How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: The north-western Mediterranean Sea

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ABSTRACT

Contrasting to the overall oligotrophic Mediterranean Sea, the north-western basin is characterised by high productivity and marked by seasonality, which induces spatiotemporal heterogeneity of habitat. Cetaceans and seabirds are expected to perceive this repetition of the seasonal cycle and to anticipate the recurrent variability of their environment. Because phenology imposes strong constraints over marine predators, especially through reproduction, we expected them to exhibit variations in their habitat preferences over seasons. Indeed, during reproductive period, marine predators have to face their own needs and those of their young, while out of this period, they can focus on maximising their own survival only. We therefore hypothesised that some species would change their habitat preferences to exploit the most favourable habitat during each season, while other species might accommodate the same habitat all year-round, for example thanks to the use of an habitat favourable all the year. To explore these hypotheses, we used aerial surveys data conducted over north-western Mediterranean Sea during winter 2011–2012 and summer 2012. Generalised Additive Models were used to link the species density to a set of 12 physiographic and oceanographic predictors describing their environment. Habitat models resulted in deviances from 12 to 47%. Our results provided the first assessment of habitat preferences for the winter season for most of our studied species. Small-sized delphinids (mostly striped dolphins), fin whales, Globicephalinae (long-finned pilot whales and Risso’s dolphins) and small-sized shearwaters (Yelkouan and Balearic shearwaters) exhibited no habitat variations between seasons, although for the first two, abundances were lower in winter. On the contrary, bottlenose dolphins switched from coastal habitat in summer to pelagic habitat in winter, while Cory’s shearwaters and storm petrels exhibited the largest habitat variations between seasons with a complete absence during winter.

1. Introduction

Physical and biological processes in marine ecosystems are generally strongly heterogeneous in space and time (Barry and Dayton, 1991). This high environmental variability in ecosystem conditions induces patchy and variable distributions of forage resources for top predators and, as a consequence, implies the necessity for predators to cope with such variability (Hunt and Schneider, 1987; Stewart et al., 2000). However, the degree of predictability and patchiness of resources for predators depends on scales: spatial and temporal scales are known to be linked and generally to increase together (Wiens, 1989). For example, spatially large-scale features tend to be recurrent or permanent and are highly predictable; in contrast, coarse and fine-scale processes tend to be shorter and less predictable. Seasonality is a major contributor to temporal variability and operates at an intermediate temporal scale (infra-year) and from fine to large spatial scales; its effects are strongly predictable from year to year. Indeed, the winter mixing of the water column induces enrichment of the upper layer in nutrients, which allows the growth of phytoplankton when incident light and temperature increase in summer, the so-called phytoplankton bloom (Sverdrup, 1953). The development of phytoplankton then induces an impoverishment of the upper layer and, since the summer stratification of the water column inhibits the renewal of nutrients, a reduction of production occurs in summer.

Seasons result from the angle between the polar rotation axis of the earth and its revolution plan around the sun. This angle has been fairly stable with time, and hence the earth has experienced a seasonal regime for periods comparable to evolutionary times. The
amplitude of seasonal variation is minimal at the equator and increases with latitude. The location and intensity of the main seasonal processes can vary between years according to decadal fluctuations (i.e. north Atlantic oscillation) or longer-term trends (i.e. climate change). Marine mammals and seabirds living at temperate latitudes have thus evolved in a seasonal environment that has shaped their life traits and migration patterns according to the main recurrent large-scale features in physical and biological characteristics of the ocean. We define the phenology of these species as their annual cycle in distribution and associated vital functions such as reproduction, migration, and foraging.

In addition to this, meso- and micro-scale processes add less predictable heterogeneity to the marine environment that top predators have to cope with by adaptive behavioural responses largely dependent on their individual sensory and communication skills, possibly enriched by the memory of previous experiences as well as by social (horizontal transmission between individuals of the same generation) and cultural (vertical transmission between individuals of consecutive generations) traits.

Hence, we could reasonably expect top predators to perceive the repetition of the seasonal cycle (Simmonds, 2006), and to anticipate this recurrence of their environment. Since phenology imposes strong constraints over species on an annual basis, especially through reproduction, we could expect predators to change their habitat preferences seasonally to find the best compromise between ocean conditions and their own constraints during each season. For example, during the reproductive period, marine mammals and seabirds face increased energetic demands to answer both their own needs and those of their young (Stearns, 1992). As an answer, adults adapt their behaviour during the reproductive season to equilibrate the compromise between investing in their own survival or in reproduction: diet and/or foraging strategy flexibility, variations of foraging areas, increase of foraging effort in the case of an unfavourable year. Out of the reproductive season, predators are released from this compromise and can modulate their habitat preferences to optimise their own survival.

This study will focus on the north-western Mediterranean basin (hereafter NWMS). This long considered oligotrophic sea (Margalef, 1985) is today known as strongly heterogeneous. The eastern basin is oligotrophic, but the north-western basin exhibits the highest productivity of the whole Mediterranean, showing similarities with the eastern North Atlantic regarding its marked seasonality (D’Ortenzio and Ribera d’Alcalà, 2009). The NWMS is home to a diversified and abundant community of cetaceans and seabirds (see Laran et al., 2017; Pettex et al., 2017). Cetacean populations are mostly confined to the Mediterranean, whereas seabird populations include species with a permanent presence in the basin, as well as populations that predominantly use the area either during their breeding season, or conversely during non-breeding or inter-nuptial periods of their life cycles (del Hoyo et al., 2010). Few of them have been investigated for habitat use so far and, when so, mostly in the summer (e.g. Péron et al., 2013; Péron and Grémillet, 2013). Hence, basin-wide seasonal changes in distribution and habitat use by marine top predators are still poorly known.

