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Contemporary migration of fin whales through the Strait of Gibraltar

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ABSTRACT: Fin whales *Balaenoptera physalus* used to be abundant in the Strait of Gibraltar and nearby Atlantic areas until their rapid collapse due to intense whaling at the beginning of the 20th century. Recent studies seem to indicate that some fin whales, believed to belong to the North East North Atlantic (NENA) stock, now use the area to travel between the Atlantic Ocean and the Mediterranean Sea. In this study, we analyzed 15 yr of direct observations combining vessel and land-based surveys with photo-identification to characterize the migration of fin whales through the Strait. These combined observations provide a temporal and spatial analysis of the whales' movement patterns and behavioral activity. Our main findings suggest a migration of a small community of fin whales through the Strait of Gibraltar, with remarkable seasonal directionality. All whales travelled towards the Atlantic Ocean between May and October, and 69% towards the Mediterranean Sea between November and April. Observations of young whales exiting the Mediterranean Sea mainly between May and July suggest that at least part of this community is likely to calve in the basin. Due to the special sensitivity of the species to ship strikes and underwater noise, and the intense maritime traffic in the Strait of Gibraltar, we urge Spain and Morocco to cooperate through the International Maritime Organization (IMO) to ensure a safe crossing of these whales by the effective implementation and year-round extension of the existing recommendation of a seasonal vessel speed reduction to 13 knots.

KEY WORDS: *Balaenoptera physalus* · Migration · Respiratory rates · Swim speed · Ship strike · Strait of Gibraltar · Endangered species · Conservation

INTRODUCTION

Animal migrations are of particular interest to both scientists and the public as they occur in a wide range of terrestrial and marine species including birds, mammals, fishes, reptiles and arthropods (e.g. Corkeron & Connor 1999, Witt et al. 2011, Sergio et al. 2014). Over the last 2 centuries, these movements have been severely disrupted by human activities such as overhunting, anthropogenic barriers, habitat loss and climate change (Bolger et al. 2008, Singh et al. 2012). Regarding baleen whale migration, the generally accepted model worldwide has been historically described as seasonal movements between feeding and breeding grounds in high and low latitudes, respectively (e.g. Kellogg 1929), making them, as well as most wide-ranging migratory marine species, vulnerable to the effects of climate change and human activities (Clapham et al. 2008, MacLeod 2009, Lascelles et al. 2014). However, a recent review has shown that this model was too simplified to describe the diversity of migration strategies of some mysticete species, including the populations of fin whales *Balaenoptera physalus* inhabiting the Mediterranean Sea. In the latter, resident whales (hereafter, MED) are believed to use nomadic and opportunistic movement strategies within the northwestern and central Mediterranean Sea (Geijer et al.

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2016). The MED subpopulation was found to be genetically distinct from those inhabiting the North Atlantic Ocean, mainly through maternally inherited mitochondrial DNA (Bérubé et al. 1998). Their distinctiveness was also evidenced by organochlorine contaminants (Aguilar et al. 2002) and stable isotope analysis (Giménez et al. 2013, Ryan et al. 2013, Das et al. 2017), with a low recurrent gene flow between the NW Spain and MED subpopulations (Palsbøll et al. 2004).

As the only connection between the Atlantic Ocean and the Mediterranean Sea, the Strait of Gibraltar is a mandatory pathway for whales migrating between these 2 bodies of water. The first evidence of the presence of fin whales in the area was unveiled by bone remains found in excavations on both shores of the Strait dated between 1350 and 2150 yr BP (Bernal de Casasola & Monclova Bohórquez 2011). However, the first quantitative information comes from American whaling vessels, which recorded 100 sightings of fin whales between 1862 and 1889, mostly in the adjacent Gulf of Cadiz (Aguilar & Borrell 2007). In 1910–1911, a Norwegian expedition reported a high number of fin whales inside the Strait and the first modern whaling company started exploitation in April 1921 (Tønnessen & Johnsen 1982). Between 1921 and 1959, a minimum of 4535 individuals were captured (Sanpera & Aguilar 1992), reflecting a remarkable density of fin whales in the Strait of Gibraltar and the Gulf of Cadiz. In the early 1920s, catch per unit of effort (CPUE) was very high, reaching the second highest production of oil barrels per catcher boat ever achieved for one season in 1923 (Tønnessen & Johnsen 1982). In this first period, whalers reported catching migrating whales entering the Mediterranean within or nearby the Strait (Sanpera & Aguilar 1992). However, by 1930 all companies had ceased their activities due to the paucity of captures (Sanpera & Aguilar 1992, Clapham et al. 2008). Hoping that the population would have recovered, whaling activities resumed in 1948, but only 370 fin whales were caught, and the fishery was definitely abandoned in 1960 (Sanpera & Aguilar 1992).

Several authors have suggested an incursion of North East North Atlantic (NENA) whales into the Mediterranean Sea (e.g. Jonsgård 1966, Viale 1977, Notarbartolo-di-Sciara et al. 2003, Castellote et al. 2012b), but the extent of this incursion and the limits of the NENA and MED subpopulations within the Mediterranean Sea have been a subject of on-going debate during the last decade. Currently, some authors believe that NENA whales could be distributed from Gibraltar to the eastern Balearic Basin and MED whales from the western Balearic Basin to the Ionian Sea, with a temporal and spatial overlap of both subpopulations within the Balearic Basin (Notarbartolo di Sciara et al. 2016). However, Giménez et al. (2013, 2014) considered that the overlap may occur further north, due to the presence of one individual with an Atlantic isotopic signature in the northwestern Mediterranean Sea (NWMS) and a satellite-tagged individual in the NWMS that moved to the Atlantic (Bentaleb et al. 2011). Although their interpretation of the extent of overlapping area differs, all of these authors suggest that whales currently crossing the Strait of Gibraltar are NENA individuals.

Another point of debate is the seasonality in the presence of these 2 subpopulations and of their possible migration through the Strait. In the 20th century, fin whale catches were made throughout the year with apparent no seasonality in CPUE, suggesting a local, non-migratory subpopulation, but most of these captures happened outside of the Strait, in the Gulf of Cadiz (Sanpera & Aguilar 1992, Clapham et al. 2008). Previously, Viale (1977) suggested that 2 populations from a North Atlantic migrating stock cohabited in the Mediterranean Sea. A summer subpopulation was observed by whalers crossing Gibraltar to enter the Mediterranean Sea in May and June, while a second population entered in winter to breed in the NWMS and returned to the Atlantic during the feeding season, as also suggested by Jonsgård (1966). This would imply several periods of bi-directional movements through the Strait of Gibraltar.

