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Inter-specific and seasonal comparison of the niches occupied by small cetaceans off north-west Iberia

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ABSTRACT

Knowledge of species' ecological niches can be used to assess ecological interactions between different taxa. Sixteen species of cetaceans have been recorded in Galician waters and niche partitioning is expected to occur among these species in order to allow them to co-exist. In this study, the niches occupied by five of the most commonly encountered odontocete species off Galicia (NW Iberia) were compared, based on seven ecogeographic variables, using a PCA-based methodology and Classification trees. Significant differences in niche centres and niche widths were found among all the species. During the summer, the harbour porpoise occupied the narrowest and most differentiated niche when compared to the rest of the species. Three species could be compared during the winter, when long-finned pilot whales preferred colder and less variable water temperatures than did common dolphins. Seasonal differences in habitat preferences were found for bottlenose dolphins. A higher degree of specialisation was found during the summer, resulting in stronger differences in habitat use in this season, which may be related to an increment in resource availability during the upwelling period (April–September). The PCA-based methodology used in this study provides an effective multivariate approach to explore niche partitioning between co-existing species.

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1. Introduction

A species' niche is defined as the n-dimensional hyperspace, formed by relevant niche factors, where a species can occur (Hutchinson, 1957). Generally, species have ecological niches that are distinct enough (e.g. diet, habitat preferences, climatic conditions) to allow species co-existence, i.e., there is niche partitioning. If the niches of two or more species are not sufficiently distinct, it would be expected that competition between species would result in competitive exclusion (i.e. the absence of one species from a specific favourable environments due to the presence of other similar species). As a consequence, a species' fundamental niche (all areas where it can possibly occur) may be wider than its realised niche (Hutchinson, 1957; Phillips et al., 2006). In addition, there may also be seasonal shifts in the niches occupied by individual species. For example, in the marine environment, seasonal differences in temperature and/or productivity can affect cetacean distribution. In turn, modifications in a species' realized niche can result in changes in inter-specific relationships and cascade effects (i.e. Leveque, 1995; Ginger et al., 2003; Myers et al., 2007; Harihar et al., 2011).

Understanding how species interact in terms of their ecological niches is essential for understanding how they will respond to environmental changes and to alterations in the distribution, presence and/or abundance of other species that occur within a local ecosystem. For example, it is thought that common dolphin, *Delphinus delphis*, competitively excludes white-beaked dolphin, *Lagenorhynchus albisrostris*, when local temperatures increase above 13 °C around UK and Irish waters (MacLeod et al., 2008). Therefore, from a management and conservation point of view, knowledge of inter-specific and seasonal differences in species' niches is essential in order to design or improve conservation measures undertaken to protect vulnerable taxa.

Abbreviations: EGVs, Ecogeographic variables; PC, Principal component; CD, Common dolphin; RD, Risso's dolphin; PW, Long-finned pilot whale; HP, Harbour porpoise; BD, Bottlenose dolphins.

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However, few studies examining the habitat preferences and distribution of cetaceans consider how the niches of individual species interact and how competition may influence their occurrence. This is, in part, due to the fact that few existing approaches for examining habitat preferences in cetaceans (primarily based around presence–absence or abundance/density statistical methods applied to single species data sets—see Redfern et al., 2006) are appropriate for comparing specific aspects of the niches occupied by individual species such as the positioning of the niche centre and the level of specialisation (niche width).

Ordination techniques are valuable tools for exploring relationships in community ecology, which typically involve multiple species and habitat variables that may be best analysed simultaneously (Redfern et al., 2006). In this study, we apply an ordination technique (Principal Component Analysis, PCA) to compare two aspects (the niche centre and the niche width) of the niches occupied by sympatric cetacean species, a method that has been recently applied to define and compare species' ecological niches in the eastern tropical Atlantic (e.g. Weir et al., 2012). In addition, in the present paper, classification trees are used to identify intraspecific seasonal differences in habitat preferences for cetaceans in the area. Again, there are few published examples using tree-based models to explore cetacean-habitat relationships or interspecific competition in cetaceans (e.g. Friedlaender et al., 2006, 2009; MacLeod et al., 2007, 2008) and this is the first time that this technique is used to account for seasonal changes in habitat preferences. These approaches have an important advantage over traditional statistical techniques as they do not require reliable absence data (which are often difficult to obtain for cetacean species—MacLeod et al., 2008) in order to compare the niches occupied by different species or in different seasons. As a result, these techniques can be used to analyse sightings databases where information on effort is not available or where data are combined from different data sets which lack comparable measures of survey effort.

We demonstrate these approaches by comparing the niches occupied by cetacean species in the waters of NW Iberia, in relation to seven ecogeographic variables which may help to define the niches occupied by marine mammal species. This area is particularly interesting because regional upwelling enhances primary productivity, mainly between April and September (Fraga, 1981; Prego and Bao, 1997; Figueiras et al., 2002), resulting in a strong seasonality in productivity. This, in turn, may result in differences in niche interactions among species between summer and winter months. For this analysis, we concentrate on the five most commonly-sighted cetacean species in NW Iberian waters (López et al., 2002, 2003, 2004; Pierce et al., 2010). These are common dolphin, bottlenose dolphin, *Tursiops truncatus*, long-finned pilot whale, *Globicephala melas*, harbour porpoise, *Phocoena phocoena* and Risso's dolphin, *Grampus griseus*. If differences in habitat preferences between species do exist, higher productivity would result in a greater level of specialisation (narrower niches) and greater apparent differences between species' niches (less overlap, although most likely with no change in the distances between niche centres). On the other hand, if the species considered have similar habitat preferences (i.e. compete for the same resources), higher productivity may reduce the pressure to maintain separate realised niches hence resulting in smaller differences between niche centres.

Among these species, bottlenose dolphins, common dolphins and harbour porpoises are mainly piscivorous (Santos et al., 2001, 2004, 2007, 2013a; Wells and Scott, 2002; Bjørge and Tolley, 2002; Pusineri et al., 2007) while long-finned pilot whales and Risso's dolphins are, in principle, teuthophagous (González et al., 1994; LeDuc, 2002; Fernández et al., 2009; Santos et al., 2013b). However, several prey categories (e.g. blue whiting, hake) can contribute to the diet of most of these species in the research area (Santos et al., 2007, 2013a, 2013b; Méndez-Fernández et al., 2012) and previous studies found a partial dietary overlap of the foraging niche between harbour porpoises and bottlenose dolphins in the Bay of Biscay (Spitz et al., 2006). These facts suggest the potential for competition for limited resources, which could result in niche partitioning between species.

