Scale-dependent interactions of Mediterranean whales with marine dynamics

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Abstract

We investigated the influence of the ocean circulation at different spatiotemporal scales on the seasonal distribution of a large marine predator, the Mediterranean fin whale, by comparing multisatellite data with the positions of eight fin whales equipped with Argos tracking devices from August 2003 to June 2004. At the western Mediterranean basin scale, fin whales were associated with the anticlockwise gyre in the northern part of the western Mediterranean Sea, which defines the habitat of krill, the whales’ main prey. At mesoscale and submesoscale, and only during the seasonal phytoplankton biomass minimum in summer, whales exhibited a preference for the periphery of eddies and they were often associated with filaments indicative of submesoscale fronts. Timescales of these mesoscale and submesoscale features are comparable with the ecological timescales of the lower levels of the trophic chain. Whales were not associated to productive areas, probably due to the spatiotemporal lag between phytoplankton and krill. Our results suggest that stirring by eddies may create filaments that are favorable foraging grounds for predators searching for aggregated prey during the most oligotrophic period of the year.

The interaction of a predator with its environment is a process that occurs at several spatiotemporal scales, particularly in marine ecosystems (Bost et al. 2009). Indeed, foraging marine predators are integrators of a variety of ecological processes, and in particular of the numerous interactions between environmental forcing and the growth, behavior, and distribution of marine organisms at lower trophic levels (Nicol et al. 2000). Although the large-scale (1000 km) distribution of predators is well explained by large oceanic features such as climatological fronts (Tynan 1998; Bost et al. 2009), the environmental drivers of their distribution at finer scale (10 to 100 km) in the open sea are still not well identified (Etnoyer et al. 2006). When considering large pelagic predators such as fish, turtles, seabirds, and marine mammals, these organisms searching for prey have to cope with a puzzle of oceanographic features, often nested by scales, shaping their heterogeneous environment. Many studies have related the distribution and behavior of predators with the oceanographic context either from oceanographic cruises (Nicol et al. 2000) or from telemetric studies using predators to sample their environment (Bailleul et al. 2007). However, only a few studies have considered the relationships between the distribution of predators and their marine environment at several scales simultaneously, which is fundamental to understand the complete picture of a predator’s foraging strategy (Fauchald et al. 2000). Indeed, although interdisciplinary cruises collect valuable information on both physical and biological processes, i.e., in space, they usually report snapshots of a given situation at a specific period and do not provide for the investigation of temporal patterns.

Such multiscale analysis is now possible thanks to satellite technology that permits both animal tracking and synoptic descriptions of the marine environment in which they operate (surface currents, temperature, and chlorophyll). The relatively high spatiotemporal resolution of satellite data and their large spatial cover make it possible to observe the variability of the environment on scales ranging from the seasonal and ocean basin scale, to the scale of oceanic eddies (hereafter “mesoscale,” ~ 100 km and weeks to months) and filaments (hereafter “submesoscale,” 1–10 km and days to weeks) principally resulting from eddy–eddy interactions. Evidence that mesoscale eddies affect the distribution and the dynamics of primary production and lower-level pelagic ecosystems has been accumulating during the last decades (Angel and Fasham 1983; Strass et al. 2002; d’Ovidio et al. 2010). There is also growing evidence for the importance of eddies in providing foraging opportunities for various marine predators such as turtles (Polovina et al. 2006; Lombardi et al. 2008), seals (Ream et al. 2005), and seabirds (Nel et al. 2001; Weimerskirch et al. 2004; Cotté et al. 2007).

At submesoscale, the ocean surface is characterized by filamentary structures with temporal scales comparable with those of phytoplankton blooms (~ 10 d) (Lévy 2008;
Pérez-Muñuzuri and Huhn 2010). These filamentary structures mainly result from the horizontal stirring induced by the deformation velocity field associated with eddies (Lévy 2008; d’Ovidio et al. 2009). Filaments have been shown to strongly influence lower trophic levels (phytoplankton) by creating environmental conditions favorable for the stimulation of biological production, and by structuring this production in space and time (Lehahn et al. 2007; Lévy et al. 2008). The effect of filament dynamics on phytoplankton production has been found to be particularly important in oligotrophic conditions—like the interior of subtropical gyres or the shallow and nutrient-depleted photic layer occurring in summertime. The main mechanisms are mesoscale- and submesoscale-driven upwelling or lateral intrusion of nutrients, and development of patchiness by horizontal stirring. The influence of these filaments on the distribution of marine predators is, however, still poorly known. Recently, Tew-Kai et al. (2009) have shown the strong association of the frigatebird positions with surface submesoscale filaments in the Mozambique Channel. This result suggests that the presence of submesoscale features may explain part of the distribution and behavior of foraging marine top predators.

