



ELSEVIER

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsr

Scale-dependent habitat use by a large free-ranging predator, the Mediterranean fin whale

Cédric Cotté^{a,b,*}, Christophe Guinet^b, Isabelle Taupier-Letage^a, Bruce Mate^c, Estelle Petiau^b

^a Université de la Méditerranée, OSU/Centre d'Océanologie de Marseille, CNRS, Laboratoire d'Océanographie Physique et de Biogéochimie, Antenne de Toulon, BP330, 83507 La Seyne, France

^b Centre d'Études Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France

^c Department of Fisheries and Wildlife, Coastal Oregon Marine Experimental Station, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA

ARTICLE INFO

Article history:

Received 16 May 2008

Received in revised form

9 December 2008

Accepted 21 December 2008

Available online 25 December 2008

Keywords:

Foraging predator

Mesoscale oceanographic processes

Habitat use

Spatial and temporal scales

Whale

ABSTRACT

Since the heterogeneity of oceanographic conditions drives abundance, distribution, and availability of prey, it is essential to understand how foraging predators interact with their dynamic environment at various spatial and temporal scales. We examined the spatio-temporal relationships between oceanographic features and abundance of fin whales (*Balaenoptera physalus*), the largest free-ranging predator in the Western Mediterranean Sea (WM), through two independent approaches. First, spatial modeling was used to estimate whale density, using waiting distance (the distance between detections) for fin whales along ferry routes across the WM, in relation to remotely sensed oceanographic parameters. At a large scale (basin and year), fin whales exhibited fidelity to the northern WM with a summer-aggregated and winter-dispersed pattern. At mesoscale (20–100 km), whales were found in colder, saltier (from an on-board system) and dynamic areas defined by steep altimetric and temperature gradients. Second, using an independent fin whale satellite tracking dataset, we showed that tracked whales were effectively preferentially located in favorable habitats, i.e. in areas of high predicted densities as identified by our previous model using oceanographic data contemporaneous to the tracking period. We suggest that the large-scale fidelity corresponds to temporally and spatially predictable habitat of whale favorite prey, the northern krill (*Meganctiphanes norvegica*), while mesoscale relationships are likely to identify areas of high prey concentration and availability.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Spatio-temporal variations in the distribution of foraging marine top predators are interpreted as a direct response to changes in prey distribution, density and availability, which in turn largely depend on biophysical processes at different spatio-temporal scales (Hunt et al.,

1999). Very large-scale oceanographic features such as the circumpolar boundary (Tynan, 1998) to fine-scale processes such as small fronts (Sims and Quayle, 1998) were therefore reported to affect prey distribution, which in turn influenced the distribution of foraging predators. However, direct information on prey abundance and distribution are generally lacking because of the difficulty of assessing these parameters over large areas. As a consequence, the spatial distribution of large marine predators, such as large baleen whales, is investigated in relation to biophysical oceanographic features that are known to structure the abundance of prey (e.g., Tynan et al., 2005; Friedlaender et al., 2006). In the context of the

* Corresponding author at: Centre d'Études Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France. Tel.: +33 5 49 09 78 39; fax: +33 5 49 09 65 26.

E-mail address: cecotte@cebc.cnrs.fr (C. Cotté).

heterogeneous marine environment, where biophysical processes are highly dynamic in space and time, interactions of predators with their marine environment must be investigated at adequate spatial but also temporal scales. Environmental variability, which affects the foraging activities of predators, has been found to be decisive at some scales and not others (Jacquet et al., 1996; Guinet et al., 2001; Austin et al., 2006). Identification of appropriate scales of environmental processes is thus important to understanding of the predator–environment relationship.

Fin whales are the largest free-ranging predators of the semi-enclosed Mediterranean Sea. This species feeds primarily on the northern krill *Meganyctiphanes norvegica*, which is common in the North Atlantic but is also found in the Western Mediterranean (WM), the southernmost location of the species. Numerous studies have reported that high densities of fin whales are located in the northern WM during summer (Forcada et al., 1996), although the geographical imbalance between eastern and western basin is partly due to a lack visual effort in the eastern basin (Notarbartolo di Sciara et al., 2003). Fin whales have also been reported to be markedly pelagic and are typically found in areas of colder surface water relatively to the whole WM (Forcada et al., 1996) and in areas of high productivity during the preceding spring season (Notarbartolo di Sciara et al., 2003; Littaye et al., 2004). However, very little information is available concerning the habitat of fin whales and their possible movement patterns because of the paucity of data from the southern part of the WM and from the winter season. To our knowledge, spatial and temporal scales have rarely been taken into account in studies of the interactions of large free-ranging predators, such as fin whales, with their environment. There is growing evidence of the importance of biophysical processes at the mesoscale, spatially considered to be 20–100 km and temporally to be weeks to months (Lévy, 2008) in the foraging strategies of various land-based predators such as turtles (Hays et al., 2006; Polovina et al., 2006; Lombardi et al., 2008), seals (Ream et al., 2005), and penguins (Cotté et al., 2007). Along the marine circulation of the WM, mesoscale processes, such as eddies, modulate biological activity, implying high spatial and temporal variability (Morel and André, 1991; Lévy et al., 1998; Taupier-Letage et al., 2003). This mesoscale activity could substantially affect interactions between the physical environment, prey, and their predators through the local enhancement of productivity, aggregation processes, and availability of prey to free-ranging predators.

In order to examine interactions of a predator with its environment, a properly designed sampling protocol is needed to detect patterns over a range of temporal and spatial scales. As specified by ecologists (Fauchald et al., 2000) and oceanographers (Taupier-Letage, 2008), this leads to a trade-off between the spatial coverage of large areas to detect large-scale patterns and small sampling intervals to examine small-scale processes. Indeed, environment–predator interactions at scales smaller than the nominal resolution would be missed because of unsuitable sampling. Here we carried out such a sampling

strategy through surveys across the WM at high spatial resolution for both predators and environmental parameters during one year. Obtaining such fine-scale data is needed to analyze the variability of cetacean distribution appropriate to the spatio-temporal variability of the environmental features. The challenge of developing habitat-use models that take into account the spatio-temporal environmental variability has been recently put forward by Redfern et al. (2006). This approach relies on careful selection of environmental variables that have their own spatio-temporal scale of variability, requiring previous knowledge of the variability of each of them.

In this study, we conducted an interdisciplinary investigation of the scale-dependent habitat use of a large free-ranging predator, the fin whale, to understand the consequence of predator–environment interactions on foraging activity. We used the combination of year-long whale sighting data and in-situ/remote sensing oceanographic data, collected along transects crossing the WM, to model fin whale densities according to oceanographic parameters. Using an independent dataset from satellite tracking of several individual fin whales, we then compared the observed Argos locations of the tagged whales to predicted habitat use estimated from oceanographic data contemporaneous to the tracking period.