Little information is currently available about fin whales in the vicinity of the Strait of Gibraltar (Bayed & Beaubrun 1987, Notarbartolo-di-Sciara et al. 2003). The few reported observations may represent either stragglers from the MED subpopulation or remnants of the once-abundant Gibraltar subpopulation (Clapham et al. 2008). De Stephanis et al. (2008) reported only 3 (<1%) observations of fin whales out of 606 cetacean sightings during summers from 2001 to 2004. Moreover, between 1989 and 2013 <4% (n = 19) of 511 cetacean strandings were identified as fin whales on the Spanish and Moroccan shores of the Strait, from Trafalgar Cape to Europa Point on the northern shores, and from Cape Espartel to Almina Point on the southern coast (Fernández-Maldonado 2015, Masski & De Stéphanis 2015). However, male fin whale songs were detected continuously in the Strait of Gibraltar between November and January, suggesting a regular winter presence for the species (Castellote et al. 2012b).

In this study, we investigated the current migration of fin whales through the Strait of Gibraltar by combining land- and vessel-based surveys with photo-identification. We used the whales' behavioral activity documented via respiratory rates, movement direction and speed to characterize temporal and spatial patterns of observations, and discussed what could motivate these patterns.

MATERIALS AND METHODS

Data collection

Surveys were performed in the Strait of Gibraltar (between 5.1 and 6.0° W; Fig. 1) from the 10 m research boat 'Elsa' between 2001 and 2014 following protocols described in de Stephanis et al. (2008). Transects were conducted year-round without any pre-defined track for each survey, but were designed to provide even coverage. Two observers scanned the 180° area in front of the boat with 7 × 50 binoculars, when Douglas sea state was <4. The geographic position of the ship was recorded every 1 min with a Logger 2010 (IFAW). When fin whales were sighted, they were approached and photo-identified when possible. The number of animals from each age class (calf, juvenile, adult) was estimated visually based on body length, with juveniles measuring two-thirds, and calves one-half the size of an adult. Behavior and swimming direction were also recorded. In 1999 and 2000, the same data were collected opportunistically from a whale-watching boat.

Additionally, a land-based platform was used biannually from 2009 to 2013 to characterize fin whale observations during 2 periods (May to July and November to December), except in winter 2013. The land station was located on the northern shore of the Strait, 217 m above sea level and 900 m from shore (see Fig. 2). At the station, 2 teams of 4 people operated in summer (09:00 to 15:00 h and 15:00 to 21:00 h local time) and 1 team of 5 people in winter (09:00 to 18:00 h), approximately matching daylight time. Search effort was recorded hourly or when a change occurred, and stopped when Douglas sea state was >4 and/or visibility decreased to less than one-third of the study area due to fog or rain. Two spotting observers scanned the area of almost 180° using 7 × 50 binoculars with compass and reticules. Once a whale was sighted by a spotter, a theodolite operator located the animal using a surveyor's theodolite (Leica T1000) (Würsig & Würsig 1979). The vertical and horizontal angles measured by the theodolite were transmitted to a laptop running the Cyclops Tracker v.2.6 whale tracking software (unpublished software, E. Kniest, University of Newcastle, NSW, Australia), which automatically calculated the position of the animal. When possible, the location was also communicated to the vessel to confirm group size and age classes, as well as to perform photo-identification. The theodolite operator aimed to record the whale's position at least once per surfacing bout (i.e. when the whale is blowing several times at the surface between longer dives; see 'Respirations, surface and dive time' below) to track its movements through the Strait, until the

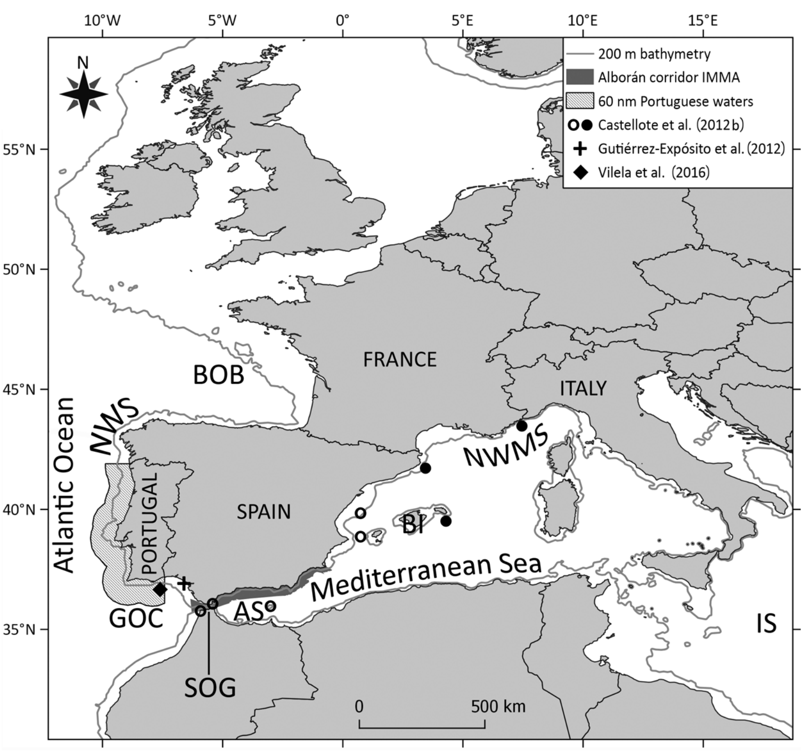

Fig. 1. Study area (SOG; Strait of Gibraltar) and places mentioned in the text. BOB: Bay of Biscay; NWS: northwestern Spain; GOC: Gulf of Cadiz; AS: Alboran Sea; BI: Balearic Islands; NWMS: northwestern Mediterranean Sea; IS: Ionian Sea. Light grey shaded area shows Portuguese waters up to 60 nautical miles while the dark grey shaded area shows the 'Alborán Corridor Important Marine Mammal Area' (IMMA) (IUCN Marine Mammal Protected Areas Task Force 2016). Open (North East North Atlantic [NENA] fin whale songs) and closed circles (resident Mediterranean Sea [MED] fin whale songs) indicate approximate hydrophone locations from Castellote et al. (2012b). Diamond and cross indicate locations of Vilela et al. (2016) and Gutiérrez-Expósito et al. (2012), respectively

