
Preliminary study of Beaked whale (Ziphiidae) distribution, movements, acoustics, and habitat use in the Lesser Antilles

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Abstract

Cetaceans are an umbrella group of species; their diversity and population are used as an indicator for the ecosystem health. The Lesser Antilles is described as a hotspot for cetacean species, in which beaked whales (Ziphiidae) are accounted for. However, despite the high interest in cetology, that family remains poorly studied due to the cryptic and elusive behaviour of its members. Beaked whales spend up to 70% of their time underwater and surface for a short period of time, providing small opportunities to visually observe and study them. Some species such as Cuvier's, Gervais' and Blainville's beaked whales, are believed to occur in the Lesser Antilles. The Caribbean Cetacean Society have been conducting boat survey data collection for over 3 years from 2021 to 2023 to gain insights into the beaked whale distribution and habitat preferences in the Lesser Antilles Arc. We have been able to predict the areas of highest use by beaked whales in that area using bathymetric and climatologic oceanographic data, computed in Generalized Additive Models. It is likely that distance to the isobath 1000meters, Eddies Kinetic Energy and Sea Surface Temperature are best explaining their configuration in the area. Beaked whales are highly vocal animals, that perform sounds that are species-specific. Beaked whale's echolocation clicks were distinguished by analysing their waveform, spectrogram, and spectrum. The verification process relied on specific criteria, including frequency modulation (up-sweeps), and the inter-click-interval between successive clicks. While Gervais' beaked whales exhibit known patterns of clicks with upsweeps peaking at 39KHz and 46KHz and with ICI around 0.34ms, Cuvier's beaked whales seemed to present a unique click pattern, respecting the known peak frequencies but do not show click trains when vocalizing. One detection of Blainville's beaked whale was found, indicating their presence in the Lesser Antilles.

1. Introduction

Knowing the structure of a species helps conservationists to propose adequate management measures. The approach to conservation focused on marine megafauna often has a positive impact on high-trophic species, thus promoting the preservation of marine habitats (Hooker et Gerber, 2004). Cetaceans, as umbrella species, govern the food web. It is thus primordial to understand their distribution and behaviour in order to assess the health of the global marine ecosystem.

With 22 species in 6 different genera, making them the second biggest cetacean family, beaked whales inhabit deep offshore waters of all oceans worldwide, from the temperate tropical waters to the cold polar environment (Hooker *et al.*, 2019). Beaked whales, part of the odontocetes group, make up about a quarter of all known cetaceans but are one of the least understood families (Claridge, 2006; Li and Rosso, 2021). Their preferred habitat is believed to be continental slope and abyssal plains that are usually far offshore (DeAngelis *et al.*, 2018). Yet they are poorly studied as they spend most of their time underwater (Schorr *et al.*, 2014; Hooker *et al.*, 2019), estimations indicate hour-long foraging deep dives for a few minutes of non-foraging surfacing dives (Joyce *et al.*, 2019; Sweeney *et al.*, 2022). Beaked whales are defined as rare, cryptic individuals and morphologically alike when at the surface, hence making visual observations biased, even in perfect conditions. Most of the information has only been gathered from stranded individuals (Li and Rosso, 2021). Global population trends and density are poorly documented, thus most beaked whale are globally classified as Least Concern or Data Deficient in the IUCN Red List (IUCN, 2024). There is a need to recognize their presence in all oceans and acknowledge their specific habits. Moreover, despite that they can be found in all oceans, they usually inhabit offshore waters, complexifying their study (Hazen *et al.*, 2011).

Beaked whales, like other apex predators are influenced to choose their environment

depending on prey availability, reproduction suitability and possibly to get proper protection against predators (Claridge, 2006). Like so, understanding the characteristics of a habitat allow to model a species distribution by describing the availability in prey, nutrients, and seafloor shape (Virgili *et al.*, 2021). Yet in the Lesser Antilles, little to no studies have showed a proper map of the distribution and movement of beaked whales (Boisseau *et al.*, 2006). What is known in the area is to a wider point of view; the Caribbean Sea or up-north in the Bahamas and the Gulf of Mexico (Rosario-Delestre *et al.*, 1999; Boisseau *et al.*, 2006; Claridge, 2006; Dunn *et al.*, 2013; Luksenburg, 2013; Hildebrand *et al.*, 2015). Indeed, the Caribbean Sea can be described as a biodiversity hotspot, as it contains the greatest concentration of marine species in the Atlantic Ocean (Miloslavich *et al.*, 2010). However, this area remains poorly studied when it comes to marine life. The Lesser Antilles arc is located on the southeastern side of the Caribbean Sea and represents the entrance of the counter clock current, consequently offering unique hydro-geologic features harbouring a diverse array of species (Miloslavich *et al.*, 2010; Seibert *et al.*, 2020). The Wider Caribbean Region is home to 32 of the world's 86 recognized cetacean species (Ward *et al.*, 2013) To this extent, evidence of Blainville's Beaked whale (*Mesoplodon densirostris* (Blainville, 1817)), Cuvier's beaked whale (*Ziphius cavirostris*, (Cuvier 1823)) and Gervais' beaked whale (*Mesoplodon europaeus* (Gervais, 1855)) were found in the Caribbean Sea and potentially spotted in the Lesser Antilles (SEPENMAR, 2003; Debrot *et al.*, 2011; Luksenburg, 2013; Shelltone Whale Project, 2024). Yet, there is no study explaining the distribution of these species within the Lesser Antilles habitat.

Like most cetaceans, they are threatened by human activity including by-catch, and vessel collisions which often occurs (Reeves *et al.*, 2013). Beaked whales are particularly sensitive to noise disturbances, indeed mass-strandings events have been recorded due to military sonar activity in the Bahamas (Balcomb III and Claridge, 2001) and in the Pacific (Simonis *et al.*,

2020), hence noise is believed to disrupt their physiological response to stress affecting their diving and communication capacities (Rolland *et al.*, 2016, Cholewiak *et al.*, 2017). That sensibility to noise raises interrogations on their use of sound, diving behaviour and interactions with human activity (Johnson *et al.*, 2006). These interrogations have led to numerous studies. Thus acoustics of beaked whales is a well-studied research field (Frantzis *et al.*, 2002; Johnson *et al.*, 2004; Johnson *et al.*, 2006; Gillespie *et al.*, 2009; Kowarski *et al.*, 2018; Malinka *et al.*, 2020; McCullough *et al.*, 2021; Stanistreet *et al.*, 2022; Boisseau *et al.*, 2023). Researchers identified various click types based on the activity and species of beaked whales. A foraging beaked whale will perform Frequency-Modulated (FM) upsweep echolocation clicks to navigate its environment to detect prey items. Once detected, it localises prey items with rapid rate buzz clicks that are unmodulated (Johnson *et al.*, 2008). We differentiate species from their beak, which is difficult to observe when on field, combining acoustic information with visual encounters offer a better understanding of the population structure.

On the other hand, beaked whales perform sounds that are species-specific, meaning that it is possible to identify them by studying the nature of sounds, associating a frequency length to a species (Baumann-Pichering *et al.*, 2013). Combining their acoustic personality to the distribution of their favourite prey, i.e. cephalopods and deep-sea fish (Santos *et al.*, 2001; 2007; MacLeod *et al.*, 2003) through analysis of the environmental conditions, will allow to model how they use their habitat and design ways to protect them and their environment.

One of the objective of the Caribbean Cetacean society is to complete the lack of knowledge on the cetacean species in the Caribbean. As part of the “Ti whale an nou” program, several scientific expedition have been organized in the Lesser Antilles. From 2021 to 2023, more than 6 expedition of 15 days each have been organized each year, to cover all the islands of the lesser

Antilles from Anguilla to Grenada. All have been using the same standardised protocol, with a combination of line transect, visual survey, acoustic monitoring and photo identification. Herein, this preliminary study aims to lay the essential knowledge base to document the geographic distribution, possible migratory movements, acoustic patterns and habitat use of beaked whales of the Lesser Antilles. While the seas surrounding the Lesser Antilles represent a complex and diverse ecosystem, beaked whales, as key components of this environment, are of particular interest due to their enigmatic behaviour and potentially crucial role in the balanced local ecology. Using data collected in the last 3 years during the ‘Ti Whale An Nou’ program, we analysed visual information, modelled their distributions and movements depending on the environmental features of the Lesser Antilles. The objective here is to draw their density as a family-species in the Lesser Antilles and draw the variation of their distribution within the different island’s waters. We want to find if they exhibit a preference in habitat structure. With acoustics, we will be able to describe the click patterns of the different species found in the Lesser Antilles from their species-specific frequency and interclick-interval. The main distribution of ziphiids have been estimated using visual encounters from 2021 to 2023. Using the non-invasive photo-identification method, we will be able to recognize the possible movements of beaked whales within the study area. Static and dynamic environmental variables that can influence the distribution of these cetaceans were considered for performing the General Additive Model (GAM) and estimate their density. With a census of acoustic recordings using the Passive Acoustic Monitoring (PAM) method, the aim is to describe individuals to a species-level and to describe their click patterns. Hence, with this study, we hope to confirm the presence of ziphiids in the area, identifying the specific species present and describing the habitat usage patterns of this family as well as their acoustic characteristics.

2. Materials and Methods

2.1 Study zone

The Lesser Antilles Arc extends from 12-19°N and 61-65°W, covering a total area of 69,105 km², in this study. Given the amplitude of the study area, sub-zones have been defined as follows: the southern zone includes the islands of the south, Saint Lucia, Saint Vincent and the Grenadines (SVG), and Grenada; the central zone concentrates around Dominica, Guadeloupe, and Martinique; and the northern zone spans from Montserrat to Anguilla (Antigua-Barbuda, Saint Kitts and Nevis, Sint-Eustatius, Saint Martin (FR&NL), Saint-Barthelemy, Saba (Figure 1A). These three zones are located both in the Caribbean Sea (west coast of the island arc) and the Atlantic Ocean (east coast of the island arc). Indeed, the islands of the Lesser Antilles are formed by a series of volcanic arcs, a result of the subduction of the South American plate beneath the Caribbean plate along the

Caribbean Trench. Consequently, the geomorphological and oceanic characteristics of the sea and ocean on either side of this area can significantly differ (Macdonald *et al.*, 2000). On the Caribbean side, analysis of bathymetric data such as isobath distances of 200m, 1000m, and 2000m revealed that great depths are more common (Figure 1B). There are also a various number of canyons on this side, principally concentrated at the centre of the Lesser Antilles (Guadeloupe, Dominique and Martinique) from the study point of view, adding depth to the environment, and hence prey productivity (Moors-Murphy, 2014). The shape of canyons can affect how sound travels through water. The walls of canyons can reflect and refract sound waves, creating complex acoustic environments. This can enhance the ability of whales to detect and localise sound sources using echolocation (Moors-Murphy, 2014).