2. Material and methods

2.1. Study area and surveys

The study area includes shelf and slope waters of N Portugal and NW Spain (Fig. 1). Data on cetacean sightings in this region were obtained from three different types of survey: (1) opportunistic surveys onboard fishing vessels; (2) dedicated cetacean surveys; and (3) oceanographic cruises primarily dedicated to determine pelagic fish abundance by means of acoustic and trawl surveys.

2.1.1. Surveys onboard fishing vessels

During two research periods (1998–1999 and 2001–2003), trained marine mammal observers accompanied commercial fishing vessels that used several different gears and covered a range of ports along the Galician coast ($N=98$ during 1998–1999 and $N=119$ during 2001–2003). Covered routes were determined by the primary activities of the boats. One marine mammal observer was onboard during each trip recording data on presence of cetaceans, fishing haul composition and environmental conditions (e.g. sea state, weather conditions, visibility). Marine mammal observations were carried out continuously except when catch compositions were being recorded. For further details on the protocol followed see López et al. (2004) and Spyrakos et al. (2011).

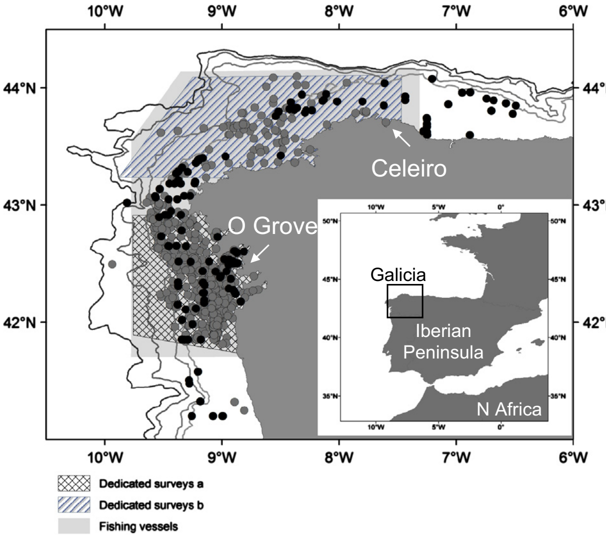

Fig. 1. Map of the study area, Galicia, NW of the Iberian Peninsula. Sighting locations are indicated: Grey circles: summer sightings (May–October). Black circles: winter sightings (November–April). Grey polygon: approximate area covered by fishing vessels, Lined polygon: approximate area where dedicated cetacean surveys onboard Santiago Apóstolo took place, Checkered polygon: approximate area covered by all other dedicated cetacean surveys. Oceanographic cruises covered shelf waters delimited by the map up to the 200 m isobath with occasional prospections over deeper waters. The situation of *O Grove* and *Celeiro* harbours are indicated. Depth contours of −200 m, −1000 m, −2000 m and −2500 m are shown in greyscale.

2.1.2. Dedicated cetacean surveys

Dedicated cetacean surveys have been performed periodically over the Galician shelf by the local NGO CEMMA from April to October since 2003. The present paper includes data recorded between 2003 and 2008. Research tracks were followed onboard the ships "Nauja" (22 m length, $N=68$ surveys), "Íbero" (12 m length, $N=15$ surveys), "Nieves" (32 m length, $N=4$ surveys), "Elda Dos" (6 m length, $N=4$ surveys) and "Black Knight" (17 m length, $N=1$ survey). Cruises started from the base port of O Grove (Fig. 1) on 47 occasions and ended in O Grove 43 times. For the remaining trips, the base port varied and surveys were carried out over Galician shelf waters.

In addition, CEMMA carried out one survey in Galician offshore waters (>100 nm from the coastline) in September 2007 onboard the vessel "Santiago Apóstolo" (33 m). Sightings recorded over the Galician shelf and slope during outward and return journeys to and from the base port of Celeiro (Fig. 1) have been included in the present analysis.

Standard methodology for marine mammal sightings was used (Evans and Hammond, 2004). At least two experienced observers were working at all times recording data on cetacean presence. Periodic scans of the horizon were carried out with naked eyes and with the help of binoculars covering an angle of 90° from the bow to each side of the vessel (total angle of 180°). Environmental conditions were recorded every 30 min. For further details on the protocol followed, see VVAA (2007).

Opportunistic sightings (off-effort due to, for example, bad weather conditions) were available from 27 dedicated trips carried out in 2008 onboard the vessels "Íbero" and "Nauja" and were also included in the present research.

2.1.3. Oceanographic cruises

In 1998, a dedicated marine mammal observer was deployed on 12 occasions onboard the RV 'Cornide de Saavedra' (67 m length), operated by the Instituto Español de Oceanografía, IEO, as part of the annual DEMERSALES trawling survey. Information on cetacean presence was recorded by scanning the horizon periodically with naked eyes and with the help of binoculars. Data on environmental conditions were also recorded. For further details on the protocol followed see López et al. (2004).

Surveys carrying marine mammal observers were conducted by the IEO, in the spring (March–April) of 2007, 2008 and 2009, onboard the RV "Thalassa" (74 m length) as part of the annual PELACUS survey series which aims to monitor and study the distribution and abundance of the main small pelagic fish resources of the northern Iberia shelf using acoustic methods and pelagic trawls. A series of transects perpendicular to the coast and spaced 8 nm apart was followed, covering the continental shelf (up to 200 m depth) from N Portugal to the Cantabrian Sea (N Spain). Occasionally, areas of the continental slope were also surveyed. Two dedicated observers worked simultaneously searching for cetaceans and seabirds within an angle of 180° (90° per observer) ahead of the bow. Observers also recorded information on environmental conditions. A total of 76 survey days was carried out covering Galicia and Cantabrian shelf waters although the effort fell within the research area of interest for the present study only during 41 days (399 transects of around one hour duration). Therefore, only sightings recorded during those 41 days of survey were analysed here. For further details on the protocol followed see Certain et al. (2008).

Data come from a range of different surveys and research projects but in all cases, sightings were recorded during daylight by experienced marine mammal observers. In the present paper, cetacean sighting records during all the above-mentioned surveys were accessible for analysis, although information on effort was only available for the acoustic spring surveys carried out in 2007, 2008 and 2009. On every occasion, GPS (Global Positioning System) coordinates of boat position were used as a proxy of cetacean sighting location. Data were recorded during all sighting conditions, and all positively identified sightings were considered in the analysis regardless of visibility or sea state.

