

Spatiotemporal patterns of marine mammal distribution in coastal waters of Galicia, NW Spain

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Abstract The spatial and seasonal distribution of cetaceans and possible links with environmental conditions were studied at the Galician continental shelf. Data were collected between February–August 2001 and June–September 2003 during opportunistic surveys onboard fishing boats. Seven species of cetaceans were identified from 250 sightings of 6,846 individuals. The common dolphin (*Delphinus delphis*) was by far the most frequently sighted and the most widely distributed species. Spatiotemporal trends in cetacean distribution and abundance, and their relationships with environmental parameters (sea depth, SST and chlorophyll-*a*) were quantified using generalised additive models (GAMs). Results for all

cetaceans were essentially the same as for common dolphins alone. Modelling results indicated that the number of common dolphin sightings per unit effort was higher further south. The number of individual common dolphins seen per sighting of this species (i.e. group size) was however higher in the north and west of the study area, higher later in the year and higher in 2001 than in 2003. In contrast, the number of common dolphin calves seen (per sighting of this species) was higher in the south. Models including environmental variables indicated larger common dolphin group sizes in deeper waters and at higher chlorophyll concentrations (i.e. in more productive areas). There was also a positive relationship between survey effort and group size, which is probably an artefact of the tendency of the survey platforms (fishing boats) to spend most time in areas of high fish abundance. Numbers of common dolphin calves per sighting were found to be higher in shallower waters. The results are consistent with common dolphins foraging mainly in deeper waters of the Galician continental shelf, while more southern inshore waters may represent a nursery area.

Keywords Cetaceans sighting · GAMs · GIS · Galician waters

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Introduction

Defining geographical ranges and distribution limits for highly mobile marine species such as cetaceans is

intrinsically difficult. Nevertheless, many studies have shown that the distribution of cetaceans (especially in relation to foraging areas) is linked to environmental features, both physiographic (e.g. water depth) and oceanographic (such as temperature and chlorophyll-*a* (chl-*a*) concentrations) at various scales (e.g. Evans, 1987; Baumgartner et al., 2001; Murase et al., 2002; Tynan et al., 2005; Marubini et al., 2009; Scott et al., 2010). Such relationships may be either direct or indirect. Thus, temperature may have direct and indirect effects on cetacean distribution, for example through its effects on the energetic costs of thermoregulation (MacLeod et al., 2009) and on the distribution of fish, cephalopod and zooplankton prey (Rubín, 1994; Baumgartner, 1997; Davis et al., 1998; Murase et al., 2002; Tynan et al., 2005). As evident from recent interest in defining characteristics of Essential Fish Habitat (e.g. Valavanis, 2008), the distributions of fish and cephalopods have been found to be related to numerous oceanographic and environmental features, including depth (Gil de Sola, 1993), upwelling (Guerra, 1992; Rubín, 1997) and fronts, which create hotspots of primary and secondary production (Rubín, 1994).

The horizontal and vertical mobility of the prey of cetaceans, combined with temporal variability, make it difficult to predict habitat use of cetaceans over small spatial and temporal scales. In general, it is easier to measure environmental parameters accurately than fine-scale prey distribution. According to Torres et al. (2008), environmental parameters can generate better models of cetacean habitat preferences than models derived from prey distribution data, due to the difficulty of accurately measuring the latter at an appropriate scale.

Understanding the relationships between cetacean distribution and environmental factors is necessary to identify cetacean habitat requirements, to predict their distribution and provide insights into their feeding habits. In turn, this provides valuable information to underpin conservation measures directed at cetaceans, for example identifying areas suitable for designation as Special Areas of Conservation (as required under the EU 'Habitats Directive', Directive 92/43/EEC, in relation to bottlenose dolphins and harbour porpoises) and mitigating impacts of anthropogenic threats such as naval sonar trials, collisions with ships and fishery by-catch (e.g. Redfern et al., 2006). In addition, implementation of the Ecosystem

Approach to Fisheries Management (EAFM) and the Marine Strategy Framework Directive (MSFD) require collection of data on the status of all ecosystem components, including top predators.

Over the last two decades, most studies on cetacean ecology and conservation in the coastal waters of Galicia (NW Spain), e.g. on interactions with fisheries (López et al., 2003), have been carried out by or based on data and samples provided by the non-governmental organisation Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA, see López et al., 2002). Diets of common and bottlenose dolphins along the Galician coast have been described in several previous studies (e.g. González et al., 1994; Santos et al., 2004, 2007). The most important prey of common dolphins in Galician waters are blue whiting (*Micromesistius poutassou*) and sardine (*Sardina pilchardus*) (Santos et al., 2004) while the most important prey of bottlenose dolphin are blue whiting and hake (*Merluccius merluccius*). The majority of the main prey species of these cetaceans are of high commercial importance in Galician waters. Although there considerable overlap in the diets of the three main cetacean species in these waters (e.g. the generally high importance of blue whiting), dietary differences may reflect different habitat preferences.

Geographical Information Systems (GIS) offer a powerful tool in ecosystem studies, facilitating mapping of species occurrence and abundance in relation to a range of environmental variables, construction of empirical habitat preference models and suggesting hypotheses about mechanisms that determine species distribution (e.g. Meaden & Do Chi, 1996; Sakurai et al., 2000; Eastwood et al., 2001; Wang et al., 2003; Koubbi et al., 2006). Among the statistical tools available for constructing habitat models, Generalised Additive Models (GAMs), first proposed by Hastie & Tibshirani (1990), are particularly appropriate. GAM is a non-parametric generalisation of linear regression, allowing non-normal distributions and non-linear relationships between an independent variable and multiple predictors. In the context of variation of species abundance along ecological gradients, non-linear relationships are more common than linear relationships (Oksanen & Minchin, 2002), while the capability to use non-normal distributions permits the use of presence-absence (binomial) or count (e.g. Poisson or negative binomial) data as

response variables. GAMs have been regularly used to analyse distributions of commercially exploited marine species in relation to geographical and environmental variables (e.g. Swartzman et al., 1992; Daskalov 1999; Bellido et al., 2001; Maravelias & Papaconstantinou, 2003; Valavanis et al., 2008) and there are increasing numbers of applications to marine mammal habitat use (see Redfern et al., 2006 for a review).

A frequent problem in studies of marine mammal distribution is that dedicated surveys are time-consuming and expensive. An alternative is to use opportunistically collected sightings data, e.g. from observers placed on ferries or fishing boats. Clearly, this tends to result in imperfect survey designs, with non-random distribution of survey effort, so that variation in survey effort must be taken into account in the model-building process. In addition, when data are collected by fishery observers, the efficiency of detection of marine mammals is inevitably reduced (especially when the catch is being sampled), and the reliability of absence records may therefore be doubtful.

There are few published studies about marine mammal distribution in Galician waters. López et al. (2004) summarised results on cetacean distribution and relative abundance from opportunistic boat-based surveys in Galician waters during 1998 and 1999. Pierce et al. (2010) reported on spatiotemporal and environmental trends in land-based sightings of cetaceans along the Galician coast and identified some broad-scale relationships between local cetacean occurrence and productivity. However, there have been no similar studies on relationships between at-sea cetacean occurrence and oceanographic parameters (e.g. SST and chl-*a* concentration) in this area.

The present study utilises GIS and statistical modelling to analyse data collected by fishery observers during 2001 and 2003 and aims to (a) describe spatiotemporal (geographical, seasonal, between-year) trends in distribution of different cetacean species in Galician continental shelf waters, (b) test whether relative local abundance is dependent on environmental conditions, specifically, depth, SST and chl-*a* concentration, (c) for the most common cetacean species (common dolphin), to identify potential ‘nursery areas’ (i.e. where calves were present) and determine their characteristics.

Methodology

Study area

Galicia (NW Spain) has a coastline of about 1,200 km (Fig. 1). It has a relatively narrow continental shelf with a total surface area of approximately 15,000 km² (Fariña et al., 1997). The Galician continental shelf and the Galician rías (coastal fjords according to Vidal-Romaní, 1984) lie at the northern edge of one of the major upwelling areas in the world, the eastern boundary system off NW Africa and SW Europe (Wooster et al., 1976). The frequent upwelling of cold and dense North Atlantic Central Water (NACW) results in nutrient enrichment of the area (Blanton et al., 1984) and this area is among the most productive oceanic regions of the world. Upwelling reaches its highest intensity during summer (April to September) (Fraga, 1981; Prego & Bao, 1997). Up to 300 species of fish (Solórzano et al., 1988) and around 80 species of cephalopods (Guerra, 1992) have been recorded in Galician coastal waters. The area constitutes an important nursery ground for several commercially important fish species, e.g. hake, *Merluccius merluccius* (Pereiro et al., 1980; Fariña et al., 1985). The broad-scale distribution of fish assemblages over the continental shelf area is mainly determined by depth and hydrographic structure and, in general, density, biomass and species richness all decrease with increasing depth (Fariña et al., 1997), reflecting the general phenomenon that species with more restricted depth ranges tend to occur in the shallowest waters (Smith & Brown, 2002). Galician waters are also an important area for marine mammals, including 16 cetacean and four pinniped species. Resident cetaceans in Galicia include the common dolphin (*Delphinus delphis*), the bottlenose dolphin (*Tursiops truncatus*) and the harbour porpoise (*Phocoena phocoena*). These three species are seen all along the Galician coast, although with different geographical patterns of local abundance (López et al., 2004; Pierce et al., 2010), and are listed as vulnerable in Spain’s National Endangered Species Act (Cañadas et al., 2002).

Data collection and processing

Cetacean sightings data were collected from Galician coastal waters by four observers on-board a total of

