

Population identity and migration movements of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea and Strait of Gibraltar

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ABSTRACT

Seafloor recorders were deployed in the western Mediterranean Sea, Strait of Gibraltar and in adjacent Atlantic waters during 2006-2009 to further contribute to knowledge regarding fin whale (*Balaenoptera physalus*) movement patterns and population structure within and outside of the Mediterranean basin. Analysis of 24,280 recording hours revealed typical long, patterned sequences of 20-Hz pulses, back beats, 135-140 Hz notes and downsweeps. Acoustic parameters (inter pulse interval, pulse duration, bandwidth, centre and peak frequency) were compared between signals from the Mediterranean Sea and northeast North Atlantic Ocean (NENA) to compare and characterize fin whale sounds from the Mediterranean population. Detection results suggest that an important number of Mediterranean fin whales aggregating in the northwestern Mediterranean basin during summer migrate through French and Spanish waters towards Southern Mediterranean regions, but do not migrate into the Atlantic Ocean. Fin whale calls attributable to the NENA population, probably East or West Icelandic, were detected off northern Morocco, crossing the Strait of Gibraltar and wintering in the southwestern Mediterranean basin (Alboran Sea). These results suggest that the NENA fin whale wintering grounds extend into the southwest Mediterranean basin, and spatial and temporal overlap may exist between this population and the Mediterranean fin whale population.

INTRODUCTION

The fin whale (*Balaenoptera physalus* L. 1758) is the only commonly observed mysticete in the Mediterranean Sea. Its presence has been documented since ancient times (Notarbartolo di Sciarra *et al.* 2003) but because of its pelagic distribution, this species is among the least known of all cetaceans in the Mediterranean Sea.

The degree of protection of the fin whale is important. It has recently been declared as an endangered species by the IUCN and Mediterranean fin whales are of high priority for the ACCOBAMS to better understand their population structure in order to assess their conservation status.

No population estimates exist for the entire Mediterranean region. However, line-transect surveys yielded estimates of 3,583 fin whales (S.E. 967, 95% C.I. 2.130-6.027) over a large portion of the western Mediterranean in 1991 (Forcada *et al.* 1996), and 901 (S.E. 196, 95% C.I. 591-1.374) in the Corsican-Ligurian-Provençal basin in 1992 (Forcada *et al.* 1995). Based on the information available, there are fewer than 10,000 mature individuals and they are subject to ongoing threats that may be causing a decline, but population trends are still unknown (Reeves and Notarbartolo di Sciarra 2006).

Mediterranean fin whales are currently defined as a distinct subpopulation from the North Atlantic locales, perhaps extending out to southern Portugal (IWC, 1992, 2007 & 2009). Genetic analyses indicates differences between the Mediterranean population, which is thought to be resident, and fin whales in North Atlantic coastal waters of Canada, Greenland, Iceland and Spain, based on mitochondrial DNA but no differences have been observed on nuclear DNA (Bérubé *et al.*, 1998), suggesting a model of isolation by distance. Further genetic analyses (Palsbøll *et al.*, 2004) better supported a male mediated low recurrent gene flow between Mediterranean

and northeast North Atlantic populations. Few other population marker data is available for a better understanding of the possible isolation and current distribution limits of Mediterranean fin whales. Results from satellite tagged fin whales and stable isotope analysis from baleen plates suggest that a small proportion of Mediterranean fin whales show seasonal migrations to the North Atlantic Ocean through the Strait of Gibraltar to feed (Guinet *et al.*, 2005). However, visual observations of fin whales in the Strait of Gibraltar and adjacent waters show different seasonal movement trends than the general pattern described in the western Mediterranean basin (Raga and Pantoja, 2004; Salazar-Sierra *et al.*, 2004). Therefore, the hypothesized movement of Mediterranean whales visiting the North Atlantic is not fully supported. To date, the distribution limits and the relationship between NE North Atlantic and Mediterranean fin whales are still puzzling and the identity of observed whales crossing the Strait of Gibraltar has still to be determined.

Multidisciplinary approaches to assess the population structure of mysticetes including both traditional and alternative population markers are improving our current knowledge (Donovan, 1991; Mellinger and Barlow, 2003; Clapham *et al.*, 2008). Alternative population markers are becoming more popular and acoustic methods are among those most commonly cited as worthy of further investigation (Mellinger and Barlow, 2003; McDonald *et al.*, 2006). The growing body of evidence indicating regional variations in vocalizations in a number of terrestrial and marine species, including several marine mammal species (see McDonald *et al.*, 2006) already allowed the description of populations over a broad geographical scale for the fin whale (e.g. Hatch and Clark 2004), the blue whale (e.g. McDonald *et al.*, 2006) and the humpback whale (e.g. Cerccio *et al.*, 2001). More particularly, in species such as fin whales where genetic assessment of population structure is hindered by logistic difficulties in collecting sufficiently large sample sizes of tissue, geographic variations in songs may offer a good alternative, provided they track meaningful biological units from a management point of view (Delarue *et al.*, 2009).

Several acoustic parameters of fin whale song have proven to be useful to identify their population. In particular, time intervals between pulses and pulse bandwidth allowed to explain up to 80 % of the song variability between populations in the North Atlantic Ocean (e.g. Hatch and Clark, 2004).

Acoustic methods have been already proposed as a potential tool for cetacean conservation in the Mediterranean Sea (e.g. Nortarbartolo di Sciarra and Gordon, 1997). However, little effort, if any, has been made in this direction so far. This study aims to the acoustic identification of fin whale populations present in the western Mediterranean Sea and Strait of Gibraltar in order to improve our knowledge of the current population structure in this significantly small basin. Results presented here will allow better conservation management actions to reduce the already important human pressure on this highly protected whale species.