2. Methods

2.1. Observation, tracking, and environmental data

We used so-called “platforms of opportunity” to collect whale sighting data because of the ships’ regular and frequent paths over the WM. Data were collected during 18 surveys between 12 September 2006 and 26 July 2007 on a ferry crossing from Marseille (France) to Algiers and Bejaïa (Algeria) (Fig. 1). Observations were made from the bridge (25 m high) of the ship, with the unaided eye and binoculars equipped with eyepiece reticles and compass. A visual angle of 90° centered on the trackline was surveyed to ensure as much as possible that all animals directly on the trackline were spotted, the $g(0) = 1$ assumption of distance sampling protocols (Buckland et al., 2001). The ferry travelled at 20 knots mean speed. Two observers alternated observation duties continuously during daytime at 1-h intervals. This defined the on-effort period, the off-effort period corresponding to nighttime. When a cetacean school (single or several individuals) was sighted, the ship’s location, the time, the radial distance and angle from the ship to the sighting, and group size were recorded. Information on meteorological factors that could affect sighting conditions was also recorded.

Environmental data were obtained from in-situ and satellite sources. The oceanographic and meteorological in-situ data were collected underway with a system installed on-board the ferry in TRANSMED program framework (test phase to develop a network to monitor the surface of the Mediterranean using ships of opportunity, from a CIESM (Commission Internationale pour l’Exploration Scientifique de la Méditerranée) initiative). It is composed of a thermosalinometer, which records

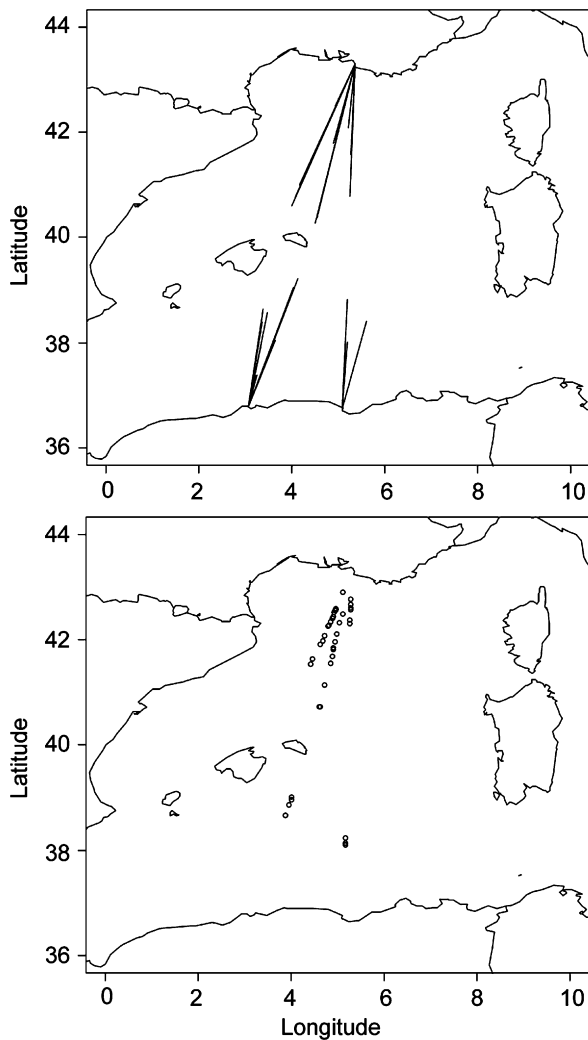


Fig. 1. Surveys tracks in the study area and locations of fin whale sightings.

hydrological parameters of sea-surface temperature (SST) and salinity, and a fluorometer that estimates the phytoplankton chlorophyll concentration from the fluorescence signature of sampled seawater. Surface water (~3 m depth) was pumped to the on-board system that took one measurement per minute. We also used satellite observations of the SST, of the chlorophyll concentrations (visible/ocean color imagery) and of sea level (altimetry). The NOAA/AVHRR (National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer, available at <http://poet.jpl.nasa.gov/>) sensor, measuring the SST, is an extremely efficient tool for tracking mesoscale oceanographic features (e.g. Taupier-Letage, 2008). Chlorophyll-*a* (Chl-*a*) images are obtained from MODIS (Moderate Resolution Imaging Spectroradiometer, available on <http://oceancolor.gsfc.nasa.gov>). The spatial resolution of both datasets ranges from ~1 to 4 km, and the WM is fully covered within one daytime period. To reduce gaps in the satellite data coverage due to cloud

coverage, we used 3-day composite images corresponding to the environmental conditions at the time and location of the corresponding observation data. For sea circulation we used satellite-derived sea-surface altimetry data in the form of weekly merged products of absolute dynamic topography (ADT) at $1/8^\circ$ resolution (Ssalto/Duacs distributed by Archiving Validation and Interpretation of Satellite and Oceanographic data (AVISO), available on <http://atoll-motu.aviso.oceanobs.com>). These high temporal and spatial resolutions were relevant in our investigations of mesoscale interactions between whale distribution and fast-moving environmental processes. Bathymetric data were extracted from the ETOPO2 database (from the national geophysical data center, available on <http://www.ngdc.noaa.gov>). Temperature and chlorophyll gradients, bottom slope, and geostrophic currents were computed as described in Cotté et al. (2007).

During August 2003, 8 fin whales were equipped with satellite tracking devices. These semi-implantable tags (26 cm in length \times 1.9 cm in diameter) consisted of a Telonics[®] Argos ST-15 transmitter in a stainless steel tube, incorporating a flexible 12.5-cm whip-antenna, a flexible 4-cm saltwater switch (SWS), and two solid flanges (0.9 \times 1.5 cm) to prevent inward migration. Half of the upper housing was coated with 2.5 g of Gentamycin[®] sulfate antibiotic in methacrylate (Eudragit[®]), designed for extended time-release of the antibiotic. The tag was applied using an air-powered applicator (Heide-Jorgensen et al., 2001) with 7 bar pressure from an elevated 1-m bow pulpit mounted on a 6-m rigid-hull inflatable boat with a 115 hp outboard motor at a distance of <3 m from the whale. Tags were deployed 2–0 m in front of the dorsal fin area on the dorsal surface of the whale. To conserve batteries and extend tag operation, tags transmitted for only four 1-h periods daily for 90 days and then every 4th day thereafter. A saltwater switch and microprocessor were used to conserve battery power by limiting transmissions to times when the tag was out of the water and coinciding with optimal Argos satellite coverage. We used screening criteria for Argos location classes 0–3 based on feasible swimming speeds (Mate et al., 1999).

