Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain

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Abstract

The northeastern section of the Alboran Sea is currently under consideration as a Special Area for Conservation under the European Union’s Habitat Directive. Within this framework, the present study focuses on the distribution of cetaceans in this area and is part of the Spanish Ministry of the Environment’s “Program for the Identification of Areas of Special Interest for the Conservation of Cetaceans in the Spanish Mediterranean”. Shipboard visual surveys were conducted in 1992 and from 1995 to 2001 in the north-eastern Alboran Sea, covering 14,409 km. A total of 1,134 sightings of cetaceans were made. From the data collected, the distribution of seven species of odontocete was examined with respect to two physiographic variables, water depth and slope. Analyses of $\chi^2$ and fitting of GLMs demonstrated significant differences in distribution for all species, mainly with respect to depth. Kruskal–Wallis tests, factor analysis and discriminant function analysis showed that the species could be classified into two major groups, shallow-waters (short-beaked common dolphin and bottlenose dolphin) and deep-waters (striped dolphin, Riss’s dolphin, long-finned pilot whale, sperm whale and beaked whale), respectively. Preferred habitats in terms of water depth were areas deeper than 600 m for the deep-water group, and the shallower ranges from shore to 400 m for the other. The distribution of cetaceans was further matched with that of their most common prey in order to establish which habitats could be considered important for their feeding. The resulting analysis highlighted two areas in the region as important habitats for the conservation of the most vulnerable species in the Mediterranean, the bottlenose and the common dolphin.

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1. Introduction

The primary influence of the physical environment over cetacean distribution is probably the aggregation of prey species (Rubin, 1994; Baumgartner, 1997; Davis et al., 1998). Studies in the Gulf of Mexico (Mullin et al., 1994; Baumgartner, 1997; Davis et al., 1998), eastern North Pacific
(Hui, 1979, 1985; Perrin et al., 1985; Taylor, 1992), and North Atlantic (Scott et al., 1985; Kenney and Winn, 1987; Forcada et al., 1990; Hooker et al., 1999) have suggested the possibility of defining habitat in terms of physiography for several species of cetaceans. In the case of benthic or demersal prey species, physiography plays a very important role in limiting distribution directly by depth, slope, and type of substrate (Gil de Sola, 1993). For other species of cetacean prey, such as pelagic fish or cephalopods, physiography could play a more indirect role through mechanisms such as topographically induced up-welling of nutrients (Guerra, 1992; Rubin, 1997), increased primary production, and aggregation of zoo-plankton due to the enhanced secondary production or convergence of surface waters (Rubin et al., 1992; Rubin, 1994).

The present study is part of the Spanish Ministry of the Environment’s “Program for the Identification of Areas of Special Interest for the Conservation of Cetaceans in the Spanish Mediterranean”. It takes a first step in analyzing the importance of the physiography of the northeastern Alboran basin for several species of cetaceans within the context of national and international biodiversity conservation frameworks (European Union’s Habitats Directive, the Bonn Convention’s ACCOBAMS agreement and the Barcelona Convention).

This study focused primarily on two delphinids, the bottlenose dolphin (Tursiops truncatus) and the short-beaked common dolphin (Delphinus delphis) considered to be declining in the Mediterranean biogeographical region (Pelegri, 1980; Viale, 1980, 1993; Laurent, 1991; Aguilar, 1991; Notarbartolo di Sciara, 1993; Gannier, 1995), both being included in Spain’s National Endangered Species Act as vulnerable (BOE, 2000) and the bottlenose being included in the European Union’s Habitats Directive Annex I. Other species included in this study are striped dolphin (Stenella coeruleoalba), long-finned pilot whale (Globicephala melas), sperm whale (Physeter macrocephalus), Risso’s dolphin (Grampus griseus), and beaked whales of the Ziphiidae family.

The research site was the northeastern Alboran Sea (Fig. 1), a region that stands out in the Mediterranean as especially important for these two target species. Common dolphins, at present found only in small groups in the southern part of the central Mediterranean basin (Lauriano and Notarbartolo di Sciara, 1995; Notarbartolo di Sciara et al., 1993, Politi, 1998; UNEP, 1998), are abundant only in the Alboran Sea, where the population is estimated to be 15,072 (95% CI = 7,337 and 30,960) (Forcada and Hammond, 1998). Moreover the region has also been highlighted as especially important for the long-finned pilot whale (Cañadas and Sagarminaga, 2000).

The Alboran Sea has been defined as the transition zone between the Mediterranean Sea and the Atlantic Ocean (Rodríguez, 1982). Parallel to its importance for maintaining a possible gene flow between Mediterranean and Atlantic populations (Natoli et al., 2001), the Alboran Sea plays a vital role in the oceanography of the Mediterranean basin. The important circulation pattern of the Atlantic surface water in the Alboran Sea is often referred to as the hydrologic motor of the western Mediterranean basin (Rodríguez, 1982) and makes this area one of the most productive regions of the Mediterranean (Rubin et al., 1992). The research area, in the northeastern section of the Alboran Sea, has a relatively narrow continental shelf, somewhat wider within the large bay of Almeria. The shelf edge starts its drop at around 150 m. There is great variability in the slope of the shelf edge, from very steep escarpments to gently sloping plains. The abyssal plain is very narrow because of the presence of ridges and volcanic mountains such as those giving rise to the island of Alboran (Parrilla and Kinder, 1987) (Fig. 1). The particular physiography of the Alboran basin directs the currents (Parrilla and Kinder, 1987), which, favored by atmospheric and meteorological conditions (Cheney and Doblar, 1979), give rise to processes of convergence and divergence of water masses creating areas of enhanced productivity (Rubin et al., 1992).