In this work, we focus on the seasonal distribution and preference of fin whales in the Mediterranean Sea relative to circulation features. The general circulation in the Mediterranean is a counterclockwise permanent flow along the continental slope (Millot and Taupier-Letage 2005). This main circulation is markedly unstable and generates mesoscale and submesoscale features. This dynamic activity is known to be higher in the south of the basin and temporally stronger during winter (d’Ovidio et al. 2004; Millot and Taupier-Letage 2005). The Mediterranean Sea is known to be an oligotrophic environment where large populations of predators such as tuna, seabirds, and cetaceans are paradoxically found. Within this apparent inhospitable environment, the fin whale, Balaenoptera physalus, is the largest predator feeding almost exclusively on northern krill, Meganyctiphanes norvegica (Orsi Relini and Giordano 1992). The summer preference of fin whales for the northwestern Mediterranean sea is well known since the synoptic survey of the western basin (Forcada et al. 1996). Partial information on the seasonal distribution over the year has been very recently examined along a transect crossing the basin from French to Algerian coasts (Cotté et al. 2009).

Because the Mediterranean is generally poorly productive and because the whales need concentrated food to meet their large energetic demand (Nemoto 1970), we hypothesized that these large free-ranging predators adjust their distribution to the distribution of their prey in response to mesoscale and submesoscale processes. The presence of rich mesoscale and submesoscale activities (Taupier-Letage et al. 2003; Isern-Fontanet et al. 2006) in this oligotrophic environment is purported to be particularly important in modulating the regional and seasonal variability of the biological production. As no data set on krill distribution was at our disposal, we examined the distribution of fin whales in relation to the marine environment at large scale (basin-wide circulation), mesoscale (eddies), and submesoscale (filaments) within the western Mediterranean Sea. Our data set covers a period of 10 months, which allowed us to discriminate the relationships during a strongly oligotrophic period (summer) and a relatively more productive one (winter).

Methods

**Whale tracking**—During August 2003, eight fin whales were equipped with Argos satellite-tracking devices. These instruments allowed tracking of the whales’ positions at intervals ranging from a few hours to a few days, and for a period of 1 to 10 months, depending on the device (Table 1; Fig. 1). Most whales were tagged within the same area, centered on 6°E and 42.5°N (gray full circles in Fig. 2), and were tracked over several months, although only a few locations were obtained for some whales (Table 1; Fig. 2).

More precisely, the semi-implantable tags (26 cm in length × 1.9 cm in diameter) consisted of a Telonics® Argos ST-15 transmitter in a stainless steel tube. The tag was applied using an air-powered applicator (Heide-Jorgensen et al. 2001) with 7 bar pressure at a distance of less than 3 m from the whale. Tags were deployed in front of the dorsal fin area on the dorsal surface of the whale. To save batteries and extend tag operation, tags transmitted for only four 1-h periods daily during the first 90 d and every 4 d thereafter. A saltwater switch and microprocessor were used to save battery power by limiting transmissions to

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**Table 1.** Summary of whale tracking from the eight devices.

<table>
<thead>
<tr>
<th>Device No.</th>
<th>First location</th>
<th>Last location</th>
<th>Location number (summer–winter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2910836</td>
<td>12 Aug 2003</td>
<td>16 Jan 2004</td>
<td>9 (6–3)</td>
</tr>
<tr>
<td>2910838</td>
<td>18 Aug 2003</td>
<td>16 May 2004</td>
<td>57 (34–23)</td>
</tr>
<tr>
<td>2910842</td>
<td>16 Aug 2003</td>
<td>01 Jan 2004</td>
<td>43 (19–24)</td>
</tr>
<tr>
<td>2923029</td>
<td>18 Aug 2003</td>
<td>02 Oct 2003</td>
<td>12 (12–0)</td>
</tr>
<tr>
<td>2923032</td>
<td>18 Aug 2003</td>
<td>30 Sep 2003</td>
<td>10 (10–0)</td>
</tr>
<tr>
<td>2923033</td>
<td>04 Aug 2003</td>
<td>22 Dec 2003</td>
<td>9 (2–7)</td>
</tr>
<tr>
<td>2923041</td>
<td>08 Aug 2003</td>
<td>30 Jan 2004</td>
<td>5 (4–1)</td>
</tr>
</tbody>
</table>
times when the tag was out of the water and coinciding with optimal Argos satellite coverage. Although we used all location classes for the analyses, we used screening criteria for Argos location classes 3–0 (accuracy < 150 m, < 350 m, < 1000 m respectively and classes 0, A, B, and Z with no designated accuracy) on the basis of feasible swimming speeds (Mate et al. 1999). We removed all locations on the basis of the assumption that whales rarely travel at speeds > 15 km h\(^{-1}\) for > 1 h. The higher error associated with Argos LC0 locations (which is about several kilometers) is equal or less than the submesoscale features, which are 1–10-km wide and ~ 100-km long.

Satellite data—Sea-surface currents were derived from satellite sea-surface altimetry data. We used the surface velocities computed from weekly merged products of absolute dynamic topography (ADT) at 1/8\(^{\circ}\) resolution (12 km) on a Mercator projection (Ssalto-Duacs) distributed by Archiving Validation and Interpretation of Satellite and Oceanographic data (AVISO, http://www.aviso.oceanobs.com) (Le Traon et al. 1998; Ducet et al. 2000).