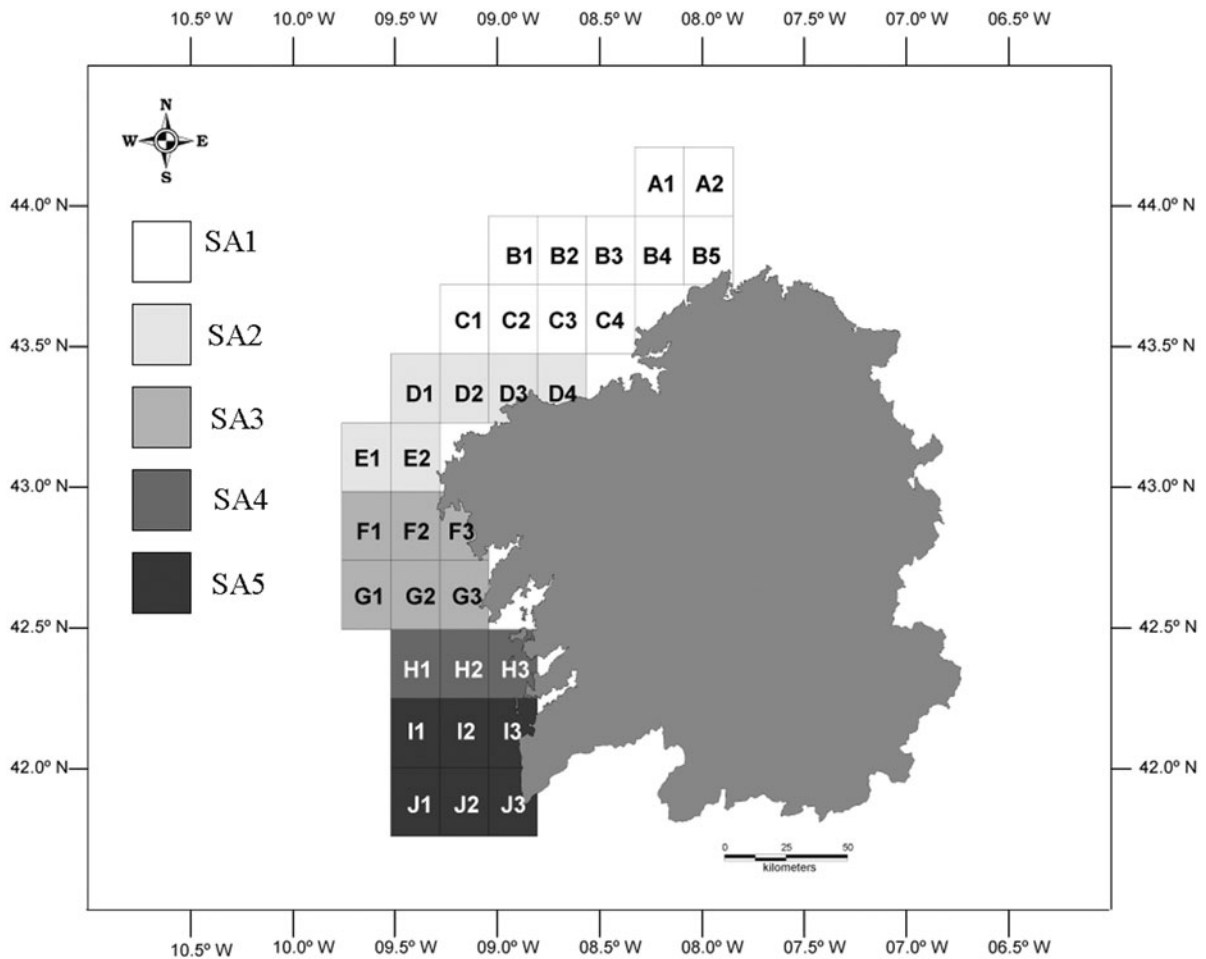


Fig. 1 Map of Galicia and its coastal waters, showing the grid system used (32 cells, from with A1 and A2 in the north to J1... J3 in the south). The five sub-areas are identified by differing shading (north to south: SA1, SA2, SA3, SA4 and SA5)

16 Galician fishing vessels working out of ports all along the Galician coast (between A Guardia in the south and A Coruña in the north), during February–August 2001 and June–September 2003. The survey routes were determined by the primary activity of the fishing vessels (i.e. fishing and travelling to and from fishing grounds).

The observers were responsible for monitoring both fishing activity and presence of cetaceans. All observers had previous experience in detecting and counting cetaceans at sea. While an observer was on-board, vessel location was recorded using a GPS system, every 15 min (providing a set of ‘control points’ and allowing effort to be quantified in terms of 15-min periods) and whenever the boat changed its

route. Cetacean observations were carried out continuously during daylight hours except while catch compositions were being recorded. All cetacean observations involved scanning with the naked eye supplemented by occasional scans with binoculars.

The following data were recorded for each cetacean sighting: location of the fishing vessel, identity (to the lowest possible taxonomic grouping; to species where possible), number of individuals present (the average of minimum and maximum counts of individuals), presence and number of calves and a description of behaviour. Distance and bearing of the cetacean from the boat were not recorded and boat position was therefore used as a proxy for the location of sighted cetaceans. Nevertheless, most sightings are

thought to have been within 1 km of the position of the boat and in any case the final analysis uses a coarser-scale (grid cell) spatial resolution.

The study area was divided into a base-grid of 32 cells of dimensions 14'12" longitude and 14'42" latitude (area approximately 530 km²), which covered the area of Galician coastal waters between latitudes 41° to 45°N and longitudes 7° to 12°W. This grid size was a compromise between the aim of determining environmental relationships and the need to avoid the majority of cells having no sightings (this being a function of the amount of survey effort). A grid-based approach also reduces potential problems with autocorrelation in the data. Five sub-areas were also defined along the north–south axis (Fig. 1). Survey routes and sightings positions data were imported into GIS (MapInfo; Idrisi Taiga). The system used included detailed bathymetry data.

Satellite-derived sea surface temperature (SST) data were sourced from Plymouth Marine Laboratory (Natural Environment Research Council, UK). All level-2 images used in this study were geo-referenced and masked out manually in black for clouds, land and sun-glint. The SST images were from the AVHRR (Advanced Very High Resolution Radiometer) sensor onboard the NOAA satellite series. Satellite-derived images of chl-*a* concentration were from the SeaWiFS (Sea Viewing Wide Field-of-View Sensor) colour sensor. Treatment of SeaWiFS images included application of nearest neighbour interpolation. Raster data were extracted on a standard digital 0–255 colour or grey-scale value for each pixel. Chl-*a* concentration is calculated based to the reflectance ratio between 490 and 555 nm (McClain, 1997). Both satellite sensors provide data with a 1.1 km on-ground resolution in nadir.

The conversion from the standard Digital Number (DN) 0–255 scale integer value stored in the image, to obtain the real-world SST values (°C), used the AVHRR Oceans Pathfinder SST algorithm (Walton, 1988; Walton et al., 1990): $SST = DN \times 0.1 + 5.0$. Conversion from DN to real values of Chl-*a* (mg/m³) used the following equation: $Chl-a = 10^{((0.015 \times DN) + \log_{10}(0.01))}$.

Information on calendar day, depth (m) and associated effort was available for all cetacean observations. In addition, depth (minimum, maximum and average) and total effort were derived for each grid

cell. Satellite-derived data for SST and chl-*a* were available for slightly over half of the sightings records (missing values are due to cloud cover).

Data analysis

Data were analysed at two levels of temporal resolution, by cell over the whole study period and by cell per day. The former provides a coarse-scale view of distribution without the possibility to examine temporal trends but avoids problems of temporal autocorrelation. The latter is potentially more powerful but the daily by-cell sightings data included a very high proportion of zero values, making model fitting difficult and with a high likelihood of significant temporal (or spatial) autocorrelation. In addition, at present, satellite data have not been obtained for all the absence records. Therefore, fine-scale analysis was restricted to an analysis of trends in cetacean abundance among the subset of presence records. Note that a further option for analysing the data would have been to use (15 min) survey legs as the basic unit of data. However, this suffers similar limitations to the by cell by day analysis.

Daily survey effort within a grid cell was estimated from the number of GPS positions recorded within the cell, counting only the 'control point' position records, i.e. those taken at 15-min intervals. To generate summary statistics we expressed total survey effort per cell as a percentage of the total number of control points over the whole study area and period ($N = 2,002$ within the study grid). Thus, a figure of 1% represents approximately 5 h of observation time ($2,002 \times 0.25 \text{ h}/100$).

To provide overall indices of relative abundance, totals for sightings and survey effort were extracted by grid cell, and two measures of sighting rate were derived: sightings per unit effort (SPUE, i.e. number of sightings per 15 min search effort) and individuals per unit effort (IPUE, number of individuals per 15 min search effort).

The environmental characteristics of locations at which each species was seen were summarised: although absolute values may be biased due to uneven distribution of effort, comparisons between species are potentially informative.

Generalised additive models were used to determine environmental relationships for (a) cetacean sightings rate per cell over the study period and

(b) for the subset of cetacean sightings records, variation in numbers of cetaceans (given presence). In the latter case, search effort for the relevant grid cell, day and year combination was used as one of the explanatory variables. Since common dolphins were by far the most frequently recorded species, both analyses were repeated for common dolphin sightings only. Finally, the analysis of numbers given presence was also repeated for common dolphin calves.

Between-cell variation in abundance

The overall cetacean SPUE by cell and common dolphin SPUE by cell were modeled as a function of grid cell location (as northing and easting, i.e. equivalent to latitude and longitude) and average sea depth. Since all three explanatory variables are continuous variables they were fitted as smoothers. SPUE was assumed to be normally distributed and an identity link function was used. The assumption of normality was validated by examining the distribution of model residuals. Separate GAMS were not fitted for any other cetacean species since there were insufficient non-zero records.

Abundance given presence

For this analysis, each sighting was treated as a separate data point, with the response variables being (a) number of cetaceans sighted, (b) number of common dolphins sighted and (c) number of common dolphin calves sighted. The suite of explanatory variables tested was: grid cell location (as northing and easting), year, calendar day, depth, effort (for the cell and day) and satellite image-derived values for SST and chl-*a*. Since some of the available explanatory variables potentially explain the same variation in abundance, three types of models were fitted:

- (1) models with only effort, time and location used as explanatory variables, i.e. models describing spatiotemporal variation in abundance;
- (2) models with environmental variables used in place of the time and location variables, i.e. models to test the proportion of spatiotemporal variation that can be ascribed to environmental conditions;
- (3) models using all available explanatory variables, thus allowing both ‘environmental’ and

‘non-environmental’ components of spatiotemporal patterns to be included (although the latter may of course be a consequence of environmental variables not included in the analysis).

Since SST was significantly correlated with calendar day ($r = 0.69$), we derived residual SST from a Gaussian GAM model of SST in relation to calendar day for use in models which included both calendar day and SST. Thus, the seasonal component of SST variation will be contained within the variable ‘calendar day’ while residual variation in SST is included as a separate explanatory variable. Chl-*a* values showed a complex and non-linear relationship with bathymetry, in that both the highest values and the widest range of values were found in shallow waters. Data on SST and chl-*a* were not available for all sightings, mainly due to high cloud cover on some days. Therefore, for those models which included ‘environmental’ variables, we separately tested use of (i) depth alone and (ii) depth, SST and chl-*a*.

Initial GAM fits using a Poisson distribution for abundance data indicated substantial overdispersion of the response variable. Adult numbers were markedly more overdispersed than those for calves so a negative binomial distribution was used for the former and quasi-Poisson for the latter, in both cases using a log-link function. Abundance of other cetacean species was too low to fit separate models.

For all GAMS, the final model was selected on the basis of the AIC, individual significance of explanatory variables and examination of diagnostic plots (e.g. residual plots, hat values, etc.). To avoid overfitting, the maximum value of k (knots, i.e. a measure of the maximum complexity of the fitted curve) was set at 4 for all explanatory variables. Note that, since we used grid cells as spatial units, there were few unique values of latitude and longitude and higher k values could not have been used for these variables. F tests were used to compare the nested models (Zuur et al., 2007). Significance of smooth terms is reported along with an indication of the estimated degrees of freedom, a measure of the complexity of the curve, where $\text{edf} = 1$ indicates a linear fit and higher values indicate curves. Brodgar software (www.brodgar.com), a menu-based interface for R (R Core Development Team, 2006), was used for fitting GAMS.

