Habitat preferences of Ziphiids: an analysis of physiographic variables associated to beaked whales sightings in French temperate and tropical waters

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Abstract

Beaked whales are among the most poorly known cetacean worldwide, including basic information related to their distribution and habitat characteristics. Here, we describe the distribution, occurrence (or encounter rates) and habitat in relation to physiography of beaked whales in French temperate (Bay of Biscay, NE Atlantic) and tropical waters (French Guyana, French Antilles, French Polynesia and SW Indian Ocean). Information was based on dedicated aerial surveys conducted in tropical waters and from multiple sources for the Bay of Biscay region, including ship-based, aerial-based dedicated surveys and opportunistic sightings. Cuvier's beaked whale was the most frequently sighted species in all regions. We reported sightings of Blainville's beaked whales in tropical regions only. Northern bottlenose whales were reported in Bay of Biscay. Longman's beaked whales were detected on three occasions in the SW Indian Ocean, especially in NW and NE Madagascar. Our study also highlights some spatial variations of beaked whale occurrence, especially in tropical waters. In the French Antilles and off French Guiana, beaked whale occurrence was relatively low. However, in the Mozambique Channel, the occurrence of beaked whales was the highest. In French Polynesia, encounter rates were highly variable, and the Marquesas had the highest beaked whale occurrence. An important outcome of our study is the relatively similar overall encounter rates between tropical regions (French Antilles, French Guiana, south-west Indian Ocean and French Polynesia) but more variable within areas. Our preliminary analysis highlighted some habitat differences between species within regions. In particular, *Indopacetus pacificus* seemed to be concentrated over higher slopes than the other species in south west Indian Ocean. In French Polynesia *Mesoplodon sp.* appeared to occur closer the 200m isobaths than *Ziphius cavirostris*. In the Bay of Biscay *Hyperrodon ampullatus* were sighted at lower depths than the other ziphiids.

INTRODUCTION

Since the 2000s, there is a growing interest in beaked whale studies at the global scale (e.g., Journal of Cetacean Research and Management, Vol. 7, Issue 3, Donovan, 2006). One of the main reasons is the increasing evidence of their vulnerability to anthropogenic sound as shown by temporal and spatial association of atypical mass strandings of some beaked whale

species with certain naval exercises and use of low-frequency active sonar (e.g. Frantzis, 1998, Jepson *et al.*, 2003).

Beaked whales (family Ziphiidae) consist of 21 recognized species, which represents almost a quarter of worldwide cetacean diversity. Conversely, they remain poorly understood species that have essentially been studied from few stranded specimens (Reyes *et al.*, 1991; Dalebout *et al.*, 2002; Dalebout *et al.*, 2002). However, as they tend to occur in deep-water habitats (Mead 2002) and frequently associate with continental slopes (e.g. Waring et al., 2001), i.e. far from most shores. Consequently, they may not be accurately represented in strandings records.

For conservation and management purposes, baseline information on beaked whales is critically needed. It includes quantitative analysis of spatial and temporal distribution, abundance (or at least relative abundance) and habitat preferences. Canadas *et al.* (2002) examined the distribution of ziphiids with respect to depth and slope in the Mediterranean Sea using GLMs and found that depth was a better predictor than slope. MacLeod (2005) identified a general beaked whale niche in the North Atlantic frontier, characterized by deep waters and high slope seabeds. Hooker *et al.* (2002) found that northern bottlenose whale *Hyperoodon ampullatus* had a discrete distribution within a submarine canyon, the Gully, off eastern Canada, associated with water depth between 500 and 1500 m and relatively steep topography. Therefore physiographic variables appear to be relevant parameters in ziphiid distribution. However, most studies focused on particular beaked whales species in certain regions.

The vast extent of the French Economic Exclusive Zone (EEZ, Figure 1), the second largest in the world, amounting to 11 million of km² and distributed in all three oceans over temperate and tropical regions, covering shelf, slope and abyssal plain habitats, gives an opportunity to study beaked whales distribution at a large geographical scale.

Since 2008, REMMOA surveys (*REcensement des Mammifères marins et autre mégafaune pélagique par Observation Aérienne* - Census of marine mammals and other pelagic megafauna by aerial survey), were conducted in French tropical and neighboring waters (in total 4 tropical regions shown as black boxes on Figure 1). The addition of beaked whales sightings from different surveys conducted in the Bay of Biscay (the temperate region, see black box on Figure 1), enabled us to identify key regions in French EEZ in terms of diversity and density. In addition, beaked whale sightings (in total 4 identified genera) were examined with respect to five physiographic variables: distance from the nearest coast, distance from the 200m isobath, distance from the 2000m isobath, depth and slope. In this short preliminary paper, we compared ziphiids distribution within regions but also between regions to highlight presence or absence of geographical variation.
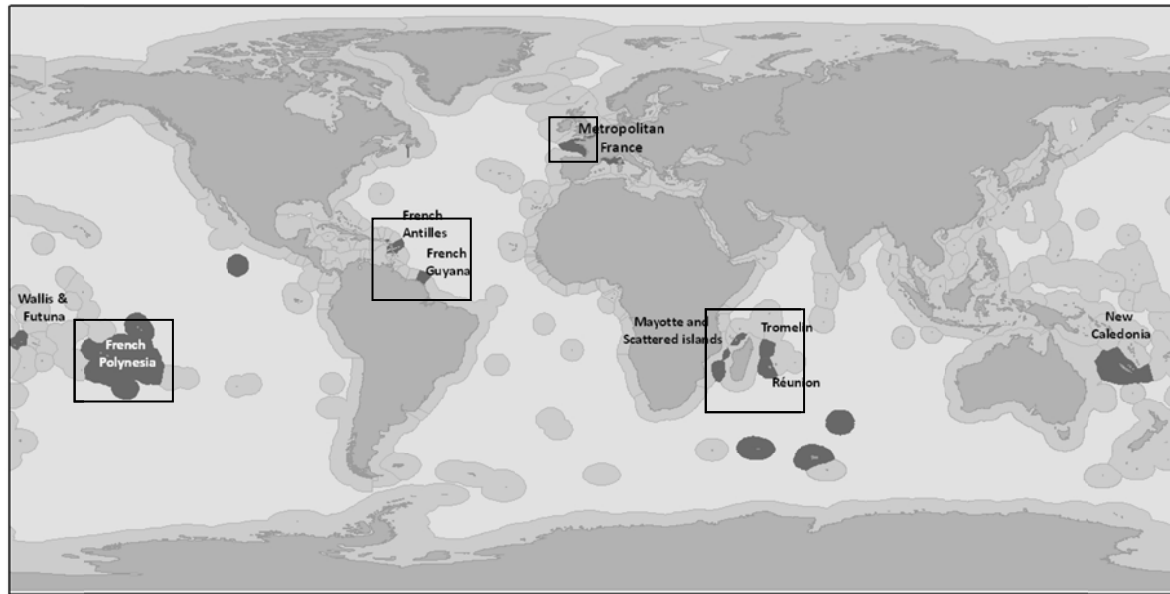
Figure 1: The French Economic Exclusive Zone (in dark grey) stretches across all three oceans approximately 50°N to 50°S. The black boxes show the different regions retained in this paper to study beaked whales distribution (four tropical regions: French Polynesia, French Antilles, French Guiana and south west Indian Ocean and one temperate region: the bay of Biscay).

MATERIAL AND METHODS
1-Origin of data

1-1-French temperate waters (Bay of Biscay)

Beaked whales sightings were extracted from dedicated aerial and ship based surveys conducted in the Bay of Biscay (Appendix 1) and various opportunistic sightings.

1-2-French tropical and neighboring waters

Beaked whales sightings were extracted from REMMOA surveys (*REcensement des Mammifères marins et autre mégafaune pélagique par Observation Aérienne* - Census of marine mammals and other pelagic megafauna by aerial survey) conducted in French tropical waters. The dedicated aerial survey methodology follows the general SCANS methodology (Hiby and Lovell, 1998) adapted to aircrafts. A zigzag track layout is used and transects are sampled at a target altitude of 180 m and ground speed of 90 nm.h^{-1} (167 km.h-1). Survey platforms are high-wing, double-engine aircrafts fitted with bubble windows (see Ridoux et al., 2010 SC/62/E14 for more details on the survey protocol). Presence and group size of marine mammals (and other pelagic megafauna) were collected as well as perpendicular distance from the transect line. Covariates collected on board included sea-state, turbidity, glare and cloud coverage.

