

## Original Articles

## Living apart together: Niche partitioning among Alboran Sea cetaceans

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## ABSTRACT

Co-occurring species are expected to distribute themselves unevenly throughout ecological niche dimensions to avoid competitive exclusion. However, few studies have previously investigated spatial and trophic factors structuring an entire cetacean community. Here, we combined density surface models (DSMs) with two dimension ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) isotopic niche spaces in order to identify the mechanistic processes underlying niche partitioning for the most abundant cetacean species inhabiting the Alboran Sea: the long-finned pilot whale (*Globicephala melas*), the Cuvier's beaked whale (*Ziphius cavirostris*), the Risso's dolphin (*Grampus griseus*), the bottlenose dolphin (*Tursiops truncatus*), the striped dolphin (*Stenella coeruleoalba*), and the short-beaked common dolphin (*Delphinus delphis*). DSMs provide a spatially-explicit assessment of species distribution through key spatial and environmental gradients, whereas isotopic niches characterize habitat and resource use. Our isotopic niche approach pointed to habitat and/or trophic segregation between the small (striped and short-beaked common dolphins) and large-sized cetacean species (Risso's and bottlenose dolphins, and long-finned pilot whales). Conversely, DSMs suggested a larger degree of spatial segregation among species by depth, with some overlap for offshore species (long-finned pilot, Cuvier's beaked whales and Risso's dolphins) and also between bottlenose and common dolphins. Thus, both components of the ecological niche apparently played an important role in explaining niche partitioning among species, which, in turn, might explain the high abundance and diversity of cetaceans in the Alboran Sea. Further, when both methodologies were applied in isolation, the structure and functioning of this cetacean community was poorly resolved. The combination of both approaches is therefore desirable when investigating niche partitioning among ecologically similar species within communities.

## 1. Introduction

Within communities, species are expected to distribute themselves unevenly throughout different niche dimensions (n-hypervolume *sensu* Hutchinson, 1957) thereby avoiding competitive exclusion (Gause, 1934; Hutchinson, 1957; Pianka, 1973; Schoener, 1974). These dimensions include both biotic (i.e. resources that species use; “Eltonian niche”, Elton 1927) and scenopoietic axes (i.e. environmental

conditions where species perform; “Grinnellian niche”, Grinnell 1917). Identifying the most influential ecological niche dimensions that structure communities is fundamental to approach a panoply of important ecological questions including resource use and niche partitioning, species abundances and distribution, geographic diversity or adaptation to changing environmental conditions (McGill et al., 2006; Geange et al., 2011). Thereby, these understanding can help in the design and improvement of conservation measures that allow niche

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conservationism (Wiens et al., 2010).

The renewed interest in the niche concept and its application to different ecological questions has recently emerged as a consequence of the computational and technological advances in modelling techniques (i.e. multivariate statistics or species distribution models) to inform about the Grinnellian niche (Rödder and Engler, 2011). On the other hand, the Eltonian niche, traditionally approached through conventional stomach content analysis, can be now explored throughout stable isotope approaches. So, the isotopic niche concept has arisen as a potentially powerful approach to inform questions traditionally considered within the broad domain of the ecological niche studies (Newsome et al., 2007). This concept includes both bionomic and scenopoetic axes because  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures inform on habitat use and trophic position, respectively (Post, 2002; Bearhop et al., 2004; Newsome et al., 2007). Furthermore, stable isotopes are also well suited to investigate the niche breadth using the variance of the stable isotope composition (Bearhop et al., 2004) or other metrics of individual isotopic variation (reviewed in Bolnick et al., 2002).

The Alboran Sea is an important feeding and breeding ground for cetaceans, and one of the most important areas in the Mediterranean for marine mammal conservation (Cañadas et al., 2005; Micheli et al., 2013). The most frequently recorded species in the area are pilot whales (*Globicephala melas*), bottlenose dolphins (*Tursiops truncatus*), striped dolphins (*Stenella coeruleoalba*) and common dolphins (*Delphinus delphis*). Although less frequently, the Risso's dolphin (*Grampus griseus*) and Cuvier's beaked whale (*Ziphius cavirostris*) also occur in this area (Cañadas and Sagarminaga, 2000; Cañadas et al., 2002, 2005; Cañadas, 2006; Cañadas and Hammond, 2006, 2008; Cañadas and Vázquez, 2014), as well as sperm whales (*Physeter macrocephalus*) and fin whales (*Balaenoptera physalus*) (Cañadas et al., 2005). The observed species richness and abundance might be partially explained by niche partitioning among cetacean species (Giménez et al., 2017a). However, to date no study has considered all common cetaceans inhabiting the Alboran Sea in conjunction. Accordingly, the roles of trophic and spatial factors structuring this cetacean community are poorly known. In general, few studies have previously simultaneously investigated both spatial and trophic factors structuring cetacean communities (e.g. Gross et al., 2009; Giménez et al., 2017a), nevertheless it is common in other taxa such as fish (Sala and Ballesteros, 1997; Piet et al., 1999; Garrison, 2000) and seabirds (Wilson, 2010; Navarro et al., 2013; Navarro et al., 2015). This is partly because of the lack of data for entire communities, but also because parametrizing continuous variables informing on particular niche dimensions might be challenging, thus commonly resulting in inoperative and disused niche dimensions.

The objective of the study is to investigate niche partitioning among the main cetacean species inhabiting the Alboran Sea. In particular, we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in skin samples as a proxy for the bionomic and scenopoetic niche components, whereas Density Surface Models (DSMs) based on cetacean sightings and spatially-explicit information such as chlorophyll-*a*, sea surface temperature, depth, and primary productivity were used to approximate the scenopoetic niche. We provide an evaluation of the main trophic and spatial drivers of the structure and functioning of this cetacean community, which may find useful applications for management and conservation purposes.

## 2. Material and methods

### 2.1. Study area

The Alboran Sea, located in the western Mediterranean Sea, is the transitional zone between the Atlantic Ocean and the Mediterranean Sea. It is one of the western Mediterranean areas with the highest rates of primary production (Vargas-Yañez et al., 2010; Rodríguez, 2011). It is characterized by a complex hydrology with Atlantic surface currents and deep Mediterranean waters, two main anticyclonic gyres, strong fronts and upwelling areas (Rubín et al., 1992; Rodríguez, 2011). All

these features make the Alboran Sea the hydrological motor of the western Mediterranean basin (Rodríguez, 1982) and promotes its high biodiversity (Gascard and Richez, 1985; Parrilla and Kinder, 1987; Tintoré et al., 1988; Rubín et al., 1992; Templado, 1993). The high cetacean diversity found in the Alboran Sea may be explained by the high heterogeneity in habitat types (e.g. coastal habitat, deep-waters, canyons, rocky bottoms, sandbanks, sea mountains) present in the basin and the close proximity between habitats. The narrow continental shelf means that coastal and deep waters are relatively close. Moreover, its location is such that Atlantic and Mediterranean species co-occur here, including several migratory species such as the sperm and the fin whale. This results in a relatively high cetacean diversity compared with other Mediterranean areas of comparable size (Coll et al., 2010).

### 3. Density surface modelling

Cetacean sightings were collected in the Alboran Sea from the research vessel "Toftevaag" from summer months between 1992 and 2009. The surveyed area was sailed at a medium speed of 5 knots with a constant sighting effort. Although the study area was not sampled with a systematic design due to logistic constraints (see Cañadas and Hammond, 2008), cruise tracks crossed depth contours and covered as much area as possible. Two trained observer occupied the lookout in 1 h shifts to avoid visual fatigue. Observations were done during daylight with a visibility over 3 nmi by naked eyes assisted with a 7x50 binoculars. Adequate sighting conditions were considered with Douglas sea state of 2 or lower. A total of 528 sightings of long-finned pilot whales, 108 sightings of Risso's dolphins, 421 sightings of bottlenose dolphins and 71 sightings of Cuvier's beaked whales were obtained during 67,900 km of tracks on effort (with adequate searching conditions, i.e. sea state below 3 Douglas, Appendix A). The research area was divided into regular grid cells of 2 x 2 min latitude–longitude of resolution. Several spatial and environmental variables (latitude, longitude, depth, the standard deviation of depth, slope, distance from the coast and from several isobaths, chlorophyll *a*, sea surface temperature, primary productivity and distance to Seco de los Olivos i.e. a seamount south of Almería) were extracted for each grid cell and used in the models as covariates. Depth was obtained from ETOPO (<http://maps.ngdc.noaa.gov/viewers/wcs-client/>) and an average was obtained for each grid cell. Additional variables were obtained through Geographic Information System analysis, namely latitude and longitude, slope, distance from the coast, distance from 200, 500 and 1000 m depth contours and distance to Seco de los Olivos. Environmental dynamic variables, namely sea surface temperature, chlorophyll *a*, and primary productivity were downloaded from NOAA Ocean Watch ([http://las.pfeg.noaa.gov/oceanWatch/oceanwatch\\_safari.php](http://las.pfeg.noaa.gov/oceanWatch/oceanwatch_safari.php)), in all cases monthly averages for every month of every year. Mean values for the survey period analyzed were then used as covariates.

