

ICES CM 2004/THEME SESSION Q:09 (Recent Advances in the Oceanography and Biology of the Iberian Waters and Adjacent Shelf Seas: Results from Integrated Multidisciplinary Projects)

Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991-2003 and relationship with prey abundance

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Analyses of marine mammal diets in Galician waters have been carried out over the last 13 years as part of four consecutive European funded projects. The species that is best represented in samples from stranded animals is the common dolphin *Delphinus delphis*, for which 414 non-empty stomachs were analysed during 1991-2003. We quantified interannual and seasonal variation in the diet, as well as differences between the diets of male/female and juvenile, sub-adult and adult dolphins. Although sampling is based on stranded dolphins, the majority showed evidence of having died as a consequence of interactions with fisheries (by-catch). The influence of cause of death on stomach contents was examined. The most important prey species were (small) blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*) and scad (*Trachurus* sp.), all of high commercial importance in Galician waters, and (in the first quarter of the year), sand smelt *Atherina* sp. Interannual trends in the importance of sardine in the diet of common dolphins appear to track trends in spawning stock biomass. Preliminary estimates are also made for the amount of fish removed by the common dolphin population in Galician waters.

KEYWORDS: *sardine, common dolphin, diet, fisheries*

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Introduction

Galician waters with their seasonal upwelling (Fraga, 1981) sustain high productivity and high biodiversity, including nearly 300 species of fish (Solórzano *et al.*, 1988) and over 75 species of cephalopods (Guerra, 1992). At least 19 species of marine mammals (16 cetaceans and 3 pinnipeds) have also been recorded in the area. Over a period of 13 years, 4 consecutive European funded projects have studied the interactions between marine mammals and their prey: *The impact of marine mammals on Northeast Atlantic Fisheries* (Training and Mobility of Researchers-TMR Programme 1994-96); *Modelling the Impact of Marine Mammals on NE Atlantic Fisheries* (TMR Programme, 1996-97); *Impacts of Fisheries on Small Cetaceans in Coastal Waters of Northwest Spain and Scotland* (DG Fisheries Study Project 97/089, 1998-00) and *Bioaccumulation of persistent organic pollutants in small cetaceans in European waters: transport pathways and impact on reproduction* (V Framework Programme, 2001-03). The present study presents the results of the most abundant species, the common dolphin (*Delphinus delphis*).

Delphinus delphis is one of the most common and widely distributed cetacean species (Evans, 1994). In the Atlantic, it ranges from Norway and Iceland in the east and the coasts of Nova Scotia in the west, extending south to the Cape of Good Hope in Africa and Península Valdés in South America (Gaskin, 1992). It is very abundant off the coasts of Spain, Portugal, the Gulf of Gascony and Brittany (Cabrera, 1914; Casinos & Vericad, 1976; Duguy, 1977; Evans, 1980; Sequeira & Teixeira, 1988; Dos Santos *et al.*, 1988). Sequeira & Inácio (1992) reported that it was the most common cetacean off the Portuguese coast. Evidence from strandings, reported by-catches, and sightings, suggests that it is the most abundant cetacean on the Galician coast (López *et al.*, 2002, 2003, 2004). There are few recent population estimates for common dolphins in the NE Atlantic. The MICA survey, in 1993 produced an estimate of approx 62,000 common dolphins in offshore waters to the West of France (Goujon *et al.*, 1993b), while the 1994 SCANS survey estimated common dolphin abundance in the Celtic Sea to be around 75,000 (Hammond *et al.*, 2002). Data from opportunistic boat-based surveys during 1998 and 1999 indicated a preliminary population estimate for Galician waters of around 8000 animals (López *et al.*, 2004).

Since early times, common dolphins were perceived as competitors by fishermen and were killed in an effort to protect dwelling fish stocks or were hunted for their meat and blubber, e.g. in the Black Sea where a target fishery for dolphins was in operation (Tomilin, 1957). This belief was supported by a common observation in many early studies on diet that single dolphin stomachs sometimes contained many thousands of fish otoliths (e.g. 15,191 from a female in the Mediterranean coast of Spain, Schmidt, 1923 which led the author to note the dolphin's "enormous consumption of fish").

In the present day, common dolphins and all other cetacean species are protected by law from direct take but by far the main threat to common dolphin (and other cetacean) populations is the "incidental killing" in fisheries operations (by-catch) (Evans, 1994, Tregenza *et al.*, 1997, Tregenza & Collet, 1998). In the Cantabrian Sea (N Spain), common dolphins were the most frequently by-caught cetacean species, especially in fixed nets (Nores *et al.*, 1992). In Portugal, the highest mortality takes place in the gillnet fishery (Sequeira & Ferreira, 1994). Interview surveys of fishermen suggest that large numbers are caught in Galician fisheries (López *et al.*, 2003).

Early studies reported common dolphin stomachs contents to be predominantly remains of pelagic, shoaling fish such as anchovy (*Eugraulis encrasicolus*), mackerel (*Scomber scombrus*), sardine (*Sardina pilchardus*, *Sardinops coerulea*), herring (*Clupea harengus*) and sprat (e.g. Legendre, 1922; Schmidt, 1923; Frost, 1924; Fraser, 1937; Brown & Norris, 1956; Sergeant & Fisher, 1957; Cadenat, 1959; Nishiwaki, 1972; Norris & Prescott, 1961; Anon., 1965; Fiscus & Niggol, 1965; Fitch & Brownell, 1968; Jones, 1981; Fiscus, 1982). Probably the most detailed studies on the diet of common dolphins took place in the Black Sea and adjacent areas where thousands of stomachs from the dolphin fishery were examined (see Tomilin, 1957). The main prey was pelagic fish, mainly anchovy and sprat (*Sprattus sprattus*) and diet varied between seasons and areas. Sprat was the main prey of dolphins captured in the open sea in summer, while dolphins captured closer to the shore, between January and October, had mainly anchovy and pipefish (Syngnathidae) in their stomachs (Tomilin, 1957).

With the setting up of stranding schemes in many countries and the collection of by-caught specimens during the 1980s and 1990s, various more detailed studies on common dolphin diets were carried out (e.g. Collet, 1981; Ross, 1984; Desportes, 1985; Waring et al., 1990; Overholtz & Waring, 1991; Sekiguchi *et al.*, 1992; Kuiken *et al.*, 1994; Young & Cockcroft, 1994; Berrow & Rogan, 1995; Osnes-Erie, 1995; Cooperus, 1998; Silva, 1999). These studies support the general conclusions that diet varies between areas and seasons and that the main prey are small pelagic shoaling fish. Several authors suggested that common dolphins feed opportunistically, with their diet reflecting local prey abundance and availability (e.g. Evans, 1994; Young & Cockcroft, 1994). However, this hypothesis has not actually been tested. Despite the large number of studies on common dolphin diet, only Desportes (1985) working on common dolphins stranded in France, and Silva (1999) in Portugal attempted to analyse variability in the diet.

Little previous information is available on common dolphin diet in Galicia, an important nursery ground for hake (*Merluccius merluccius*), scad (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*), all of which are of high commercial value. During the study period (1991-2003), stocks of sardine and blue whiting off the Iberian peninsula have fluctuated markedly, with blue whiting stock size more than doubling and sardine abundance varying by a factor of two between peaks in 1995 and 2003 and minima in 1991 and 2000 (Anon., 2004a,b,c). Thus the present study examines whether dolphin diet tracks abundance trends in the main fish stocks. In addition to examining the relationship between diet and fish abundance we determine whether there is seasonal, geographical, size-related and sex-related variation in diet.

Material & Methods

Collection of samples

Common dolphins stomach contents were collected from animals stranded between 1991 and 2003. Stranded common dolphins were identified and sampled by AL and collaborators from Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA), a voluntary organisation which runs the stranding network in Galicia. Biological data available normally include sex and length. Cause of death was diagnosed in some cases, the most frequent diagnosis being by-catch (following Kuiken's, 1994 criteria).

One animal sampled had an occluded gut and many thousands of otoliths had accumulated in the stomach. Data for this animal were excluded, leaving a total of 413 animals. The composition of the sample in terms of season, size class, sex, etc is indicated in Table 1.

Prey identification

Prey remains consisted principally of fish otoliths, bones and lenses, and cephalopod mandibles (beaks). Few crustacean remains were present and these were not identified in all cases, due to the poor state of preservation. Fish otoliths and bones were identified using reference material and published guides (Härkönen, 1986; Watt *et al.*, 1997). The number of fish was estimated from the number of otoliths or jaw bones (for species with fragile otoliths, e.g. sardines), whichever was higher. Fish sizes were estimated by measuring the otoliths, using callipers or a binocular microscope fitted with an eyepiece graticule. For stomachs in which one fish species was represented by >30 otoliths, a random sample of 30-60 otoliths was measured. Usually otolith length was measured, except for the otoliths of herring, sardine and Gobiidae, for which width is the standard measurement (Härkönen, 1986), and for any otolith broken lengthways. Fish length and weight was calculated from standard regressions (see Santos *et al.*, 2004). For otoliths identifiable to one of a group of species, regressions based on combined data from all the species in the group were used. To reconstruct total prey weight, each otolith was assumed to represent 0.5 fishes. Thus, when both otoliths were present, the estimated fish weight was the average of the weights estimated from the two otoliths.

Cephalopods 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 both upper and lower beaks using a binocular microscope. Dorsal mantle length and body weight of the animals were estimated using standard regressions (Clarke, 1986). Complete pairs of cephalopod beaks were rarely present and in all cases weight was estimated from either the upper or the lower beak. Cephalopod remains from seventeen of the dolphins were previously identified by Dr. Angel González (IIM) and these partial results have been published (González *et al.*, 1994). All fish material from those seventeen animals and the entire stomach contents of all the remaining animals were identified and measured by MBS.

The importance of individual prey species in each stomach was evaluated by presence/absence, number and estimated weight. For overall diet, relative importance was estimated as (a) percentage frequency of occurrence, (b) proportion of the total number of prey and (c) proportion of total prey weight. Since fish were not always represented by otoliths, and only otoliths were used to reconstruct weight, %weight values were adjusted based on the ratio of measured to unmeasured individuals of each prey species.

Multivariate analysis: correlation of dietary and environmental similarity matrices

This analysis was based on data on prey numbers, since these are subject to fewer errors than (back-calculated) weight estimates. Each stomach was treated as a sample. All prey taxa occurring in only one or two dolphins were excluded from analysis. Where more than one species in a family was recorded but the majority of occurrences of the family were not identifiable to species, only data for the family as a whole were used, e.g. Sepiolidae,

Ommastrephidae. This left a total of 40 prey categories. All data on prey numbers were then db-RDA transformed as follows:

$$y'_{i,j} = \frac{y_{i,j}}{\sqrt{\sum_{j=1}^p y_{i,j}^2}}$$

where

$y_{i,j}$ = abundance of prey category i in dolphin stomach j

p = the number of dolphin stomachs

Following this transformation, the Euclidean distance between two samples is equal to the chord distance (Legendre & Gallagher, 2001).

An “environmental” dataset was constructed containing year, season, location, size and sex data. Although maturity and age data were available for some animals (notably for 2001-03), due to the absence of such data for the majority of animals we use size as a proxy. Length was divided into three categories: animals ≤ 150 cm in length are probably up to around 2 years old and will include all animals still associated with the mother (full independence is thought to be reached at an age between 6 months to 1-2 years). Although regional variation in size at maturity is reported, most animals >190 cm in length will be sexually mature (Hui, 1979; Collet, 1981; Collet & Saint Girons, 1984; Pierce *et al.*, 2004). Locations were recorded (latitude, longitude) and categorised into “areas”: López *et al.* (2003) divided the Galician coastline into 6 areas (see Fig. 1). Very few stomach samples were obtained from the two most northerly areas (1, 2) so data were finally divided into four area categories (1-3, 4, 5, 6). All environmental variables were recoded as dummy variables taking the value 0 or 1. There were thus 12 yearly variables (1991, 1992, ..., 2002), three season variables (Q1, Q2, Q3), three location variables (A1-3, A4, A5), two size-class variables (L1, L2) and a variable coding sex. Since location, sex and length data were missing for some animals, a series of sub-sets of the data were created, e.g. all animals with location data, all animals with location and sex data, etc. This was repeated for the subset of known by-catches, leading to a total of 9 subsets of data (see Table 2). In each case, the associated environmental dataset included only those variables for which information was complete. In each case, any dietary variables for which there were two or fewer non-zero values were dropped from the dataset.

Data were analysed using PRIMER 5 software (Primer-E Ltd). Similarity matrices for dietary and environmental datasets were derived using Euclidean distances. The “RELATE” routine was used to test the null hypothesis that there was no multivariate relationship between dietary and environmental data. The “BIOENV” routine was used to select the set of environmental variables best explaining patterns the dietary data. This computes rank correlations between dietary and environmental similarity matrices using different permutations of the environmental variables. Note that the set of environmental variables selected is not necessarily the set of variables that, individually, correlate most highly with dietary variation. If two environmental variables are strongly correlated with each other, once the first has been selected as a predictor the second will add little to predictive power and is unlikely to be selected.