Five regions were surveyed: French Caribbean, French Guiana, South West Indian Ocean and French Polynesia. South West Indian Ocean was divided in 6 areas: Comoros-Mayotte-Glorieuses-Madagascar (CMGM), Juan de Nova-Madagascar (JNM), Europa-Bassas de India-Madagascar (EBM), Tromelin-Madagascar (TM), La Reunion-Mauritius (RM) and Seychelles (SE). French Polynesia was divided in 6 areas: Society islands (SOC), Australes islands (AUS), Tuamotu North (TUN), Tuamotu South (TS), Gambier islands (GAM) and Marquesas (MAR).

In each survey three gross bathymetry strata (shelf, slope and abyssal plain) were sampled.

2-Effort and encounter rates

We did not compile effort data for Bay of Biscay as beaked whales sightings were extracted from several different surveys. Therefore encounter rates were not calculated for this region. Encounter rates were calculated for the four tropical regions, for which the survey methodology was standardized and effort was available as the number of kilometers flown on effort. Encounter rates were then calculated as the number of groups sighted (occurrence only) per 1000km of effort.

The ability to detect beaked whales, characterized by long dive times and short surface times, changes with sighting conditions (e.g. Barlow et al, 2006) (in particular with sea state, the most frequently used detection covariate in cetacean surveys). Therefore 5% of the furthest sightings were removed in all regions (Buckland et al., 2001). Truncation was made at a perpendicular distance of 700 m from both sides of the transect on the basis of the histogram of beaked whales sightings in south west Indian Ocean (Figure 2).
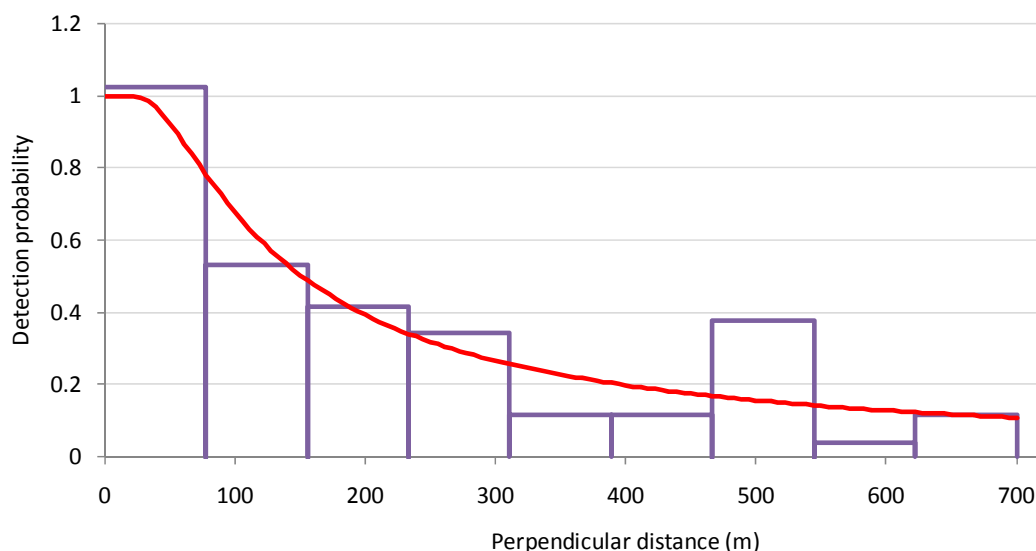

Figure 2: Histogram of beaked whales sightings in south west Indian Ocean, with 5% of the largest perpendicular distances truncated at 700m (n=81) and hazard rate model (AIC = 1024 ; ESW = 238m).

3-Analysis of associations with physiographic features

We explored habitat associations using *ArcView 10.0* (ESRI, 2010) by overlapping beaked whales sightings and physiographic features. Retained physiographic variables included distance from the nearest coast, distance from the 200m isobath (representing the top of the slope), distance from the 2000m isobath (representing the bottom of the slope), depth and slope.

Depth was derived from the GEBCO 08 grid one minute resolution (General Physiographic Chart of the Ocean ; http://www.gebco.net/). Then bathymetric contours (coastline, 200m isobath, and 2000 isobath) were isolated with *XToolsPro7.1.0* extension for ArcGIS (Data East 2010, available from http://www.xtoolspro.com/). When the sighting was located between the coast and the isobath (200m or 2000m) we affected a minus to the distance from the isobath, whereas when it was located beyond the isobaths we affected a plus to the distance from the isobath. Slope was compiled with *Spatial Analyst* (ESRI, 2010) and was expressed in percentage.

Descriptive statistics mean and standard errors where compiled for each region and each species or genera. Mann-Whitney non parametric tests were performed to compare the distribution of ziphiids with respect to physiographic variables (1) between species (or genera) within each region and (2) between region within each species (or genera). Mann-Whitney tests were not performed when sample sizes were lower than 5.

RESULTS

1- Effort and encounter rates

The REMMOA aerial surveys covered a total of 194,704 km (8,486 km in French Antilles, 7,775 km in French Guiana, 83,627 km in the south-west Indian Ocean and 94,814 km in French Polynesia; Appendix 2). In total beaked whales were sighted on 153 occasions in tropical regions, of which 53 sightings were *Ziphius cavirostris*, 42 sightings were *Mesoplodon densirostris* or unidentified *Mesoplodon*, 3 sightings were *Indopacetus pacificus* (exclusively in south-west Indian Ocean) and 55 sightings were unidentified beaked whales (Table 1). In the Bay of Biscay, beaked whales were sighted on 20 occasions (*Ziphius cavirostris*: n=7, *Hyperoodon ampullatus*: n=4, and unidentified ziphiids: n=9; Table 1).

Overall, the Cuvier's beaked whale was the most commonly sighted ziphiid, both in temperate and tropical waters.

In French Antilles, *Ziphius cavirostris* was the only identified ziphiid species. Beaked whales sightings were exclusively beyond the 2000m isobath and were more numerous around Martinique island (Figure 3A). In Guiana *Ziphius cavirostris* and *Mesoplodon sp* were detected and also appeared to be distributed beyond the 2000m isobath (Figure 3B). However the overall encounter rate was higher in Guiana than in French Caribbean (Figure 4A; Appendix 2).

In the south-west Indian Ocean diversity appeared to be higher with Cuvier's beaked whale, Blainville's beaked whale, *Mesoplodon sp* and Longman's beaked whale (*Indopacetus pacificus*) detected from the air (Figure 3C). *Indopacetus pacificus* were sighted on three occasions in the northern part of Madagascar. Overall encounter rates varied greatly among areas, and was the highest in the center and south of Mozambique channel and the lowest around the Mascareignes islands (Figure 4B; Appendix 2). A higher encounter rate of *Ziphius cavirostris* is notable in the center of Mozambique channel.

In French Polynesia, *Ziphius cavirostris, Mesoplodon densirostris* and *Mesoplodon sp* were sighted (Figure 3D). Like in south west Indian Ocean encounter rates varied greatly among areas. Marquesas islands had the highest encounter rates (notably a high encounter rate of *Mesoplodon sp* compared to the other areas) whereas the southern Tuamotu had the lowest encounter rate (Figure 4C; Appendix 2).

In the bay of Biscay *Ziphius cavirostris* and Northern bottlenose whale *Hyperoodon ampullatus* were regularly sighted. Conversely to tropical waters, sightings appeared to be more concentrated over the slope (particularly *Hyperoodon ampullatus*) (Figure 3E).

In summary, beaked whales encounter rates were quite similar between regions (varying between 0.6 and 0.9 encounters per 1000 km of effort), with maximal values in south west Indian Ocean and minimal values in French Polynesia. However they showed important variations within south-west Indian Ocean and French Polynesia.

