore, we looked for alternative indicators of local abundance and used indices derived from an annual survey covering the Spanish shelf waters of interest.

The decline in sardine abundance in recent years potentially allows us to test what happens to the diet of an abundant top predator when a preferred prey species becomes less available. Here, our interest was in the consequences for diet composition, although, in the longer term, a reduction in availability of energy-rich prey may also impact individual predator health and ultimately population distribution and abundance, as evidenced by various studies on seals (e.g. Thompson et al. 1997, Rosen & Trites 2000).

The availability of ZINB models undoubtedly offers greater analytical power to deal with such 'difficult' data sets, although currently at the expense of model complexity. It remains debatable whether stomach content data include false 0s in the sense implied by zero-inflated models but, in any case, ZINB and binomial GAM analyses of factors affecting dietary importance of the main prey species gave generally similar results.

Our results provide an indication of the form of the relationship between sardine abundance and its importance in the diet of common dolphins, which may be thought of as equivalent to the functional response of this predator (Holling 1959). Although the wide confidence bands around the fitted smoothers make it difficult to specify the precise form, it does not appear as though the relationship is asymptotic. Holling (1959) defined both functional and numerical responses, the former referring to the actions of a single predator, the latter to the population (and representing a combination of aggregation and demographic responses, although over a short time scale it will mainly refer to an aggregation response). Here it is, strictly speaking, difficult to distinguish these phenomena, since the probability of finding a particular prey species in an individual stomach depends on both. However, we would argue that dietary analysis permits quantification of average population functional responses.

Our results for the 3 main prey species (see Tables 5 & 6), taken together, seem to be more consistent with an opportunistic foraging strategy than with selective predation. Although we only tested 3 prey species, the wide variety of prey species taken by common dolphins is also weak evidence against selective feeding. Opportunistic predation is expected to occur when prey availability is unpredictable or the abundance of preferred prey is low — as has been the case of sardine in recent years. Assuming that sardines would be a preferred prey due to their high energy density compared to hake and blue whiting, the absence of an asymptote in the functional response for common dolphin feeding on sardines implies that 'predator saturation' is not reached at current sardine stock levels. Obviously, other factors could also affect whether a prey species is preferred, for example, its handling time (which would presumably be shorter for a smaller fish), ease of capture and other factors affecting encounter rate.

Caution is necessary when interpreting these results, as ZINB and binomial models did not always agree (although usually in the sense that one picked up a trend and the other did not). Although the absence of trends can also be argued to provide relevant evidence, it can arise due to a low signal to noise ratio in the data. An additional complication is that recruitment and SSB do not follow exactly the same trends, as might be expected from the generally weak nature of stock–recruitment relationships. There were also positive (or broadly positive) relationships between importance of a species in the diet and abundance of one of the other species, e.g. predation on hake increased with sardine SSB (although not with sardine recruitment). These trends, if not coincidental, are not consistent with theory. In addition, sometimes the highest or lowest presence or numerical importance of a prey species in stomach contents was seen at intermediate abundance levels of that species or of another prey species. Such relationships may also be coincidental, reflecting the fact that (by chance alone or some unknown cause) years of high sardine abundance may have coincided with low or intermediate abundance years for some other prey species.

It would be interesting to investigate effects of fish abundance on dolphin diet at smaller spatial and temporal scales. However, it should be borne in mind that it is difficult to be sure where an individual dolphin had been feeding prior to its death: stranding location may not be a good proxy for feeding location. In theory, access to detailed commercial fishery catch data might provide evidence of short-term temporal shifts in fish abundance in the study area, but it would be difficult to rule out or control for other (e.g. economic) factors which affect catches. One aspect of diet selection which is amenable to further study, however, is size selectivity. Although fish sizes in stomachs are likely to be underestimated due to otolith erosion, it ought to be possible to relate shifts in the size composition of the diet to age-class abundance in the fish prey.

Top predators are believed to have significant effects on prey populations, although there is also considerable debate about whether the dynamics of marine ecosystems typically involve top-down, bottom-up or wasp-waist control. Cury et al. (2003) suggested that bottom-up control predominates in marine ecosystems, while top-down control plays a role in dampening ecosystem-level fluctuations, and wasp-waist control is most probable in upwelling systems, of which the Galician coast is an example. A recent ecosystem model for the Bay of Biscay (Lassalle et al. 2011) revealed that the continental shelf food web was strongly bottom-up controlled. Thus it is pertinent to ask what effect changes in fish abundance currently have (and have had in the past) on dolphin populations. Fisheries also have direct impacts on dolphin populations, and fishery by-catch is thought to be a significant cause of mortality for common dolphins in Galician waters (López et al. 2002, 2003, Fernández-Contreras et al. 2010). Published studies refer to data collected more than a decade ago, and to date there has been insufficient on-board observation to obtain a reliable estimate of numbers killed. The only population size estimate available for common dolphins in the region is that for the mid-2000s derived from the SCANS II and CODA surveys (Cañadas et al. 2009), and further large-scale surveys are urgently needed to identify trends in abundance.

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