Results

Survey effort

Surveys took place during 119 non-consecutive days over 2 years, with observers present on-board Galician fishing vessels during February–August 2001 (85 days) and June–September 2003 (34 days). A total of 136 observer-days at sea was achieved (102 and 34, in 2001 and 2003, respectively), with 2,116 control points acquired over a broad area within Galician coastal waters, 2,002 of which fell within the grid. There was considerable variation in the survey coverage within each grid-square, mainly due to the routes and preferred fishing areas of the fishing

vessels. Grid cell B1 (Fig. 1) was not surveyed during the entire study period but all the other 31 grid cells were surveyed at least once. Total survey effort within the grid was $2,002 \times 0.25 \text{ h} = 500.5 \text{ h}$, with effort per grid cell ranging from 0.25 h (0.05% of the total) to 69.2 h (13.84%) (Fig. 2). Most effort (40.6% of the total) was recorded in sub-area SA5, i.e. the southernmost area. The mean number of grid cells surveyed per day was 4 (SD = 2.34, range 1–11).

Cetacean diversity, abundance and distribution

In total, there were 250 cetacean sightings, comprising 6,846 individuals belonging to at least seven species (Table 1). The common dolphin (*Delphinus*

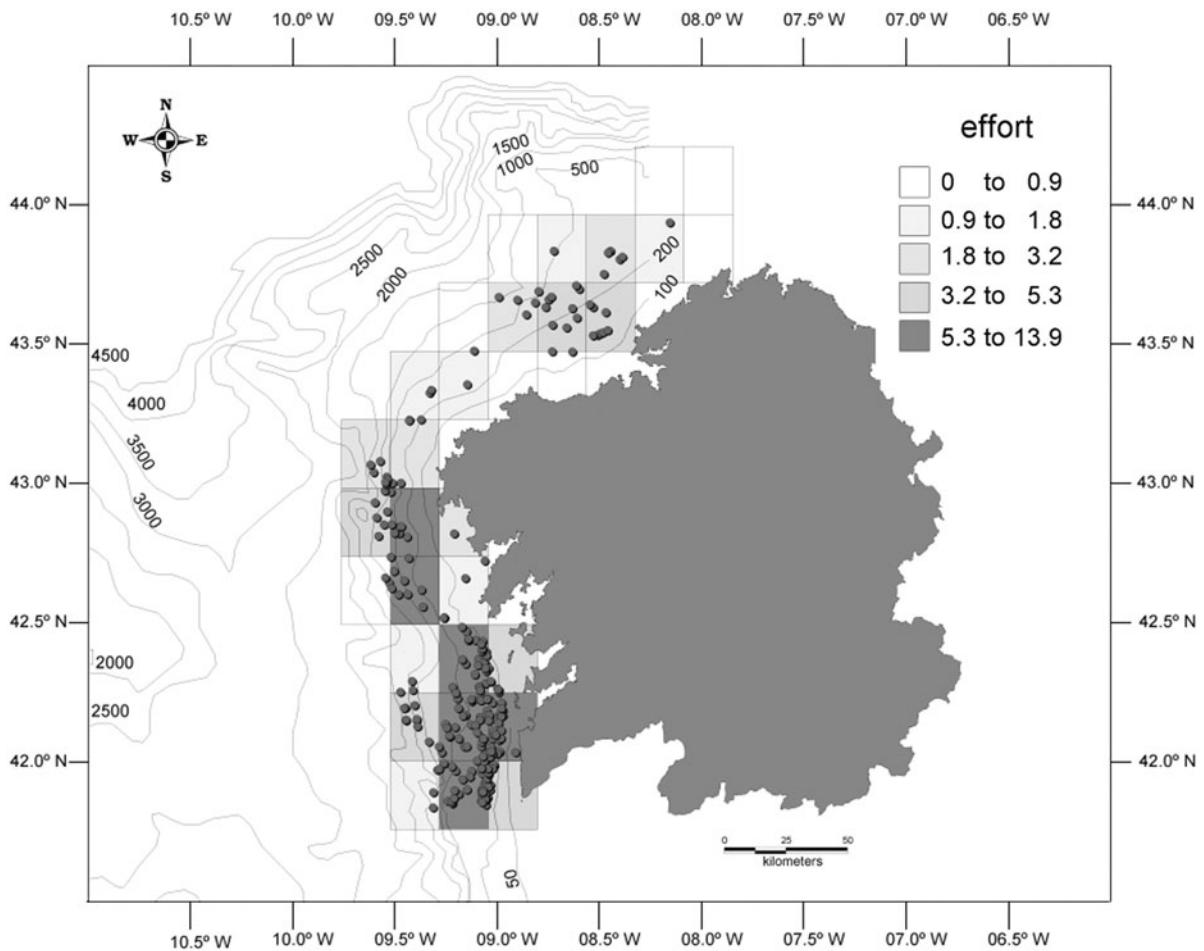


Fig. 2 Cetacean distribution (sightings locations) in relation to survey effort by grid cell. Here survey effort is expressed as a percentage of the total, with 1% point being equivalent to

approximately 5 h of observation (see text). Also shown are bathymetry contours (50, 100, 200, 500, 1000, ... 4500 m)

Table 1 Number of cetaceans recorded during surveys, by species: number of sightings, sums of minimum, maximum and mean counts, total number of groups seen and mean group size

Species	Sightings	Minimum	Maximum	Mean	Number of groups	Mean group size
<i>Delphinus delphis</i>	205	5410	7368	6389	252	25.4
<i>Globicephala melas</i>	13	208	265	236.5	20	11.8
<i>Tursiops truncatus</i>	7	69	90	79.5	9	8.8
<i>Grampus griseus</i>	6	61	86	73.5	6	12.3
<i>Phocoena phocoena</i>	5	8	8	8	5	1.6
<i>Stenella coeruleoalba</i>	4	25	30	27.5	4	6.9
<i>Balaenoptera physalis</i>	1	1	1	1	1	1
Unidentified mysticeti	5	6	6	6	5	1.2
Unidentified delphinid	2	18	25	21.5	2	10.8

delphis) was by far the most frequently sighted species (205 sightings, 82.4% of the all-species total). The other species recorded were long-finned pilot whale (*Globicephala melas*) (13 sightings), bottlenose dolphin (*Tursiops truncatus*) (9), Risso's dolphin (*Grampus griseus*) (6), harbour porpoise (*Phocoena phocoena*) (5), striped dolphin (*Stenella coeruleoalba*) (4) and fin whale (*Balaenoptera physalis*) (1). In addition, there were two sightings of unidentified Delphinidae and five sightings of unidentified mysticetes. For further analysis, the unidentified mysticetes and the fin whale were grouped as mysticetes.

Delphinus delphis was also the most abundant species in the study area, accounting for 93.3% of individual cetaceans seen. *G. melas* was the second most abundant species (3.5%), followed by *T. truncatus* (1.3%) and *G. griseus* (1.1%). Common dolphins tended to be seen in large groups while mysticetes were seen alone or in very small groups.

Calves were recorded during 60 sightings (24% of the total), with numbers ranging from 1 (21 sightings) to 18 (1 sighting) individuals. Calves of five species were recorded: *D. delphis* (158 individuals from 48 sightings), *G. melas* (18 individuals, 8 sightings); *T. truncatus* (2 individuals, 2 sightings); *G. griseus* (2 individuals, 1 sighting) *P. phocoena* (1 individual, 1 sighting).

Two sightings of *T. truncatus* were outside the pre-defined study area and therefore excluded from further analysis. Of the remaining 248 sightings, the highest percentages were recorded in sub-areas SA5 (40.6% of sightings) and SA3 (20.2%, Fig. 2). Most sightings in

SA5 occurred between the 100 and 200 m isobaths although further north there appear to be fewer sightings in such shallow waters. Taking into account survey effort, overall the sightings rate (SPUE) per grid cell was generally higher in the south (Fig. 3) while the spatial pattern in abundance (IPUE) is less clear (Fig. 4). The highest values of both SPUE (0.24) and IPUE (10.86) were seen in SA5.

Delphinus delphis was the most widely distributed cetacean and was present in all sub-areas, although over half of the sightings (51.3%) were in SA5 (Fig. 5), *G. melas* was present all along the coast but mostly seen in SA3 and SA1 (38.5 and 30.8%, respectively) and generally not close to the shore (Fig. 6). For the other species, the small number of sightings precludes any firm conclusions about distribution, although *T. truncatus* was most often sighted in SA5 (40%) and *P. phocoena* was only sighted in SA5.

Delphinus delphis was sighted mainly in May to August, although it should be noted that the months June to August were the only months sampled in both years. The second most frequently sighted species, *G. melas* ($N = 13$) was seen most often in May.

Cetacean distribution and abundance in relation to environmental parameters

Cetacean sightings were recorded in water depths ranging from 7–1,432 m. The majority of *D. delphis* sightings were in waters of less than 200 m depth, although it was also the only species sighted in waters over 1,050 m depth (11 out of 205 sightings). Once

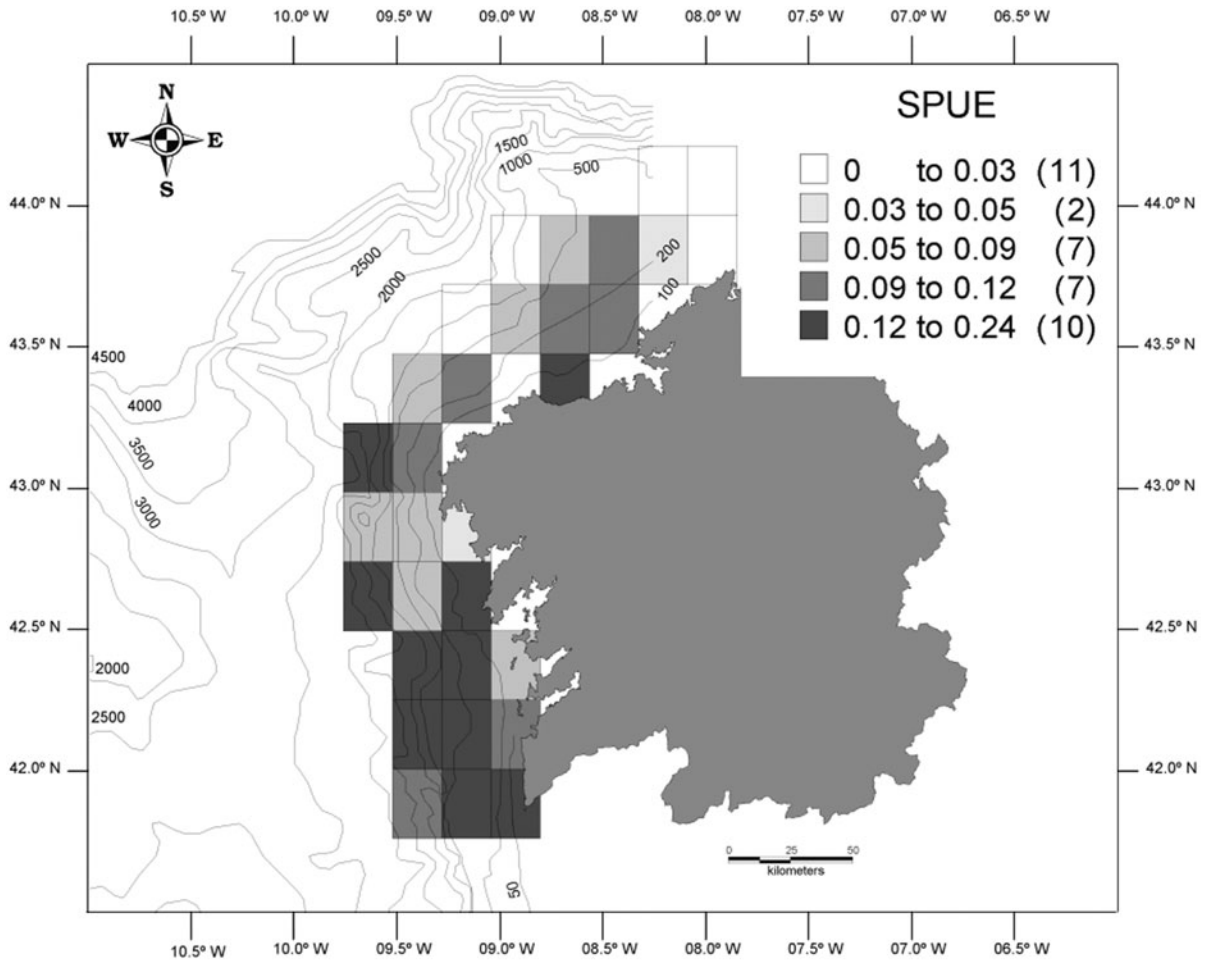


Fig. 3 SPUE per grid cell, SPUE being the number of cetacean sightings events per 15-min track segment, over the whole study period

survey effort was taken into account, it became apparent that this species was relatively more abundant (higher SPUE) in deeper waters (Table 2). *D. delphis* was seen in areas with SST ranging from 14.8–21.5°C, with most sightings in waters of 18–19°C.