METHODS

Two types of archival bottom-mounted audio recorders were used in this study. Marine Autonomous Recording Units (Clark *et al.*, 2002) for deployments made in 2006-2007 and Ecologic Acoustic Recorders (Lammers *et al.*, 2008) for deployments made in 2007-2009. Recorders were deployed in nine different areas (figure 1). Six deployment areas in the western Mediterranean Sea: Liguian Sea, off Cape Begur, off Menorca, Columbretes Marine Reserve, Ibiza Channel and Alboran basin. Two deployment areas in the Strait of Gibraltar: off Algeciras bay and off Cape Espartel, and one deployment area in the northeast North Atlantic Ocean, in Azores archipelago. Sample size comprised 12 deployments of 3,3 months on average duration, for a period of 2 years and 5 months from August 2006 to January 2009. Deployment depths varied between 100 to 1100 m. Sound recording was set continuous for the MARU and on a 33% duty cycle (5 minutes every 10 minutes) for the EAR. Sample rate was 2000 Hz for all units and all deployments.

Sound recordings were analyzed using the Matlab based code Extensible Bioacoustic Tool (XBAT) release 5 (<http://www.xbat.org>). An automated detector was built using the XBAT template detector tool to search for 20-Hz pulses and reject other sound sources in this frequency band to reduce false detections in each of the data sets. Other fin whale signals, like back-beats or downsweeps were discarded for the analysis. All detections were manually validated and two different logs were created, one log with highest signal to noise ratio 20-Hz pulses to obtain acoustic parameter measurements within each pulse and another log with 20-Hz pulses from sequences that could be unambiguously attributed to a single singer to measure the interval time between pulses. Measurements were made using the in house code Energy Measurement Tool for XBAT. Based on results from Hatch and Clark (2004), acoustic parameters within pulses selected for this study were central frequency, peak energy frequency, pulse bandwidth and pulse duration. In order to obtain time intervals between pulses, central time of each pulse was also selected from the energy measurement tool output, and pulse intervals were obtained by subtracting each central time from consecutive pulses. All acoustic measurements of each song were grouped

together because of the risk of non-independence of data. Here we apply the definition of song by Watkins *et al.* (1987), where different songs are separated by silent periods longer than 2 hours. All acoustic measurements grouped by songs were explored using a hierarchical regression analysis (Bryk and Raudenbush 1987, 1992; Goldstein *et al.* 1998; Snijders and Bosker 1999). This analysis allows variance in outcome variables to be analyzed at multiple hierarchical levels, as opposed to a single level allowed in simple linear and multiple linear regression analyses. Thus, this method is more appropriate for use with nested data, such as acoustic measurements made in 20-Hz pulses organized in sequences within different songs. Sources of variance are hierarchically organized in different levels. Our dataset includes a first level corresponding to 20-Hz pulses and a second level corresponding to songs. The covariable study area is included in the second level to assess its effect in the variability of the acoustic parameters between songs. Differences and similarities in the acoustic parameters of songs between study areas were further explored by multiple comparisons using the Bonferroni correction. Finally, acoustic measurements were divided in two groups by oceanic influence: Mediterranean and North Atlantic and compared using a one way analysis of variance (ANOVA) to explore potential differences and similarities in acoustic parameters between both basins.

RESULTS

A total of 29,822 hours of recording were analyzed detecting 103,664 fin whale 20 Hz pulses (table 1). Other detected fin whale signals included back-beats, downsweeps and 135-140 Hz upsweeps (figure 2). Recorders deployed in Cape Begur were lost and off Menorca failed to record data due to malfunctioning.

The obtained sample size for Ibiza channel and Alboran basin deployments in summer of 2007 were too small to be included in the statistical analysis. Therefore, these data sets were omitted for the hierarchical regression analysis.

The null model analysis allowed exploring the variability of acoustic parameters within or between songs. Statistically significant differences were observed between but also within songs. The variance of acoustic parameters between songs ranged between 43 to 79 % (table 2). When the study area was included in the second level as a covariate, a statistically significant effect was detected in all the acoustic parameters (table 3). Pseudo-R² values (Snijders and Bosker, 1999) were calculated for each acoustic parameter in order to assess the proportion of variance explained by study area effect. The variance of acoustic parameters of songs between study areas ranged between 22 to 96 % (table 4). Results from the area multiple comparison using Bonferroni correction (table 5) showed interesting relationships for pulse interval and pulse bandwidth: pulse interval showed no statistical differences between songs recorded in the Azores archipelago, Strait of Gibraltar and Alboran Sea, but differed from those recorded in Columbretes archipelago and Provenzal basin. Pulse bandwidth from songs recorded in Columbretes archipelago and Provenzal basin areas did not differ, however did so for pulse interval. These two acoustic parameters were of highest pseudo-R² values. All other measured acoustic parameters did not show any other clear relationships between study areas.

Pulse interval differences and similarities between study areas denote two clear patterns in these data sets. Fin whale songs recorded in areas of strictly Mediterranean influence (Provenzal basin and Columbretes archipelago) included pulse intervals of almost 15 seconds while songs recorded in study areas of North Atlantic influence (Alboran basin and Strait of Gibraltar) or strictly North Atlantic (Azores archipelago) included pulse intervals of 12-13 seconds (figure 3).