By using observational data from aerial surveys conducted in the NWMS during both the summer and winter seasons, the present study was aimed at testing whether predators modulated their habitat preferences in response to seasonal changes of their environment, and explore which parameters were involved in these potential variations. To do so, we investigated seasonal changes in habitat preferences of species underlying their changes in distribution through habitat modelling using Generalised Additive Models (GAMs) to seasonally model the relationships between species density and a set of variables describing their environment. This approach allowed us both to provide robust insights into those relationships and to compute predictions of potential species distributions based on their observed habitat preferences.

2. Material & methods

2.1. Study region

The NWMS is characterised by a complex topography, with large continental shelves in the Gulf of Lion and the Tyrrenhian Sea and steep slopes indented by numerous canyons elsewhere (Fig. 1). The general circulation is dominated by deep Atlantic-originated waters entering the area from the eastern Mediterranea through the Tyrrenhian Sea, and flowing across the Ligurian Sea to the Balearic Sea, along the continental slope. This current is known as the Liguro-Provençal or Northern Current (Millot, 1999).
Wind regime, topography and general circulation generate two permanent fronts: the Ligurian Front along the steep slopes of the Ligurian Sea and the North-Balearic Front (Sournia et al., 1990). The Gulf of Lion remains a particular area within the NWMS, where the combined effect of winds and fluvial discharge, mainly from the Rhône river, generates high productivity throughout the year (Morel and André, 1991). The Rhône river plume spreads out up to hundred kilometres from the river delta (Sournia et al., 1990; Morel et al., 1990).

The strong NWMS seasonality (D’Ortenzio and Ribera d’Alcà, 2009) is characterised by a strong summer stratification limiting phytoplankton growth and overall biological production, whereas water mixing during winter due to the combination of low surface temperatures and strong winds results in the breakdown of water stratification and in deep water nutrients being upwellled to the surface layer. This enrichment of the euphotic layer allows phytoplankton bloom and mesotrophic conditions to develop in the NWMS from late winter to spring (Auger, 2011; Morel and André, 1991; Sournia, 1973; Bosc et al., 2004).

2.2. Aerial survey and data collection

SAMM (Suivi Aérien de la Mégafauna Marine, Aerial Census of Marine Megafauna) aerial surveys were conducted from late November to mid-February 2012 (13,762 km of sampled transect) and from mid-May to early August 2012 (18,451 km of sampled transects). Sampling transects followed a zig-zag layout, and were manually designed to both maximise the use of flight time and cover the variety of marine habitats found in the NWMS, while ensuring an equal coverage probability within each stratum. Effort covered most of the NWMS north of 41°N (Fig. 1).

Observations were conducted following a standardised protocol designed for aerial surveys. For cetaceans, the protocol was based on line-transect methodology (Buckland et al., 2001): all sightings of cetaceans were recorded with the declination angle, based on line-transect methodology (Buckland et al., 2001): all cetaceans were recorded at the lowest taxonomic level possible, with as many observations as possible. Common and striped dolphins (Delphinus delphis and Stenella coeruleoalba) were grouped as small-sized delphinids since, for most observations, it was not possible to tell apart the two species with certainty; however, it is admitted that striped dolphin largely dominates in the NWMS (Forcada and Hammond, 1998). The bottlenose dolphins Tursiops truncatus were identified at the species level. All sightings of “unidentified dolphins” were removed from the dataset. Although they can easily be told apart, long-finned pilot whales Globicephala melas and Risso’s dolphins Grampus griseus were pooled together (the Globicephalinae group) due to low sighting numbers for each species taken separately. Fin whales Balaenoptera physalus could not be confused with any other cetacean in the area. Regarding seabirds, we focused on three groups of procellariiforms: storm petrels Hydrobates pelagicus, Cory’s shearwaters Calonectris diomedea and small-sized shearwaters, including both the yellow-eyed Puffinus yellow and Balearic P. mauretanicus shearwaters (two species indiscernible from the air). As for delphinids, unidentified procellarids were left apart.

2.3. Habitat modelling

Transects flown in effort were first subdivided into legs of identical observation conditions and then into 10 km-long segments. For each segment, numbers of sighted individuals of each group were summed up. To perform habitat modelling on the best quality data, we retained only segments with a Beaufort sea-state from 0 to 3, and subjective conditions from medium to excellent, representing 95% and 93% of the total survey effort in winter and summer, respectively.

Generalised Additive Models (GAMs) were used to model the relationship between the number of individuals per segment (response variable) and several environmental predictors (Hastie and Tibshirani, 1990; Wood, 2006) with a quasi-Poisson distribution, due to the over-dispersion of our data (Hedley and Buckland, 2004). We used a log-link function to relate the response variable to predictors, and set the sampled area per segment as model offset. The sampled area associated with each segment was the segment length multiplied by twice the corresponding ESW for cetaceans (see Laran et al., 2017, and Appendix S2 for more details), or by twice 200 m for seabirds.

We used a set of twelve environmental predictors (Table 1). First, we included four physiographic variables: bathymetry (depth), its gradient (slope), distance to the closest coast and distance to the closest colony for seabirds. Colony locations were compiled from several sources and geolocated (Appendix S1). Second, we included eight oceanographic variables: sea surface temperature (http://www.science.oregonstate.edu/ocean.productivity/), surface chlorophyll and euphotic depth (http://oceancolor.gsfc.nasa.gov/cgi/l3), and Eppley-VGPM model based on MODIS products was used to compute surface Net Primary Production (http://www.science.oregonstate.edu/ocean.productivity/). The ODYSEEA product from Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu) was used to compute mean, variance and gradient of sea surface temperature. The Mediterranean Sea Physics Analysis and Forecast (MSPAF) products from My Ocean project were used to compute mean and standard deviation of sea surface height.