Globicephala melas was seen in waters of up to approximately 900 m depth, with only 2 out of 13 sightings in waters of less than 200 m depth. Maximum SPUE was in the depth range 200–500 m (Table 2). For all other species, there were fewer than 10 sightings and results on depth distribution should thus be treated with caution. *T. truncatus* was seen in both shallow (<200 m) and deep (>800 m) waters, *S. coeruleoalba* was seen over water depths of up to 940 m and *G. griseus* over depths of up to 470 m.

Both *P. phocoena* and *Mysticetes* were seen only in waters of <200 m depth.

Models of distribution and abundance

Distribution of sightings

Average all-species SPUE per cell was related to latitude (edf = 1, $P < 0.0001$), with a linear decline in sightings rate further north. Once latitude was included in the model, depth and longitude had no significant effects and were therefore excluded from the final model. The model explained 41.6% of deviance. The final model for common dolphin SPUE also included only latitude (edf = 1, $P = 0.0002$) and explained 38.3% of deviation ($N = 31$). It

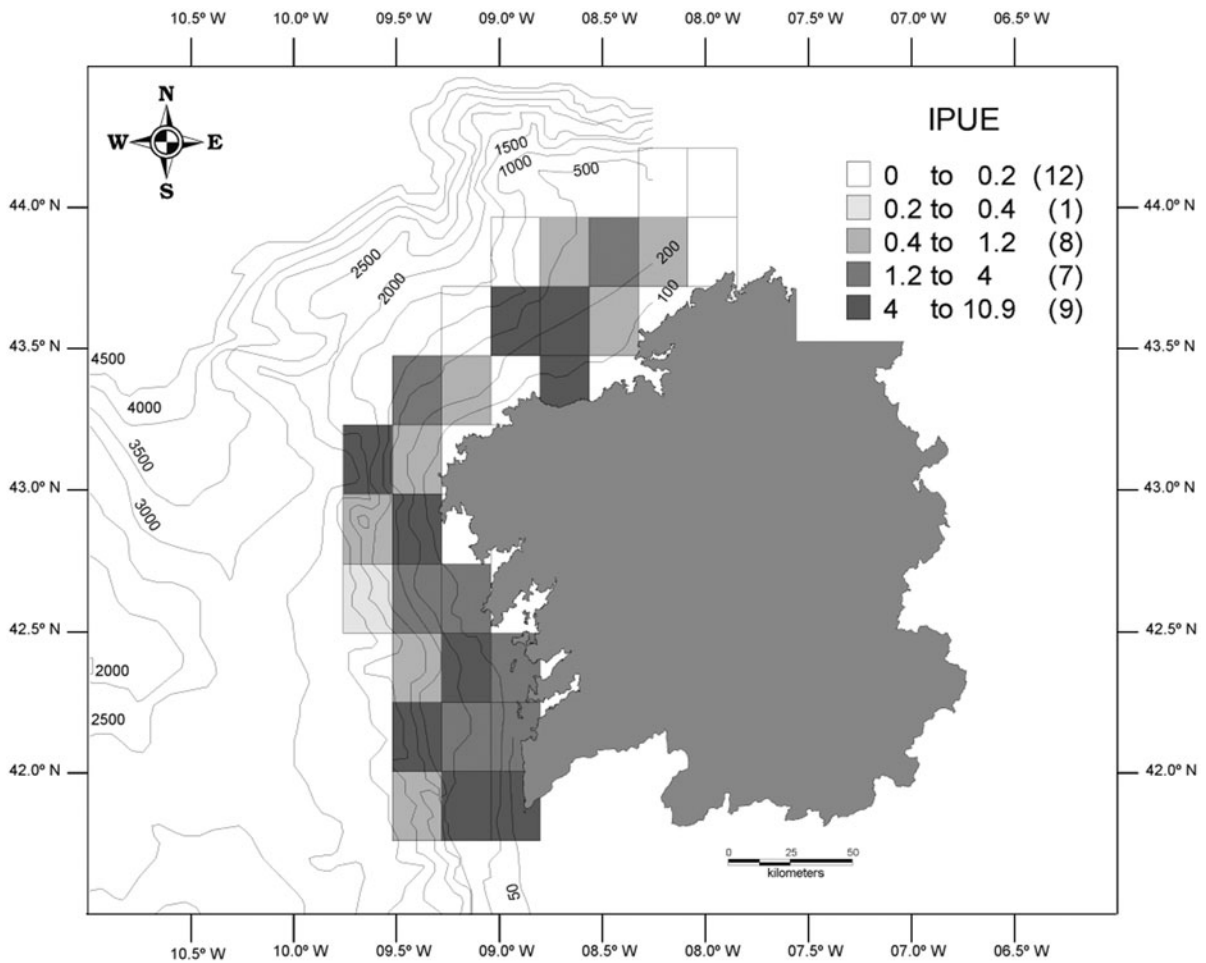


Fig. 4 IPUE per grid cell, IPUE being the number of individual cetaceans sighted per 15-min track segment, over the whole study period

indicated a similar trend of lower SPUE further north. Examination of diagnostic plots indicated no important patterns in residuals, which were approximately normally distributed.

Abundance variation in space and time and in relation to survey effort

The best (negative binomial GAM) model for spatial, temporal and effort-related patterns in the number of cetaceans sighted (when sightings took place) included all five explanatory variables. The trends were for higher numbers per sighting in the north (latitude, $\text{edf} = 1.38$, $P = 0.1182$) and west (longitude, $\text{edf} = 2.78$, $P = 0.0593$) of the study area, higher numbers later in the year ($\text{edf} = 2.71$, $P < 0.0001$),

lower numbers where survey effort was lowest ($\text{edf} = 2.46$, $P = 0.0002$, Fig. 7) and higher numbers in 2001 than in 2003 ($P = 0.0022$). Although individual effects of latitude and longitude were not statistically significant, removing either of them resulted in a significantly poorer fit; the reduction in goodness of fit from removing latitude ($F = 5.21$, $P = 0.0061$) was greater than that resulting from removing longitude ($F = 3.49$, $P = 0.0374$). An apparent trend for lower numbers at the highest levels of effort cannot be confirmed due to the very wide confidence limits in this part of parameter space. Overall this model explained 19.4% of deviance ($N = 248$).

The best (negative binomial GAM) model for spatial, temporal and effort-related patterns in the number of common dolphins sighted, when sightings

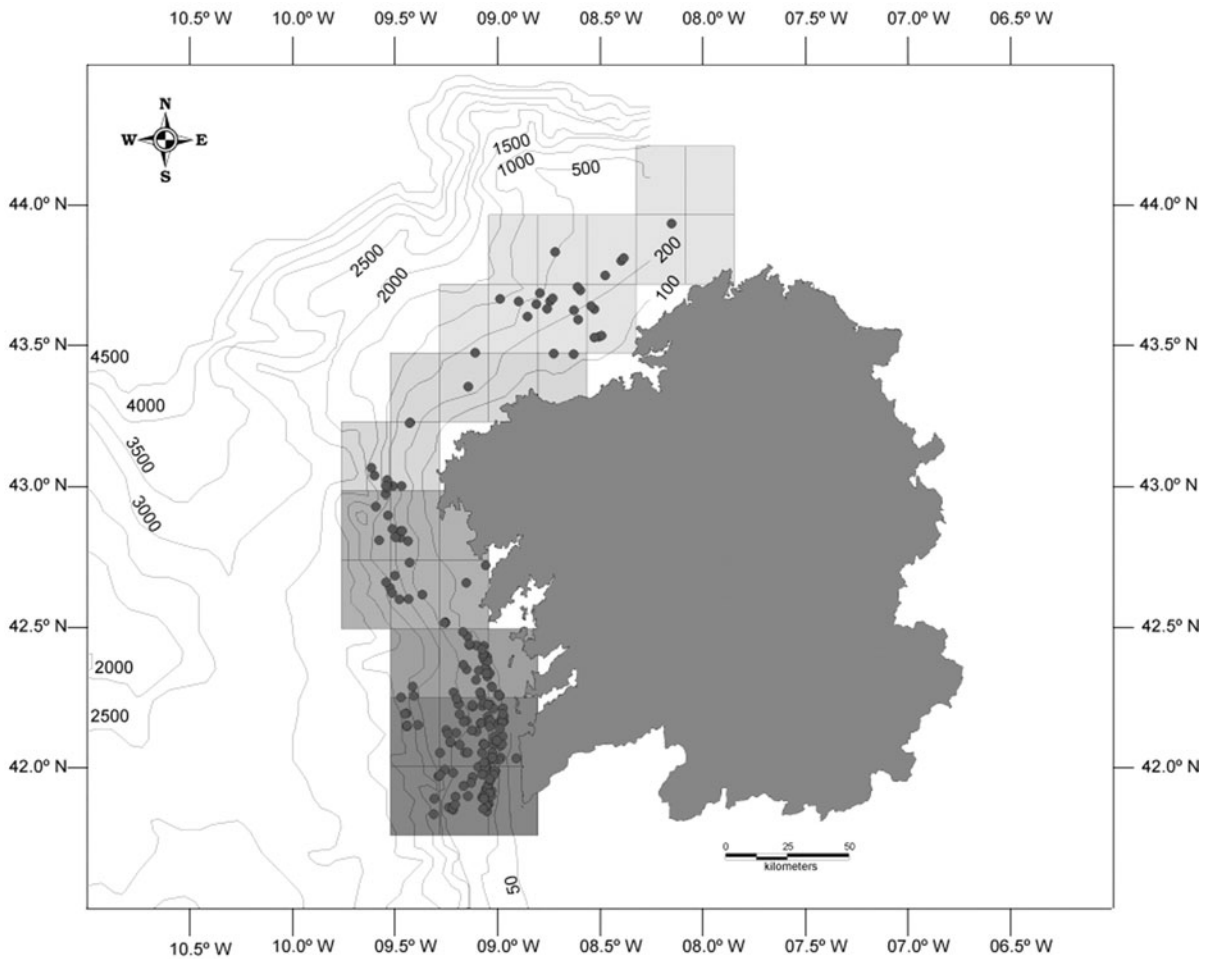


Fig. 5 Locations of *Delphinus delphis* sightings. Shading indicates different sub-areas

took place, also included all five explanatory variables. As seen for the all-species model, trends were for higher numbers in the north (edf = 1, $P = 0.0287$) and west (edf = 2.73, $P = 0.0576$) of the study area, higher numbers later in the year (edf = 2.71, $P = 0.0025$), lower numbers where survey effort was lowest (edf = 2.345, $P = 0.0001$; see Fig. 8) and higher numbers in 2001 than in 2003 ($P = 0.0017$). Overall the model explained 19.9% of deviance ($N = 205$).