Based on the identified pattern for the pulse interval in fin whale songs, data sets from all other acoustic parameters were grouped by oceanic influence and analyzed with one way ANOVA. Pulse bandwidth and pulse duration results further evidenced significant differences between both groups, although differences within groups were also statistically significant (table 6 and figure 4).

Data sets from Ibiza channel area and Alboran basin in 2007 were too small to be included in the hierarchical regression analysis but 20 Hz pulse intervals from both data sets and pulse bandwidth from Ibiza channel were obtained from a selection of pulses with best signal-to-noise ratio (table 7). The values of these acoustic parameters for both study areas matched those of the North Atlantic group.

DISCUSSION

Results from the acoustic analysis of male fin whale songs detected in all study areas from the Mediterranean Sea, Strait of Gibraltar and Azores archipelago allowed the identification of two clearly differentiated populations. However, the distribution of these did not correspond with the limits of the Atlantic and

Mediterranean basins, which is a common assumption in the current literature (e.g. IWC, 1992, 2007 & 2009; Cañadas *et al.*, 2005).

The presence of songs in the Columbretes archipelago area in fall and their absence in the Ibiza Channel in summer is in accordance with the well documented seasonal concentration of fin whales in their primary feeding ground in Liguria during summer. The pulse interval obtained in these areas is close to 15 seconds, matching the interval described by Clark *et al.* (2002) in Liguria, therefore confirming that whales detected in these areas belong to the same Mediterranean population.

The presence of fin whales in the Alboran basin and Strait of Gibraltar in fall and winter could be related to the already suggested southward migration of Mediterranean whales from their primary feeding ground in Liguria to southern areas to spend the winter (Marini *et al.*, 1996). These whales could continue their migration movement, crossing the Strait to enter the North Atlantic Ocean, as it has been suggested by Guinet *et al.* (2005) and recently supported by other authors (e.g. Cotté *et al.*, 2009; Gauffier *et al.*, 2009). However, fin whale songs recorded during fall and winter in the Alboran basin and Strait of Gibraltar reveal that their pulse intervals of 12-13 seconds as well as their pulse bandwidths of 6,5 Hz are different from values obtained in strictly Mediterranean areas. Their acoustic features match those obtained in songs recorded in northeast North Atlantic areas such as cape Espartel and Azores archipelago as well as results from other studies from the North Atlantic Ocean (e.g. Hatch and Clark, 2004; Delarue *et al.*, 2009). Furthermore, the area multiple comparison analysis grouped songs from Alboran basin and Strait of Gibraltar with those from Azores and cape Espartel instead of songs from the western Mediterranean Sea. Therefore, our results strongly suggest that the whales detected in Alboran basin and Strait of Gibraltar in fall and winter correspond to a northeast North Atlantic population.

Fin whale songs with Mediterranean acoustic features were never detected in the Alboran basin or the Strait of Gibraltar areas, suggesting that the fall-winter distribution of this population does not include these regions of the basin. Since Mediterranean fin whales are known to be primarily concentrated in northwestern areas in late spring and summer (Notarbartolo di Sciara *et al.*, 2003), it is improbable that the distribution range of this population includes the Alboran basin and Strait of Gibraltar during this period either.

The presence of 135-140 Hz upsweeps as well as some songs composed exclusively of back-beats suggest that the whales detected in the Azores archipelago, Cape Espartel, Strait of Gibraltar and Alboran basin correspond to a northeast North Atlantic population, because these particular signals of the fin whale repertoire have been exclusively reported in these populations (Hatch and Clark, 2004) and more precisely in the north Atlantic Ocean above 55° N (Clark and Gagnon, 2004), (see fig. 5).

Results from this study indicate that fin whales from the northeast North Atlantic population cross the Strait of Gibraltar and enter the Mediterranean Sea, remaining in these areas at least during winter. Results also suggest that Mediterranean whales do not include these areas within their distribution range. Therefore, distribution limits and possible overlap range between these two populations must occur within the Mediterranean basin, east of the Alboran Sea.

Results from the hierarchical regression analysis shows that 96 % of the pulse interval variation is explained by differences between study areas even if there is considerable variation within songs of the same study area. From a biostatistical point of view, one single factor that explains this high percentage of variance is extremely rare (Dytham, 1999), conveying strong biological significance to the specific time intervals between pulses used by fin whales when singing. Since fin whale pulses can travel extreme distances in the open ocean (Payne and Webb, 1971) and propagation loss degrades signal structures (Urlick, 1983), it could be possible that selective pressure has favoured fin whales to codify information of biological significance for long range communication in acoustic features that are robust against propagation loss, such as the time interval between pulses in a sequence. This communication characteristic is robust against environmental distortion (Morton, 1975), and has already been suggested to be used by other cetacean, the sperm whale, clicking in rhythmic patterns that allow group differentiation (André and Kamminga, 2000).

The population differentiation suggested by the pulse interval analysis was not so apparent for all other acoustic features explored in the hierarchical regression analysis. In fact, results from all other acoustic features indicated considerable variance within areas. Between 43 to 58 % of the variability of acoustic features is explained by song differences in the null model. Only pulse bandwidth differences between Mediterranean and North Atlantic songs show statistically significant results. In fact, pulse interval and pulse bandwidth have also been described as the two more effective parameters for fin whale population identity within the North Atlantic Ocean (Hatch and Clark, 2004).