<table>
<thead>
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<th>Type</th>
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<th>Units</th>
<th>Source</th>
</tr>
</thead>
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<td>GEBCO-08</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>degrees</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Distance to the closest</td>
<td>km</td>
<td></td>
</tr>
<tr>
<td></td>
<td>coast</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Distance to the closest</td>
<td>km</td>
<td>Manually referenced</td>
</tr>
<tr>
<td></td>
<td>sea surface height</td>
<td>meters</td>
<td></td>
</tr>
<tr>
<td>Oceanographic</td>
<td>Mean surface Chlorophyll</td>
<td>g m⁻²</td>
<td>MODIS</td>
</tr>
<tr>
<td></td>
<td>Production</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean euphotic depth</td>
<td>meters</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean SST</td>
<td>°C</td>
<td>ODYSEEA</td>
</tr>
<tr>
<td></td>
<td>Variance of SST</td>
<td>°C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean gradient of SST</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean sea surface height</td>
<td>meters</td>
<td>MSPAF</td>
</tr>
<tr>
<td></td>
<td>Standard deviation of SSH</td>
<td>meters</td>
<td></td>
</tr>
</tbody>
</table>
temperature (SST) mean, variance (SST\textsubscript{var}) and gradient (SST\textsubscript{grad}), computed as the difference between minimum and maximum values among the eight neighbours of each cell), sea surface height (SSH) mean and standard deviation (SSH\textsubscript{SD}), surface chlorophyll a concentration (Chl), surface net primary production (NPP) and mean euphotic depth (Zeu). These oceanographic predictors were dynamic and, hence, introduced with two temporal resolutions: dynamic predictors were summarised over the 7 and 28 days prior to each sampled day. An overview of environmental conditions in the study area was obtained by averaging predictors over the survey period for winter and summer seasons (Fig. 2). These predictors were all distal variables, given that no proximal variables (i.e. prey) were available at this scale for the study periods. Although proximal variables are expected to better explain the distributions of species, the variables used here were environmental characteristics of known importance to approximate the distribution of prey.

We implemented a selection procedure which tested models with at least one and up to four covariates (including covariates at both temporal resolutions) and excluding all combinations of covariates with an absolute value of correlation higher than 0.7 (correlation matrices are presented in Appendix S3). The maximum degree of freedom for smoothers was constrained to 3 to avoid over-fitting of the data (4, considering the offset). The

**Fig. 2.** Environmental conditions averaged over the two study periods. A – averaged conditions in winter (from late November 2011 to mid-February 2012); B – averaged conditions in summer (from mid-May 2012 to early August 2012).
with depth, mean SST (7d), SSTvar (7d) and Chl (28d) as selected accounted for 11.8% of the total deviance (Table 3, Fig. 3A). The SSHSD had overall important contributions, with a preference for deep waters (3000 m deep). The most contributing covariate was depth, with a relationship indicating a preference for oligotrophic waters, inducing negative contributions in the Gulf of Lion (which was productive). Then, the relationships with the last two covariates showed a preference for cooler waters and a fairly high weekly variance of SST. The model predicted small-sized delphinids to be present in oceanic waters, with higher densities in the southern, deep oligotrophic waters (Fig. 4B). CVs were overall low for both seasons, with higher CVs in the Gulf of Lion and along northern Tuscan coast in winter, but higher CVs outside the studied area in summer (Appendix S5, Figure S5.1).

3. Results

3.1. Sightings

The four groups of cetaceans were present in both seasons, but the only seabirds to be abundant in both seasons were the small-sized shearwaters (Table 2, Appendix S4). For the two other seabird groups, numbers of sightings in winter were too low to allow habitat modelling.

3.2. Seasonal habitat models and predicted distributions

3.2.1. Small-sized delphinids

In winter, the selected habitat model for small-sized delphinids accounted for 11.8% of the total deviance (Table 3, Fig. 3A). The selected covariates were depth, slope, Zeu (7d) and SSHSD (28d). The most contributing covariate was depth, with a relationship highlighting a preference for deep waters (3000–1500 m deep). The SSHSD had overall important contributions, with a preference for medium values (the lower the value, the higher the water column stability). The relationships to Zeu and slope, respectively, indicated a preference for oligotrophic waters and high slope values. This model predicted an exclusively oceanic distribution, completely avoiding shelves (Fig. 4A).

In summer, explained deviance reached 20.5% (Table 4, Fig. 3B), with depth, mean SST (7d), SSTvar (7d) and Chl (28d) as selected covariates. As in winter, depth was the most important covariate, with a similar relationship. Chl seemed to be an important covariate as well, with a relationship indicating a preference for oligotrophic waters, inducing negative contributions in the Gulf of Lion (which was productive). Then, the relationships with the last two covariates showed a preference for cooler waters and a fairly high weekly variance of SST. The model predicted small-sized delphinids to be present in oceanic waters, with higher densities in the southern, deep oligotrophic waters (Fig. 4B). CVs were overall low for both seasons, with higher CVs in the Gulf of Lion and along northern Tuscan coast in winter, but higher CVs outside the studied area in summer (Appendix S5, Figure S5.1).

