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Cédric Cotte, Christophe Guinet, Isabelle Taupier-Letage, Estelle Petiau. Habitat use and abundance of striped dolphins in the western Mediterranean Sea prior to the morbillivirus epizootic resurgence. *Endangered Species Research*, 2010, 12, pp.203-214. 10.3354/esr00301 . hal-00527424

**HAL Id: hal-00527424**

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Submitted on 23 Sep 2022

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# Habitat use and abundance of striped dolphins in the western Mediterranean Sea prior to the morbillivirus epizootic resurgence

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**ABSTRACT:** Although the striped dolphin *Stenella coeruleoalba* has a world status of Least Concern, a recent IUCN Red List assessment has proposed that the Mediterranean population be listed as Vulnerable and stresses the need for an estimate of abundance and distribution. While substantial efforts have been made to study cetaceans in regions of the western Mediterranean Sea (WM), we have little knowledge of their large-scale distribution and interaction with oceanographic features at various scales. We conducted 18 basin-wide surveys from ferry platforms within the WM from early September 2006 to late July 2007 and used spatial modelling to investigate the distribution, abundance and habitat use of striped dolphins. Most striped dolphins were sighted north of the Balearic Islands, where they are closely associated with the counter-clockwise circulation defined by negative absolute dynamic topography. In the Algerian basin, dolphins were mostly found in recent Atlantic water mass. Densities of striped dolphins were also related to high gradients of sea surface temperature and high chlorophyll concentrations. Moreover, we found similar results (1) when the northern and southern data sets were pooled and (2) in the northern area only, where the majority of sightings occurred. These relationships suggest that dolphins were found in dynamic and productive areas generated by mesoscale processes which could create favourable foraging conditions. Despite our relatively small data set, dolphins were found year-round. We estimated the number of striped dolphins in the area between 3° and 6° E to have been 38 600 (95 % CI: 25 900 to 53 900) before the resurgence of the morbillivirus epizootic in summer 2007. This is considerably more than the estimate from the 1991 WM survey, which reported a 43 % lower abundance, probably affected by the 1990 epizootic. Platforms of opportunity are therefore relevant not only to assess animal ecology but also to monitor population in a given area. Such interannual monitoring is especially important to detect and quantify the response of animal populations, in terms of distribution and density, to environmental stresses.

**KEY WORDS:** Habitat use · Abundance and distribution modeling · Mesoscale oceanographic processes · Striped dolphin · *Morbillivirus* epizootics

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## INTRODUCTION

Knowledge of cetacean distribution in the western Mediterranean Sea (WM) is not spatially and temporally homogeneous, especially with regard to relationships with the animals' oceanographic environment. Because most of the data come from visual observations, this knowledge is inherently limited in space and time. Spatially, observations have mostly been carried

out in the northern part of the WM, i.e. the Ligurian Sea including the Pelagos Sanctuary (e.g. Panigada et al. 2008, Laran & Gannier 2008), and along the Spanish coasts (Cañadas et al. 2005, Cañadas & Hammond 2008, Gómez de Segura et al. 2006). These surveys were often undertaken in the framework of conservation of wildlife populations through establishment of marine protected areas. A large-scale survey conducted during summer 1991 still applies as a reference

for distribution and abundance of cetacean populations in the WM (Forcada & Hammond 1998). Despite the attempts of a few previous studies to study large-scale patterns such as the seasonal abundance of cetaceans in the Ligurian Sea (Laran & Drouot-Dulau 2007), data acquisition is often limited to the summer season (review in Aguilar 2000). Thus no studies have yet assessed the distribution of cetaceans in the WM at both large and annual scales.

From an IUCN report (Reeves & Notarbartolo di Sciarra 2006) and its recent updates, striped dolphin *Stenella coeruleoalba* in the Mediterranean is currently proposed to be listed on the IUCN Red List as Vulnerable. The Mediterranean population of striped dolphin is particularly exposed to high levels of chemicals and heavy metals, which have severe effects on their reproduction and immune system (Aguilar & Borrell 1994). Moreover, Reeves & Notarbartolo di Sciarra (2006) reported that the association of mortality in pelagic driftnets (thousands of animals per year) and the residual effects of a large-scale die-off from an epizootic in the early 1990s provided the main basis for the proposed listing as Vulnerable. The population was quantified at 117 880 (95% CI = 68 379 to 214 800) individuals in the WM immediately after the 1990 die-off due to a morbillivirus epidemic (Forcada et al. 1994, Forcada & Hammond 1998). Information on striped dolphin distribution and abundance is therefore needed to assess current estimates and highlight possible population trends.

The biological production of the oligotrophic Mediterranean Sea, from primary production to top predators, is influenced at a basin scale by circulation and air–sea interactions. Within this basin circulation, physical phenomena such as meanders and eddies affect biological activity, implying a high mesoscale spatial and temporal variability (Morel & André 1991, Taupier-Letage et al. 2003). This can lead, locally and episodically, to unexpectedly high biological production in the WM (Taupier-Letage et al. 2003). Many previous studies on marine ecology have linked distribution and abundance of marine predators to high biomasses of resources through biological stimulation and/or aggregation (e.g. Guinet et al. 2001). However, most of these studies are snapshots of a given, and maybe ephemeral, situation of the environment, and they are not designed to consider dynamic marine processes. In order to accurately describe interactions between cetaceans and their environment in such a dynamic oceanographic context, especially considering the mesoscale phenomena, it is crucial to design a relevant mesoscale-dedicated sampling strategy. This approach needs to include multidisciplinary high-resolution and long-term (at least annual) monitoring. Only such a data set would capture the variability in cetacean distribution and its links

with the Mediterranean marine environment (Millot & Taupier-Letage 2004).