animal was lost or too far away from the land station to follow. When a group of whales (i.e. several whales separated by <1000 m) was sighted, the theodolite operator tried to take a position of the same whale (e.g. the 'leading' whale). Although this was generally feasible during one surfacing bout, it was not always possible to ensure that the same whale was tracked in subsequent surfacing bouts. However, group cohesion was generally very high, so the error should be small. The second spotter resumed scanning the area as soon as possible. All fin whale tracks were plotted in QGIS v.2.18 (QGIS Development Team 2016).

All calculations and comparisons were run in R v.3.2.5 (R Core Team 2016), unless stated otherwise. When applicable, normality was tested using a Shapiro-Wilk test and homoscedasticity using a Levene test from the 'car' package (Fox & Weisberg 2011). Although the main target species was fin whale, other cetacean species were recorded opportunistically when sighted from the land stations. Boxplots of distances from the land station for each species with more than one observation were compared using a Wilcoxon rank sum test to provide a way of assessing detection bias over the study area.

Using a Wilcoxon rank sum test, the total annual number of observations and photo-identified animals from the research vessel were compared for years with or without land-based surveys. This provided an assessment of the benefits of land-based assistance to vessel activities, to determine if indeed land-based assistance increased observations.

Swimming speed and linearity

Speed and linearity were calculated for each land-based track by Cyclops Tracker v.2.6 using whales' positions. Minimum swimming speed was calculated as the distance between initial and final locations of a track divided by total duration. Linearity was the straight distance between initial and final locations divided by the cumulative distance between all pairs of consecutive positions. Only tracks with more than 3 positions in total were used for this analysis. Both variables were compared for whales swimming west- and eastwards, using a Wilcoxon rank sum test.

Encounter rates

Encounter rates (ERs) were calculated as the number of sightings per hour for the land-based observations for each survey; ERs were then compared annually between periods using a 2-proportion z-test. Sea state conditions showed great spatial heterogeneity but were similar for both seasons.

For boat-based observations, ER was calculated monthly as number of sighting per 100 km searched in the area, and Wilson's confidence intervals were calculated using the 'binom' package (Dorai-Raj 2014).

Respirations, surface and dive time

Respirations were recorded from land and vessels for several purposes. One was to compare blow detection from each platform as a way to further assess the capacity of detection from the land station. Respiration rates were also used to define a surfacing period and to calculate blow intervals and diving duration (see below), which can give an indication about whale behavior. From the land station, all respirations were called out by an assigned spotter and recorded to the closest second; however, individuals were not distinguishable except for pairs of adults with calves. From the vessel surveys, respiration rates were monitored beginning in 2009. Each respiration was recorded to the closest second at the individual level when the animals were distinguishable without error due to natural markings (see 'Photo-identification' below), or otherwise at the group level.

Blow intervals were calculated only from respirations recorded by the vessel, for solitary animals or groups of 2 animals with recognizable features, excluding calves. Respiratory intervals were divided between intra-bout dives (i.e. short duration submergences during surface activity clusters) and inter-bout dives (i.e. longer terminal dives) (CeTAP 1982). The breakpoint between surface bouts and dives was estimated by a log survivorship analysis (Fagen & Young 1978). Additionally, the duration of surfacing time was calculated by adding intra-bout intervals between 2 dives. Mean duration and standard deviation of intra- and inter-bouts intervals as well as surfacing time were also calculated.

When fin whales were simultaneously tracked from both platforms, the number of respirations recorded from each one was compared using a paired t-test or Wilcoxon signed rank test with continuity correction.

Photo-identification

Whenever possible, photographs of the whole fin whale body were taken, as well as close-ups of the rostrum, dorsal fin and peduncle, from both left and right sides of the animal. These images were used to create 2 catalogues. The main catalogue compiled only individuals with recognizable features (available at www.cetidmed.com), including nicks on their dorsal fins and severe scarring. Coloration patterns on the head (or chevron) were not always visible due to bad light or water covering the area and were therefore only used as complimentary information. A secondary catalogue was also created for each year with the best photographs of each individual per sighting regardless of their marking. While the main catalogue was used to investigate possible resightings over different years, the secondary catalogue allowed the comparison of poorly marked individuals, mainly based on temporary scarring, within the same year.

RESULTS

Sightings

A total of 254 fin whales were sighted in the Strait of Gibraltar between 1999 and 2014, consisting of 155 observations (some observations contained more than one individual) from the following platforms: 72 from the vessel only, 65 from land only and 18 from both platforms (Table 1, Fig. 2). Overall, the direction of migration was known for 93% (n = 239) of individuals. All whales with known travelling direction were headed towards the Atlantic Ocean between May and October (n = 185), while 69% (n = 38) were travelling towards the Mediterranean Sea during the rest of the year. Eastbound whales were only observed in the winter period, specifically in November and December (Table 1).

Animals with estimated age classes (n = 128) were mostly adults (76%), although a lower proportion of juveniles (12%) and calves (12%) were also observed. Juveniles and calves were mainly observed between May and July (Fig. 3). Age classes could not be determined for most animals seen exclusively from land, except a few obvious smaller animals travelling with adults which were considered calves. Whales travelled alone or in groups up to 5 individuals (mean ± SD = 1.6 ± 0.8). In general, only one sighting was recorded during the same day from any platform (82%), but a maximum of 5 sightings totaling 10 individuals were observed once.