2.2. Modeling whale densities

Line transect sampling from design-based methods is the standard tool to provide information on abundance and distribution in cetacean population (Buckland et al., 2001). An alternative technique relevant to surveys that have not initially been designed to achieve equal coverage probability is the model-based approach (Hedley et al., 1999; Marques, 2001), in which line transect sampling is combined with spatial analysis. Data from such surveys can then be combined when fitting descriptive models of heterogeneity in animal density, thus imparting information on how animals use their habitat, and how populations behave over time (Williams et al., 2006). We used here a method based on modeling distances between detections, called waiting distances (Hedley, 2000). This method has theoretical appeal as it avoids the subjective

choice of cell size and zeros inflated datasets generated by the classical method of dividing transects into separate cells (Henrys, 2005). Waiting distance models have been used to estimate density because in areas of high density the waiting distance between detections is short (Buckland et al., 2004). The waiting distances were modeled using generalized additive models (GAMs, Hastie and Tibshirani, 1990) with a logarithmic link function to the set of spatial environmental covariates. Data were fitted to GAMs in package “mgcv” of the statistics program R (Wood, 2001). We used GAMs in our analysis because they offer flexibility through smooth functions applied to each explanatory variable (Wood, 2003). Smoothing splines were fitted using multiple generalized cross-validation (mgcv). The amount of flexibility given to a model term is determined in a maximum likelihood framework by minimizing the GCV scores of the whole model. The general structure of the model was

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

where l_i is the waiting distance, β_0 the intercept, f_k the smoothed functions of the explanatory covariates, z_{ki} the value of the k th explanatory covariate in the i th observation, and n is the number of observations. While the optimal amount of smoothing is automatically determined by mgcv, the decision on including/dropping a model term is not. We adopted the model specification procedure proposed by Wood (2001), essentially based on the lowest generalized cross-validation (GCV) score. To handle over-dispersion, a gamma distribution was used. The density surface was then obtained by calculating the inverse of the waiting area, defined as twice the effective strip half-width times the waiting distance:

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

where $\hat{\mu}$ is the effective strip half-width and l_i the waiting distance. We then multiplied by the estimated cluster size to calculate the total whale density.

To obtain $\hat{\mu}$, we estimated the best (from AIC) detection function from distance sampling method using the software DISTANCE 5.0 beta 5 (Thomas et al., 2002). We selected the multiple covariate distance sampling (MCDS) method (Marques, 2001; Thomas et al., 2002), as covariates, particularly meteorological parameters, may influence the detection probability. The perpendicular distances were right truncated prior to the analysis, following the recommendation of Buckland et al. (2001). The best detection function was selected using Akaike's information criterion (AIC) and chi-squared goodness of fit test. Effective strip half-width and estimated cluster size were computed and used in the formula for density estimation using waiting distance. The mean cluster size was estimated by DISTANCE to detect school size bias, i.e. the tendency of detection for large and small school at the same distance range. The approach fits a least-squares regression of log of school size versus distance, which yields a slope when bias is present (which is not the case here).

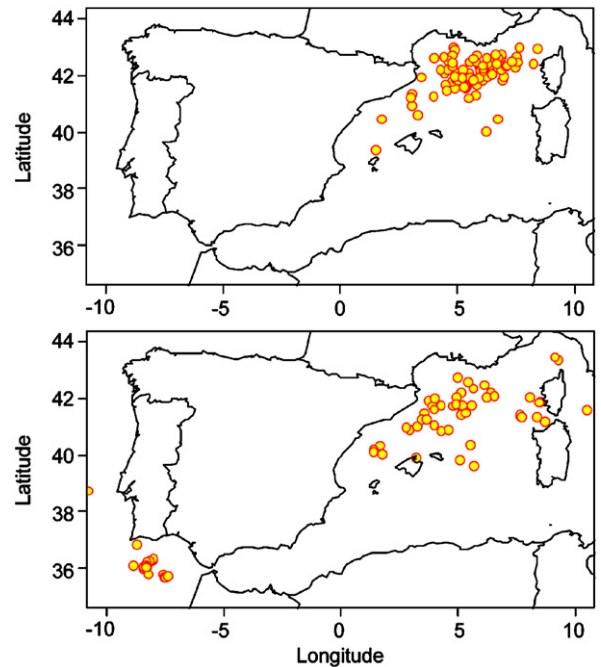


Fig. 2. Locations of the eight satellite telemetry tagged fin whales during the summer (August–October, upper panel) and winter (November–May, lower panel).

2.3. Habitat use and predicted densities

The analysis of habitat use compared environmental conditions corresponding to the visual observations or Argos locations and the environmental conditions available within the entire sampled area. For the whale sighting dataset, the sampled area was the ferry transect corresponding to a given observation. For the Argos location dataset, we considered the sampled area as the area covered by most of the locations, i.e. between 3°E and 9°E north of the Balearic Islands (Fig. 2).

Since we had two independent datasets at our disposal (ferry observations in 2006–2007 and Argos locations in 2003–2004), we were able to test the efficiency of our model constructed from the transect dataset by comparing the distribution of Argos location data within the habitat predicted by the model. We considered our model efficient whenever fin whale Argos location distribution skewed toward predicted favorable fin whale habitat, i.e., areas of high predicted whale densities as derived from the transect study and using the weekly satellite oceanographic parameters temporally appropriate to the fin whale tracking period being analyzed.

3. Results

A total of 7422 km were surveyed on-effort during which 40 sightings of fin whale schools were observed over the year. The Balearic area was not covered by transects. Most of the sightings ($N = 33$) occurred in the northern part of the WM, i.e., north of the Balearic Islands

(Fig. 1). Satellite locations from the eight tracked fin whales from August 2003 to June 2004 were also found mainly in the northern WM, and only one whale made a short excursion out into the Atlantic Ocean (Fig. 2). The tracked fin whales were thus found mostly in the northern part of the WM, where they were aggregated during summer. Their winter distribution was more dispersed but still north of the Balearic Islands for all but one individual.