2.2. Ecogeographic variables

Seven ecogeographic variables (EGVs) were used to compare the niches occupied by cetacean species in NW Iberian waters. These include both fixed and dynamic variables. Fixed variables were depth, slope, standard deviation (SD) of slope, and distance to the coast. The dynamic variables used were chlorophyll (Chl-a) concentration, Sea Surface Temperature (SST) and SD of SST.

A grid of 1 km resolution of "distances to the coast" (Euclidean distances) was created based on a Universal Transverse Mercator (UTM) projection of the European coastline file provided by the General Bathymetric Chart of the Oceans (http://www.gebco.net/) centred in our study area using ArcGIS (ESRI) Spatial Analyst tools. A depth grid of one arc-minute (approximately 1 km) resolution was obtained from the General Bathymetric Chart of the Oceans. This depth grid was converted into a 1 km depth grid using ArcInfo (ESRI) with an appropriate UTM projection before it was used to derive slope using the surface analysis tools within the Spatial Analyst extension for ArcGIS 9.2. A grid of SD of slope was calculated based on the slope grid and using a 5 by 5 cell square centred on an individual grid cell, applying neighbourhood statistics within the Spatial Analyst extension of ArcGIS 9.2.

Monthly SST (°C) and Chl-a (mg/m^3) data were obtained as monthly composites from the NASA OCEANCOLOR website (http://oceancolor.gsfc.nasa.gov) for MODIS 4 km SST and Chl-a (July 2002 onwards) and for SeaWiFs 9 km Chl-a (January 1998–July 2002). The tool DLR EOWEB-NG (https://centaurus.caf.dlr.de:8443/) was used to obtain 1.4 km Advanced Very High Resolution Radiometer (AVHRR) SST monthly composites (January 1998–July 2002). All monthly composites were transformed to regular grids using ArcGIS and resampled to a common 1 km resolution grid. Grids of SD of SST were calculated based on the monthly composites of SST using a 5 by 5 cell square centred on an individual grid cell, applying neighbourhood statistics within the Spatial Analyst extension.

For each sighting, based on its GPS coordinates, values of each EGV were extracted using ArcInfo. However, satellite-derived information on Chl-a and SST was unavailable on some occasions because of cloud cover and/or proximity to the coastline. As a result, the number of sightings with missing values of Chl-a and SST was assessed and, preliminary analyses were performed separately with and without those dynamic variables, which had a considerable amount of missing information. The present study focuses, for each season, exclusively on those identified cetacean species for which there were more than 10 sightings.

2.3. Data analysis

Only data points where a cetacean species was recorded were included in the analysis. Thus, while the present study provides information on the relative habitat preferences of different species in different seasons, it does not necessarily provide information on the absolute habitat preferences of any individual species. Data were analysed in two ways: firstly, a PCA was used to derive a measure of the habitat occupied by the species, taking into account potential interactions between the variables used. This measure allowed information on the niche centre and niche width for each cetacean species to be extracted and compared. Secondly, classification trees were used to determine intra-specific differences in habitat preferences for the cetacean species considered between summer (April–October) and winter (November–April).

2.3.1. PCA

When comparing the niches occupied by different species, traditionally each habitat variable has been considered separately. However, different habitat variables may interact meaning that a species may only occur when certain combinations of individual habitat variables are present (MacLeod et al., 2009). For example, a species may only occur within a specific depth range if the water temperature is also suitable, and it will not occur when only one of these variables falls within a species preferred range. Therefore, it is important that such potential interactions are considered when assessing how species differ along any individual niche axis. In this study, this is achieved by using a PCA analysis.

A PCA summarises all explanatory ecogeographic variables (EGVs) into a few uncorrelated factors or axes (the Principal Components, PC) retaining most of the information. However, this calculation assumes that all variables are on a comparable scale. Therefore, before conducting the PCA, each EGV value for each data point was standardized by subtracting the mean value for that variable (across all species) and dividing it by its standard deviation. PCA analyses were conducted on these standardized values and using all possible combinations of the EGVs.

Each PC has an associated eigenvalue that indicates the amount of variance it explains. One limitation of PCA is the need to decide how many PCs to present (Zuur et al., 2007). For this study, only the most important PCs (those that cumulatively captured more than 80% of the total variance) were selected and considered in further statistical analyses (Zuur et al., 2007). Another limitation of the method is that PCA cannot cope with missing values. Missing values can be replaced by sensible estimates or, as in the present study, the entire observation can be omitted from the analyses. Finally, PCA measures linear relationships between variables for each PC while relationships are typically non-linear in ecology research. However, by using several PCs, potential non-linear relationships can be integrated into the model. PCA analysis was carried out using Minitab (Minitab Ltd.).

2.3.1.1. Niche centre comparisons. For each considered PCA axis, the niche centre of a species was defined as the median value of the PC score of all locations where that species was recorded. To test if there was a significant niche centre difference between at least some of the species being examined, a Kruskal–Wallis test was carried out. If significant variation was identified, individual pair-wise comparisons were conducted using Mann–Whitney tests to determine which species differed from each other. As these pair-wise comparisons consist of multiple tests, which could result in type I (α) errors, the Bonferroni correction was applied and a new significance level was calculated as 0.05 divided by the number of tests performed for each PC ($N=10$ in summer, $N=3$ in winter). Statistical tests were performed in R 2.9.1.

2.3.1.2. Niche width comparisons. For each PCA axis considered, a species' niche width can be identified from the amount of variation in its PC scores for the locations occupied by that species. Differences in niche widths between species within the surveyed area would indicate different levels of specialisation. Homogeneity of variance tests (Bartlett-Box test) were performed to compare PC score variance between species. If a significant difference was identified, individual pair-wise comparisons of variances were based on *F* tests. The Bonferroni correction was applied, dividing 0.05 by the corresponding number of tests performed for each PC ($N=10$ in summer, $N=3$ in winter). Statistical tests were performed in R 2.9.1.