Significantly more fin whales were observed (Wilcoxan rank sum test, $W = 54$, $p < 0.01$) and photo-identified ($W = 50$, $p = 0.01$) in years with combined land and vessel effort, with a maximum of 29 sight-

Table 1. Annual boat- and land-based fin whale sightings and individual counts from 1999 to 2014. For the period of November to April, the given year applies to November. 'Direction' indicates the direction animals were swimming: west (W), east (E) or unknown (?); age classes were estimated when possible as adult (A), juvenile (J) or calf (C). Photo ID is the number of individuals in each annual catalogue

Year	Sightings							Individuals												Photo ID
	May–October			November–April			Total	May–October					November–April						Total	
								Direction		Age class			Direction			Age class				
	Boat	Land	Both	Boat	Land	Both		W	?	A	J	C	E	W	?	A	J	C		
1999[a]	5						**5**	7				1							**7**	1
2000[a]	12			1			**13**	17							1	0			**18**	7
2001				1			**1**								3		3		**3**	3
2002	5						**5**	8		3	1								**8**	5
2003[b]	2				3		**5**	2		1			1	1	1				**5**	
2004	1						**1**	1		1									**1**	1
2005	4						**4**	6		2									**6**	4
2006	2	2		2			**6**	3	1	2					2	1	1		**6**	2
2007	7			1			**8**	8	3	9	1	1				1			**12**	7
2008	2						**2**	1	1	2				1					**2**	1
2009[c]	3	8			8		**19**	27		7		2	9	4					**40**	5
2010[c]	4	3	4		8		**19**	20		12		3	9			1		1	**29**	18
2011[c]	2	4	2	1	17	3	**29**	21		8	2	1	17	9	3	10		1	**50**	12
2012[c]	3	10	8	1	2		**24**	35		19	4	2	2						**38**	19
2013[d]	7		1				**8**	15		10	3	2		1					**15**	14
2014	6						**6**	14		8		2							**14**	14
Total	**65**	**27**	**15**	**7**	**38**	**3**	**155**	**185**	**5**	**84**	**11**	**14**	**38**	**16**	**10**	**13**	**4**	**2**	**254**	**113**

[a]Data collected from whale-watching boats. [b]Land-based pilot project in winter 2003 and summer 2006. [c]Biannual dedicated land-based surveys in May–July and November–December. [d]Dedicated land-based survey only in summer

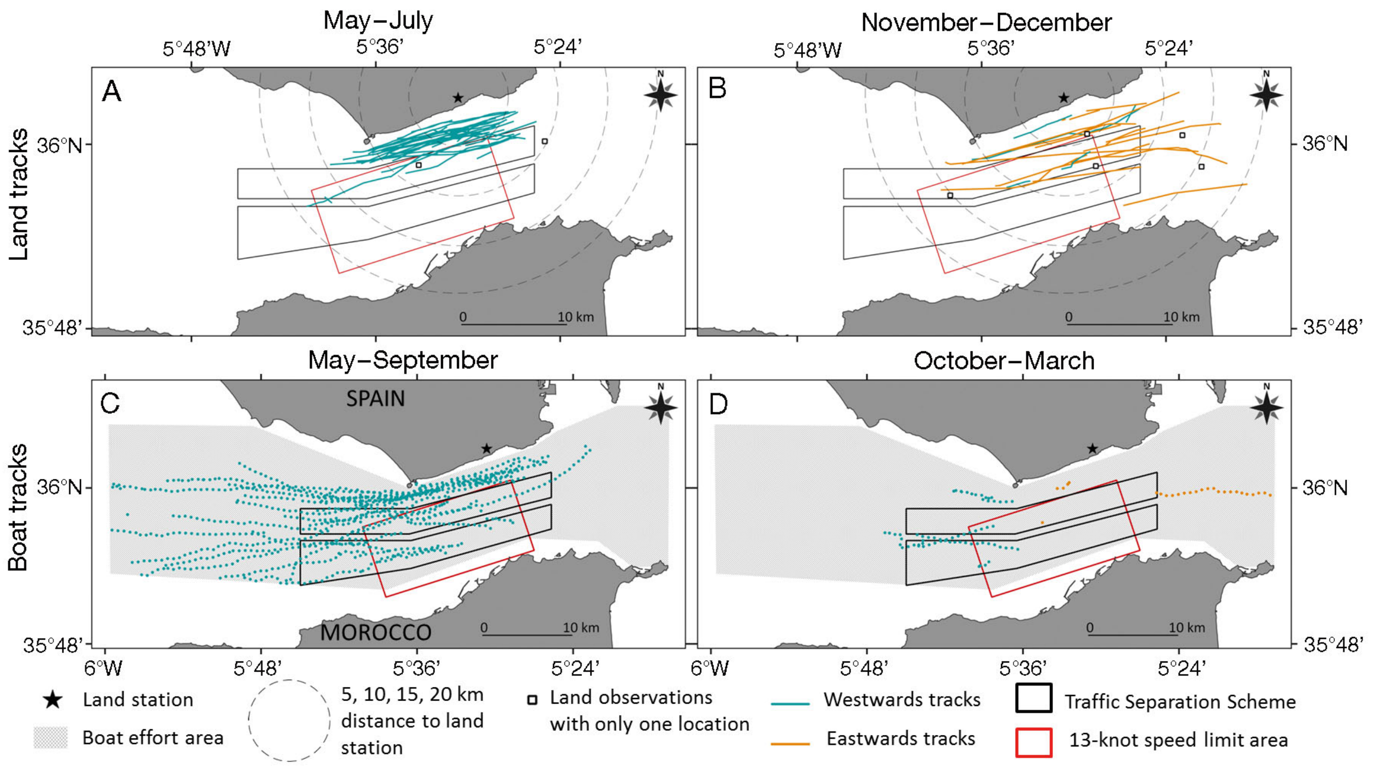

Fig. 2. Fin whale tracks from (A,B) the land station (continuous lines) and (C,D) the vessel (dotted lines). Some tracks correspond to the same sighting from both platforms

ings of 50 individuals in 2011. From November to April (2011), a maximum of 21 sightings of at least 29 whales were observed; 21 sightings of 35 whales were observed between May and September (2012) (Table 1).

The majority of fin whales observed in the summer were travelling in the northern half of the Strait of Gibraltar, especially those observed from land, which occurred mostly in a 5 km strip from the Spanish shore (Fig. 2C). Fin whale observations were more widespread in the rest of the year (Fig. 2D).