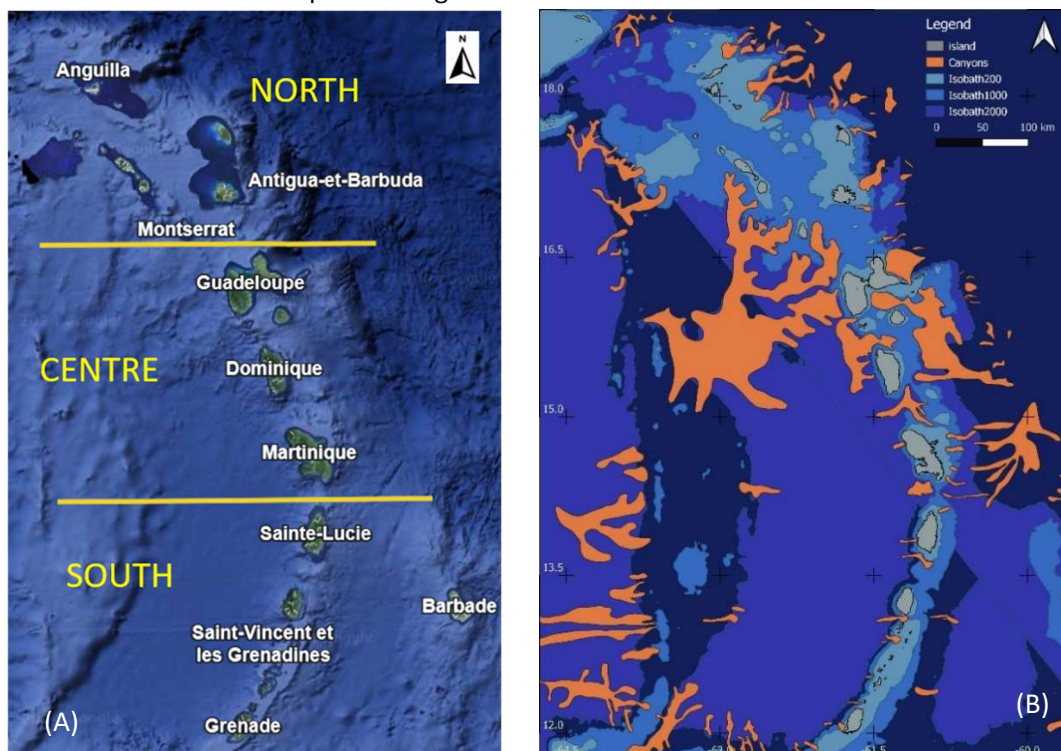


Figure 1. Study area separated in study zones (A) Geomorphologic features of the study area (B)

2.2 Data collection

All expeditions departed from Martinique aboard a catamaran (between 40 and 46 feet). Monitoring typically took place on the Caribbean side, instead of the Atlantic, where

meteorological conditions were more favourable. Expeditions took place yearly between March and August. Each expedition lasted 15 days (\pm 2 days) as they followed the islands previously cited. In this way, each zone was individually sampled at least twice a year.

Some expeditions were led in September, in Martinique, Saint Lucia or Guadeloupe, and added material to the dataset (Supplementary material). Due to data availability, this study concentrated only on the years 2021 to 2023. Statistical analysis using Kruskal-Wallis tests was run to estimate the sampling effort of each studied island.

The Caribbean Cetacean Society has established a standardised protocol for observing cetaceans which is used in all expeditions. On-effort sampling occurred depending on daylight hours, from 06:00 to 18:00. If meteorological conditions (rain, Beaufort >4, wind speed >21knots) became unsuitable for observation, the survey was terminated. During all on-effort time, Obsenmer software created by the “Groupe d’Etude des Cétacés du Cotentin” (GECC, 2018) was used to record the boat GPS position, observation and tracking of cetaceans, as well as other relevant information (Supplementary materials).

Visual data

On board, 2 observers had the role to spot and identify cetaceans; they were positioned at the front of the boat to be able to cover a 180° zone around the boat and the horizon (Figure 2A). Once cetaceans were sighted, the GPS position of the boat was recorded alongside the

estimated distance between the observers and the cetacean, the number of individuals and possible juveniles.

Other members of the team had the role of photographing the dorsal fin or fluke of sighted animals, which then served for photo-ID. As part of this study, only information concerning beaked whales was used.

Photo-identification

Photo-identification is a non-invasive method for long-term monitoring of cetaceans. Once collected, visual data were treated with Flukebook (2015). This is a collaborative software that uses artificial intelligence to recognize cetaceans. It linked possible pictures of distinctive features such as dorsal fins to GPS points where the individual was observed. Considering the shape and noticeable notches or scars, for example on the dorsal fin, it ran an algorithm that reviewed all the elements recorded by the software from various research structures, with regards to the species specified. This enabled to detect possible match between projects and expeditions, to observe their position and possible movements. It should be noted that the software makes suggestions, but the final choice is made by the user, ensuring human verification. It also constitutes the creation of individual catalogues.

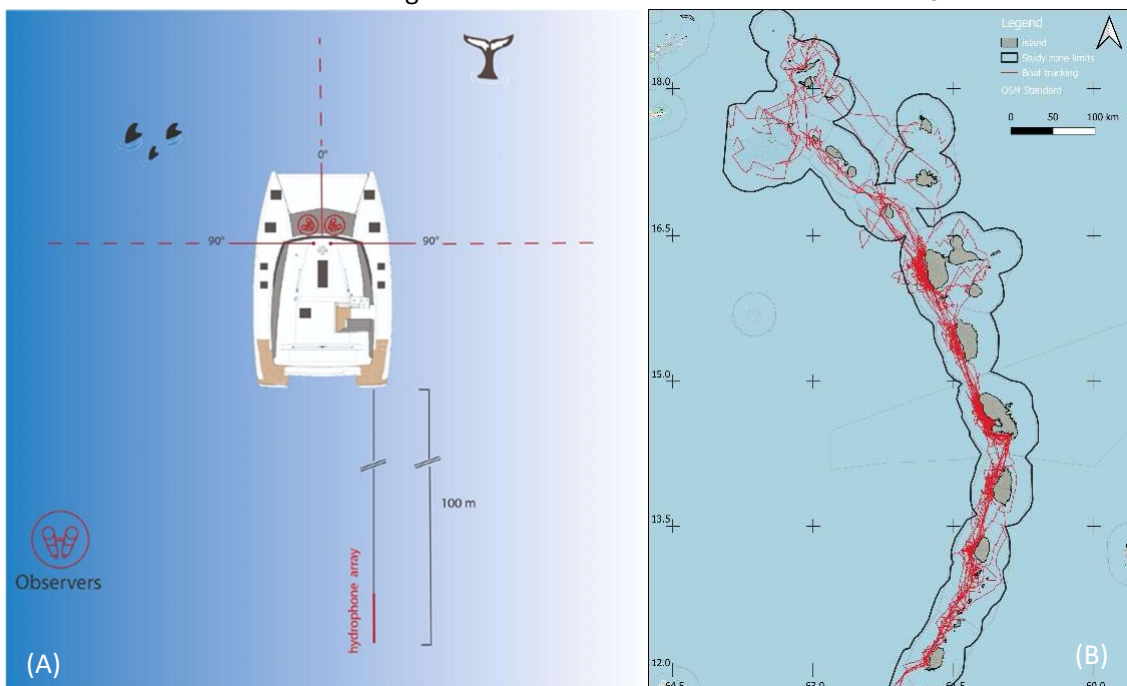


Figure 2. Schema of standardized protocol (A) and the boat track line of the “Ti Whale An Nou” project (2021 to 2023) (B)

Group size

Group size was determined by the mean individuals encountered at each observation with consideration to the coefficient of variation estimated with the minimum and maximum of cetaceans possibly sighted.

2.3 Modelling the distribution – GAM

In case of highly mobile marine organisms such as cetaceans, species distribution models are widely used in the literature to provide essential comprehension of habitat use and distribution. In this study, we employed Generalized Additive Models (GAMs) to investigate the distribution and habitat preferences of beaked whales in the Lesser Antilles. GAMs offered a flexible and powerful framework for modelling complex relationships between predictor variables and response variables without imposing rigid assumptions about linearity. By incorporating functions of covariates, GAMs could capture non-linear and non-parametric relationships, making them particularly well-suited for ecological studies where relationships might have been inherently complex (Hastie and Tibshirani, 1986). Different distribution families can be employed; in this study, the Tweedie distribution family was selected as it encompassed various distribution types including Normal, Gamma, exclusively discrete Poisson distributions, and the class of compound Poisson-Gamma mixed distributions (Tweedie, 1984). A logarithmic link function was applied in this study. The fitting process utilized Restricted Maximum Likelihood (REML) to select the smoothness, and smooth terms were derived using a thin-plate splines basis with a dimension of 4 to avoid overfitting (Hastie and Tibshirani, 1986). Models were organised and chosen based on Akaike Information Criterion (AIC) scores, which were generated in parallel to the models using the R package “mgcv” (Wood, 2017). The Akaike weight indicated the probability that a particular model was the best model among the set of candidate models under consideration. The delta AICs ($AIC_i - AIC_{min}$) was defining the probability of the model. We pondered that a delta AICs inferior to 2 was considered highly

plausible. The Akaike weights were calculated with the function “Akaike.weights” from the “qpcR” package on R (Spiess, 2018). AIC penalized model complexity, discouraging the inclusion of unnecessary predictors or smooth terms. In GAMs, smooth terms could be particularly flexible and prone to overfitting if not properly controlled. AIC helped prevent overfitting by favouring simpler models, providing a balance between model accuracy and parsimony. Higher Akaike weights indicated that a model was more likely to be the best model among the alternatives. Models with higher Akaike weights were generally preferred as they provided an equilibrium between goodness of fit and simplicity. GAMs input every combination of variables into test models to see which fit best (Hastie and Tibshirani, 1986; Wood, 2017). However, in that case combinations were computed with a maximum of 4 variables.