2. Methodology

Transects did not follow a systematic design with random probability sampling, but were
designed as triangles to cross depth contours as perpendicularly as possible and to cover as much as the area as possible, although it was not covered homogeneously (Fig. 2). Searching effort stopped at sighting and started again when the sighting was ended, with a return to the course previously established. A ‘sighting’ was defined as a group of animals of the same species seen at the same time showing similar behavioral characteristics and at distances of less than 1500 m from each other (SEC, 1999).

The survey transects (Fig. 2) were conducted from the Alnitak research motorsailer “Toftevaag”, sampling the study area throughout the months of April, June, July, August and September in 1992 and from 1995 until 2001. Surveys were also made during the month of November in 1999, 2000 and 2001 and January in 2001. The observation platform had two searching platforms (crow’s nest and deck) with an eye height of 12 and 2.5 m, respectively, above sea level. To maintain consistent sighting effort, one trained observer (of a team of five) occupied the look-out posts in one hour shifts during daylight with visibility of over 3 nmi (5.6 km), assisted with 7 × 50 binoculars, covering 180° ahead the vessel. Volunteers participating in this research (mostly untrained) contributed 2.1% of the total observations made from an additional look-out post on deck. Sighting effort was measured as the number of miles traveled with
adequate sighting conditions (i.e. with sea state Douglas 0 to 2 and good visibility) and observers on the lookout posts. Sighting effort stopped with sea states of 3 Douglas or more (the approximate equivalence to Beaufort wind force scale in offshore, current-free conditions, of 3 Douglas is Beaufort 3 to 4). Four categories of sighting effort were considered according to sea state and position of trained observers, as crow’s nest watch was canceled with excessive swell: 1 (sea state 1 in Douglas scale and one observer in the crow’s nest), 1S (sea state 1 and no crow’s nest watch), 2 (sea state 2 with crow’s nest watch) and 2S (sea state 2 and no crow’s nest watch). The geographic position of the ship was continuously recorded by the ship’s computer from a GPS navigation system using Logger, the IFAW Data Logging Software (NMEA data automatically recorded every minute in a database). Data concerning time, species, number of individuals, behavior, and other relevant data during sightings were recorded together with other complementary environmental data.

The research area was divided into 548 quadrats with a cell resolution of 2 min latitude by 2 minutes longitude each. Encounter rate for each species was calculated for each quadrat as the number of sightings per mile searched. That is $100 \times \left( \frac{n}{L} \right)$ where $n$ is the number of sightings and $L$ the number of miles of sighting effort. Here, we analyze only occurrence, so the number of individuals in each sighting is not considered.
Encounter rate was stratified by type of sighting effort, as this factor can greatly affect the detectability of the animals.

2.1. Physiographical features

Two features were measured for describing the physiography: depth and slope. Mean depth and slope were calculated for each quadrat. Depth was derived from the nautical charts of the “Instituto Hidrográfico de la Marina” (Spain). Mean depth was calculated as the average of the maximum and the minimum depth recorded in each quadrat. Slope was calculated as \( \frac{(D_{\text{max}} - D_{\text{min}})}{D_I} \) where \( D_{\text{max}} \) the maximum depth in the quadrat, \( D_{\text{min}} \) is the minimum depth in the quadrat, and \( D_I \) the distance in meters between the points of maximum and minimum depth of the quadrat, and expressed in units of meters per km. Depth and slope, were not correlated (Pearson \( r = 0.0408 \)).

2.2. Analysis

To determine if the different species of cetaceans were distributed non-uniformly with respect to depth and slope, two techniques were used: a chi-square analysis of a bivariate contingency table and a Generalized Linear Model (GLM). Results from the bivariate contingency table were used to assess which depth/slope ranges could be considered as preferred by the different species, if any.

For the chi-square analysis, the expected frequencies were obtained (after Hui, 1979) as: 
\[
E_i = \frac{(n \times L_i)}{L_T},
\]
where \( E_i \) = expected number of sightings in class \( i \), \( n \) is the total number of sightings, \( L_i \) is the amount of effort in class \( i \), and \( L_T \) the total effort. Cetaceans found off-effort or during other sightings were not included in the analysis. For depth and slope five and four classes, respectively, were arbitrarily defined: depth 0–200, 201–400, 401–600, 601–1000 and 1001–1600 m; slope 0–20.0, 20.1–40.0, 40.1–80.0 and 80.1–220 m km\(^{-1}\). Nevertheless, for some species some classes had to be pooled to avoid small sample size. This classification was defined in order to have enough sample size in each of the classes, given the restriction in chi-square tests that requires that all expected frequencies exceed 5 (Sokal and Rohlf, 2000).

For the GLMs, each quadrat was classified by depth and slope. As there was no restriction similar to that of chi-square tests regarding sample size in each class, a more detailed classification was used here. Fifteen depth ranges at 100 m intervals (except for the first two: 0–50 and 51–100 m, and the deepest one: 1300–1600 m) and 16 slope ranges at 5 m km\(^{-1}\) intervals up to 50 m km\(^{-1}\) and at larger intervals in the steeper areas (because of the smaller number of quadrats falling in these classes) were arbitrarily chosen. This gave 240 possible combinations, of which only 77 were found in the survey, hereafter referred to as ‘physiographic types’. The response variable was the encounter rate, which was calculated for each species for each of the 77 physiographic types. Given the nature of the response variable, with value ‘0’ for the encounter rate in many classes and decreasing frequencies of increasing encounter rates, the Poisson distribution and the log link function were chosen. Data were visually inspected, through the construction of univariate scattergrams of encounter rate against depth or slope, to get an idea of what would be likely to be important in the full model and to assess if quadratic or cubic functions should be included (Figs. 3 and 4). An interaction term between depth and slope was also included. The best model was selected with a stepwise method, using AIC (Akaike Information Criterion) as selection criteria.