Multivariate analysis: redundancy analysis

Redundancy analysis (RDA) is a type of direct gradient analysis and was applied using BRODGAR 2.3.4. software (Highland Statistics Ltd). Application was restricted to the 412 animals with known location and the dataset for by-caught animals with complete length and sex data (N=102). Models were fitted using a forward selection procedure.

The response variables were the db-RDA transformed prey numbers data used in PRIMER analysis. The set of explanatory variables was also as used in PRIMER, but with the addition of variables representing annual fish abundance: sardine spawning stock biomass and recruitment for ICES fishery sub-divisions VIIIc and IXa, blue whiting spawning stock biomass and recruitment (combined estimates for fishery sub-divisions I-IX, XII and XIV) and survey abundance of blue whiting during September trawling surveys in fishery sub-division IXa (i.e. off the Galician coast). These values were taken from Anon (2004 a,b,c) and from unpublished data held at IEO. For the “full” set of dolphin samples, the explanatory variables sex and length were not available due to many missing values. Year, quarter and area were entered as nominal variables. A forward selection procedure was used to fit the optimum model.

Triplots and biplots were used to visualise correlations between explanatory variables, prey numbers (response variables) and individual dolphins (samples). Numerical output includes eigenvalues for the RDA axes, weightings showing the contribution of each prey category to each axis, and significance test values for each explanatory variable.

Univariate analyses of dietary variability in relation to fishery data

Where trends were suggested by multivariate analyses, Kruskal-Wallis tests on individual prey categories and single explanatory variables were used to explore the nature of the trends.

The dietary importance (in prey numbers and back-calculated prey weight) of the two main species in the dolphin diet (blue whiting and sardine) was modelled as a function of putative explanatory variables. Analyses were carried out using Brodgar 2.3.4 statistical software (Highland Statistics Ltd.). Dietary variables were rescaled using the square root transformation. Data exploration indicated generally non-linear (although probably monotonic) relationships with explanatory variables. Initial models were fitted using a Generalised Additive Model (GAM) with Poisson distribution and log link indicated that data were overdispersed. A quasi-Poisson error distribution was therefore assumed. Relationships with explanatory variables were fitted using loess smoothers (4 degrees of freedom), except when sex was included, as a nominal variable.

The explanatory variables considered were:

- (a) Annual fishery data (from Anon, 2004a,b,c): sardine spawning stock biomass (SSB), sardine recruitment, blue whiting recruitment, blue whiting SSB and blue whiting survey abundance (as smoothers);
- (b) Dolphin characteristics: estimated length (as a smoother), sex (as a nominal variable);
- (c) Stranding time and location: year, month, area (as smoothers).

Because not all explanatory variables were available for all samples, the analysis was carried out in 3 different datasets:

- (i) The 412 common dolphin stomachs for which location was known (the variables “estimated length and sex were not included due to many missing values);
- (ii) An “intermediate” dataset (330 stomachs) comprised of those animals for which estimated length was also known;
- (iii) A “reduced” dataset (102 stomachs) of animals for which cause of death had been identified as by-catch and both estimated length and sex were available.

The best models for each dataset were chosen based on the Akaike Information Criterion.

Food consumption by common dolphins

Annual consumption of the three main prey species (I , tonnes) by the common dolphin population in Galician waters was estimated using the following simple equation:

$$I = N * P_i * F * T$$

Where:

N (common dolphin population size) was taken from López *et al.* (2004) estimates of 8,137 (4,388-13,678) common dolphins in Galician waters based on data from opportunistic sightings surveys. Population size was assumed to be constant during the study period.

P_i (adjusted proportion by weight of prey species i in the diet taking into account all prey remains) was calculated, pooling together all the diet data for common dolphins stranded in Galicia during the study period.

F (average weight of food eaten daily per common dolphin), was calculated from the value of 6.5% of dolphin weight. This value is based on Innes *et al.* (1987), applying their equation for an animal of 100 kg, and is probably rather conservative for the Galician population since the average weight of stranded individuals was considerably less than 100 kg. Dolphin weight was calculated from dolphin length, for each of the common dolphins stranded in the area of the study for which length was known, using a regression equation previously established using data on 127 common dolphins (Pierce *et al.*, 2004). A mean value for F was then obtained. This is assumed to be representative of the population as a whole.

T (number of days when prey and predator are in contact) was assumed to be 365.

This approach ignores seasonal and regional variation in diet and furthermore treats each dolphin as an “average dolphin”, ignoring population structure. However, the data available do not justify a more detailed approach.

Results

Composition of the sample

Numbers of stomachs examined each year, tabulated by area, quarter, sex, size and cause of death, are summarized in Table 1. The majority of samples came from the southern part of the study area (areas 5 and 6, $n = 175$ and 117 respectively, Fig. 1) with only one sample

originating in area 2 and two in area 1. More than one third of the dolphins examined exhibited signs of by-catch, such as cuts (in flippers and abdomen), absence of the tailstock or the presence of ropes in the tail. In two cases, dolphins had marks of shark teeth, one dolphin had been shot and another had marks consistent with an attack by a bottlenose dolphin (*Tursiops truncatus*). The remaining 258 dolphins did not show clear signs of by-catch, although it was not normally possible to exclude this as a cause of death because, in many cases, carcasses were found in an advanced stage of decomposition. [Pathological and histopathological analyses for a sub-sample of 45 animals from 2001-03 revealed 21 by-catch mortalities and 16 deaths from pathological causes, the majority of the latter being parasitological or infectious pneumonia; see Pierce *et al.*, 2004b].

Of the 390 dolphins for which sex was known, almost two thirds were males. Most strandings occurred in the first half of the year: 44% in the first quarter, 30.5% in the second quarter, 10.6% in the third quarter and 14.8% in the fourth quarter.

General description of diet and estimates of prey consumption

Remains of at least 46,058 fish were recovered from the stomachs together with remains belonging to 5,657 cephalopods, 796 crustaceans and 28 polychaetes. Twenty-five fish taxa and fifteen cephalopod taxa were identified from these remains (Table 3). Crustacean remains were found in one third of the stomachs but consisted mainly of parasitic isopods. Polychaete remains were found in twenty-two stomachs.

Blue whiting and sardine were the most important prey categories by reconstructed weight, together making up more than 56% of the diet, while gobies (Gobiidae) were the most numerous prey group. The next most important prey categories were scad and *Atherina* sp. Each making up slightly under 9% of the reconstructed prey weight. Of the cephalopod prey, the common squid *Loligo* sp. (there are two species of this genus present in Galician waters with very similar mandibles, *L. vulgaris* and the less common *L. forbesi*) was the main prey by reconstructed weight, followed by another member of the same family, *Alloteuthis subulata*. By number, bobtail squids (Sepiolidae) were the main cephalopod prey but due to their small size they contributed little to total prey mass. Remains of two 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 very little (Table 4): the importance (by reconstructed weight) of sardine and mackerel rose from 13.7% and 1.3% to 21.6% and 4.8% respectively, while blue whiting importance decreased correspondingly from 36.9 % to 34.9%.

The estimated length of blue whiting eaten by all dolphins ranged from 5.5 to 30.5 cm total length, with a mode at 15.5 cm, while sardine eaten ranged from 15.5 to 22.5 cm total length with a mode at 18.5 cm. Scad eaten by dolphins ranged from 3.5 to 36.5 cm with a mode at 12.5 cm. When only dolphins which had died as a result of by-catch were considered, the estimated length of blue whiting eaten ranged from 7.5 to 29.5 cm total length with a mode at

the larger size of 17.5 cm, sardine lengths from 16.5 to 22.5 cm with the mode still at 18.5 cm and scad lengths ranged from 3.5 to 32.5 cm with the mode still at 12.5 cm (Figure 2).

Taking into consideration that age 0 blue whiting has a mean length of 16.9 cm (Anon., 2003), 60% of the fish consumed by the dolphins comprised recruits. When only the by-caught dolphins are considered, the percentage of recruits in the diet decreases to 46.5%. These results however, were not corrected for otolith erosion due to digestion so the importance of small fish is probably overestimated.

The mean estimated body weight of the common dolphins stranded in Galicia for which an estimated length was available (330) was 74.23 kg (standard deviation 25.35 kg). The estimated average weight of food eaten daily per common dolphins (calculated as 6.5% of dolphin weight) was 4.83 kg (standard deviation 1.52 kg).

Calculations of the annual population consumption of common dolphins in Galician waters give figures of around 5000 tonnes of blue whiting, 3600 tonnes of sardine and 1200 tonnes of scad (Table 4). For comparison, Table 4 also includes official landings figures for Spain and Portugal for 2003 for blue whiting and 2002 for sardine and scad (Anon. 2004a,b,c). It can be seen that estimated dolphin consumption is a rather small proportion of the Spanish annual landings of scad (4.1%) from ICES areas VIIIc and IXa in 2002. For sardine, the estimated amount consumed by dolphins is equivalent to 18.0% of the 2002 landings and, for blue whiting, estimated consumption is equivalent to 36.2% of 2003 landings.

Analysis of dietary and environmental similarity matrices

Analysis of prey number data using PRIMER showed that diet was significantly related to the “environmental” data set, with season and year being the most important factors. In particular, the diet in quarter 1 differed from that in other quarters of the year, and the diet in 1997 was different to that of other years (Table 2). This was rather consistently observed across all subsets of data even when other explanatory variables were available.

Kruskal-Wallis test results confirmed that there was highly significant seasonal variation in the number of blue whiting eaten ($H = 43.3$, $P < 0.001$), with least taken in quarter 1 (only around 1/3 of stomachs from quarter 1 contained blue whiting whereas more than half contained blue whiting in all the other seasons). There was no significant seasonal variation in the amount of sardine eaten. Kruskal-Wallis tests also suggested that interannual variation in blue whiting consumption was statistically significant ($H = 31.86$, $P = 0.001$) whereas this was not (quite) the case for sardine ($H = 20.96$, $P = 0.051$).

Redundancy analysis

Model for all dolphins

The final model for the 412 dolphins with location data included significant effects of year ($F = 1.480$, $P = 0.040$), quarter ($F = 4.113$, $P = 0.005$), area ($F = 2.832$, $P = 0.005$), blue whiting SSB ($F = 2.835$, $P = 0.005$), sardine SSB ($F = 1.596$, $P = 0.010$) and blue whiting survey abundance ($F = 3.108$, $P = 0.005$). The sum of all canonical eigenvalues is 0.004 indicating that all the explanatory variables used in the analysis together explain only 4% of the variation in the

response variables. The first two axes together explain 92% of the variation in the data that can be explained with all the explanatory variables. Plots of explanatory variables, response variables, and a bi-plot for both sets, appear in Figure 3.

Axis 1 was most strongly related to the effect of quarter (Fig. 3a), and the response variables most strongly affected appear to have been numbers of gobies (Gobiidae), sand smelts (*Atherina* sp.) and the small squid *Alloteuthis* in the stomach contents (Fig. 3b,c). Kruskal-Wallis tests confirmed significant seasonal variation in numbers of all three taxa (H values 43.91, 33.97 and 28.03 respectively, $P < 0.001$ in all cases). All three taxa were much more important in quarter 1 than at other times of year.

The explanatory variables blue whiting SSB and blue whiting survey abundance were quite strongly correlated with each other and were positively related to numbers of sandeels and polychaetes in stomachs and negatively related to numbers of scad, unidentified clupeids and myctophids (see Fig. 3c). Simple correlation analysis confirms these relationships.

The area effect is strongly (negatively) related to blue whiting numbers in the stomachs (Fig. 3c). Kruskal-Wallis test results ($H=32.8$, $P < 0.001$) confirm that there is significant between-area variation in number of blue whiting in stomach contents, with fewer blue whiting generally being seen further south: indeed there is a significant positive correlation ($R=0.305$, $P < 0.001$) between blue whiting numbers in stomach contents and latitude.

Model for by-caught dolphins

The final model for the 102 by-caught dolphins with location, length and sex data included significant effects of year ($F=1.618$, $P=0.015$), quarter ($F=2.340$, $P=0.005$), length ($F=1.625$, $P=0.020$), blue whiting SSB ($F=1.785$, $P=0.005$), sardine SSB ($F=1.573$, $P=0.015$) and blue whiting survey abundance ($F=1.990$, $P=0.005$). The sum of all canonical eigenvalues is 0.15 indicating that all the explanatory variables used in the analysis together explain 15% of the variation in the response variables. The first two axes together explain 69% of the variation in the data that can be explained with all the explanatory variables. Plots appear in Figure 4.

The effect of quarter appears to be strongly correlated to several (dietary importance) response variables (Fig. 4), notably blue whiting, while the effect of blue whiting survey abundance was most strongly correlated with sea breams (Sparidae) – and negatively correlated with the importance of sardine in the diet. However, it was essentially uncorrelated with the importance of blue whiting in the diet.