3.2.2. Bottlenose dolphins

The bottlenose dolphin winter model explained 20% of deviance (Fig. 5A). Selected covariates were mean SST (28d), SSTvar (28d), SSTgrad (28d) and Zeu (28d). According to the contribution maps, all covariates seemed to be more or less equivalent in their overall contributions. Relationships indicated a preference for deep Zeu, for high monthly variations of SST, warmer waters and an avoidance of medium monthly thermal fronts. According to the model, bottlenose dolphins were predicted to spread across oceanic waters (Fig. 4A), with higher densities in the strong frontal zone off Catalonia and in the frontal zone induced by the interaction between cyclonic and anticyclonic eddies in the Tyrrenian Sea.

In summer, the model explained 27.1% of deviance (Fig. 5B). Selected covariates were depth, mean SST (28d), mean SSH (28d) and SSHSD (28d). Once again, the four selected covariates resulted in similar importance in the linear predictor. Bottlenose dolphins showed a preference for waters deeper than 1000 m, waters around 22, low SSH and SSHSD. This model predicted a more coastal distribution for bottlenose dolphins in summer (Fig. 4B), the species being predicted all along the slope from Catalonia to the Gulf of Lion, the Ligurian Sea shelf, around Corsica and Sardinia, the Tuscan Archipelago and the northern Tyrrenian Sea. However, coupled with a preference for high SST, highest densities were predicted in the Balearic shelf and west of Sardinia, two areas located outside the surveyed area. CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.3. Globicephalinae

Given the small sample size and the absence of Globicephalinae from the Gulf of Lion, the effort conducted in the area has been excluded from the dataset prior to performing habitat model selection, since when the Gulf was included, no habitat models stood out. Explained deviances for the selected model were quite high, with 53.1% in winter and 39.6% in summer (Fig. 6A, B). In winter, selected covariates were depth, SSTgrad (7d), mean SST (28d) and SSHSD (28d). Mean SST was the most contributing covariate, especially along the slope and the oceanic area off the Gulf of Lion, with a relationship denoting a preference for cooler waters. Relationship to depth highlighted a preference for shallower waters, inducing positive contributions along the coasts, while the relationship to SSTgrad indicated a preference for

| Table 2 |
| Number of sightings, number of individuals and encounter rates for each studied groups in winter and summer. |

<table>
<thead>
<tr>
<th>Species</th>
<th>Winter</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of sightings</td>
<td>Number of individuals</td>
<td>Encounter rate (ind. km⁻¹)</td>
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<tr>
<td>Small-sized delphinids</td>
<td>163</td>
<td>979</td>
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<tr>
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<td>56</td>
<td>209</td>
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<tr>
<td>Globicephalinae</td>
<td>20</td>
<td>42</td>
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</tr>
<tr>
<td>Fin whales</td>
<td>13</td>
<td>13</td>
<td>0.001</td>
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<tr>
<td>Small-sized shearwaters</td>
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<td>1540</td>
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<td>2</td>
<td>1.45 x 10⁻⁴</td>
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<tr>
<td>Storm petrels</td>
<td>7</td>
<td>13</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Summer</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Number of sightings</td>
<td>Number of individuals</td>
<td>Encounter rate (ind. km⁻¹)</td>
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<tr>
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<td>101</td>
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Table 3
Summary of selected models for winter. Selected covariates for each group are indicated with the tick mark for physiographic variables, but with their temporal resolution (7 or 28 days) for oceanographic variables. All selected covariates were significant.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Small-sized delphinids</th>
<th>Bottlenose dolphins</th>
<th>Globicephalinae</th>
<th>Fin whales</th>
<th>Small-sized shearwaters</th>
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<td>28d</td>
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<tr>
<td>SST$_{grad}$</td>
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<td>7d</td>
<td>28d</td>
<td>28d</td>
<td>28d</td>
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<tr>
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<td>7d</td>
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<td>Mean SSH</td>
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<td>28d</td>
<td>28d</td>
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<td>28d</td>
<td>28d</td>
<td>28d</td>
<td>7d</td>
<td>28d</td>
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<td>Explained deviance (%)</td>
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<td>20.0</td>
<td>53.1</td>
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</table>

medium weekly thermal gradients, hence positive contributions along the slope. The relationship with the last covariate indicated a preference for reduced SH$_{SD}$. The model predicted Globicephalinae to be present mostly in the cooler waters of the Liguro-Provençal Current, and east of Corsica (Fig. 4A).

In summer, the selected covariates were NPP (7d), Zeu (7d), SST$_{var}$ (28d) and SH$_{SD}$ (28d). Zeu and NPP were the most important covariates, with similar contributions. Their relationships indicated a preference for high productivity areas (hence positive contributions for NPP along the Liguro-Provençal Current), and for deep Zeu (positive contributions for Zeu within oceanic waters and the Tyrrenhian Sea). For the remaining two covariates, contributions were lower and positive all over the area. Their relationships indicated a preference for low monthly variance of SST and low SH$_{SD}$. This model predicted highest densities along the slope and shelf of the Iberian coast and Balearic Islands, and around the Tuscan Archipelago (Fig. 4B). CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.4. Fin whales

The winter model-explained deviance was 24.8% (Fig. 7A), with depth, NPP (7d), SST$_{var}$ (28d) and mean SH (28d) as selected variables. Depth was the most important covariate, with high contributions over the whole area highlighting a clear preference for deep waters. NPP had high positive contributions in the Gulf of Lion and around the Tuscan Archipelago due to a relationship indicating a preference for productive areas. The other two covariates were less important, with a relationship denoting a preference for high variance of SST and lower mean SH. The resulting prediction showed the species being distributed over all deep waters across the region (Fig. 4A).