Table 1: Number of beaked whales sightings per region (in bold) and area (see abbreviation for areas in text)

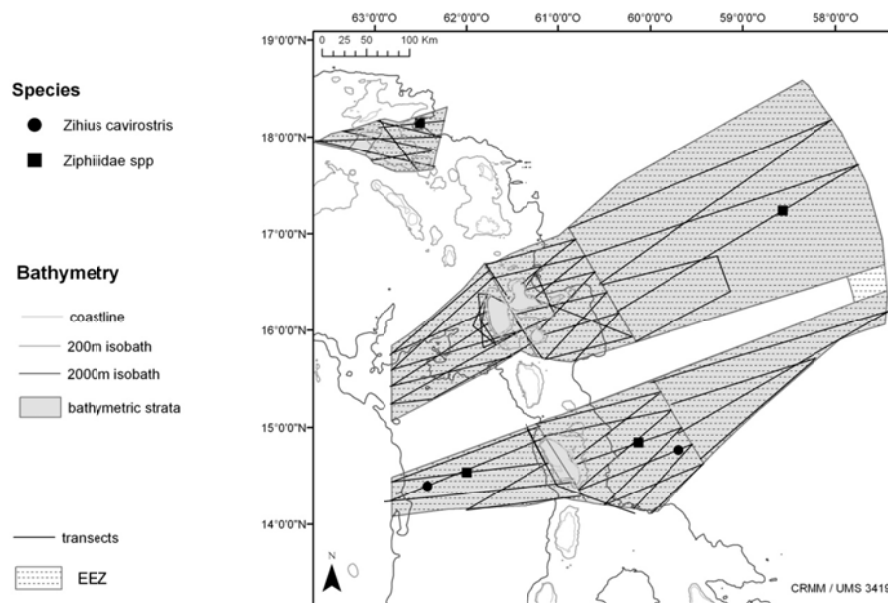| Regions and areas	*Ziphius cavirostris*	*Mesoplodon densirostris*	*Mesoplodon sp*	*Indopacetus pacificus*	*Hyperoodon ampullatus*	*Ziphiidae spp*	Total
Bay of Biscay	**7**	**0**	**0**	**0**	**4**	**9**	**20**
French Antilles	**2**	**0**	**0**	**0**	**0**	**4**	**6**
French Guiana	**3**	**0**	**2**	**0**	**0**	**2**	**7**
SW Indian Ocean	**24**	**4**	**20**	**3**	**0**	**32**	**83**
CMGM	2	1	3	2	0	7	15
EBM	3	0	4	0	0	5	12
JNM	7	0	3	0	0	10	20
RM	4	0	2	0	0	6	12
SE	5	3	2	0	0	3	13
TM	3	0	6	1	0	1	11
French Polynesia	**24**	**6**	**10**	**0**	**0**	**17**	**57**
SOC	4	1	2	0	0	3	10
AUS	5	5	0	0	0	4	14
TUN	5	0	1	0	0	2	8
TUS	2	0	2	0	0	1	5
GAM	5	0	1	0	0	1	7
MAR	3	0	4	0	0	6	13

Figure 3A: Beaked whale sightings in French Antilles.
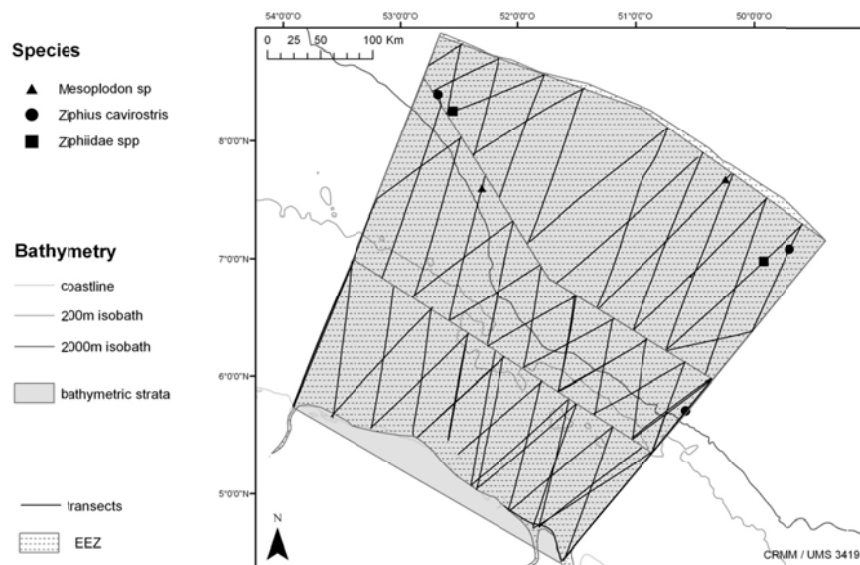
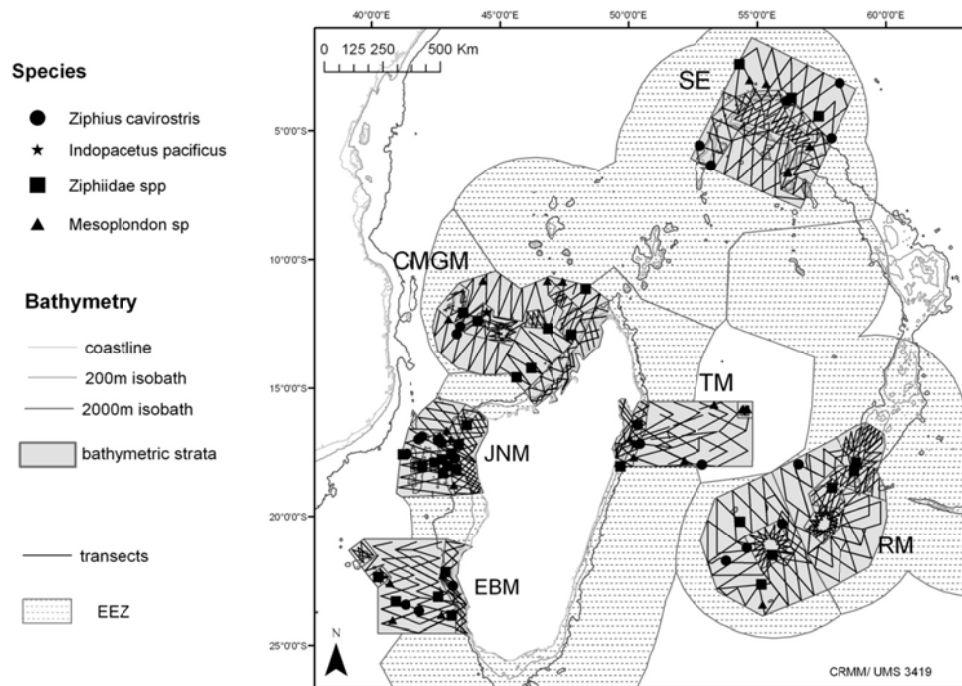Figure 3B: Beaked whale sightings in French Guiana.

Figure 3C: Beaked whale sightings in south west Indian Ocean. South west Indian Ocean was divided into 6 areas: Comoros-Mayotte-Glorieuses-Madagascar (CMGM), Juan de Nova-Madagascar (JNM), Europa-Bassas de India-Madagascar (EBM), Tromelin-Madagascar (TM), La Reunion-Mauritius (RM) and Seychelles (SE).
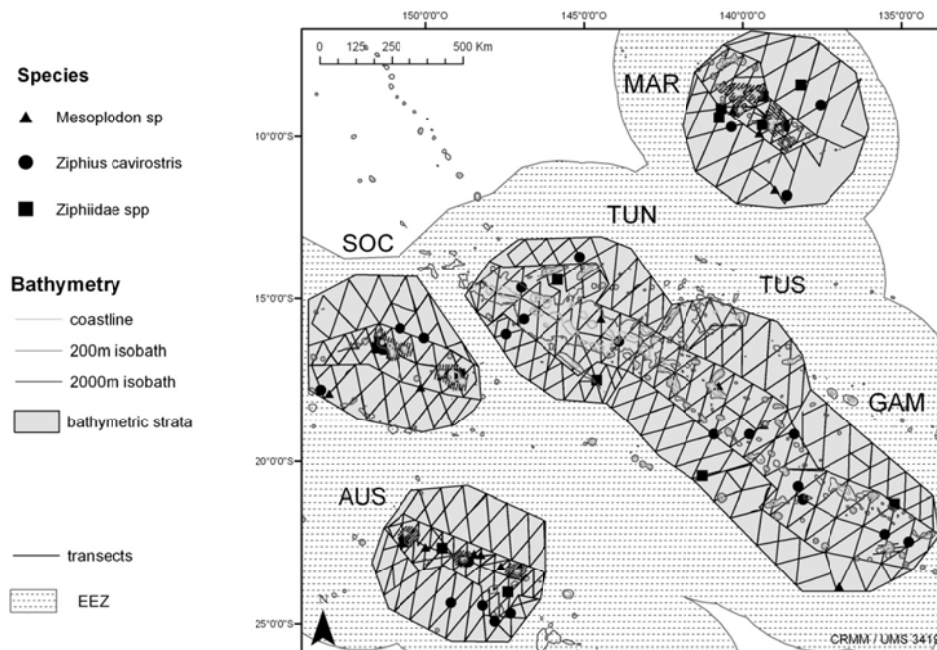
Figure 3D: Beaked whale sightings in French Polynesia. French Polynesia was divided in 6 areas: Society Islands (SOC), Austral Islands (AUS), Tuamotu North (TUN), Tuamotu South (TS), Gambier islands (GAM) and Marquesas (MAR).
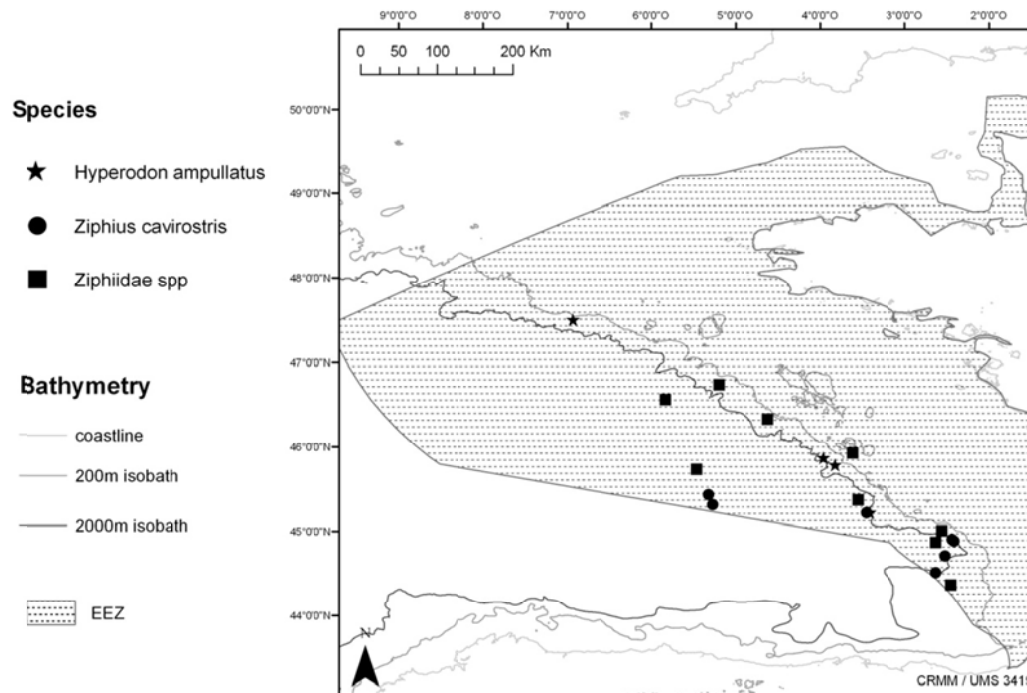