The velocities obey the following relations:

\[
\begin{align*}
u &= - \left( g/f \right) \frac{\partial \text{ADT}}{\partial y} \\
v &= \left( g/f \right) \frac{\partial \text{ADT}}{\partial x}
\end{align*}
\]

where \(g\) is the acceleration due to gravity (9.81 m s\(^{-2}\)), \(f\) is the Coriolis parameter, and \(\delta x\) and \(\delta y\) are the eastward and northward distances, respectively. The ADT is obtained by satellite-derived anomalies to which the Rio05 mean dynamic topography (Rio et al. 2007) is added. The period 2003–2004 of our study has one of the best altimetric coverage, with a four-satellite constellation (Jason-1, Topex-Poseidon, Envisat, and Geosat Follow-on [GFO]).

Sea-surface temperature (SST) was derived from the MODerate-resolution Imaging Spectroradiometer (MODIS) Aqua global level 3 monthly gridded product at 9-km resolution. Data are provided by the Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory.

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Fig. 2. Tracking of fin whales. Gray full circles represent the first obtained locations and the black crosses represent the last locations.
Laboratory (http://podaac.jpl.nasa.gov/). We also used surface chlorophyll a (Chl a) concentration from the merged Sea-viewing Wide Field-of-view Sensor (SeaWiFS), MODIS, and the medium-resolution imaging spectrometer (MERIS) instrument. We used weekly and monthly data from composite products at 9-km resolution provided by GlobColour (http://www.globcolour.info/). The satellite data used in this study are summarized in Table 2.

Seasonality—The oceanographic environment, through ADT (see Fig. 3a,b) and Chl a (see Fig. 3c,d), showed a strong seasonal modulation between the beginning (summer 2003) and the end (winter 2003) of the whale tracking period, as expected for our study area. This seasonal trend is clearly observed in SST and sea-surface Chl a temporal variations (see Fig. 3e) with a continuous decrease of SST associated with an increase of Chl a (Bosc et al. 2004). To account for this seasonal change, we based our analysis on two periods, of approximately equal durations: the first period was from August to October 2003 and covers the end of summer and the beginning of fall. For simplicity, we will refer to this period as “summer.” Summer is strongly oligotrophic (Fig. 3c), except along coastal areas. This oligotrophy mainly results from strong stratification that isolates the nutrient-depleted surface layer from the nutrient-rich layers below (Levy et al. 1998). The second period (hereafter “winter”) was from November 2003 to January 2004. It is more productive in terms of Chl a (Fig. 3d) because of the breaking of the surface stratification by winter cooling, allowing convective supply of nutrients all over the basin. Because of this strong summer oligotrophy we did not use thereafter the Chl a gradient as additional information to the Chl a concentration.

As defined above, the summer and winter periods include 90% of the locations obtained from Argos devices. We defined the whale-preferred areas as the area prospected by whales during each period (dotted black contours in Fig. 3). This preferred area corresponds to the whale home range defined by the 95% kernel polygon (Worton 1989). To take into account the nonuniform distribution of whales within the preferred areas, we have used in the following analyses the utilization distribution from the 95% to the 50% kernel polygon. The latter is considered the core area (illustrated by the continuous black contours in Fig. 3) and corresponds to the nonuniform distribution of whale density probabilities from locations within the home range of whales. The summer and winter mean circulations were defined by averaging ADT and associated geostrophic currents during each period (Fig. 3).

Eddy detection and estimation of whale–eddy distance—To detect eddies, we adopted a geometrical approach using the “winding-angle method” (Chaigneau et al. 2008, 2009), on the basis of the curvature of the streamline functions. This method (hereafter referred as “WA method”) uses geometric criteria defined by Robinson (1991), which characterized a vortex by instantaneous streamlines exhibiting a roughly circular or spiral pattern. The WA of the streamline corresponds to the cumulated sum of the angles between all pairs of consecutive segments. A streamline is associated with an eddy if its WA is higher than \(2\pi\). The WA eddy identification method consists of, first, automatically identifying eddy centers by local extrema in ADT (minima for cyclonic, counterclockwise rotating eddies and maxima for anticyclonic, clockwise rotating eddies). Then, for each possible cyclonic (or anticyclonic) center, the algorithm searches for closed ADT contours with an increment (or decrement) of \(10^{-3}\) m (Chaigneau et al. 2009). The closer ADT contour, which corresponds to a closed streamline, and embedding only the considered center, corresponds to the eddy edge. To quantify the relative position of whales to eddies, we estimated the distance of whale locations relative to the center and the edge of the nearest eddy detected by the WA method, by the ratio:

\[
p = \frac{d}{r}
\]

where \(d\) is the distance (in km) between the whale location and the center of the nearest eddy, and \(r\) corresponds to the corresponding eddy radius (in km) along the \(d\)-axis. A whale is considered associated to the eddy edge for \(p = 1 \pm 0.2\), inside an eddy for \(p \leq 0.8\), and outside for \(p > 1.2\) (values chosen from relative vorticity exhibited by eddies studied by Levy et al. (2001): the edge was \(\sim 20\)-km wide for a radius of eddies of \(\sim 50\) km). To estimate the significance of these locations relative to eddies, they were compared with random locations. We adopted a Monte Carlo approach by using bootstrap tests of significance. We calculated the \(p\) from \(n\) random locations, with \(n\) corresponding to the number of real whale locations obtained from tag deployments (92 locations during summer and 48 during winter, once the North Atlantic locations of a whale that traveled there had been removed).