Observation effort

To fit a GAM, the observations of the studied species were used to create the observation effort. To do so, a hexagonal grid of 1.7km long per unit (totalling 7.8km²) was created alongside the study area. Using boat tracking (Figure 2B), this allowed to determine whether a grid cell was considered sampled, and with the coordinates of an observation whether the sampled grid cell contained the observation of the desired cetacean. Considering the reduction in cetacean detection probability with distance, four buffers following the tracking line were created and associated with a detection probability (1, 0.75, 0.5 and 0.25). These probabilities were affiliated to a distance, so if the probability was 1, it was considered that the maximum (100%) of cetaceans within this distance were detected, this probability was determined using the distance where a maximum of cetaceans was observed. Once the percentile of the first threshold of the buffer zone was estimated, the rest of the distance distribution was divided into three equivalent quantiles. These percentiles established the distance thresholds for each buffer zone. To mitigate buffers overlapping, straight-line micro-segments were generated at

each inflection point of the boat's trajectory, corresponding to instances when the boat travelled in a straight line. Buffer zones were created around boat trajectory segments and overlapped with the hexagonal grid cells in QGIS. This allowed for the calculation of the sampled area and detection probability within each hexagon. The detection probability for each buffer zone level was multiplied by its respective area within each grid cell. These values were then aggregated within each hexagon to represent the total effort. The effort per hexagon was standardized and used as an offset in the beaked whale distribution model. Obtaining this sampling effort was crucial for weighting the observations in the distribution model by this effort, meaning to account for the fact that one area has been sampled more than another, which could impact the final prediction.

General Additive Models graphs and other statistical analysis were drawn using the R software (R Core Team, 2021).

Environmental factors

In this GAM analysis a suite of environmental covariates known or hypothesized to influence ziphiids distribution was considered from the literature (Moulins *et al.*, 2007; Cañadas *et al.*, 2018; Virgili *et al.*, 2019; Virgili *et al.*, 2021; Tournier, 2022). Studies distinguished two types of environmental variables that induced or govern a species distribution; static conditions (that never change) and dynamic conditions (that vary over time) (Virgili *et al.*, 2021). As static variables, this included bathymetric data (depth, slope and roughness – the variability of the seabed floor surface), depth data were retrieved from the General Bathymetric Chart of the Oceans (GEBCO, 2024). From depth data and using the function “terrain” from the “terra” R package (Hijmans, 2023), the slope and roughness were extracted, isobath distances (200, 1000, 2000m) were generated with the “Distance” function of “raster” R package (Miller *et al.*, 2019) using depth and the canyon shape in the area, these depth conditions were considered as it has been previously proved that beaked whale favoured deep sub-marine canyons, seamounts or the end of the

continental slope as habitat (Waring *et al.*, 2001; D’Amico *et al.*, 2003), thus distance to canyons was also considered. The different isobaths also represented the repartition of preys in the water column (Virgili *et al.*, 2022). Sea surface temperature (SST), sea bottom temperature (SBT), sea surface height (SSH - above geoid, i.e. the equipotential surface that best approximated the shape of the Earth), oceanographic currents velocity (eastward and northward) as well as Eddies Kinetic Energy (EKE), mixed layer depth (ML) and chlorophyll a concentration (CHL - used as an indirect proxy for net primary production) was qualified as dynamic variables. These dynamic variables were retrieved from the Copernicus Marine Service website (<https://marine.copernicus.eu/fr>). The EKE was particularly interesting as it explained the redistribution of sediment particles in the water column (either to the surface or to the bottom depending on the direction of the eddies) (Virgili *et al.*, 2022).

The EKE variable was calculated using the eastward and northward current variables and the following formula:

$$EKE = \frac{1}{2}(u^2+v^2), \text{ where } u \text{ is the eastward current and } v \text{ the northward current.}$$

These variables were considered as they represented a proxy for prey aggregation, it referred to a measurable or observable factor that served as an indirect indicator of the concentration or grouping of prey organisms within an ecosystem. It helped describing variables such as habitat complexity, food availability, or predator behaviour. By incorporating these variables as smooth terms in the GAM, the aim was to elucidate the underlying ecological drivers shaping the spatial distribution of beaked whales within the study area. All variables were estimated by mean and standard deviation (SD) of data from January 2021 to December 2023 collected monthly and then recorded in the grid by collecting the mean of all the values of the variable inside the hexagon. Environmental information at observation points were retrieved from maps in QGIS. In total, 14 variables were tested to assess

their impact on beaked whales, they are listed in the table below (table 1).

Each of them (mean and SD) was normalized to fit the scale and tested by pair with Pearson's correlation test. If tested variables were highly correlated ($|R| > 0.7$) then they are not considered in the same model (Dormann *et al.*,

2013). We removed outliers from environmental variables which means excluding or eliminating data points that deviated significantly from the expected range. This was done to ensure that the model was not unduly influenced by extreme or unusual observations, which could potentially distort the model's predictions.

<i>Environmental variables</i>	<i>Resolution</i>	<i>Possible effect on Ziphiids</i>	<i>Source</i>
<i>Static variables</i>			
<i>Depth (m)</i>	15 arcsec	Forage at deep depth	GEBCO
<i>Slope (°)</i>	15 arcsec	Indirect proxy for prey aggregation Associated with currents	Function 'Terrain' from 'Terra' R package using Depth data
<i>Roughness</i>	15 arcsec	Can affect acoustic properties	Function 'Terrain' from 'Terra' R package using Depth data
<i>Isobaths distance (200m, 1000m, 2000m) (km)</i>	15 arcsec	Preferred habitat Influence the presence of prey in the water column	Function 'Distance' from raster' R package using depth and canyon surface data
<i>Distance to the canyon (m)</i>	15 arcsec	Preferred habitat	GEBCO & Blue Habitat (https://bluehabitats.org/)
<i>Dynamic variables</i>			
<i>Sea Surface Temperature (°C)</i>	0.083° × 0.083°, Daily	Indirect proxy for prey aggregation	Copernicus Marine service
<i>Sea Surface Height (m)</i>	0.083° × 0.083°, Daily	Indirect proxy for prey aggregation	Copernicus Marine service
<i>Eastward current (m s-1)</i>	0.083° × 0.083°, Daily	Indirect proxy for prey aggregation	Copernicus Marine service
<i>Northward current (m s-1)</i>	0.083° × 0.083°, Daily	Indirect proxy for prey aggregation	Copernicus Marine service
<i>Eddies Kinetic Energy (m s-1)</i>		Indirect proxy for prey aggregation redistribute sediment particles in the water column	
<i>Chlorophyll a concentration (mg/m3)</i>	4km x 4km, Daily	Indirect proxy for prey aggregation Indicates Net Primary Production	Copernicus Marine service
<i>Mixed Layer Depth (m)</i>	0.083° × 0.083°, Daily	Indirect proxy for prey aggregation	Copernicus Marine service

Table 1. Summary of the hypothesized environmental variables used in the distribution model of beaked whales in the Lesser Antilles

2.4 Acoustic data collection

A hydrophone array was towed 100m behind the boat, at depth of 5m ±2m, during every expedition from 2021 to 2023 and recorded every sound of the environment at any time during the day, when on effort, comprising

vocalisations and environmental sounds like anthropic noise or physical noise (Figure 2A). The network of hydrophones comprised 2 low-frequency hydrophones and 2 high-frequency hydrophones recording sample rate frequencies up to 500kHz. Here, only the high-frequency

hydrophones were used and digitised at 192kHz sample rate. The hydrophones are linked to a computer with the PAMguard software designed for passive acoustic monitoring (PAM) of marine environments. It detected, and analysed sounds produced by marine organisms, such as whales, dolphins, and other marine life. PAMguard was specifically developed for the analysis of bioacoustics data, allowing researchers and scientists to monitor and study the behaviour and presence of marine species through their vocalizations (Gillespie *et al.*, 2008).

Acoustics analysis

Defined as deep-divers, acoustic study of beaked whales gives massive information on their behaviour as they spend around 70% of their time at deep depth, performing sound for most 20% of their dive (Hooker *et al.*, 2019). PAMguard could be configurate to recognize the specific sound patterns of the different species of beaked whales. PAMguard employed detection algorithms to detect and extract beaked whale clicks from the audio recordings. PAMguard offered several methods for click detection including sound level thresholds, algorithms based on specific beaked whales' models, etc.

Beaked whales perform a various panel of vocalisations, depending on their activity. As odontocetes, they use clicks to navigate, forage and communicate. Three kinds of clicks have been identified; 'normal' click, Frequency-Modulated upsweeps clicks and buzz (McCullough *et al.*, 2021). Each species has a dedicated frequency to which they vocalise, interclick-interval (ICI) is also specific to the species. These unique features that are FM upsweeps are proper to beaked whale echolocation clicks (Yack *et al.*, 2013). When foraging, beaked whales perform buzz that are a series of close non-FM clicks with an ICI smaller than 0.1s (Johnson *et al.*, 2006). When visual data are difficult to access, acoustic brought precious lacking information. In the area, three species are thought to be present: Cuvier's beaked whale, Gervais' beaked whale and Blainville's beaked whale.

PAMguard 2.01.05 Beta was configurated to post-process the data with a sixth-order bandpass Butterworth pre-filter with cutoff frequencies from 16 to 90kHz and a trigger threshold set at 10dB from 16 to 90kHz.

In this study case, semi-automated methods were used. Click classifiers were set depending on peaks frequency. Like so, PAMguard ran every sound files with detectors identifying 4-15kHz peak, 15-30kHz peak, 30-50kHz peak, 30-50kHz upsweeps, 50-80kHz peak and unclassified clicks (clicks that are possibly under or above the click range), these click classifiers was described by Keating and Barlow (2013). All these parameters enabled to filter out any unwanted sounds recordings such as dolphin whistles, sperm, pilot whales or *Kogia* spp. clicks from this analysis. *Ziphius* sp. and *Mesoplodon* spp. clicks ranged between 15 and 50kHz, depending on the species. At this stage, the algorithms did not discern the sounds to a species-level but as a family guild, this was done manually. Once clicks were detected, it was possible to extract relevant acoustic features for each click. This included measures such as duration, intensity, type and interclick-interval. From this information, it was feasible to identify the species of the individual.