2.3.2. Classification trees

Classification trees were applied for each species to identify the key differences between summer (May–October) and winter (November–April) sightings that would indicate seasonal variations in their ecological niches. Classification trees identify such differences by way of recursive binary partitioning of data into increasingly homogenous groups with respect to dependent variables (see Redfern et al., 2006). The first split is based on the value of the most important variable as it produces two subsets with the greatest difference. Each successive split represents the next most important variable, resulting in a tree-like structure consisting of a series of nodes. Cross-validation was applied and pruning was performed to keep the final trees relatively simple (Zuur et al., 2007) and to allow only the most important variables to be identified. Thus, only predictor variables that create homogeneous data subsets, and hence explain some of the variation in the response variable, are retained in the model (Redfern et al., 2006). Only fixed EGVs were considered in the analysis because seasonal differences in SST and/or Chl-a would result in obvious summer/winter variation that will not represent real thermal preferences but would reflect habitat availability. Analyses were conducted using the software Brodgar (www.highstat.com).

3. Results

3.1. Sighting composition

A total of 734 cetacean sightings was recorded, including five cetacean species: common dolphin *Delphinus delphis* ($N=534$), bottlenose dolphin *Tursiops truncatus* ($N=99$), long-finned pilot whale *Globicephala melas* ($N=50$), harbour porpoise *Phocoena phocoena* ($N=35$) and Risso's dolphin *Grampus griseus* ($N=16$; Fig. 1).

A considerable proportion of sightings of bottlenose dolphins (41 out of 99) had missing values for Chl-a concentration. Chl-a data was also unavailable for 18 sightings of common dolphins. Missing values of SST were less frequent, with no information regarding sea temperature for 8 sightings of bottlenose dolphins and 4 records of common dolphins. To avoid sample size reduction, preliminary analyses were performed with and without Chl-a as an explanatory variable. Results showed that Chl-a concentration was an important factor contributing to habitat preference differentiation between species. Therefore, Chl-a was retained as explanatory variable in the analyses. Final sighting composition used for Classification trees analyses (Table 1) and PCA analyses (Table 4, Table 6) are indicated (see also Fig. 2).

3.2. Comparisons of niche centres and niche widths

3.2.1. Summer

For summer sightings, PC1 and PC2 accounted for 47.2% and 16.9% of the total variation respectively. The first four components explained 87.0% of the deviation and, therefore, subsequent statistical analyses were based on these first four axes (Table 3). There were significant differences in the median scores of the first, second and third PCs across the five species examined (Kruskal–Wallis, $p<0.001$), suggesting that at least two of the groups considered have significantly different niche centres for each of the examined axes (Fig. 3). No significant differences in median scores were found along the fourth PC (Kruskal–Wallis, $p=0.438$). There were significant niche widths differences between species based on the first (Bartlett-Box, $p<0.001$), third (Bartlett-Box, $p=0.005$) and fourth (Bartlett-Box, $p<0.001$) axes. No significant differences were found along the second axis (Bartlett-Box, $p=0.073$). Bottlenose dolphins showed a wide range of scores

Table 1
Total number of encounters per species used for data analysis. Summer: May–October, Winter: November–April.

Species	Fishing vessels		Oceanographic cruises		Dedicated surveys		Opportunistic cruises		Total	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Bottlenose dolphin	16	7	0	10	43	8	12	3	71	28
Common dolphin	265	24	10	39	167	4	22	3	464	70
Long-finned pilot whale	16	4	0	19	11	0	0	0	27	23
Harbour porpoise	5	0	0	0	28	0	2	0	35	–
Risso's dolphin	7	0	0	3	4	2	0	0	11	5
Total									**608**	**126**