The best fitting model of detection probability was a half-normal key function with no adjustment terms, i.e., no covariate effects on the probability of detection. The lack of influence of sea state on detection function may be due to the high platform of ferries allowing a better detection of whales (as in Williams et al., 2006). The expected mean cluster size of fin whales was 1.27, and the effective strip half-width was estimated to be 864 m (see Web Appendix B). Based on the lowest GCV score, the selected spatial model includes months ($F_{3,25} = 2.26$,

$p = 0.081$), SST ($F_{3,73} = 4.29$, $p = 0.018$), SST gradient ($F_1 = 5.15$, $p = 0.039$), Chl-*a* gradient ($F_{5,85} = 4.47$, $p = 0.010$), ADT ($F_{2,36} = 2.76$, $p = 0.061$), and geostrophic current amplitude ($F_1 = 3.06$, $p = 0.099$). Depth, bottom slope, and Chl-*a* failed to enter the model as covariates. The explanatory power of this model was very high; the adjusted R^2 score (Wood, 2001) for the model was 0.68, and the deviance explained by the model was 81.8% of the observed data distribution. The shapes of the functional forms for the smoothed covariates, conditional on the other covariates being included in the models, are shown in Fig. 3. Waiting distance was low, i.e., density was high, during the summer season and, conversely, waiting distance was high in winter, corresponding to a decrease in whale density from summer to winter. Density was high in colder water and in areas with a high-temperature gradient. The relationship with the Chl-*a* gradient is quite complex since it included periods of phytoplankton bloom

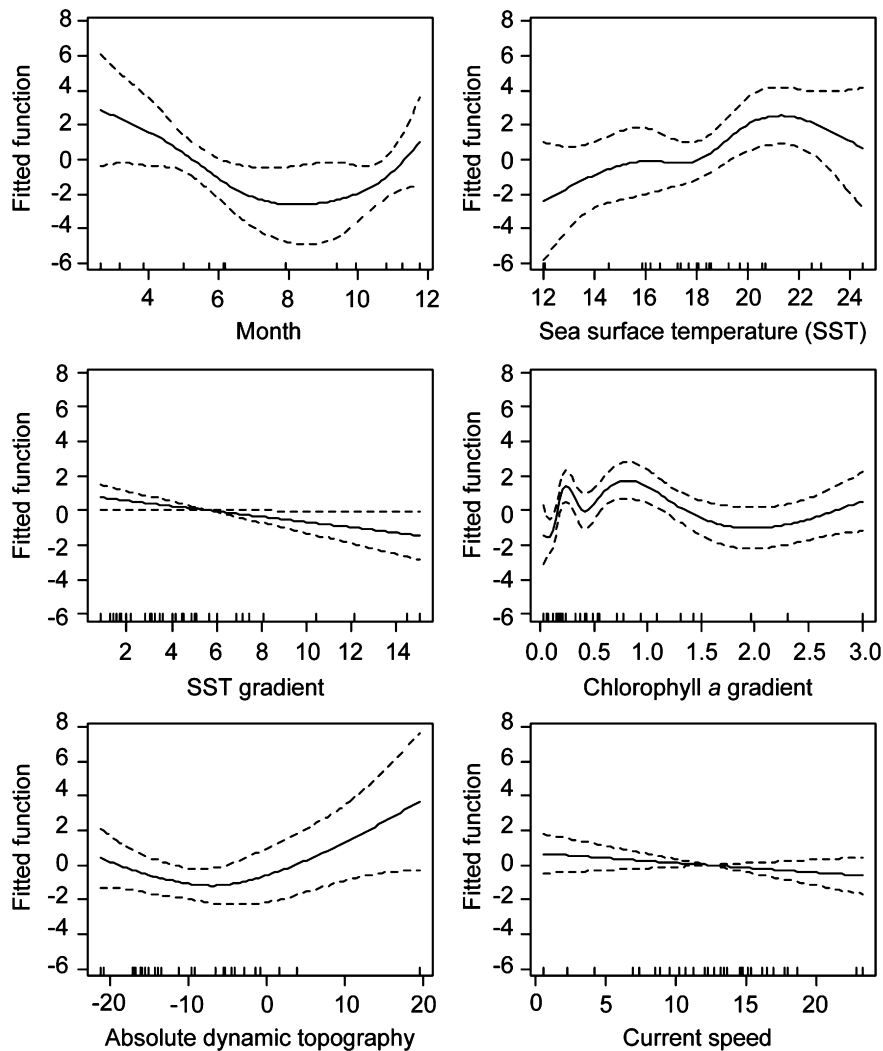


Fig. 3. Functional forms for the smoothed covariates included in the GAM. Units are °C for SST, % for SST and Chlorophyll-*a* gradients, cm for absolute dynamic topography, and cm s^{-1} for current speed.

(high Chl-*a*) and oligotrophic (low Chl-*a*) periods. Density was also high in areas with low (negative) ADT and where the speed of derived geostrophic current was high.

When the environmental parameters at each observation were compared to the corresponding mean value of the transect when on-effort, fin whales were found in colder and saltier waters where the gradients of SST, and Chl-*a* to a lower extent, were marked (Table 1). This confirmed the relationships in the model between whale density and the measured environmental parameters. One illustrative survey is given in Fig. 4, where fin whales were observed in northern and southern WM (corresponding to the colder and saltier waters in the temperature–salinity diagram).

Table 1

Mean±SE of difference between environmental parameters at each observation and the corresponding mean value of the transect (from the departure of the boat until dusk, corresponding to the southern or northern part of the trip).

| Environmental parameters | TRANSMED in-situ measurements | Satellite measurements |
|-------------------------------------|-------------------------------|------------------------|
| SST (°C) | -0.31 ± 0.65 | -0.50 ± 0.69 |
| SST gradient (%) | – | 0.64 ± 1.86 |
| Fluorimetry (relative unit) | 0.14 ± 0.76 | – |
| Chl <i>a</i> (mg m^{-3}) | – | 0.04 ± 0.13 |
| Chl- <i>a</i> gradient (%) | – | 0.13 ± 0.34 |
| Salinity | 0.12 ± 0.18 | – |

A similar analysis was conducted with tracking data, where environmental parameters from satellite altimetry corresponding to each Argos location were compared to the mean value over the entire area at the tag location period (Fig. 5). Fin whales were located mostly in areas of lower ADT and stronger currents in summer and through late fall (see the animation in Appendix A). In winter these tendencies tend to disappear, before strengthening in late spring. However, the scarcity of data for that latter period could lead to incorrect interpretations.

As a validation of the model, frequency distribution of predicted densities at whale locations from Argos tracking is significantly different from the distribution of predicted densities in the whole area, i.e. all the pixels between 3° and 6°E (two-sample KS test, $p < 0.001$) (Fig. 6). Thus, the tracked whales were found in areas where high densities of whales were predicted by the model, showing that tracked whale locations correspond to predicted favorable areas.