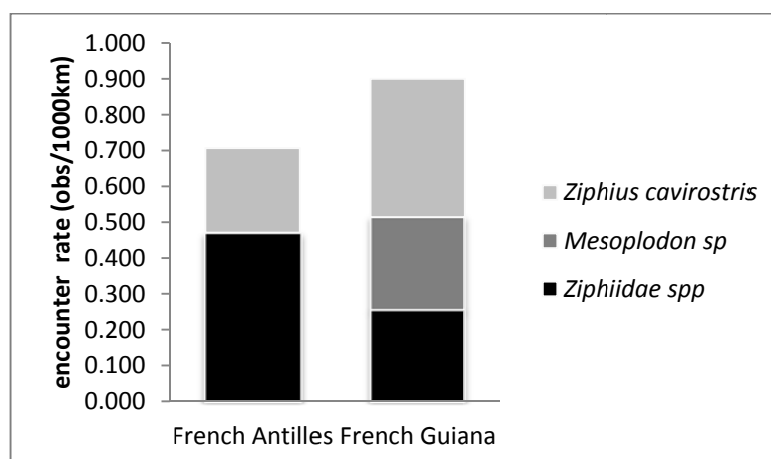Figure 3E: Beaked whale sightings in bay of Biscay.

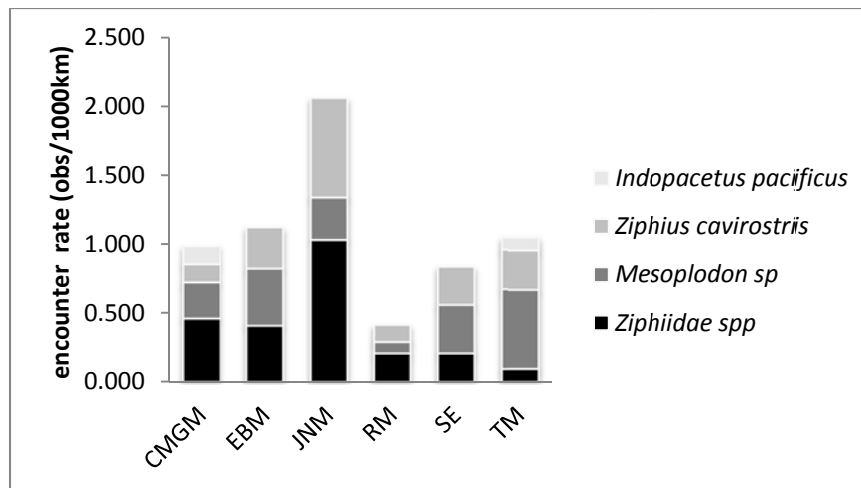Figure 4A: Encounter rates of beaked whales in French Antilles and Guiana.

Figure 4B: Encounter rates of beaked whales in south west Indian Ocean per area (Comoros-Mayotte-Glorieuses-Madagascar (CMGM), Europa-Bassas de India-Madagascar (EBM), Juan de Nova-Madagascar (JNM), La Reunion-Mauritius (RM), Seychelles (SE) and Tromelin-Madagascar (TM)).
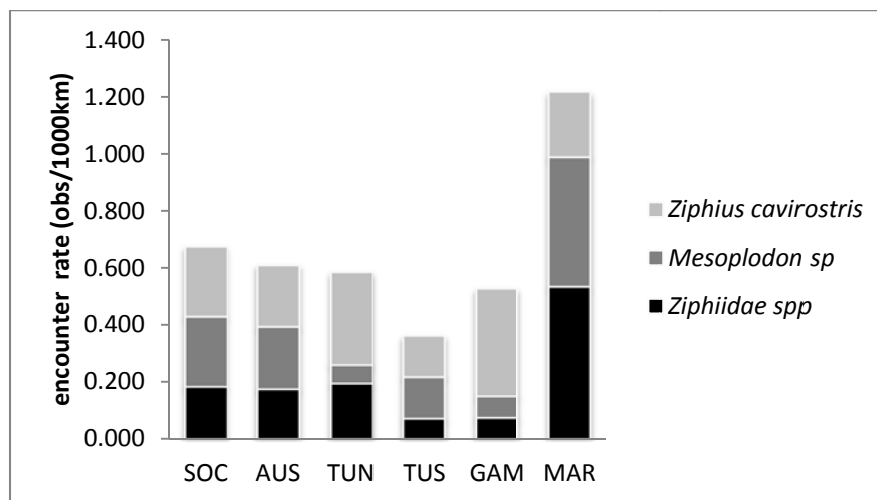

Figure 4C: Encounter rates of beaked whales in French Polynesia per area (Society islands (SOC), Australes islands (AUS), Tuamotu North (TUN), Tuamotu South (TS), Gambier islands (GAM) and Marquesas (MAR)).

3-Analysis of association with physiographic features

3-1-Within-region comparisons

In French Antilles the two Cuvier's beaked whales were encountered in similar physiographic habitats, resulting in a more narrow distribution than unidentified ziphiids. *Ziphius cavirostris*

seemed too occur less deeper than ziphiidae spp but both were located around a 4% slope (Figure 5A; Appendix 3).

In French Guiana *Ziphius cavirostris* and *Mesoplodon sp* occurred at a similar depth (on average 3500m) but *Ziphius cavirostris* seemed to be located around greater slopes (Figure 5B; Appendix 3).

In south west Indian Ocean, *Indopacetus pacificus* showed a very different physiographic habitat related to the other species: they occurred at a lower depth (less than 1000m) and at greater slopes (around 15%) (Figure 5C; Appendix 3). *Ziphius cavirostris* and *Mesoplodon sp* seemed to share relatively similar physiographic habitats (however with no significant differences).

In French Polynesia *Ziphius cavirostris* occurred at a significantly greater distance from the 200m isobath than *Mesoplodon sp* and *Ziphiidae spp* (respectively p-value = 0.03123 and 0.04786) and closer to the coast (no significant differences) (Figure 5D; Appendix 3).