Generalized additive models for numbers of prey in stomach contents

Blue whiting numbers

The final model for blue whiting numbers eaten, for the “full” set of samples (AIC = 4.91, deviance explained = 24.8%) included month (M, $\chi^2=68.02$, $P < 0.0001$), area (A, $\chi^2=15.03$, $P=0.0052$), blue whiting spawning stock biomass (BS, $\chi^2=20.27$, $P=0.0005$) and sardine spawning stock biomass (SS, $\chi^2=14.22$, $P=0.0073$) and took the form:

$$Y1 \sim +s(M, fx=T, b=5) + s(A, fx=T, b=5) + s(BS, fx=T, b=5) + s(SS, fx=T, b=5)$$

Smoothers are illustrated in Figure 5. There is a clear summer (July) peak in predation on blue whiting, and more blue whiting was eaten in the northern areas 3 and 4 than in the southern areas 1 and 2. The relationships with spawning stock biomass appear somewhat counter-intuitive, with most blue whiting eaten in years of high sardine stock biomass and at low and intermediate blue whiting stock biomass. An alternative model using blue whiting recruitment rather than spawning stock biomass had a slightly higher AIC (4.97) and rather similarly shaped smoothers.

The final model for blue whiting numbers eaten, for the intermediate set of samples (AIC = 4.56, deviance explained = 34%) included month ($\chi^2=41.34$, $P<0.0001$), estimated length ($\chi^2=25.54$, $P<0.0001$), sub-area ($\chi^2=19.11$, $P=0.0009$), blue whiting spawning stock biomass ($\chi^2=24.23$, $P=0.0001$) and sardine spawning stock biomass ($\chi^2=16.11$, $P=0.0034$). Smoothers are illustrated in Figure 6. Results were essentially as seen for the full data set, with an additional clear trend for larger dolphins to have eaten more blue whiting. Again, an alternative model using blue whiting recruitment rather than spawning stock biomass had a slightly higher AIC (4.67) and rather similarly shaped smoothers.

The final model for blue whiting numbers eaten, for the by-catch set of samples (AIC = 4.45, deviance explained = 55.7%) included sex ($T=-0.77$, $P=0.4426$), year ($\chi^2=8.59$, $P=0.0830$), month ($\chi^2=17.16$, $P=0.0035$), estimated length ($\chi^2=21.95$, $P=0.0006$), sub-area ($\chi^2=11.06$, $P=0.0333$), blue whiting spawning stock biomass ($\chi^2=6.10$, $P=0.2033$) and sardine spawning stock biomass ($\chi^2=11.88$, $P=0.0245$). The terms for sex, year and blue whiting spawning stock biomass were not individually significant. Smoothers for the significant terms are illustrated in Figure 7. Animals by-caught in the fishery had eaten most blue whiting towards the end of the year. The amount eaten generally increased with body size but dropped sharply in the largest animals. As seen for the larger dataset, more blue whiting was eaten in the more northern areas and there was a slight tendency for more blue whiting to be eaten in years of higher sardine stock biomass.

Blue whiting weight

The final model for weight of blue whiting eaten, for the full set of samples (AIC = 23.49, deviance explained = 21.7%) included month ($\chi^2=48.53$, $P<0.0001$), sub-area ($\chi^2=14.74$, $P=0.0058$), blue whiting spawning stock biomass ($\chi^2=12.43$, $P=0.0154$) and sardine spawning stock biomass ($\chi^2=14.22$, $P=0.0217$). The smoother plots (not illustrated) confirm the strong similarity between this model and the model for numbers of blue whiting eaten.

The final model for weight of blue whiting eaten, for the intermediate set of samples (AIC = 22.53, deviance explained = 27.4%) included month ($\chi^2=23.44$, $P=0.0001$), estimated length ($\chi^2=19.05$, $P<0.0010$), sub-area ($\chi^2=14.91$, $P=0.0030$), blue whiting recruitment ($\chi^2=7.05$, $P=0.1363$) and sardine spawning stock biomass ($\chi^2=16.11$, $P=0.0056$). The term for blue whiting recruitment is not itself statistically significant. Smoothers (Figure 8) were broadly similar to those for the model for blue whiting numbers, although blue whiting consumption is seen to fall off at the highest levels of sardine stock biomass.

The final model for weight of blue whiting eaten, for the by-catch set of samples (AIC = 21.44, deviance explained = 55.6%) included year ($\chi^2=9.86$, $P=0.0520$), month ($\chi^2=15.88$,

P=0.0056), estimated length ($\chi^2=21.15$, P=0.0008), sub-area ($\chi^2=12.47$, P=0.0197), blue whiting spawning stock biomass ($\chi^2=7.30$, P=0.1325) and sardine spawning stock biomass ($\chi^2=10.99$, P=0.0341). The terms for year and blue whiting spawning stock biomass were not individually significant. Smoothers for the significant terms (not illustrated) were rather similar in shape to those for the equivalent model of number of blue whiting eaten.

Sardine numbers and weight

No significant model could be fitted for numbers of sardine eaten based on either the full data set or the by-catch data set, or for weight of sardine for the full data set.

The final model for sardine numbers eaten, for the intermediate set of samples (AIC = 3.02, deviance explained = 8.7%) included year ($\chi^2=5.79$, P=0.2182), month ($\chi^2=6.80$, P=0.1497), sub-area ($\chi^2=4.49$, P=0.3464), blue whiting spawning stock biomass ($\chi^2=4.26$, P=0.3740) and sardine spawning stock biomass ($\chi^2=9.66$, P=0.0488). Of these terms, only the last is statistically significant, and then only marginally so. The smoother for sardine stock biomass is illustrated in Figure 9. It can be seen that more sardine were taken when sardine abundance was higher.

The final model for weight of sardine eaten, for the intermediate set of samples (AIC = 16.94, deviance explained = 10.7%) included year ($\chi^2=5.51$, P=0.2419), month ($\chi^2=6.62$, P=0.1606), sub-area ($\chi^2=3.42$, P=0.4913), blue whiting spawning stock biomass ($\chi^2=5.93$, P=0.2070) and sardine spawning stock biomass ($\chi^2=10.05$, P=0.0417). Again only the last term is statistically significant. The smoother for sardine stock biomass is illustrated in Figure 10. It can be seen that a bigger total weight of sardine was taken when sardine abundance was higher.

For the by-catch data set, the best model to predict weight of sardine eaten (AIC = 17.46, deviance explained = 21.3%) included month ($\chi^2=4.43$, P=0.3581), blue whiting recruitment ($\chi^2=10.71$, P=0.0369) and sardine spawning stock biomass ($\chi^2=5.32$, P=0.2649). Of these terms, only that for blue whiting recruitment was significant and the shape of the smoother suggested that, generally, a bigger weight of sardine was eaten when blue whiting recruitment was low (Figure 11).

Discussion

Composition of the sample

In any dietary study on cetaceans (or any other marine mammals) a major problem is the collection of enough samples to allow an investigation into the feeding habits to be something more than a simple description of stomach contents. The problems arising from the use of stranded specimens in dietary analysis have been extensively discussed and reviewed elsewhere (e.g. Pierce & Boyle, 1991; Sekiguchi *et al.*, 1992). Stranded cetaceans can be considered an “opportunistic” resource, the composition of which depends on many factors (currents carrying the carcasses to the coast, favourable wind conditions, accessibility of coastal regions, state of preservation, etc.). Four general points may be made about the composition of the sample analysed in this study: there were many more males than female dolphins, strandings were concentrated in the first part of the year and in the south of Galicia, and a substantial proportion of mortality was related to by catch. All these findings were first reported by López *et al.* (2002).

López *et al.* (2002) highlighted the high incidence of by-catch mortality amongst cetaceans in Galician waters, based on strandings records, and this was supported by results from an interview survey of fishermen (López *et al.*, 2003). Entanglement in fishing gear was also found to be the most frequent cause of death for common dolphins stranded on the coasts of England and Wales (Kuiken *et al.*, 1994; Kirkwood *et al.*, 1997). In contrast to strandings, by-catches may provide “healthy” animals accidentally drowned in fishing gear. However, it might be expected therefore, that results on diet could be biased towards target species of the fishery and associated species. However, such a bias has rarely, if ever been demonstrated in studies on cetacean diets. It remains true, as commonly noted that strandings can be biased towards sick animals and those feeding recently in coastal waters.

López *et al.* (2002) also commented on the preponderance of males in the strandings. The under-representation of females and mature animals in the sample could be due to age- and sex-related habitat differences. Kuiken *et al.* (1994) found segregation, in relation to sexual maturity and sex, in common dolphin stranding locations on the Southwest coast of England in 1992, suggesting the existence of at least two types of groups of dolphins, including separate groups of sub-adult males. In the Northwest Atlantic, Irvine *et al.* (1981) observed that groups of sub-adult males common dolphins formed bachelor groups that rarely mixed with sexually mature adult males. If bachelor groups of sub-adult male common dolphin exist off Galicia, there is still the question of why they seem to be the group most vulnerable to by-catch. Perhaps different herds of dolphin are spatially separate and sub-adult male groups feed in areas also used by the fishery. Alternatively, juvenile dolphins may be more at risk of entrapment because of their lack of experience with nets (although this does not explain the predominance of males in the samples).

The seasonal trend in numbers of samples obtained may relate to changes in the number of dead animals that reach the shore. In Galician waters the predominant winds from the south and southwest in winter would carry carcasses towards the coast. Similarly, the reverse direction of winds in spring and summer, associated with upwelling, may lead to a decrease in the number of carcasses reaching the shore (López *et al.*, 2002). Storms are more frequent during the autumn and winter and this could influence strandings, both by carrying carcasses towards the coast and by causing the death of animals in poor condition (Cendrero, 1993).

Lastly, the geographical trend, aside from its likely relationship to prevailing winds, may reflect the higher human population density in the south of Galicia, and indeed the strandings network is also co-ordinated from the south of Galicia.

Diet, estimated prey consumption and interactions with fisheries

Common dolphins in Galician waters had eaten a wide variety of prey over the study period. The majority of the prey were pelagic species (e.g. blue whiting, sardine and scad), although demersal and inshore species (e.g. sandeels, scaldfish, sole, gobies, garfish, *Atherina* sp.) were also found. Of the cephalopod species taken by common dolphins, most are neritic, living over the continental shelf (e.g. sepiolids, *Loligo vulgaris*, *Alloteuthis subulata*, *Eledone cirrhosa* and *Octopus vulgaris*). On the other hand, oceanic species such as *Gonatus* sp., *Histioteuthis reversa*, *Chiroteuthis* sp., *Teuthowenia megalops* and *Todarodes sagittatus* were also found in the stomachs. A high number of different prey species is usually considered to be an indication of an opportunistic feeding behaviour (Collet, 1981; Klinowska, 1991, Sekiguchi *et al.*, 1992). Following the definition of opportunism, if opportunistic, common dolphins would eat the most abundant and easily captured prey in a given area at a particular time. If this is true, we would expect to find variability in the diet in relation to year, season, area and perhaps, if habitat segregation takes place in the common dolphin population, also by sex and/or age group.

In our study, the PRIMER analysis mainly highlighted seasonal and interannual differences in diet, with diet in the first quarter of the year, and in 1997 and 1998, standing out as distinct. Redundancy analysis confirmed the marked difference for quarter 1, and indicated significant interannual differences were present, although 1997 and 1998 did not stand out. It also indicated effects of location, dolphin length, and spawning stock biomass for both blue whiting and sardine, although these were not significant in all models.

Redundancy analysis confirmed the strong effect of quarter, which was related to higher numbers of gobies, sand smelts and small squid (*Alloteuthis* sp.) in the stomach contents in quarter 1. An area effect was also apparent, related to the higher incidence of blue whiting in stomach contents of dolphins from the north of Galicia.

Other studies on common dolphin diet in the Northeast Atlantic have also shown dolphins preying in a wide variety of fish and cephalopod, although generally no more than 3 or 4 species made up most of the diet (in Portugal, Silva, 1999; in France, Collet, 1981; Desportes, 1985; in Ireland, Berrow & Rogan, 1995; and in the UK, Pascoe, 1986; Kuiken *et al.*, 1994).

Silva (1999) found four pelagic species (sardine, blue whiting, *Atherina* sp. and scad) to be the most common prey of 42 common dolphins stranded on the Portuguese coast between 1987 and 1997. Collet (1981) and Desportes (1985) found blue whiting, *Trisopterus* spp. and scad to be the most frequent prey consumed by 103 and 50 dolphins respectively stranded and by-caught on the Atlantic French coast from 1972 to 1985. The authors noted that the wide variety of prey, together with some seasonal and geographical variation in the diet (Desportes, 1985) supported the idea of opportunistic feeding, with dolphins consuming preferentially pelagic prey commonly found between 0-400 m depth.

Berrow & Rogan (1995) found *Trisopterus* spp. to be the most frequent and most numerous prey in stomach contents of 26 stranded and by-caught dolphins on the Irish coast. Other prey

found included both pelagic (herring and scad) and demersal (whiting) species, including small amounts of oceanic squid (*Gonatus* sp., *Histioteuthis* sp.) and the octopus *Eledone cirrhosa*.

Kuiken *et al.* (1994) examined two groups of common dolphins stranded in the South-west of England. The first group, 10 dolphins stranded during 1990 to 1991, had mainly mackerel and *Trisopterus* spp. in the stomachs. In the second group (32 dolphins stranded in 1992), mackerel and sardine were the main prey. These results agree with the findings of Pascoe (1986) for two common dolphins by-caught in the same area in 1982, which had mackerel and sprat in their stomachs. Cooperus (1998) found mackerel and scad to be the most important prey in the stomachs of seven common dolphin by-caught between 1992 and 1995 in the Dutch trawl fishery, for mackerel and scad, Southwest of Ireland.