Although fin whales were the target species observed, all 7 cetacean species commonly inhabiting the Strait of Gibraltar (de Stephanis et al. 2008) were sighted at least once from the land stations in both seasons, including bottlenose dolphins *Tursiops truncatus*, striped dolphins *Stenella coeruleoalba*, common dolphins *Delphinus delphis*, long-finned pilot whales *Globicephala melas* and sperm whales *Physeter macrocephalus*. A group of 4 killer whales *Orcinus orca* was observed on 3 December 2011 and a humpback whale *Megaptera novaeangliae* on 10 July 2013. Boxplots of distances from the land station of fin, sperm and pilot whales as well as grouped dolphin species show that fin whales and dolphins were detected over a similarly wide range of distances, while pilot and sperm whales were sighted only at greater distances (Fig. 4).

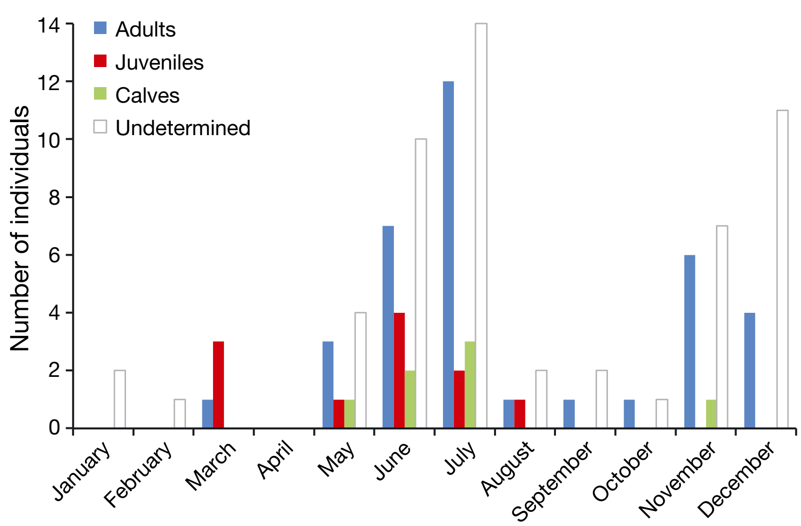

Fig. 3. Maximum monthly number of individual fin whales sighted by estimated age class. Data include both land- and boat-based sightings

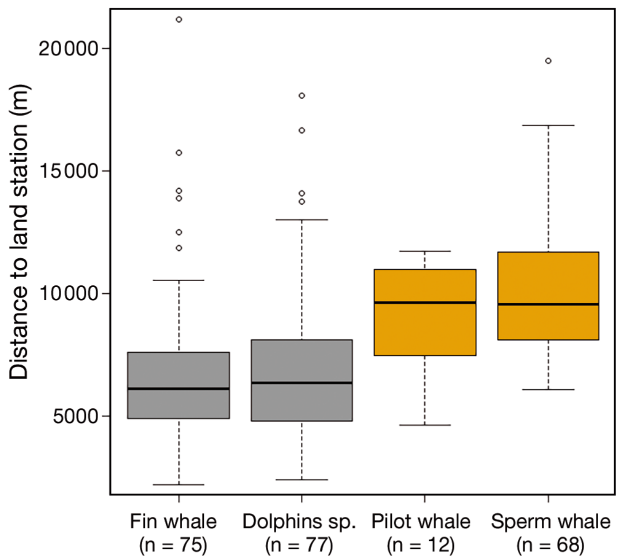

Fig. 4. Distance from the land station of each first observation of fin whales and other cetaceans. Species with significantly different distances are displayed with different colors (Wilcoxon rank sum test, $p < 0.05$). The box spans the first to third quartiles. The thick horizontal line represents the median. The whiskers show the minimum and maximum value within 1.5 interquantile range, i.e. excluding outliers (circles)

Encounter rates

Total effort from the land station from May to July (798 h) was more than twice that during November and December (307 h). Conversely, encounter rates were overall 2 times lower in summer, with 0.05 fin whale sightings h^{-1} compared to 0.12 sightings h^{-1} in winter ($z = 4.28$, $p < 0.001$) (Fig. 5). However, a large inter-annual variation was found within each period, with ERs ranging from 0.01 to 0.07 and from 0.03 to 0.20, respectively.

Additionally, a total of ca. 46 000 km was searched between 1999 and 2014 over the study area with 85% of the effort concentrated between May and October (Fig. 2A,B). Fin whale observations made solely from the research vessel were recorded year-round, except in April and November (Fig. 6). May, and especially June and July were the months with highest ER values, between 0.19 and 0.27 sightings per 100 km. In comparison, August, September and October had lower values (0.05 to 0.09) but still a reasonable amount of effort. The other 6 months had sporadic effort and ERs showed greater variability.

Swimming speed and linearity

Most whales showed a quasi-linear track west- or eastwards (Fig. 2). Two whales observed on 28 November 2011 from both platforms presented a convoluted swimming pattern which could indicate foraging activity (Whooley et al. 2011). While swimming eastward at the surface, they would then reappear further to the west after each longer dive, but no surface feeding events were observed during the study period.

Speed and linearity were calculated from 44 (53%) land-based sightings. Average speed for the whales swimming eastwards (6.0 ± 1.9 knots, n = 7) was greater than for whales swimming westwards (3.7 ± 0.2 knots; $W = 221.5$, $p < 0.01$, n = 37), i.e. 2.3 ± 2.1 knots higher for easterly whales. However, average linearity was similar for both directions (0.9 ± 0.02; $W = 137$, $p = 0.8$) and very close to a completely linear trajectory.