The best (quasi-Poisson GAM) model for spatial, temporal and effort-related patterns in the number of common dolphin calves sighted, when sightings of this species took place, included effects of latitude (edf = 2.79, $P = 0.0002$), calendar day (edf = 2.71, $P = 0.0393$) and year ($P = 0.0069$). The trends were for more calves to be seen in the south of the study

area (the opposite to the trend for total numbers of common dolphins), more towards the end of the year (Fig. 9) and more in 2001 than in 2003. Effects of longitude and effort were not significant and were dropped from the final model. This model explained 19.1% of deviance ($N = 205$).

Models of environmental effects on local abundance of all cetaceans combined

The best ‘environmental’ model (i.e. excluding direct descriptors of time and location) for numbers of cetaceans seen per sighting contained only the effect of depth (edf = 2.89, $P < 0.0001$). The trend was for numbers sighted to increase over greater water depths, at least up to around the 400 m isobath (Fig. 10a). This model explained 11.9% of deviance

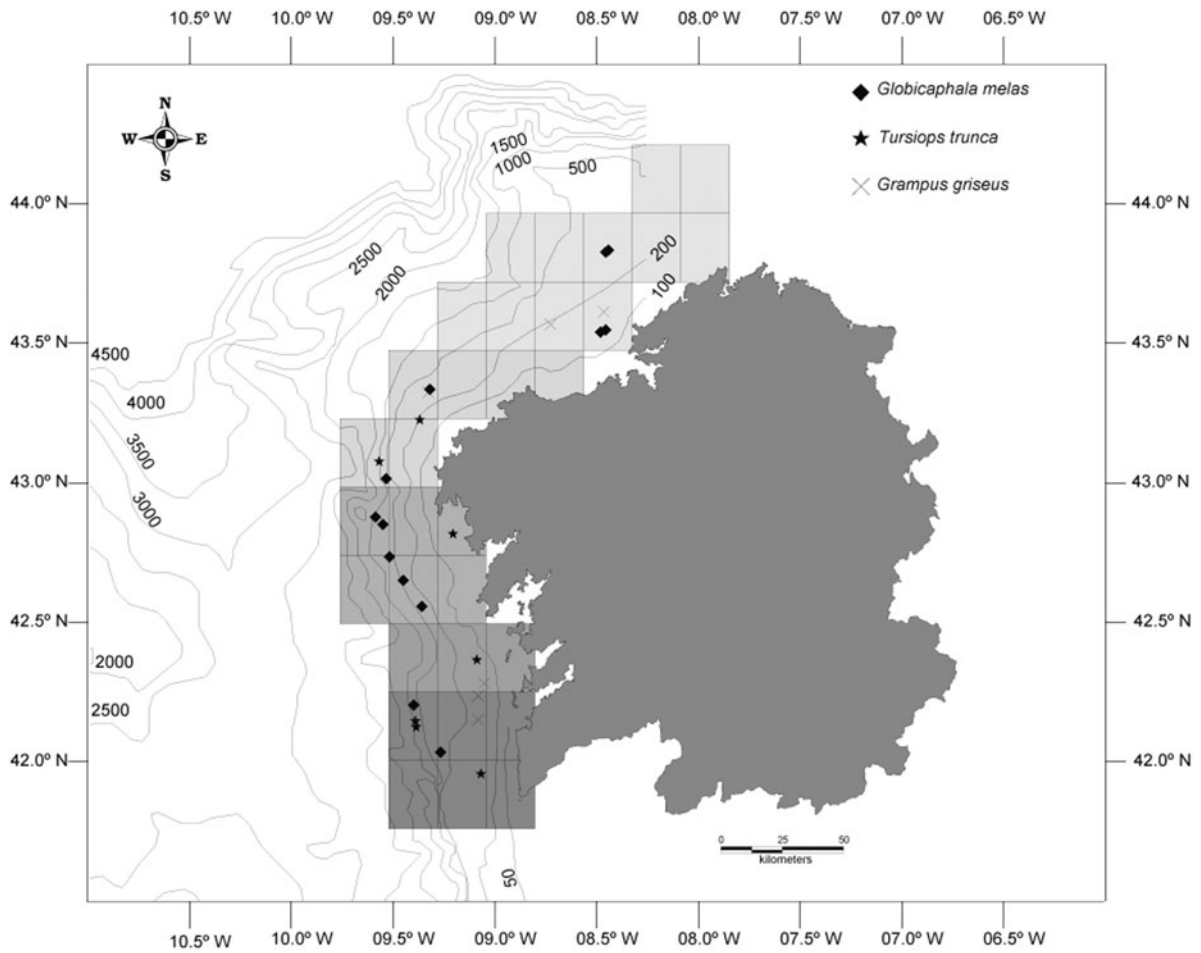


Fig. 6 Locations of sightings of *Globicephala melas*, *Tursiops truncatus* and *Grampus griseus*. Shading indicates different sub-areas

Table 2 Species IPUE per depth interval: mean \pm SD (with sample size, N , in parentheses)

Species	<100 m	101–200 m	201–500 m	501–800 m	>800 m
<i>Balaenoptera physalus</i>	–	0.2 (1)	–	–	–
<i>Delphinus delphis</i>	3.39 \pm 4.82 (21)	4.40 \pm 6.61 (110)	5.87 \pm 6.85 (37)	8.10 \pm 12.20 (16)	6.36 \pm 6.36 (21)
<i>Globicephala melas</i>	–	2.63 \pm 3.00 (2)	3.29 \pm 3.30 (6)	3.01 \pm 0.96 (3)	1.93 \pm 1.12 (2)
<i>Grampus griseus</i>	–	1.74 \pm 1.41 (4)	2.14 \pm 2.06 (2)	–	–
<i>Tursiops truncatus</i>	1.40 (1)	0.82 \pm 0.96 (3)	–	–	1.59 \pm 1.00 (3)
<i>Phocoena phocoena</i>	–	0.30 \pm 0.39 (5)	–	–	–
<i>Stenella coeruleoalba</i>	1.25 (1)	0.90 \pm 0.28 (2)	–	–	0.5 (1)
Unidentified delphinids	–	1.46 \pm 0.47 (2)	–	–	–
Unidentified mysticetes	–	0.14 \pm 0.13 (5)	–	–	–

($N = 248$). Addition of chl-*a* or SST as explanatory variables did not improve this model. When the effect of adding the spatiotemporal explanatory variables

was explored, two alternative ‘best’ models were encountered, which are difficult to compare due to the great difference in sample size. However, common

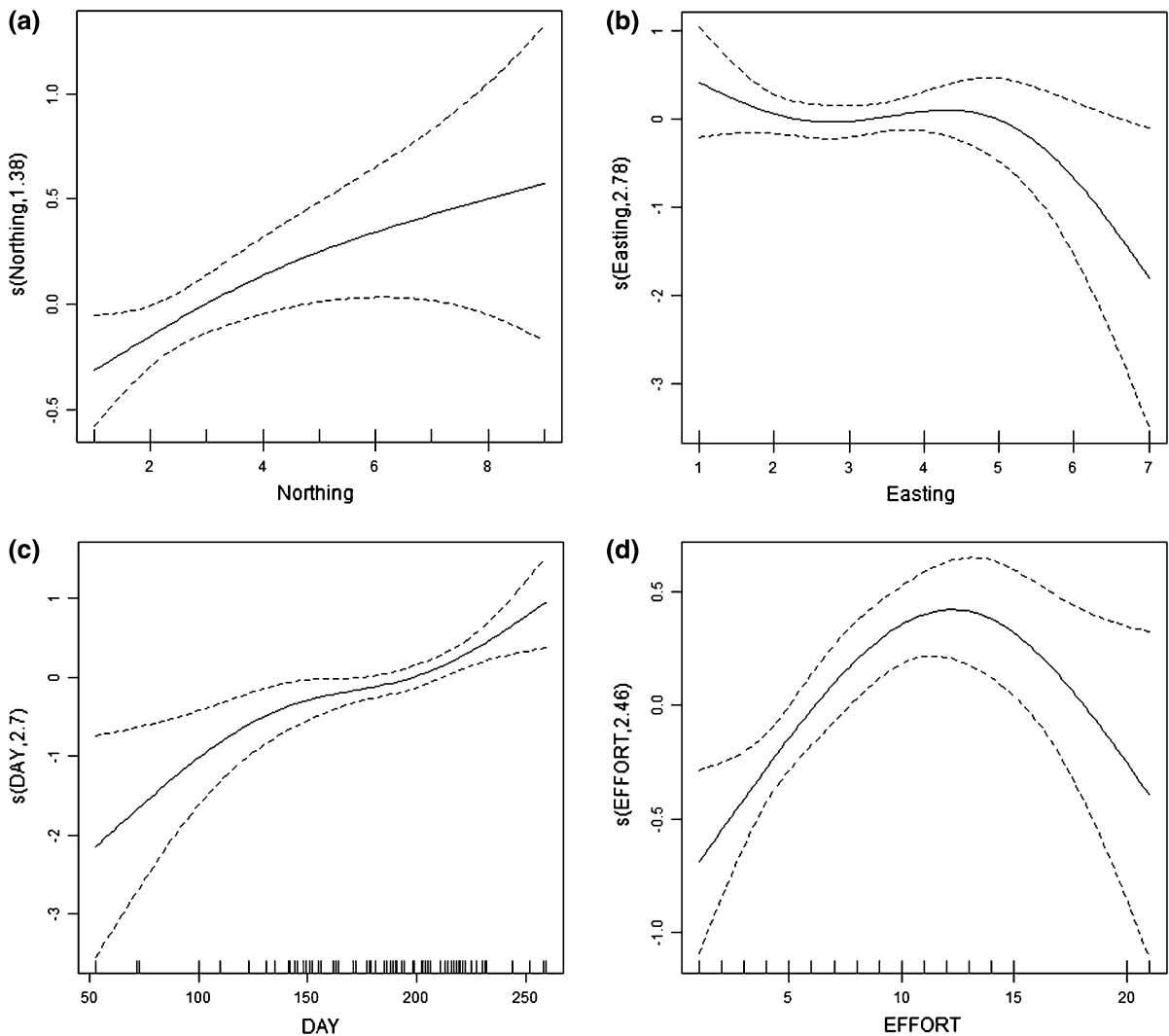


Fig. 7 GAM results: models of cetacean abundance (all spp) given presence: smoothers showing partial effects on number of cetaceans recorded during a sighting, for: **a** latitude (expressed as northing, where 1 is the southernmost grid cell

row), **b** longitude (expressed as easting, where 1 is the westernmost grid cell column), **c** calendar day and **d** search effort (number of control points in the grid cell in which the sighting occurred, on that day)

patterns are apparent in both of these models. The first ‘best’ model (Fig. 10b–d) included positive effects of depth (edf = 1, $P < 0.0001$) and chl-*a* (edf = 1, $P = 0.0220$), higher numbers in 2001 than in 2003 ($P = 0.0114$) and a positive effect of effort (edf = 2.28, $P = 0.0039$) at low effort levels. This model explained 27.2% of deviance but, due to missing values for chl-*a*, had a relatively small sample size ($N = 138$). The second of the ‘best’ models (Fig. 10e–g) also included a positive effect of depth (edf = 2.67, $P = 0.0017$) and a positive effect of effort (edf = 2.28, $P = 0.0036$) at low effort

levels. In addition, numbers were seen to be higher later in the year (edf = 1.93, $P = 0.0009$) and higher in 2001 than in 2003 ($P = 0.0036$). This model explained 19% of deviance ($N = 248$).