Seasonal variation in the diet has been reported only in a few studies. Collet (1981) records that common dolphins on the French coast ate sardine, sprat, anchovy, mackerel and scad mainly in the winter months, while eel, garfish and snipefish were found mainly in the stomachs of dolphins stranded in summer. Desportes (1985) found seasonal differences in the diet of dolphins stranded in the Northern part of the Gulf of Biscay, with dolphins eating more pelagic prey in spring-summer.

In the present study, the most important prey of common dolphins in Galician waters were found to be blue whiting and sardine, both very abundant species off the Iberian coast and of considerable economic value, being the target of important directed fisheries in both Spain and Portugal. The sardine fishery, which in both Atlantic Spain and Portugal is one of the most ancient in the region (Porteiro *et al.*, 1993), was estimated to be the main pelagic fishery in the area, not only by level of captures but also due to its socio-economic importance (Pérez *et al.*, 1985).

Blue whiting is a “typical” prey species for common dolphins: a shoaling mesopelagic fish, living over depths of 160-3000 m in midwater, 30-400 m from the surface, and rising to surface waters at night, with seasonal and spawning migrations (Whitehead *et al.*, 1989). Its high abundance can also be inferred from its importance as the main prey for other predators in the area: other cetaceans (e.g. bottlenose dolphins, Santos *et al.*, 1997), fish (e.g. hake, González *et al.*, 1985; Olaso *et al.*, 1994), cephalopods (e.g. *Loligo forbesi*, *L. vulgaris*, Rocha *et al.*, 1994 and *Todaropsis eblanae*, Rasero *et al.*, 1996), and for predators in adjacent Portuguese waters. (e.g. common dolphins and several fish species, Silva *et al.*, 1997).

Sardine is also a pelagic shoaling species, living 25-55 m from the surface during the day and 15-35 m at night) (Whitehead *et al.*, 1989). Its abundance shows cyclic fluctuations in Iberian waters (Anon., 2004d). Common dolphins stranded in Portugal seem to have a higher proportion of sardine in their diets than animals stranded on the Spanish coast (Silva, 1999). Estimates of number of sardine from spring acoustic surveys carried out by both countries since 1986 showed that the species is more common in Portuguese waters than off Galicia (Carrera & Porteiro, 2003).

Our results demonstrated a relationship between diet and two of the fishery variables describing blue whiting abundance: blue whiting trawl survey abundance in area IXa and blue whiting spawning stock biomass. These were positively correlated with the importance of sandeels and polychaetes and negatively correlated with the importance of scad, myctophids

and unidentified clupeids. These trends may imply foraging further offshore in years of lower blue whiting abundance

GAMs for the amount of blue whiting in stomach contents were generally “better” (in terms of variation explained) than those for sardine. This is consistent with the finding (from Kruskal-Wallis tests) that there was more pronounced seasonal and interannual variation in blue whiting consumption than in sardine consumption.

However, the latter models, although statistically much weaker, were plausible in terms of predictions about the effect of fish abundance on predation: more sardine were predicted to be taken in years of higher sardine abundance and lower recruitment of blue whiting. If sardine were the “preferred prey”, or if predation on sardine was completely opportunistic, predation on sardine would be expected to depend on sardine abundance.

Models for blue whiting predation included interesting seasonal and regional trends but suggest a slightly implausible relationship with fish abundance, i.e. consumption of blue whiting is predicted to be higher in years of high sardine abundance. The occurrence of the two species in stomach contents was not correlated (at the individual dolphin level). It is possible that high sardine abundance leads to dolphins feeding in areas where both fish species occur. Dolphins would then be more likely to take blue whiting in good sardine years even if they took sardine preferentially.

It would be expected that dolphins should normally “prefer” to eat more energy-rich fish species, thereby maximizing their rate of energy intake – this is a basic tenet of optimal foraging theory (OFT), (Charnov, 1976, Pyke *et al* 1977). Sardine is a species with higher energetic content than blue whiting (130 Kcal/100 g as opposed to 74 Kcal/100g, data from Sociedad Española de Nutrición Básica y Aplicada, SENBA), although energetic content may be expected to vary seasonally.

Even if our calculations of fish consumption by dolphins can be considered a “back of the envelope” exercise (we are ignoring seasonal, regional and interannual variation in diet and dolphin population structure) it is useful to compare the numbers potentially removed by common dolphins with Spanish and Portuguese official landings for the three main commercially important prey species (Table 3). The most significant overlap concerns blue whiting – although it must be stressed that overlap between diet and fishery catches does not and cannot demonstrate that competition actually occurs (Pierce *et al.*, 2004b).

When size of prey is taken into account, dolphins could avoid direct competition by exploiting different size classes, for example smaller than those targeted by the fishery. In the case of blue whiting, dolphins ate fish ranging from 5.5 to 30.5 cm, with just over 70% of the blue whiting consumed below the minimum landing size established for the species (18 cm). For scad, dolphins ate fish ranging from 3.5 to 36.5 cm, with more than 71% below the minimum landing size (15 cm). However, sardine taken by dolphins (between 15.5 to 22.5 cm) are well above the minimum landing size (11 cm). Studies in Portugal showed that Portuguese dolphins stranded between 1987 and 1997 ate smaller sized prey, with blue whiting ranging from 6.10 to 22.67 cm with a mean of 12.50 cm, scad ranging from 7.51 to 27.78 cm with a mean of 14.43 cm and sardine ranging from 8.19 to 21.03 cm with a mean of 15.91 cm (Silva, 1999).

Small fish consumed by dolphins would not be available as adults for the fishery, although it is difficult to know how many would otherwise have survived to be taken by the fishery (e.g. other predators might take them). Furthermore, the high number of juvenile fish eaten by common dolphins in Galicia could originate, at least in some part, in the fishery itself (discards of undersized fish). Common dolphins have been observed feeding on disabled fish that escaped the net or discards (Leatherwood & Reeves, 1983). This aspect, the interaction with fisheries, is difficult to quantify due to the lack of estimates of discards, and also the existence of an important market for undersize fish for sardine, scad and more importantly hake (“xouba”, “chincho” and “carioca” respectively), which tend to be landed and sold in spite of the control measures (involving heavy fines) in place.

Nevertheless, the present results provide clear indication that there is potential for direct competition between common dolphins and at least two important fisheries in NW Spain. There is also further evidence of interactions taking place with frequent by-catch of dolphins in offshore trawls (Aguilar, 1997; López *et al.*, 2003). In our sample, of 413 dolphins samples, more than 1/3 (151) had clear signs of having died as a consequence of entanglement in fishing gear. For many more carcasses cause of death could not be unequivocally assigned but it is likely it would include further examples of interactions. López *et al.* (2003) estimated an annual by-catch of 764 common dolphins in Galician waters based on on-board observations, a voluntary reporting scheme and an interview survey among fishermen. The authors acknowledge the fact that all 3 sources of data (and collection an examination of stranded animals) will tend to underestimate the rate of cetacean by-catch due to the impossibility of covering all the sectors of the fishery and the self-selecting nature of the sample of co-operating fishermen. In any case, 764 common dolphins from an estimated population of slightly over 8000 represents an annual removal of more than 9% of the population. The International Whaling Commission has stated that the anthropogenic removal rate of any cetacean population should not exceed half the maximum net growth rate of the population (IWC, 1995). At the second meeting of ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas) in 1997, it was agreed that, in general, an anthropogenic removal of more than 2% of the best available population estimate was an “unacceptable interaction”.

Acknowledgements

We thank all the members of CEMMA, the ECOBIOMAR research group and the Instituto de Investigaciones Marinas in Vigo, members of the public and various local authorities in Galicia for their assistance with data and sample collection. Data collection was funded by the CEC.

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Table 1. Summary of sampled dolphins in each year, by (a) area, (b) season (quarter), (c) sex, (d) size class, (e) cause of death. Areas are as shown in Figure 1. Size classes are (S) ≤ 150 cm, (M) 151 - 190 cm, (L) > 190 cm. Causes of death are (T) killed by *Tursiops*, (B) fishery by-catch, (Sh) shoot, (Sa) shark attack, (O) Other or undiagnosed. (Note: location was not determined in one case)

Year	N	By area						By quarter				By sex		By size			By cause of death				
		1	2	3	4	5	6	Q1	Q2	Q3	Q4	F	M	S	M	L	T	B	Sh	Sa	O
1991	9	0	0	1	2	6	0	5	0	0	4	2	6	1	6	2	0	3	0	0	6
1992	17	0	0	1	5	3	8	2	3	0	12	4	12	0	13	3	0	6	0	0	11
1993	19	0	0	6	2	6	5	4	11	2	2	9	8	2	9	8	0	5	0	0	14
1994	23	0	0	5	4	10	4	8	7	1	7	5	16	1	15	7	0	12	1	0	10
1995	34	0	0	9	11	10	4	15	11	1	7	8	25	3	20	9	0	12	0	0	22
1996	47*	0	0	4	12	22	8	16	13	10	8	15	28	2	13	15	0	21	0	0	26
1997	25	0	0	2	2	14	7	16	4	1	4	14	10	0	12	7	0	17	0	0	8
1998	60	0	0	11	13	19	17	24	26	8	2	18	39	0	19	23	0	23	0	1	36
1999	40	0	0	3	2	17	18	28	5	3	4	15	25	3	24	5	1	18	0	1	20
2000	40	0	0	2	5	17	16	30	6	2	2	14	19	3	12	10	0	2	0	0	38
2001	28	1	1	2	0	14	10	11	5	11	1	14	13	2	9	12	0	11	0	0	17
2002	32	0	0	2	2	19	9	14	12	2	4	15	17	3	12	13	0	10	0	0	22
2003	39	1	0	2	7	18	11	9	23	3	4	19	20	6	16	10	0	151	0	0	28
Total	413	2	1	50	67	175	117	182	126	44	61	152	238	26	180	124	1	1	1	2	258

Table 2. Summary results of multivariate analysis

Subset	Cause of death	“Environmental” variables	Dolphins	Prey types	Overall Rho*	Best predictor	Best 2 predictors	Best 3 predictors
1	All	Y, Q	413	39	0.105 (P = 0.001)	Q1 (R = 0.113)	Q1, 1998 (R = 0.129)	Q1, 1997, 1998 (R=0.132)
2	All	Y, Q, A	412	39	0.091 (P = 0.001)	Q1 (R = 0.113)	Q1, 1998 (R = 0.122)	Q1, 1997, 1998 (R=0.132)
3	All	Y, Q, A, S	390	39	0.086 (P = 0.001)	Q1 (R = 0.110)	Q1, 1997 (R = 0.115)	Q1, 1997, 1998 (R=0.125)
4	All	Y, Q, A, L	330	38	0.098 (P = 0.001)	Q1 (R = 0.122)	Q1, 1998 (R = 0.135)	Q1, 1997, 1998 (R=0.134)
5	All	Y, Q, A, L, S	320	38	0.097 (P = 0.001)	Q1 (R = 0.117)	Q1, 1998 (R = 0.124)	Q1, 1997, 1998 (R=0.134)
6	By-catch	Y, Q, A	151	33	0.080 (P = 0.001)	Q1 (R = 0.112)	Q1, 1997 (R = 0.143)	Q1, 1997, 1998 (R=0.150)
7	By-catch	Y, Q, A, S	146	33	0.074 (P = 0.001)	Q1 (R = 0.116)	Q1, 1997 (R = 0.134)	Q1, 1997, 1998 (R=0.149)
8	By-catch	Y, Q, A, L	104	33	0.077 (P = 0.006)	Q1 (R = 0.133)	Q1, 1997 (R = 0.162)	Q1, 1997, 1998 (R=0.186)
9	By-catch	Y, Q, A, L, S	102	33	0.069 (P = 0.007)	Q1 (R = 0.130)	Q1, 1997 (R = 0.160)	Q1, 1997, 1998 (R=0.184)

Y = year, Q = quarter (season), A = area, L = length, S = sex

* P values are based on a randomisation test with 1000 repeats.

Table 4. Estimated annual consumption (tonnes) by common dolphin in Galician waters for the three main prey categories. Values in bold are the original estimates. Also given are the estimates ± 1 standard deviation based on the information for dolphin population size given by López *et al.* (2004). N = estimated number of common dolphins in Galician waters, P_i = proportion by weight of prey species i in the diet (taking into account all prey remains), F = average weight of food eaten daily per common dolphin (kg), T = number of days when prey and predator are assumed to be in contact. For further explanation see the main text. The table also shows Spanish and Portuguese official landings (tonnes) for 2003 for blue whiting (ICES subareas VIII and IX), landings in 2002 for sardine (Divisions VIIIc and IXa) and landings in 2002 for scad (Divisions VIIIc and IXa) (Divisions VIIIc and IXa).