4. Discussion

The necessity of using interdisciplinary approaches to understand the foraging tactics of marine predators has been established through comparison of their distribution, abundance, and at-sea movements with environmental processes, as well as their associations with prey distribution data (Johnston et al., 2005; Friedlaender et al., 2006; Tynan et al., 2005). However, these interdisciplinary

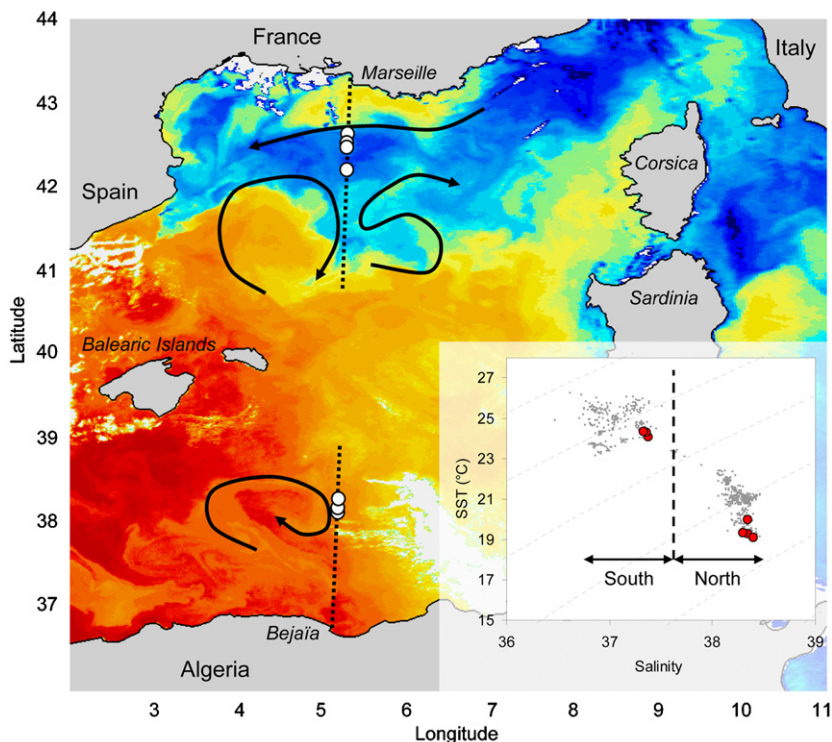


Fig. 4. Map of sea surface temperature, plotted locations of whale observations, and TS (temperature–salinity) diagram for the survey period 28–30 September 2006. Arrows indicate circulation, white circles are fin whale observations, dotted lines are on-effort transects, and red points in the TS diagram are TS conditions at the locations of whale observations.

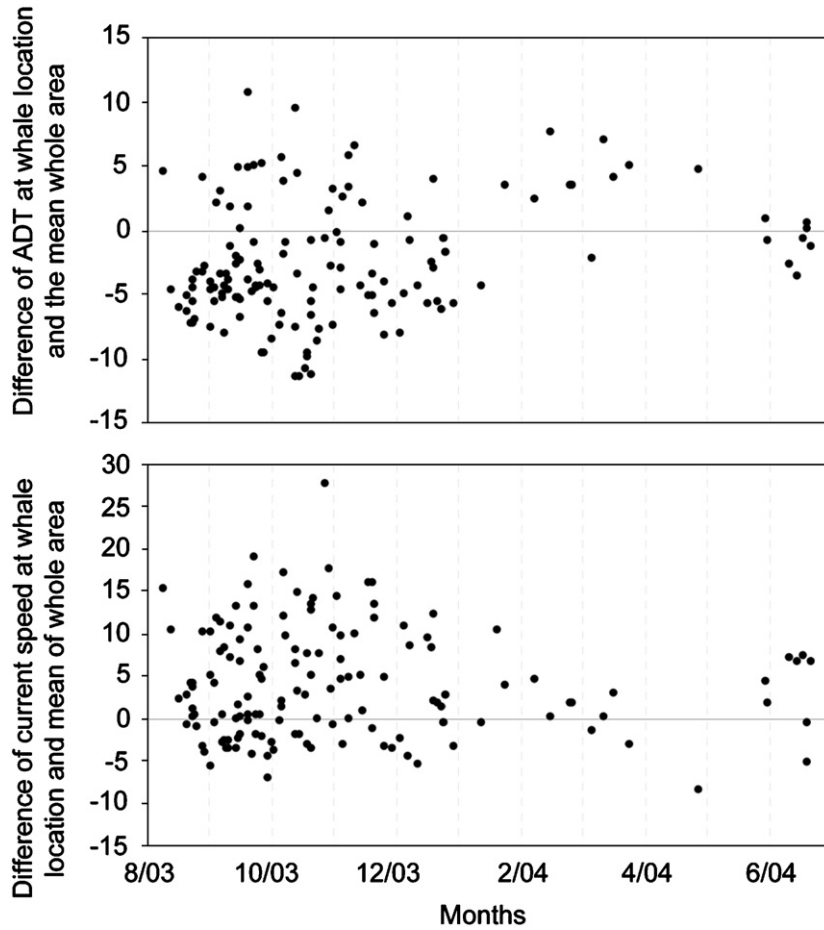


Fig. 5. Temporal altimetry preferences of remotely sensed fin whales. Difference between ADT at the whale’s location and the mean ADT of the whole area covered by all whale locations (upper panel). Idem for current speed (lower panel), over time.

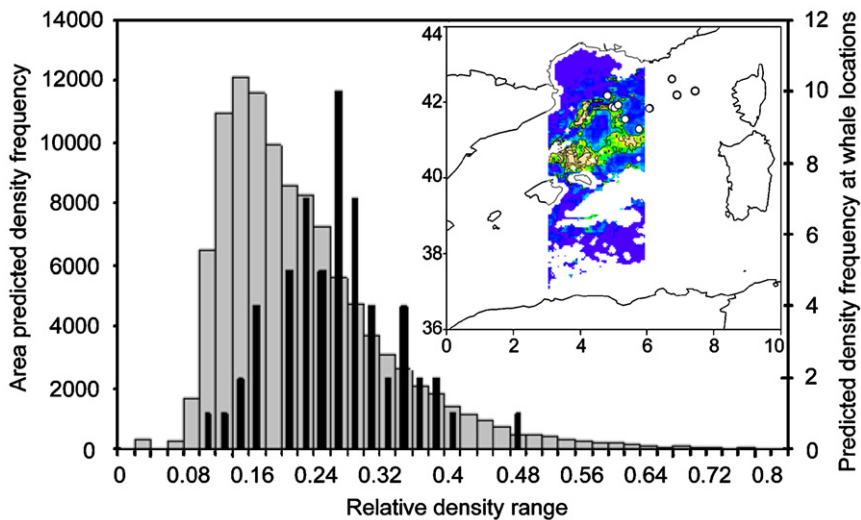


Fig. 6. Frequencies of predicted densities in the whole area (3–6°E), in gray, and frequencies of predicted densities at remotely sensed whale locations, in black, from August to December. The inside panel shows a weekly situation of predicted densities corresponding to the period of plotted whales locations (white circles).

studies are usually snapshots of a given situation at a given period and do not consider the temporal scales. Adaptive sampling strategies are therefore required to catch spatial and temporal interactions from large to fine scales, implying that sampling effort must achieve large-scale coverage with high sampling intensity.