<table>
<thead>
<tr>
<th>Oceanographic parameter</th>
<th>Satellite</th>
<th>Spatial and temporal resolution</th>
<th>Link (URL)</th>
</tr>
</thead>
</table>

Table 2. Summary of the oceanographic remotely sensed data sets.
The dates of the random locations were the same as the real locations. The generation of random location procedure was weighted by the density probabilities from 95% to 50% utilization distribution from the kernel analysis. We repeated this procedure to obtain 1000 replicates for which results converged. Frequencies of $p$ were thus obtained for the classes inside the eddy, on the edge of the eddy, and outside the eddy from whale locations and a range of frequencies (from the 1000 bootstrap) was also estimated from $p$ corresponding to random locations for the summer and winter periods (Fig. 4).

Filament detection and colocalization with whale positions—To detect filament position, we used the finite-size Lyapunov exponent (FSLE) method (Boffetta et al. 2001; d’Ovidio et al. 2004). This method measures the rate of divergence of trajectories initialized for each point in space and time at small distances (in our case, in the range 1–10 km). The frontal regions associated with filament boundaries can be detected by this technique as regions of large Lyapunov exponents when the calculation is performed backward in time. This occurs for fronts generated by the confluence between water masses of different origin—hence of large separation for trajectories initialized in nearby positions over the front and followed backward in time (illustrated in d’Ovidio et al. 2009, Fig. 1). An advantage of the FSLE is that it is a Lagrangian diagnostic, i.e., its value is computed along particle trajectories. As a consequence, the FSLEs depend on both the spatial and temporal variability of the velocity field and in this way they are able to reproduce the cascade toward small scales induced by mesoscale turbulence and responsible for the formation of tracer submesoscale anomalies. The FSLEs have been shown to reproduce submesoscale structures of tracers like chlorophyll and SST filaments from mesoscale altimetric velocity fields (Lehahn et al. 2007; d’Ovidio et al. 2009). In its simplest formulation, the FSLE is defined as:

$$\lambda = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0}$$  

where $\delta_0$ is the initial separation of the trajectories’ initial positions, $\delta_f$ is a prescribed final separation, and $\lambda$ is the first time at which a separation of $\delta_f$ is reached. Therefore, the Lyapunov exponent has the dimension of time $^{-1}$. Its value corresponds to the timescale of the frontogenesis.
between the scale $d_0$ and $d_f$ induced by horizontal stirring. When computing submesoscale structures in the ocean, typical FSLE values along filament boundaries fall in the range $0.1$–$1 \, d^{-1}$, indicating that a large-scale tracer anomaly can be structured into a submesoscale filament within the space of a few days. Following d'Ovidio et al. (2004), we set the separation $d_0 = 0.01 \, u$ (equivalent to about 1 km in the study region) when visually inspecting the filaments present in the region. Since in the Mediterranean Sea mismatch between altimetry-derived fronts and tracer (SST) fronts have been found on the order of a few kilometers (d'Ovidio et al. 2009), we used $d_0 = 8 \, km$ when colocalizing whale positions and FSLE-detected filament boundaries. We chose $d_f = 60 \, km$, which is smaller than eddy radii detected by altimetry. Lagrangian trajectories are obtained by integrating altimetry-derived surface velocities with a fourth-order Runge-Kutta integrator at a fixed time step of 6 h. Altimetry velocities (gridded at $1/8^\circ$ and 1 week) are interpolated linearly in space and time. Although Lagrangian structures obtained in both forward and backward time directions have dynamical information, here (unlike Tew-Kai et al. 2009) we restricted our analysis to the backward calculation, since the forward analysis depends on the velocity field in the future of the day being analyzed and therefore cannot have a causal effect on whale positions. More details on FSLE calculation in the Mediterranean Sea can be found in d'Ovidio et al. (2009).

To quantify the association between whale locations and filaments, we compared individual whale positions with the simultaneous filament situation within the preferred area. We also performed bootstrap tests of significance with the same bootstrap procedure previously described for the WA method. We extracted the FSLE at $n$ random locations, with $n$ corresponding to the number of real whale locations, on the same date. Following d'Ovidio et al. (2009), we separated filaments in two categories using a threshold of FSLE of $0.1 \, d^{-1}$. This threshold value corresponds to frontogenesis timescales faster than 1 month, which is a realistic time span over which the structuring of phytoplankton patches may occur. Frequencies of FSLE were thus obtained for the classes $< 0.1$ and $> 0.1 \, d^{-1}$ from whale locations and a range of frequencies (from the 1000 bootstrap) was also estimated from random locations for the summer and winter periods (Fig. 5).