Species were identified using recognisable patterns in the sound files. Cuvier's frequency peaked from 18kHz to 39kHz, Gervais' started at 30/33kHz and had a frequency peak at 38-40kHz with a secondary peak at 46kHz when Blainville's started at 26kHz, for a duration of ~0.3 to 0.5ms. ICI were different regarding to genus; *Ziphius* sp. ICI was estimated at 0.4-0.6s, when *Mesoplodon* spp. ICI was estimated between 0.2-0.4s (Baumann-Pickering *et al.*, 2013; DeAngelis, 2019). Wigner-Ville transformation plot was used to check for the verification of Frequency-Modulated upsweep clicks. These plots were quadratic time-frequency representation used to investigate the time-frequency structure of cetacean clicks (Yack *et al.*, 2013), it visually indicated the form of the FM clicks, which were species-specific figures. Click recognition was also made using the click waveform display and frequencies were

checked with the click spectrum, both available on PAMguard.

This author differentiated certain detection against potential detection. A detection was declared certain if the click had a clear waveform, frequencies and Wigner plot resembling those of published and mentioned earlier, but also potentially formed a click train. A potential detection was considered when the click forms and frequencies were uncertain for the acoustician point of view or not exactly as expected from the literature. Single click that did not form a click train but matched with species-specific characteristics was considered uncertain.

3. Results

3.1. Effort

Observations were realised in the Exclusive Economic Zone (EEZ) of each sampled islands.

Most Ziphiidae ($n = 12$) were sighted in the south or centre of the Lesser Antilles, across the years (Figure 3A). Few individuals were observed in the northern region, only one was sighted near Saba in the North in 2022. Nor Antigua and Barbuda nor Montserrat and the other northern islands present any observations. The southern region accounts for almost half of the sample. Saint-Vincent and the Grenadines are the islands with the highest number of sightings with six observations. Both Saint Lucia's and Martinique's waters account for five observations each. Dominique and Guadeloupe draw a tendency to less sightings as it goes north with three and two observations, respectively. The sampling effort is significantly not the same around all islands (Kruskall-Wallis, p -value < 0.001). The standardized sampling effort have been illustrated in figure 3B.

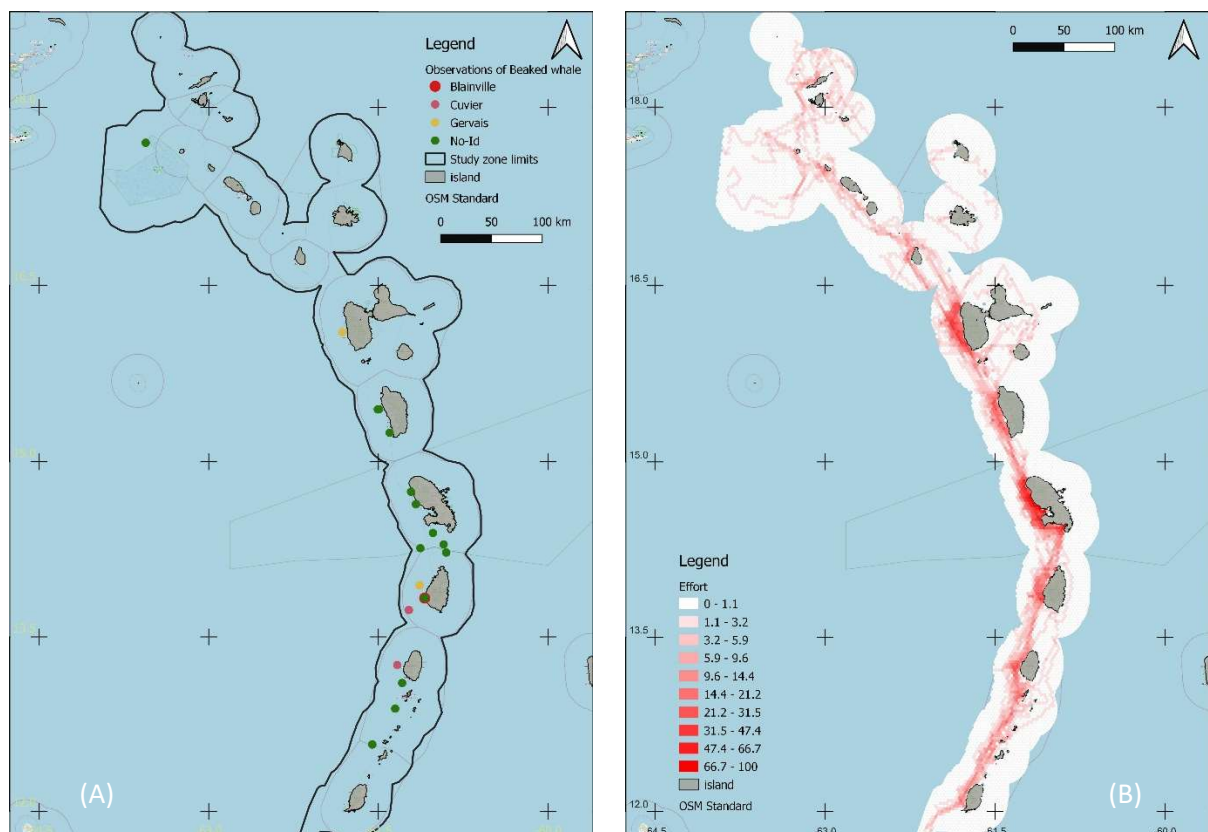


Figure 3. (A) Map of the observation points of beaked whale and (B) map of the observation effort of the 'Ti Whale An Nou' project between 2021 and 2023

Some areas have been sampled with a bigger intensity (Figure 4.), especially the Caribbean side of the Martinique and Guadeloupe ZEEs, in

fact, some areas of Martinique have been sampled at 100% for a coverage of 25% of the ZEE. In Guadeloupean waters, prospection for

beaked whales sometimes reached almost 50% in certain areas. However, Martinique ZEE is the most sampled ZEE compared to size considering our study zone. Dominica ZEE is the second most covered ZEE with 10%. The least studied islands were the Saint-Martin islands (Collectivity of Saint-Martin (FR) and Sint-Marteen (NL)), Saint-Barthelemy and Saint Kitts and Nevis.

Knowing the region repartition of the islands, there is an apparent difference in beaked whale prospecting between the North area and the Centre and South areas, that are visibly more investigated. Most sampling took place on the Caribbean side, resulting in underrepresentation of the Atlantic Ocean.

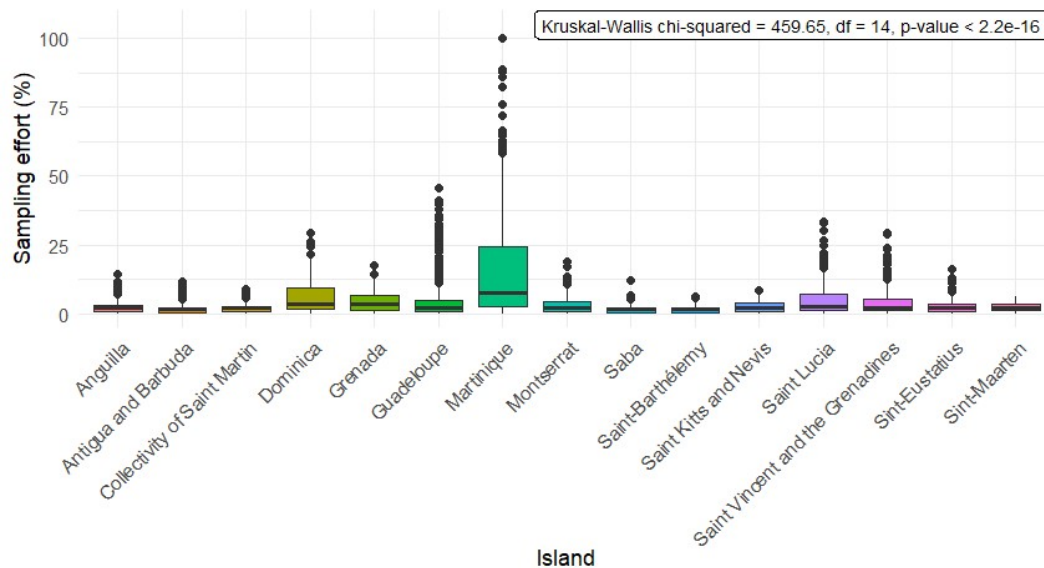


Figure 4. Repartition of the sampling effort for each island's EEZ between 2021 and 2023, dots represent the normalised effort in the sampled hexagon of the study grid.

3.2 Visual study

In total, 18 expeditions have been led in the Lesser Antilles by the CCS between 2021 and 2023. Beaked whales were witnessed 22 times (2021: n= 4, 2022: n= 10 and 2023: n= 8), photo-identification data were collected in 11 of the 22 observations (Figure 2A).

In most cases, identification was limited to the family level and did not enable species identification. In that case, they were classified as “unidentified beaked whale”. The detection was also classified as certain or uncertain, in total 8 observations out of 22 were classified as certain. When possible, with sufficient visual clues individuals could be identified to a species level and classified as Gervais’ beaked whale or Cuvier’s beaked whale. Post analysis of pictures allowed us to specialize the authentication of some unidentified Ziphiidae. From that, one

individual was identified as a possible Blainville’s beaked whale, visual confirmation of this sighting was not possible due to the photo-id quality. At the end, 16 observations were visually classified as unidentified beaked whale, three as Cuvier’s beaked whale, another three as Gervais’ and one as Blainville’s. With these data, we were able to create a catalogue of 28 potential individuals classified according to the shape and form of their dorsal fins, all uploaded into the website Flukebook. Despite a dedicated algorithm specially designed for this study on Flukebook, no match were detected. From the CCS observations only, no individual was seen twice.

In terms of population structures and according to the estimation of group sizes, at least 48 individuals were perceived (max = 62, min = 43), within groups on average of 3.53 individuals

(CV= 62.03%). Three calves were witnessed with adults.

3.3 Distribution model

From these 23 observations of beaked whales and the distance they were sighted from, a density graph based on detection distance was established. A maximum of beaked whales was detected at 166.5m from the boat (maximum of the density graph), which corresponds to the associated probability of 1, which means that between 0m (i.e. the boat) and 166.5m, we consider that all possible beaked whales are detected. The rest of the densities were divided in three equal parts that correspond to the probability of 75%, 50%, and 25% of observing beaked whales. The associated distance ranges were respectively assigned to 166.5-261m, 261-500m, 500-1000m, meaning that after 1000m, the possibility to detect ziphiids is outdated (Figure 5).