Species	N	P_i	F	T	Total (tonnes)	Landings (Spain)	Landings (Portugal)	Landings (Total)
<i>Blue whiting</i>	4388	34.9	4.8	365	2697	13825	2651	16476
	8137	34.9	4.8	365	5001			
	13678	34.9	4.8	365	8407			
<i>Sardine</i>	4388	25.8	4.8	365	1983	20448*	67536	87984
	8137	25.8	4.8	365	3678			
	13678	25.8	4.8	365	6183			
<i>Scad</i>	4388	8.8	4.8	365	677	30348*	14270	44618
	8137	8.8	4.8	365	1255			
	13678	8.8	4.8	365	2109			

*Excluding Cádiz landings

Table 3. Overall importance of prey species identified from Galician common dolphins (N=413). The first estimate (%F) indicates the percentage of stomachs containing each prey category. The estimates for total number of individuals are based on (N₁) otoliths and beaks only and (N₂) all prey remains. Measurements on otoliths and beaks were used to derive the first estimate of total prey weight (W₁, g), while the second estimate (W₂, g) is adjusted to take account of fish and cephalopods identified from other remains. All four latter estimates are also expressed as percentages.

PREY SPECIES	% F	N1	N2	%N1	%N2	W1	W2	%W1	%W2
Fish	99.0	42719	46058	88.4	87.7	583179	628761	90.9	91.5
Sardine (<i>Sardina pilchardus</i>)	63.4	1734	2948	3.6	5.6	87440	148658	13.6	21.6
Anchovy (<i>Engraulis encrasicolus</i>)	7.3	196	206	0.4	0.4	14	15	0.0	0.0
Herring (<i>Clupea harengus</i>)	0.2	1	1	0.0	0.0	7	7	0.0	0.0
All Clupeoids	83.5	1931	3915	4.0	7.5	87536	177475	13.7	25.8
Argentine (<i>Argentina</i> sp.)	11.9	338	352	0.7	0.7	5749	5987	0.9	0.9
Lanternfish (Myctophidae)	9.4	1071	1136	2.2	2.2	1218	1292	0.2	0.2
Pearlsides	0.2	518	518	1.1	1.0	282	282	0.0	0.0
Barracudinas (Paralepididae)	0.2	3	3	0.0	0.0	-	-	-	-
Whiting (<i>Merlangius merlangus</i>)	0.2	2	3	0.0	0.0	25	38	0.0	0.0
Blue whiting (<i>Micromesistius poutassou</i>)	50.6	11614	11768	24.0	22.4	236474	239610	36.9	34.9
Trisopterus spp. (<i>T. esmarkii</i> , <i>T. minutus</i> , <i>T. luscus</i>)	36.1	2028	2062	4.2	3.9	28726	29208	4.5	4.3
Silvery pout (<i>Gadiculus argenteus thori</i>)	23.2	1999	2025	4.1	3.9	5343	5412	0.8	0.8
5-bearded rockling (<i>Ciliata mustela</i>)	0.7	5	5	0.0	0.0	137	137	0.0	0.0
All Gadidae	71.2	15779	16061	32.6	30.6	272239	277104	42.5	40.4
Hake (<i>Merluccius merluccius</i>)	22.8	324	353	0.7	0.7	22413	24419	3.5	3.6
Snipefish (<i>Macroramphosus scolopax</i>)	2.4	-	179	-	0.3	-	-	-	-
Garfish (<i>Belone belone</i>)	3.4	4	35	0.0	0.1	647	5661	0.1	0.8
Scad (<i>Trachurus</i> sp.)	42.1	1577	1667	3.3	3.2	57154	60416	8.9	8.8
Sea bream (Sparidae)	12.6	640	690	1.3	1.3	19708	21248	3.1	3.1
Labridae	2.9	6	14	0.0	0.0	175	408	0.0	0.1
Sandeel (<i>Ammodytes</i> spp.)	26.2	1893	1932	3.9	3.7	23448	23931	3.7	3.5
Dragonet (Callyonimidae)	3.9	73	83	0.2	0.2	627	713	0.1	0.1
Gobiidae	46.5	14043	14147	29.0	26.9	18624	18762	2.9	2.7
Mackerel (<i>Scomber scombrus</i>)	23.5	59	233	0.1	0.4	8307	32806	1.3	4.8
<i>Atherina</i> sp.	21.5	4182	4209	8.7	8.0	59858	60244	9.3	8.8
Scaldfish (<i>Arnoglossus</i> sp.)	2.9	68	132	0.1	0.3	482	936	0.1	0.1
Sole (<i>Solea solea</i>)	1.7	37	39	0.1	0.1	2061	2172	0.3	0.3
All Flatfish	9.4	212	287	0.4	0.5	5190	7026	0.8	1.0
Unidentified Fish	24.0	65	244	0.1	0.5	-	-	-	-
Cephalopoda	72.9	5634	5657	11.6	10.8	58068	58305	9.1	8.5
Cuttlefish (<i>Sepia</i> spp.)	2.7	31	32	0.1	0.1	201	207	0.0	0.0
Sepiolid (<i>Sepioida atlantica</i>)	9.2	218	217	0.5	0.4	312	311	0.0	0.0
Sepiolid (<i>Sepietta oweniana</i>)	3.1	36	36	0.1	0.1	193	193	0.0	0.0
All Sepiolidae	46.0	2570	2567	5.3	4.9	6004	5997	0.9	0.9
Squid (<i>Loligo</i> sp.)	23.7	498	499	1.0	0.9	25167	25218	3.9	3.7
Squid (<i>Alloteuthis subulata</i>)	44.6	1964	1965	4.1	3.7	9728	9733	1.5	1.4
Squid (<i>Illex coindetti</i>)	1.2	15	15	0.0	0.0	1225	1062	0.2	0.2
Squid (<i>Todaropsis eblanae</i>)	1.0	5	5	0.0	0.0	274	274	0.0	0.0
Squid (<i>Todarodes sagittatus</i>)	0.2	1	1	0.0	0.0	883	883	0.1	0.1
All Ommastrephidae	24.7	440	446	0.9	0.8	10947	11096	1.7	1.6
Squid (<i>Gonatus steenstrupi</i>)	1.9	22	24	0.0	0.0	2099	2290	0.3	0.3
Squid (<i>Histioteuthis reversa</i>)	0.2	1	1	0.0	0.0	28	28	0.0	0.0
Squid (<i>Chiroteuthis</i> sp.)	2.2	51	51	0.1	0.1	1291	1291	0.2	0.2
Squid (<i>Mastigoteuthis</i> sp.)	0.2	1	1	0.0	0.0	90	90	0.0	0.0
Squid (<i>Teuthowenia megalops</i>)	0.7	8	8	0.0	0.0	366	366	0.1	0.1
Octopus (<i>Octopus vulgaris</i>)	4.1	25	25	0.1	0.0	869	869	0.1	0.1
Octopus (<i>Eledone cirrhosa</i>)	3.4	19	18	0.0	0.0	1133	1073	0.2	0.2
Unidentified Cephalopoda	3.9	3	18	0.0	0.0	-	-	-	-
Crustacea	32.7	-	796	-	1.5	-	-	-	-
Polychaeta	5.3	-	28	-	0.1	-	-	-	-

Figure 1. Map of study area, showing division of the coastline into 6 (sub-) areas.

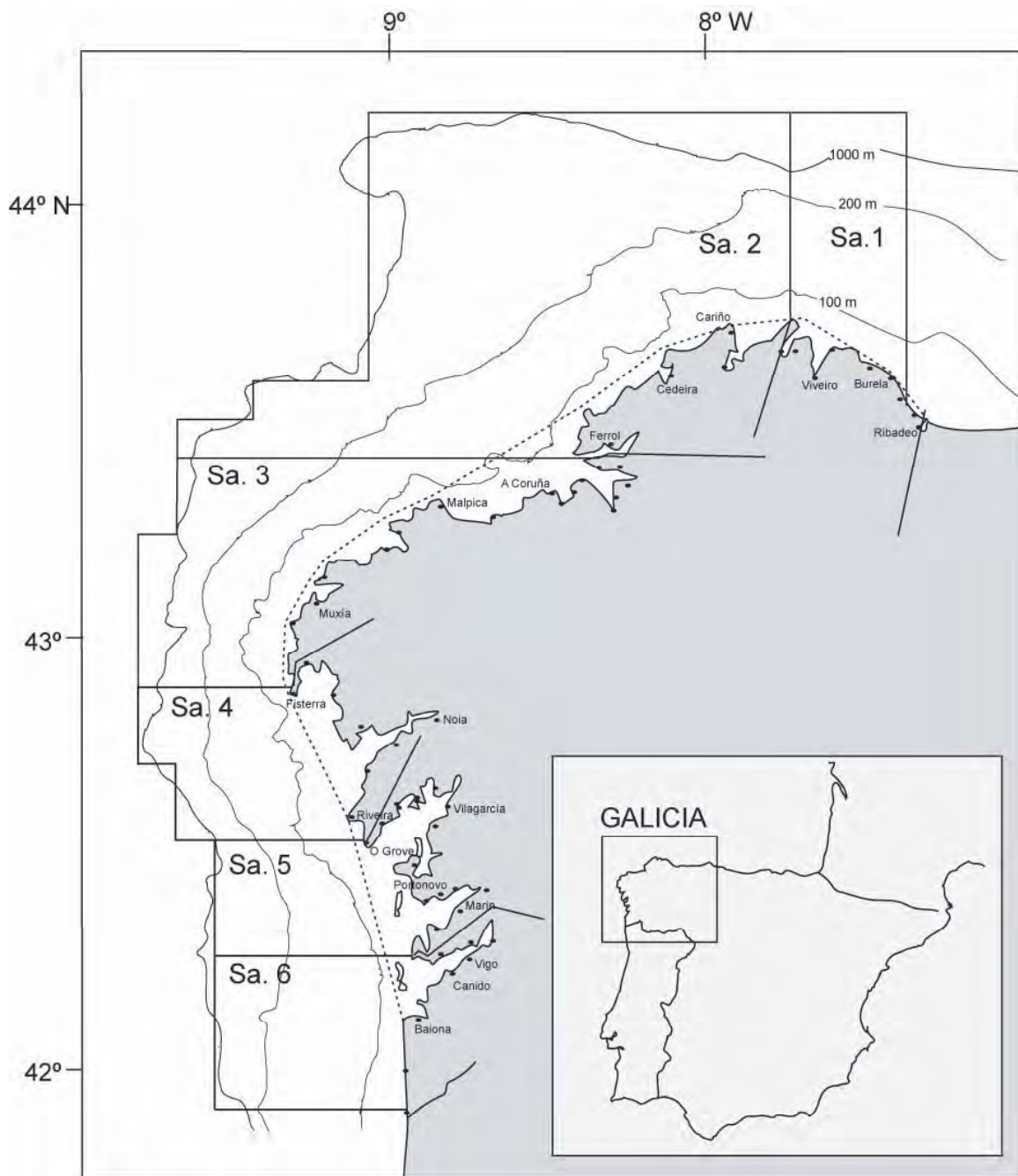


Figure 2. Frequency distributions of estimated size of (a) blue whiting, (b) sardine and (c) scad eaten by common dolphins in Galician waters. Frequencies are shown, cumulatively, for all dolphins and for those dolphins that had died as a result of by-catch.