Songs recorded in Ibiza Channel and Alborán basin in summer of 2007, although too short to be included in the general analysis, show interesting features. Based in the pulse interval and bandwidth values, songs detected in these two areas should be attributed to North Atlantic fin whales. These results support the absence of

Mediterranean fin whales in these areas of the Mediterranean basin in summer, in agreement with the hypothesis proposed by Marini *et al.* (1996). These authors suggested that Mediterranean fin whales migrate seasonally from northern feeding grounds to southern breeding areas near the North African continental shelf. Also, summer presence of North Atlantic whales within the Mediterranean basin emphasize the importance of the western Mediterranean Sea in their distribution range: whales from this population enter the Mediterranean sea not only in winter but also in summer and their visit is not limited to just the Alboran Sea. This suggests that the possibilities of distribution overlap between Mediterranean and North Atlantic populations are higher than expected. These observations allow a different interpretation of data obtained by Guinet *et al.* (2005), Cotté *et al.* (2009) and Gauffier *et al.* (2009). These authors suggest that a small proportion of Mediterranean whales move seasonally towards the North Atlantic Ocean to feed. However, an interpretation that better fits with our acoustic results would be that the whales they observed or sampled were North Atlantic individuals seasonally visiting the Mediterranean basin and moving back to the Atlantic Ocean.

Observations of fin whale movements in the Strait of Gibraltar and nearby areas support the entrance of North Atlantic fin whales into the Mediterranean basin even if the authors do not suggest it (e.g. Raga and Pantoja, 2004; Salazar-Sierra *et al.*, 2004). They describe a general movement trend towards the Atlantic Ocean in spring-summer and towards the Mediterranean Sea during fall-winter. Our acoustic results showed that northeast North Atlantic fin whales entered the Mediterranean Sea in fall and winter and the absence of detections in summer suggest that they left the basin in spring.

Comparative genetic analyses between Mediterranean and North Atlantic populations show a high level of isolation based on mitochondrial DNA but not on nuclear DNA (Berubé *et al.*, 1998; Palsbøll *et al.*, 2004). The authors propose that this genetic scenario could be explained by a male mediated low recurrent gene flow between populations. This hypothesis is in accordance with the acoustic results obtained in this study, where songs from male northeast North Atlantic fin whales have been detected within the Mediterranean basin during breeding season.

Fin whales were intensively exploited during the past two centuries off the Strait of Gibraltar (reviewed in Aguilar and Borrel, 2007). This led some authors to suggest that the use of this habitat has been lost in the population, explaining the lack of fin whale sightings in the area (Clapham and Hatch, 2000; Clapham *et al.*, 2008). Our results show how northeast North Atlantic fin whale songs are abundant and continuously detected throughout the winter in the Strait of Gibraltar and Cape Espartel areas, contradicting this hypothesis.

The current description of different fin whale stocks defines one single subpopulation into the Mediterranean Sea (IWC, 1992, 2007 and 2009; Cañadas *et al.*, 2005). Our acoustic results strongly suggest that two different populations use the Mediterranean basin. This new interpretation has important conservation implications since it implies that the distribution range of Mediterranean fin whales is smaller than previously defined and that two populations are exploiting the same Mediterranean niche, competing for same resources. Human pressure can easily affect the ecological balance of this competition since the allostatic load of Mediterranean resident whales might be heavier. In fact, this effect is already occurring as shown by differences in chemical contaminant loads between North Atlantic and Mediterranean fin whale samples (Fossi *et al.*, 2006; Aguilar *et al.*, 2002).

Finally, our results are in accordance with several hypotheses that have been unresolved for decades. Richiardi (1874) proposed that fin whales were entering the Mediterranean Sea from the Atlantic Ocean. Jonsgård (1966) proposed that fin whales from West Scotland were feeding near the Strait of Gibraltar or even into the Mediterranean Sea. Duguy and Vallon (1976) proposed that some fin whales were resident but others were leaving the basin seasonally. Viale (1977 and 1985) proposed that whales from NW Scotland were entering the Mediterranean basin in winter to breed. It is surprising to see that even if several authors have suggested a seasonal entrance of North Atlantic fin whales into the Mediterranean basin, this hypothesis has barely been considered in the current literature regarding the population identity of Mediterranean fin whales.

CONCLUSIONS

This work further supports the validity of acoustic monitoring of Mediterranean fin whales to better understand their population identity. Two well defined acoustic patterns, based on pulse interval and pulse bandwidth, have been identified allowing the description of two different populations of fin whales within the Mediterranean basin, one being resident and another being a seasonal visitor from the northeast North Atlantic Ocean. This new proposed population structure match with the current genetic knowledge of Mediterranean fin whales as well as with the movement trends described in the Strait of Gibraltar and adjacent waters. Northeast North Atlantic fin whale wintering grounds extend into the southwest Mediterranean basin, and spatial and temporal overlap may

exist between this population and the Mediterranean fin whale population. The current distribution range of these stocks should be reviewed based in the results of this study.

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Table 1: Sample size for each study area.

Study area	Hours of audio recordi	% analyzed	# 20 Hz pulses
Provenzal basin	2133 h	15 %	927
Columbretes	4296 h	100 %	91.327
Ibiza Channel	2856 h	100 %	23
Alboran 2006	4271 h	100 %	2.202
Alboran 2007	3572 h	100 %	41
Gibraltar Strait	5718 h	100 %	4.137
Cape Espartel	2847 h	100 %	4.089
Azores archipelago	4129 h	22 %	911
Total	29.822 h		103.664

Table 2: Intraclass correlation coefficient (ICC) denoting the variance of acoustic parameters between songs obtained in the null model from multilevel analysis.