In bay of Biscay *Hyperoodon ampullatus* showed a different physiographic habitat and were encountered significantly closer to the 2000m isobath and at a lower depth than *Ziphius cavirostris* (respectively p-value = 0.01212 and 0.01212). They appeared to be located over higher slopes but the differences was no significant (Figure 5E; Appendix 3).
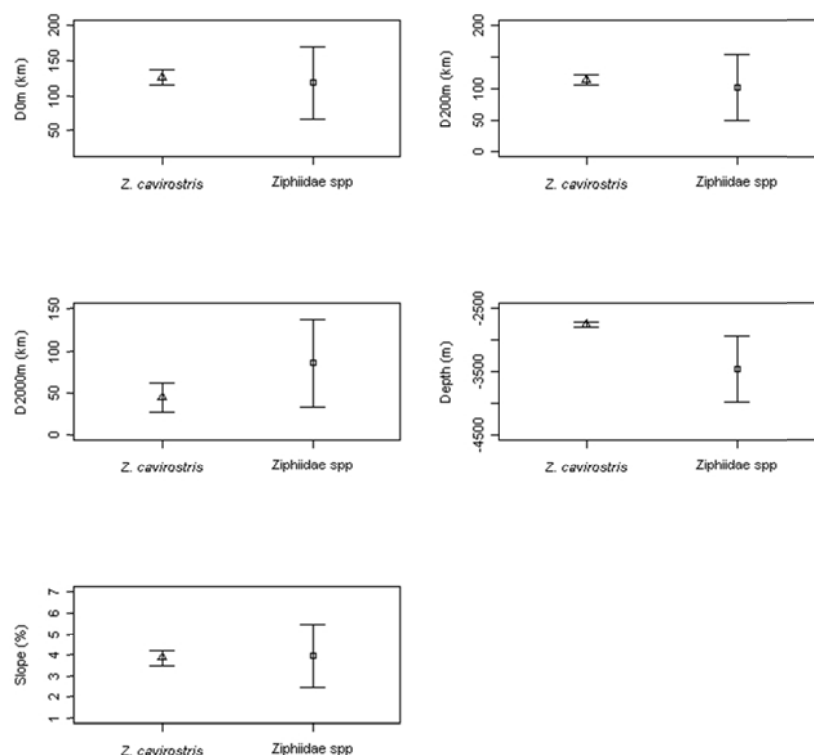

Figure 5A: Distribution of beaked whales related to the five physiographic variables (mean and standard error) in French Antilles
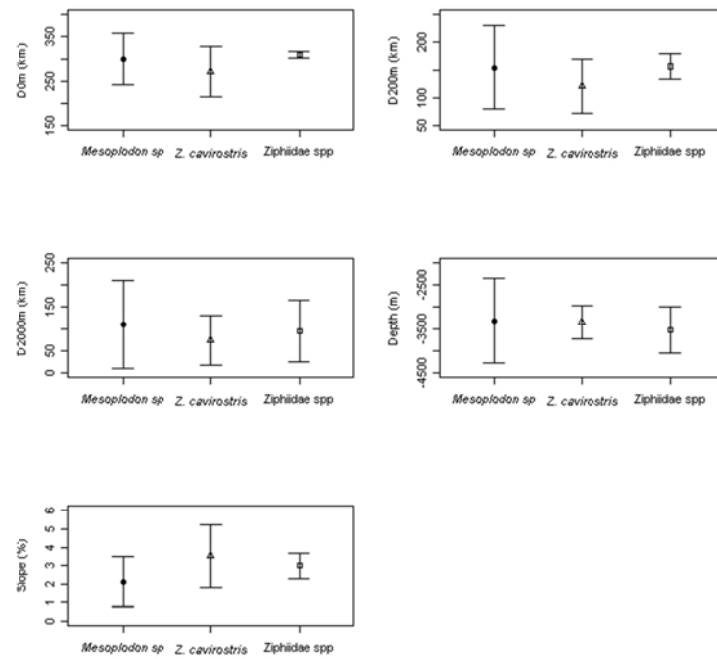
Figure 5B: Distribution of beaked whales related to the five physiographic variables (mean and standard error) in French Guiana
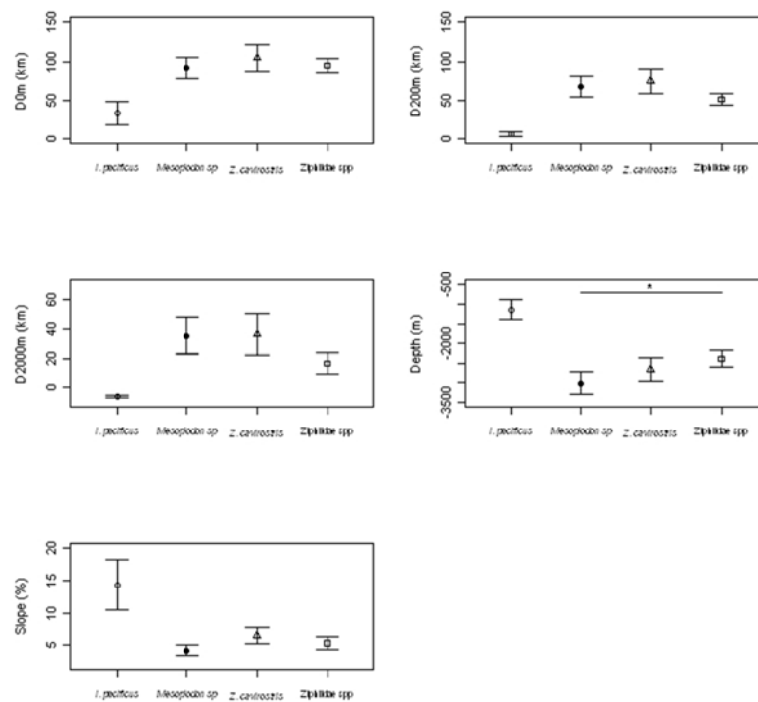

Figure 5C: Distribution of beaked whales related to the five physiographic variables (mean and standard error) in south west Indian Ocean
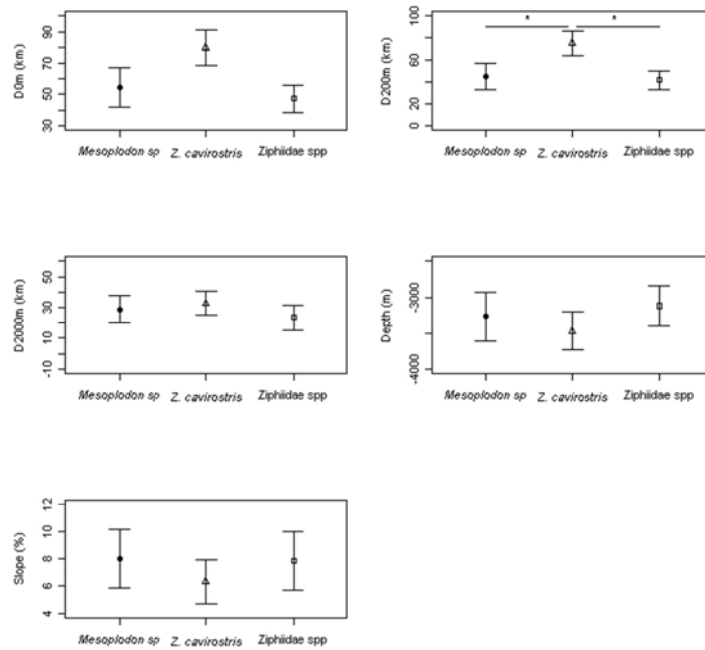
Figure 5D: Distribution of beaked whales related to the five physiographic variables (mean and standard error) in French Polynesia
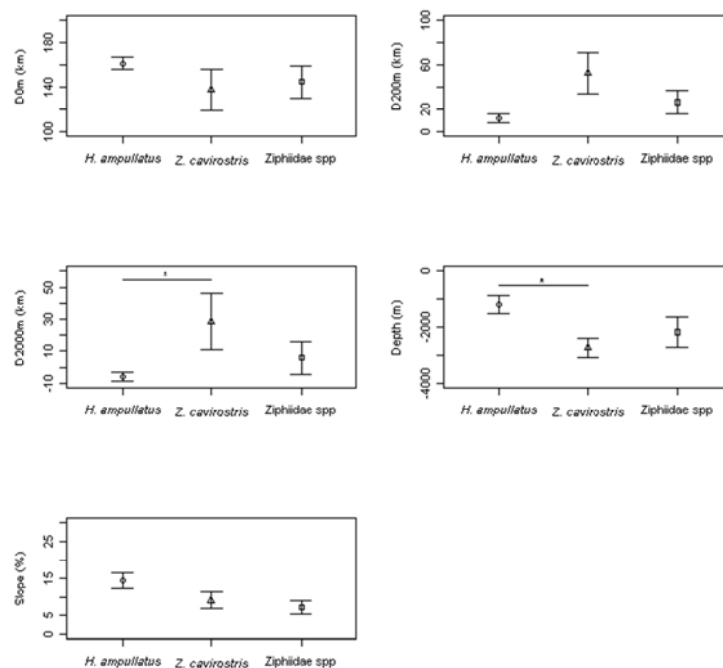

Figure 5E: Distribution of beaked whales related to the five physiographic variables (mean and standard error) in Bay of Biscay.