To test whether different species could be differentiated based on physiographic variables, several techniques were used. Factor analysis based on principal components was conducted to explore the spatial coincidence between species, using a matrix of encounter rates for all species in each of the 77 physiographic types. Discriminant function analysis was used to test the significance of both depth and slope in differentiating species or groups of species.

All analyses were performed on two different data sets, one using only effort type 1 (the best sighting conditions) and the other one using the four effort types pooled together. In all cases results were very similar for both datasets. Therefore we present here the results obtained with the analysis considering the four effort types pooled together to increase sample size. On 66 occasions,
mixed groups of two species were encountered, mainly mixed groups of striped and common dolphins, but also a few of pilot whales with common dolphins or bottlenose dolphins.

In 1999, an important shift in the distribution of common dolphins was observed by the authors in the research area (unpublished data). This shift was not observed in other species. As a result, for

Fig. 3. Scattergram plots of encounter rates vs. depth ranges for the eight groups of species. Quadratic or cubic functions have been fitted to the scattergrams as suggested by the GLMs.
all analysis, the sightings of common dolphins were separated into two groups: 1999 alone and all other years with the exception of 1999 (Dde99 and Dde2001, respectively, hereafter). In 42 common dolphins sightings, feeding behaviour could be assessed (feeding behaviour being defined as the
observation of dolphins chasing and eating fish on surface, either by direct visual observation or by underwater video filming of the animals).

3. Results

The shipboard surveys covered a total of 7780 nmi (14,409 km) with adequate sighting effort (conducted in sea states of less than 3 Douglas) from 1992 until 2001 (with the exception of 1993 and 1994, see Fig. 2). During this period, cetaceans were sighted 1134 times, of which 105 sightings were of baleen whales or unidentified species of small dolphins, giving 1029 sightings of identified odontocetes. Mean depths and slopes for encounters for monospecific groups are given in Table 1.

3.1. Tursiops truncatus

One of the most coastal species encountered was the bottlenose dolphin, showing a clear distribution throughout both the continental shelf and shelf edge. From 1992 to 2001 on effort 132 groups were encountered, seven sightings were classified as mixed groups with pilot whales. The GLM analysis selected a model with depth, slope, a quadratic function for depth, and the interaction between depth and slope (see Table 2). Bottlenose dolphins showed a clear preference for steep areas between 200 and 400 m, and avoided depths over 600 m, with a highly significant difference ($\chi^2 = 87.2, n = 125, df=9, p \leq 0.001$).

3.2. Delphinus delphis

On effort 313 sightings of this species were made; 53 were mixed groups of common and striped dolphins, five were common dolphin with pilot whales and one with Risso’s dolphin. Data were pooled for all years, 1999 alone (Dde99) and all years without 1999 (Dde9201) (Tables 1). A significant difference was found for depth between Dde99 and Dde9201 ($U = 2731$, $p < 0.0001$), but not for slope. When the year 1999 was analyzed, four variables were selected in the GLM: slope, its

<table>
<thead>
<tr>
<th>Table 1 Descriptive statistics of the distribution by depth (a) and slope (b) for the seven cetacean species or group of species, ordered by increasing means</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
</tr>
<tr>
<td>-----</td>
</tr>
<tr>
<td>(a) Depth</td>
</tr>
<tr>
<td>Common dolphin (except 1999)</td>
</tr>
<tr>
<td>Bottlenose dolphin</td>
</tr>
<tr>
<td>Common dolphin (total)</td>
</tr>
<tr>
<td>Common dolphin (1999)</td>
</tr>
<tr>
<td>Striped dolphin</td>
</tr>
<tr>
<td>Long-finned pilot whale</td>
</tr>
<tr>
<td>Sperm whales</td>
</tr>
<tr>
<td>Risso’s dolphin</td>
</tr>
<tr>
<td>Beaked whales</td>
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<tr>
<td>(b) Slope</td>
</tr>
<tr>
<td>Common dolphin (1999)</td>
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<tr>
<td>Common dolphin (total)</td>
</tr>
<tr>
<td>Common dolphin (except 1999)</td>
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<tr>
<td>Striped dolphin</td>
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<tr>
<td>Beaked whales</td>
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<tr>
<td>Long-finned pilot whale</td>
</tr>
<tr>
<td>Sperm whales</td>
</tr>
<tr>
<td>Bottlenose dolphin</td>
</tr>
<tr>
<td>Risso’s dolphin</td>
</tr>
</tbody>
</table>
quadratic function, the quadratic function of depth and the interaction between depth and slope (Table 2), although the model did not fit very well according to the plots of residuals. This year, common dolphins showed a preference for the deepest areas with intermediate slopes (40–80 m km\(^{-1}\)), especially above 600 m (\(\chi^2 = 22.0, n = 42, df = 6, p < 0.005\)). When the period from 1992 to 2001 excluding 1999 (Dde9201) was considered, the GLM incorporated the depth and its quadratic and cubic function (Table 2). During this period, common dolphins showed a preference for areas with depths between 1 and 400 m (especially below 200 m) and slopes between 0 and 40 m km\(^{-1}\) (\(\chi^2 = 39.2, n = 212, df = 9, p < 0.001\)).