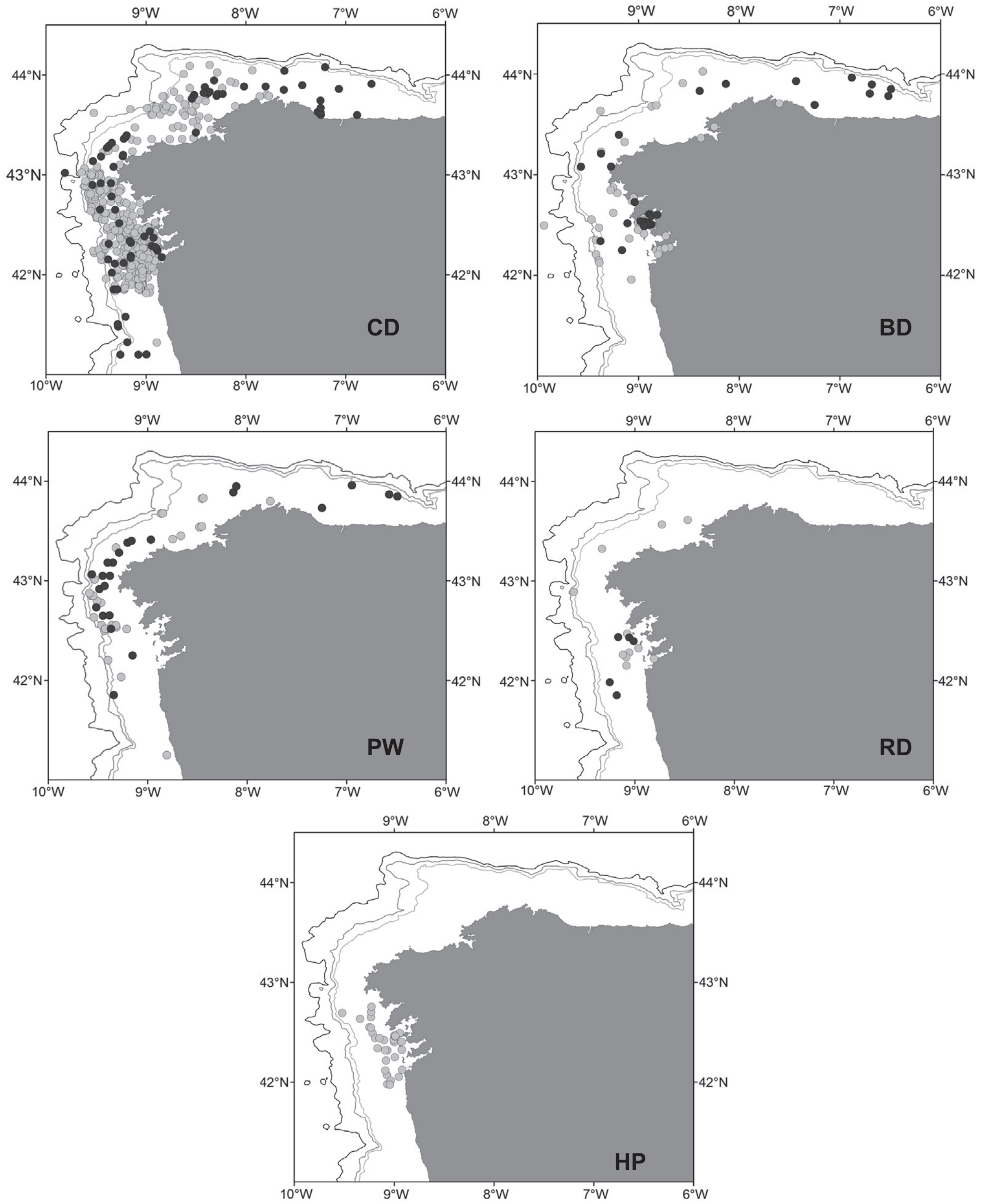

Fig. 2. Distribution map of species sightings. Grey circles: sightings during the summer. Black circles: sightings during the winter. Depth contours of −500 m, −1000 m and −2000 m are shown in greyscale. CD: common dolphin, BD: bottlenose dolphin, PW: long-finned pilot whale, RD: Risso's dolphin, HP: harbour porpoise.

for PC1 and PC2 while long-finned pilot whale showed a broad range of scores on PC1 and PC3. Harbour porpoises showed the largest variance along PC4 (Fig. 3).

The Bonferroni correction was applied to the results obtained from the subsequent pair-wise comparisons and significance level decreased to 0.005.

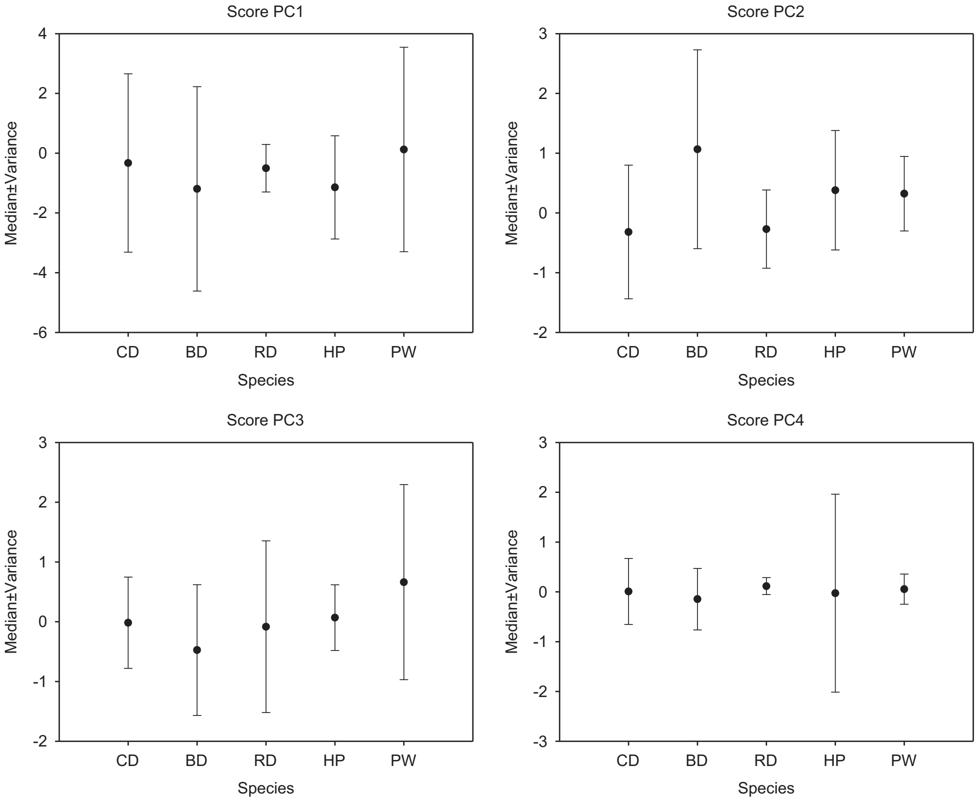

Fig. 3. PC scores in summer: Median ± Variance for each species. CD: common dolphin, BD: bottlenose dolphins. RD: Risso's dolphin, HP: harbour porpoise, PW: long-finned pilot whale.

Table 2
Mean and Standard Deviation (SD) of each variable (a measure of variance) and species during summer (S) and winter (W) months.

	SST (°C)		*SD_SST*		*Chl-a* (mg/m^3)		*Depth* (m)		*Dist. coast* (Km)		*Slope*		*SD_Slope*	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bottlenose dolphin, S	16.84	1.60	0.42	0.31	2.40	1.98	−150.07	362.74	8.48	15.63	1.96	3.95	0.50	0.77
Bottlenose dolphin, W	13.47	0.73	0.33	0.30	1.17	0.70	−75.07	90.58	12.88	13.56	1.40	2.27	0.59	1.12
Common dolphin, S	16.90	1.10	0.19	0.14	1.62	1.76	−184.34	203.15	16.00	11.58	2.01	3.40	0.53	0.90
Common dolphin, W	13.96	0.97	0.15	0.13	1.14	1.57	−233.16	374.23	20.91	12.43	2.84	4.65	0.70	0.93
Long-finned pilot whale, S	15.87	1.62	0.12	0.07	1.30	1.23	−274.74	211.81	22.54	9.28	4.27	4.85	0.94	0.95
Long-finned pilot whale, W	13.17	0.34	0.12	0.07	1.10	0.72	−165.15	68.57	21.11	9.22	2.15	3.12	0.87	1.32
Harbour porpoise, S	16.33	0.81	0.22	0.14	3.38	3.03	−87.39	50.92	8.27	6.99	1.07	0.78	0.34	0.36
Risso's dolphin, S	16.55	1.11	0.20	0.14	1.68	1.57	−165.58	174.07	12.97	8.37	1.45	2.86	0.20	0.17
Risso's dolphin, W	14.31	0.77	0.14	0.11	1.56	0.90	−108.21	37.72	14.48	11.75	0.51	0.22	0.23	0.10

3.2.1.1. *First axis.* The harbour porpoise showed a significantly different PC1 score to common dolphin and pilot whales (Table 4a). Variation in PC1 was mainly related to the fixed EGVs considered in the analysis; positive relationships with distance to the coast, slope and SD of slope and a negative relationship with depth (note that depth was introduced in the analysis as a negative variable). As a consequence, species with high median PC1 scores (i.e. long-finned pilot whales) will be found in areas at greater distances to the coast, with stronger and more variable slopes, and in deeper waters in relation to the other species, while the opposite can be said for species with low median PC1 scores (i.e. harbour porpoise; Fig. 3).