3-2-Between region comparisons

Ziphius cavirostris were encountered at greater (and more variable) distances from the coast in French Guiana but the small sample size (n=3) prevented the computation of statistical tests. Cuvier's beaked whales were encountered significantly further from the coast but at significantly lower depth in bay of Biscay than in French Polynesia (respectively p-value = 0.007692 and 0.03778). Moreover they occurred significantly deeper in French Polynesia than south west Indian Ocean (p-value = 0.03635). They also appeared to be at greater slopes in the Bay of Biscay than in other regions but without significant differences (Figure 6A; Appendix 3).

Mesoplodon sp (including *Mesoplodon densirostris*) were sighted in French Guiana, south west Indian Ocean and French Polynesia. Like *Ziphius cavirostris* they were encountered further from the coast in French Guiana than the other two regions. Moreover they were encountered significantly further from the coast in south west Indian Ocean than in French Polynesia (p-value = 0.03605). They seemed to occur at greater slopes in French Polynesia but differences were not significant (Figure 6B; Appendix 3).

Unidentified ziphiids were also encountered significantly further from the coast in the Bay of Biscay than in south west Indian Ocean and French Polynesia (respectively, p-value = 0.01867 and 7.681e-06). They were sighted significantly further from the coast in south west Indian Ocean than in French Polynesia (p-value = 0.001724). In French Guiana they appeared to be further from the coast (on average 300km) than in the other regions. Ziphiidae spp occurred significantly deeper in south-west Indian Ocean than in French Polynesia (p-value = 0.03969) (Figure 6C; Appendix 3).

DISCUSSION AND CONCLUSION

This paper describes preliminary results of ziphiid distribution, occurrence and habitat in relation to physiographic variables in the French EEZ and some neighboring waters (these latter specifically in the SW Indian Ocean). We did not compile effort data in the Bay of Biscay as sighting methodology differed from the other regions. Consequently encounter rates were not available for this area. For certain areas, the insufficient number of sightings for several species (e.g. French Antilles and French Guiana) prevented the computation of statistical tests to examine differences and similarities in physiographic habitats. Finally, even if it covers a considerable spatial extent, our dataset only reflects a snapshot of beaked whale distribution for a particular period in a particular region (especially summer, both for temperate and tropical waters).

Cuvier's beaked whale was the most frequently sighted species in all regions. We reported sightings of Blainville's beaked whales in tropical regions only, even if this species is known to be widely distributed in tropical, subtropical and warm temperate waters (MacLeod *et al.*, 2006). Northern bottlenose whales, which are endemic of the North Atlantic Ocean (MacLeod *et al.*, 2006), were reported in Bay of Biscay. Longman's beaked whales were detected on

three occasions in the SW Indian Ocean, especially in NW and NE Madagascar. This species was previously reported in south-west Indian Ocean, including in the northern Mozambique Channel islands of the Comoros (Anderson *et al*., 2006).

Our study also highlights some spatial variations of beaked whale occurrence, especially in tropical waters. In the French Antilles and off French Guiana, beaked whale occurrence was relatively low. However, in the Mozambique Channel, the occurrence of beaked whales was the highest. In French Polynesia, encounter rates were highly variable, and the Marquesas had the highest beaked whale occurrence.
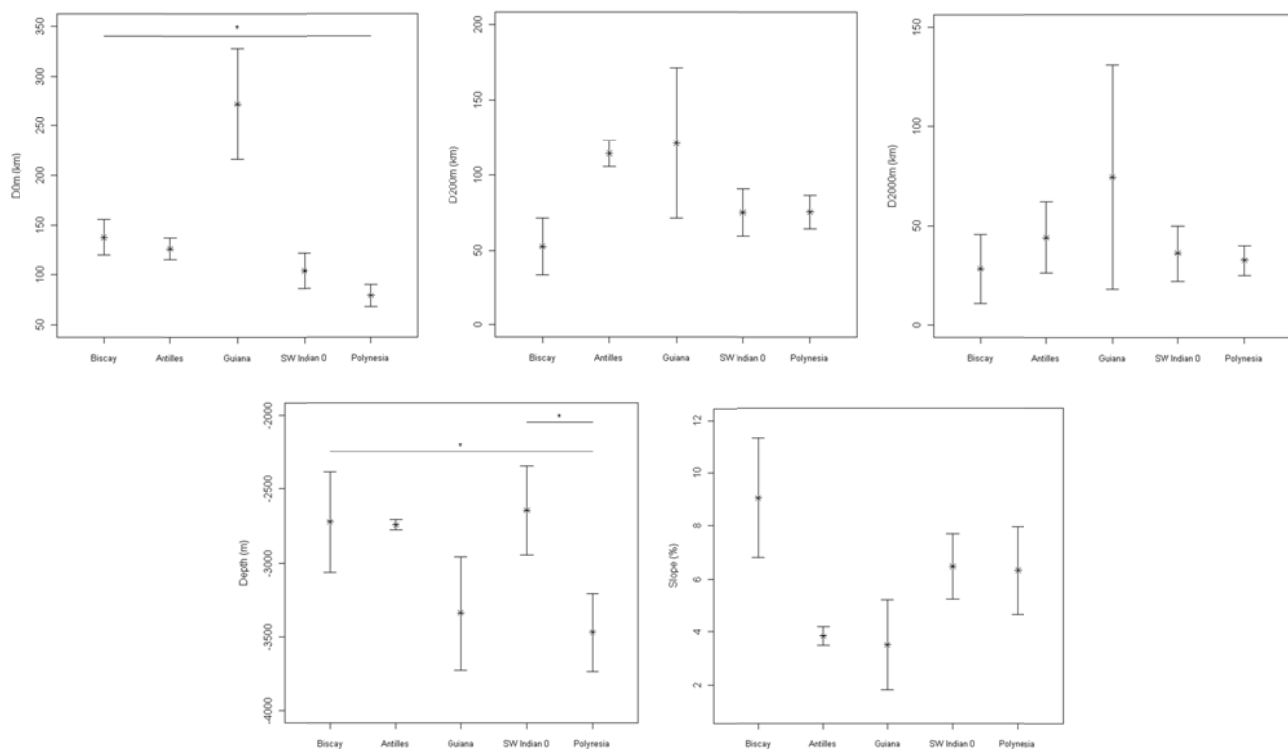