Our results reveal two distinct scales of interactions between predators and their environment. At large scale, fin whales exhibited a well-marked seasonal cycle in time, and basin-wide pattern in space. The link with ADT suggests that whales were found mostly within the mean cyclonic circulation in the northern part of the WM, limited to the north by the Northern Current and to the south by the North Balearic front (Rio et al., 2007). Since most historical information on fin whale distribution in the WM had been obtained only from the northern part of the WM and from the summer season, fin whale seasonal movement patterns were the subject of considerable speculation, but little substantive data. In our study, change in density of whale sighting along transects and satellite tracking established that fin whales do not migrate during winter, but instead dispersed with a clear tendency to remain north of the Balearic Islands, reflecting a regional fidelity to the northern WM exhibited by most individuals. However, we could not delimit precisely the southern boundary of whale distribution from the sightings since the Balearic area was not covered by transects. Our results confirm year-round presence of whales, even if less abundant during winter, as reported from observations in the Ligurian Sea (Laran and Drouot-Dulau, 2007) and from acoustic records (Clark et al., 2002). Movements were also recorded across the Tyrrhenian Sea and Gibraltar Strait, confirming the linkage of recently reported wintering areas within the Mediterranean, where fin whales were observed feeding on another krill species *Nyctiphanes couchi* (Canese et al., 2006), and in Atlantic Ocean (Bentaleb et al., submitted). However, combining the approaches of stable isotopes in the baleen plates and satellite tracking, Bentaleb et al. (submitted) report that fin whales migrating in the Atlantic are a small proportion of the population (less than 20%). Most of fin whale seasonal movements appear to be better characterized as movements across a flexible habitat margin, i.e. aggregation and dispersal in the northern WM, than the dispersal of individuals between discrete habitats, i.e. migration outside the northern WM including the Atlantic. Colder and saltier waters are important parameters at basin scale, as they are generally characteristic of the northern water of the WM (Millot, 1999), the preferred habitat of the northern krill in the WM. Indeed, modified Atlantic water in the northern part of the WM, where most whales have been observed or remotely located, are globally more productive than recent Atlantic water in the southern part of the WM (Morel and André, 1991). These environmental factors, particularly the high spring productivity in the northern modified Atlantic water, sustain krill occurrence and population dynamics (Labat and Cuzin-Roudy, 1996).

The high explanatory power of the model proposed here for WM fin whales is probably due to the fact that both large and mesoscale whale–environment interac-

tions have been captured through the multiple covariates. While the large-scale pattern is characterized by higher densities of fin whales during summer than winter in the northern colder water of the WM, other relationships reveal that mesoscale processes affect whale distribution. At mesoscale, higher whale densities are found in areas defined by high current speed and steep change in temperature. High-temperature change and geostrophic current speed, estimated on a weekly resolution (i.e., non-smoothed by monthly or seasonal composites) are indicative of dynamic areas generated by the mesoscale processes in the WM. Nested within large-scale patterns actually corresponding to their prey habitat, whales seemed to specifically target dynamic areas at mesoscale. Since the mesoscale activity modulates the distribution of primary production and probably krill distribution, taking into account mesoscale processes through relevant oceanographic parameters permit one to cope with the large interannual variability observed in fin whale distribution (Panigada et al., 2005; Monestiez et al., 2006), which is not possible with static physiographic parameters. That is why our model, constructed from 2006 to 2007 visual data, is able to retrospectively predict whale locations in 2003–2004.

Mesoscale features in the WM are mostly depicted by eddies, meanders, and fronts, and they are particularly variable in time and space. Association of top predators with mesoscale fronts has also been reported in the open ocean (Sims and Quayle, 1998; Cotté et al., 2007) and within the Mediterranean for red tuna (Royer et al., 2004). As they have a strong aggregative potential, mesoscale processes can be important for whales since they consume large zooplankton biomasses. Indeed krill patchiness is often associated to advective processes (Fiedling et al., 2001; Cotté and Simard, 2005). The northern krill is an active vertical swimmer (diel vertical migration) but is strongly influenced by horizontal currents as it cannot sustain swimming speeds equivalent to the speeds of these currents (Cotté and Simard, 2005). In addition to this prey patchiness generated at the mesoscale, oceanographic processes probably also influence the availability of these prey to predators. Indeed, these mesoscale processes are often linked to vertical and shearing movements of water masses that can lead to a localized elevation of prey in the water column. This increase of prey accessibility is likely important for Mediterranean fin whales as their dives are the deepest recorded for mysticete species (470 m from Panigada et al., 1999) because of the atypically deep krill layer in the WM (Sardou et al., 1996). Energy expenditure associated with diving activity should be substantially decreased in the case of shallower prey patches. Although most whales in this study were observed or satellite tracked in the northern WM, whale observations in the southern WM were also systematically associated with the edge of eddies (as shown in Fig. 4). Eddies are dynamical features that dominate the circulation of the Algerian basin along a basin-wide path limited by the Northern Balearic front. They propagate at up 3–5 km/day, and they evolve in shape, amplitude and depth, with a lifetime that was reported to reach 3 years (Puillat et al., 2002), so they are

supposed to be extremely important in term of conditioning and structuring the production of the whole area. High densities of zooplankton acoustical detection have been reported to co-occur with the presence of cetaceans in the highly dynamic context of the Algerian basin (Viale and Frontier, 1994).

The seasonal pattern of mesoscale habitat use by remotely tracked fin whales (Fig. 5) suggests that the close association of predators with dynamic areas decreases in winter. This denotes a seasonal foraging strategy, with an active summer foraging season during which fin whales aggregated in the regional habitat of krill, especially within areas of highly mesoscale dynamics, while during the winter season, whales dispersed within the northern WM and tended to target less specifically dynamic areas. Even if opportunistic feeding events can occur, the winter period may be allocated to other activities of the whale life cycle such as reproduction. This shows that whale–environment interactions could be season-dependent corresponding to a shift of whale activity, probably in response to seasonal changes in prey availability. While habitat use has been reported to be dependent on spatial scale several times, the influence of temporal scale, i.e., change of habitat use of large marine predators over time, has rarely been investigated (Boyd, 1996). These results are particularly interesting since they suggest that most fin whales remain all year in Mediterranean, mostly in the northern WM, as a means of coping with the seasonal changes in the life cycle of their prey. Blue whales were also reported to use the region off southern Chile as both a feeding and nursing area (Hucke-Gaete et al., 2004), contradicting the general pattern of whales to fast and breed in temperate waters and migrate to polar waters to feed. This peculiarity of staying in the northern WM all year long is, to our knowledge, the first described for fin whales as evoked by Notarbartolo di Sciara et al. (2003).