In summer, the selected model resulted in 33.3% of explained deviance (Fig. 7B). Depth and NPP (28d) were the most important covariates, with high contributions all over the area. The relationships showed a preference for deep waters on one hand, and productive waters on the other. The relationship with the two other covariates (SST$_{var}$ 28d and mean SST 7d) indicated a preference for low weekly variance of SST and warmer waters. This model predicted fin whales to be present in high densities in all oceanic zones from the Ligurian Sea to the Balearic Front (Fig. 4B), where high productivity was coincident with deepest waters. CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.5. Small-sized shearwaters

Small-sized shearwater models resulted in explained deviances of 46.6% in winter and 41% in summer (Fig. 8A). In winter, distance to the closest coast was the most important covariate, with a relationship indicating a preference for 50 km from the coast, and inducing positive contributions along the coasts. The other selected covariates were SH$_{SD}$ (7d), SST$_{var}$ (28d) and Chl (28d). Relationships showed a preference for reduced SH$_{SD}$ (negative contributions in the Gulf of Lion), high monthly variations of SST and high Chl (positive contributions in the Gulf of Lion). This model resulted in higher predicted densities where high Chl were close to shores, in the Gulf of Lion (especially in the Rhône river plume) and off the Catalonian and Tuscan coasts (Fig. 9A).

In summer (Fig. 8B), the most important covariates were depth and mean SH (7d). The two other selected covariates, SST$_{var}$ (7d) and SST$_{grad}$ (7d) had lower contributions. The relationships indicated a preference for shallow waters, medium SH, reduced weekly variance of SST and strong weekly thermal gradients. This model predicted a summer distribution pattern quite similar to the winter one, with highest densities mostly predicted in coastal frontal zones, especially in the Gulf of Lion, the northern Tuscan coast and over the Sardinian shelf (Fig. 9A). CVs were overall low for both seasons, with no pattern in summer but higher CVs both close and far away from coasts in winter (Appendix S5, Figure S5.2).

3.2.6. Cory’s shearwaters

The summer model for Cory’s shearwaters gave 37.5% of explained deviance (Fig. 10), with depth as the most important covariate, and mean SST (28d), NPP (28d) and distance to the closest colony as the three other selected covariates, with similar overall contributions. Relationships highlighted a preference for shallow waters (positive contributions along the coast), warmer waters (negative contributions in the Gulf of Lion and Tyrrenhian Sea) and productive waters (positive contributions over the Liguro-Provençal Current) within 50 km of colonies. The predicted distribution was quite contrasted (Fig. 9B), the species being predicted in highest densities in shallow, warm and productive waters close to shores, such as the Tuscan shelf, western Sardinia, around the Balearic Islands and in the Gulf of Lion (particularly in the Rhône river plume). In winter, Cory’s shearwater sightings were too scarce for habitat modelling. CVs were low, with higher values within the Tyrrenhian Sea (Appendix S5, Figure S5.2).

3.2.7. Storm petrels

The summer model resulted in 23.4% of explained deviance (Fig. 11), Selected covariates were mean SST (7d), SST$_{grad}$ (7d), SH$_{SD}$ (7d) and mean SH (28d). According to the contribution maps, mean SST and mean SH were the most important covariates. The relationships indicated a preference for 22°C, medium SH, low weekly thermal gradients and strong SH$_{SD}$. The model predicted quite homogeneous distribution (Fig. 9C), the species
Fig. 3. Habitat model selected for small-sized delphinids: A – in winter (explained deviance = 11.8%), B – in summer (explained deviance = 20.5%). Each panel spatially represents the contribution of the concerned covariate to the linear predictor for each sampled segment, with the dot size proportional to the covariate relative contribution regarding the three other covariates contributions in that point. Grey dots represent points with negative covariate contribution, black dots where it is positive. Corresponding GAMs curves are inserted in corresponding panels, representing the relationship between the covariate (abscissa) and the linear predictor (log(individuals) ordinate). The two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range must be avoided, since the smooth splines might not be reliable.
being predicted mostly over deep oceanic waters north of 40 °N up to the Gulf of Lion, and deep waters of the Ligurian Sea. High densities were also predicted in the southern Tyrrhenian Sea. As for Cory’s shearwaters, in winter, storm petrels sightings were too scarce to permit habitat modelling, and no model was fitted. CVs were low and without clear pattern (Appendix S5, Figure S5.2).

4. Discussion

4.1. General

The present work analyses the summer and winter distribution and habitat used by marine mammals and seabirds in the NWMS, an area of major importance with regard to human activities at
Relative densities were modelled under GAMs by using a variety of physiographic and oceanographic variables of potential biological importance to the different taxa of interest. While fitting the models, variables that contributed the most to the heterogeneity of seabird and cetacean densities were identified in the selection process and provided some representation of the habitat preferences of each taxon. Major strengths of the two seasonal data sets include: (1) the synoptic view of two seasonal situations in a large marine area permitted by an airborne survey methodology; (2) the homogeneity of treatment, both during the sampling phase and the analytical phase, between seasons and taxa allowing ample comparisons; (3) the unprecedented amount of effort per unit surface area yielding large data sets; and (4) the simultaneous sampling of multiple target taxa of the marine megafauna that not only reduces relative costs of data sets but also allows for more ecosystemic analyses and interpretations. The main weaknesses are mostly related to the downside of the survey strategy: (1) no protocol was implemented within this particular aerial survey to allow detection probability to be properly estimated; (2) identification at specific level from the air can be impaired for groups of species with similar colour, shape and size patterns such as small-sized delphinids, auks and several groups of larids; (3) the timing of the surveys relative to the dynamic of marine ecosystems makes it impossible to provide instant views of summer or winter cetacean and seabird distributions, instead the two seasonal data sets correspond to composite sampling over periods of 2–3 months of predominantly summer or winter conditions; and finally (4) the phenology of the different taxa cannot always match the timing of the surveys. The results have thus to be interpreted and discussed within these limitations.