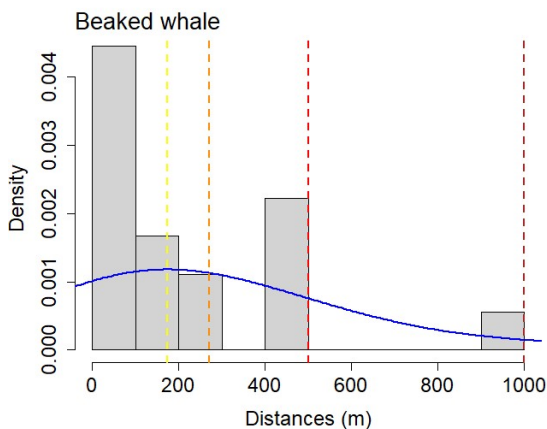


Figure 5. Observation density based on detection distances. The yellow line indicates the maximum of beaked whales detected around 166.5m, the other lines (orange, red, brown) are affiliated to the detection distances (261m, 500m, 1000m, respectively).

To model the distribution of beaked whales in the Lesser Antilles, 14 environmental predictors were considered. Both mean (indicated by the name of the variable) and standard deviation of the environmental variables were tested to look for correlation between them using Pearson's correlation test (Figure 6). Highly correlated variables were removed from the same model framework.

Environmental variables	Abbreviation
Depth	Depth
Slope	Slope
Roughness	Roughness
Isobath distance 200m	dist_iso200
Isobath distance 1000m	dist_iso1000
Isobath distance 2000m	dist_iso2000
Distance to the canyon	dist_canyon
Sea surface temperature	SST
Sea surface height	SSH
Eastward current	East_Currents
Northward current	North_Currents
Eddies Kinetic Energy	EKE
Chlorophyll a concentration	CHL
Mixed layer depth	Mixed_Layer

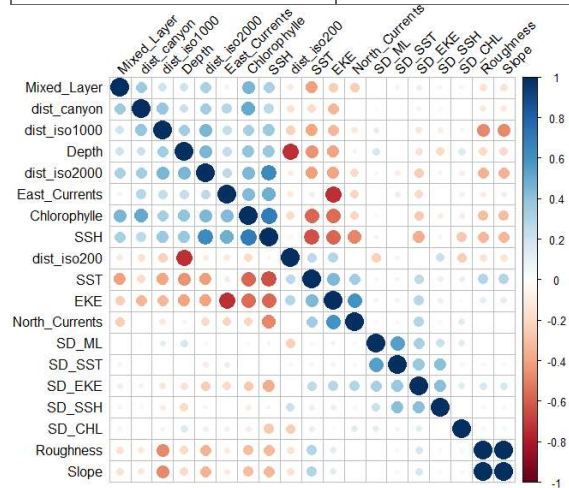


Figure 6. Correlation matrix of the environmental variables (top) and table of the abbreviation used in the matrix (bottom).

With consideration to the correlation between variables, a total of 4577 different associations of one to four variables were tested. To choose which model was most appropriate, we used the delta AIC. In that way, seven models were retrieved from the simulation (table 2), they each present variables that could influence the distribution of the target species. In all these simulations, one variable is recurrent in every one of them, which is the EKE. Variables related to the bathymetry is also quite repetitive, as either the 1000m isobath distance or the depth are illustrated. For the first two model predictions, three variables are identical (isobath 1000m distance, EKE and SD_EKE), these variables are thus capital. The lowest AIC

score (i.e. 114.3491) suggests that the most relevant model incorporates the distance to the 1000-meter isobath, Eddies Kinetic Energy (both mean and standard deviation) and the standard deviation of the sea surface temperature as the most plausible model.

These variables appeared as the most relevant variables to model the distribution of Ziphiids in this study, however each considered covariates have been classified depending on the importance it has in the weight of the model combination.

.	Model	AIC	ExpDev	Delta.AIC	RELM	Akaike.weight
1	dist_iso1000 + EKE + SD_EKE + SD_SST	114,3491	21,1	0	1	0,028267
2	dist_iso1000+ EKE + SD_EKE + SD_ML	114,4201	21	0,070977	0,965134	0,027282
3	EKE + SD_EKE + SD_SST + SST	114,8876	20,6	0,538436	0,763977	0,021595
4	EKE + SD_EKE + SD_ML + SST	115,2363	20,4	0,887181	0,641728	0,01814
5	dist_iso1000 + EKE + SD_CHL + SST	115,5304	19,8	1,181227	0,553987	0,01566
6	Depth + EKE + SD_CHL + SST	115,6681	21,8	1,319001	0,51711	0,014617
7	Depth + EKE + SD_EKE + SD_SST	116,0348	21,9	1,685682	0,430486	0,012169

Table 2. First seven models explaining the distribution of beaked whales. AIC: Akaike Information Criterion. ExpDev: Explained Deviance (%). Delta.AIC: Delta Akaike Information Criterion. RELM: Restricted Maximum Likelihood.

So, the number of time a variable is computed into a model distribute its importance. The weight of each covariate was assessed by counting the number of times it appeared in the model combinations, weighted by the Akaike weight of the model. The variable with the highest weight (importance) is defined as the most relevant variable to assess the distribution. Hence, model 1 is the best model for the distribution of beaked whales.

It should be noted that the importance of covariates is not directly related to the model. EKE is the most important covariate with 88.9%, followed by the SST with 47.4%. this second

covariates is however not represented in the model (Figure 7.). In the chosen model, the standard deviation of the sea surface temperature was chosen but stands 7th most important covariate, meaning that it does not weigh much in the model combinations but does have a strong influence on the distribution. Also, the distance to the isobath 1000m despite being the first variable in the distribution model, only weigh for 39.2% in all the model combinations.

The smoothed functions of the selected model's variables were plotted (Figure 8.) and acknowledge the contribution of each predictor by representing the relation between it and the response variable. The Y axis speaks for the prediction of the observation's frequency when the X axis speaks for the values of the predictor in the area. The black dashes on the X axis represent the distribution of the variable's values in the targeted area. The associated maps (Figure 9.) offer a better visualisation of the predictors and their variation in the area with the observation points of beaked whales.

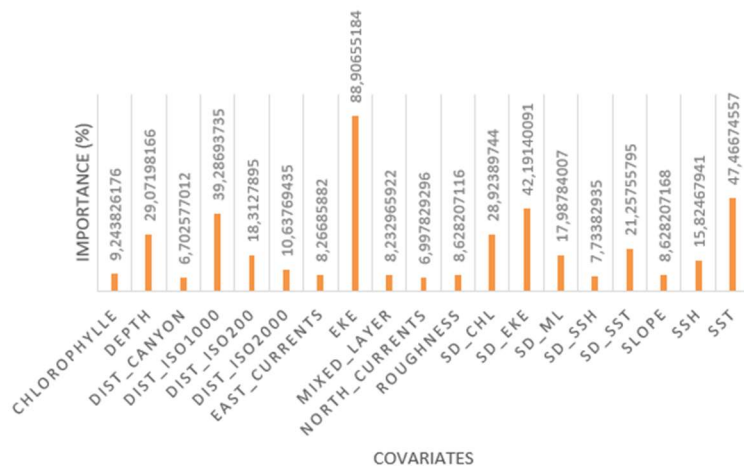


Figure 7. Importance of covariates considered in the models.

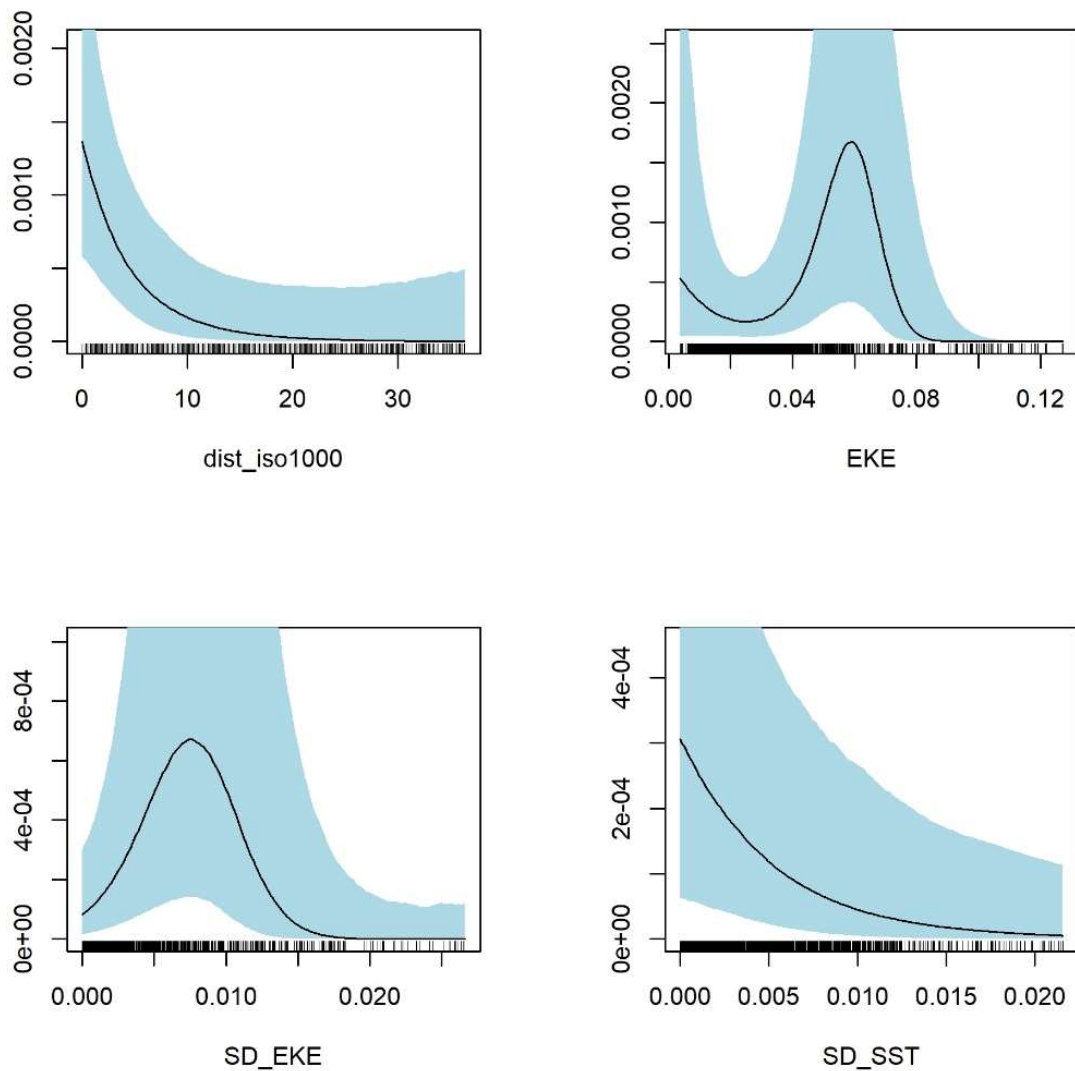


Figure 8. Smooth functions of selected variables for the distribution model of beaked whales. On the Y axis is the prediction of the observation's frequency. The X axis is the values of the predictor in the area. The black dashes on the X axis represent the distribution of the variable's values in the targeted area. The continuous lines represent the estimated smoothing functions, and the blue areas correspond to the 95% confidence intervals.