Density surface models (DSM) were performed to investigate the spatial abundance of the cetacean species inhabiting the Alboran Sea following the methodology of Cañadas and Hammond (2006, 2008). Prior to running the models, all on-effort transects were divided into small segments (mean = 2.8 km) each with homogeneous type of effort and low variability in environmental features along them. DSM were chosen due to the flexibility and statistical power to predict the abundance of animals combining information of line transect sampling with spatial covariates (Hedley et al., 1999; Buckland et al., 2004; Miller et al., 2013). Spatial abundance estimates were performed in five steps (Cañadas and Hammond, 2006, 2008): i) Estimation of the detection function in DISTANCE 6.0 using the multiple covariate distance sampling (MCDS) method (Marques, 2001; Thomas et al., 2002), ii) Estimation of the ESW (Effective Strip Width) in each segment, iii) Modelling the abundance of groups using a Generalized Additive Model (GAM), iv) Modelling of group size using a GAM, v) Combination of steps III and IV and extrapolation to the whole study area to obtain the final density of animals (see Appendix B for more details). Spatially-

explicit abundance outputs were joined with data analyzed in Giménez et al. (2017a) for striped and common dolphins that followed the same methodology

### 3.1. Identification of high-density areas and spatial overlap

The areas encompassing the highest 40% of estimated abundances for each species (hereafter, core distribution areas) were selected following the methodology of Cañadas and Vázquez (2014) and also applied by Giménez et al. (2017a). The methodology consisted of sorting all grid cells by their estimated abundance in decreasing order, assigning them the percentage of the total estimated abundance and selecting those that comprised the highest 40% of abundance in the whole area of distribution. The segregation between each pair of species is calculated as the relative number of grid cells not shared by one species with respect to their whole core spatial distribution, with values ranging from 0 (complete overlap) to 100 (complete segregation). The 40% threshold used for identifying the core distribution areas is the same percentage used for depicting those main isotopic areas within the multidimensional  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  niche spaces (i.e.  $\text{SEA}_B$ , see below), thus allowing a comprehensive comparison between habitat use and trophic preferences.

### 3.2. Biological sampling

Skin biopsies from free-ranging long-finned pilot whales ( $n = 50$ ), Risso's dolphins ( $n = 5$ ), and bottlenose dolphins ( $n = 22$ ) were obtained between 2001 and 2013. A crossbow and a modified darts with sterilized stainless-steel biopsy tips was used to obtain skin biopsies following a minimally invasive protocol described in Giménez et al. (2011). Adults and sub-adults were the main targets and no calves were sampled. Samples were frozen at  $-20^\circ\text{C}$  after collection. Additionally, stable isotope data presented by Giménez et al. (2017a) of adults and sub-adults striped ( $n = 61$ ) and common dolphins ( $n = 20$ ) were used to perform a community wide analysis for the Alboran Sea. These additional samples were obtained using the same methodology (Giménez et al. (2017a)).

### 3.3. Laboratory analyses

Stable isotopes were used as ecological tracers of habitat ( $\delta^{13}\text{C}$ ) and trophic position ( $\delta^{15}\text{N}$ ). Carbon stable isotope values characterize the main source of primary production incorporated into food webs (DeNiro and Epstein, 1978) and provides insights about the inshore versus offshore and benthic versus pelagic consumption (Rubenstein and Hobson, 2004; Fry, 2006), while nitrogen stable isotope chiefly reflects the trophic position occupied by each species in the trophic web (DeNiro and Epstein, 1981; Post, 2002). Stable isotope analyses were performed in skin samples following standard protocols, where samples were dried at  $60^\circ\text{C}$  during 48 h and powdered with a mortar and pestle. Lipids were removed using sequential extractions with chloroform:methanol solution (2:1) because high lipid concentration can skew the values by decreasing the  $^{13}\text{C}$  content (DeNiro and Epstein, 1978). Subsamples of powdered material (0.3 mg) were weighed into tin capsules for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  determinations. Isotopic analyses were carried out at the Laboratorio de Isótopos Estables de Estación Biológica de Doñana (LIE-EBD, Spain; [www.ebd.csic.es/lie/index.html](http://www.ebd.csic.es/lie/index.html)). All samples were analyzed using a continuous flow isotope-ratio mass spectrometry system by means of Flash HT Plus elemental analyser coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). The isotopic compositions are reported in the conventional delta ( $\delta$ ) per mil notation (‰), relative to atmospheric  $\text{N}_2$  ( $\delta^{15}\text{N}$ ) and Vienna Pee Dee Belemnite ( $\delta^{13}\text{C}$ ). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of  $\pm 0.2\text{‰}$  and  $0.1\text{‰}$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively.

### 3.4. Stable isotope analyses

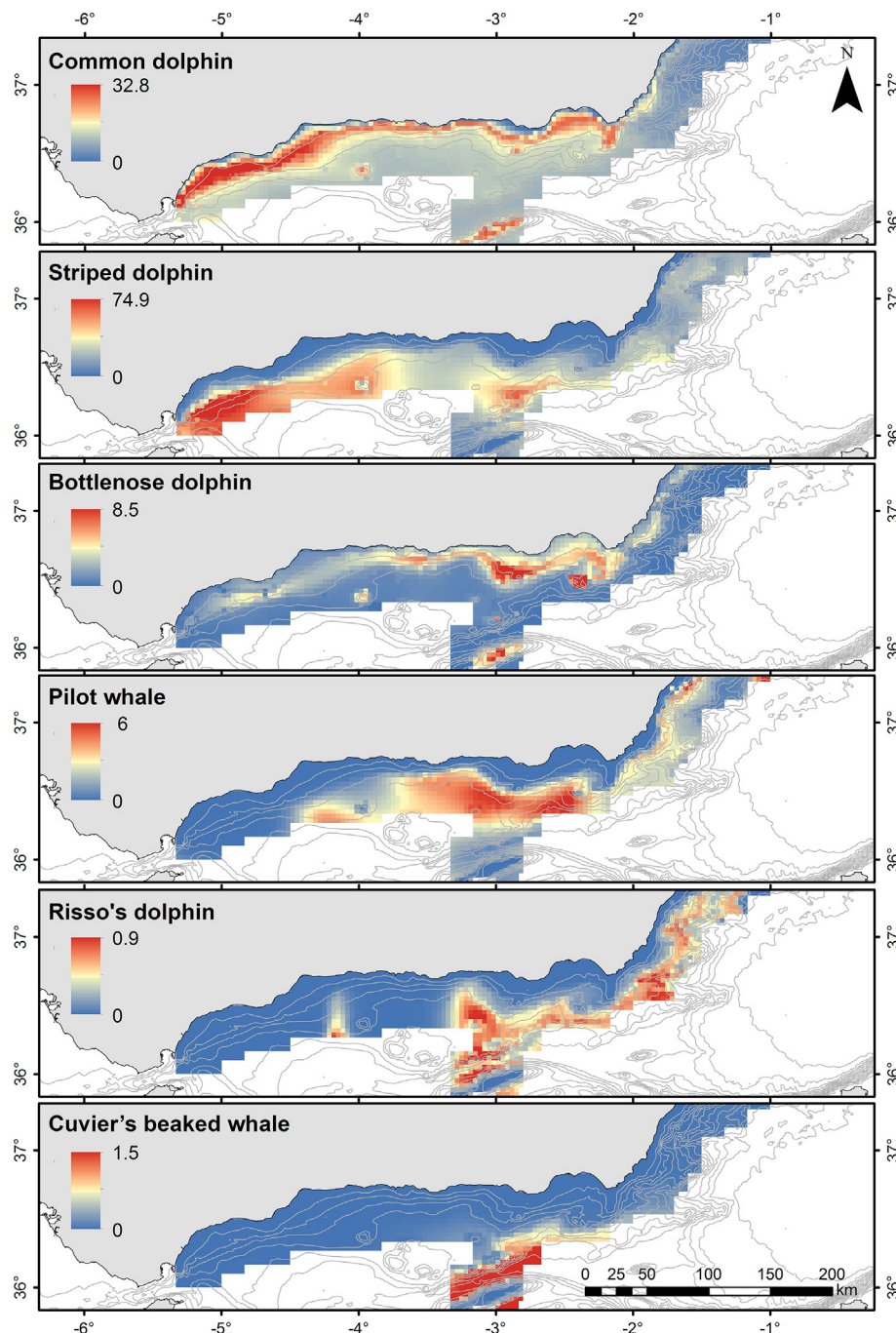
Standard ellipses areas ( $\text{SEA}_C$ , i.e. area containing approximately 40% of the data; Jackson et al., 2011) and Layman metrics (Layman et al., 2007) were used to quantify isotopic niche variation among species. Some Layman metrics are sensitive to extreme data points (i.e.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  range (NR and CR) and Total Area (TA) measured via the convex hull), so they were avoided for further analysis. Instead, we used the *mean distance to centroid* (CD) which is a measure of the average degree of trophic diversity, the *mean nearest neighbour distance* (MNND) as a measure of the overall density or packing of individuals (i.e. trophic redundancy) and the *standard deviation of nearest neighbour distance* (SDNND), as a measure of the evenness of packing of individuals in the bi-plot space. All these metrics were bootstrapped ( $n = 1000$ ) to derive confidence limits (Jackson et al., 2012). Additionally,  $\text{SEA}_B$  (Bayesian SEA) was used to quantify the niche width and overlap between species. The Bayesian framework takes into account the uncertainty in the sampled data and naturally incorporates the error arising from the sampling process, propagating it through to the derived metric (Jackson et al., 2011). Furthermore the estimation via Bayesian inference allows robust comparison to be made among data sets comprising different sample sizes (Jackson et al., 2011).  $\text{SEA}_B$  was computed using 10,000 posterior draws. Differences in stable isotopes among species were analyzed by one-way ANOVA and a Tukey Honest Significant Difference test as a post-hoc analysis for each stable isotope after checking the homoscedasticity with a Levene's test. The open-source program R v.2.6.2 (<http://cran.r-project.org/>) was used for all the isotopic analysis. The SIBER package was used to calculate all isotopic niche metrics (Jackson et al., 2011).