So far, no similar synoptic and multitarget survey has been conducted in such a large area with a dual seasonal focus to the summer and winter seasons as well. However, many studies, although of taxonomically and spatially more limited scope, provided insights into the distribution and habitat preferences of cetacean and seabirds in the NWMS, but mostly during the summer season. These studies encompassed some dedicated shipborne surveys of cetaceans (Cañadas et al., 2002), observer programs from platforms of opportunity with yearly coverage as well as some telemetry studies on seabirds (mainly shearwaters; Péron and Grémillet, 2013). Only a few surveys included a seasonal component, but did not focus on such a large area (see for example Panigada et al., 2011). Therefore, in complement with these previous studies, our results provided the first assessment of habitat preferences driving the seasonal distributions of some poorly known species in the area, such as storm petrels, and provided a refined understanding of habitat preferences for some species such as bottlenose dolphins.

### 4.2. Ecological preferences

**Small-sized delphinids:** The small-sized delphinids oceanic distribution was driven by a clear preference for deep and oligotrophic waters in both seasons, and a preference for moderate to low monthly eddy dynamic and steep slope in winter. Those two last conditions were met along the Provencal coast and in the deep Ligurian Sea, where higher densities were predicted, and could match an optimum for prey habitat. In summer, their overall preferences for oligotrophic waters shifted towards areas with SST around 21°C, and moderate weekly variations in SST. Those optimum conditions were met in the Tyrrhenian Sea, along the lower slope of the western Sardinia/Corsica margin and the south Balearic Islands. These areas of high density were consistent with the habitats of the known forage species, such as blue whiting Micromesitis poutassou for example (Würtz and Marrale, 1993).

Small-sized delphinids were mostly composed of identified striped dolphins and unidentified small-sized delphinids (unidentified between striped or common dolphin: 23% of sightings in summer, 42% in winter), with only one identified common dolphin in summer. This composition of aerial survey data is consistent with previous knowledge in the NWMS (Bearzi et al., 2003). The clear oceanic pattern revealed in this study also concur with the majority of unidentified sightings being of striped dolphins, since both the observed and predicted distribution patterns were well consistent with the known ecology of the species (Forcada and Hammond, 1998; Cañadas et al., 2002).

Bottlenose dolphins: Concerning bottlenose dolphins, the seasonality resulted in a complete inversion of habitat preferences from winter to summer. Seasonal changes in preferences might be linked to a compromise equilibrium set in favour of the optimization of phenological constraints, with bottlenose dolphins moving inshore during summer for calving and growth of their young. Indeed, the bottlenose dolphin is a plastic species and can adapt to changing conditions, hence the species could easily sustain such a compromise.

Bottlenose dolphins showed the most contrasted predicted distribution between seasons among all studied cetaceans. Indeed, in winter, the species was overall oceanic, avoiding the northern NWMS, from the Gulf of Lion to the Ligurian Sea, and aggregated over the predictable and monthly frontal zones of the Balearic and Tyrrhenian Seas. Contrarily, in summer, the species was more inshore, with a preference for warmer waters (22°C, as for small-sized delphinids) with calm hydrography. It was only around the Tuscan Archipelago, eastern Corsica and in the Ligurian Sea that...
coastal waters were used throughout the year. This contrast in seasonal distribution has, to our knowledge, never been described in the NWMS, since the bottlenose dolphin is considered inhabiting mainly continental shelves: previous studies reported bottlenose dolphins to be present only over the shelf, within the 200 m isobath (Cañadas et al., 2002; Gnone et al., 2011). In

Fig. 5. Habitat model selected for bottlenose dolphins A – in winter (explained deviance = 20%), B – in summer (explained deviance = 27.1%). See Fig. 3 for figure explanation.
contrast, we showed here that, even in summer, bottlenose dolphins were also frequent in offshore waters up to 1000 m deep. To our knowledge, only one study suggested variations in abundance between seasons within the shelf, around the Balearic Islands (Forcada et al., 2004). Considering our results, these variations of abundance might be due to movements between neritic and

![Habitat model selected for Globicephalinae](A) Winter - Model Deviance = 53.1%

- Depth (m)
- SST gradient (°C) - 7d
- Mean SST (°C) - 28d
- SD SSH (m) - 28d

![Habitat model selected for Globicephalinae](B) Summer - Model Deviance = 39.6%

- NPP (log g/m²/d) - 7d
- Euphotic depth (m) - 7d
- SST var. (°C) - 28d
- SD SSH (m) - 28d

Fig. 6. Habitat model selected for Globicephalinae A – in winter (explained deviance = 53.1%), B – in summer (explained deviance = 39.6%). See Fig. 3 for figure explanation.
Fig. 7. Habitat model selected for fin whales A – in winter (explained deviance = 24.8%), B – in summer (explained deviance = 33.3%). See Fig. 3 for figure explanation.
Fig. 8. Habitat model selected for small-sized shearwaters A – in winter (explained deviance = 46.6%), B – in summer (explained deviance = 41%). See Fig. 3 for figure explanation.
Fig. 9. Predicted distributions of seabirds based on habitat models, for small-sized shearwaters (A), Cory's shearwater (B) and storm petrels (C). Distributions were scaled in relative densities: densities were divided by the maximum predicted density over the two seasons, for each group. As a consequence, scales are not comparable between groups. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1). Black dots on Cory's Shearwaters prediction (B) are colonies locations.