Because of their regular and frequent path across the WM, opportunistic platforms like ferries are relevant to this type of study. Spatial modelling, increasingly used in cetacean studies (Hedley 2000, Redfern et al. 2006), can indeed accurately analyse data from such platforms (Marques 2001, Henrys 2005, Williams et al. 2006). In addition to presenting several advantages, such as mapping animal abundance and investigating relationships between density and environmental covariates, the feasibility of this approach and precision of estimates have been tested by comparisons with conventional line transect analysis (Gómez de Segura et al. 2007). Moreover, methods based on generalized additive models (GAMs; Hastie & Tibshirani 1990) were reported to predict cetacean densities on smaller spatial scales than conventional line transect analyses (Ferguson et al. 2006), enabling us to investigate in particular the influence of oceanographic mesoscale features. We focused our effort on straight transects, crossing the WM from northern to southern shores. Sightings of striped dolphins, *in situ* oceanographic data and remote-sensing images were used simultaneously to examine the spatio-temporal variability of striped dolphin distribution and its relationship with oceanographic conditions. This variability could also give insights into the potential movements of striped dolphins, for which different seasonal patterns have been reported (Gómez de Segura et al. 2006, Laran & Drouot-Dulau 2007) according to the region.

A large-scale and high-resolution multidisciplinary study was conducted shortly before the recent resurgence of a dolphin morbillivirus epizootic in 2007 (Raga et al. 2008). We report the pre-epidemic ecological status and abundance of a WM population of striped dolphin.

## MATERIALS AND METHODS

**Observation and environmental data.** Observations were originally planned for a 2 wk period; however, the meteorological conditions and the ship's schedule limited this effort. Data were collected during 18 trips between 12 September 2006 and 26 July 2007 on a ferry crossing the WM from Marseille (France) to Algiers and Bejaïa (Algeria) (Fig. 1). Each trip was 2 d long and consisted of 2 transects (continuous on-effort search time): one from the French coast to the north of the Balearic Islands (during daytime on Day 1), and the other from the Algerian coast to the south of the Balearic Islands (during daytime on Day 2). The northern and southern transects never joined in the middle

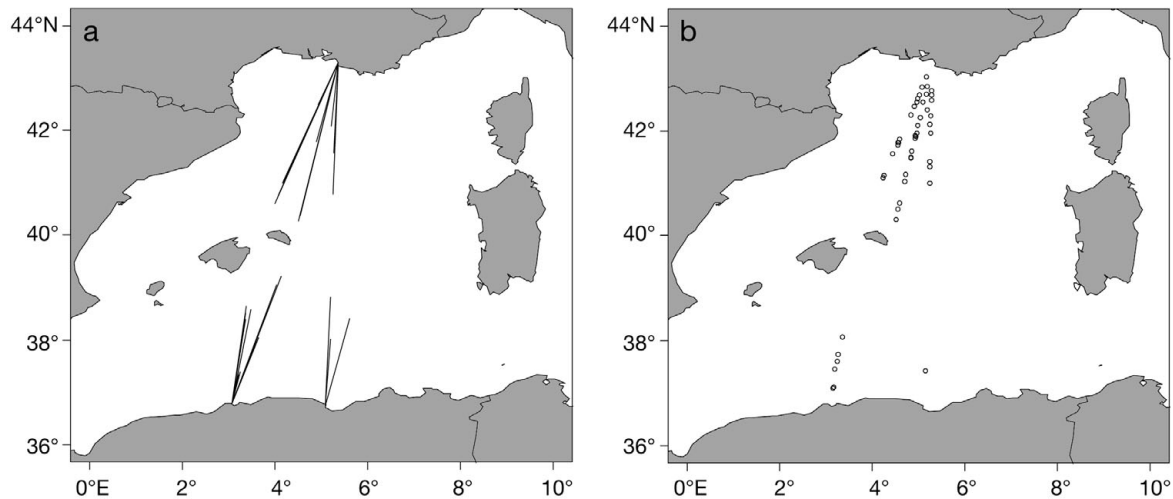


Fig. 1. (a) Transects of the ferries in the study area, the western Mediterranean Sea, used as platforms to observe striped dolphins *Stenella coeruleoalba*. (b) Locations of striped dolphin sightings along the transects

part of the basin, avoiding the violation of independence of data by surveying the same area on 2 straight days. Observations were made from the bridge (25 m high) of the ship, with the naked eye and with binoculars equipped with reticle and compass. To ensure the  $g(0) = 1$  assumption of distance sampling (Buckland et al. 2001), a visual angle of  $90^\circ$  centred on the trackline (ahead of the boat,  $45^\circ$  port,  $45^\circ$  starboard) was surveyed to optimize the detection of all animals directly on the trackline. Although the ship represents a platform of opportunity, we ensured this  $g(0) = 1$  assumption by avoiding bias of the observers. Consequently, the effort and sightings were carried out using standardized (one platform) survey methods by the same trained observers. The 2 observers relayed continuously, on an hourly basis (one observing, one resting) during daytime. When a striped dolphin school (single or several individuals) was sighted and identified from other dolphin species (at a maximum 4 Beaufort sea state), ship location, time, radial distance and angle to the sighting, and group size were recorded. Minimum and maximum group size was estimated from the first sighting of a group until the group left the observer's field of view. The mean of minimum and maximum group size was then used in the analyses. Meteorological factors that could affect sighting conditions were also recorded. The ferry travelled at an average speed of  $\sim 20$  knots.

Environmental data were obtained from *in situ* and satellite sources. The oceanographic and meteorological *in situ* data were collected at approximately 3 m depth with a system installed on-board the ferry (TRANSMED program<sup>1</sup>). It consisted of a thermosalinometer, pumping surface water and recording the hydrological parameters (temperature and salinity),

and a fluorometer, estimating the phytoplankton chlorophyll *a* (chl *a*) concentration, at a resolution of 1 measurement per minute. Satellite observations of sea surface temperature (SST), chl *a* concentrations (visible/ocean color imagery) and sea level (altimetry) were used. The NOAA Advanced Very High Resolution Radiometer (AVHRR; <http://noaasis.noaa.gov/NOAA-SIS/ml/avhrr.html>) satellite sensor, measuring SST, is an extremely efficient tool that we used to track the mesoscale features (e.g. Taupier-Letage 2008). Chl *a* images were obtained from Moderate Resolution Imaging Spectroradiometer (MODIS, <http://modis.gsfc.nasa.gov/>). Their spatial resolutions range from  $\sim 1$  to 4 km, and the WM was fully covered within 1 daytime period. Owing to cloud coverage, we used satellite 3 d-composite images corresponding to environmental conditions of observation data. We also used weekly merged products of absolute dynamic topography (ADT) at  $\frac{1}{8}^\circ$  resolution (Ssalto/Duacs, Aviso, <http://atoll-motu.aviso.oceanobs.com>). Bathymetric data were extracted from the ETOPO2 database (National Geophysical Data Center, [www.ngdc.noaa.gov](http://www.ngdc.noaa.gov)). Temperature and chl *a* gradients and geostrophic currents were computed as described in Cotté et al. (2007).