Models of environmental effects on local abundance of common dolphins

As for the all-species data, the best environmental model for common dolphin numbers contained only an effect of depth (edf = 2.84, $P < 0.0001$). This effect was positive from the coast to the 400 m

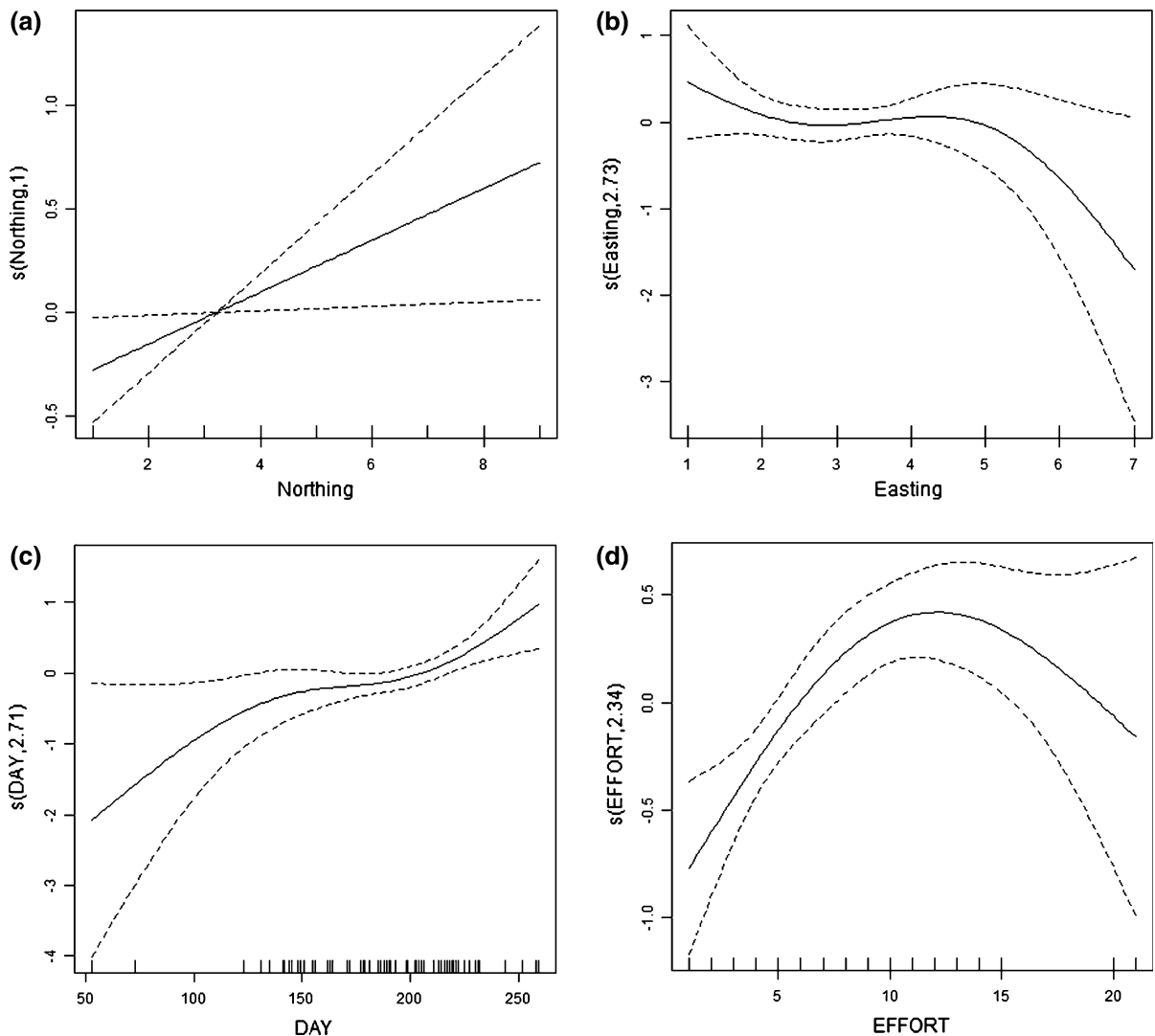


Fig. 8 GAM results: models of common dolphin abundance given presence: smoothers showing partial effects on number of common dolphins recorded during a sighting, for: **a** latitude (expressed as northing, where 1 is the southernmost grid cell

isobath (Fig. 11a) and the model explained 11.9% of deviance ($N = 205$). Again, once spatiotemporal explanatory variables were also considered, two ‘best’ models were obtained. The first model (Fig. 11b–d) explained 18.2% of deviance ($N = 205$) and included effects of depth (edf = 1, $P = 0.0001$), effort (edf = 2.16, $P = 0.0030$), day (edf = 1, $P = 0.0436$) and year ($P = 0.0008$). All effects were essentially as previously described for the equivalent all-species model. The second model (Fig. 11e–g) explained 34.3% of deviance but, again was based on a much smaller sample size ($N = 109$).

row), **b** longitude (expressed as easting, where 1 is the westernmost grid cell column), **c** calendar day and **d** search effort (number of control points in the grid cell in which the sighting occurred, on that day)

The model contained effects of depth (edf = 1, $P < 0.0001$), effort (edf = 2.20, $P = 0.0026$), chl-*a* (edf = 1, $P = 0.0298$) and year ($P = 0.0012$). Again these effects are as previously described for the equivalent all-species model.

The best pure environmental model for common dolphin calf numbers contained only the effect of depth (edf = 2.01, $P = 0.0451$), with most calves seen in the shallowest waters (Fig. 11h). This model explained only 4.13% of deviance ($N = 205$). When spatiotemporal explanatory variables were also considered, depth dropped out and the resulting best

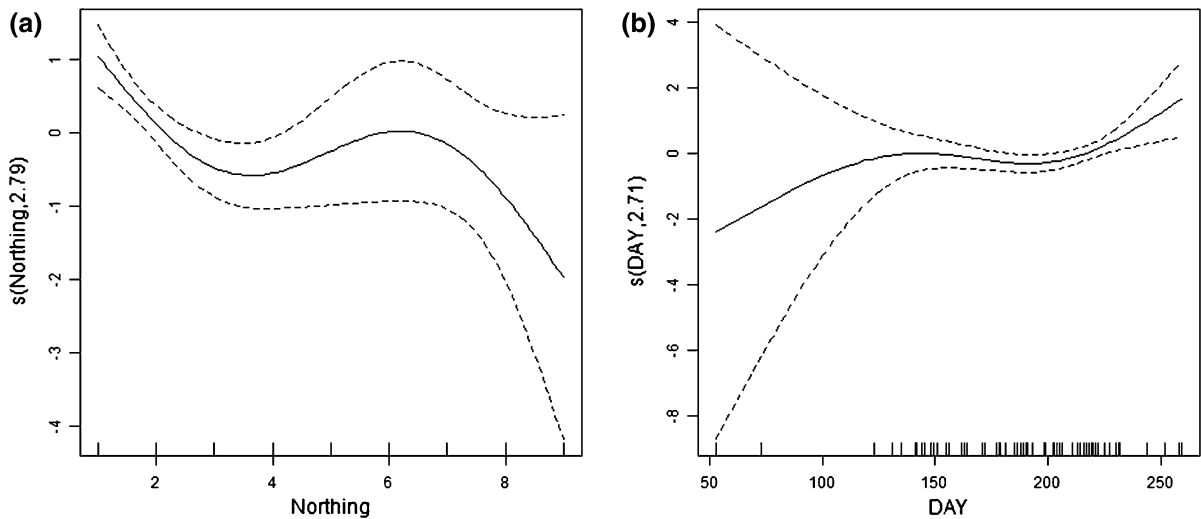


Fig. 9 GAM results: models of common dolphin calf abundance given presence of common dolphins: smoothers showing partial effects on number of calves recorded during a sighting,

model was that obtained originally for spatiotemporal variation in calf abundance (i.e. with latitude, day and year).

Discussion

Of the seven cetacean species that were identified from sightings during this study, *D. delphis* was by far the most frequently sighted. This result is in agreement with previous studies in Galician waters which suggest that common dolphin is the most abundant cetacean in the region (Aguilar, 1997; López et al., 2004). *D. delphis* were observed most frequently in the south of Galicia and in waters of <200 m depth (Fig. 5). Once survey effort was taken into account, there was no relationship between sightings frequency and depth, although a north–south gradient was confirmed, with fewer sightings in the north. However, the number of animals seen per sighting was higher in the north and in deeper waters (which is indicative of larger group sizes). López et al. (2004) previously noted higher abundance of this species in deeper waters off Galicia. This apparent preferential use of deeper waters may relate to foraging preferences. One of the two main prey species, blue whiting, is a shoaling mesopelagic fish which lives in mid-water, mainly over depths of 160–3,000 m—although immature fish are found in

for: **a** latitude (expressed as northing, where 1 is the southernmost grid cell row) and **b** calendar day

shallow water in summer (Wheeler, 1969; Whitehead et al., 1989). Model results also suggested a weak positive effect of chl-*a* concentration on common dolphin abundance (see below for further discussion).

Although the present surveys did not take place all year round, and the trends identified were not strong, modelling results indicate that common dolphin calves were most numerous later in the year and (opposite to the overall geographical trend in numbers of individuals sighted) higher numbers were seen in shallower waters to the south of the study area, suggesting that southern Galician coastal waters could represent a nursery area for this species.

Other cetacean species

Globicephala melas was the second most frequently recorded species in this study and was seen mainly in deeper waters (>200 m). This species is essentially oceanic and is known to dive to 600 m, enabling it to exploit a wide diversity of prey species (Mead & Brownell, 2005). However, it is known to forage occasionally in more coastal waters and coastal cephalopod species appear in its diet (González et al., 1994; M.B. Santos, unpubl. data). Long-finned pilot whales account for around 5% of cetacean strandings along the Galician coast (López et al., 2002).