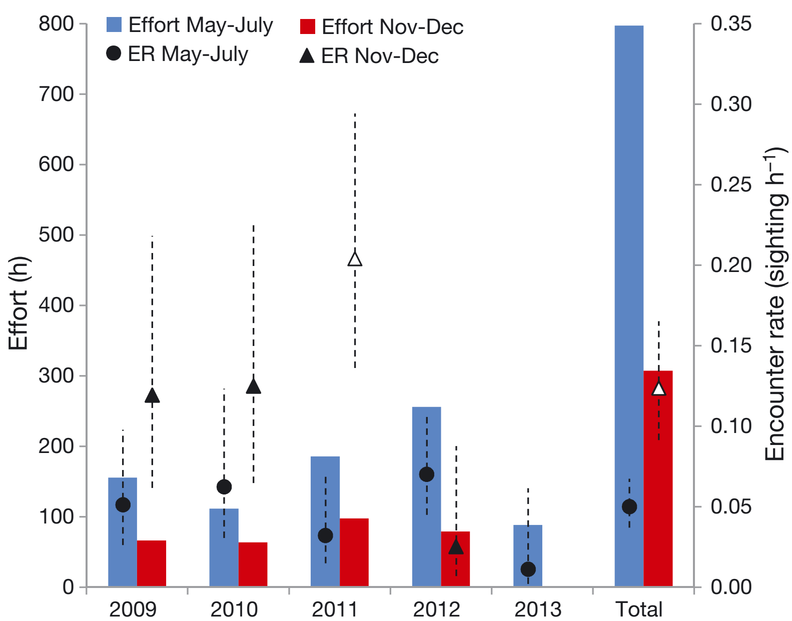

Fig. 5. Annual effort in hours from the main land station (bars) and encounter rate (ER) as sightings h^{-1} (dots). Vertical lines: 95% CI. No effort was made in winter 2013. Periods within a year with significantly different ERs are displayed with open versus closed symbols (z-test, $p < 0.001$)

Respirations, surface and dive time

Fin whale respirations relative to 16 vessel observations were recorded during 23 h and 16 min, a total of 2563 respirations. A total of 1224 blow intervals (mean = 80 s) ranged from 4 to 829 s (13.82 min), with a breakpoint of 22 s between intra- and inter-bout intervals.

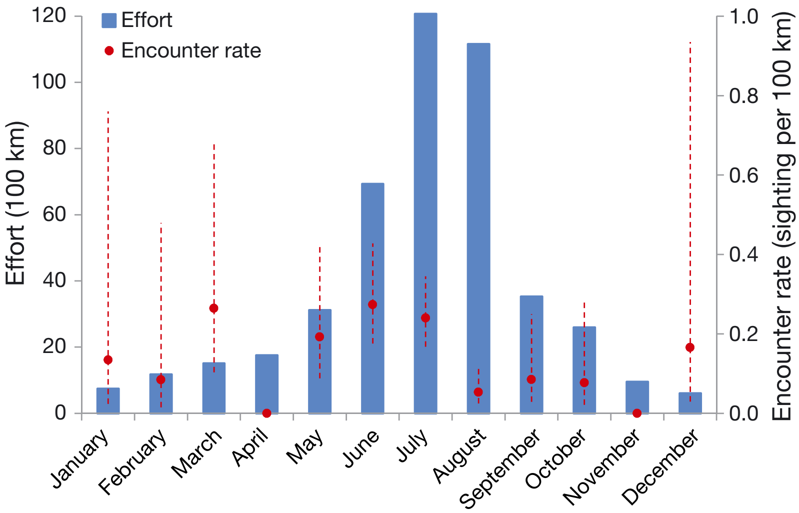

Fig. 6. Monthly effort in km searched by the research vessel from 1999 to 2014 (blue bars) and encounter rate as fin whale sightings per 100 km (red dots). Red vertical dotted lines: 95% CI

Consequently, 641 intra-bout intervals had a duration of 16 ± 4 s and 583 dives lasted 151 ± 170 s (2.52 min). On 109 occasions, whales breathed only once between 2 dives; therefore, no intra-bout interval could be calculated. Mean surfacing time was 74 ± 46 s (1.23 min) with a maximum of 4.02 min. Three extreme values (7.87, 14.67 and 27.77 min), coming from the same solitary animal sighted on 19 August 2010, were discarded from this calculation.

A total of 6 simultaneous and independent observations were used to compare blow detectability from land and vessels totaling 3 h and 53 min of tracking, including one observation of a possible mother–calf pair group. No difference was found between the number of respirations recorded from each platform, both with (Wilcoxon signed rank test with continuity correction, $U = 13$, $p = 0.17$) and without the mother–calf pair (paired $t = 1.34$, df = 5, $p = 0.24$). On 6 occasions, although a blow was not spotted from land, a body was seen on the surface and recorded as a 'no blow rise' observation. All corresponded to blows recorded from the vessel. A total of 64 blows were recorded from the vessel for the mother–calf observation, compared to 38 from land; most missed blows were from the calf (n = 15). Additionally, information was available at the individual level for 2 boat sighting of possible mother–calf pairs (including the one described above) during 3 h and 40 min. In both cases, a greater number of respirations were recorded for the calf (55 to 59%) than for its suspected mother (41 to 45%).

Photo-identification

Nearly 21000 photographs were analyzed and 50 individuals were included in the main catalogue. From these animals, 5 individuals (10%) were resighted twice over the study period from 9 mo to 3 yr apart (Table 2). All 5 animals were sighted between June and September swimming towards the Atlantic Ocean, but they were not spotted when entering the Mediterranean Sea in between these sightings. Two individuals were travelling in groups during both encounters, but their travelling partners were different on each occasion. Regarding the annual catalogues, up to 19 individuals were photo-identified during a single year, and no resighting happened within the same calendar year. Two individuals (including the resighted BP_GIB_007) showed heavy scarring on their peduncle that could have been caused by a past ship strike (Fig. 7).

DISCUSSION

Our work supports evidence of a bi-directional migration of a small community of fin whales through the Strait of Gibraltar, with a main flow towards the Atlantic Ocean between May and July and towards the Mediterranean in November and December. This temporal pattern corresponds to one of the early hypotheses about Gibraltar whales (Jonsgård 1966, Viale 1977). Moreover, while the summer peak was clear from both platforms, the winter peak was only detected by land observations. It is important to highlight that higher ERs were detected in the winter even if the effort in hours was much smaller in this

Table 2. Individual fin whales resighted during the study period (dates are dd/mm/yyyy)

Individual code	1st sighting	Group size	2nd sighting	Group size	Difference Days	Difference Years
BP_GIB_003[a]	25/07/2005	3	17/07/2008	6	1088	3.0
BP_GIB_007[a]	22/09/2006	1	20/06/2007	2	271	0.7
BP_GIB_030	25/06/2008	1	20/07/2010	2	755	2.1
BP_GIB_048	20/06/2009	3	12/07/2012	2	1118	3.1
BP_GIB_065	19/08/2010	1	06/07/2012	2	687	1.9

[a]Data reported in Gauffier et al. (2009)

Fig. 7. Two fin whale individuals, (a) BP_GIB_007 and (b) BP_GIB_068, showing heavy scarring on their peduncle that could have been caused by a past ship strike

season. Periods of 9 mo to 3 yr separated 2 observations of the same individuals on their migration towards the Atlantic Ocean, showing that the animals can spend as little as a few months in and out of the Mediterranean Sea. Indeed, at least one animal crossed the Strait of Gibraltar no less than 3 times over 9 mo, as it was spotted 2 times exiting the Mediterranean and therefore must have entered at some time in between. This suggests that some individuals must exhibit at least a bi-annual migration through the Strait, comparable to other marine species such as bluefin tuna *Thunnus thynnus* (Block et al. 2005) or Balearic shearwaters *Puffinus mauretanicus* (Guilford et al. 2012).