## 4. Results

### 4.1. Spatial dimension

Density surface models show that segregation of species core areas is present in almost all species studied (Figs. 1 and 2, Table 1). Two main groups can be differentiated, bottlenose and common dolphins tend to distribute near the coast while the rest can be considered off-shore species. Depth is the main enabler of species coexistence, being statistically significant in all spatial models (Appendix C). Bottlenose dolphins tend to occur in areas of 400–500 m depth and close to the seamount “Seco de los Olivos” ( $36^\circ31'00''\text{N}$  /  $2^\circ49'59''\text{W}$ ) while common dolphins aggregate in area from 200 to 400 m depth with higher density of groups towards the cooler western waters but with larger groups in the eastern part of the Alboran Sea (excluding the Gulf of Vera). Regarding offshore species, pilot whales abundance is high between 500 m and 2500 m with a steep decrease in shallower waters, Risso's dolphins are found between 500 and 2000 m depth with steep decrease below and over those depths, Cuvier's beaked whale present a more or less steady increase of abundance from over 500 m toward deep waters but concentrated around the Alboran Island, and finally striped dolphins generally preferring waters between 600 and 1800 m depth. The deviance explained in the four models of abundance of groups ranges between 11.3% for bottlenose dolphins to 40.7% for Cuvier's beaked whales. The more restricted habitat for a population, given that adequate covariates are selected, the more variance gets explained. A species with a broader habitat is found more widely dispersed in terms of ranges of environmental features, and therefore it is more difficult to explain the variability (deviance explained) with the available covariates. This is the case for bottlenose dolphins, which despite having a strong attraction towards the Seco de los Olivos, it is also found elsewhere. The deep divers, however, and especially Cuvier's beaked whales, have a more restricted range, both in terms of depth and longitude (restricted to the eastern part) and therefore the model manages to explain more of its reduced variability with the available covariates.





**Fig. 1.** Abundance distribution of common, striped, bottlenose dolphins, pilot whales, Risso's dolphins and Cuvier's beaked whales in the Alboran Sea. Higher abundance depicted in red and lower abundances in blue. Isobath lines for each 200 m are represented in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 4.2. Trophic dimension

The isotopic-biplot clearly identifies two isotopic groups; one composed by the small cetacean species (*i.e.* common and striped dolphins) and another by the deep divers (*i.e.* Risso's dolphins and pilot whales) and the bottlenose dolphins. Statistical difference were found among species in carbon (Fig. 3;  $F_{(4,153)} = 92.63$ ,  $p\text{-value} < 0.001$ ) and nitrogen stable isotopes (Fig. 3;  $F_{(4,153)} = 97.93$ ,  $p\text{-value} < 0.001$ ). All species segregate by both stable isotopes except between striped and common dolphins and between pilot whales and Risso's dolphins, where no statistical differences were found for any of the tracers (Fig. 3). Furthermore, bottlenose dolphins and Risso's dolphins did not

present differences in  $\delta^{15}\text{N}$ , while bottlenose dolphins and pilot whales were similar in  $\delta^{13}\text{C}$  (Fig. 3). Segregation in the first group (small cetaceans) is smaller compared to the second group (Fig. 4, Tables 2 and 3). Regarding the isotopic niche, striped dolphins present the smallest isotopic standard ellipses area ( $\text{SEA}_b$ ) followed by pilot whales, common, bottlenose and Risso's dolphins. All species present similar mean distance to the centroid ( $\text{CD}_b$ ), except the bottlenose dolphins that show a higher distance. The mean nearest neighbor distance ( $\text{MNND}_b$ ) is higher for common and bottlenose dolphins and the standard deviation of the nearest neighbor distance ( $\text{SDNND}_b$ ) is higher for common and bottlenose dolphins (Fig. 5, Appendix D).