Figure 6A: Between region distribution of *Ziphius cavirostris* related to the five physiographic variables (mean and standard error). Horizontal bars on the top of the graphs show significant differences.
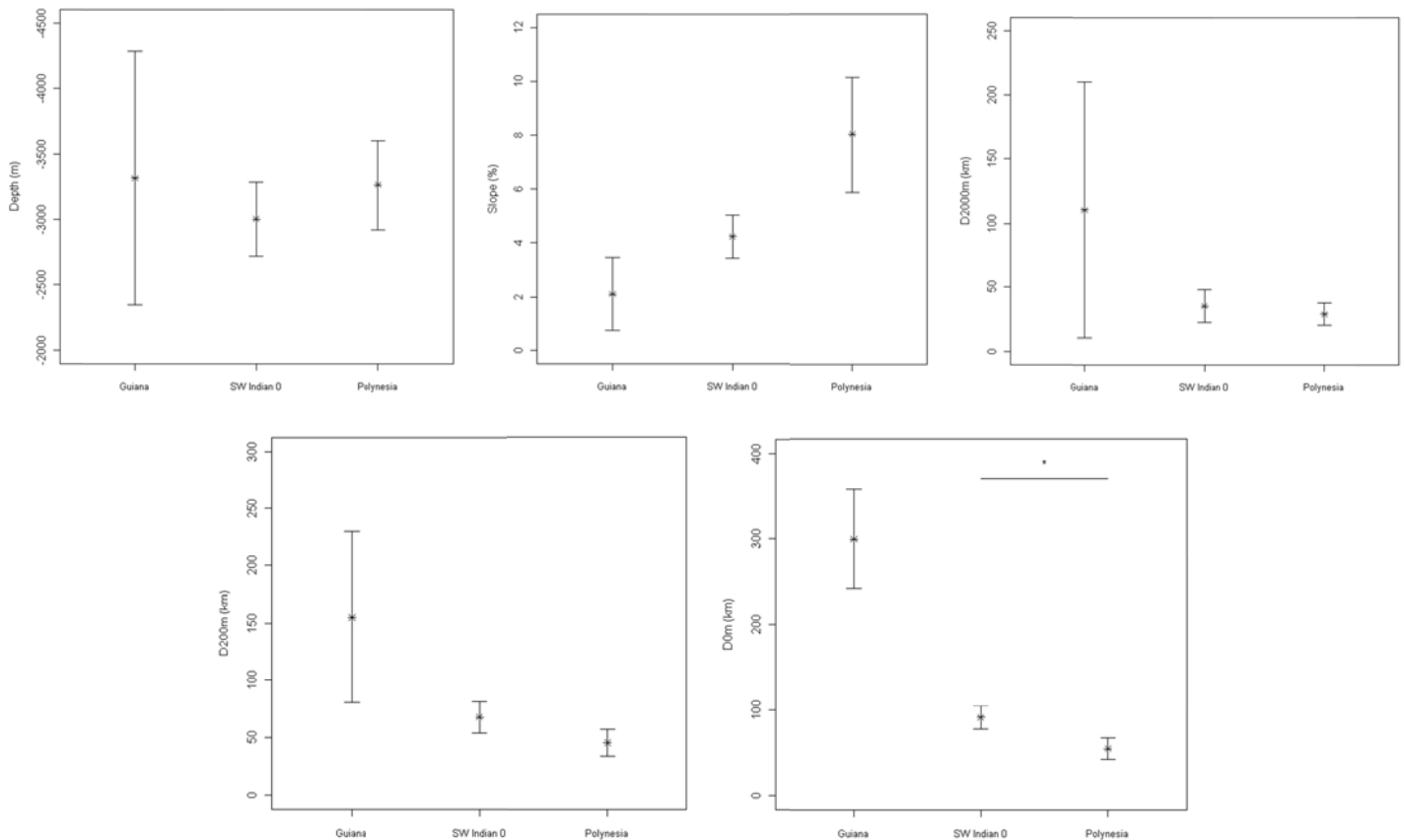
Figure 6B: Between region distribution of *Mesoplodon sp* related to the five physiographic variables (mean and standard error). Horizontal bars on the top of the graphs show significant differences.

An important outcome of our study is the relatively similar overall encounter rates between tropical areas (French Antilles, French Guiana, south-west Indian Ocean and French Polynesia) but more variable within areas. In particular the south and center areas of Mozambique channel were identified as a hot-spots for beaked whales. The Mozambique channel is characterized by mesoscale eddies (100-300km) which are essential for a number of processes influencing dynamics of top predator community (Tew-Kai and Marsac, 2009, Weimerskirch et al., 2004). Beaked whales may take advantage of these mesoscale features, that promote good foraging conditions. In Marquesas islands ziphiids encounter rates were higher than in the other areas of French Polynesia. Marquesas are characterized by an enhanced phytoplankton production attributed to the island mass effect that creates a persistent phytoplankton bloom (Signorini et al., 1999). This phenomenon is likely to enhance secondary production and thus prey densities for beaked whales.
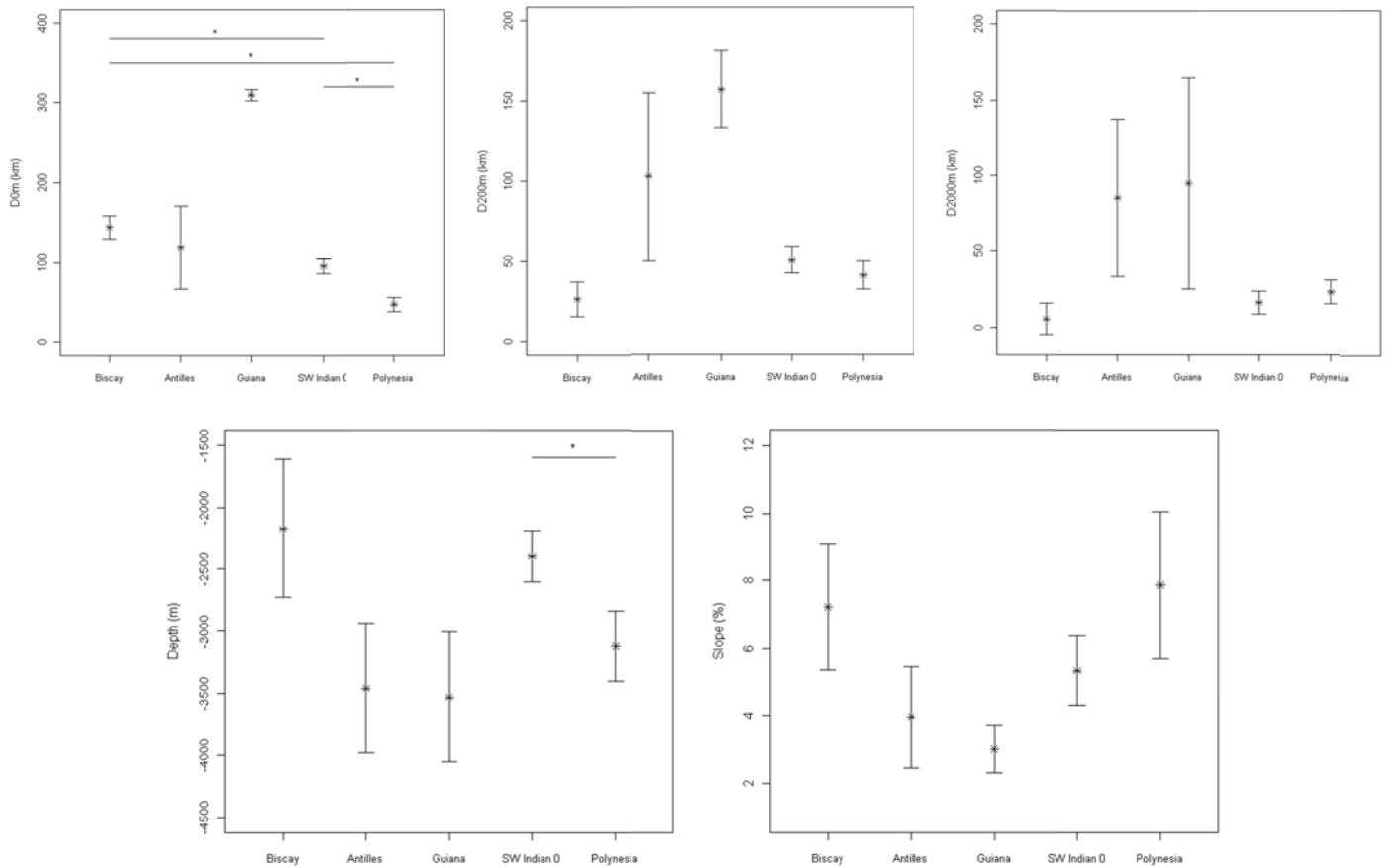
Figure 6C: Between region distribution of unidentified ziphiids related to the five physiographic variables (mean and standard error). Horizontal bars on the top of the graphs show significant differences.

A recurrent issue in field studies is the difficulty of identifying beaked whales to species level (e.g. Barlow *et al.*, 2006). This is even more problematic in aerial surveys sighting time is limited. However photographs could sometimes help to with species identification. Within the genus *Mesoplodon*, identification was particularly problematic because for the co-occurrence of several species, field identification is impossible for juveniles or females and only groups with mature males can be identified to species level (Barlow *et al.*, 2006). As a result most *Mesoplodon* sightings are only identified to genus level and many sightings are classified as "unidentified ziphiids". As Cuvier's beaked whale was the most commonly sighted species it is likely to represent a high proportion of "unidentified ziphiids".

Our preliminary analysis highlighted some habitat differences between species within regions. In particular, *Indopacetus pacificus* seemed to be concentrated over higher slopes than the other species in south west Indian Ocean. In French Polynesia *Mesoplodon sp.* appeared to occur closer the 200m isobaths than *Ziphius cavirostris*. In the Bay of Biscay *Hyperrodon ampullatus* were sighted at lower depths than the other ziphiids.