The large-scale pattern of whale habitat use is probably driven by the cycle of krill in association with environmental conditions. Biological production in the WM is defined by a seasonal cycle, with intense mixing in winter, stratification of the water column and increasing light conditions in spring, leading to higher phytoplankton grazing by krill in summer (Labat and Cuzin-Roudy, 1996). However, the abundance and distribution of the krill, constituting the variable part of the production of whale prey patches, is likely to be modulated by the major mesoscale dynamic processes. These mesoscale processes are characterized by lower predictability than the large-scale production and distribution of krill (for a review of the predictability of resources for marine predators, cf. Weimerskirch, 2007). However, although the mesoscale prey concentration processes are highly variable in time and space, they are associated with physical processes, i.e. frontal zones and strong currents. These environmental features can potentially indicate areas of prey aggregation at the mesoscale. This foraging behavior was suggested by fractal analysis on a previous Mediterranean whale trajectory (Mouillot and Viale, 2001). The foraging strategy of whales implies a trade-off between searching for the most concentrated food while remaining in the large and persistent area of krill habitat, i.e. the northern

WM relatively to the whole Mediterranean Sea, which is generally known to be “oligotrophic”. It can be supposed that whales associated with the edge of eddies in the southern WM, i.e., outside the main krill habitat, may not yet be engaged in intense but opportunistic foraging, as they were observed in the early and late foraging periods, or they be representative of animals feeding on prey other than krill, possibly copepods, an alternative feeding strategy suggested by low isotopic nitrogen ratios (Bentaleb et al., submitted) and macrozooplankton biomasses (Riandey et al., 2005).

Investigations of environment–predator interactions to understand their foraging strategy is now possible thanks to the greater availability of remote sensing data and imagery products for large areas of the world’s oceans, containing information on a variety of physical and biological parameters at several temporal and spatial scales. The modeling approach we used in this study, and which we have validated with an independent satellite tracking dataset, enabled us to examine which environmental processes possibly drive the distribution and foraging scale-dependant tactics of a large, wide-ranging marine predator, the fin whale. However, these analyses require previous knowledge of temporal and spatial scales of environmental parameters supplied to the models that may affect these interactions. In addition to addressing important ecological questions, our predictive distribution and density modeling approach could be a useful tool to predict whale habitat in the context of growing human maritime traffic that has produced unusually high rates of collisions between ships and whales in recent decades, usually with lethal consequence for the whales (Panigada et al., 2006).

Acknowledgments

We are grateful to the Société Maritime Corse Méditerranée (SNCM) and the ferry crews for their help, and for the contribution of the Commission Internationale pour l’Exploration Scientifique de la Méditerranée (CIESM) and SeaKeepers for the Trans-Mediterranean Network (TRANSMED) on-board system. We appreciate the statistical comments of Pascal Monestiez, and we wish to thank Robert Gisiner and the editor for revising the English of this paper. Comments of anonymous reviewers improved the paper. The Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory (National Aeronautics and Space Administration, NASA), the Ocean Biology Processing Group (NASA), the Collecte Localisation Satellites (Space Oceanography Division, support from the Centre National d’Études spatiales), and Météo France are thanked for the distribution of satellite images.

This study was supported by the US Office of Naval Research (ONR awards: N0014-02-1-0885 and N0-176A). Cédric Cotté is funded by a Provence-Alpes-Côte d’Azur regional council fellowship.

Appendix A. Supplemental data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2008.12.008.