The land station maximized the number of fin whale encounters, which would otherwise have been much fewer. When assisting boat activities, it was especially important for photo-identification as it greatly increased the possibility of finding resighted animals. Additionally, observations of other cetaceans at greater distances than fin whales provided strong evidence for a good detectability of our target species over the study area and are consistent with the distribution of these species in the Strait of Gibraltar (de Stephanis et al. 2008). Furthermore, when tracked simultaneously from the land station and the vessel, no difference was found in the number of blows detected from each platform, although blows from calves accompanying an adult were missed more often, as with humpback whales in eastern Australia (Godwin et al. 2016). In turn, the vessel allowed for confirmation of group size, age classes and photo-identifying animals; thus, surveys combining land and vessel platforms appear to be the best way to study fin whales in the Strait of Gibraltar. Fin whale swimming behavior was consistent with travelling and/or migrating, presenting an almost fully linear movement and short diving times (Croll et al. 2001, Lafortuna et al. 2003). Respiratory parameters such as blow intervals, surface and dive times were similar to other studies on the species (Leatherwood et al. 1982, Stone et al. 1992, Kopelman & Sadove 1995, Lafortuna et al. 2003). Swimming speed was about 2 knots higher for easterly than westerly whales. This difference could be explained by the presence of a main easterly current in the upper water layer of the Strait of Gibraltar (Lacombe & Richez 1982). Fin whales have been found to stay near the surface and spend most of their time at <100 m depth, especially when not foraging (Panigada et al. 1999, Croll et al. 2001, Stimpert et al. 2015). At this depth in the Strait, longitudinal currents range from slightly positive to a maximum of almost 3 knots, and even with the influence of tides, the overall average current flows easterly at about 1 knot (Lacombe & Richez 1982, Wang 1993, Sánchez Garrido et al. 2008), which corresponds to the difference in fin whale swimming speed.

In November and December, most animals were travelling eastwards, consistent with a main migratory flow entering the Mediterranean Sea, but a small proportion was swimming in the opposite direction. This could suggest that some animals use both sides of the Strait of Gibraltar as a wintering ground, as proposed by Castellote et al. (2012b). Bentaleb et al. (2011) also suggested that 2 individuals stranded on the coast of Malaga (i.e. in the northern Alboran Sea) were mainly feeding in the Mediterranean Sea with short incursions in contiguous Atlantic waters due to the longitudinal variations of their $\delta^{13}C$ stable isotope values along their baleen plates. However, regardless of their origin, a posterior analysis suggested these animals had spent at least the last 2 yr of their life foraging in the Mediterranean Sea (Giménez et al. 2013). Although both matched the isotopic values of Mediterranean whales, one animal showed values close to the Atlantic data set (Giménez et al. 2013), which could reflect intermediate prey values found in the Gulf of Cadiz (Varela et al. 2013) or nearby areas. Interestingly, an individual satellite-tagged in the NWMS visited historic whaling grounds in the Gulf of Cadiz and offshore Portugal in November and December (Bentaleb et al. 2011). Indeed, some fin whale populations also feed outside of the summer

(Aguilar et al. 2014, Geijer et al. 2016), and winter feeding grounds have been identified in the Mediterranean basin near Lampedusa Island in the Strait of Sicily and in the Tunisian Plateau (Marini et al. 1996, Panigada et al. 2017). Potential fin whale foraging habitat in the Mediterranean Sea is more widespread in winter (Druon et al. 2012), leading to the dispersion of whales after the summer (Notarbartolo-di-Sciara et al. 2003, Panigada et al. 2017). Thus, the mild meteorological and climatic conditions of the Mediterranean Sea might have provided year-round resident MED fin whales with an extended calendar of feeding opportunities (Notarbartolo-di-Sciara et al. 2003). NENA whales could also benefit from these feeding opportunities if they use some of the same winter grounds as MED whales. Nevertheless, the location of the winter grounds of NENA whales remains unclear but could include the Gulf of Cadiz, the Alboran Sea and part of the NWMS (Sanpera & Aguilar 1992, Castellote et al. 2012b, Giménez et al. 2013, Notarbartolo di Sciara et al. 2016).

In the present study, fin whales were observed travelling towards the Atlantic Ocean with juveniles and even small calves mainly between May and July. This could indicate that these whales use the Mediterranean Sea for breeding and calving in the winter, as proposed by Castellote et al. (2012b). If these are the main reasons for NENA whales to enter the Mediterranean Sea, then it would be crucial to assess the degree of possible mixing of these animals with the resident MED population. Indeed, there is some evidence of spatial and temporal overlap between these 2 subpopulations (Castellote et al. 2012b, Giménez et al. 2013, 2014, Notarbartolo di Sciara et al. 2016) that could explain the recurrent gene flow of 2 females per generation between northern Spain and the NWMS (Palsbøll et al. 2004). Alternatively, NENA whales could take advantage of the mild winter conditions in the Mediterranean basin compared to the North Atlantic Ocean while breeding separately from the MED subpopulation, as suggested by the different types of songs recorded in the basin (Castellote et al. 2012b). Although newborn calves have been observed in the Mediterranean Sea, precise calving locations have not been identified and evidence suggests that breeding may be dispersed throughout the basin (Notarbartolo-di-Sciara et al. 2003). As with other mysticete species, it is generally assumed that young fin whales may learn migratory routes from their mothers and at least some populations show maternally directed site fidelity (Clapham & Seipt 1991, Mizroch et al. 2009, Kennedy et al. 2014). This remains to be investigated for the populations of fin whales inhabiting the Mediterranean Sea, and especially for the animals crossing the Strait of Gibraltar.