The vast spatial extent covered by the REMMOA surveys gave the opportunity to test the geographical variation of physiographic habitats. However we must be careful in the interpretation of differences between areas because underwater topography varies greatly between regions. For example *Ziphius cavirostris* was seen significantly further to the coast in the Bay of Biscay than in French Polynesia but the Bay of Biscay is characterized by a vast continental shelf compared to Polynesia islands. Our analysis showed than Cuvier's beaked whales and unidentified ziphiids tend to occupy deeper habitats in French Polynesia than in south west Indian Ocean. In addition species of the genus *Mesoplodon* and unidentified ziphiids were encountered closer to the coast in French Polynesia than in south west Indian Ocean.

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APPENDIX 1: References of surveys from which beaked whales sightings were extracted in Bay of Biscay

Survey	platform	reference
ATLANCET	aircraft	
ROMER	aircraft	
SCANS 2	ship and aircraft	SCANS-II 2008. Small Cetaceans in the European Atlantic and North Sea (SCANS-II). Final report to the European Commission LIFE Nature programme on project LIFE04NAT/GB/000245. Available at http://biology.st-andrews.ac.uk/scans2/.
CODA	aircraft	CODA 2009. Cetacean Offshore Distribution and Abundance in the European Atlantic (CODA). Available at http://biology.st-andrews.ac.uk/coda/.
PELGAS	ship	
PELACUS	ship	

APPENDIX 2: Group size (mean and standard deviation) and encounter rate (number of sightings in the 700m bandwidth / 1000km) per species and site

Region	Effort (km)	*Ziphius cavirostris* group size	*Ziphius cavirostris* enc_rate (obs/1000km)	*Mesoplodon sp* group size	*Mesoplodon sp* enc_rate (obs/1000km)	*Indopacetus pacificus* group size	*Indopacetus pacificus* enc_rate (obs/1000km)	*Ziphiidae spp* group size	*Ziphiidae spp* enc_rate (obs/1000km)	Total group size	Total enc_rate (obs/1000km)
French Antilles	8486	1.5 (0.70)	0.236	-	-	-	-	2.00 (0.81)	0.471	1.83 (0.75)	0.707
French Guiana	7775	1.67 (0.58)	0.386	2.00 (1.41)	0.257	-	-	1.00 (0)	0.257	1.57 (0.79)	0.900
SW Indian Ocean	83627	2.29 (2.03)	0.263	2.00 (1.96)	0.287	1.33 (0.58)	0.036	2.40 (2.02)	0.359	2.22 (1.96)	0.945
IO-CMGM	15198	2.00 (0)	0.132	3.25 (2.22)	0.263	1.00 (0)	0.132	3.71 (3.73)	0.461	3.00 (2.83)	0.987
IO-EBM	9785	4.67 (4.04)	0.307	3.25 (3.86)	**0.409**	-	-	2.00 (1.22)	0.409	3.08 (2.97)	**1.124**
IO-JNM	9700	2.43 (2.15)	**0.722**	1.00 (0)	0.309	-	-	2.50 (1.08)	**1.031**	2.25 (1.52)	**2.062**
IO-RM	24053	1.00 (0)	0.125	1.50 (0.71)	0.083	-	-	1.67 (1.03)	0.208	1.42 (0.79)	0.416
IO-SE	14420	1.6 (0.89)	0.277	2.00 (1.22)	0.347	-	-	1.67 (1.15)	0.208	1.77 (1.01)	0.832
IO-TM	10471	2.67 (1.53)	0.287	1.00 (0)	**0.573**	2.00 (NA)	0.096	1.00 (NA)	0.096	1.54 (1.03)	**1.051**
French Polynesia	94816	1.67 (0.92)	0.253	2.12 (1.26)	0.200	-	-	1.47 (0.87)	0.200	1.74 (1.03)	0.654
FP-SOC	16293	1.75 (1.5)	0.246	2.33 (1.53)	0.246	-	-	1.00 (0)	0.184	1.70 (1.25)	0.675
FP-AUS	22880	1.8 (0.45)	0.219	2.20 (1.64)	0.219	-	-	1.75 (0.96)	0.175	1.93 (1.07)	0.612
FP-TUN	15405	1.6 (0.89)	**0.325**	2.00 (NA)	0.065	-	-	1.50 (0.71)	0.195	1.62 (0.74)	0.584
FP-TUS	13814	1.00 (0)	0.145	2.00 (0)	0.145	-	-	2.00 (NA)	0.072	1.60 (0.55)	0.362
FP-GAM	13285	1.6 (0.55)	**0.376**	4.00 (NA)	0.075	-	-	1.00 (NA)	0.075	1.86 (1.07)	0.527
FP-MAR	13 139	2.00 (1.73)	0.228	1.50 (1)	**0.457**	-	-	1.50 (1.22)	0.533	1.61 (1.19)	**1.218**

APPENDIX 3: Descriptive statistics of beaked whales sightings related to the five physiographic variables in the different regions

Table A: Descriptive statistics of beaked whales sightings related to the five physiographic variables (mean and standard deviation) in French Antilles

Species (n obs)	Dcoast :mean (sd)	D200m:mean (sd)	D2000m:mean (sd)	Depth:mean (sd)	Slope:mean (sd)
Ziphius cavirostris (2)	127 (15)	114.3 (12.3)	44.3 (25.4)	-2748 (50.2)	3.85 (0.51)
Ziphiidae sp (4)	118.7 (104.2)	103.1 (104.7)	85.5 (104.1)	-3457 (1043.7)	3.96 (3)

Table B: Descriptive statistics of beaked whales sightings related to the five physiographic variables (mean and standard deviation) in French Guiana

Species (n obs)	Dcoast :mean (sd)	D200m:mean (sd)	D2000m:mean (sd)	Depth:mean (sd)	Slope:mean (sd)
Ziphius cavirostris (3)	272 (96.4)	121.3 (86.9)	74.4 (97.8)	-3344 (664.2)	3.52 (2.95)
Ziphiidae sp (2)	309.9 (10.3)	157.5 (33.3)	94.9 (98.2)	-3528 (740.3)	2.99 (0.97)
Mesoplodon sp (2)	299.5 (81.8)	155.2 (105.7)	110.7 (141.3)	-3318 (1365.4)	2.11 (1.92)

<u>Table C</u>: Descriptive statistics of beaked whales sightings related to the five physiographic variables (mean and standard deviation) in South West Indian Ocean

Species (n obs)	Dcoast :mean (sd)	D200m:mean (sd)	D2000m:mean (sd)	Depth:mean (sd)	Slope:mean (sd)
Ziphius cavirostris (24)	105.08 (85.88)	75.12 (77.87)	36.14 (68.77)	-2649 (1459)	6.47 (5.97)
Indopacetus pacificus (3)	32.71 (26.23)	6.27 (4.77)	-6.04 (0.78)	-1135 (465)	14.36 (6.70)
Ziphiidae sp (32)	95.07 (50.97)	51.04 (45.05)	16.45 (42.58)	-2395 (1158)	5.33 (5.84)
Mesoplodon sp (24)	91.51 (65.15)	67.6 (67.18)	35.24 (61.71)	-3005 (1376)	4.23 (3.96)

<u>Table D</u>: Descriptive statistics of beaked whales sightings related to the five physiographic variables (mean and standard deviation) in French Polynesia

Species (n obs)	Dcoast :mean (sd)	D200m:mean (sd)	D2000m:mean (sd)	Depth:mean (sd)	Slope:mean (sd)
Ziphius cavirostris (24)	80.11 (55.60)	75.36 (53.75)	32.69 (37.48)	-3472 (1292)	6.33 (8.05)
Ziphiidae sp (17)	47.40 (35.97)	41.83 (35.93)	23.43 (32.29)	-3118.06 (1161.23)	7.86 (8.98)
Mesoplodon sp(16)	54.65 (51.29)	45.34 (47.76)	28.84 (34.67)	-3266 (1369)	8.01 (8.61)

Table E: Descriptive statistics of beaked whales sightings related to the five physiographic variables (mean and standard deviation) in Bay of Biscay

Species (n obs)	Dcoast :mean (sd)	D200m:mean (sd)	D2000m:mean (sd)	Depth:mean (sd)	Slope:mean (sd)
Ziphius cavirostris (7)	137.74 (48.9)	52.58 (49.46)	28.36 (46.49)	-2726 (894)	9.06 (5.95)
Ziphiidae sp (9)	144.78 (43.70)	26.55 (31.83)	5.88 (30.61)	-2171 (1663)	7.22 (5.55)
Hyperoodon ampullatus (4)	161.63 (11.48)	12.28 (8.37)	-5.73 (5.34)	-1182 (639)	14.38 (4.32)