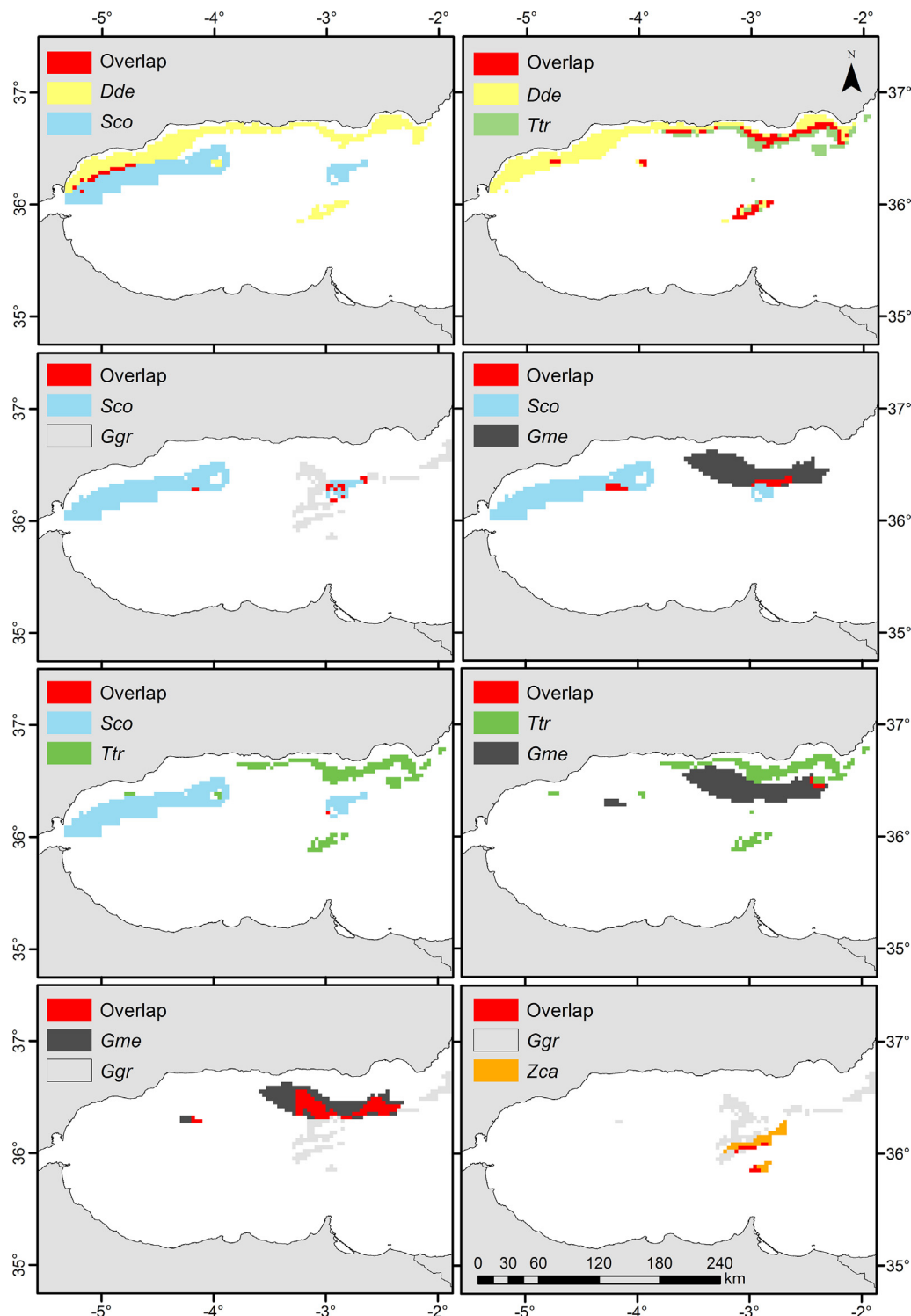


Fig. 2. Spatial overlap between all species in the Alboran Sea. Combinations of species that do not present overlap are not shown. Dde: Common dolphin, Sco: Striped dolphin, Ttr: Bottlenose dolphin, Ggr: Risso's dolphin, Gme: Pilot whale, Zca: Cuvier's beaked whale.

## 5. Discussion

Niche partitioning has been observed in several species of a range of different taxa (e.g. Tilley et al., 2013; Bocher et al., 2014), including cetacean species (e.g. Méndez-Fernandez et al., 2012, 2013; Fernández et al., 2013; Giménez et al., 2017a,b) to reduce competition. Here we used a multidisciplinary approach, based on DSMs and stable isotope analysis, to unravel how an entire cetacean community is structured within a multivariate niche-space. We demonstrated that different

species within this community segregated both in the spatial and/or the trophic niche dimensions allowing coexistence. In part, this may explain the high abundance and diversity of cetaceans in the Alboran Sea in conjunction with the high productivity of the basin (Font, 1987; Videau et al., 1994; Gascard and Richez, 1985; Parrilla and Kinder, 1987; Tintoré et al., 1988; Rubín et al., 1992; Templado, 1993), and pointed to the contrasting ecological needs and, potentially, conservation requirements for these co-occurring species.

According to our results, the spatial overlap is mainly occurring in

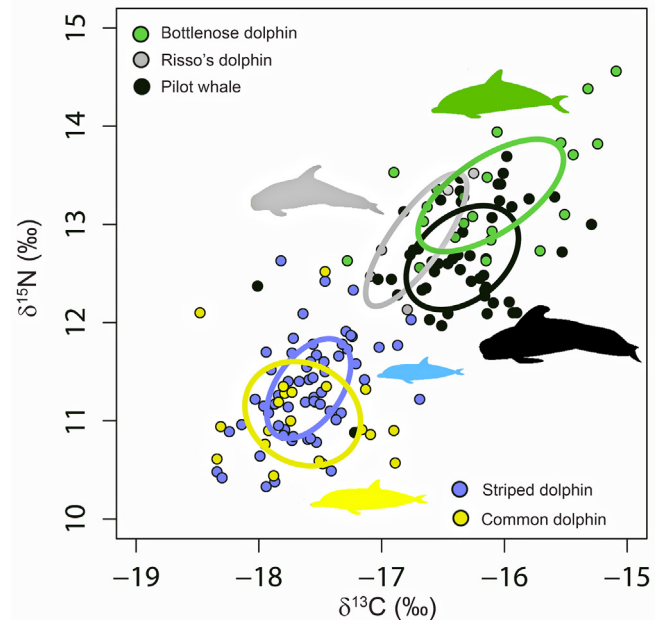
**Table 1**

Spatial core area segregation between the species (should be read as the percentage of segregation of the area of species in the first column versus the ones of the first row). Dde: Common dolphin, Sco: Striped dolphin, Ttr: Bottlenose dolphin, Ggr: Risso's dolphin, Gme: Pilot whale, Zca: Cuvier's beaked whale.

	Dde	Sco	Ttr	Gme	Ggr	Zca
Dde	–	95.17	76.99	100	100	100
Sco	94.12	–	99.65	90.66	94.81	100
Ttr	51.50	99.40	–	97.01	100	100
Gme	100	88.66	97.90	–	62.18	100
Ggr	100	92.46	100	54.77	–	93.97
Zca	100	100	100	100	76.92	–

deep waters of the Alboran Sea between pilot whales and Risso's dolphins, as well as between this latter species and Cuvier's beaked whales. Common and bottlenose dolphins co-occur in coastal waters, but segregate trophically as indicated by the observed differences in their isotopic niche spaces. Among offshore species, depleted isotopic values observed for striped dolphins suggest a trophic segregation between this small species and the other two, large-sized cetaceans, *i.e.* Risso's dolphins and pilot whales. In contrast, these two latter species showed similar isotopic composition, thus pointing to trophic similarity and a certain degree of competition. However, isotopic similarity does not necessarily imply real ecological or dietary overlap, as different food resources may present similar isotopic compositions (Moreno et al., 2010; Ramírez et al., 2011).

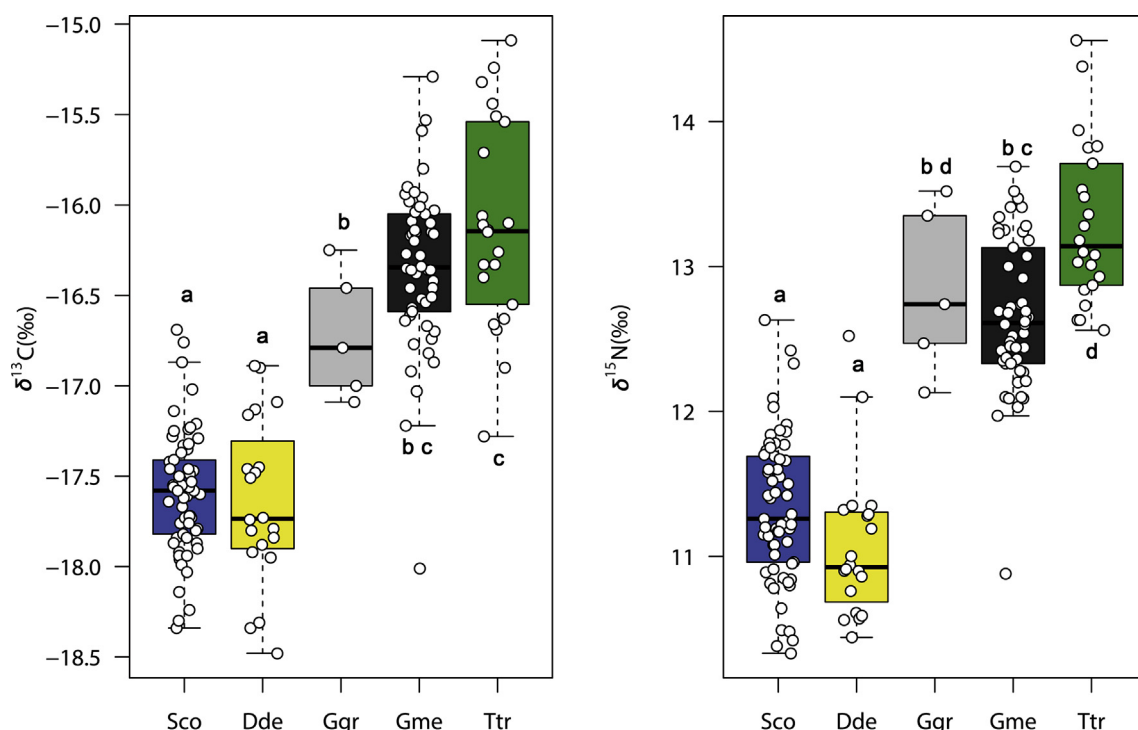
Interspecific competition occurs when co-occurring species rely on overlapping limited resources (Pianka, 1981; Schoener, 1982). In the contrary, coexistence in a stable competitive equilibrium can be expected when feeding resources are abundant (González-Solís et al., 1997). The Alboran Sea, unlike other oligotrophic Mediterranean areas, is considered a highly productive area due to its hydrographic characteristics (Font, 1987; Videau et al., 1994). Then, we do not expect that deep-divers are food-limited, so a competitive equilibrium is plausible. Nevertheless, no information about their diets in the Alboran Sea is available, so they might be feeding on abundant preys and/or on



**Fig. 4.** Standard Ellipse Area corrected (SEAc). Striped dolphins in blue, common dolphins in yellow, Risso's dolphins in grey, pilot whales in black and bottlenose dolphins in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

different food resources with similar isotopic compositions. To what extent they are competing remains therefore elusive. In Galician waters (north-western Iberian Peninsula) a similar stable isotope topology is found (Méndez-Fernández et al., 2013) indicating a possible niche conservatism in these species that should be tested in future studies.