**Modeling dolphin densities.** Line transect sampling from design-based methods is the standard tool to provide information on abundance and distribution in cetacean populations (Buckland et al. 2001). An alternative technique relevant to surveys that have not ini-

<sup>1</sup>Test phase to develop a network to monitor the surface of the Mediterranean using ships of opportunity, an initiative of the Commission Internationale pour l'Exploration Scientifique de la Méditerranée (CIESM).

tially been designed to achieve equal coverage probability is the model-based approach (Hedley et al. 1999, Marques 2001), in which line transect sampling is combined with spatial analysis. Data from such surveys can then be combined when fitting descriptive models of heterogeneity in animal density, thus imparting information on how animals use their habitat and how populations behave over time (Williams et al. 2006). In the present study we used a method based on modeling distances between detections, called waiting distances (Hedley 2000). This method has theoretical appeal as it avoids the subjective choice of cell size and zero-inflated data sets generated by the classical method, which consists of dividing transects into separate cells (Henrys 2005). Waiting distance models were used to estimate density because in areas of high density the waiting distance between detections is short (Buckland et al. 2004). The waiting distances were modeled using GAMs (Hastie & Tibshirani 1990) with a logarithmic link function of the set of spatial environmental covariates. To handle over-dispersion, a gamma distribution was used. We used GAMs in our analysis because they offer flexibility through a smooth function applied to each explanatory variable (Wood 2003). Smoothing splines were fitted using multiple generalized cross-validation (mgcv) in R (Wood 2001). The amount of flexibility given to a model term is determined in a maximum likelihood framework by minimizing the generalized cross-validation (GCV) score of the whole model. The general structure of the model was:

$$g[E(l_i)] = \beta_0 + \sum_k f_k(z_{ki}), \quad i = 1, \dots, n \quad (1)$$

where  $g$  is the link function between expected waiting distances  $E(l_i)$  and the covariates,  $\beta_0$  is the intercept,  $f_k$  are smoothed functions of the explanatory covariates,  $z_{ki}$  is the value of the  $k$ th explanatory covariate in the  $i$ th observation, and  $n$  is the number of observations. While the optimal amount of smoothing is automatically determined by mgcv, the decision as to whether to include or drop a model term is not. We adopted the model selection procedure in the framework recommended by Wood (2001), essentially based on the lowest GCV score. The saturated (including all remotely sensed covariates) models were fitted to the data, and a term was dropped from the final model if it satisfied the following conditions: for each model term, the estimated number of degrees of freedom was examined to see if it was near 1. If its 95% confidence intervals included zero across the range of observations, the term was removed temporarily, to see if the GCV score dropped. The density surface between observations, given by  $D(x_{i+1}, 0)$  was then obtained using the formula:

$$D(x_{i+1}, 0) = \frac{1}{2\hat{\mu} \cdot l_{i+1}} \quad (2)$$

where  $\hat{\mu}$  is the effective strip half-width. Because the data set available for the analysis was relatively small, we chose not to incorporate interaction terms into the GAM models to avoid the risk of overfitting. We then multiplied by the estimated clustered size to calculate the total dolphin density. Using a gridded data set of the explanatory variables included in the model, abundance was estimated by integrating the density surface under the area. The non-parametric bootstrap was used to obtain 95% confidence intervals for the estimates of abundance. The trips, not transects, were used as the resampling units and were sampled 1000 times with replacement.

The covariates used in this procedure are remotely sensed environmental variables: SST and its gradient (gSST), chl  $a$  concentration and its gradient (gchl  $a$ ), ADT, derived absolute geostrophic velocity (AGV), sea level anomaly (SLA), derived geostrophic velocity anomaly (GVA) and depth. Moreover, there is no formal rule for specifying the maximum number of covariates that can be included in any analysis, although larger samples (number of observations) tolerate more covariates than smaller samples. Potential covariates are often strongly correlated and so examination of the cross-correlation can be a useful basis for eliminating some combination between the covariates. First, we identified strongly correlated ( $|r_s| > 0.5$ ) predictors by estimating all pairwise Spearman's rank correlation coefficients (cross-correlation analysis). Second, once the non-correlated environmental covariates were identified, models were built for all possible combination of predictors.

To obtain  $\hat{\mu}$ , we estimated the best detection function from conventional and multi-covariate (conditions of sightings) distance sampling (MCDS) methods (Marques 2001, Thomas et al. 2002) using the software DISTANCE 5.0 beta 5 (Thomas et al. 2002). The perpendicular distances were right-truncated prior to the analysis, following the recommendations of Buckland et al. (2001). The best detection function was selected using Akaike's information criterion (AIC) and the chi-squared goodness-of-fit test. The mean cluster size was also estimated by DISTANCE to detect school size bias, i.e. the tendency of detection for large and small schools at the same distance range. The approach fits a least-squares regression of log of school size on the distance, which yields a slope when bias is present (not the case here).

Since out of a total of 48 sightings, only 7 were made south of the Balearic Islands, we split the data. The first analysis was realized on the major core of the data, belonging only to the northern area (strati-

Table 1. Surveyed distance and number of sightings of striped dolphin *Stenella coeruleoalba* in the western Mediterranean from early September 2006 to late July 2007

Region	On-effort distance (km)	Number of sightings
North of Balearic Is.	4351	41
South of Balearic Is.	3071	7
Total	7422	48

fied data), while the second model analysis was realized on the whole data set, i.e. southern and northern data (pooled data).