The harbour porpoise showed significantly lower variation in PC1 scores than all other species except Risso's dolphin (Fig. 3; Table 4a). Therefore, porpoises in this area show a preference for more specific combinations of depths, slopes, SD of slopes and distances to the coast than the other species studied here (Table 2). Bottlenose dolphins showed a significantly broader environmental niche than common dolphins for PC1.

3.2.1.2. *Second axis.* Common dolphin showed a significantly different PC2 niche centre to all other groups except Risso's dolphin (Table 4a). Variation along the second axis was principally explained by a positive relationship with SD of SST, Chl-a and SD of slope. These findings suggest that species with higher median PC2 scores, such as bottlenose dolphins, long-finned pilot whales and harbour porpoises, will be found in waters with more variable SST, higher Chl-a concentration and more variable slope than species of lower median PC2 scores (i.e. common and Risso's dolphin). After applying the Bonferroni correction, niche width differences were not found along the second axis.

3.2.1.3. Third axis. Long-finned pilot whales showed the most differentiated mean PC3 score, being different to all other groups except Risso's dolphin (Table 4b). Variation in the third axis was mainly explained by a negative relationship with SST. Therefore, the higher PC3 scores displayed by long-finned pilot whales indicate a preference for colder waters during the summer.

Significant differences in PC3 niche width were found between long-finned pilot whales and both common dolphins and harbour porpoises. The results suggest that common dolphins and harbour porpoises favour a significantly narrower range of SST than long-finned pilot whales.

3.2.1.4. Fourth axis. Niche centre differences were not found along the fourth axis. The harbour porpoise showed a significantly more variable PC4 score than all the other groups (Table 4b). Variation along the fourth axis was mainly explained by a negative relationship with Chl-a. Consequently, the harbour porpoise favours waters characterised by a broader range of Chl-a than the other species considered.

3.2.2. Winter

Only three species were included in the winter analyses (common and bottlenose dolphins, and long-finned pilot whales) since <10 sightings were available in this season for both harbour porpoise ($N=0$) and Risso's dolphin ($N=5$). PC1 and PC2 explained 41.9% and 18.6% of the variation respectively. The first four components explained 85.6% of the deviation (Table 5). Significant differences in median scores across the three species examined were found only for the third axis (Kruskal–Wallis, $p<0.001$), suggesting that at least two of the groups considered have significantly different niche centres along this PC (Fig. 4). There were significant differences between species' niche widths based on the first, (Bartlett-Box, $p\equiv0.01$) and third ($p\equiv0.008$) axes but not based on the second ($p=0.128$) and fourth ($p=0.073$) axes. Further analyses refer exclusively to the first and third PCs.

The Bonferroni correction was applied to the results obtained from the subsequent pair-wise comparisons and significance level decreased to 0.016.

3.2.2.1. First axis. Common dolphin showed a wider range of PC1 scores than pilot whale (Fig. 4; Table 6). As for summer sightings, variation along the first axis during the winter was mainly related to fixed EGVs; a positive relationship with distance to the coast, slope and SD of slope and a negative relationship with depth. Therefore, common dolphins show a preference for a wider variety of values of fixed variables than pilot whales during the winter.

3.2.2.2. Third axis. There was a significant difference in median PC3 scores between common dolphin and long-finned pilot whale (Fig. 4; Table 6). Variability along PC3 is mostly explained by a negative relationship with SST. Therefore, species with high PC scores for this axis, such as the long-finned pilot whale, will be found in waters with lower values of SST when compared to species with lower PC3 scores, such as the common dolphin.

When comparing niche widths based on PC3, long-finned pilot whale showed a significantly narrower range of PC3 scores than common and bottlenose dolphins. Consequently, during the

Table 3

PCA results for all species considered during summer months. Eigen vectors and coefficients of each explanatory variable are indicated for the first four principal components.

EGVs	PC1	PC2	PC3	PC4
Chl	−0.286	0.426	−0.138	−0.808
SST	0.214	−0.400	−0.807	−0.234
SD_SST	−0.246	0.486	−0.558	0.537
Depth	−0.467	−0.113	0.112	0.021
Distance_Coast	0.475	−0.200	0.045	−0.045
Slope	0.449	0.420	0.009	−0.032
SD_Slope	0.409	0.441	0.056	−0.008
Eigen value	3.307	1.833	0.881	0.721
Proportion	0.472	0.169	0.126	0.103
Accumulated variation explained	0.472	0.641	0.767	0.870

Table 5

PCA results for all species considered during winter months. Eigen vectors and coefficients of each explanatory variable are indicated for the first four Principal Components.

EGVs	PC1	PC2	PC3	PC4
Chl	−0.175	−0.580	−0.260	−0.724
SST	0.300	0.326	0.650	−0.107
SD_SST	−0.225	−0.416	−0.536	0.648
Depth	−0.428	0.024	0.356	0.091
Distance_Coast	0.485	0.187	0.014	−0.046
Slope	0.490	−0.384	0.112	0.091
SD_Slope	0.412	−0.449	0.290	0.164
Eigen value	2.932	1.303	1.025	0.734
Proportion	0.419	0.186	0.146	0.105
Accumulated variation explained	0.419	0.605	0.751	0.856

Table 4

Summer comparison of **niche centres/niche widths** between pairs of species. *P* values are shown from Mann–Whitney tests (before slash) to compare medians and from *F* tests (after slash) to compare variances. Statistically significant differences after the Bonferroni correction was applied ($p<0.005$) are highlighted in **bold**. NA: not available. (Table 4a) Results based on PC1 are shown below the diagonal and results based on PC2 are shown above the diagonal. (Table 4b) Results based on PC3 are shown below the diagonal and results based on PC4 are shown above the diagonal.