The bottlenose dolphin is one of two cetacean species (the other being the harbour porpoise) for

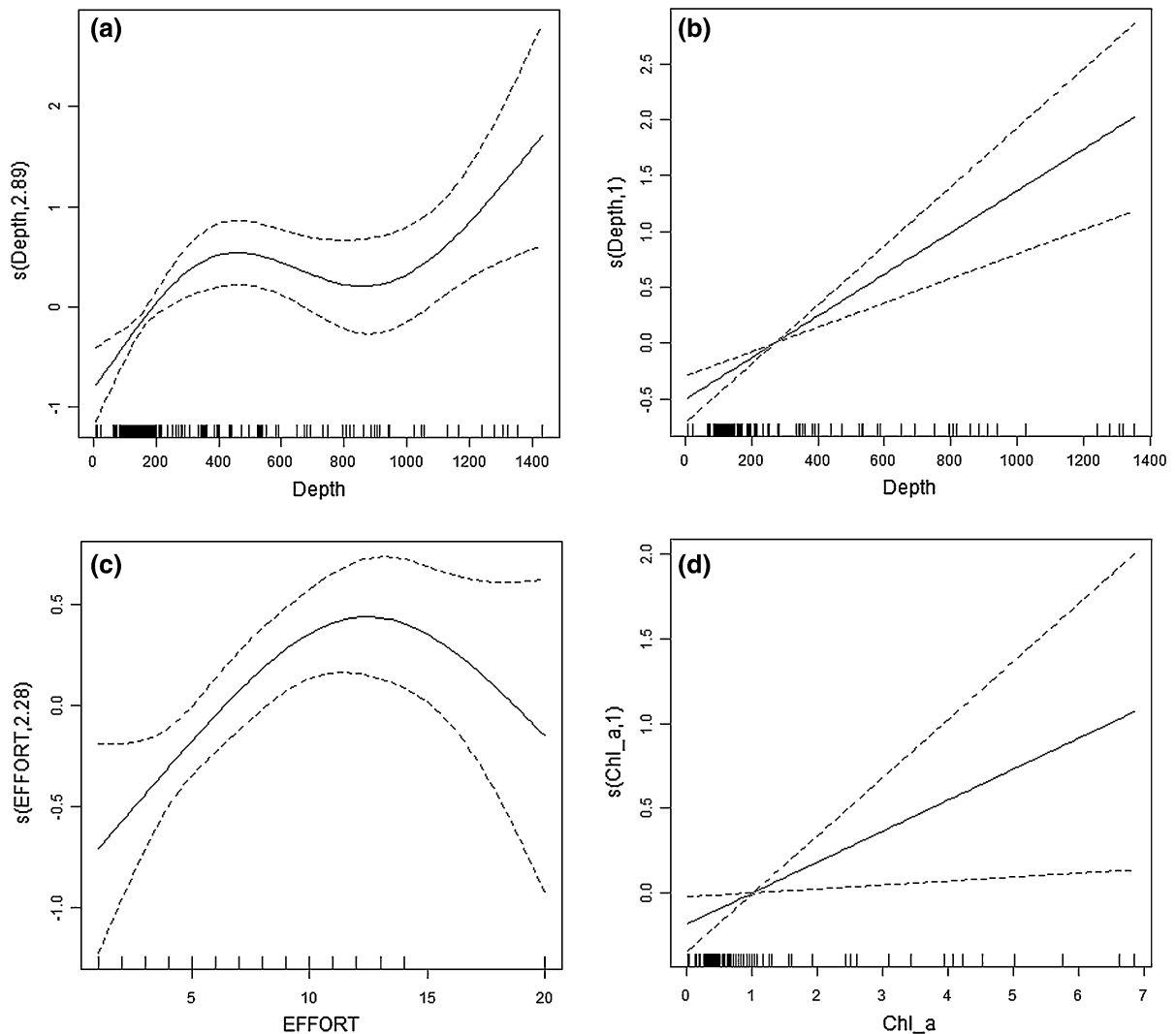


Fig. 10 GAM for numbers of individuals per sighting: environmental model for all spp., **a** effect of depth (in m). ‘Combined’ model 1 for all spp.: effects of **b** depth, **c** effort, **d** chl-*a*. Combined model 2 for all spp.: effects of **e** depth, **f** effort and **g** day

which the EU Habitats Directive requires designation of Special Areas of Conservation. The low frequency of sightings reflects the fact that the study did not extend into the inshore waters of the rias. It is known that *T. truncatus* is present within the platform and inshore waters of the southern part of the study area, including the Ria of Vigo (Fernández-Cordeiro et al., 1996) and this appears to be a resident population. In the past, two hypotheses have been proposed to explain the occurrence of this species in offshore waters: there could be a separate offshore population or members of the resident population may sometimes travel offshore to forage (López et al., 2004).

The most recent evidence, from studies on stable isotopes and microsatellite DNA suggest that animals from the southern rías differ both ecologically and genetically from animals occurring further north and generally in offshore waters (Fernández et al., 2011a, b).

Harbour porpoises in the NW Iberian peninsula appear to be genetically isolated from those in the rest of Europe (Fontaine et al., 2007). These findings have led to increasing interest in the conservation of the species in Galicia. Although coastal sightings and strandings suggest that this is the third most abundant cetacean in coastal waters of Galicia (López et al.,

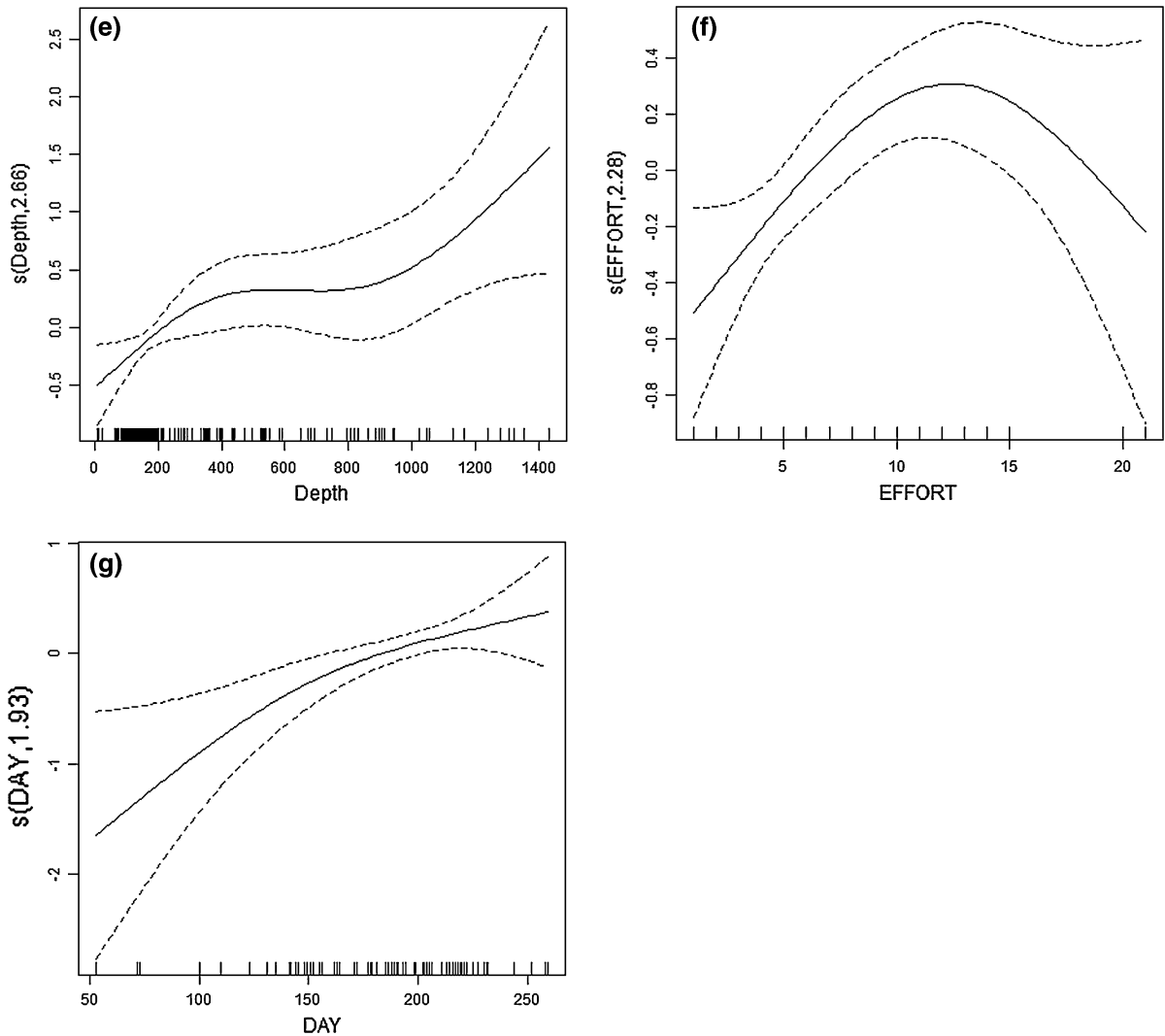


Fig. 10 continued

2002; Pierce et al., 2010), during the present study, individuals of *P. phocoena* were sighted on only five occasions, all in the southern part of the study area, within continental shelf waters (100–200 m depth). It is true that this species is difficult to observe at sea, mainly due to the small body size, the absence of large groups and the relative inconspicuous behaviour of individuals when they are at the surface. However, the infrequency of sightings in the present study is also consistent with results of the boat-based sightings study in 1998–1999 (López et al., 2004) and suggests that at least part of the reason for the contrast between results from strandings and

land-based surveys on the one hand, and at-sea surveys on the other, could be that porpoises are found mainly close to the coast. The main prey species recorded in porpoise stomachs in Galicia are scad (*Trachurus trachurus*), *Trisopterus* spp., garfish (*Belone bellone*) and blue whiting (Pierce et al., 2010; Santos, unpubl. data). Scad occurs near the coast in warmer months of the year but moves to deeper water in winter, while garfish is basically an oceanic species that regularly enters coastal waters. Bib (*Trisopterus luscus*) is the most common member of its genus in Iberian peninsula waters and is a coastal species (Wheeler, 1969).