Bottlenose dolphins stand out as the top predator of the cetacean community in the Alboran Sea, as revealed by its relatively high mean  $\delta^{15}\text{N}$  value (DeNiro and Epstein, 1981; Post, 2002), whereas its high



**Fig. 3.** Boxplot of carbon and nitrogen stable isotopes. Raw data is plotted as white dots. Post-hoc Tukey Honest Significant Difference test between species is denoted by different letters. Dde: Common dolphin, Sco: Striped dolphin, Ttr: Bottlenose dolphin, Ggr: Risso's dolphin, Gme: Pilot whale, Zca: Cuvier's beaked whale.

**Table 2**

Summary table of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes values (‰). Mean, standard deviation (sd), minimum (Min), and maximum (Max) values for each species.

	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean $\pm$ sd	Min to Max	Mean $\pm$ sd	Min to Max
Striped dolphins	$-17.59 \pm 0.34$	-18.34 to -16.69	$11.33 \pm 0.5$	10.33 to 12.63
Common dolphins	$-17.64 \pm 0.46$	-18.48 to -16.89	$11.07 \pm 0.52$	10.44 to 12.52
Long-finned pilot whales	$-16.34 \pm 0.45$	-18.01 to -15.29	$12.66 \pm 0.52$	10.88 to 13.69
Risso's dolphins	$-16.72 \pm 0.36$	-17.09 to -16.25	$12.84 \pm 0.59$	12.13 to 13.52
Bottlenose dolphins	$-16.11 \pm 0.58$	-17.28 to -15.09	$13.29 \pm 0.58$	12.56 to 14.56

$\delta^{13}\text{C}$  values pointed to a diet composed mainly of benthic species (Fry, 2006). Nevertheless, its food preferences seem to be diverse due to its width isotopic niche area and the high scores in all Layman metrics considered. This large variation in isotopic values is typical from generalist predators feeding on a considerable number of prey items (e.g. Tilley et al., 2013) or generalist populations composed by specialist individuals feeding on different food resources (Bolnick et al., 2003). These results are in concordance with the stomach contents results of bottlenose dolphins from western Mediterranean Sea, where this species feeds on at least 19 prey species with high predominance of hake *Merluccius merluccius* and European conger *Conger conger* (Blanco et al., 2001). Furthermore, it is also in accordance with other food web studies around Europe where bottlenose dolphins play a top role in the system consuming a large variety of prey (e.g. Giménez et al., 2017b; Hernández-Milián, 2014; Torres et al., 2013). Although being the top predator of the cetacean community, some isotopic overlap is found with the deep-diving species. This might be explained, in part, because bottlenose dolphins can supplement their diet with a certain amount of cephalopods species such as the common octopus *Octopus vulgaris* and the common squid *Loligo vulgaris* (Blanco et al., 2001), prey that are also commonly consumed by deep-diving species (i.e. Risso's dolphins and pilot whales). In this particular case, niche segregation seems to occur preferentially in the spatial dimensions as bottlenose dolphins preferentially occur in coastal waters (around 400 m depth) and close to a sea mountain (i.e. Seco de los Olivios), whereas deep-diving species are mainly associated to deeper waters. In addition, the spatial overlap between bottlenose and common dolphins may not indicate trophic competition due to preference towards mesopelagic preys of common dolphins in the Alboran Sea (Giménez et al., 2018) and their different isotopic values.

Deep-diving species presented a lower trophic level compared to

bottlenose dolphins, but higher than the small delphinids (i.e. common and striped dolphins). Pilot whales showed a narrow isotopic area and low values for Layman metrics in general. Therefore, they seem to be feeding on a reduced number of species, being more specialist than the rest of cetacean excluding the striped dolphins. Information of stomach content analysis in the Mediterranean Sea indicate that pilot whales mainly feed on cephalopod species (Cañadas and Sagarminaga, 2000; Astruc, 2005; Praca et al., 2011). Pilot whales in the north-western Mediterranean basin seem to feed at a lower trophic level than do other teuthophagous species, such as Risso's dolphins (Praca and Gannier, 2008; Praca et al., 2011). Nevertheless, in the Alboran Sea their nitrogen stable isotope values are higher than in the north-western Mediterranean Sea ( $12.66\text{‰} \pm 0.52$  vs.  $9.8\text{‰} \pm 0.3$ ) and similar to Risso's dolphin values.

Risso's dolphins and pilot whales overlapped both spatially (off-shore areas in the eastern Alboran Sea) and isotopically, thus pointing to a certain degree of competition or competitive equilibrium. However, our isotopic results contrast with those from the north-western Mediterranean Sea, where a complete isotopic segregation was found between these two, large-sized cetacean species (Praca et al., 2011). Owing to the small sample sizes used for stable isotope analysis in Risso's dolphins, all isotopic metrics showed large uncertainties, so we must interpret our results with caution, and cannot rule out the existence of certain trophic segregation between these two species in Alboran waters.

Our isotope results also contrasts with those from Pedà et al. (2015), who found some partial dietary overlap between Risso's dolphins and striped dolphins in the Ligurian Sea. Stomach content analyses of Risso's dolphins in other Mediterranean locations indicate a preference for pelagic octopods (Blanco et al., 2006), but also mesopelagic and deep-water cephalopods are found, such as ommastrephid squids (Würtz et al., 1992; Clarke, 1996; Blanco et al., 2006; Bearzi et al., 2011 and Pedà et al., 2015). The complete isotopic segregation found for these two species may indicate, therefore, a higher ingestion of teuthophagous species by Risso's dolphins compared with a more piscivorous diet by striped dolphins.

Although our spatial analysis indicates similar depth preferences for Cuvier's beaked whales and Risso's dolphins, only small spatial overlap was found between them due to the preference of the first species towards deeper waters around the Alboran Island. Unfortunately, no skin samples are available for Cuvier's beaked whales and further sampling campaigns should be focused on this species to facilitate a better comprehension of its feeding ecology. In addition, detailed information on stomach content of deep-diving species is crucial to gain more insights into the taxonomic composition of their diet to disentangle the degree of competition between them in the Alboran Sea.

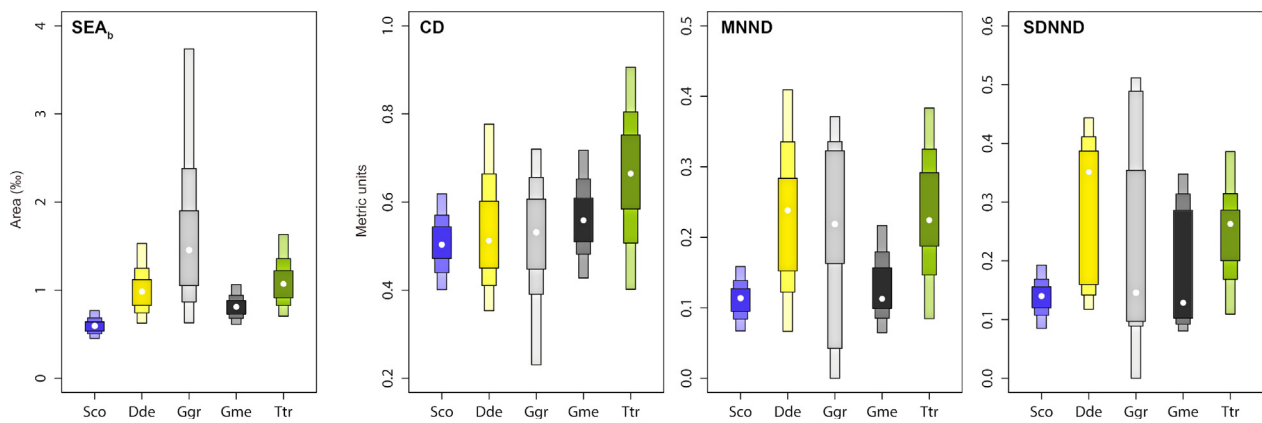
Finally, spatial segregation seems to be also the main enabler for the coexistence of the small cetaceans throughout niche partitioning, with common dolphins being more coastal than the striped dolphins that prefer offshore areas. As occurs for the other species, isotopic similarity

**Table 3**

Median isotopic standard ellipses area segregation between the species (should be read as the percentage of segregation of the isotopic area of species in the first column versus the ones of the first row). 25% and 75% percentiles are given in parenthesis. Dde: Common dolphin, Sco: Striped dolphin, Ttr: Bottlenose dolphin, Ggr: Risso's dolphin, Gme: Pilot whale, Zca: Cuvier's beaked whale.