**Robustness analysis of the Lagrangian calculation**—Altimetry data provide an approximation to the real surface velocities. In addition to the choice of $d_0$ described above, we have dealt with the influence of the possible errors in the altimetry-derived velocity field into the Lagrangian diagnostics by performing a robustness analysis of the particle advection scheme. To our knowledge, this is the first time that this technique has been used on altimetry data. Some
...of the terms from which errors can be expected are the presence of ageostrophic components (e.g., due to wind), spatiotemporal variability in sea-surface heights unresolved by the satellites (or filtered when constructing the gridded product), and measurement errors. Borrowing a method proposed in atmospheric Lagrangian simulations (Legras et al. 2005), we verified the effect of unresolved scales by repeating the Lagrangian calculations with a random noise component, corresponding to a lateral turbulent diffusion. Two numerical experiments, with noise intensity corresponding to a turbulent diffusion of 50 and 200 m$^2$ s$^{-1}$, have been compared with noise-free FSLE calculations. The two values bound a realistic range in our case. The first one is a typical value used in submesoscale resolving models, hence corresponding to unresolved velocity components. The second value corresponds to diffusivities used in eddy-permitting–resolving models (see Lévy et al. 2001 for the relation between model resolution and choice of horizontal diffusivities). To achieve numerical convergence, 16 independent FSLE estimations were averaged for each pixel in the calculation with noise. We derived a simple theoretical calculation that indicates the effect of these diffusivities on the FSLE calculation, which allowed comparison of the noise-free and noisy cases quantitatively. Given a diffusivity of $D$ (m$^2$ s$^{-1}$), in the absence of other dynamics, the second moment of a particle distribution is given by the classical theory of diffusion:

$$\langle x^2 \rangle = \langle x^2 \rangle_0 + 2nDt \quad (5)$$

where $x$ is the position of a particle with respect to the center of the particle ensemble, $n$ is the number of spatial dimensions (in our case, 2), and $t$ is time, where the average is taken over the particle ensemble. We now want to use this relation to compute the time $t$ at which two particles initially separated by a distance $\sqrt{\langle x^2 \rangle_0} = \delta_0$ and reach a final separation $\sqrt{\langle x^2 \rangle} = \delta_t$. To do this, we doubled the dispersion since we dealt with two-particle separations. Also, considering that the relation above provides an average, whereas the FSLE calculation computes the fastest separation, we have obtained an inequality:

$$\delta_t^2 \geq \delta_0^2 + 8Dt \quad (6)$$

From this relation we calculated an upper estimation of the time needed to reach the separation $\delta_t$ from an initial separation $\delta_0$ as:

$$t \leq \frac{\delta_t^2 - \delta_0^2}{8D} \quad (7)$$

Plugging this value into Eq. 4 and considering the effect of noise as additive, we obtained a lower estimation of the diffusion contribution to the Lyapunov calculation in a noisy environment as:

$$\lambda_{\text{noise}} \geq \lambda + \frac{1}{(\delta_t^2 - \delta_0^2)} \log \frac{\delta_t}{\delta_0} \quad (8)$$

This approximated analysis shows that in the presence of diffusion, an additional contribution to the FSLE should be expected, whose order of magnitude is provided by Eq. 8.

**Statistical analyses**—We tested the following hypotheses: (1) Whales were preferentially associated with eddies and (2) they were mainly found in regions of strong filament activity. We used the nonparametric maximum likelihood statistical significance tests ($G$ tests, Sokal and Rohlf 1994) for testing the independence of the $p$ distribution and FSLE frequencies from whale locations and random positions. Using this statistical $G$ test, we also investigated the relationship between whale locations and Chl $a$ concentration. Chl $a$ concentration was extracted at real whale locations and at random locations within the preferred area following the bootstrap procedure previously described and split into two categories. These categories were defined using thresholds equal to mean summer and winter Chl $a$ concentrations within preferred whale areas. Although serial autocorrelation in tracking studies with Argos devices is usually taken into account, here the temporal resolution is low, i.e., the time intervals between successive locations is long. Despite locations in the data set being sparse, we have tested the serial autocorrelation using the Durbin–Watson test.

**Results**

**Description of whale tracks**—Although all eight whales started in August and exhibited long-distance movements, their later trips were oriented differently. The whales remained within the northern sector of the western Mediterranean, except for one whale that moved into the Atlantic after 87 d of tracking (Fig. 2, device 2910842). Their mean speed between two successive locations with a time interval not exceeding 2 d was 0–4 km h$^{-1}$, with maximum speed reaching up to 14 km h$^{-1}$. The mean number of locations obtained during these tracks was 20 ± 17 (range 5–57; Table 1).