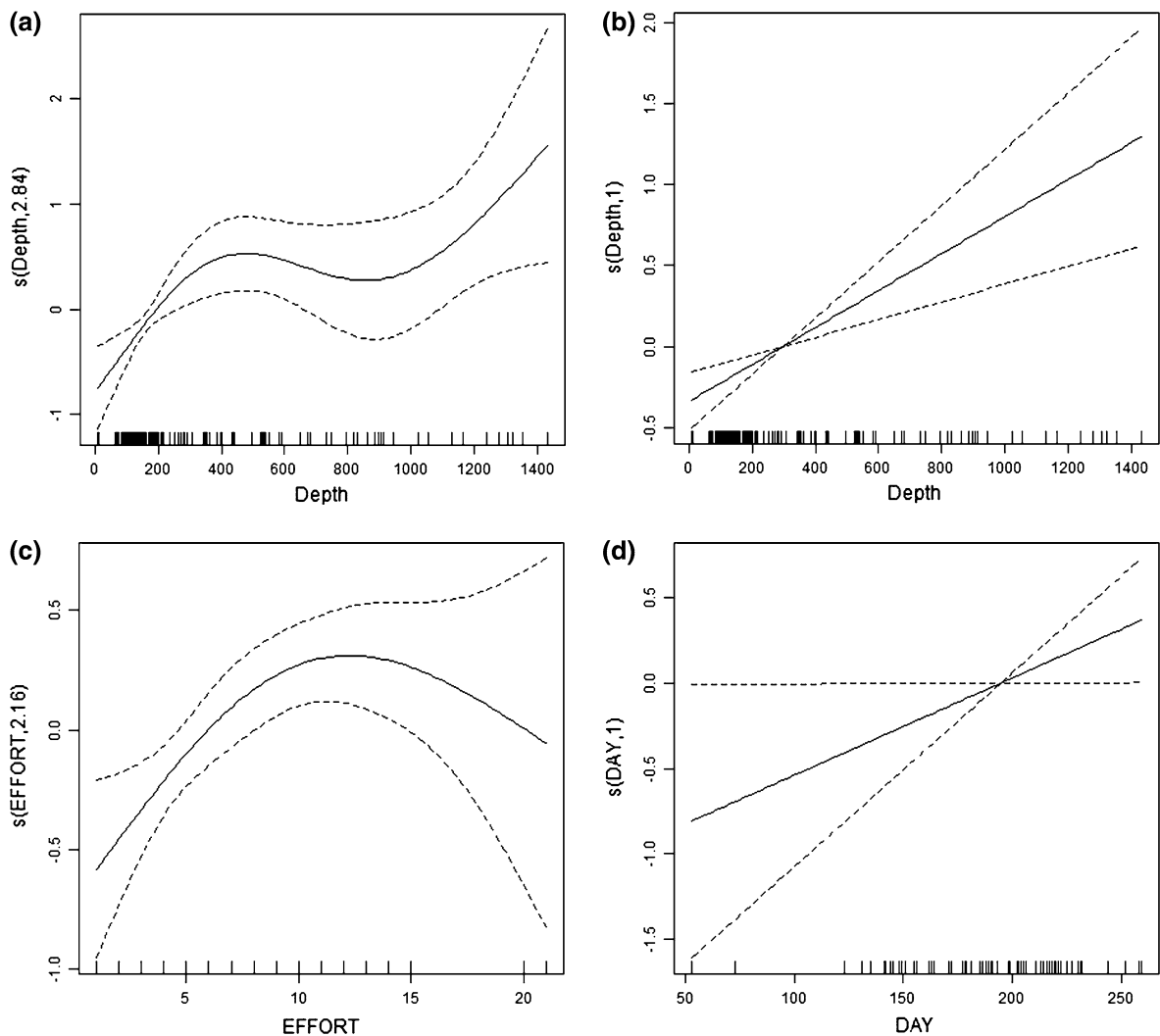


Fig. 11 GAMs for numbers of individual common dolphins per sighting of common dolphins: environmental model for common dolphins: **a** effect of depth. Combined model 1 for common dolphins: effects of **b** depth, **c** effort and **d** day.

Combined model 2 for common dolphins: effects of **e** depth, **f** effort and **g** chl-*a*. Environmental model for calves: **h** effect of depth

The other cetacean species recorded during this study period were *Balaenoptera physalus* (along with several Mysticetes which were not identified to species), *Grampus griseus*, and *Stenella coeruleoalba*. None of these species was sighted frequently and they are probably not abundant in the surveyed area. Data from strandings suggest that *S. coeruleoalba* is the most numerous of the three species (López et al., 2002), although coastal sightings suggest that *G. griseus* is more common (Pierce et al., 2010). In the present study *S. coeruleoalba* was sighted in depths of 100–500 m along both the western and

northern coasts of Galicia. Mysticetes were seen only towards the south of the study area (sub-areas 4 and 5) in waters less than 200 m deep. In the western North Atlantic, fin whales regularly feed over continental shelf waters less than 200 m in depth (Katona et al., 1993). Nevertheless, in Galicia, *B. physalus* probably occurs primarily in offshore waters: it was the most frequently sighted cetacean species in offshore Galician waters during the CODA survey (CODA, 2009) and indeed, historically, was one of the main species taken by Galician whalers (Valdés Hansen, 2010).

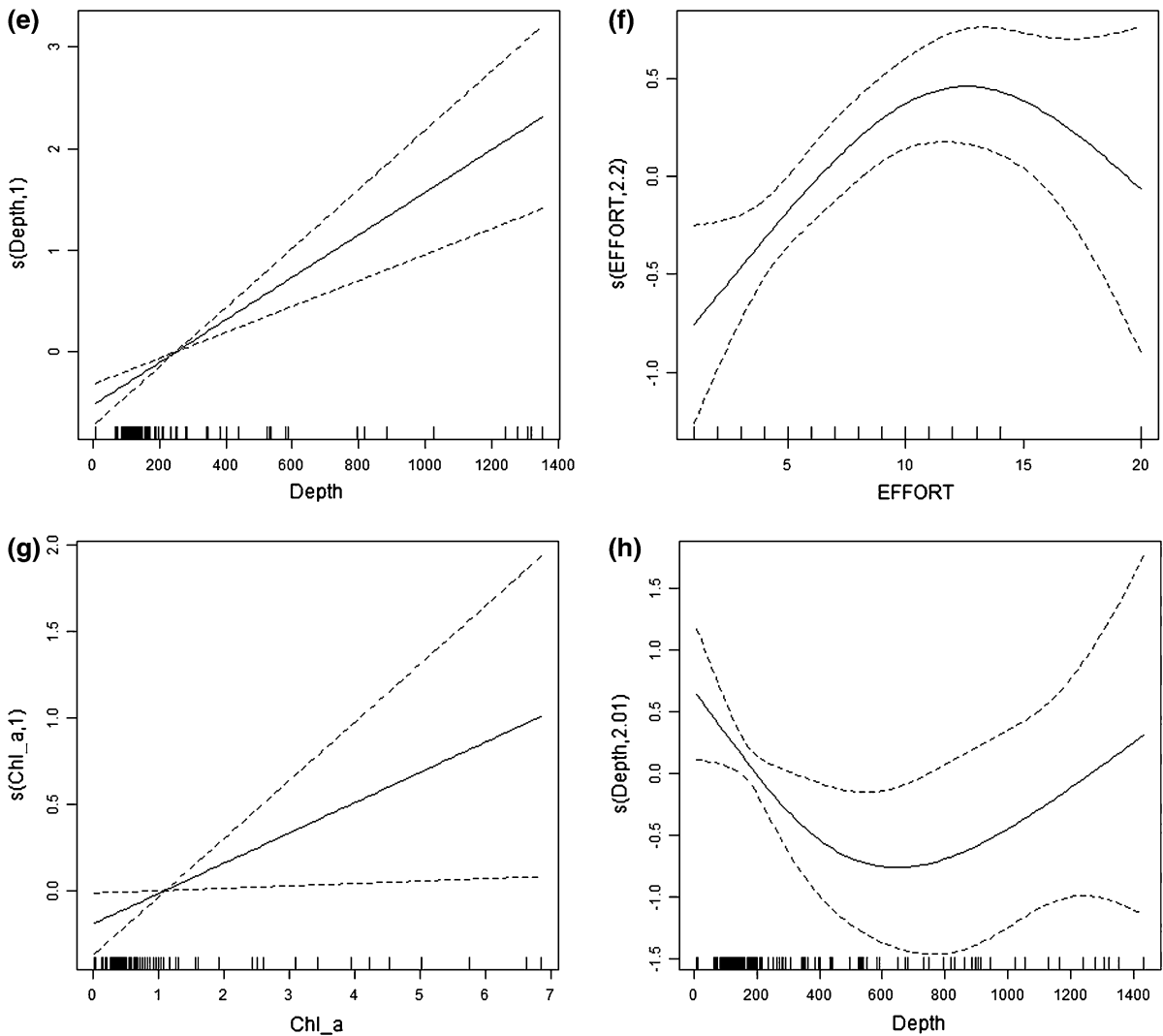


Fig. 11 continued

Environmental relationships

In quantifying environmental relationships it is important to be able to control for variable search effort, especially in opportunistic studies where this is not wholly under the investigator's control. In the present study, there was a trend for numbers of animals sighted (given occurrence of a sighting) to be positively related to search effort in a given grid cell on a given day. The most likely explanation is that, since the study was based on opportunistic use of fishing vessels which, clearly, tend to go to areas of high fish abundance, there was more observer effort in areas where some species of cetaceans are also likely to congregate.

The environmental trends identified in the present study were higher numbers of cetaceans to be seen in deeper waters (except in the case of calves) and in areas of higher chl-*a* concentration. The majority of cetaceans seen were common dolphins and the trends observed thus essentially concern this species; we have insufficient data to determine environmental relationships for the other species. Note also that the analysis concerns the number of cetaceans present per sighting, rather than the presence of cetaceans per se.

Cetaceans are known to actively select habitats with certain measurable and consistent oceanographic qualities (Tynan et al., 2005) and the association (at various scales) of a range of pelagic predator species

in areas of high productivity (including meso-scale fronts and upwelling areas) is well-documented (e.g. Jaquet & Whitehead, 1996; Zainuddin et al., 2006). Thus, the association of higher cetacean numbers with higher chlorophyll concentrations is not unexpected. Higher numbers of common dolphins were seen over deeper waters, although the survey did not extend beyond the shelf waters used by the fishing fleet. Oceanic cetaceans may undertake feeding excursions into coastal waters, congregating in areas where there is high abundance of prey, thus feeding at relatively shallow depths (Katona et al., 1993). This is likely in the Atlantic (western) area of Galician waters, where the effect of coastal upwelling (during April–September) is known to be more intense (Fraga, 1981; Blanton et al., 1984; Castro et al., 1994) and prey availability would be higher than in offshore waters (FAO, 1987; Fariña et al., 1997; Cañadas et al., 2002; Smith & Brown, 2002).

Understanding the spatiotemporal relationships linking oceanographic variables such as SST and chl-*a* to diversity and abundance of cetaceans is not straightforward, e.g. due to questions about the appropriate scale at which relationships will be seen. Hotspots of primary production resulting from oceanographic phenomena are often localised in both space and time. In addition, as pointed out by Grémillet et al. (2008), we tend to forget that top predators do not consume phytoplankton and the relationship between primary production and the presence of cetaceans may involve significant time-lags (e.g. several weeks) and/or spatial displacement (e.g. tens of kilometres) (e.g. Brown & Winn, 1989; Littaye et al., 2004; Walker, 2005). Without good knowledge of local oceanography and current systems and of the ecology of the cetaceans, such relationships can easily be missed. An additional logistical issue associated with fine-scale studies is the availability of cloud-free satellite images for the desired area and time-window.

Although the present study provides some useful preliminary indications of habitat preferences and environmental relationships in Galician cetaceans, further studies on cetacean habitat preferences in the area are needed and would benefit from use of on-board CTD, permitting measurement of additional oceanographic variables and providing the further benefit of allowing whole water column profiles to be constructed (Scott et al., 2010).

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