	Dde	Sco	Ttr	Gme	Ggr
Dde	–	47.1 (30.74–63.11)	100 (100–100)	100 (100–100)	100 (100–100)
Sco	58.77 (51.17–73.88)	–	100 (100–100)	100 (100–100)	100 (100–100)
Ttr	100 (100–100)	100 (100–100)	–	69.55 (52.05–82.74)	83.63 (53.99–100)
Gme	100 (100–100)	100 (100–100)	72.94 (57.05–84.23)	–	89.55 (67.98–100)
Ggr	100 (100–100)	100 (100–100)	88.15 (72.07–100)	90.56 (72.97–100)	–





**Fig. 5.** Density plots showing the isotopic niche metrics: SEA<sub>B</sub> (Bayesian Standard Ellipse Area); CD (Mean distance to centroid); MNND (Mean nearest neighbour distance); SDNND (Standard deviation of the nearest neighbour distance). Striped dolphins (Sco) in blue, common dolphins (Dde) in yellow, Risso's dolphins (Ggr) in grey, long-finned pilot whales (Gme) in black and bottlenose dolphins (Ttr) in green. The boxed areas reflect the 95, 75 and 50% credible intervals for SEA<sub>B</sub> and the confidence intervals for the rest of metrics. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between common and striped dolphins may suggest certain trophic overlap, but also the use of different resources with similar isotopic compositions (see also Giménez et al., 2017a).

The combination of stable isotope analysis and spatial density models is an excellent way to assess the niche partitioning of species for stable coexistence. Stable isotopes alone cannot resolve properly the coexistence of these species in the Alboran Sea due to the limitations of the technique (e.g. putative differences between baselines and similarity of stable isotope values between different prey species). Then, the combination with other techniques, such as DSMs, is beneficial and enhances the interpretation of the results. This study has provided a better understanding of the coexistence of the cetacean community in the Alboran Sea. This information about the contrasting ecological needs of species within communities is essential for effective community-based conservation. In other words, conservation must be focused not only in conserving species but also on preserving its ecological needs, combined with species-specific conservation actions. Future research must consider the variation in the isotopic composition of prey sources and a description of stomach content analysis to better understand the role and the resource utilization of these cetaceans, as well as temporal variation in spatial utilization.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the

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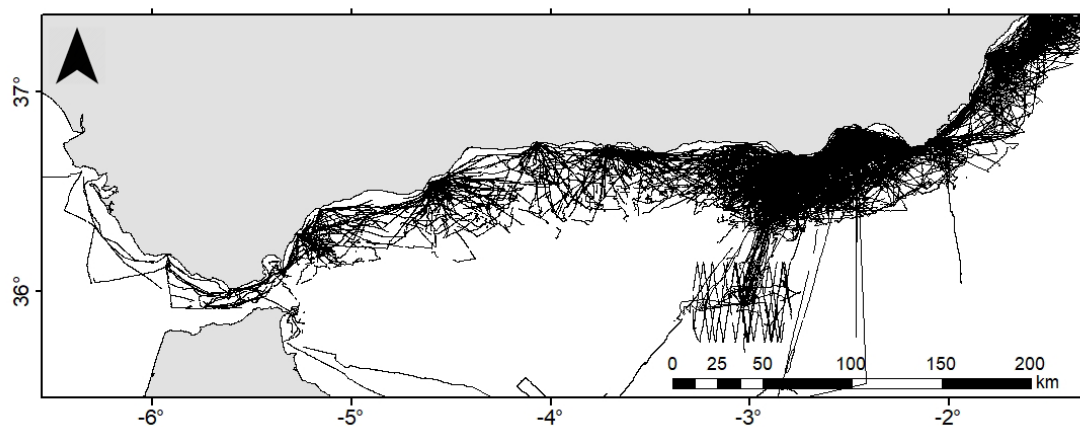
## **Living apart together: niche partitioning among Alboran Sea cetaceans**

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## APPENDIX A

### Density surface modelling effort



**Figure S1:** Effort transect performed in the research area between 1992 to 2009 in the Alboran Sea.

## **APPENDIX B**

### **Density surface modelling methodology**

Spatial abundance estimates were performed following the methodology of Cañadas and Hammond (2006, 2008). Five steps were performed:

i) Estimation of the detection function from the distance data and covariates that could affect detection probability; the software DISTANCE 6.0 was used to estimate the detection functions for each species, using the multiple covariate distance sampling (MCDS) method (Marques 2001, Thomas et al. 2002). Covariates considered for inclusion in the detection functions were effort related covariates (ship, observation platform height, position of observer, speed of vessel, sea state, swell height, sightability conditions) in order to apply the effective strip width to all on effort segments.

ii) Estimation of the ESW (Effective Strip Width) in each segment from the detection function equation and the covariates involved in it.

iii) Modelling the abundance of groups; the response variable used to formulate the spatial models of abundance of groups was the count of groups (N) in each segment (Hedley et al. 1999) using a Generalized Additive Model (GAM) with a logarithmic link function, and a Tweedie error distribution, with a parameter  $p$  of 1.1, very close to a Poisson distribution but with some over-dispersion.

iv) Modelling of group size; group size was also modelled using a GAM with a logarithmic link function. The response variable was the number of individuals dolphins counted in each group and, given the large overdispersion due to the wide range of group sizes (1 – 1000), a quasi-Poisson error distribution was used, with the variance proportional to the mean. See equations and their description in Cañadas and Hammond (2008).



v) Combination of steps 3 and 4 and extrapolation to the whole study area to obtain the final density of animals; the estimated abundance of animals for each grid cell was calculated as the product of its predicted abundance of groups and its predicted group size in each cell.

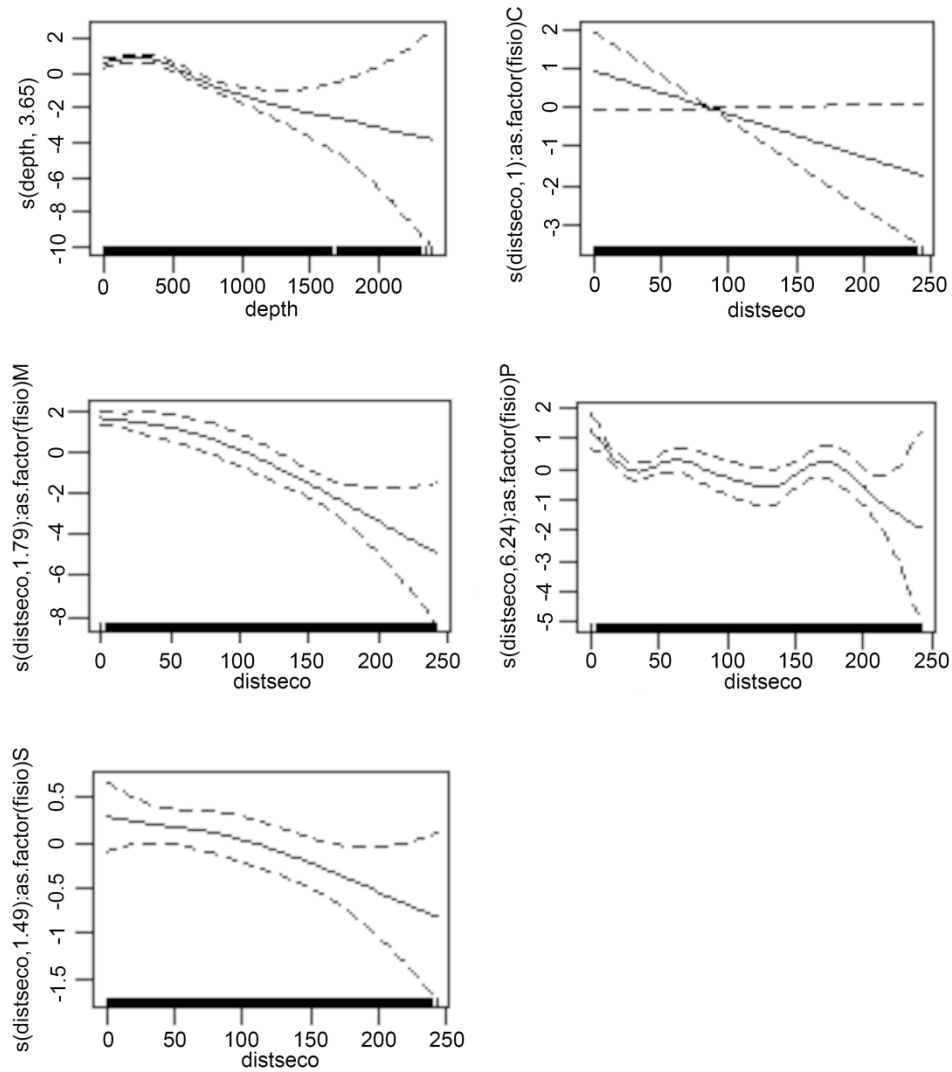
All models were fitted using package 'mgcv' version 1.7 for R (Wood 2001). Model selection was done manually using three diagnostic indicators: (a) the GCV (Generalized Cross Validation score), an approximation to AIC (Wood 2001); (b) the percentage of deviance explained; and (c) the probability that each variable was included in the model by chance.