Fig. 10. Habitat model selected for Cory's shearwaters in summer (explained deviance = 37.5%). See Fig. 3 for figure explanation.
oceanic waters. Interestingly, although habitat preferences were contrasted between winter and summer, bottlenose dolphins were always related to monthly covariates, indicating a preference for more persistent patterns.

The observed shift in habitat use may be due to different reasons, such as a shift in main prey, a seasonal migration of prey, or phenological constraints. The calving period for this species occurs during summer (between July and August), and it is thought that females favour shallower waters during this period, for shelter against open-ocean agitation or predation (Blanco et al., 2001). Moreover, they could find prey without having to perform long dives, thus calves could easily learn to forage (Blanco et al., 2001). According to stranding data (mostly spring and summer strandings; Blanco et al., 2001), bottlenose dolphins in the NWMS would mainly forage on demersal and benthic prey (mainly hake), with occurrence of epipelagic species (pilchard and anchovy, possibly due to indirect ingestion, given that these species are fed on by hake). The authors hypothesised that the highlighted differences in diet according to sex and age might be due to lactation or calf care. Given that the selected model for summer corresponded to warm, shallow and calm waters, during summer, a significant fraction of bottlenose dolphin populations would dwell in coastal waters for calving and thus forage on demersal and benthic prey, whereas in winter, when calves are older, they would switch towards deep oceanic waters where they would have to forage on different species.

Globicephalinae: Most studies exploring long-finned pilot whales and Risso’s dolphins habitat preferences in the NWMS used physiographic covariates, including depth, slope and distance to the shore or to the 200 m isobath, as well as oceanographic variables such as SST, always in summer (Cañadas et al., 2002; Praca and Gannier, 2008). However, our results showed that the taxon was more related to dynamic processes enhancing productivity in both seasons. In winter, they showed a preference for the frontal zone in the Ligurian Sea and the deep convection area off the Gulf of Lion (Auger, 2011), both variables being involved in the enrichment of the surface layer in nutrients. In summer, these species showed a preference for productive and dynamic waters occurring from the Balearic to the Ligurian Sea associated to the Liguro-Provençal Current, as well as for productive waters around the Tuscan Archipelago.

Fin whales: Fin whales, unlike bottlenose dolphins and Globicephalinae, proved to be similarly distributed between the two seasons, albeit at a lower density in winter. In the NWMS, in summer, fin whales are known to forage mostly on Meganyctiphanes norvegica, which has a patchy distribution with the main concentration found in the Liguro-Provençal Front (Astruc et al., 2005). Parameters selected for the summer model were precisely related to the anticlockwise gyre of the Liguro-Provençal Current, hence fin whales were predicted to be the most abundant in this area. Our model therefore seemed to relate fin whales directly to habitats where krill concentrations are the most predictable. Moreover, summer habitat preferences were consistent with previous studies in the same season, showing that fin whales preferred waters with a SST around 23°C (Laran and Gannier, 2008; Panigada et al., 2008) and depth around 2500 m. Beside this, during periods of low productivity, fin whales were shown to respond to weekly environmental processes (Littaye et al., 2004), while during periods of high productivity they responded to monthly processes (spring bloom). Our results were consistent with this, since the summer best model related fin whales to 28 days NPP, while the winter model related them to 7 days NPP. In winter, information concerning habitat preferences of fin whales is scarce, but it is admitted that the population would migrate to other Mediterranean subregions, such as the central Mediterranean Sea. Fin whales may perform a migration from the
PELAGOS sanctuary to around Lampedusa Island, through the Messina Strait (Aïssi et al., 2008). Other studies have shown that some animals fitted with Argos tags moved to the Alboran Sea and the Gibraltar Strait (Cotté et al., 2009). These movements might explain the lower predicted densities in winter. Some studies demonstrated a shift in foraging strategies potentially linked to variations in resource availability between regions, as was the case for fin whales around Lampedusa Island foraging on Nyctiphanes couchii rather than Meganyctiphanes norvegica (Canese et al., 2006). However, in the NWMS, we could reasonably suggest that wintering fin whales remaining in the area still forage on krill during winter since they exhibit the same habitat preferences as in summer.

Small-sized shearwaters: Habitat models clearly indicated that small-sized shearwaters exhibited no seasonal variations of their preferences for coastal waters. In winter, they showed a clear preference for inshore rich waters (high Chl) averaged at a monthly scale. They were concentrated north of the study area, mostly in the Gulf of Lion, and Catalonian Tuscan coasts. In summer, their distribution was similar, but higher densities were predicted around Sardinia, the Balearic Islands and the Tuscan Archipelago. Interestingly, this pattern reproduced well the distribution of known colonies for Yelkouan and Balearic shearwaters, although distance to the closest colony was not selected in the best model; this suggests that colonies would be established close to recurrently favourable habitats. Indeed, our results indicated that during summer, individuals relied on predictable weekly frontal zones over the plateau. Yelkouan and Balearic shearwaters therefore seemed to select similar coastal habitats throughout the year, although the drivers were a bit different.

This summer distribution was consistent with known foraging habitats of these two species. Yelkouan shearwaters breeding on the Provençal coast islands are known to perform most of their foraging trips to the Gulf of Lion with some flights up to Cape Creus (Péron et al., 2013; Péron and Grémillet, 2014). The Catalonian coast, around Cape Creus, was identified as an important foraging ground for Balearic shearwaters breeding in Balearic colonies (Louza et al., 2011), but the Gulf of Lion was recently shown to be regularly used by Balearic shearwaters in spring (Meier et al., 2015). When comparing results from telemetry (Péron et al., 2013; Péron and Grémillet, 2014) and predictions from habitat models presented in this study, it seems surprising that our model does not predict the high densities of individuals close to the Provençal colonies. However, individuals sighted around those colonies were very coastal, and predictors used for this study did not provide any information for very coastal cells, depending on their resolutions. Therefore, no prediction was available in those areas.