## RESULTS

Throughout the year, most of the sightings of striped dolphin schools (~85%, Table 1) occurred in the northern part of the WM, i.e. north of the Balearic Islands (Fig. 1). Encounter rates (number of dolphin schools per km) in the northern part of the WM throughout the

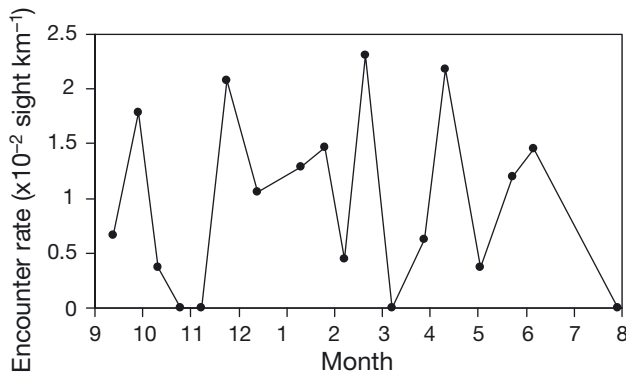


Fig. 2. Encounter rate of striped dolphins from September 2006 to July 2007

year would suggest that there is no seasonal trend, and especially no marked difference between winter and summer periods (Fig. 2). So, despite the relatively small number of sightings, striped dolphins occurred year-round in the northern part of the WM.

The best-fitting model of detection probability was a half-normal key function with cosine series expansion and adjustment terms. No environmental covariate (not even Beaufort sea state) seemed to affect the detection of dolphins. The expected mean cluster size of striped dolphin was 8.8 (95% CI = 6 to 12.8) and the effective strip half-width was estimated to be 224 m. All non-correlated explanatory covariates (Table 2) were included within the models. Based on the lowest GCV score, the selected spatial models exclude the temporal covariate. This also suggests that the densities of dolphins did not markedly vary over the year, i.e. there was a year-long occurrence of striped dolphin at least in the northern area. From the pooled data set, the selected model includes ADT ( $F = 4.40$ ,  $df = 3.87$ ,  $p = 0.006$ ), SST gradient ( $F = 2.88$ ,  $df = 2.04$ ,  $p = 0.040$ ) and chl *a* concentration ( $F = 2.95$ ,  $df = 1.48$ ,  $p = 0.049$ ). The deviance explained by this model is 50.1%. The shapes of the functional forms for the smoothed covariates, conditional on the other covariates being included in the models, are shown in Fig. 3. To prevent the over-fitting of our relatively small data set, we imposed a threshold of the degree of freedom of the smoothing spline equal to 4. Waiting distance was low, i.e. density was high, in areas with low ADT. Density was also high in areas with high chl *a* concentration and high SST gradients. We obtained similar results from the stratified (northern) data. The selected model also includes ADT ( $F = 3.82$ ,  $df = 3.51$ ,  $p = 0.019$ ), SST gradient ( $F = 3.13$ ,  $df = 2.08$ ,  $p = 0.041$ ) and chl *a* concentration ( $F = 2.61$ ,  $df = 1.82$ ,  $p = 0.061$ ). The deviance explained by this model is 57.5%. The shape of the functional form for the ADT (Fig. 4) corresponds to the

Table 2. Results of the cross-correlation analysis of environmental variables based on the Spearman's rank correlation coefficient  $r_s$  ( $|r_s| > 0.5$  in **bold**) and corresponding significant levels (lower and upper diagonal). The environmental variables are: sea surface temperature (SST) and its gradient (gSST), chlorophyll *a* concentration (chl *a*) and its gradient (gchl *a*), absolute dynamic topography (ADT), derived absolute geostrophic velocity (AGV), sea level anomaly (SLA), derived geostrophic velocity anomaly (GVA) and depth. Significance levels set at  $<0.05$ ,  $<0.01$  and  $<0.001$ ; NS: not significant

	SST	gSST	chl <i>a</i>	gchl <i>a</i>	ADT	AGV	SLA	GVA	Depth (m)
SST	–	NS	0.001	0.001	0.001	NS	0.001	NS	0.05
gSST	0.238	–	NS	NS	NS	NS	NS	NS	NS
chl <i>a</i>	<b>-0.604</b>	-0.133	–	0.001	0.001	NS	0.01	NS	0.05
gchl <i>a</i>	<b>-0.544</b>	-0.073	<b>0.803</b>	–	0.01	NS	0.05	NS	0.05
ADT	<b>0.580</b>	0.118	-0.431	-0.427	–	NS	0.001	NS	0.01
AGV	0.275	0.214	-0.101	-0.132	0.231	–	NS	0.001	NS
SLA	<b>0.515</b>	0.134	-0.378	-0.352	<b>0.715</b>	0.135	–	0.05	NS
GVA	0.243	0.061	-0.257	-0.279	0.251	0.479	0.347	–	NS
Depth	-0.361	0.071	0.354	0.337	-0.372	0.176	-0.022	-0.055	–

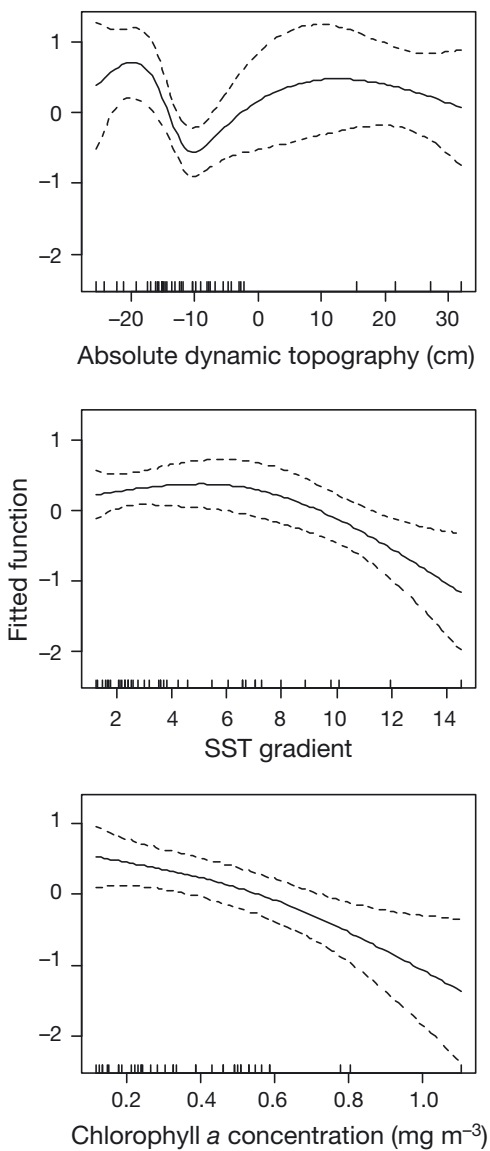


Fig. 3. Functional forms of the waiting distance for the smoothed covariates included in the generalized additive model from the northern and southern data (pooled data set)

left part of the curve from the pooled data set (i.e. range = -25 to 0 cm; Fig. 3), while the other forms were similar and appear to be less affected by the southern data (Fig. 4). For both data sets (stratified and pooled), depth, SST, geostrophic currents and chl *a* concentration gradient failed to enter the model as covariates.