The feeding behaviour was significantly more often observed in shallow waters between 1 and 200 m than in the other areas (\(\chi^2 = 28.4, n = 42, df = 3, p < 0.001\)). In some of these sightings prey species were identified (garfish—Belone belone, gilt sardine—Sardinella aurita, flying fish—Exonastes rondeletii). At the same time, much larger group sizes were observed in shallower waters than in deeper waters (\(x = 117.7, sd = 137.31, n = 188\) for areas of 1–400 m vs. \(x = 40.0, sd = 57.04, n = 119\) for areas deeper than 400 m).

### 3.3. Stenella coeruleoalba

On effort 324 groups of striped dolphins were seen. The variables that showed significant GLM fits were depth and its quadratic function (Table 2). The striped dolphin was not uniformly distributed through all the physiographic types considered (\(\chi^2 = 487.0, n = 270, df = 12, p < 0.001\)). This species was very rarely found on continental shelf waters (only five sightings of monospecific groups), showing instead a preference for waters of more than 600 m (with increasing encounter rates for increasing depths) with intermediate slopes (between 20 and 80 m km\(^{-1}\)).
3.4. *Globicephala melas*

The long-finned pilot whale, of which one hundred and eighty-three groups were encountered on effort (12 in association with either common or bottlenose dolphins), showed a very widespread distribution throughout pelagic waters. The GLM model selected depth and its quadratic and cubic functions (Table 2). The preferred physiographic types for this species were areas with depths greater than 600m and intermediate slopes between 20 and 80 m km\(^{-1}\) \((\chi^2 = 397.0, n = 171, \text{df}=9, p \leq 0.001)\).

3.5. *Grampus griseus*

Risso’s dolphin was only encountered 31 times. Five variables were selected in the GLM: depth, its quadratic and cubic functions, slope, and the interaction between depth and slope (Table 2), although the model didn’t seem to fit very well, according to the plots of residuals, maybe because of the small sample size. This species was not distributed uniformly through all the physiographic types, preferring areas with depths over 600 meters (with no sightings below 400m) and, within these, the steepest ones (more than 40 m km\(^{-1}\) \((\chi^2 = 90.0, n = 31, \text{df}=4, p \leq 0.001)\)).

3.6. *Ziphiidae*

Beaked whales were only encountered 33 times. The only terms included in the GLM were depth and its quadratic function (Table 2). This group showed a strong preference for deep and steep areas of more than 600 m depth and slopes of more than 40 m km\(^{-1}\) \((\chi^2 = 107.3, n = 33, \text{df}=4, p \leq 0.001)\).

3.7. *Physeter macrocephalus*

The small sample size of sightings of this species \((n = 15)\) constituted a difficulty when the chi-square test and the GLM were applied, but the encounter rates in the scattergram showed a preferential depth of more than 700m and no patterns regarding slope (Figs. 3 and 4).

3.8. Comparison among species

A Kruskal–Wallis one-way ANOVA was used to compare the distribution among the different species (in monospecific groups). Common dolphins were introduced as two separate groups: Dde99 and Dde9201. Highly significant differences were found for both variables, although the statistic was much higher for depth than for slope (depth: \(k = 456.26, n = 896, p < 0.0001\); slope: \(k = 45.39, n = 896, p < 0.00001\)). A chi-square test of medians showed highly significant differences among the species regarding depth \((\chi^2 = 354.48, n = 896, \text{df}=7, p < 0.0001)\); species fell into two groups: common (Dde9201) and bottlenose dolphins in one group and all the others in another. The first group were found in shallower water while the second group were found in deeper water. For Dde99, the observed values were equal to expected. The chi-square test of medians for slope also showed highly significant differences among the species \((\chi^2 = 21.65, n = 896, \text{df}=7, p = 0.0029)\). As for depth, common dolphins (Dde9201) had more observed values than expected lower than the overall median, and Dde99 equal number. Bottlenose dolphins and sperm whales had observed values equal to expected.

Factor analysis was used to classify the associations between species using both variables at the same time. The factor loadings (Table 3) showed

### Table 3

The factor loading for the seven types of cetacean groups from the factor analysis

<table>
<thead>
<tr>
<th></th>
<th>Factor 1</th>
<th>Factor 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottlenose dolphin</td>
<td>0.3859</td>
<td>-0.4186</td>
</tr>
<tr>
<td>Striped dolphin</td>
<td>*-0.8365</td>
<td>0.2434</td>
</tr>
<tr>
<td>Long-finned pilot whale</td>
<td>*-0.7873</td>
<td>0.3336</td>
</tr>
<tr>
<td>Risso’s dolphin</td>
<td>*-0.7455</td>
<td>0.1037</td>
</tr>
<tr>
<td>Sperm whale</td>
<td>-0.6916</td>
<td>-0.3724</td>
</tr>
<tr>
<td>Beaked whales</td>
<td>*-0.8314</td>
<td>-0.1699</td>
</tr>
<tr>
<td>Common dolphin (1999)</td>
<td>-0.4893</td>
<td>-0.6488</td>
</tr>
<tr>
<td>Common dolphin (except 1999)</td>
<td>-0.0206</td>
<td>0.5425</td>
</tr>
<tr>
<td>Expl.Var</td>
<td>3.4335</td>
<td>1.2393</td>
</tr>
</tbody>
</table>

Expl. Var. is the variance explained by a factor. Marked loadings are >0.7.
that striped dolphins, pilot whales, Risso’s dolphins and beaked whales load strongly and are associated with the first factor, with sperm whales very closely related. In the second factor none of the species loaded more than 0.7, although it was dominated by 1999 common dolphins. Both bottlenose dolphins and common dolphins excluding 1999 were far from the first group in the first factor. In a plot of the factor loadings (Factor 1 vs. Factor 2, Fig. 5), three groups can be clearly distinguished: striped dolphins, pilot whales, Risso’s dolphins, beaked whales and sperm whales in one group, common dolphins excluding 1999 in a second group, and bottlenose dolphins in a third group. Common dolphins in 1999 appear close to the first group.