Acoustic parameters	Variance estimates (null model)		ICC
Pulse interval	$\hat{\sigma}_e^2$	0,27	0,79
	$\hat{\sigma}_u^2$	0,98	
Pulse duration	$\hat{\sigma}_e^2$	0,02	0,48
	$\hat{\sigma}_u^2$	0,02	
Pulse bandwidth	$\hat{\sigma}_e^2$	0,61	0,58
	$\hat{\sigma}_u^2$	0,85	
Center frequency	$\hat{\sigma}_e^2$	0,56	0,43
	$\hat{\sigma}_u^2$	0,42	
Peak frequency	$\hat{\sigma}_e^2$	0,53	0,53
	$\hat{\sigma}_u^2$	0,61	

Table 3: Multilevel analysis fixed (study area) and random (song) effect estimates and significance level for all the acoustic parameters measured in fin whale songs.

Fixed effects					
Variable	Study area	γ_{00}	Std. Error	D.F.	Level sig.
Pulse interval	C. Provenzal	15,07	0,04	195,553	p<0,01
	I. Columbrete	14,81	0,04	155,02	p<0,01
	I. Alborán	12,89	0,04	148,76	p<0,01
	Estrecho de G.	13,05	0,04	172,08	p<0,01
	I. Azores	12,92	0,04	177,555	p<0,01
Pulse duration	C. Provenzal	0,88	0,03	159,84	p<0,01
	I. Columbrete	1	0,04	163,7	p=0,028
	I. Alborán	0,97	0,03	173,66	p<0,01
	Estrecho de G.	0,98	0,03	173,47	p<0,01
	I. Azores	1,08	0,02	166,7	p<0,01
Center frequency	C. Provenzal	-0,87	0,11	152,24	p<0,01
	I. Columbrete	-1,07	0,13	157,27	p<0,01
	I. Alborán	-1,14	0,1	172,42	p<0,01
	Estrecho de G.	-1,24	0,1	170,27	p<0,01
	I. Azores	22,61	0,07	162,19	p<0,01
Pulse bandwidth	C. Provenzal	-2,01	0,12	158,25	p<0,01
	I. Columbrete	-1,8	0,15	163,3	p<0,01
	I. Alborán	-0,28	0,12	177,33	p=0,018
	Estrecho de G.	-1,05	0,11	175,75	p<0,01
	I. Azores	6,9	0,08	167,64	p<0,01
Peak frequency	C. Provenzal	-0,83	0,12	130,23	p<0,01
	I. Columbrete	-1,12	0,14	134,37	p<0,01
	I. Alborán	-1,07	0,11	145,72	p<0,01
	Estrecho de G.	-1,65	0,11	144,51	p<0,01
	I. Azores	22,52	0,08	137,85	p<0,01
Random effects					
Variable	Parameter	Variance	Std, Error	Wald Z	Level sig,
Pulse interval	u_{0j}	0,04	0,01	6,24	p<0,01
	e_{ij}	0,27	0,01	44,20	p<0,01

Pulse duration	u_{0j}	0,02	0,00	7,99	p<0,01
	e_{ij}	0,02	0,00	47,64	p<0,01
Pulse bandwidth	u_{0j}	0,24	0,03	7,46	p<0,01
	e_{ij}	0,61	0,01	47,71	p<0,01
Center frequency	u_{0j}	0,18	0,02	7,14	p<0,01
	e_{ij}	0,56	0,01	47,70	p<0,01
Peak frequency	u_{0j}	0,22	0,03	6,80	p<0,01
	e_{ij}	0,53	0,01	47,49	p<0,01

Table 4: pseudo- R^2 estimates of each acoustic parameter measured in fin whale songs, based on results from null and fixed models of multilevel analysis.

Variable	Parameter	Variance	pseudo- R^2
Pulse interval	$\hat{\sigma}_u^2$ null model	0,98	0,96
	$\hat{\sigma}_u^2$ fixed model	0,04	
Pulse duration	$\hat{\sigma}_u^2$ null model	0,02	0,22
	$\hat{\sigma}_u^2$ fixed model	0,02	
Pulse bandwidth	$\hat{\sigma}_u^2$ null model	0,85	0,72
	$\hat{\sigma}_u^2$ fixed model	0,24	
Center frequency	$\hat{\sigma}_u^2$ null model	0,42	0,57
	$\hat{\sigma}_u^2$ fixed model	0,18	
Peak frequency	$\hat{\sigma}_u^2$ null model	0,61	0,65
	$\hat{\sigma}_u^2$ fixed model	0,22	

Table 5: multiple comparisons using Bonferroni correction for pulse interval and pulse bandwidth values from songs recorded in all study areas.

Pulse interval						Pulse bandwidth					
Area 1	Area 2	Mean diff.	Std. Error	D.F.	Level sig.	Area 1	Area 2	Mean diff.	Std. Error	D.F.	Level sig.
GIB	PROV	-2,02	0,06	183,03	p<0,01	GIB	PROV	0,96	0,12	164,52	p<0,01
	COL	-1,77	0,06	162,74	p<0,01		COL	0,76	0,15	167,63	p<0,01
	ALB	-0,16	0,06	161,08	0,04		ALB	-0,77	0,12	186,10	p<0,01
	AZO	-0,13	0,05	174,41	0,15		AZO	-1,05	0,11	175,75	p<0,01
PROV	COL	0,26	0,06	172,01	p<0,01	PROV	COL	-0,21	0,16	158,04	1
	ALB	-2,18	0,05	171,90	p<0,01		ALB	-1,73	0,13	166,23	p<0,01
	AZO	-2,16	0,05	187,29	p<0,01		AZO	-2,01	0,12	158,25	p<0,01
COL	ALB	-1,92	0,06	152,36	p<0,01	COL	ALB	-1,53	0,15	168,71	p<0,01
	AZO	-1,90	0,06	163,58	p<0,01		AZO	-1,80	0,15	163,30	p<0,01
ALB	AZO	-0,03	0,05	161,82	1	ALB	AZO	-0,28	0,12	177,33	0,18

Table 6: One-way ANOVA results for all acoustic parameters measured in fin whale songs clustered in two groups by oceanic influence: Mediterranean and North Atlantic.