One can notify that most observations of beaked whales follow the line of the isobath 1000m. The closer to this isobath, the denser the distribution is. It appears that most observed beaked whales were located in a 5 km range from this isobath.

Eddies Kinetic Energy variable appears twice in the selected model, in the mean and standard deviation forms. The graphs indicate that most

beaked whales were spotted around a mean value of 0.06 m.s-1 with a low associated variation (SD =0.008 m.s-1). In brief, most observations were where the EKE was slow with little to no variation to that speed. Despite that the variation of sea surface temperature within the Lesser Antilles is very low, most observations of beaked whales were recorded where there was almost no variation (SD = 0.005°C).

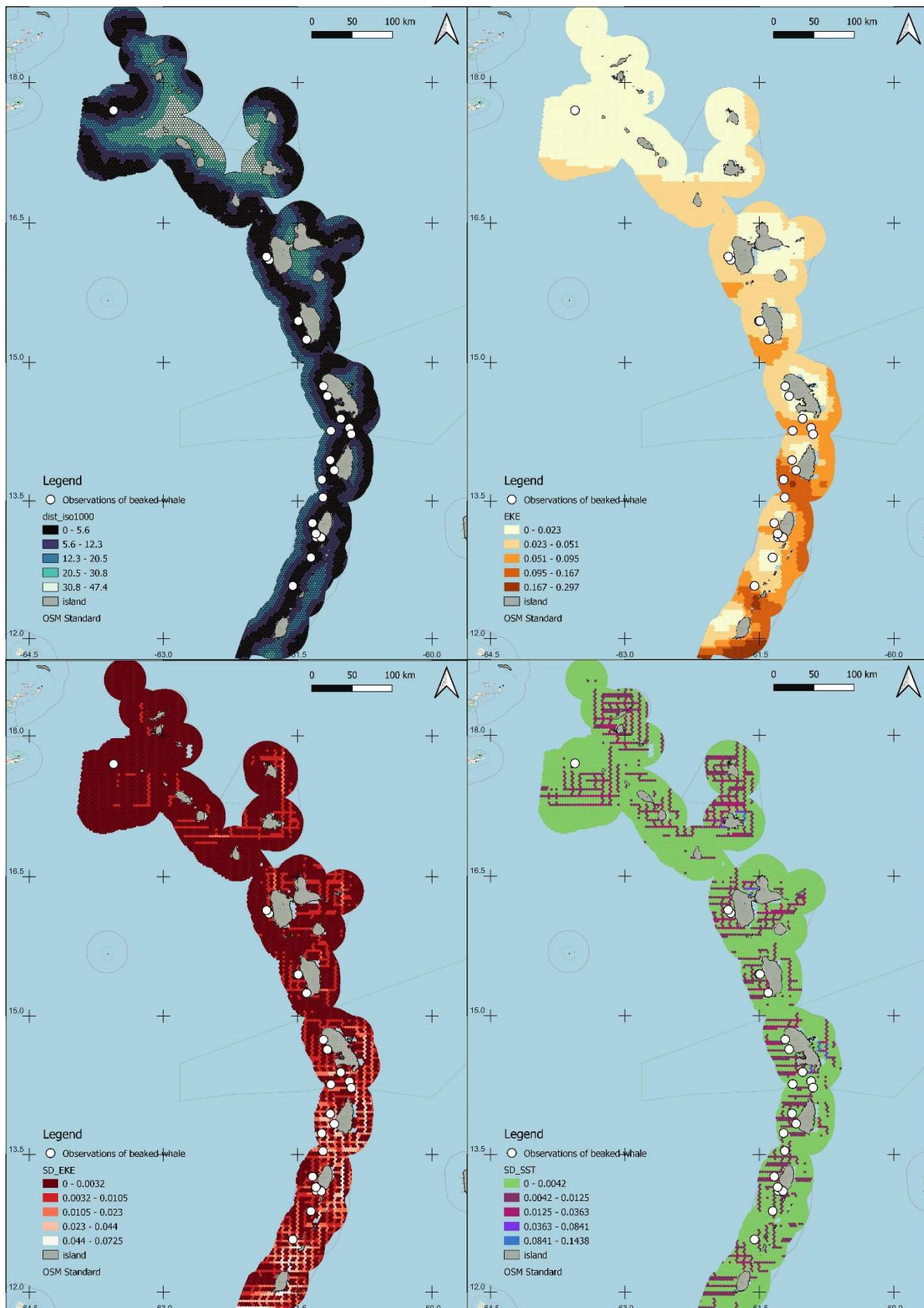


Figure 9. Mapping of the four environmental variables within the study area selected for the modelling of the distribution of beaked whales in the Lesser Antilles. Top left represents the distance to the isobath 1000m (km), top right is the mean EKE, bottom left represents the standard deviation of the EKE and bottom right is the standard deviation of the sea surface temperature. Observations of beaked whales are indicated on each map in white.

Once the model was selected, we were able to draw maps of the relative density of beaked whales. The prediction obtained was associated with its uncertainty, estimated using the coefficient of variation. This illustrates the possible distribution in the Lesser Antilles.

Figure 10 (left) indicates that the potential distribution of beaked whales is mostly concentrated around Martinique in the Channel to Saint Lucia. The probability to encounter

beaked whales in this region of the study area is between 0.01 and 0.02 individual/7.8km² when the density is basically null in the centre and north region. It seems that the biggest density (0.03 individual/7.8km²) of beaked whales is located on the Atlantic side of Martinique. There is a very small probability to encounter beaked whales on the Caribbean side of SVG and Grenada (density ≤ 0.01 individual/7.8km²).

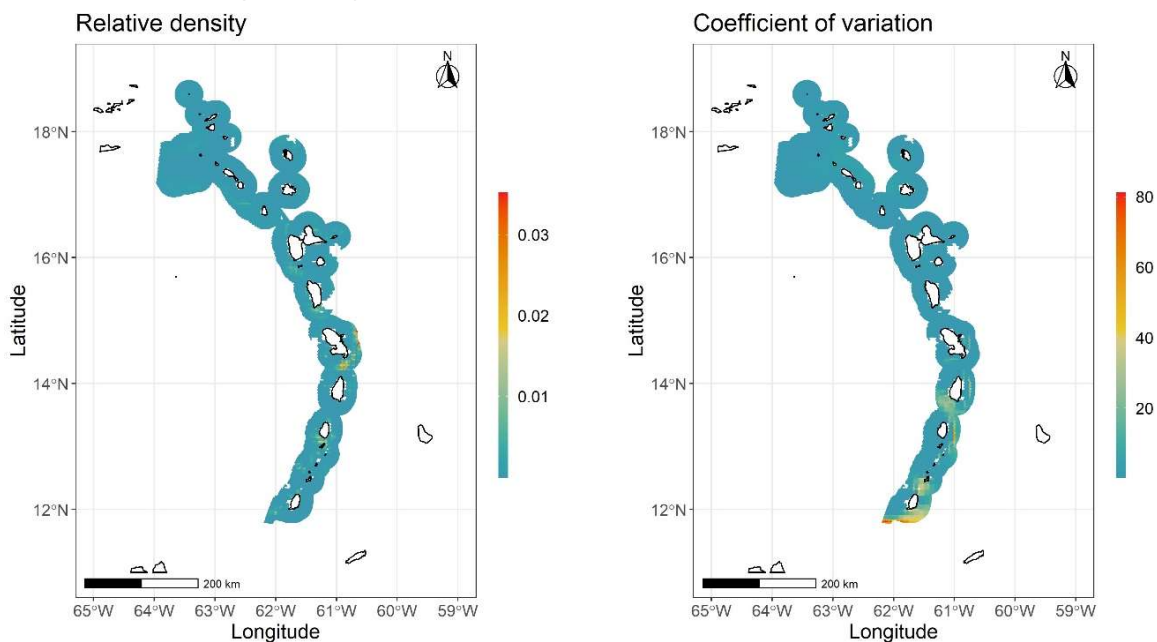


Figure 10. Map showing the prediction for the distribution (individual/7.8km²) of beaked whales in the Lesser Antilles under the four chosen predictors (left). The associated uncertainty map given by the coefficient of variation (%) on the right.

The map of the coefficient of variation (Figure 10 right) reveals strong variations at the south limits of the study area (CV >60%). These coefficients are weak (CV < 30%) in the rest of the study zone, especially within the zones where the prediction for the density of beaked whales were the highest. In both relative density and coefficient of variation, the northern zone is considered null.

3.3 Acoustic study

A total of 226 days of recordings have been collected over the 3-year project, totalling 1785 hours of acoustic data. However, in this analysis, we discarded acoustic data from the 2021 campaigns due to defective recordings. The detection effort was concentrated on days where visual data of beaked whales were acquired. Like so, when observers labelled a

sighting as ‘undetermined’, it is possible to identify the species acoustically. Within these recordings, beaked whales’ signals have been detected at least 132 times over 10 possible detections. In 11 opportunities, no acoustic signals were perceived, either because of a malfunction in the recordings or that they were simply not found, as in no echolocation clicks were visible on the PAMguard software. Among these click types we identified consistent clicks that matched species characteristics such as Gervais’, Blainville’s and Cuvier’s beaked whales. This study is showing one sample of each species detected to show the possible pattern, but all detection were accounted for and considered in the analysis.