Species		Common dolphin	Risso's dolphin	Pilot whale	Harbour porpoise	Bottlenose dolphin
(a)						
	N	449	11	27	35	41
Common dolphin	449	–	0.781/NA	**0.003/**NA	< **0.001**/NA	< **0.001**/NA
Risso's dolphin	11	0.367/0.307	–	0.071/NA	0.080/NA	0.021/NA
Pilot whale	27	0.013/0.569	0.023/0.236	–	0.714/NA	0.062/NA
Harbour porpoise	35	< **0.001/** < **0.001**	0.063/0.105	< **0.001/** < **0.001**	–	0.194/NA
Bottlenose dolphin	41	0.014/ < **0.001**	0.478/0.012	0.013/0.026	0.811/ < **0.001**	–
(b)						
	N	449	11	27	35	41
Common dolphin	449	–	NA/0.021	NA/0.018	NA/ < **0.001**	NA/0.816
Risso's dolphin	11	0.574/0.092	–	NA/0.342	NA/ < **0.001**	NA/0.034
Pilot whale	27	< **0.001/0.002**	0.108/0.818	–	NA/ < **0.001**	NA/0.059
Harbour porpoise	35	0.215/0.240	0.960/0.036	< **0.005/** < **0.005**	–	NA/ < **0.001**
Bottlenose dolphin	41	0.060/0.093	0.160/0.513	< **0.001/**0.249	0.030/0.043	–

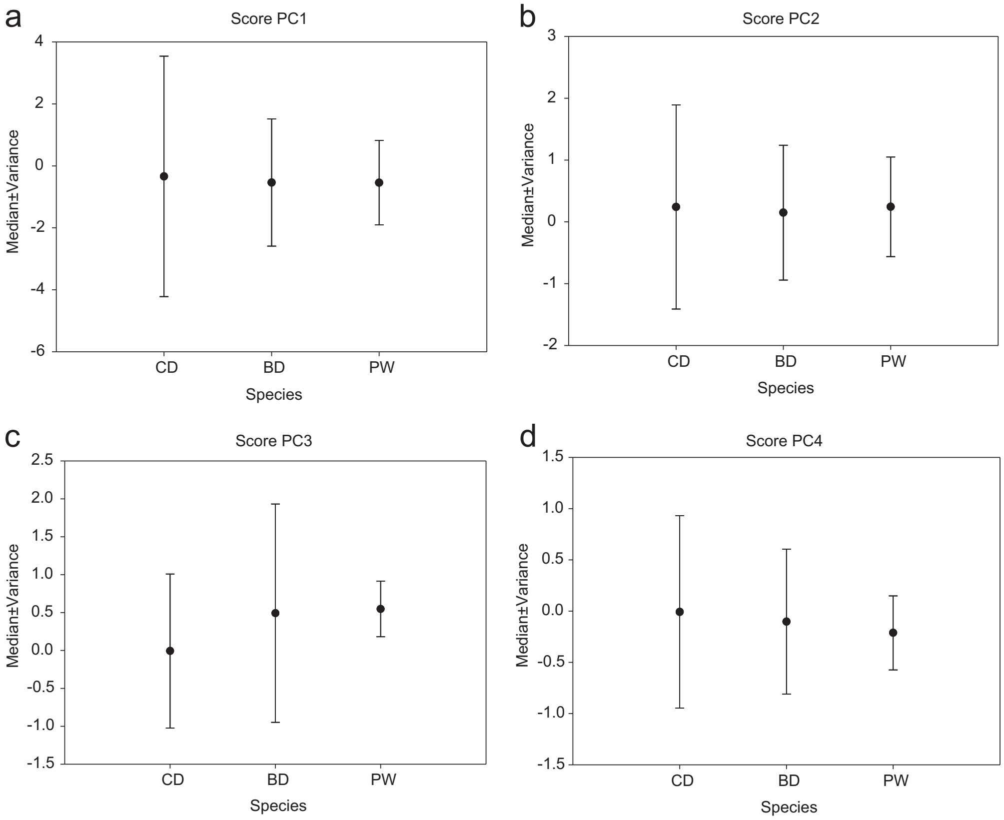

Fig. 4. PC scores in winter: median ± variance for each species. CD: common dolphin, BD: bottlenose dolphins, PW: long-finned pilot whale.

Table 6
Winter comparison of **niche centres/niche widths** between pairs of species. *P* values are shown from Mann–Whitney tests (before slash) to compare medians and from *F* tests (after slash) to compare variances. Statistically significant differences after the Bonferroni correction was applied ($p < 0.016$) are highlighted in **bold.** NA: not available. Results based on PC1 are shown below the diagonal and results based on PC3 are shown above the diagonal.

Species		Common dolphin	Pilot whale	Bottlenose dolphin
N		65	23	17
Common dolphin	65	–	< **0.001/0.008**	0.095/0.261
Pilot whale	23	NA/**0.008**	–	0.460/**0.002**
Bottlenose dolphin	17	NA/0.154	NA/0.368	–

winter, long-finned pilot whales favour waters of less variable SST than the other two species.

3.3. Seasonal comparisons

Differences in habitat use were found when comparing winter and summer sightings of bottlenose dolphin. Results suggest that bottlenose dolphins prefer waters at distances to the coast smaller than 18 km during the summer. However, of the 12 summer sightings further from the coast (17% of sightings of this species in summer), all but one were in waters deeper than 339 m. In contrast, during the winter, although again there were more sightings close to the coast (< 18 km), those sightings occurring further offshore were all in waters shallower than 339 m. Common dolphin, long-finned pilot whales and Risso's dolphin showed no seasonal variation in habitat preferences. Seasonal comparisons were not feasible for the harbour porpoise due to the absence of sightings during the winter.

4. Discussion

There were significant differences in the niche widths and niche centres occupied in summer months by the five cetacean species analysed. The first axis of the PCA analysis, related to fixed EGVs, highlighted differences between more coastal (harbour porpoise) and more pelagic (common dolphin and long-finned pilot whale) species. The classification of Risso's dolphin and bottlenose dolphin is less clear as they prefer, on average, shallower waters and smaller distances to the coast than the pelagic groups and, at the same time, their niche centre based on PC1 does not differ from that of the harbour porpoise. When considering the second and third axes, which are more related to dynamic variables, particular differences between species were identified during the summer. For example, the two pelagic species (common dolphins and long-finned pilot whales) differed from each other with the former species preferring warmer waters, higher Chl-a concentrations and less variability in SST that the latter.

During the winter, a significant difference in the niches centres was found between common dolphin and long-finned pilot whale. Since both species are considered to be pelagic, it is not surprising that this niche difference was mainly based on a dynamic variable, SST, with long-finned pilot whales consistently showing a preference for colder waters. SST has been previously found to be one of the main drivers of long-finned pilot whale distribution in other areas such as the Canadian Gully Canyon (Gowans and Whitehead, 1995) and the West of Scotland (MacLeod et al., 2007).