We then compared *in situ* oceanographic parameters, especially salinity (the only parameter not available from remotely sensed imagery), at each sighting with the mean value of the corresponding transect when on-effort (Fig. 5). In the south only, dolphins were found in water masses with a lower salinity than those along the transects. *In situ* SST and chl *a* fluores-

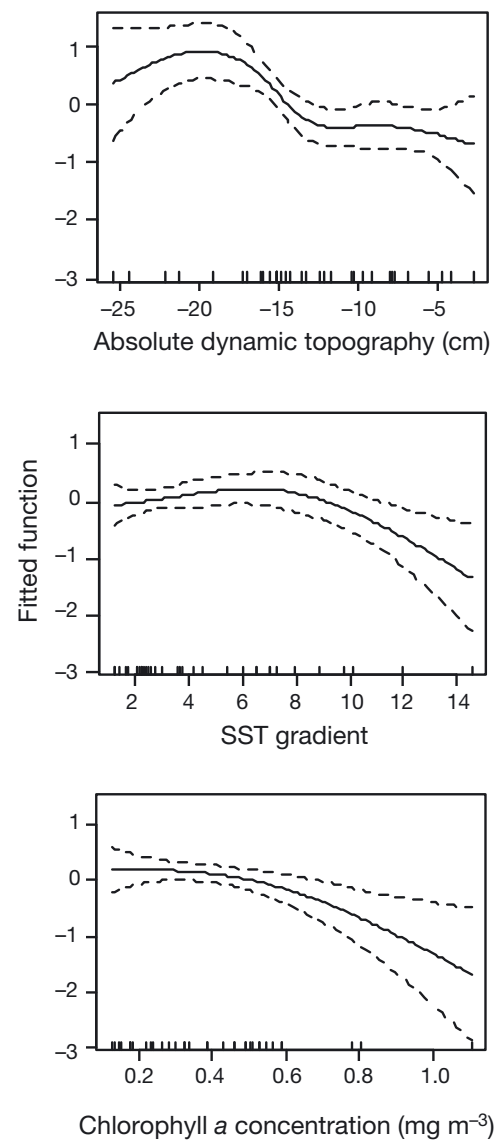


Fig. 4. Functional forms of the waiting distance for the smoothed covariates included in the generalized additive model from the northern data (stratified data set)

cence data confirmed the previous results of the model. In both northern and southern areas, dolphins were not found in water masses with a specific SST range relative to water masses along the transects. However, they were clearly found in higher chl *a* concentrations in both the northern and southern regions of the WM.

The transect carried out in late September (28–29 September 2006) shows sightings of striped dolphins in both the northern and southern regions of the WM (Fig. 6). The *in situ* oceanographic profiles of the surface water from the on-board system depict a typical summer situation, with colder and saltier water in

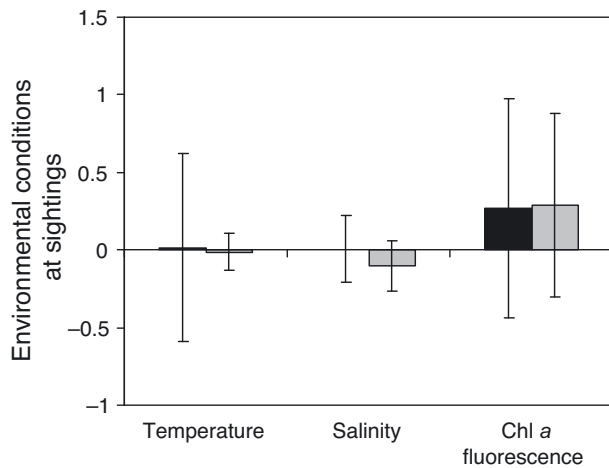


Fig. 5. Environmental preference of striped dolphins. Difference between the *in situ* value of sea surface temperature (SST), salinity and chlorophyll *a* (chl *a*) fluorescence at time of sighting and the mean ( $\pm$ SD) of the corresponding transect in the north (black bars) and south (grey bars)

the north, and warmer and lower salinity water (recent Atlantic water) in the south. However, in both regions there is spatial variability. In the north there is a weak relative minimum of salinity shorewards corresponding to the Northern Current's signature during summertime. In the south the amplitude of the variability is also well marked, especially with respect to salinity. Dolphins were sighted in areas where steep changes in SST and high chl *a* fluorescence (*in situ* proxy of chl *a* concentration) occurred. These parameters underline the mesoscale circulation highlighted by high-resolution satellite imagery (1 km in space and 0.1°C for SST precision) and *in situ* data. In the northern transect, sightings were associated with the external border of the Northern Current and with the edge of an eddy. In the southern transect, the sighting was associated with the edge of a coastal Algerian eddy, well marked by low salinity, SST variability and a peak in chl *a* fluorescence. The transect was also located along another eddy just north of the previously mentioned coastal