Fin whale counts in the Strait of Gibraltar were low, even during peak season, and with a high resighting rate which points to a small number of individuals crossing the Strait of Gibraltar on a regular basis. Based on passive acoustics and stable isotopes (Castellote et al. 2012b, Giménez et al. 2013), it was suggested that these whales belonged to the northeastern North Atlantic Ocean, an estimated population of about 20 000 fin whales, mainly distributed in the offshore Bay of Biscay (Hammond et al. 2011). If this is the case, only a small proportion of these animals was detected during the present study, even if some whales could have crossed undetected at night. More information is needed on the connectivity of Gibraltar whales with neighboring areas and populations. Indeed, if Gibraltar whales exhibit a unique migration pattern, they might not belong to the abundant northeastern North Atlantic population, and could therefore be a remnant from the historic non-migrating population. In that case, the conservation status of what would be a small subpopulation needs to be urgently assessed.

Information about the current presence of fin whales in the Gulf of Cadiz is scarce. Between 1986 and 2011, only 7 fin whales out of 303 (2%) stranded cetaceans were recorded on a 60 km Spanish beach of the Gulf of Cadiz at about 6.5°W longitude (Gutiérrez-Expósito et al. 2012). Further west, 30 nautical miles offshore south Portugal (around 7.5 to 8°W), a spring survey found 0.5 encounters of the species per 100 km in waters from about 200 to 750 m depth, mainly in April (Vilela et al. 2016). Although 1035 fin whales were caught between 1925 and 1951 off the west central Portugal coast (Brito et al. 2009), recent distance sampling surveys from cargo ships travelling from mainland Portugal to Madeira Island between July and October only found a maximum encounter rate of 0.03 sighting per 100 km for unidentified baleen whales (which might include *Balaenoptera physalus* but also *B. acutorostrata*; Correia et al. 2015). In coastal Portuguese waters up to 60 nautical miles (see Fig. 1), fin whales are quite rare (Brito et al. 2009, Vingada et al. 2011, Santos et al. 2014, Goetz et al. 2015). Southward, low numbers of fin whale strandings occur along the Moroccan Atlantic coast with no apparent seasonality (Masski & De Stéphanis 2015), and few whales were confirmed to belong to this species off Mauritania (Baines & Reichelt 2014). This information seems to indicate that if fin whales are regularly detected in the Gulf of Cadiz in winter (Castellote et al. 2012), they must either leave the area the rest of the year, or stay offshore where no recent data are available, or in poorly studied inshore locations. It further suggests that either the proportion of NENA whales that undertake a migration back and forth to the Strait is small, or that the route is located far offshore mainland Portugal and the peak migration does not occur between July and October. The latter temporally matches the decrease in fin whale encounter rates from the end of July to early November in the Strait of Gibraltar reported in the present study. If Gibraltar whales do migrate to the Atlantic Ocean in summer for feeding purposes, it could be to take advantages of different feeding grounds, including different prey items. Indeed, while summer feeding grounds in the Mediterranean Sea seem to be restricted to the NWMS, the Bay of Biscay and other areas of the North Atlantic offer a larger prey biomass to support the abundant NENA population (Hammond et al. 2013). Moreover, while fin whales from the Mediterranean and NW Spain seem to feed exclusively on krill (Aguilar 1985, Notarbartolo-di-Sciara et al. 2003, Canese et al. 2006, Borrell et al. 2012), individuals from Irish and Icelandic waters also feed on small schooling fishes such as sprat, herring capelin or anchovies (Ryan et al. 2014, Vighi et al. 2016). In NW Spain, fin whales used to be caught on a feeding ground from July to October (Sanpera & Aguilar 1992) and recent population estimates for the Bay of Biscay are higher in the summer (Laran et al. 2017). However, foraging whales have been observed around the Azores archipelago in spring (Visser et al. 2011), then migrating to west Iceland and east Greenland feeding grounds in the summer (Silva et al. 2013), while some whales feed in Irish waters from autumn to spring (Ryan et al. 2014, Baines et al. 2017). Future research should focus on where Gibraltar whales are going when they are not in the Strait, either through direct evidence such as matching photo-identification catalogues with other areas and deploying satellite tags, or indirectly by comparing genetic and isotopic data with neighboring populations.

This small community of fin whales regularly travels through one of the most transited shipways in the world (Abdulla & Linden 2008), and some show signs of possible past collisions. In fact, the species has been recognized as especially vulnerable to ship strike and underwater noise (Laist et al. 2001, Panigada et al. 2006, Castellote et al. 2012a). Therefore, special effort should be made to ensure the safe crossing of these whales through the Strait of Gibraltar, an area identified as a cetacean critical habitat by the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic area (ACCOBAMS 2007) and an important marine mammal area by the IUCN (IUCN Marine Mammal Protected Areas Task Force 2016). Nevertheless, with nearly 110 000 ships navigating in the area in 2014 (Sociedad de Salvamento y Seguridad Marítima 2014), automatic information system (AIS) monitoring indicates that mariners are not adhering to the 13 knot vessel speed limit recommended by the International Maritime Organization (IMO) since 2007 for the Strait of Gibraltar traffic separation scheme (TSS) (Silber et al. 2012, see Fig. 2). Migrating fin whales use this seasonal vessel speed reduction area, which was initially created for sperm whales from April to August, in both summer and winter. There is therefore an urgent need for an effective application of this measure and its extension to the rest of the year, which will require the international cooperation of Morocco and Spain through the IMO. Indeed, restrictions of shipping activities through this international organization are believed to be most effective at reducing the risk of ship–whale strikes (Geijer & Jones 2015). Moreover, slowing maritime traffic would also reduce ship noise, as shown in the eastern Mediterranean Sea, where the noise level decreased by 50 to 65% when steaming speed decreased from 15.6 to 13.8 knots over 6 yr (Leaper et al. 2014). Finally, future analyses should identify higher risk areas within the Strait, while actions to mitigate anthropogenic disturbances and to increase awareness of maritime stake holders as well as the general public should be implemented as soon as possible.

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