The stepwise discriminant analysis selected both depth (Wilk’s $\lambda = 0.962, p < 0.000001$) and slope (Wilk’s $\lambda = 0.474, p = 0.00004$) as explanatory variables in the distinction among the 8 monospecific groups considered. The percentage of correctly predicted classifications for the model was high only for two species: striped and common dolphins excluding 1999 (Table 4). Bottlenose dolphins were classified mainly as common dolphins. Common dolphins in 1999 were mainly classified as striped dolphins. The other four species, pilot whales, Risso’s dolphins, sperm whales and beaked whales were classified almost completely as striped dolphins. Hence, the results of the discriminant analysis for the species suggested that at least two groups could be differentiated. One group consisting of striped dolphins, pilot whales, Risso’s dolphins, sperm whales and beaked whales, with little differentiation within it, and another one consisting of common dolphins (Dde9201) and possibly bottlenose dolphins. The situation of common dolphins in 1999 remained unclear, with 43% of the cases assigned as common dolphins and 57% as striped dolphins.

Based on all the previous results, from the Kruskal–Wallis analysis of variance, the factor analysis and the discriminant analysis, a clear
distinction between common and bottlenose dolphins in one (or two) group and striped and Risso’s dolphins, pilot whales, beaked whales and sperm whales in the second group is apparent. We named these groups as shallow-water (SW) and deep-water (DW) groups, respectively, because, according to the results, the first two species seemed to prefer shallow waters while the second group seemed to prefer deeper waters than the first one.

The mean depth and slope for both groups are shown in Table 5. Highly significant differences were found between the two groups of SW and DW, in terms of both depth and slope when a univariate Mann–Whitney U test was performed (depth: $U = 19,821$, $n = 896$, $p < 0.00001$; slope: $U = 77,090$, $n = 896$, $p < 0.00001$). A discriminant function analysis was used to explore the difference between these two groups (Table 6). Since the common dolphin distribution in 1999 was different from that observed in other years, the discriminant analysis was performed in two ways: including Dde99 in the SW group, and excluding it. In the first case, only depth was significant and included in the model (depth: Wilk’s $\lambda = 0.993$, $p < 0.000001$; slope: Wilk’s $\lambda = 0.514$, $p = 0.333$), and a high percentage of the cases were correctly classified (82.1% of the SW and 88.0% of the DW). When common dolphins of 1999 were excluded, again only depth was significant and included in the model (depth: Wilk’s $\lambda = 0.995$, $p < 0.000001$; slope: Wilk’s $\lambda = 0.461$, $p = 0.154$), and the percentage of correctly predicted classifications increased (84.9% of the SW and 89.6% of the DW).

Differences were observed within both groups. The distribution of bottlenose and common
dolphins (1999 excluded) within the SW group, was significantly different both for depth and slope (depth: $U = 11,134.5$, $n = 337$, $p = 0.014$; slope: $U = 10,425.5$, $n = 337$, $p = 0.0011$). Within the DW group also highly significant differences were obtained but only for depth (depth: $K = 32.29$, $n = 517$, $p < 0.0001$; slope: $K = 1.43$, $n = 517$, $p = 0.839$). The chi-square test of medians showed that striped dolphins and pilot whales had more observations than expected lower than the overall median, as opposed to the other 3 species, both for depth and slope. To analyze the differences found within the DW group, pairwise $t$-tests were carried out for depth. The following pairs of species were different: striped dolphins–beaked whales ($t = -4.535$, $n = 301$, $p < 0.00001$), striped dolphins—Risso’s dolphins ($t = -2.408$, $n = 300$, $p = 0.016$), long-finned pilot whales–beaked whales ($t = -4.496$, $n = 202$, $p < 0.00001$), sperm whales–beaked whales ($t = -2.585$, $n = 46$, $p = 0.013$) and Risso’s dolphins–beaked whales ($t = -2.399$, $n = 61$, $p = 0.019$).

### 4. Discussion

This study of seven odontocetes in the north-eastern section of the Alboran Sea indicates that local physiography can play a significant role in their distribution. Depth was the variable with the strongest influence, although slope also played a role for some species. Two distinct groups of species were identified according to their different distribution with respect to depth. Striped dolphins, Risso’s dolphins, pilot whales, beaked whales and sperm whales, all had a preference for deep waters. Common and bottlenose dolphins were more frequently found in shallower waters. These groups were not homogeneous, however; differences found between and within them are discussed below.

Davis et al. (2001) classified cetacean species in the Gulf of Mexico in 4 categories based on diverse criteria, including diving ability, depth preference, phylogenetic relationship and dietary preference. One of their categories, ‘squid-eaters’, included pilot whales, Risso’s dolphin and beaked whales. Sperm whales were assigned to a unique category because of their large body size, and striped dolphins were assigned to the group of oceanic stenellids with preference for deep waters.