Acoustic parameter		SS	D.F.	MS	F	Level sig.
Pulse duration	Intercept	4930,88	1	4930,88	9239,95	< 0,01
	ATL vs MED	89,84	1	89,84	168,36	< 0,01
	Error	103,53	194	0,53		
Pulse bandwidth	Intercept	4930,88	1	4930,88	9239,95	< 0,01
	ATL vs MED	89,84	1	89,84	168,36	< 0,01
	Error	103,53	194	0,53		
Centre frequency	Intercept	71372,65	1	71372,65	129151,24	< 0,01
	ATL vs MED	0,78	1	0,78	1,41	0,24
	Error	107,21	194	0,55		
Peak frequency	Intercept	70364,30	1	70364,30	84918,94	< 0,01
	ATL vs MED	0,01	1	0,01	0,01	0,91
	Error	160,75	194	0,83		

Table 7: Mean values and standard error of acoustic parameters measured in 20 Hz pulses from songs recorded in the Ibiza channel and Alboran Sea during summer 2007.

Study area	n	Pulse interval (S.E.) sec	Pulse bandwidth (S.E.) Hz
Ibiza Channel	11	11,73 (0,46)	6,41 (0,24)
Alboran 07	13	11,99 (0,55)	-

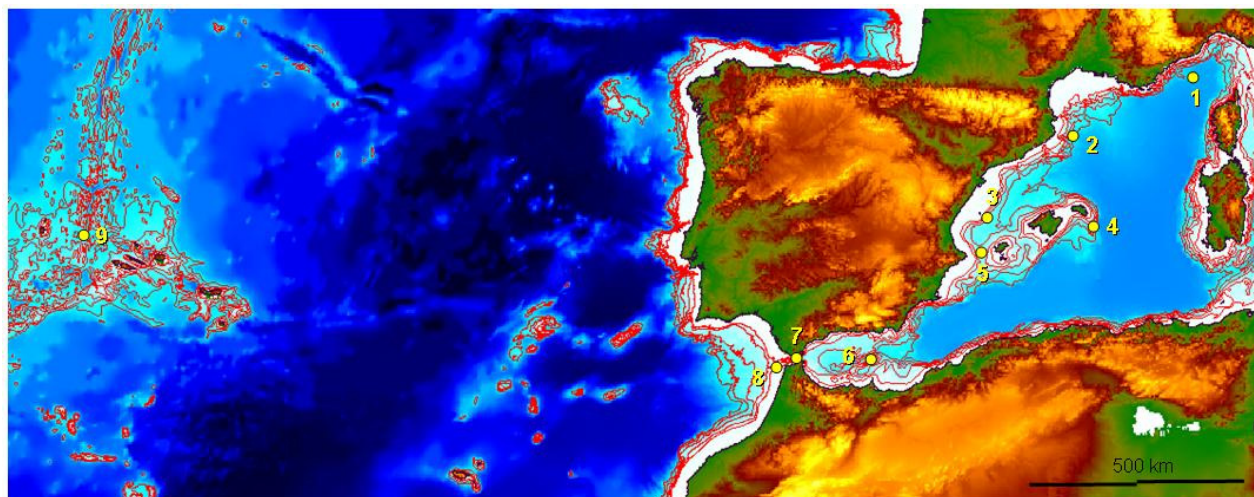


Figure 1: Deployment locations of archival bottom-mounted audio recorders. 1-Liguian Sea, 2-off Cape Begur, 3-Columbres Marine Reserve, 4-off Menorca, 5-Ibiza Channel, 6-Alboran Sea, 7-off Algeciras bay, 8- off Cape Espartel and 9-Azores archipelago.

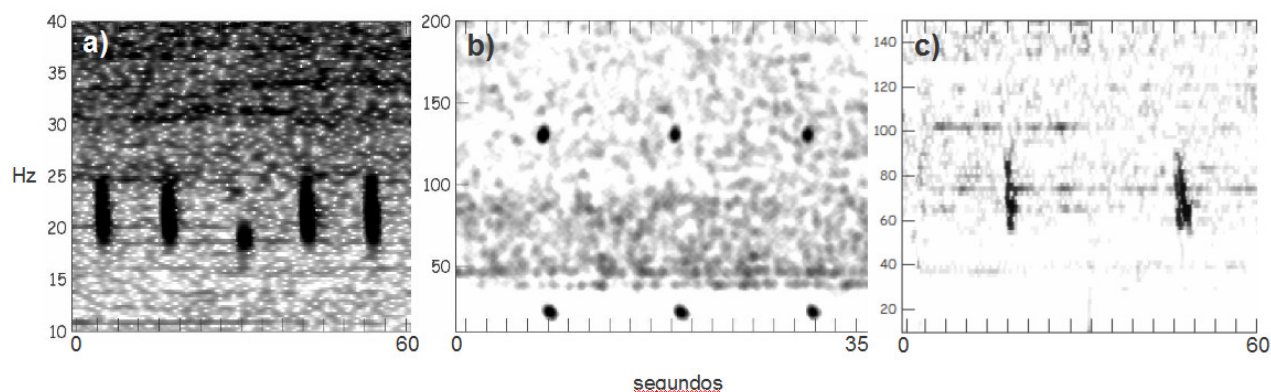


Figure 2: Spectrograms of detected a) 20 Hz pulses and back-beats, b) 20 Hz pulses and 135-140 Hz upsweeps and c) downsweeps. (Note: FFT size and x-y scales are different for each spectrogram).