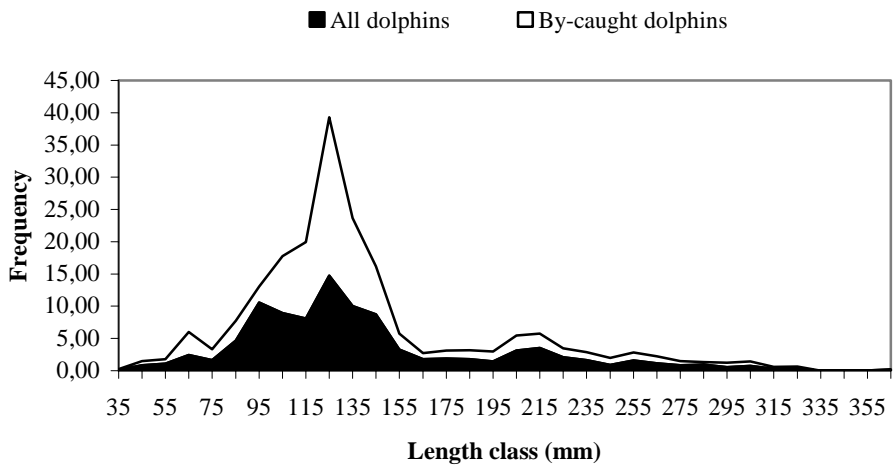
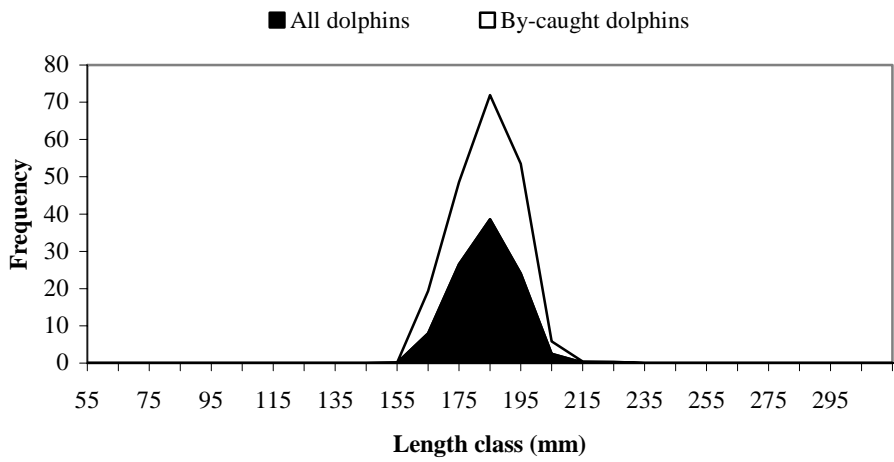
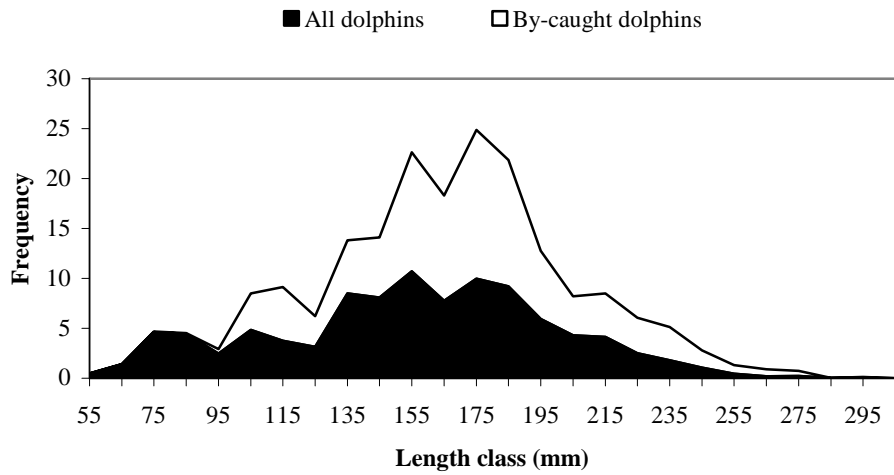


Figure 3a. Redundancy analysis (RDA) for diet of all dolphins with location data (N=412): explanatory variables plotted against the first two RDA axes. Continuous explanatory variables appear as vectors, the length and direction of which indicates the strength and direction of correlation of these vectors with scores on axes 1 and 2. Nominal explanatory variables appear as squares, the position of which also indicates strength and direction of correlations with axis scores. Explanatory variables: Y = year, Q = quarter, A = area, BR = blue whiting recruitment, BS = blue whiting SSB, B9 = blue whiting survey abundance in area IXa, SR = sardine recruitment, SB = sardine SSB.

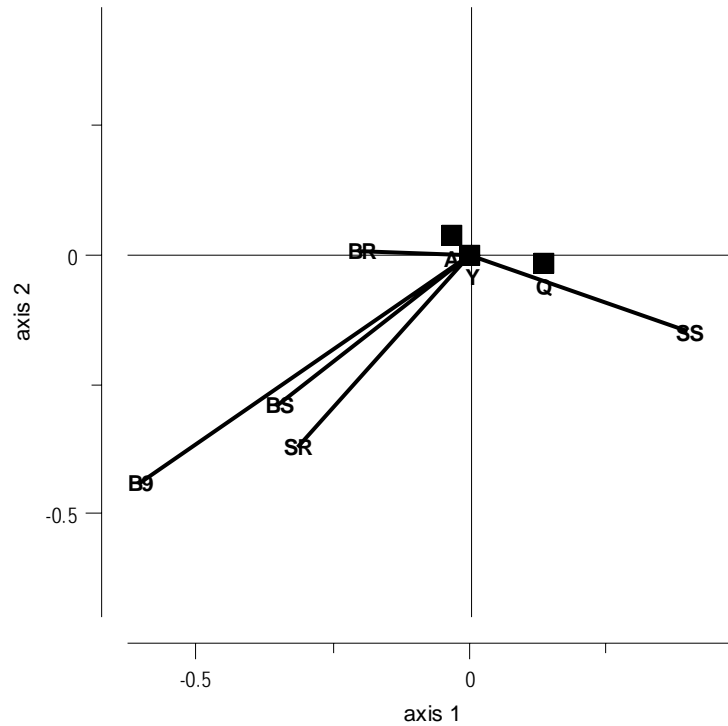


Figure 3b. Redundancy analysis (RDA) for diet of all dolphins with location data (N=412): response variables plotted against the first two RDA axes. Response variable codes: sardine (*Sardina pilchardus*) = F2, anchovy (*Engraulis encrasicolus*) = F3, unidentified Clupeoids = F4, argentine (*Argentina* sp.) = F7, Myctophidae = F8, blue whiting (*Micromesistius poutassou*) = F11, silvery pout (*Gadiculus argenteus thori*) = F13, rocklings = F14, unidentified Gadidae = F15, garfish (*Belone belone*) = F17, hake (*Merluccius merluccius*) = F18, snipefish (*Macroramphosus scolopax*) = F19, scad (*Trachurus* sp.) = F20, Sparidae = F21, Labridae = F22, Ammodytidae = F23, mackerel (*Scomber scombrus*) = F24, Gobiidae = F25, Callionymidae = F26, sand smelt (*Atherina* sp.) = F27, Bothidae = TF30, Sole (*Solea solea*) = F31, Pleuronectidae = TF32, unidentified flatfish = F33, unidentified fish = F34, cuttlefish (*Sepia* spp.) = C1, Sepiolidae = TC4, squid (*Loligo* sp.) = C5, squid (*Alloteuthis* sp.) = C6, squid (*Gonatus* sp.) = C7, Ommastrephidae = TC16, squid (*Chiroteuthis* sp.) = C17, squid (*Teuthowenia megalops*) = C18, octopus (*Eledone cirrhosa*) = C19, octopus (*Octopus vulgaris*) = C20, unidentified cephalopods = C21, Crustacea = O1, Polychaeta = O2.

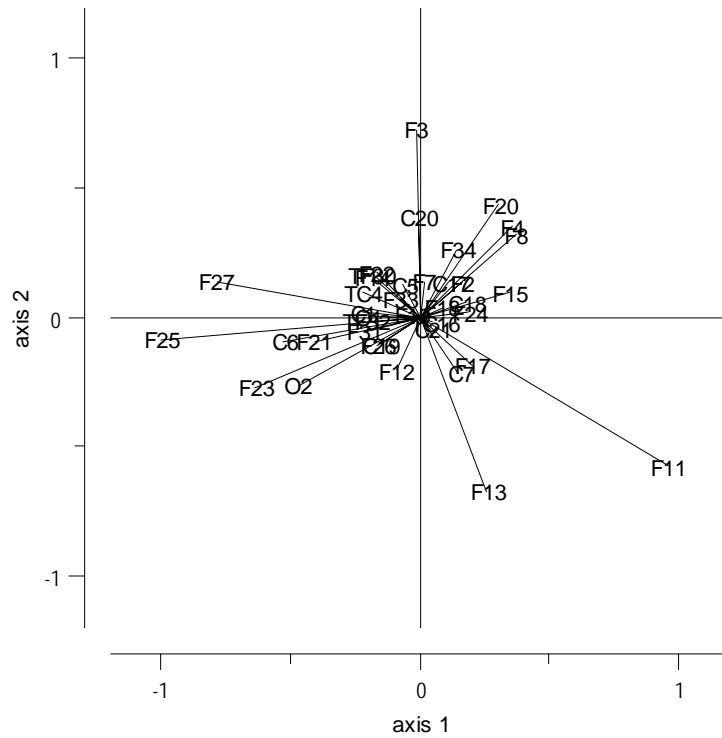


Figure 3c. RDA biplot for diet of all dolphins with location data (N=412). In addition to the explanatory variables, this plot shows vectors for prey categories (fish categories numbered F1, F2 etc, cephalopod categories as C1, C2 etc and other as O1, O2 etc). Thus relationships between explanatory and response variables can be identified visually.

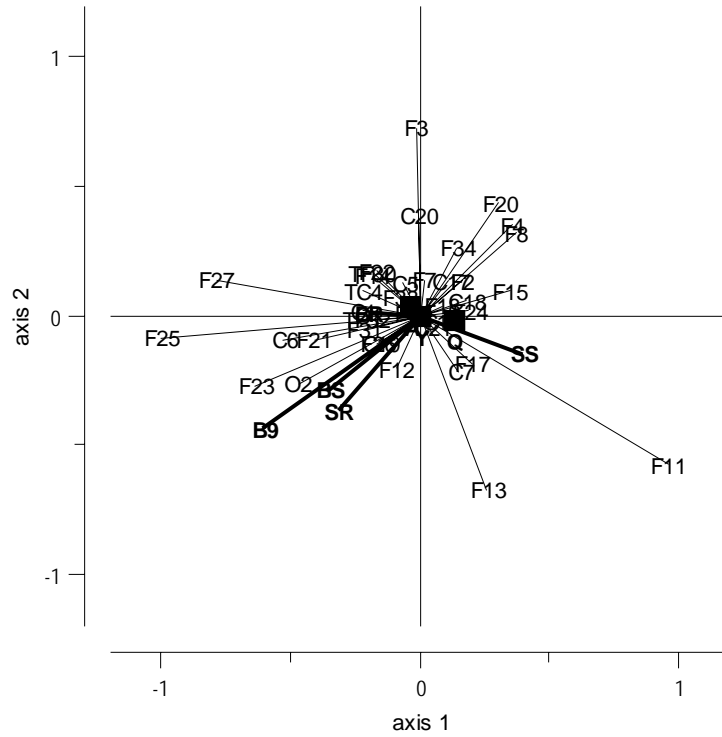


Figure 4a. Redundancy analysis (RDA) for diet of by-caught dolphins with location, length and sex data (N=102): explanatory variables plotted against the first two RDA axes. Continuous explanatory variables appear as vectors, the length and direction of which indicates the strength and direction of correlation of these vectors with scores on axes 1 and 2. Nominal explanatory variables appear as squares, the position of which also indicates strength and direction of correlations with axis scores. (Variable abbreviations as in figure 3 except for: F = female (i.e. sex), EL = estimated length).

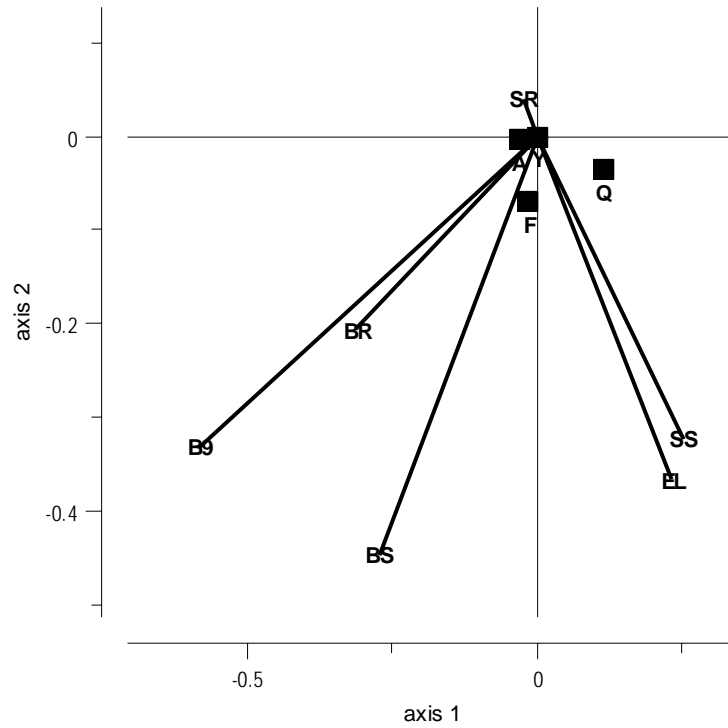


Figure 4b. Redundancy analysis (RDA) for diet of by-caught dolphins with full data (N=102): response variables plotted against the first two RDA axes. Response variable codes are as in Figure 3b.

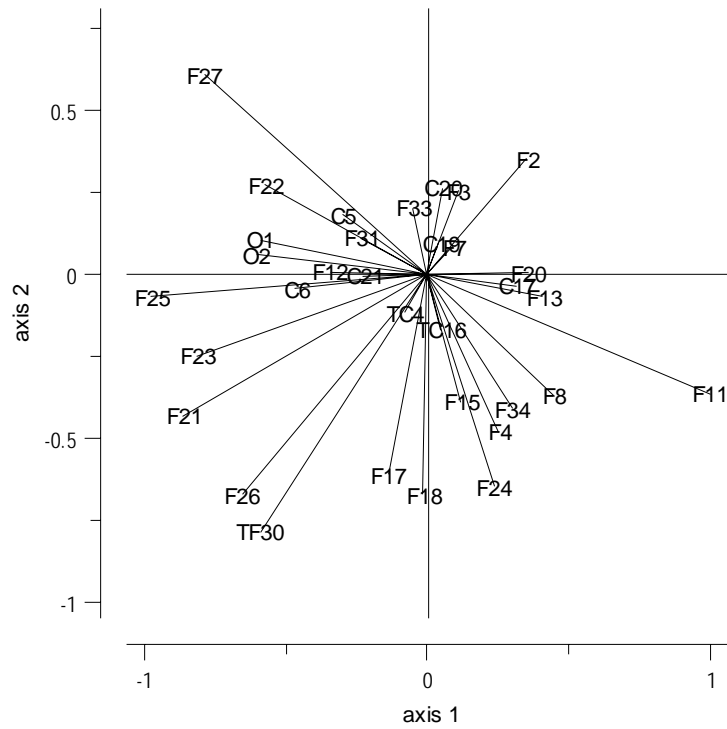


Figure 4c. Biplot for redundancy analysis for diet of by-caught dolphins with location, length and sex data (N=102). In addition to the explanatory variables, this plot shows vectors for prey categories (fish categories numbered F1, F2 etc, cephalopod categories as C1, C2 etc and other as O1, O2 etc). Thus relationships between explanatory and response variables can be identified visually. Abbreviations are as in Figure 3.