The most obvious characteristic common to all species in the DW group was their feeding habits. The five species included in this group have been frequently reported as teutophagic (Mercer, 1975; Clarke and Pascoe, 1985; Würtz et al., 1992; Blanco et al., 1995; Kenney et al., 1995; Santos et al., 1996; Gannon et al., 1997; Pauly et al., 1998; Blanco and Raga, 2000), although some species like striped dolphins have a wider spectrum of target prey. Likewise, and in contrast with the DW group, common and bottlenose dolphins (SW

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**Table 6**

Classification matrix of the discriminant function analysis for the two groups of species (SW = shallow-waters group, and DW = deep-waters group), with two variables in the model (depth and slope)

<table>
<thead>
<tr>
<th>Percent correct</th>
<th>SW</th>
<th>DW</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Including common dolphins in 1999, Wilk’s Lambda: 0.5131, $p &lt; 0.0000$.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SW</td>
<td>311</td>
<td>68</td>
</tr>
<tr>
<td>DW</td>
<td>62</td>
<td>455</td>
</tr>
<tr>
<td>Total</td>
<td>373</td>
<td>523</td>
</tr>
<tr>
<td>(b) not including common dolphins in 1999, Wilk’s Lambda: 0.4599, $p &lt; 0.0000$.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SW</td>
<td>286</td>
<td>51</td>
</tr>
<tr>
<td>DW</td>
<td>54</td>
<td>463</td>
</tr>
<tr>
<td>Total</td>
<td>340</td>
<td>514</td>
</tr>
</tbody>
</table>

Observed classifications in rows, predicted classifications in columns.
group), despite being considered as very opportu-
nistic species with a wide range of target preys
(Cockcroft and Ross, 1990; Klinowska, 1991;
Young and Cockcroft, 1994; Reynolds et al.,
2000), have shown in many dietary studies to have
preference for fish over squid (Barros and Odell,
1990; Young and Cockcroft, 1994; Kenney et al.,
1995; Cordeiro, 1996; Salomón, 1997). Hence, the
classification of odontocetes in the Alboran Sea
according to their depth preference seems to match
a broad classification according to feeding habits.

4.1. Shallow-water group

The Mediterranean Sea is currently experiencing
many human environmental pressures such as
over-exploitation of fish resources and pollution of
different sorts. Until recently, most of these
environmental pressures have affected primarily
the coastal waters of the continental shelf and shelf
edge, where human activity is most concentrated
(EEA, 1999). It is therefore not surprising that the
two species that appear to be declining during the
last decades in the Mediterranean are the common
and the bottlenose dolphin that inhabit these
waters.

4.1.1. Bottlenose dolphin

The quadrats showing a mean depth of 200 to
400 m and very high slope values, where the
highest encounter rates of bottlenose dolphins
were found, are those surrounding the “Seco de los
Olivos” sea mount (Fig. 1). This is an important
area of upwelling induced by several very steep
underwater volcanic mountains rising up to 70 m
in an area of 200 to 500 m, which has been
highlighted for having the highest concentrations
of ichthyoplankton of the northern half of the
Alboran Sea (Gilde Sola, 1994). Bottlenose
dolphins were often observed surrounding these
submarine mountains (Fayos et al., 2000), an area
also heavily exploited by local fishermen. In
general, bottlenose dolphins are widely consid-
etered as benthic or demersal feeders (Günter, 1942;
Tomilin, 1957; Evans, 1980; Barros and Odell,
1990). Although there are no studies regarding the
diet of this species in the research area, a stomach
content study was carried out in Valencia, around
400 km to the north-east along the Spanish coast
(Salomón, 1997). In this study, 95.8% of the
stomach contents was composed of fish, and
87.5% was composed of neritic-benthonic/demer-
sal prey items (hake, Merluccius merluccius, being
the main prey) while only 12.5% was composed of
pelagic prey. In the Ligurian Sea (north-western
Mediterranean Sea) and in Portugal and Galicia
(north-west Spain), fish constituted between 85% and
99% of the contents, with blue whiting
(Micromesistius poutassou), hake, some demersal
Trichiuridae and conger (Conger conger) as main
prey (Relini et al., 1994; Santos et al., 1996; Silva
and Sequeira, 1997). These prey species have a
distribution primarily confined close to the sea
floor, around depths of 100 to 600 meters and
especially at the steeper shelf edge (FAO, 1987).
Thus, the area of “Seco de los Olivos” has ideal
conditions for the presence of the bottlenose
dolphin’s favorite prey. High numbers of these
species of fish (M. poutassou, M. merluccius, T.
trachurus, G. argenteus, Mullus spp., etc.) have
been found over the continental shelf and con-
tinental slope (0–500 m) of the northern Alboran
Sea (Gil de Sola, 1994). Hence, habitats such as the
shelf or shelf edge waters around the north-eastern
Alboran Sea and shelf slopes as that of “Seco de
los Olivos” seem to be largely used by bottlenose
dolphin, and illustrate the importance of local
physiography for this species. These areas will be
considered as priority for protection within the
Project for the Identification of Areas of Special
Interest for the Conservation of Cetacean in the
Mediterranean Spanish Waters set up by the
Spanish Ministry for the Environment.

Our results show this species to be one of the
two most coastal of all odontocetes in the research
area; nevertheless, they occur in higher numbers in
intermediate depths, beyond the continental shelf,
more in accordance with the offshore ecotype of
bottlenose dolphin (Ross, 1984; Hersh and Duf-
field, 1990; Kenney, 1990; Peddemors, 1999). This
agrees with a recent study on phylogeography that
shows the Mediterranean bottlenose dolphins to
be more closely related to the offshore genotype (Natoli and Hoelzel, 2000).