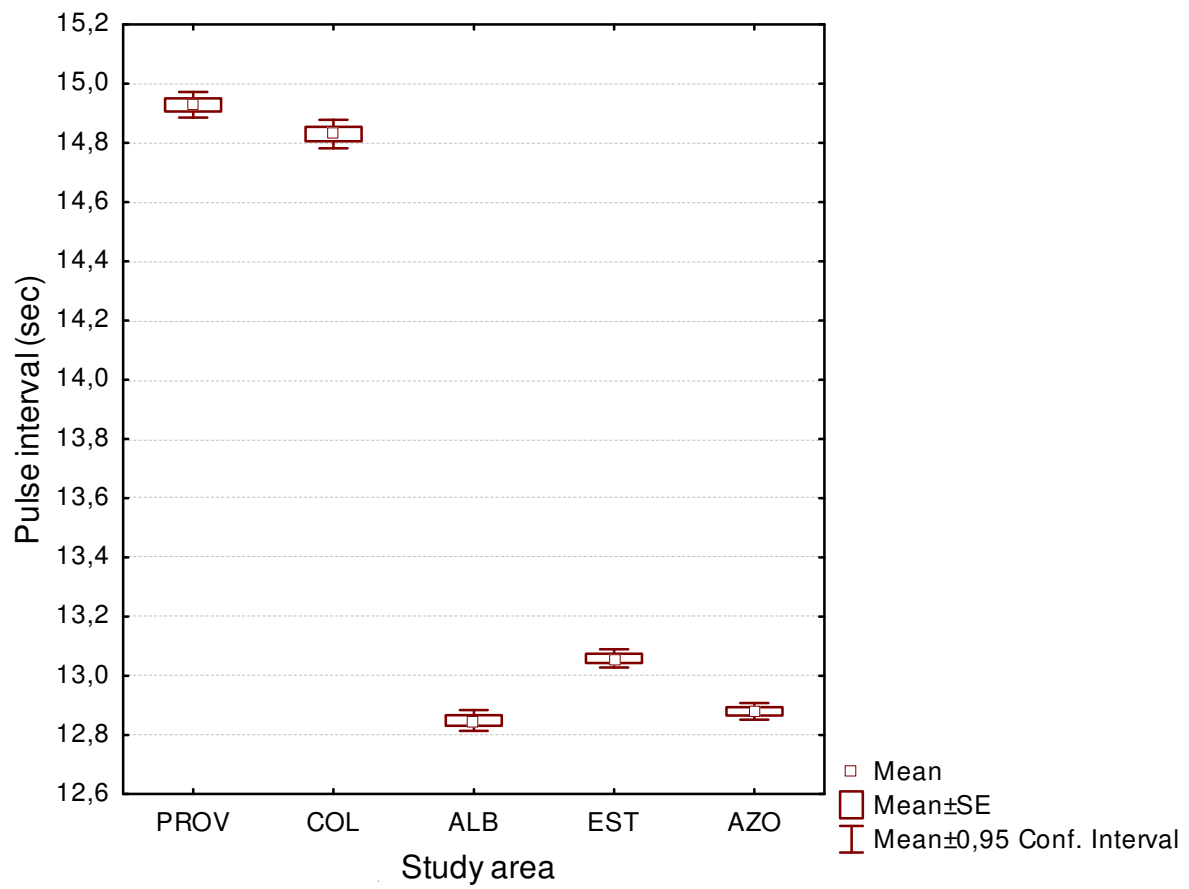


Figure 3: Mean, standard error and 0.95 confidence intervals of pulse interval values (in seconds) from fin whale songs recorded in Provençal basin (PROV), Columbretes archipelago (COL), Alboran basin (ALB), Strait of Gibraltar (EST) and Azores archipelago (AZO).