Cory's shearwaters: The summer Cory's shearwater predicted distribution was quite similar to that of small-sized shearwaters. However, the environmental parameters driving this distribution were different. The selected model indicated that Cory’s shearwater preferred monthly averaged warm productive waters close to their colonies, where they could find reliable and easily accessible resources during the breeding period. A tracking study of Cory’s shearwaters tagged during aerial survey periods provided consistent results (Péron and Grémillet, 2014): individuals breeding in the colonies of the Provençal coast performed foraging trips in the Gulf of Lion and on the Catalonian coast (Cape Creus), while individuals tagged in northern Corsica used the south Ligurian Sea, close to the Tuscan Archipelago, and individuals tagged in southern Corsica moved across the whole Bonifacio Strait. The absence of Cory’s shearwaters from the area in winter has recently been confirmed by telemetry study (Péron and Grémillet, 2013), revealing migration from the Mediterranean Sea to western Africa in autumn for all adults, juveniles and immature individuals.

Storm petrels: Storm petrels showed a predicted distribution almost opposite to that of shearwaters. Indeed, the species was predicted across all oceanic waters from the Balearic to Ligurian Seas, as well as in the Gulf of Lion, as an answer to their preference for stable waters with negative SSH and reduced surface temperature. This oceanic distribution was fairly similar to that of the fin whale, which might be linked to a partially overlapping diet between both taxa, since storm petrels are known to forage over plankton, although with a wider spectrum than whales. They forage over microzooplankton and ichthyoplankton from oceanic to coastal waters, but also over small fishes, squids, whale carcasses and offal (del Hoyo et al., 2010).

4.3. Accommodating seasonal variations

Small-sized shearwaters, Globicephalinae, small-sized delphinids and fin whales were characterised by the consistency of their habitat preferences from winter to summer. The small-sized shearwaters answered the seasonality of their environment by targeting areas exhibiting reduced seasonality: the coastal year-round productive habitats. Doing so, they exploited a habitat ensuring the satisfaction of their needs throughout the year, during the non-reproductive period as well as during the high-cost breeding and chick-rearing periods. The overall seasonality of the NWMS seemed to have no impact on the Globicephalinae habitat preference, the species being able to switch between habitats with enhanced productivity from season to season. This might be explained by the reduced energetic needs of the species linked to their deep-diving capacities, allowing them to target layers little concerned by surface seasonality. For the last two groups, habitat preferences did not vary between seasons, but a part of the population seemed constrained to migrate out of the area during the unfavourable season; e.g. fin whales and small-sized delphinids had lower abundance in winter compared to summer (see Laran et al., 2017), but their habitat preferences remained similar in both seasons. Around the Channel Islands, California, whales were also found to have consistent preferences across seasons (Croll et al., 1998); the authors demonstrated that whales exploited highly predictable patches of euphausiids that aggregate above topographic breaks when upwelling is more active, these processes being sufficiently consistent across seasons and years to correctly predict the distribution of whales. Although at a finer scale, fin whales in the NWMS showed the same pattern of foraging consistency between seasons, if not years, at least for the part of the population remaining in the area throughout the year. For these two groups, then, the habitat remained favourable throughout the year but a part of the population seems to move out of the NWMS for some unknown reasons.

In contrast to the above groups, species characterised by high plasticity seemed to have the possibility to switch between the most favourable habitats between seasons rather than accommodating the same habitat all year round. For migrating seabirds, this variation was extreme: although the NWMS seemed a good reproductive ground for Cory’s shearwaters and storm petrels, once the central-place foraging constraint was released, the two species migrated out of the Mediterranean Sea (Péron and Grémillet, 2013). This migration could indicate that the area might not, during winter, represent an optimal foraging ground, and once reproductive constraints are released, they leave the NWMS for better places. Finally, bottlenose dolphins exhibited the widest shift in habitat preferences among the cetaceans studied here, using coastal habitats during the calving period then moving to oceanic waters when calves could follow the adults. This is a good example of the well-known foraging plasticity of the species.
5. Conclusion

In the present work, our goal was to test whether the seasonality of the environment induces a modification in ecological processes underlying seasonal changes in the distribution of species, and we provided insights on which mechanisms drive the spatial distribution of species in each season.

The knowledge of habitat preferences for the studied species in the NWMS were scarce, and mostly relied on physiographic parameters such as depth or slope, plus some dynamic parameters such as SST, but always at low temporal resolution. Here, we incorporated all predictors potentially involved in the processes underlying distributions for these species. The use of two temporal resolutions (7 and 28 days) allowed consideration of the temporal lags between oceanographic processes and predator responses. Therefore, our study provided a first insight into habitat preferences of several taxa, and for all taxa the first description of their winter preferences in the NWMS.

Our goal was to test whether the seasonality of the environment induces a modification in ecological processes underlying seasonal changes in species distribution, and we showed that both ecological processes driving distributions and top predator relationships with these processes vary through seasons. The highlighting of this seasonal variation of habitat preferences implies some important advice for habitat modelling: our results clearly demonstrated that we must not try to extrapolate habitat preferences and distributions based on one season to another. That is, we should not use a summer model to predict a winter distribution or vice-versa. Indeed, the first assumption of extrapolation is that processes are stationary and are similar, in their distribution and importance for species, in the forecast region and forecast time (Elith and Leathwick, 2009), which in the present study was clearly demonstrated as wrong concerning season.

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Appendix A. Supplementary data

Supplementary data associated with this paper can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2016.06.012.

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References