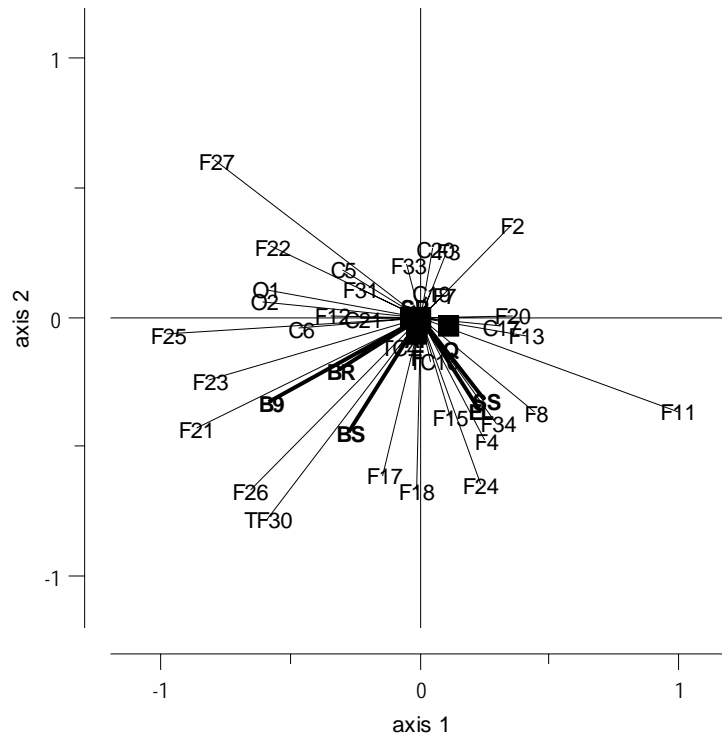


Figure 5. Smoothers for GAM fitted to blue whiting numbers in stomach contents (full data set). Clockwise from top left: month, subarea, blue whiting spawning stock biomass, sardine spawning stock biomass.

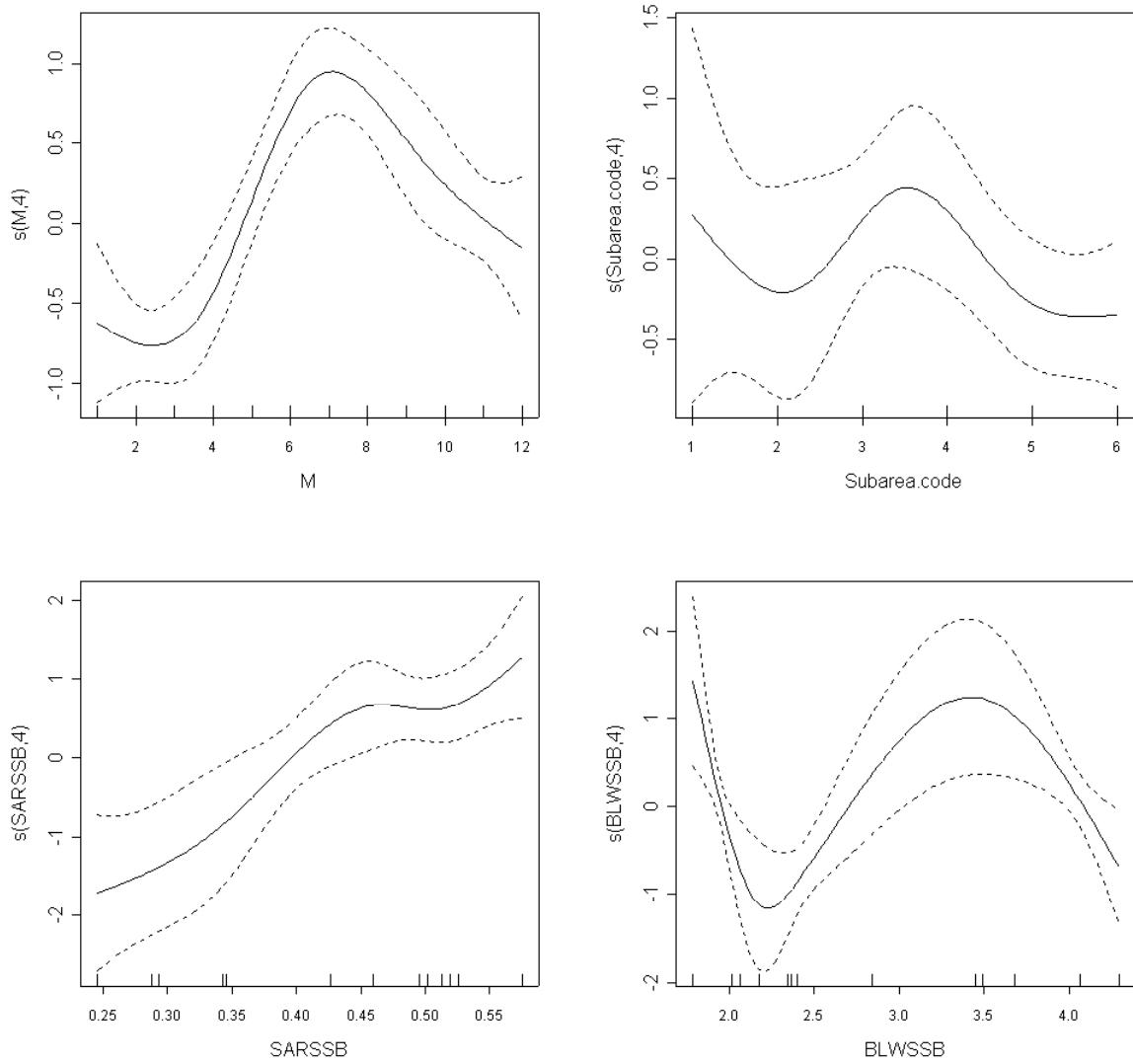


Figure 6. Smoothers for GAM fitted to blue whiting numbers in stomach contents (intermediate data set). Clockwise from top left: month, length, subarea, blue whiting spawning stock biomass, sardine spawning stock biomass.

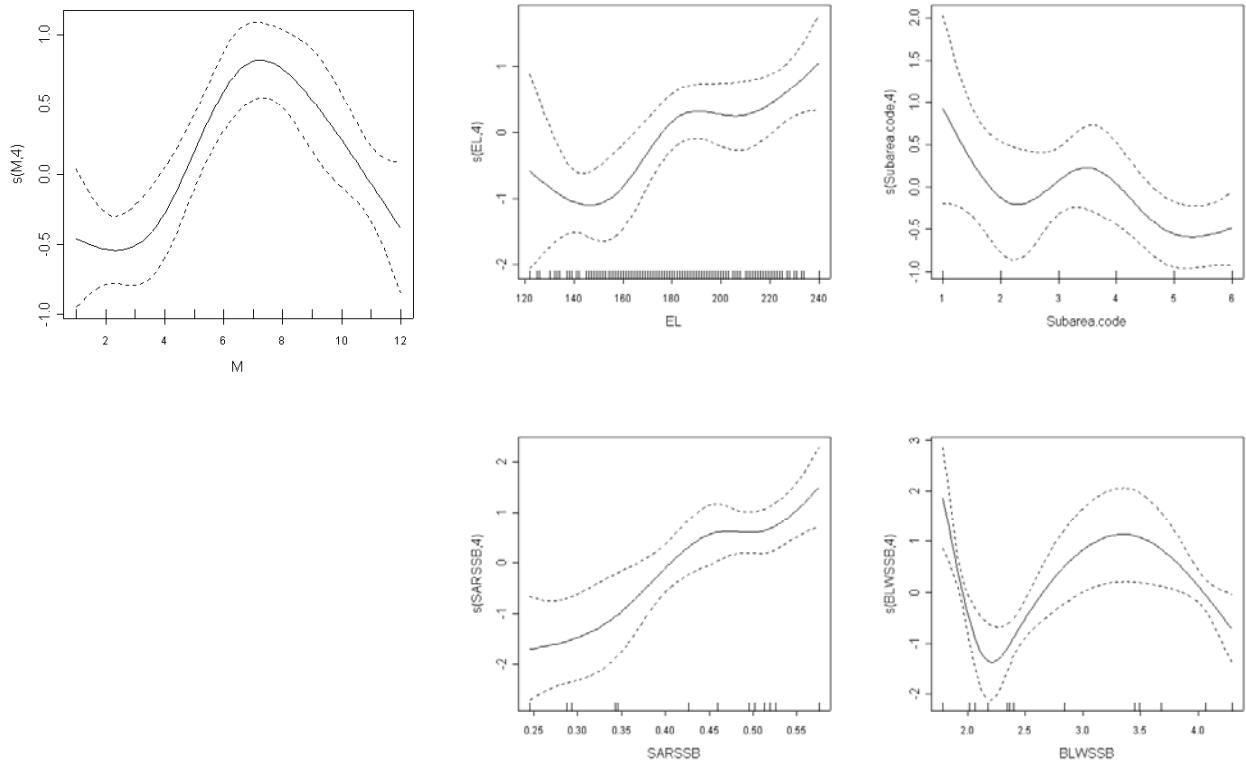


Figure 7. Smoothers for GAM fitted to blue whiting numbers in stomach contents (by-catch data set). Clockwise from top left: month, length, subarea, sardine spawning stock biomass.

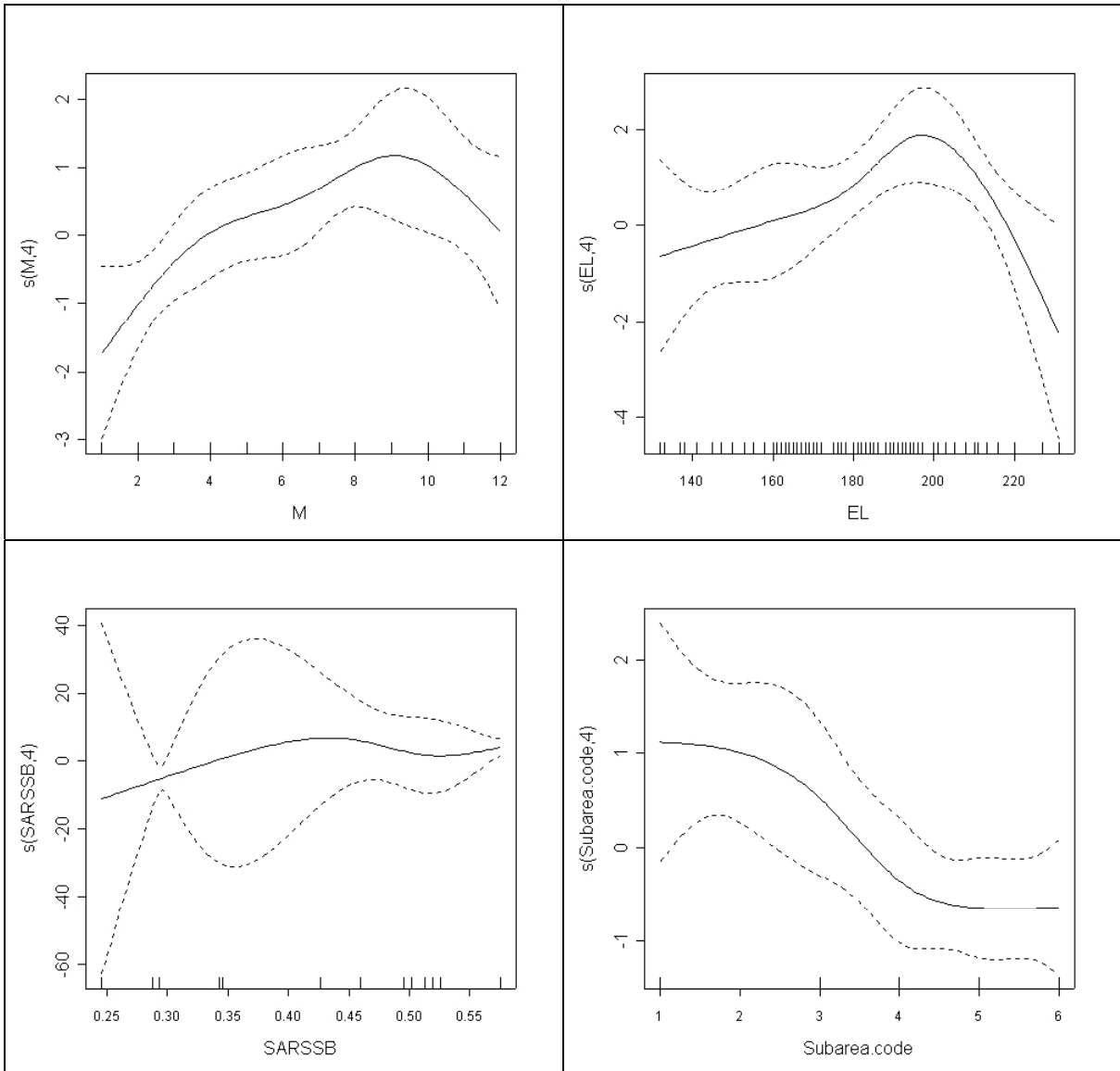


Figure 8. Smoothers for GAM fitted to blue whiting weight in stomach contents (intermediate data set). Clockwise from top left: month, length, subarea, sardine spawning stock biomass.