During the winter, differences in niche widths between the three species with sufficient data were also identified; long-finned pilot whale showed less variety of PC1 and PC3 scores than common and bottlenose dolphins. It could be argued that a higher number of common dolphin sightings ($N=65$) was included in the analyses, which could have inflated the variance in the PC scores of this species. However, as seen in the winter PC3 plots (Fig. 4), long-finned pilot whales show here a narrower niche than the bottlenose dolphin while the number of sightings of pilot whales considered in the PCA analysis is higher ($N=23$). Thus, conclusions derived from our statistical tests appear to reveal genuine differences.

Interspecific niche partitioning was less apparent during the winter. This might be related to variations in resource availability associated with an increased upwelling between April and September (Fraga, 1981; Prego and Bao, 1997; Figueiras et al., 2002). The higher abundance of resources during the summer may allow for a higher degree of specialisation, as hypothesised by MacLeod et al. (2004) to explain variations in cetacean community composition in the northern Bahamas. However, the harbour porpoise, one of the species with the most differentiated niche centre in the summer, was not included in the winter analyses (due to lack of sightings) and this could have also influenced the results. In the present study, porpoise sightings were recorded only during summer months (May–October) when it occupies a niche highly differentiated from more pelagic species. The absence of porpoise sightings during the winter could imply that this species occurs outside the study area at this time of the year. This may be due to porpoise's unique habitat requirements during the winter or to inter-specific competition, which can result in localised competitive exclusion. However, sightings of harbour porpoises from land occur all year round in Galicia (Pierce et al., 2010). It may also be that the absence of records of harbour porpoises during the winter in the present study is related to poorer sighting conditions in this period of the year. Poor sighting conditions could compromise the identification of very small and shy cetacean species such as the harbour porpoise (average body lengths of 161.8 ± 31.4 cm for females and 145.3 ± 18.2 cm for males in the research area; López, 2003).

The categories specialist/generalist have been previously used in cetacean ecology mainly to account for different feeding habits (Hoelzel et al., 1998; Santos et al., 2004, 2007). In the study area, seasonal variations have been found in the diets of long-finned pilot whale (Santos et al, 2013a) and common dolphin (Santos et al., 2013b) but not in that of the bottlenose dolphin (Santos et al., 2007a). However, opportunistic or selective behaviours have not been conclusively confirmed for any of the three species (Santos et al., 2001, 2007, 2013a, 2013b). In the present study, the terms specialist/generalist refer to the relative width of ecological niches in relation to EGVs rather than variability in diet. Here, the harbour porpoise consistently displayed a narrower occupied niche than other species regarding fixed EGVs (Depth, Slope, SD of Slope and Distance to the coast), while common dolphin, bottlenose dolphin and long-finned pilot whales are more generalist. However, when examining dynamic variables, trends were not so clear since the harbour porpoise showed a wider range of Chl-a concentrations than any other species during the summer and, at the same time long-finned pilot whales showed a narrow range of SST and SD of SST during the winter.

Classification trees were applied to identify the key differences in habitat use between summer and winter for each considered species. When applying this methodology, a similar coverage of habitat types in both seasons is assumed. In this study, the fact that no seasonal differences were found for the common dolphin, which is the most commonly recorded cetacean species, indicates that approximately the same combination of environmental variables was surveyed in both seasons. In terms of seasonal shifts in the niches occupied, between-season differences were found in only one species, bottlenose dolphin. These differences may relate to variation in upwelling, resource availability or local currents. For example, a higher abundance of resources during the summer could permit bottlenose dolphins to have a wider choice of habitats also in more pelagic waters.

Previous studies have identified two genetically distinct populations of bottlenose dolphins in Galician waters (Fernández et al., 2011a), which are characterised by differentiated trophic niches (Fernández et al., 2011b). In the present study bottlenose dolphins were considered as a single group/species since it was not possible to determine *a priori* the genetic origin of the individuals sighted. By merging the two populations, a true inter-specific comparison of the habitat niches occupied by five small cetacean species was carried out. However, future analyses in the research area should examine bottlenose dolphin intra-specific habitat preferences based on EGVs.

Previous research addressing cetacean trophic ecology in our area of interest, based on stable isotope signatures, did not find obvious niche differences between the harbour porpoise, bottlenose dolphin and long-finned pilot whales (Méndez-Fernández et al., 2012). However, the authors observed differentiated trophic niches for common and striped dolphin. The present paper, which identified niche differences between five odontocete species in NW Iberia, highlights the need to combine different approaches to track and identify species ecological preferences.

Spyrakos et al. (2011) found that common dolphin and long-finned pilot whales preferred, respectively, depths of around 200 m and >200 m in Galician waters. The present study increased substantially the dataset used by Spyrakos et al. (2011), and our findings show that average water depths of common dolphin sightings are around 200 m depth both in winter and summer months while long-finned pilot whales preferred waters that were on average >200 m depth during the summer. However, in the present study, sightings of pilot whales during the winter were mostly recorded at shallower depths (i.e. 100–200 m).

The PCA-based methodology used here applies a multivariate approach to identify niche differences between cetacean species. As such, it can detect the existence of niche differences that might otherwise be missed due to interactions between the different habitat variables being considered. In particular, when using univariate approaches, there is a risk that niche differences may be identified based on a specific variable which does not reflect true niche partitioning but is rather an artefact of co-variation with another variable on which partitioning is actually based.

The bottlenose dolphin and the harbour porpoise are recorded in the European Habitats Directive (Directive 92/43/CEE) as *species of community interest in need of strict protection* that require: (1) the setting up of an European common regime for their conservation, (2) the designation, where suitable areas exist, of Special Areas of Conservation (SAC), (3) the surveillance of their conservation status and, (4) the establishment of a system to monitor their incidental capture and killing. Improved knowledge on the habitat preferences of both species in Galicia is needed to guide surveys that aim to detect distribution range changes and to determine the best areas to establish SAC. The results presented here can provide baseline information for future conservation efforts, especially since genetically differentiated populations of both species have been identified in the area (Fontaine et al., 2007; Fernández et al., 2011a).

5. Conclusion

Niche partitioning between small cetacean species in NW Iberia is stronger during the summer, possibly due to an increase in resource availability in this period caused by regional upwelling. Seasonal shifts in local oceanographic conditions could also explain the differences in summer/winter habitat preferences displayed by bottlenose dolphins.

The harbour porpoise shows the narrowest ecological niche during the summer while long-finned pilot whales consistently show a preference for colder waters than the other species considered here. The proposed methodology represents a successful way to explore niche partitioning between cetacean species.

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Appendix A. Supplementary information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2013.05.008.

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