The figures that follow present the characteristics of typical clicks from a Gervais’ beaked whale. They were found during the

supplementary expedition on October 2nd, 2022. During this encounter, 86 beaked whale clicks have been recorded. These clicks were emitted during a short period of time, approximately 3 minutes. The duration of each click train have been estimated to 3 seconds, repeated seven times during the pinpointed period, implying gaps between frequencies that vary in duration. Identified clicks depict click trains with frequency-modulated upsweep. The click spectrum illustrates a first peak at 39kHz followed by a second peak at 46kHz, creating the upsweep (green line on figure 11B). The Wigner plot is the visual representation of that upsweep (figure 11C). The mean Interclick-interval for this encounter has been calculated to last ~0.346ms (figure 11D).

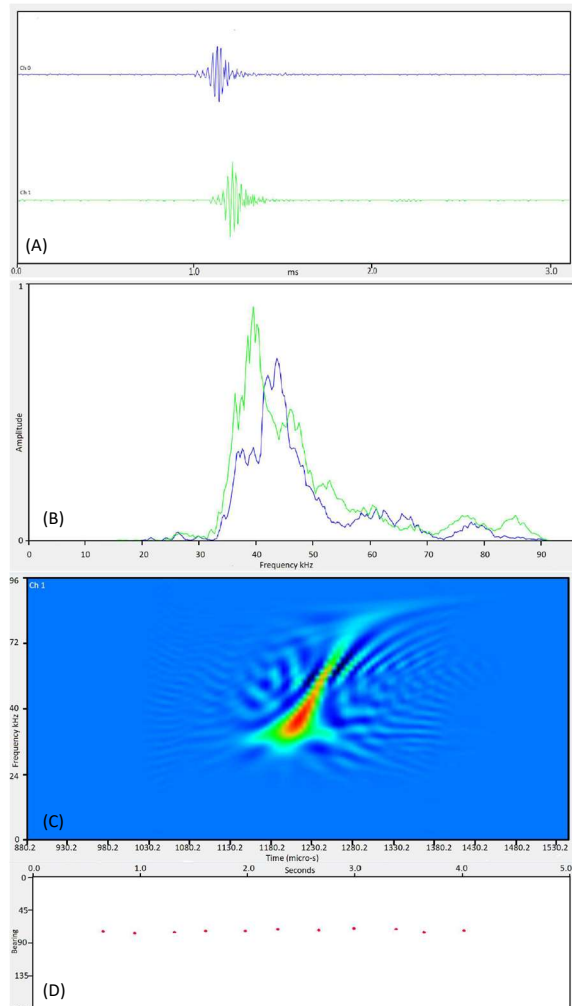


Figure 11. Description of Gervais' beaked whale click using PAMguard. (A) is the waveform display, (B) is the click spectrum, (C) is the Wigner plot and (D) is the click train showing the ICI

Cuvier's beaked whale was detected acoustically on June 26th, 2022. No click train was found, but species-specific frequencies and Wigner-Plot were recognizable over a period of ~5min that day, with 8 perceptible clicks (Figure 12.). The waveform, spectrogram (Wigner-plot) and spectrum representations of that clicks are as followed:

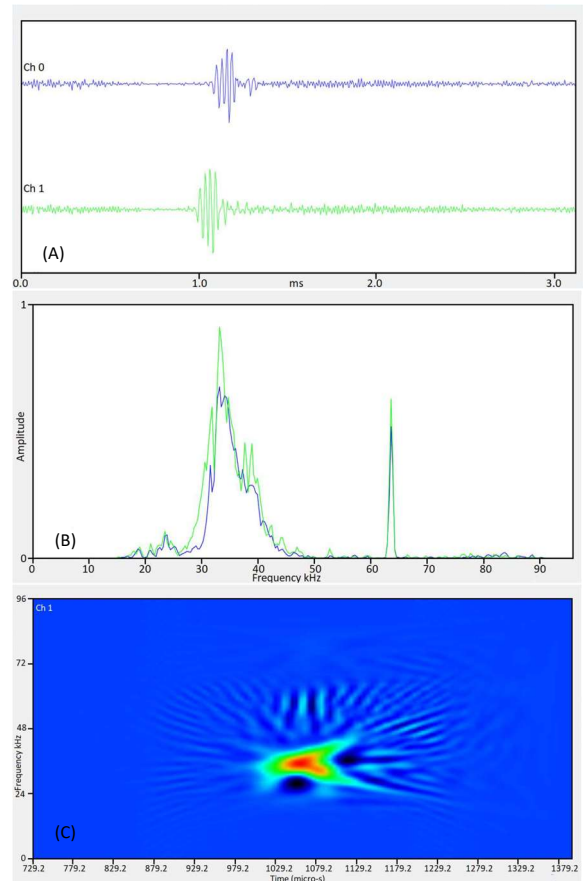


Figure 12. Description of Cuvier's beaked whale click using PAMguard. (A) is the waveform display, (B) is the click spectrum, and (C) is the Wigner plot.

In the literature, Cuvier's beaked whale clicks are described with multiple frequency peaks, here the detection matches with a first peak at 18kHz, followed by two at 23kHz and 33kHz, and finally a click at 39kHz (Figure 12B). *Z. cavirostris* have a distinctive click form (Wigner plot, Figure 12C) that is recognizable by the tail at the bottom of the upsweep. However, no click train was detected, making the estimation of the ICI impossible.

On March 15th, 2023, one click resembling a Blainville's beaked whale click was observed. This detection is classified as potential as no click train was found, also the waveform is not

clearly distinguished. This is believed to be a Blainville click as the frequencies and form of the upswing concord with other descriptions. This detection shows a long (150ms, figure 13C) click starting at 26kHz and peaking again at 33kHz (Figure 13B).

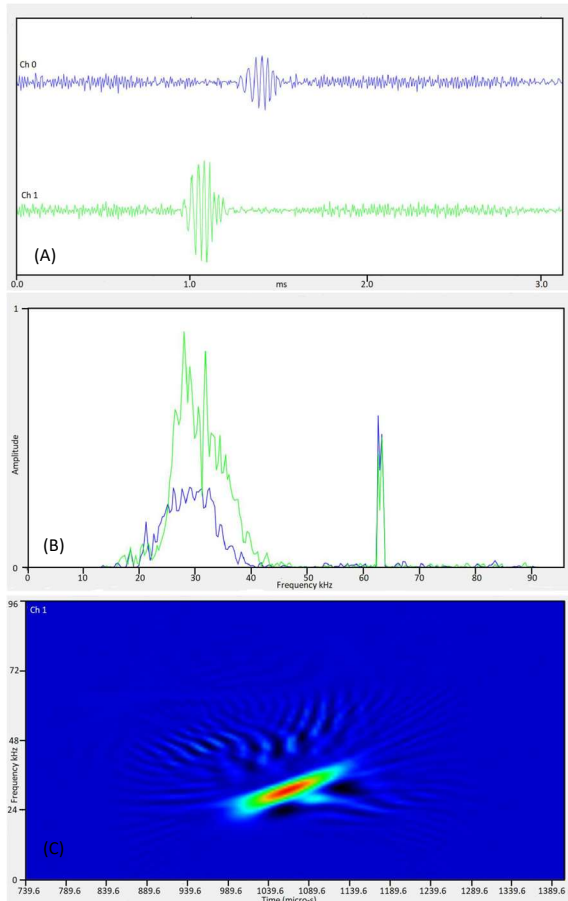


Figure 13. Description of Blainville's beaked whale click using PAMguard. (A) is the waveform display, (B) is the click spectrum, and (C) is the Wigner plot.

Throughout all the data processed, in 2022, beaked whales were encountered visually 10 times, when analysing the recordings on those dates, we counted two potential detections of Cuvier's beaked whales, one potential Gervais' and one clear detection for each species. In six occasions, recordings were either damaged (e.g. contact failure, boat noise overlapping, etc.) or did not exhibit beaked whale acoustic activity despite a visual observation. Four times, the acoustic allowed us to identify the species

of the individual sighted. Indeed, on 16/08/2022, two signals were perceived that potentially match the characteristics of Cuvier's beaked whales. On 24/08/2022, one potential signal of a Gervais' beaked whale was perceived, (however the certainty of the acoustic detection is not established in those cases) and finally on 02/10/2022, the clear detection of Gervais' echolocation patterns allowed to identify the undetermined sighted individual. On June 26th, 2022, the acoustic detection confirmed the sightings of a Cuvier's beaked whale.

In 2023, beaked whales were encountered visually eight times, however, acoustic detections were found in four occasions when analysing data at those days. This allowed to recognize possible detections of three Cuvier's beaked whales and one Blainville's beaked whale. In the four other occasions, no acoustic detections were feasible, either because of boat noise overlapping or missing recordings. Like so, on March 15th, one click of Blainville's beaked whale was found and described as well as potential Cuvier's clicks detected several times minutes apart. On this day, the sighting indicates an undetermined individual. On April 6th, 2023, when a Gervais' beaked whale was sighted, acoustic analysis likely reports three encounters of Cuvier's click characteristics. Finally, on July 26th, 2023, a potential detection of Cuvier's beaked whales was detected with a first encounter of 8 clicks and then 30min later another two clicks, on this day.

Overall, acoustic analysis allowed to detect six signals from visually unidentified beaked whales and assigned them to a species also it allowed to confirm two sightings. With no account for 2021 data, 61% of the recordings did not present beaked whales signals, either because of boat noise or simply because no detection was made.