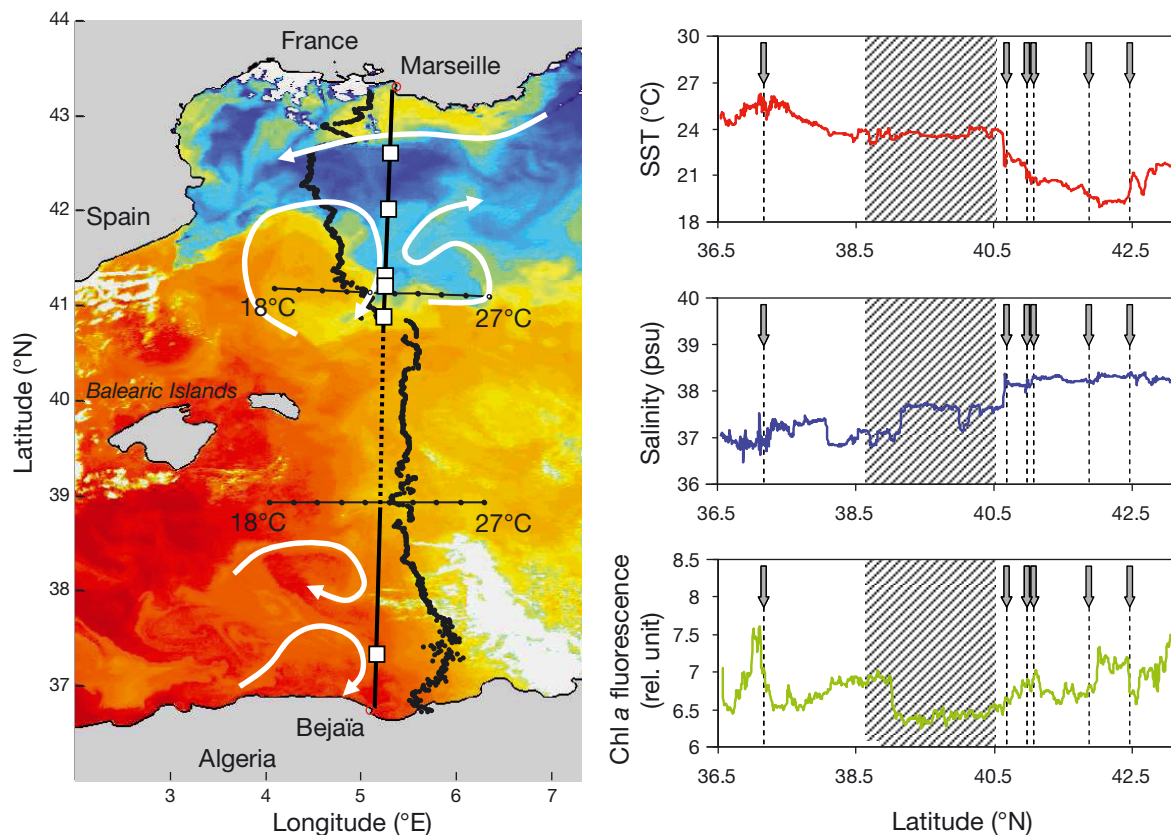


Fig. 6. Satellite sea surface temperature (SST), striped dolphin sightings and *in situ* surface parameters of the 28–30 September 2006 transect. (a) The color map represents SST from colder (blue) to warmer water (red). White arrows indicate circulation, white squares are dolphin sightings, continuous black lines are on-effort transects and dotted black lines are off-effort (nighttime). Black points on the map draw the SST profile from *in situ* data collected by the on-board TRANSMED system, using the transect line as the x-axis (the 2 y-axes are perpendicular to the transect line). (b) Dolphin sightings (gray arrows) are also located along the *in situ* oceanographic profiles of SST (upper panel, the same profile as on the map), salinity (middle panel) and chlorophyll *a* (chl *a*) fluorescence (lower panel). Hatched area: off-effort (night)



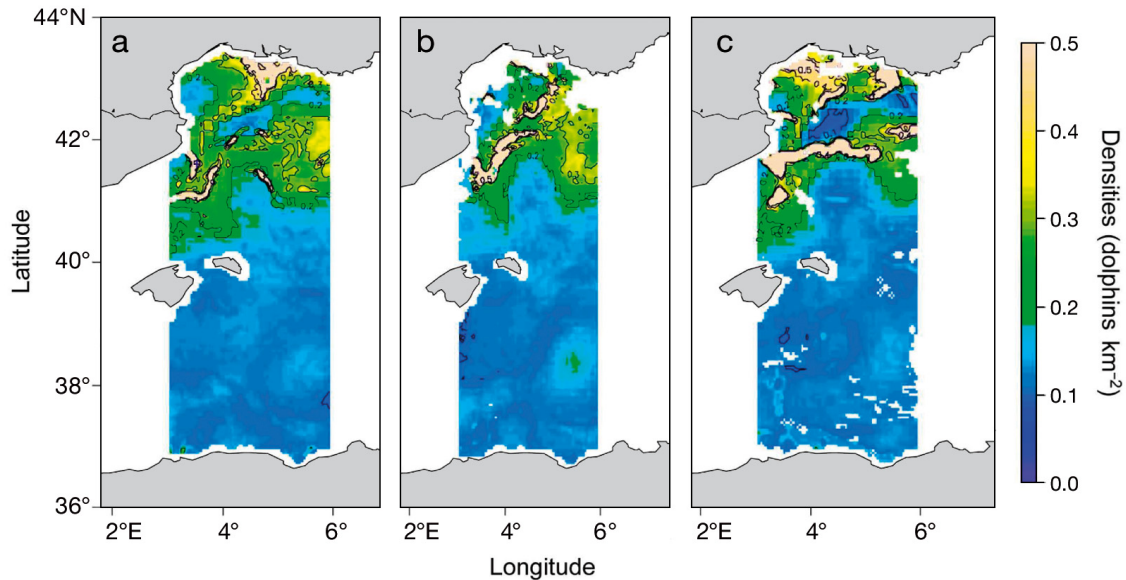


Fig. 7. *Stenella coeruleoalba*. Predicted striped dolphin densities (dolphins  $\text{km}^{-2}$ ) for (a) 31 July–2 August, (b) 15–17 August and (c) 31 August–2 September 2007. White areas within the strips indicate cloud coverage

eddy. However, no dolphins were seen within this oceanographic context, which is relatively similar to the neighbouring eddy from the *in situ* profiles. The main difference lies in the SST gradient, which is relatively low in the offshore eddy.