The existence of different, loosely defined ‘ecotypes’ of such a cosmopolitan species as the
bottlenose dolphins makes the attempts of comparison of the distribution of different populations difficult. The findings of this study agree with observations made on the same species in some areas like the Gulf of Mexico (Davis et al., 1998; Baumgartner et al., 2001) and South Africa (Peddemors, 1999) but differ from observations in other areas like the northeastern coast of the United States (Kenney, 1990). In other areas of the Mediterranean Sea the distribution by depth of this species shows great variation, e.g. northwestern Sardinia (Lauriano, 1997), Balearic Islands and Gulf of Vera (personal observations of the authors) and the Strait of Gibraltar (de Stephanis, com. pers.). However, these data are not corrected for sighting effort. Bottlenose dolphins probably take advantage, in each area, of the features that favor the aggregation of locally abundant prey species that can vary from region to region.

4.1.2. Common dolphins

There is no information on the diet of this species in the research area or other parts of the Spanish Mediterranean coast. Nevertheless, according to other studies around the world, this species appears to be an opportunistic feeder (Klinowska, 1991; Young and Cockcroft, 1994; Gannier, 1995; targeting mainly small, neritic, epipelagic fish, especially of the Clupeidae family and some of the Gadidae family, as well as a small amount of cephalopods (Young and Cockcroft, 1994; Kenney et al., 1995; Cordeiro, 1996; Santos et al., 1996).

Several species of small pelagic fish included in the diet of this species are seasonally very abundant along several parts of the continental shelf and upper slope of the Alboran region, and the continental shelf waters of the Alboran area are important breeding sites for some fishes, especially for the Clupeidae and Engraulidae families (Rodriguez, 1990; Rubin et al., 1992; Gil, 1992; Rubin, 1994). In fact, the western section of the Bay of Almería has one of the highest densities of sardines along the Spanish Mediterranean coast (Gil, 1992). In addition, gilt sardines (Sardinella aurita) and needle-fish (Belone belone) constitute an important by-catch of the local purse seining fleet (Abad et al., 1991, 1992; personal communication of local fishermen). This could explain why this region appeared to be heavily used by common dolphins (higher encounter rates, larger group sizes and observations of feeding behaviour). The combination of certain physiographic characteristics in conjunction with winds and currents can result in the existence of locally high productivity related to physiography (Medina, 1974; Rubin et al., 1992). The local physiography of the north-eastern Alboran Sea therefore appears to play an important role in concentrating the prey of common dolphin.

Moreover, a previous study on the movement patterns and orientation of common and bottlenose dolphins in the research region found common dolphins to be oriented in the same direction as the depth contours in the range between 1 and 300 m depth in the western section of the Bay of Almería (Fayos et al., 2000). As in the case of bottlenose dolphins, these areas will be considered as priority for protection within the Project set up by the Spanish Ministry for the Environment for this purpose.

Fig. 3 shows a slight bimodality in the plot of encounter rate vs. depth. An apparent bimodality in distribution by depth of common dolphins has been suggested before for the north-east Atlantic (Forcada et al., 1990; López, A. com. pers.), although no clear evidence exists for this. It has been suggested that this apparent bimodality could mean the co-existence of two sympatric populations, one neritic and one pelagic (Forcada et al., 1990), but it could also be due to age/sex segregation. Further research is needed to address this issue.

Common dolphins are present along most coasts world-wide in temperate, tropical and subtropical areas, mainly over the continental shelf, although they can be found in all depth ranges (Evans, 1994; Forcada and Hammond, 1998; Peddemors, 1999) and our results agree with this. On the other hand, it has been indicated that this species preferentially travels over underwater escarpments (Hui, 1979, 1985; Selzer and Payne, 1988; Evans, 1994), which does not seem to be the case in the north-eastern Alboran Sea. Hui (1979) suggested that common dolphins prefer prominent
underwater topography because these features promote upwelling and therefore primary and secondary production, which in turn would attract great numbers of anchovies, part of the diet of these dolphins. In the case of the Alboran Sea, primary production is higher in coastal areas due to the particular oceanographic dynamics of the region, and sardines (probably more important in the diet of common dolphins in this area because its biomass is much higher than that of anchovies) are very abundant in those coastal regions over the continental shelf (Abad et al., 1991, 1992; Gil, 1992), which could explain the lack of specific preference for steep areas shown by this study.

During the summer of 1999, a pronounced drop in sea surface temperature (SST) was recorded coinciding in time with the breeding season of the sardine along the southern coast of Almería. The temperature dropped drastically in a few days (a result of an unusually strong westerly wind), to temperatures 8–10°C lower than the normal summer SST (15–16°C versus 23–26°C) (personal observations of the authors). Several inquiries among fishermen in the area revealed that during the summer of 1999 the sardine catch dropped to a minimum along the coasts whereas sardine predators such as the horse mackerel (Trachurus trachurus) and mackerel (Scomber scomber) increased. The unusual abundance of such predators or the sudden sea surface temperature drop, which could lead to the death of most of the sardine larvae and juveniles, could explain the scarcity of sardines along the Andalusian coast during the summer of 1999. The scarcity of sardines and the cooler sea surface temperature coincided also with a displacement in the distribution of the common dolphins during that summer towards deeper areas. Hence, sightings of common dolphins in deep waters, where the most abundant small delphinid is the striped dolphin, increased considerably as did the number of mixed groups of both species (34.6% in 1999 against an average of 17% for the other years—ranging from 0 to 26%) (García et al., 2000; personal observations of the authors). The fact that the GLM did not fit very well for Dde99 was likely a combination of small sample size and that there were variables other than physiography influencing their distribution to a greater extent.