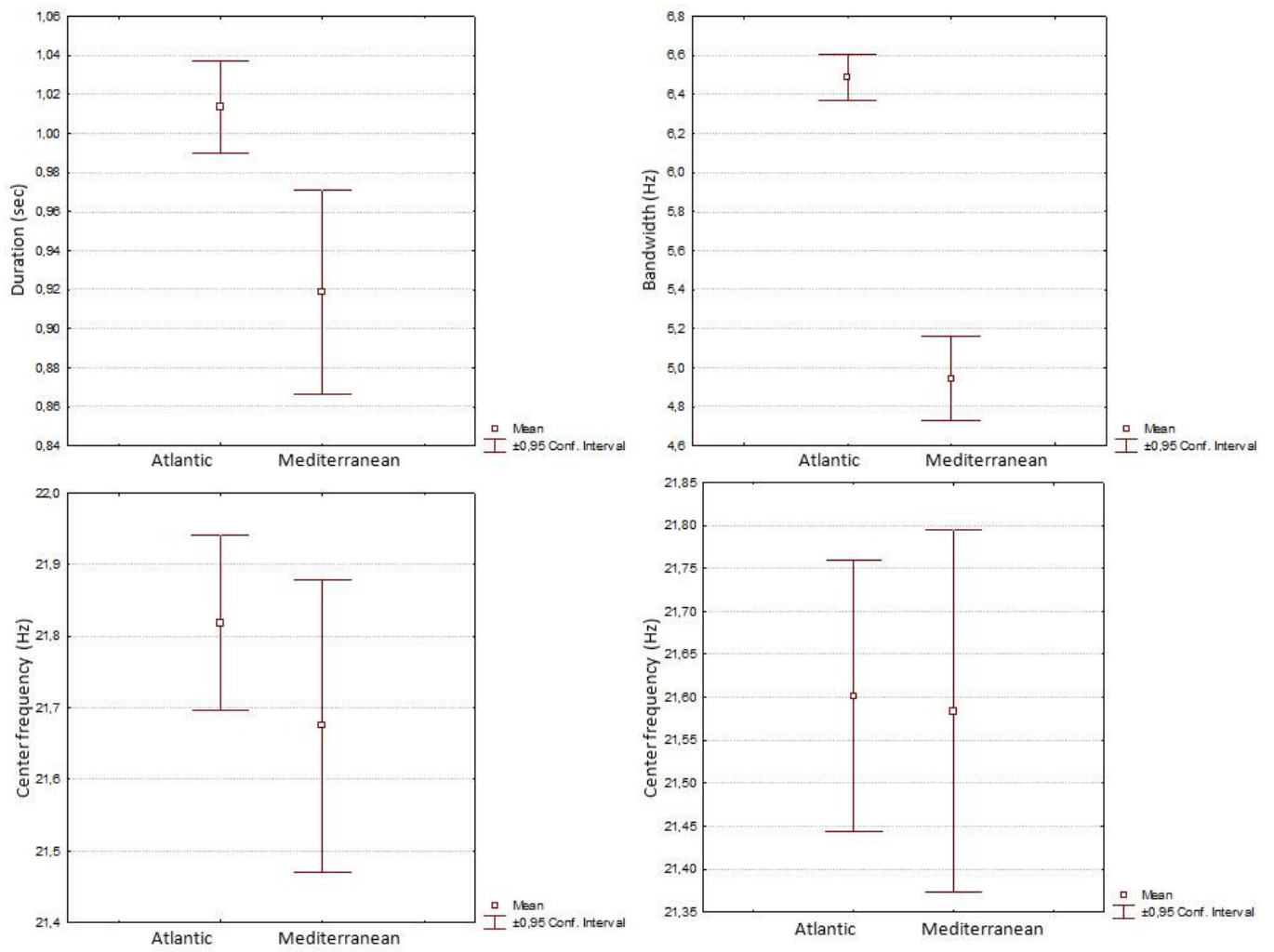


Figure 4: Mean values and 0.95 confidence intervals of all acoustic parameters measured in fin whale songs clustered in two groups by oceanic influence: Mediterranean and North Atlantic.

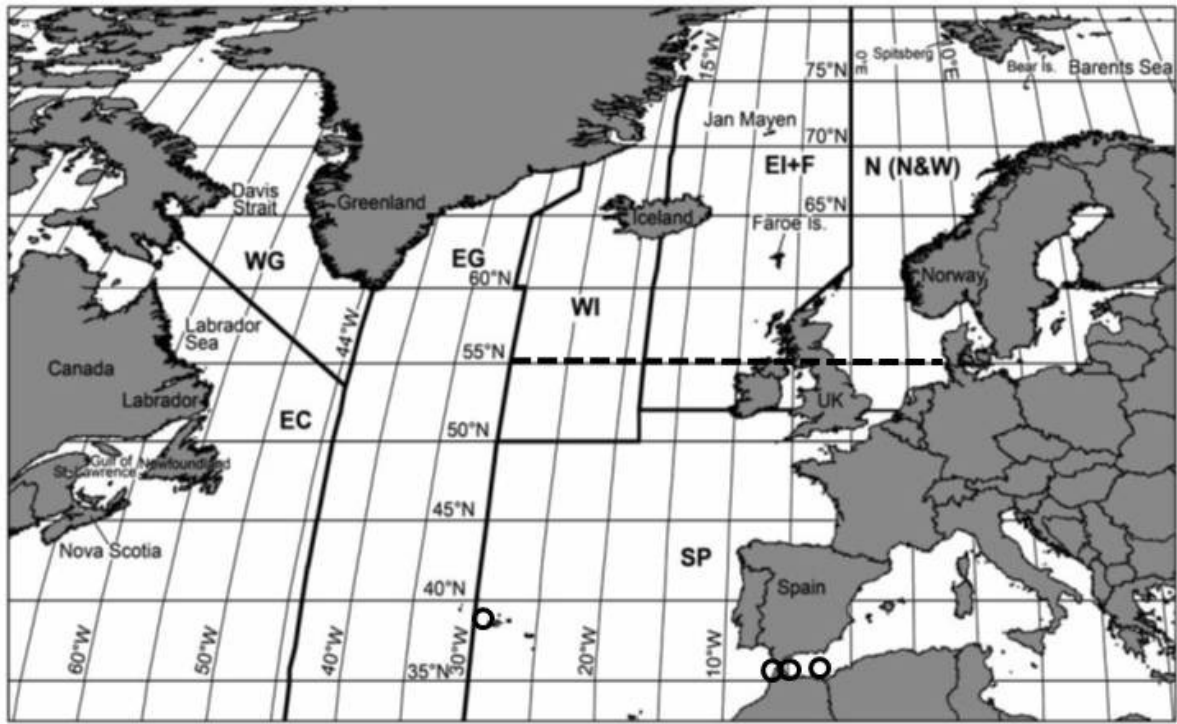


Figure 5: North Atlantic fin whale stock boundaries as defined by IWC (2008). Dashed line indicates parallel 55°N and circles indicate the locations where 135-140 Hz upsweeps were recorded, south of parallel 55°N.