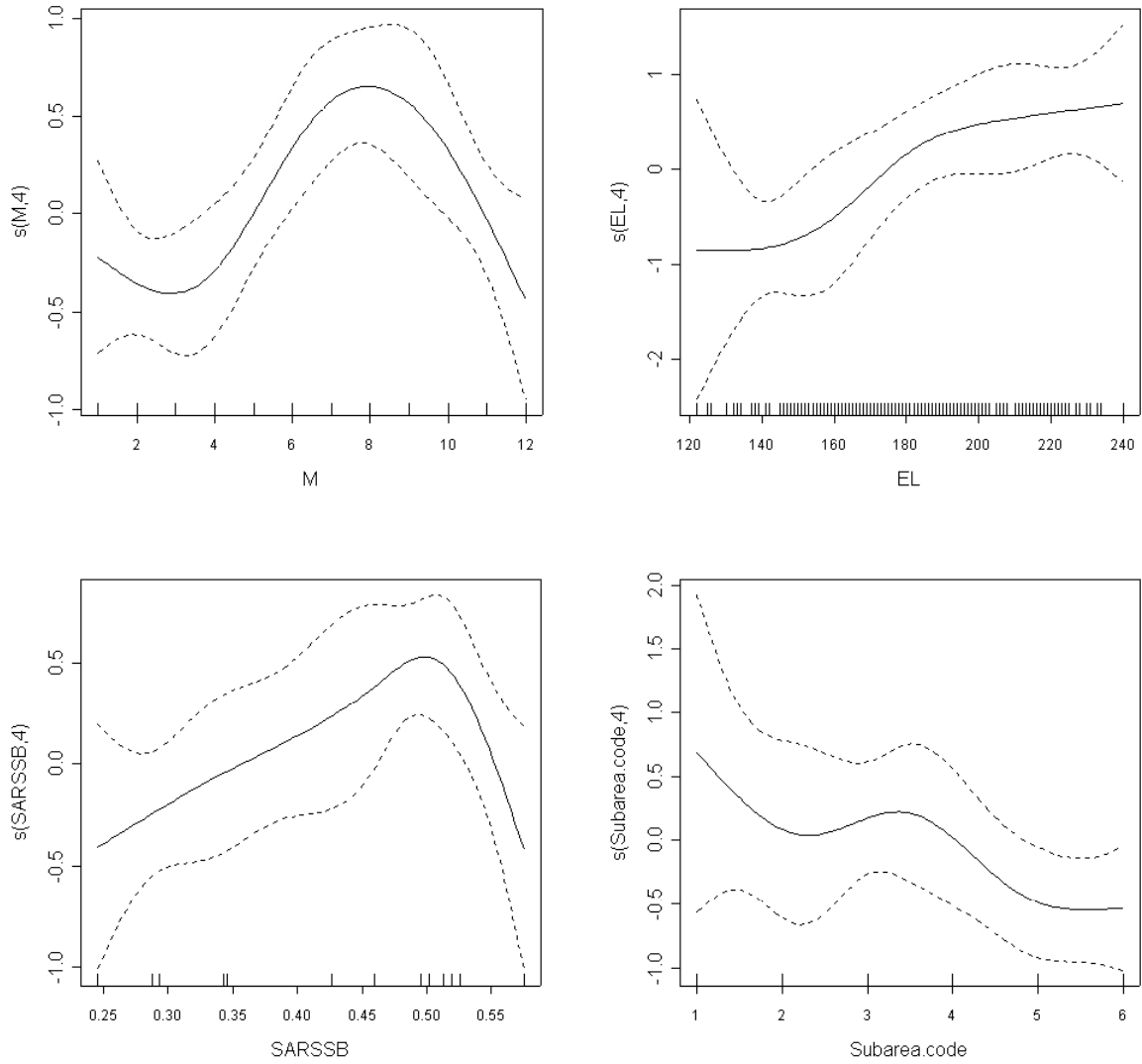


Figure 9. Smoother for GAM fitted to sardine numbers in stomach contents (intermediate data set), for effect of sardine spawning stock biomass.

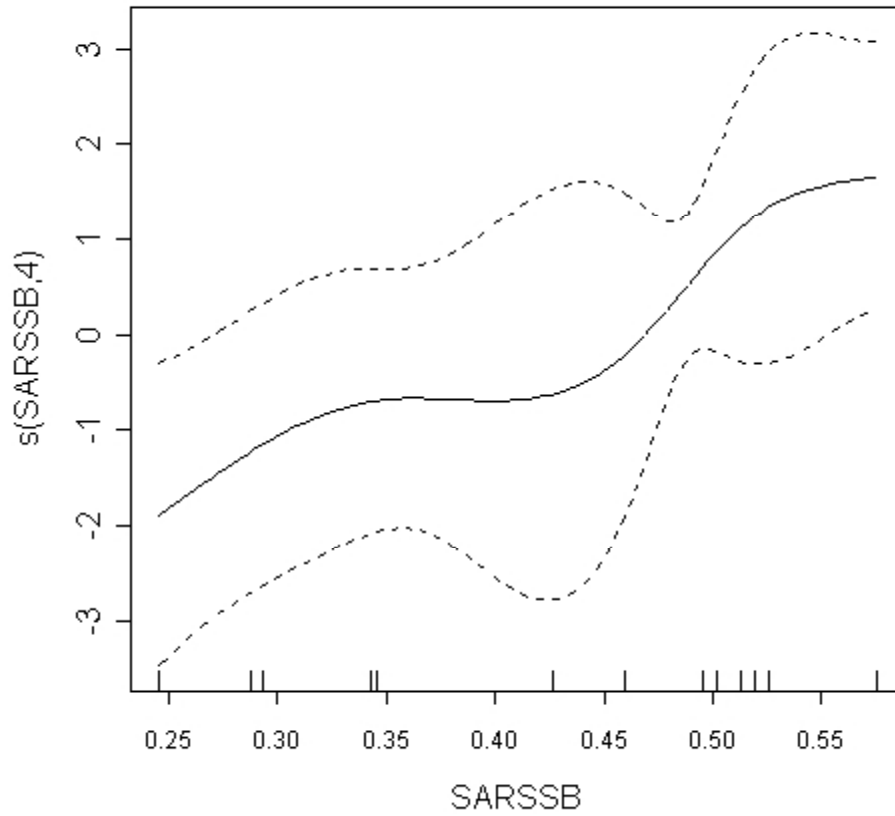


Figure 10. Smoother for GAM fitted to weight of sardine in stomach contents (intermediate data set), for effect of sardine spawning stock biomass.

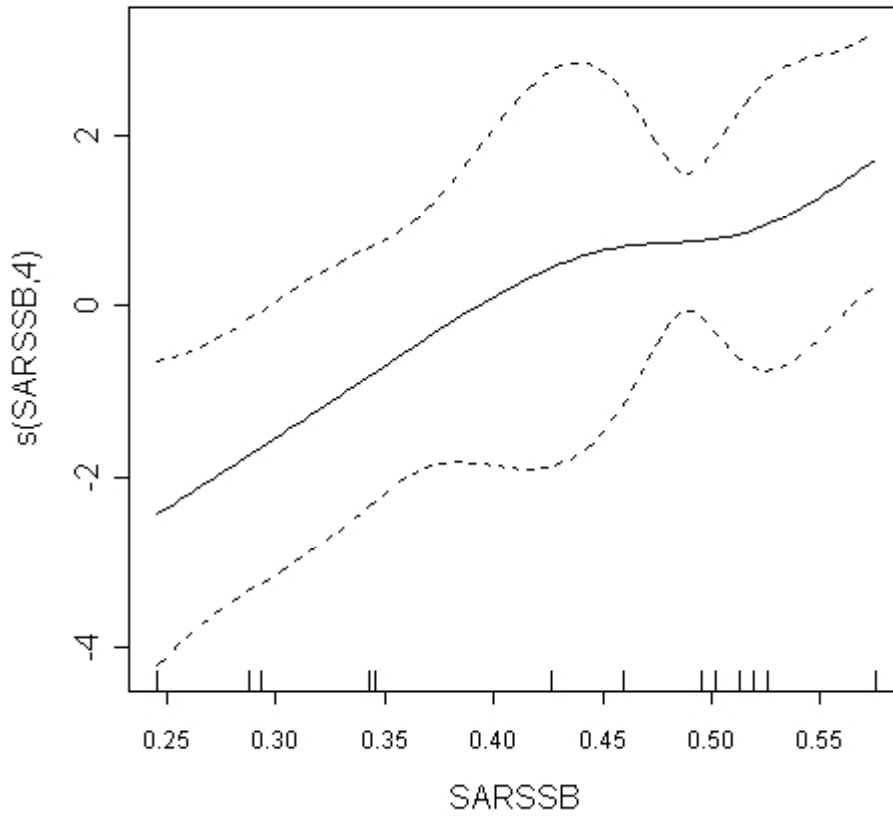
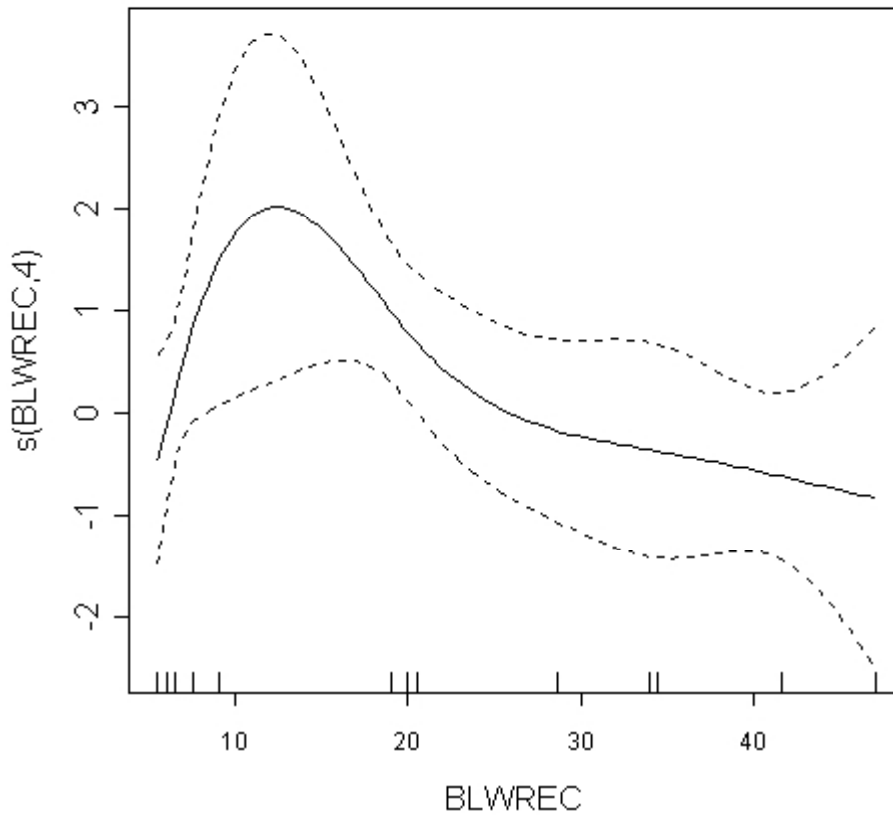


Figure 11. Smoother for GAM fitted to weight of sardine in stomach contents (by-catch data set), for effect of blue whiting recruitment.



The southeast Bering Sea shelf was relatively warm between 1999 and 2005, with winter depth-averaged temperatures over the southeastern shelf $3\text{ }^{\circ}\text{C}$ warmer than in the 1990s. Winters since 2000 have had sea ice coverage typically 30–80% less than the climatological average (1972–2000); the retreat of this ice in spring since 2001 was not only earlier, but also more rapid than average (Overland and Stabeno, 2004; Grebmeier et al., 2006). This anomalous warmth has been associated with below-normal sea level pressure (SLP) and. 104 R.D. Brodeur et al. / Progress in Oceanography 77 (2008) 10... The trawl, which had a 26.5 m headrope and 34.1 m footrope with graded mesh (10 cm at the mouth to 3.8 cm in the codend), was towed on the bottom. Fig.