**Whale distribution and large-scale circulation**—The whales remained aggregated in the northernmost part of the western basin during summer (Fig. 3a,c). They were more dispersed, but still in the northern part of the basin, during winter (Fig. 3b,d). Hence, the whale-preferred area was bigger in winter than in summer. These seasonal areas are consistent with the extension of the anticyclonic gyre that characterizes the circulation in the northern part of the basin in winter (Fig. 3a,b). The northern branch of this gyre corresponds to the Northern Current flowing along the continental slope, whereas the southern branch is associated with the North Balearic front. The anticyclonic gyre has a smaller latitudinal extent during summer (Fig. 3a) than during winter (Fig. 3b) because of the southward displacement of the North Balearic front during winter (respectively, 41°N vs. 40°N). Surface Chl $a$ concentration is higher during winter (Fig. 3b) than during summer (Fig. 3c). Seasonal changes in whale dispersal are consistent with seasonal variations in the area of high Chl $a$ concentration: It is particularly remarkable that in summer, the whales’ core area is low in Chl $a$ but is close to the area
of high Chl a extending off the Gulf of Lion. In winter, the high Chl a concentrations are more widespread, and so are the whale locations.

**Whale distribution and mesoscale eddies**—The systematic analysis performed with the WA method and shown in Fig. 4 suggests that whales tended to be located near eddy edges, particularly during summer. This quantitative analysis compared whale positions with the seven eddies (five anticyclonic and two cyclonic) that were detected within the preferred areas. A high proportion (70%) of whale locations was associated with anticyclonic eddies, whereas the lower percentage (30%) was associated with cyclonic eddies. In summer, the frequency distribution of whale positions (black bars) and random positions (gray bars) differ significantly ($G = 10.35, df = 2, p < 0.01$). Whales were often found in an area with high filament activity compared with the filamentary activity in the whole preferred area ($G = 8.92, df = 1, p < 0.01$). In other words, whales were more frequently located in FSLE detected filament boundaries than what would be expected by random distribution during summer (Fig. 5a). During winter, whale locations relative to filaments did not differ significantly from a random distribution (Fig. 5b, $G = 0.38, df = 1, p > 0.05$). Moreover, FSLE data are not significantly autocorrelated (Durbin–Watson $p > 0.05$, log-transformed data).

The large-scale spatial distribution pattern of the filamentary activity did not change significantly between the summer and the winter periods, neither inside nor outside the home range and the core area of whales (Fig. 6). According to d’Ovidio et al. (2004) the high FSLEs correspond to main current flow, here the Northern Current. Temporal evolution of the mean filament activity in the north area of the Balearic Islands shows seasonal variations (Fig. 7). As pointed out by d’Ovidio et al. (2004), the FSLEs are generally low during spring–summer. However, FSLEs were relatively high from August to January (illustrated by the gray time period, Fig. 7).

At mesoscale, the relationship between whale locations and eddies is illustrated in Fig. 8a, which shows a situation in September 2003 where six whales were located near the edge of eddies south of the Gulf of Lion. The relatively short filament lifetime (over days and weeks) allows the aggregation of whale positions with a lag of only a few days for each FSLE daily map, leaving in most cases only one position per week. A case in which several positions can be compared together is shown in Fig. 8b (6 Sep 2003). Daily maps of FSLEs and corresponding daily locations of one whale are provided as an animation in the Web Appendix (www.aslo.org/lo/toc/vol_56/issue_1/0219a.gif).
These images suggest that whale positions tend to be colocalized to Lyapunov maxima and hence to frontal regions enclosing submesoscale filaments.

Robustness of Lagrangian calculation and whale colocalization—We performed a robustness analysis of the FSLE comparison by perturbing the velocity field with a random noise. The intensity of additive noise used in a Lagrangian scheme can be quantified as a term of turbulent diffusion (see Methods for details). There was very little effect of noise on the detection of filaments in velocity fields. The analysis performed in the Methods section showed that the presence of noise increased the value of the FSLEs by a scale-dependent factor that depends on $d_f$, $d_0$, and the noise intensity. As a practical consequence, we found that noisy FSLEs have a constant additional term with a lower bound theoretical estimation (Eq. 8) of 0.03 and 0.11 d$^{-1}$ respectively for $D = 50$ m$^2$ s$^{-1}$ and 200 m$^2$ s$^{-1}$ (Fig. 9). A numerical comparison found that this difference was indeed fairly constant and of this order of magnitude (the observed value being about twice the lower bound estimation). Once the constant factor was subtracted, the noisy calculation showed structures that were similar—although blurred—to the ones of the noise-free case (Fig. 10). The correlation between whale positions and FSLE strong manifolds was maintained even for the stronger noise. As in the noise-free case, whales were more frequently located in FSLE detected filament boundaries than what would be expected by random distribution during summer (Fig. 11a, $G = 7.65$, df = 1, $p < 0.05$ for $D = 50$ m$^2$ s$^{-1}$; Fig. 12a, $G = 4.65$, df = 1, $p < 0.05$ for $D = 200$ m$^2$ s$^{-1}$), whereas whale locations relative to filaments did not differ significantly from a random distribution during winter (Fig. 11b, $G = 0.50$, df = 1, $p > 0.05$ for $D = 50$ m$^2$ s$^{-1}$; Fig. 12b, $G = 0.25$, df = 1, $p > 0.05$ for $D = 200$ m$^2$ s$^{-1}$).