## **APPENDIX C**

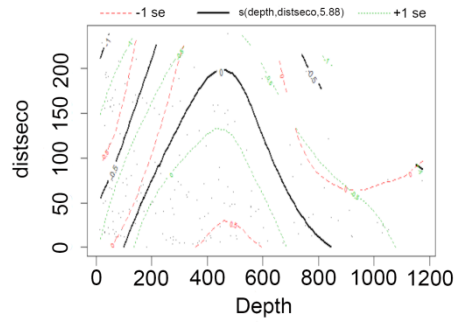
### **Density surface modelling - Functional relationships**

#### **BOTTLENOSE DOLPHINS**

Two covariates selected in the model for groups of bottlenose dolphins (Fig. S1), depth, with the higher density around 200-300m, and “distseco” (distance from Seco de los Olivos, an underwater mountain south of Almeria). Distance from Seco was selected in two forms: on itself (with clear decreasing density from the Seco to further away), and as interaction with the three bottom fisiography factor levels (C = canyon, M = mountain, P = plain). In all cases the pattern is the same: higher density closer to the Seco de los Olivos and decreasing further away. The model of group sizes (Fig. S2) selected the same two covariates but as an interaction. The larger group sizes tend to occur in areas of 400-500 m depth (x axis in the plot, high peak over 400) and closer to the Seco de los Olivos (y axis in the plot, positive trend towards 0 around 400-500 m depth).



**Figure S2:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of groups of bottlenose dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes.

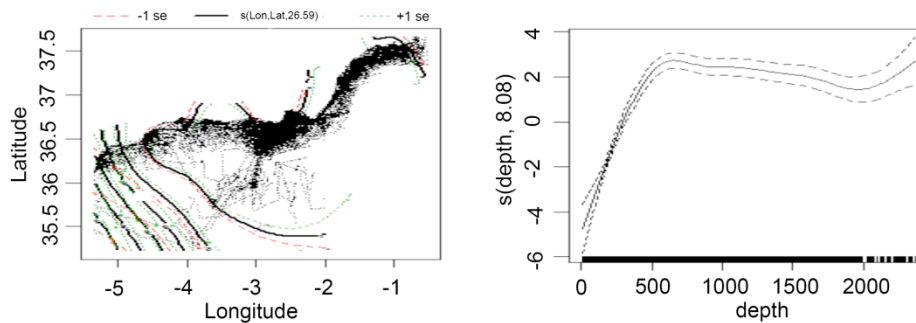


**Figure S3:** Shapes of the functional forms for the smoothed covariates used in the models for group sizes of bottlenose dolphins. The interactions between two variables are shown as two-dimensional plots. The locations of the observations are plotted as small dots. The dotted red and green lines represent -1 standard error and + 1 standard error respectively. The number on the lines indicates whether it has a positive effect (e.g. '+1'), a negative effect (e.g. '-1') or is neutral ('0').



## PILOT WHALES

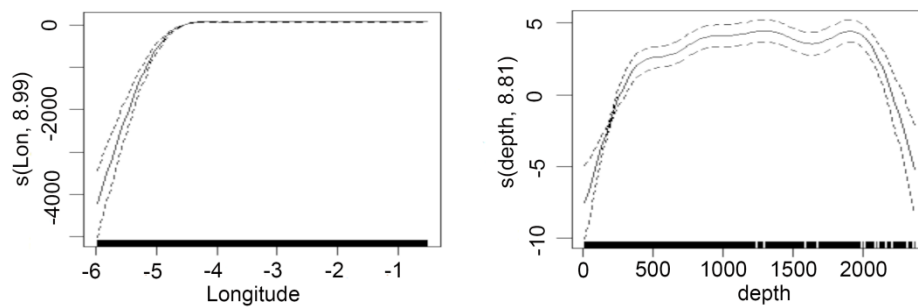
The model of groups of long-finned pilot whales (Fig. S3) selected depth and the interaction of the geographic covariates latitude and longitude. Depth shows the highest densities over 500 m, with a steep decrease in shallower waters. The interaction shows higher density towards the east with a rapid decrease towards the west.



**Figure S4:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of groups of pilot whales. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The dotted red and green lines represent -1 standard error and + 1 standard error, respectively (equivalent to the dashed lines of the univariate plots). The number on the lines indicates whether it has a positive effect (e.g. '+1'), a negative effect (e.g. '-1') or is neutral ('0').

## RISSE'S DOLPHINS

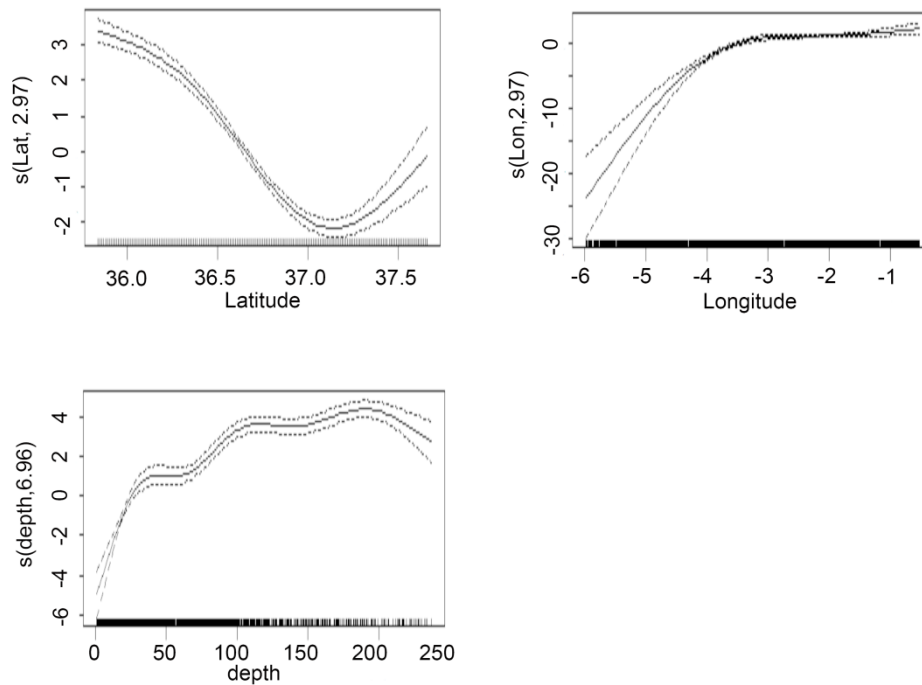
The model of groups of Risso's dolphins (Fig. S4) selected depth and the geographic covariate longitude. The highest densities are found between 500 and 2000 m depth, with steep decrease below and over those depths. The latter shows most of the density to the east of 5°W (Malaga), with very steep decrease to the west.



**Figure S5:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of groups of Risso's dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes.