Distributions, abundances and confidence intervals were estimated for 3 periods in August 2007 (early, middle and late) in order to test whether our estimates are independent of short spatial and temporal scale (i.e. local) conditions (Fig. 7). We then compared this with the abundance of striped dolphins during August 1991, during the large-scale epizootic event (Forcada & Hammond 1998). We estimated a constant abundance of 38 600 (95% CI = 25 900 to 53 900), 37 900 (95% CI = 24 800 to 52 400) and 38 600 (95% CI = 27 500 to 51 400) striped dolphins for early, middle and late August, respectively, in the area between 3° and 6°E. In this strip, predicted densities were substantially higher in the north. We estimated a mean density of 0.38 dolphins  $\text{km}^{-1}$  for the northern region area and 0.12 for the southern region. Throughout their range, densities of striped dolphin are higher offshore French and Spanish coasts and lower close to the coasts, despite high densities in the Rhône River plume due to especially high chl *a* concentrations.

## DISCUSSION

### Modeling scale-dependent habitat use

The north–south distribution of striped dolphin found in the present study confirms the large-scale

pattern of the reference work on cetaceans carried out in summer 1991, where striped dolphins were also mostly found north of the Balearic Islands (Forcada & Hammond 1998). The link with ADT suggests that dolphins were mostly found within the mean counter-clockwise circulation in the north part of the WM, limited to the north by the Northern Current and to the south by the North Balearic front. Despite the fact that a correlation exists between the dynamic height and SST (Rio et al. 2007; see Table 2), dolphins were mostly found in low ADT areas, but they did not seem to target colder waters at a large scale. Indeed, since the northern region represents the major core of the data, the higher densities were not found at the centre of counter-clockwise circulation (the highest value of ADT; Figs. 3 & 4) but at the edge (range =  $-15$  to  $0$  cm). We can only compare our temporal results with regional studies: striped dolphin abundance in the Ligurian Sea was reported to vary seasonally (Laran & Drouot-Dulau 2007) and even throughout the summer months (Azzellino et al. 2008a). However, as in the present study, dolphins were observed year-round in the central Spanish Mediterranean with no detected seasonal changes (Gómez de Segura et al. 2006). This suggests that the seasonal variation in abundance of striped dolphins depends on the particular area of the WM, with some areas used as summering and/or wintering areas, while others are used year-round. Despite a relatively small data set, the year-long occurrence of striped dolphins which we reported south of the Gulf of Lions could be associated with the high production available to dolphin prey. Indeed, the high primary production within this area is especially dri-

ven by the mixing generated by the strong NW winds (Mistral) (Morel & André 1991, Bosc et al. 2004) and, to a lesser extent, by land runoff from the Rhône, an important fertilization process and source of nutrients, combined with upwelling driven by winds (Estrada 1996). Moreover, the structure of the Northern Current, flowing along the shelf of the Gulf of Lions, changes markedly seasonally. During winter, the Northern Current is narrower and deeper than in the summer, and it displays enhanced mesoscale variability (Conan et al. 1998, Millot 1999). The mixing mechanism induced by the intensification of cross-slope current between the shelf and the slope waters may lead to the seaward export of particulate matter (Durieu de Madron et al. 1999), which may then be available to dolphin prey during the oligotrophic winter season. Besides temporal variability, it is also speculated that striped dolphins may change their habitat use as result of behavioural changes that may reflect changes in the preference for prey items (Azzellino et al. 2008a). Despite the fact that sightings did not occur very close to the coast, dolphins were observed at a range of distances from the coast. Several studies (Gaspari 2004, Valsecchi et al. 2004, Bourret et al. 2007) suggest genetic structuring of striped dolphin populations and hypothesize subdivision on the basis of distance from the coast. Because of the relatively small data set in the present study, we did not test for the differential habitat use of dolphins according to distance from the coast.

Relationships between animal densities and covariates at relatively high spatial and temporal resolutions (few km, days) allow us to interpret these interactions in the context of mesoscale dynamics. Since mesoscale dynamics modulate the oceanographic and biological environment, it is important not to spatially and temporally average the data over a long period and wide areas, because this would result in smoothing out the phenomena. This would be the case, for example, for transient upwelling cells induced by strong northerly wind events (few days) in the Gulf of Lions, or for the eddies propagating ( $3$  to  $5$  km  $d^{-1}$ ) in the Algerian sub-basin (e.g. Puillat et al. 2002), which cannot be identified on monthly to annual composite satellite images. Previous studies (e.g. Cañadas et al. 2002) in coastal areas have usually reported that cetacean densities were mainly related to static physiographic parameters, i.e. depth and slope, while dynamic environmental processes are more rarely investigated. The open sea is characterized by high environmental variability as a result of the mesoscale dynamics, despite relatively constant depth (centre of the basin). It also emphasizes the difficulty in examining relationships between environmental parameters and cetacean distribution from a temporally pooled data set.

Our results show that observed occurrences of striped dolphins are linked to the dynamic environment. This link is especially highlighted by the relationship with SST gradient, which defined frontal zones. Relationships have been documented with temporal SST gradients (Littaye et al. 2004) or deviations from seasonal averages (Azzellino et al. 2008b), and the spatial link between cetacean density and thermal fronts has been recently investigated (Gannier & Praca 2007). Such important changes in SST are found in turbulent areas generated by eddies, meanders and filaments in both the northern and southern WM. The transect shown in Fig. 6 illustrates this link with mesoscale processes. The salinity is homogeneous in the north; however, dolphins seemed to be associated with steep changes in SST. Listed north to south, the external (offshore) edge of the Northern Current (Millot & Taupier-Letage 2005), the edge of an eddy and the north Balearic front are all characterized by abrupt changes in both SST and salinity. In the south, dolphins were also associated with the edge of an eddy, corresponding here to rapid change in SST and low salinity, and a peak in high chl *a* concentrations. Although striped dolphins were found in areas with high chl *a* concentrations, it is very likely that our model overestimates the densities of dolphins in the northernmost coastal area corresponding to the eastern Gulf of Lions. Here the plume of the Rhône River corresponds to high chl *a* concentrations, but this area is too close to shore to present such high densities of striped dolphin, a species which is known to be more pelagic than other delphinids such as common and bottlenose dolphins (Cañadas et al. 2002). The mesoscale habitat use of striped dolphins is fairly similar to that of fin whales reported from concurrent observations and satellite tracking (Cotté et al. 2009). Since the frontal zones defined by steep changes in SST seem to be important for striped dolphins, our results suggest that the mesoscale dynamics create favourable foraging conditions. Although mobile and transitory, mesoscale processes could potentially present high production, attracting and aggregating both cephalopods and mesopelagic fish, the dominant prey species of striped dolphins (Blanco et al. 1995, Würtz & Marralle 1993, Astruc 2005). Such influence of the mesoscale circulation on the distribution of production and on different trophic levels including megafauna has been reported within the Algerian basin (Viale & Frontier 1994). The presence of aggregated prey is not necessarily the consequence of high chl *a* concentrations but concomitant outcomes of oceanographic processes leading to convergence at frontal zones and favourable conditions for phytoplankton growth (Franks 1992). The lack of association with geostrophic currents as reported for fin whales (Cotté et al. 2009) could be due to the strong

influence of advection on krill distribution, while mesopelagic cephalopods and fish are mobile prey. Frontal zones in the open sea have been reported to be linked with other teutophageous predators such as sperm whales in the WM (Gannier & Praca 2007).