Whale distribution and Chl $a$ concentration—We compared satellite-derived Chl $a$ concentration from whale positions to the random distribution. We chose the seasonal mean Chl $a$ concentrations within the whale-preferred areas as thresholds: 0.2 mg m$^{-3}$ in summer and 0.3 mg m$^{-3}$ in winter. The distribution of Chl $a$ concentrations at whale positions (Fig. 13) was not significantly different from a random sample of Chl $a$ concentrations in the area for either season (Fig. 13a, $G = 0.37$, df = 1, $p = 0.05$; Fig. 13b, $G = 0.45$, df = 1, $p > 0.05$).

Discussion

The foraging strategy of whales is based on high abundance and density of its prey—krill (Nemoto 1970). As a zooplankton species, the krill *M. norvegica* is strongly exposed to circulation at several scales. If krill distribution is affected by the ocean circulation then we might expect
whale locations to be related to ocean circulation when they actively search for food. Since the information on krill distribution is not currently available and the poor resolution of whale data does not allow inference of behavior, we discuss the influence of the ocean circulation on the distribution of whales mostly in terms of foraging opportunities.

At the basin scale, fin whale distribution is strongly associated with the anticlockwise gyre in the northern part of the western Mediterranean basin (Forcada et al. 1996; Cotté et al. 2009). The northern gyre is generally characterized by cold summer temperature (≈ 23°C) relative to the south part of the basin (Algerian basin, ≈ 26°C). Cool waters have been defined as a habitat preference for fin whales in the northwestern Mediterranean Sea (Forcada et al. 1996; Cotté et al. 2009). This seems also to have been the case for the peculiarly warm summer of 2003 that was induced by a heat wave. However, the warm event only corresponded to the beginning of our study period since it stopped in late August–early September 2003 (Sparnocchia et al. 2006). The northern gyre contains modified Atlantic waters separated from the southern recent Atlantic waters in the Algerian subbasin by the North Balearic front (Millot and Taupier-Letage 2005). The presence of whales in this region is expected in spring, when the primary production occurring within this area is the highest of the Mediterranean Sea (Bosc et al. 2004), suggesting a consequently high production of zooplankton. However, fin whales also appear to prefer this region continuously from summer to winter, when the primary production maximum progressively shifts to the southern basin. This regional preference was also reported in a year-long survey from ferries crossing the western basin; whales do not track maximum Chl a concentration from north to south during winter as previously hypothesized (Cotté et al. 2009). A possible explanation for this preference is the presence of the North Balearic front, considered a frontier for many environmental processes and hence a possible boundary of the krill habitat.

At meso- and submesoscales, we found statistically significant association between whales and eddy and filament structures. Several mechanisms have been documented by which eddies and filaments affect lower levels of the marine trophic chain. Cyclonic eddies have been shown to stimulate phytoplankton production by upwelling nutrients through their doming isopycnals (McGillicuddy et al. 1998). Such upwellings mainly occur in cyclonic eddies, whereas whales mainly visited anticyclonic eddies in the western basin. If whales were associated with primary production caused by nutrient upwelling, this mechanism would result in a preference of whale positions in cyclonic eddy centers, although we found that whales had a preference for eddy peripheries. An alternative mechanism by which eddies affect marine production is the presence of cells of vertical velocities found at eddy peripheries. These cells are initiated by frontogenesis through horizontal stirring and are responsible for the injection of nutrients into the surface layer (Lévy et al. 2001). The intensity of the horizontal stirring is directly measured by the FSLE calculation that provides the inverse timescale for this type of frontogenesis. These stirring regions also have the ability to structure the horizontal and vertical distribution of biological production, in particular by defining the fronts of Chl a patches (Lehahn et al. 2007) and enclosing fluid dynamical niches (d’Ovidio et al. 2010). Therefore the lack of fin whale preference for fine-scale productive areas, also found in other top predators (Guinet et al. 2001; Votier et al. 2010), is at first sight surprising. It is, however, consistent with the fact that krill production is not temporally in phase with phytoplankton, and that regions of strong stirring identified by the FSLE technique mark the fronts and not the maxima of phytoplanktonic patches (Lehahn et al. 2007). Lyapunov values at whale positions, relative to random distribution, have values in excess of 0.1 d⁻¹, corresponding to frontogenesis timescales on the order of a few days. These values indicate that such fronts are able to affect the spatial structure of tracers that are evolving on a timescale of days or longer. We note that FSLE time averages in the north of the basin, where most of the whales were located, present a relatively homogeneous spatial pattern and a lower submesoscale activity than in the south of the basin (see figs. 2 and 6 in d’Ovidio et al. 2004).
This structuring effect of submesoscale structures is particularly important for planktonic organisms such as krill. Indeed, krill generally have a heterogeneous distribution (Abraham 1997). The northern krill is an active vertical swimmer with a diel vertical migration, but its spatial concentration is strongly influenced by horizontal currents as it cannot sustain swimming speeds equivalent to horizontal current velocities (Cotté and Simard 2005). Moreover, the strong vertical movements of water masses associated with these elongated frontal zones may deform isopycnals, inducing an elevation of water masses and shallower planktonic organisms (Klein and Lapeyre 2009; Labat et al. 2009). This increase of prey concentration, especially in the most oligotrophic period of the year, may be important for Mediterranean fin whales. Their dives are the deepest recorded for mysticete species (470 m, Panigada et al. 1999) because of the atypically deep krill layer in the western Mediterranean Sea. Thus, whales would substantially decrease their energy expenditure associated with swimming and diving during foraging activities in areas with more aggregated and shallower local prey patches. Despite weaker eddy and filament activities from FSLEs in the northwestern Mediterranean Sea in summer relative to winter (d’Ovidio et al. 2004; Millot and Taupier 2005), the local injection of nutrients at the eddy peripheries can be expected to have a stronger biological influence in summertime (when the mixed layer is shallow and phytoplankton production is nutrient limited) than in wintertime (when the mixed layer is deeper than the photic layer and the limiting factor is light) (Lévy et al. 2001). Besides the frontogenesis effect on krill patchiness, this seasonal modulation may also explain the association between whale distribution and eddy peripheries in summer and not in winter.