4.2. Deep-water group

The other species considered in this study have very different feeding habits from the two previous ones. The striped dolphin is considered to have opportunistic feeding habits but seems to prefer some oceanic epi or meso-pelagic fish, mainly of the Gadidae family, Myctophidae family, and others, but especially several species of oceanic meso-pelagic cephalopods that mainly inhabit oceanic waters (Blanco et al., 1995; Kenney et al., 1995; Santos et al., 1996; Pauly et al., 1998). The long-finned pilot whale, considered to be predominantly a squid-eater (Mercer, 1975; Kenney et al., 1995; Gannon et al., 1997; Pauly et al., 1998), feeds not only on cephalopods but also occasionally on some pelagic fish (Desportes and Mouritsen, 1993; Santos et al., 1996; Pauly et al., 1998).

Risso’s dolphins are known to be exclusively teutophagic (Clarke and Pascoe, 1985; Würtz et al., 1992; Kenney et al., 1995), and their most common prey species are from the Histiotethidae, Ommastrephidae, and Sepiidae families (Gannier, 1995; Santos et al., 1996). Species of the family Ziphiidae appear to feed also only on cephalopods, and their most common prey species are from the family Histiotethidae (Kenney et al., 1995; Santos et al., 1996; Blanco and Raga, 2000), which are oceanic and meso or bathypelagic inhabiting depths of around 1000 m, with a preference for escarpments (FAO, 1987; Guerra, 1992). In general, the squids that constitute the main prey of this second group, usually inhabit offshore oceanic waters, mainly around depths of 600 to more than 1000 m, and preferentially in areas of steep slope such as submarine canyons, escarpments, etc. (Riedl, 1983, FAO, 1987; Guerra, 1992). In the case of these deep sea squid eaters, the distribution of the predators appears to match also the habitat of their prey.

In a comparison among species, the DW group was non-homogeneous in terms of distribution with respect to depth, with significant differences within the group. A gradient of depth preferences
within this group was apparent based on the median and mean depth of encounters for each species (Table 1). Species were distributed by depth as follows: striped dolphins (with the lowest mean), long-finned pilot whales, sperm whales, Risso’s dolphin and beaked whales (with the highest mean). This would explain the pairwise differences obtained with the \( t \)-test: although one element is very similar to the next one in a gradient, the ends accumulate enough differences between them to be statistically significant. But these species all showed a clear preference for waters deeper than 600 m and areas with intermediate or high slopes.

The results of this study are in accordance with the description of these five species in other areas as oceanic species with preference for deep waters over 500 m (Gannier, 1995; Baumgartner, 1997; Gannier, 1998; Davis et al., 1998; Peddemors, 1999; Baumgartner et al., 2000). Baumgartner (1997) defined the slope class of 41.6 to 402.5 m \( \times \) 1.1 km\(^{-1} \) as highly preferred for Risso’s dolphin in the Gulf of Mexico. In our study, the divisions of the slope classes were performed at fixed intervals of 20 m \( \times \) 1.1 km\(^{-1} \), and therefore, a similar class to that defined by Baumgartner would include 8 out of 10 of our classes. If we perform such a division, the same result as Baumgartner is obtained. The difference in criteria for defining the classes (equal effort for Baumgartner and equal intervals of slope for us) could explain the difference in results.

As mentioned above, based on the literature, striped dolphins appear to feed not only on squids but also on pelagic fish. Long-finned pilot whales also feed sometimes on fish, although not as much as striped dolphins. This fact separates these species from Risso’s dolphins, sperm whales, and beaked whales, which seem to feed exclusively on squid. This gradient of feeding habits appears to coincide with the gradient in their distribution by depth.

4.3. Implications for management

In the context of designing a marine protected area (MPA) in the Gully (Nova Scotia), Hooker et al. (1999) stated: “In the marine environment, species’ spatial distributions may be determined by both fixed spatial features such as topography and variable oceanographic features such as sea surface temperature and salinity… . It is therefore critical in any assessment of an area for protection that the relative importance of these fixed and fluid environmental characteristics be investigated.”

It is clear that in a region of complex oceanography such as the Alboran Sea, physiography is not the only factor affecting the distribution of cetaceans. Oceanographic variables are of paramount importance in this area, but they are fluid features that change very quickly over time, even from day to day, while physiography stays fixed. Therefore, physiography has been chosen here as a first tool for highlighting the importance of certain regions of the Alboran basin for the conservation of bottlenose and common dolphins.

The final aim of the Spanish Ministry of the Environment’s Program for the Identification of Areas of Special Interest for the Conservation of Cetaceans in the Spanish Mediterranean is to identify areas that will be designated as MPAs. From the practical point of view, in a highly dynamic environment as the Alboran Sea, in which the oceanographic features are changing so quickly, it would be very important for the relevant authorities in charge of marine management to have a “fixed” reference on which to base the future MPA, because in area-based conservation, sites are typically chosen based on unchanging physical features. From here, research will extend to other parts of the Alboran basin and its adjacent Mediterranean and Atlantic waters with analysis of abundance and habitat use incorporating other variables such as sea surface temperature, salinity and human activities.

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