References

- Austin, D., Don Bowen, W., McMillan, J.I., Iverson, S.J., 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* 87, 3095–3108.
- Bentaleb, I., Guinet, C., Mate, B., Martin, C., Mayzaud, P., de Stephanis, R., submitted. The foraging ecology of Mediterranean fin whales in a changing environment elucidated by satellite tracking and stable isotopes.
- Boyd, I.L., 1996. Temporal scales of foraging in a marine predator. *Ecology* 77, 426–434.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2004. *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.
- Canese, S., Cardinali, A., Fortuna, C.M., Giusti, M., Lauriano, G., Salvati, E., Greco, S., 2006. The first identified winter feeding ground of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea. *Journal of the Marine Biological Association of the UK* 86, 903–907.
- Clark, C.W., Borsani, F., Notabartolo di sciara, G., 2002. Vocal activity of fin whales, *Balaenoptera physalus*, in the Ligurian Sea. *Marine Mammal Science* 18, 286–295.
- Cotté, C., Simard, Y., 2005. The formation of rich krill patches under tidal forcing at whale feeding ground hot spots in the St. Lawrence Estuary. *Marine Ecology Progress Series* 288, 199–210.
- Cotté, C., Park, Y.H., Guinet, C., Bost, C.-A., 2007. Movements of foraging king penguins through marine mesoscale eddies. *Proceedings of the Royal Society of London B* 274, 2385–2391.
- Fauchald, P., Erikstad, K.E., Skarsfjord, H., 2000. Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81, 773–783.
- Fiedling, S., Crisp, N., Allen, J.T., Hartman, M.C., Babe, B., Roe, H.S.J., 2001. Mesoscale subduction at the Almeria–Oran front Part 2. Biophysical interactions. *Journal of Marine Systems* 30, 287–304.
- Forcada, J., Aguilar, A., Hammond, P., Pastor, X., Aguilar, R., 1996. Distribution and abundance of fin whales (*Balaenoptera physalus*) in the western Mediterranean Sea during the summer. *Journal of Zoology, London* 238, 23–34.
- Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D., Read, A.J., 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series* 310, 297–310.
- Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F., Donnay, J.P., 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables, a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219, 251–264.
- Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. Chapman & Hall/CRC, Boca Raton, FL.
- Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the north Atlantic Ocean. *Ecology* 87, 2647–2656.
- Hedley, S.L., 2000. *Modeling heterogeneity in cetacean surveys*. Ph.D. Thesis, University of St Andrews.
- Hedley, S.L., Buckland, S.T., Borchers, D.L., 1999. Spatial modeling from line transect data. *Journal of Cetacean Research and Management* 1, 255–264.
- Heide-Jørgensen, M.P., Nordoy, E.S., Oien, N., Folkow, L.P., Kleivane, L., Blix, A.S., Jensen, M.V., Laidre, K.L., 2001. Satellite tracking of minke whales (*Balaenoptera acutorostrata*) off the coast of northern Norway. *Journal of Cetacean Research and Management* 3, 175–178.
- Henry, P., 2005. *Spatial distance sampling modeling of cetaceans observed from platforms of opportunity*. M.Sc. Thesis, University of St. Andrews.
- Hucke-Gaete, R., Osman, L.P., Moreno, C.A., Findlay, K.P., Ljungblad, D.K., 2004. Discovery of a blue whale feeding and nursing ground in southern Chile. *Proceedings of the Royal Society of London B (Suppl.)* 271, S170–S173.
- Hunt Jr., G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., Becker, P.H., 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams, N.J., Slotow, R. (Eds.), *Proceedings of the 22nd International Ornithol. Congress, Durban*. BirdLife South Africa, Johannesburg, pp. 2040–2056.
- Jacquet, N., Whitehead, H., Lewis, M., 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. *Marine Ecology Progress Series* 145, 1–10.
- Johnston, D.W., Thorne, L.H., Read, A.J., 2005. Fin whales *Balaenoptera physalus* and minke whales *Balaenoptera acutorostrata* exploit a tidally driven island wake ecosystem in the Bay of Fundy. *Marine Ecology Progress Series* 305, 287–295.
- Labat, J.P., Cuzin-Roudy, J., 1996. Population dynamics of the krill *Meganycyptophanes norvegica* (M. Sars, 1857) (Crustacea: Euphausiacea) in the Ligurian Sea (NW Mediterranean Sea). Size structure, growth and mortality modeling. *Journal of Plankton Research* 18, 2295–2312.
- Laran, S., Drouot-Dulau, V., 2007. Seasonal variation of striped dolphins, fin- and sperm whales' abundance in the Ligurian Sea (Mediterranean Sea). *Journal of the Marine Biological Association of the UK* 87, 345–352.
- Lévy, M., 2008. The modulation of biological production by oceanic mesoscale turbulence. *Lecture Notes in Physics* 744, 219–261.
- Lévy, M., Mémery, L., Madec, G., 1998. The onset of a bloom after deep winter convection in the North Western Mediterranean Sea: mesoscale process study with a primitive equation model. *Journal of Marine Systems* 16, 7–21.
- Littaye, A., Gannier, A., Laran, S., Wilson, J.P.F., 2004. The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment* 90, 44–52.
- Lombardi, P., Lutjeharms, J.R.E., Mencacci, R., Hays, G.C., Luschi, P., 2008. Influence of ocean currents on long-distance movement of leatherback sea turtles in the Southwest Indian Ocean. *Marine Ecology Progress Series* 353, 289–301.
- Marques, F.F.C., 2001. *Estimating wildlife distribution and abundance from line transect surveys conducted from platforms of opportunity*. Ph.D. Thesis, University of St Andrews.
- Mate, B., Lagerquist, B.A., Calambokidis, J., 1999. Movements of north Pacific blue whale during the feeding season off southern California and their southern fall migration. *Marine Mammal Science* 15, 1246–1257.
- Millot, C., 1999. Circulation in the western Mediterranean Sea. *Journal Marine Systems* 20, 423–442.
- Monestiez, P., Dubroca, L., Bonnin, E., Durbec, J.P., Guinet, C., 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. *Ecological Modelling* 193, 615–628.
- Morel, A., André, J.-M., 1991. Pigment distribution and primary production in the western Mediterranean as derived and modeled from coastal zone color scanner observations. *Journal of Geophysical Research* 96, 12685–12698.
- Mouillot, D., Viale, D., 2001. Satellite tracking of a fin whale (*Balaenoptera physalus*) in the north-western Mediterranean Sea and fractal analysis of its trajectory. *Hydrobiologia* 452, 163–171.
- Notarbartolo di Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S., Airoidi, S., 2003. The fin whale *Balaenoptera physalus* (L. 1758) in the Mediterranean Sea. *Mammal Review* 33, 105–150.
- Panigada, S., Zanardelli, M., Canese, S., Jahoda, M., 1999. How deep can baleen whales dive? *Marine Ecology Progress Series* 187, 309–311.
- Panigada, S., Notarbartolo di Sciara, G., Zanardelli Panigada, M., Airoidi, S., Borsani, J.F., Jahoda, M., 2005. Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. *Journal of Cetacean Research and Management* 7, 137–145.
- Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A., Weinriche, M.T., 2006. Mediterranean fin whales at risk from fatal ship strikes. *Marine Pollution Bulletin* 52, 1287–1298.
- Polovina, J., Uchida, I., Balazs, G., Howell, E.A., Parker, D., Dutton, P., 2006. The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Research II* 53, 326–339.
- Puillat, I., Taupier-Letage, I., Millot, C., 2002. Algerian eddies lifetime can near 3 years. *Journal of Marine Systems* 31, 245–259.
- Ream, R.R., Sterling, J.T., Loughlin, T.R., 2005. Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research II* 52, 823–843.
- Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M.F., Forney, K.A., Balance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres, L., Werner, F., 2006. Techniques for cetacean habitat modeling. *Marine Ecology Progress Series* 310, 271–295.
- Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., Thibault-Botha, D., 2005. Zooplankton distribution related to the

- hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep-Sea Research I* 52, 2029–2048.
- Rio, M.-H., Poulain, P.-M., Pascual, A., Mauri, E., Larnicol, G., Santoleri, R., 2007. A mean dynamic topography of the Mediterranean Sea computed from altimetric data, in-situ measurements and a general circulation model. *Journal Marine Systems* 65, 484–508.
- Royer, F., Fromentin, J.M., Gaspar, P., 2004. Association between bluefin tuna schools and oceanic features in the western Mediterranean. *Marine Ecology Progress Series* 269, 249–263.
- Sardou, J., Etienne, M., Andersen, V., 1996. Seasonal abundance and vertical distributions of macroplankton and micronekton in the Northwestern Mediterranean Sea. *Oceanologica Acta* 19, 645–656.
- Sims, D.W., Quayle, V.A., 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* 393, 460–464.
- Taupier-Letage, I., Puillat, I., Millot, C., Raimbault, P., 2003. Biological response to mesoscale eddies in the Algerian basin. *Journal of Geophysical Research* 108, 3245.
- Taupier-Letage, I., 2008. On the use of thermal images for circulation studies: applications to the Eastern Mediterranean basin. In: Barale, V., Gade, M. (Eds.), *Remote Sensing of the European Sea*. Springer, Berlin, pp. 21–28.
- Thomas, L., Buckland, S.T., Burnham, K.P., Anderson, D.R., Laake, J.L., Borchers, D.L., Strindberg, S., 2002. Distance sampling. In: El-Shaarawi, A.H., Piegorisch, W.W. (Eds.), *Encyclopedia of Environmental Statistics*, pp. 544–552.
- Tynan, C.T., 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature* 392, 708–710.
- Tynan, C.T., Ainley, D.G., Barth, J.A., Cowles, T.J., Pierce, S.D., Spear, L.B., 2005. Cetacean distributions relative to ocean processes in the northern California Current System. *Deep-Sea Research II* 52, 145–167.
- Viale, D., Frontier, S., 1994. Surface megafauna related to western Mediterranean circulation. *Aquatic Living Resources* 7, 105–126.
- Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research II* 54, 211–223.
- Williams, R., Hedley, S.L., Hammond, P.S., 2006. Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecology and Society* 11, 1.
- Wood, S.N., 2001. mgcv: GAMs and Generalized Ridge Regression for R. *R News* 1, 20–25.
- Wood, S.N., 2003. Thin plate regression splines. *Journal of the Royal Statistical Society Series B* 65, 95–114.