This discussion leads to conjecture that fin whale distribution in this part of the Mediterranean Sea is linked to their foraging strategy by two physical mechanisms: at the basin scale, a southern boundary of the krill habitat constituted by the North Balearic front, and at mesoscale and submesoscale, zooplankton aggregation by the high filamentary activity at eddy peripheries. Like fin whales, juvenile bluefin tuna feed on krill and previous studies have reported the importance of mesoscale fronts on their distribution (Royer et al. 2004). Despite our limited sampling of eight individuals mainly during two seasons, our results suggest the generic importance of environmental forcing, and particularly at meso- and submesoscales, in structuring prey in space and time and conditioning the foraging tactic of predators relative to their dynamic environment (Viale and Frontier 1994). The suggested generic relationship between predator distribution and mesoscale dynamics does not only concern the Mediterranean Sea but also many other oceanic environments where this kind of relationship has been found. Most of these
wind events may be intense, both sources of error are present and affect our analyses. A quantitative analysis error source during Lagrangian calculations is a complex problem that the nonlinear community is starting to tackle and that requires dedicated studies on its own (I. Hernandez-Carrasco unpubl.). Nevertheless, several studies have already empirically shown the reliability of the Lyapunov technique for detecting submesoscale filaments from altimetric data. For this reason, the application of the Lyapunov technique is now being used without ad hoc revalidation (Tew-Kai et al. 2009). In the North Atlantic, where the Rossby radius is also smaller than the expected altimetry resolution, Lehahn et al. (2007) compared it with chlorophyll patches, whereas Beron-Vera and Olascoaga (2009) compared it with Lagrangian drifters. In the eastern Mediterranean d’Ovidio et al. (2009) has already compared altimetry-derived Lyapunov exponents with SST filaments, showing their superior ability in reconstructing SST mesoscale and submesoscale spatial features with respect to Eulerian diagnostics. More recently, the Lyapunov technique has been successfully used in support of a submesoscale campaign along the Antarctic circumpolar current, where wind events are extremely strong but did not appear to compromise the analysis made from purely geostrophic currents (see LOHAFEX weekly report 5 at www.lohafex.com). The regional studies cited above show typical errors of few kilometers in the detection of mesoscale and submesoscale fronts induced by lateral stirring with the Lyapunov technique. In our study, we have dealt with the possible errors of altimetry in three way. (1) Our conclusions are based on the comparison between the observed and random whale positions. If our (sub-)mesoscale analysis was dominated by spurious signal, the statistical analysis of the observed positions would not pass the bootstrap test. (2) We have taken into account the information on the error of front localization by setting a lower bound in the colocalization of Lyapunov-detected structures and whale positions at 4 km—this is done by setting $\delta_0$ at this value. (3) We have verified the robustness of filament detection by recomputing the statistics in the presence of noise. These three approaches are general, and may be useful for submesoscale biophysical analysis.

There are now novel satellite products that attempt to include some ageostrophic components in altimetry-derived surface current (Sudre and Morrow 2008). Thanks to these type of products and from the much higher spatiotemporal coverage provided by the next altimetry missions (Ka-band and wide swath altimetry), errors in the detection of submesoscale physical structures are expected to strongly decrease in the incoming years. This—together with a continuation of the tagging program—will open new possibilities for understanding the interaction between marine top predators and ocean circulation.

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