### Opportunity to monitor abundance

In their review, Redfern et al. (2006) claimed the relevancy of data sets obtained from platforms of opportunity for cetacean-habitat modeling purposes. They particularly identified the main limitation of opportunistic data as the variability in the quality and reliability of the observations (e.g. the expertise of observers). In the present study, we paid particular attention to this limitation through a rigorous and systematic survey protocol applied by the same trained observers during all transects. Moreover, our data collection was broad enough to catch spatial and temporal interactions from large to fine scales, drawing a more complete picture of striped dolphin ecology than considering only one scale (Hunt & Schneider 1987, Redfern et al. 2006, Weimerskirch 2007, Cotté et al. 2009). Despite the care taken with the protocol, the platform itself can induce inherent bias. The most important bias is linked to the assumption that animals at zero perpendicular distance were detected with certainty. This so-called  $g(0) = 1$  assumption can be underestimated in 2 ways: not all animals were available to be detected (availability bias), or observers failed to detect all available animals (perception bias, Marsh & Sinclair 1989). So the  $g(0) = 1$  assumption is valid for highly visible and frequently surfacing animals, detectable by observers. Gómez de Segura et al. (2006) report an availability bias for small schools, i.e. a mean proportion of time spent at surface estimated as 0.650 (SE = 0.1628), while there is none for large schools, i.e. there is always an individual surfacing. Because the ferry speed was relatively high (~20 knots), the estimated strip half-width was covered in ~22 s, one-third of the average dive interval of small schools (Gómez de Segura et al. 2006). Thus we can roughly estimate a ratio of available animals of ~0.8 for small schools, and a ratio of 1 for large schools. Consequently, the availability bias was likely to have resulted in minor underestimation of absolute abundance. Another possible bias in abundance estimates could be due to the small sample size in the use of GAMs (Hastie & Tibshirani 1990). The link between waiting distances and environmental covariates is based on functional relationships. The presence of outliers can thus have spurious effects. However, the influence of the few data points on the right-hand edge of the distribution should be limited, since the waiting distances determined by

these points are within the range of the other points and they do not severely change the function trend (Figs. 3 & 4)

The aim of the present study was not to provide a new assessment of the WM striped dolphin population, but to show the relevance of the platform of opportunity to assess animal ecology and abundance in a given area. Despite different methodologies adapted to dedicated and non-dedicated surveys, we cautiously compared abundance and density data from our analyses with previous studies. Our estimate of abundance and its confidence interval, in the area between 3° and 6°E, seems substantially higher (by 43%) than the 1991 estimate of a mean abundance of 22 100 dolphins from reported densities in areas north and south of the Balearic Islands (Forcada & Hammond 1998). Despite being more abundant than in 1991, dolphin densities reported in the present study from the northern region (0.38 dolphins km<sup>-1</sup>) are slightly lower than densities reported more recently in the Ligurian Sea (0.56, Gannier 1998) and in the central Spanish Mediterranean (0.49, Gómez de Segura et al. 2006). However, our densities are higher than those reported recently in the Ligurian Sea from winter aerial (Panigada et al. 2009) and summer boat (Lauriano et al. 2009) surveys. The differences in abundance between the reference study of Forcada & Hammond (1998) are higher for the northern region (where these authors reported a mean density of 0.23) than the southern region (0.08). Actually, abundance of striped dolphins from the 1991 survey was conducted after an epizootic mass mortality (Raga et al. 2008). A resurgence of the epizootic caused by the dolphin morbillivirus seems to have occurred, as there are new die-offs recorded from Spanish and French coasts. The transects carried out from September 2006 to late July 2007, therefore, give the status of the central part of the striped dolphin population prior to the 2007 epizootic morbillivirus event (Raga et al. 2008). We do not have enough information on the striped dolphin life cycle to definitively interpret the comparison between abundance during the first reported epizootic episode in 1990 (Forcada & Hammond 1998) and our pre-resurgence abundance. However, the increased density observed between 1991 and 2007 suggests that the population of striped dolphin may have recovered, at least in part, from the 1990 epizootic.

The difference in abundance between 1991 and 2007 appears especially marked north of the Balearic Islands, where densities of striped dolphins were higher compared to south of the islands. This supports the hypothesis that epizootics are density-dependent phenomena (Black 1991), i.e. high population density is likely to facilitate the emergence and propagation of morbillivirus infections like the 1990 outbreak. In order

to assess precisely the effects of this new epizootic event, similar survey protocols from platforms of opportunity should be carried out. In the current context of changes in the marine environment, it is particularly important to investigate whether the effects of environmental stresses, directly or indirectly caused by human activities, could precipitate the epizootics.

**Acknowledgements.** We are grateful to SNCM and the ferry crews for their help, and for the contribution of CIESM, Sea-Keepers and Maritech to the TRANSMED on-board system. The Physical Oceanography DAAC (Jet Propulsion Laboratory, NASA), Ocean Biology Processing Group (NASA), CLS Space Oceanography Division (support from Cnes) and Météo France are thanked for the distribution of satellite images. C.C. was funded by a Provence Alpe Côte d'Azur regional council fellowship.

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Editorial responsibility: Daniel Palacios,  
Pacific Grove, California, USA

Submitted: November 25, 2009; Accepted: June 28, 2010  
Proofs received from author(s): August 16, 2010