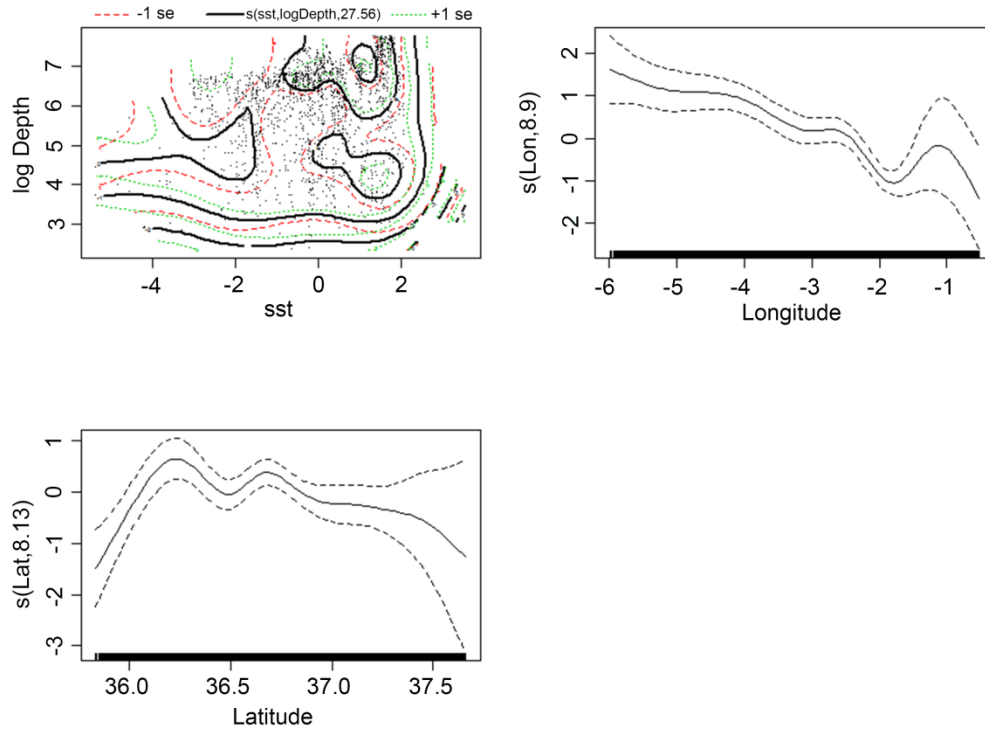
## CUVIER'S BEAKED WHALES

The model of groups of Cuvier's beaked whales (Fig. S5) selected depth, and the geographic covariates latitude and longitude without interaction. Depth shows a more or less steady increase of density from shallow waters towards deep areas over 2000m. Longitude shows a similar pattern as pilot whales and Risso's dolphins: increased density from 4-5°W towards the east. Latitude shows a decrease from south to north to a minimum around 37° - 37.4° N slightly increasing again north from this.



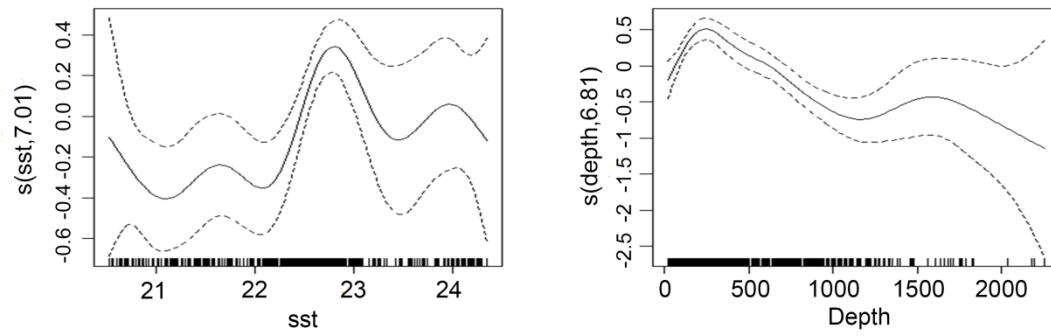
**Figure S6:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of groups of Cuvier's beaked whales. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes.

## COMMON DOLPHINS



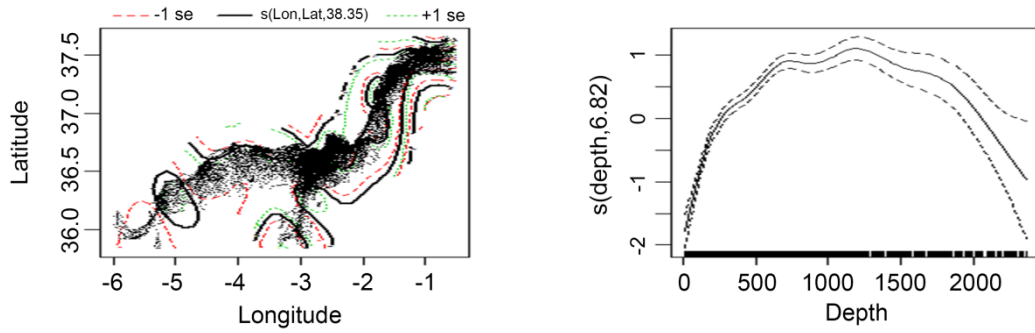
**Figure S7:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of groups of common dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The dotted red and green lines represent -1 standard error and + 1 standard error respectively (equivalent to the dashed lines of the univariate plots). The number on the lines indicates whether it has a positive effect (e.g. '+1'), a negative effect (e.g. '-1') or is neutral ('0') (extracted from Giménez et al. 2017).



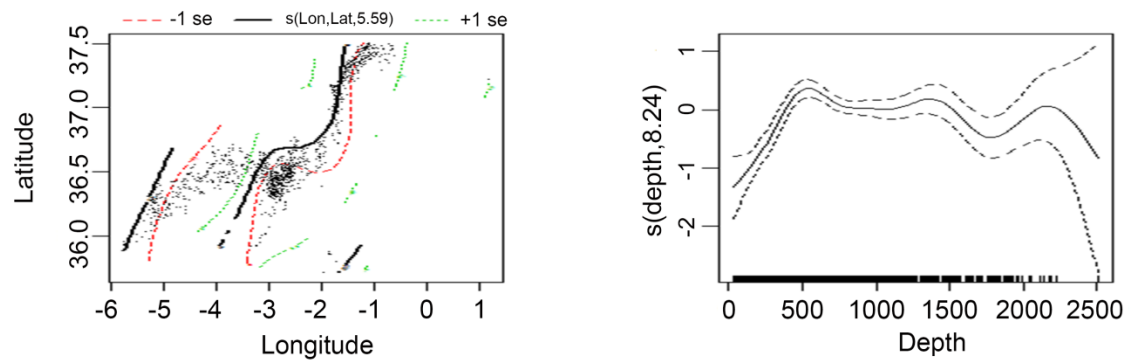


**Figure S8:** Shapes of the functional forms for the smoothed covariates used in the models for group sizes of common dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes (extracted from Giménez et al. 2017).

## STRIPED DOLPHINS



**Figure S9:** Shapes of the functional forms for the smoothed covariates used in the models for abundance of striped dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The dotted red and green lines represent -1 standard error and +1 standard error, respectively (equivalent to the dashed lines of the univariate plots). The number on the lines indicates whether it has a positive effect (e.g. '+1'), a negative effect (e.g. '-1') or is neutral ('0') (extracted from Giménez et al. 2017).



**Figure S10:** Shapes of the functional forms for the smoothed covariates used in the models for group sizes of striped dolphins. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density). The dashed lines represent twice the standard errors of the estimated curve (95% confidence band). The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The dotted red and green lines represent -1 standard error and +1 standard error, respectively (equivalent to the dashed lines of the univariate plots). The number on the lines indicates whether it has a positive effect (e.g. '+1'), a negative effect (e.g. '-1') or is neutral ('0') (extracted from Giménez et al. 2017).

## APPENDIX D

### Isotopic niche metrics

**Table S1:** Isotopic niche metrics of each species (c= corrected for small sample sizes, B = Bayesian estimate, b = bootstrapped value). 25% and 75% percentiles are given in parenthesis. **Dde:** common dolphin, **Sco:** striped dolphin, **Ttr:** bottlenose dolphin, **Ggr:** Risso's dolphin, **Gme:** long-finned pilot whale, **Zca:** Cuvier's beaked whale.

	<b>Sco</b>	<b>Dde</b>	<b>Ggr</b>	<b>Gme</b>	<b>Ttr</b>
<b><i>Siber metrics</i></b>					
SEA <sub>c</sub>	0.48	0.78	0.53	0.7	0.82
SEA <sub>B</sub>	0.6	1.1	1.71	0.82	1.11
	(0.55-0.65)	(0.88-1.19)	(1.33-2.33)	(0.75-0.91)	(0.96-1.29)
<b><i>Layman metrics</i></b>					
CD <sub>b</sub>	0.51	0.55	0.49	0.57	0.66
	(0.47-0.53)	(0.47-0.62)	(0.42-0.58)	(0.52-0.61)	(0.57-0.75)
MNND <sub>b</sub>	0.11	0.24	0.19	0.14	0.24
	(0.09-0.13)	(0.17-0.30)	(0.11-0.29)	(0.11-0.16)	(0.19-0.29)
SDNND <sub>b</sub>	0.14	0.28	0.26	0.21	0.25
	(0.12-0.16)	(0.19-0.36)	(0.15-0.36)	(0.13-0.27)	(0.21-0.29)