Date	Visual observation	Precision	Acoustic observation	Precision
08/03/2022	Undetermined	Uncertain	NO	/
28/03/2022	Undetermined	Uncertain	NO	/
26/06/2022	Gervais	Uncertain	NO	/
26/06/2022	Cuvier	Uncertain	Cuvier	Certain
15/08/2022	Undetermined	Uncertain	NO	/
16/08/2022	Undetermined	Uncertain	Cuvier	Uncertain
24/08/2022	Undetermined	Uncertain	Gervais	Uncertain
22/09/2022	Undetermined	Uncertain	NO	/
02/10/2022	Undetermined	Certain	Gervais	Certain
03/10/2022	Undetermined	Certain	NO	/
07/03/2023	Undetermined	Certain	NO	/
15/03/2023	Undetermined	Certain	Blainville	Uncertain
15/03/2023	Undetermined	Certain	Cuvier	Uncertain
16/03/2023	Undetermined	Uncertain	NO	/
06/04/2023	Gervais	Certain	Cuvier	Uncertain
13/06/2023	Cuvier	Certain	NO	/
21/07/2023	Gervais	Certain	NO	/
25/07/2023	Undetermined	Certain	NO	/
26/07/2023	Undetermined	Certain	Cuvier	Uncertain

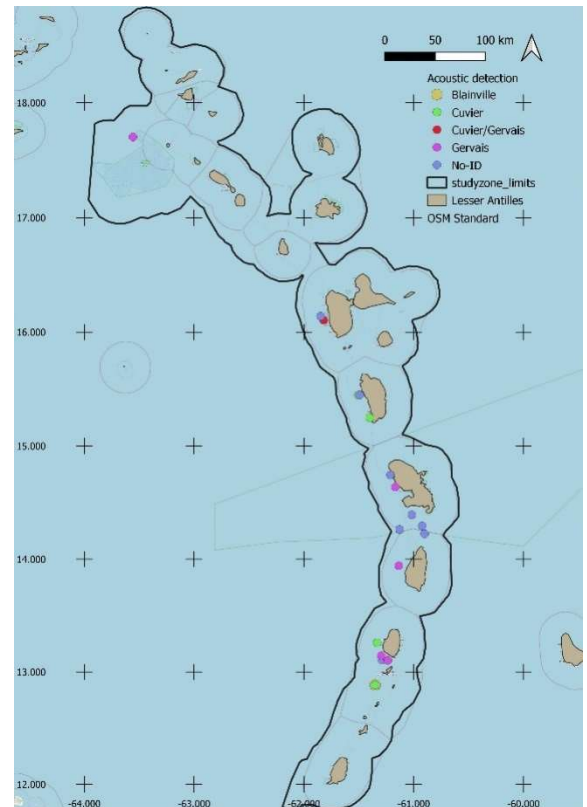


Figure 13. Table of acoustic detection (left) and Map of the locations of beaked whales detected acoustically (2022-2023). Data from 2021 are discarded (right).

In total, combining visual and acoustic identification, 14 individuals were associated with a species, when sightings allowed for seven identification (Supplementary materials). Therefore, acoustic permits to increase species identification by 50%.

4. Discussion

4.1 Study limitations

Due to the complexity of the Caribbean environment, the standardized protocol has been established to be capable of performing during every expeditions. Meteorological complications aside, the easiest way to do so was to follow the different islands of the Lesser Antilles on the Caribbean side instead of the Atlantic side. This results on uneven sampling effort making possible Atlantic population and distribution estimations biased. Also, staying quite near the coast, i.e. 12 km on average, blocks the access to more offshore data (Hazen *et al.*, 2011). Despite the prevalence for the Caribbean side, even this zone is not evenly studied. Martinique is oversampled as a result

that all expeditions leave from the marina of Le Marin at the south of the island. Also, additional expeditions are usually led around Martinique, and more generally in the Centre region, adding more sample data to this area, leading to under sampling the other islands' waters.

Sampling is not systematic. Indeed, when on effort, transects are influenced by the spotting of animals as once one is sighted, the boat changes its direction to the animal's in order to acquire photo-identification data. This does not allow a strong approach like "distance sampling" which could provide estimates of the average density across the area (Henrys, 2010). Hence, the biggest issue in this research is the lack of data. The rarity of observations of these deep divers is even more complexified by the fact that the 'Ti Whale An Nou' program is still at its early beginnings. The CCS is also not only focusing on beaked whales. With other more common cetacean species, the CCS was capable of collecting sufficient data over the three years. The cryptic behaviour of our studied species may require more time to have access

to a considerable amount of data to study their actual spatial ecology in the Lesser Antilles Arc. However, that is not an isolated case, most studies indicate an important lack of data to set up proper species distribution models in their study area if not for considerable time (10+ years) and technical means (Kasuya, 1986; McSweeney *et al.*, 2007; Arcangeli *et al.*, 2016; Rogan *et al.*, 2017; Cañadas *et al.*, 2018; Foley *et al.*, 2020).

This study was based on the tracking made over the past three years and only 22 observations came out of it. It represents an excessively low set of data to predict the distribution of a species, even more if we consider that this study looks for several species of one family. The low size sample emphasize the truncated probability to encounter on multiple occasions the same individuals, thus permitting mark and recapture estimates. Also, out of these observations, photo-identification were taken in 11 cases at most, thus limiting the individual identification capacity.

There is also the observer bias to consider; detection is greatly influenced by the observers onboard, the latter not always being professional but also simple passionate and volunteers that never had that kind of experience before. It takes time to calibrate once capability to spot cetaceans and apply the protocol set during the surveys (Oliveira-Rodrigues *et al.*, 2022).

All that combined, the detection process can be influenced and thus the distance to which they are spotted. That creates a bias in the elaboration of the sampling effort. In a cascade effect, the prediction is possibly also influenced by that overestimated effort.

GAM limitations

Despite being a performant tool to understand the spatial arrangement of a species, SDMs also present some limitations. Their effectiveness can be hindered by factors such as survey design, low sample size, or weak model performance. The 'Ti Whale An Nou' program does not exhibit a precise survey design, it comprises opportunistic sighting along a

scheduled line from a departure and an arrival point, thus some zones were more sampled than others. Nonetheless, it has previously been defined that the survey design has no major influence as long as it covers diverse environmental conditions, allowing for the identification of preferred environmental conditions for the target species (Tessarolo *et al.*, 2014).

Beaked whales are one of the rarest cetaceans to observe. With fewer data points, it becomes difficult to perform robust model selection, potentially resulting in the selection of overly complex models that do not generalize well (Fiedler *et al.*, 2023). Small sample sizes may limit the statistical power to detect meaningful relationships between predictors and the response variable, leading to inconclusive results or false negatives.

Finally, GAMs rely on the assumption that the relationships between predictors and responses are smooth, which may not always hold true in real-world scenarios, potentially leading to biased estimates. Hence, a long-term study of beaked whales in the Lesser Antilles is needed to improve the validity and fidelity of the predictions.

Acoustic limitations

When on field, meteorological conditions can degrade recordings greatly, which reduce detection probability. Boat engine noise is often overlapping the sound that the hydrophone captures as well. Like so, it is possible that some data are missing for that reason (Folegot *et al.*, 2016).

Like in visual studies, the experience of the analyst is an important bias. In this study, the lack of practice may have led the author to miss clicks and thus to not identify possible encountered individuals.

During this study, we also noticed that some acoustic files were damaged for unknown reasons and consequently impossible to analyse.

In respect to these limitations, the conclusions we make in this study must be taken with caution.

4.2 Distribution, movements, and habitat use of beaked whales

Presence of beaked whales in the Lesser Antilles

Photo-identification data were collected in 11 of the 22 beaked whale sightings. Timid apparitions of the animal combined with bad conditions (meteorological and personal, i.e. seasickness, experience, vision, etc.) complicated data acquisition. Despite that, there is a visible increase of sightings and photo-id available as the project's participants gain experience and have better means.

We are aware of the presence of beaked whales in the Lesser Antilles from previous species-inventory surveys in the area (J r mie S. (SEPENMAR), 2003 – 2019) but this lays the first ever study of the distribution of ziphiids in these waters. In three years, the CCS was able to identify several individuals of ziphiids, describing their occurrence as a family in the different areas of the Lesser Antilles Arc.

When we get the chance, species identification was made; this delivers the opportunity to verify the existence of three different species: Cuvier's beaked whale (*Z. cavirostris*), Gervais' beaked whale (*M. europaeus*), and Blainville's beaked whale (*M. densirostris*). We can explain that *Z. cavirostris* and *M. europaeus* were encountered, first and foremost because Cuvier's is the most cosmopolite beaked whale in the Atlantic tropical ocean and Gervais' is nicknamed the Antillean beaked whale, implying that the Antilles are possibly their preferred habitat in the Atlantic Ocean (McLeod et al., 2006). In fact, Gervais' beaked whales have been sighted at the top north (Gillespie et al., 2009) and bottom south of the Caribbean Sea (Rosario-Delestre, 1999), as well as in the ABC islands (Debrot et al., 2011). On the other hand, the detection of a Blainville's beaked whale is rarely reported in the Lesser Antilles,

thus exhibiting the scarcity of information on that species.

However, on-effort identification is often compromised as the surfacing angle of these animals rarely exhibit the beak properly, only Blainville's beaked whale are thought to be capable of surfacing at a low angle showing both their head and dorsal fin at the same time (Carwardine, 2020), thus when both these features were perceivable, we assumed that species identification is feasible. However, there is no record of Blainville's beaked whale in the Lesser Antilles Arc so far, except for one in the Guadeloupean Archipelago in 2003 (Rinaldi, 2007). In the Caribbean Sea, their known range is more likely to be in the Bahamas (Claridge, 2006; Dunn, 2014), it could thus be mistaken with another species that also exhibit this behaviour but hasn't been documented.

Beaked whales were rarely sighted alone, but mostly in small groups. In fact, beaked whales usually live in small groups, protection against predators such as sharks or killer whales is the hypothesized lead to explain this behaviour (Dunn, 2014). In most species, social groups are formed of one mature male and several females, this harem can count calf and juveniles. Male sub-adults are often outsiders, evolving alone until they reached maturity (Claridge, 2006; Hooker et al., 2019; Carwardine, 2020).

Movements of beaked whales

There is no evidence of migration patterns between the studied species (Foley et al., 2020). Also, there is no proof that beaked whale populations can be endemic to a given area.

With a lack of rematch during this project so far, we are unable to reckon possible movements of beaked whales within the Lesser Antilles. We were the first to use the beaked whale algorithm in Flukebook, so we were unable to assess if photo-identification research were already made in this area and with these species, and so collaboration was impossible.

Species distribution model

The combination of ambiguous identification principally due to the visual species discrimination bias, their avoidant behaviour regarding boats or any human structures and a low sample size explains why the distribution was fit into a family-guild model instead of a species-guild model. The beaked whales distribution model presented here lays the first density estimations of that family in the Lesser Antilles.

The model predicted ziphiids densities in the entire Lesser Antilles less than 0.01 individuals, with maximum densities around Martinique.

The final model for Ziphiids distribution included the distance to the isobath 1000m, Eddies Kinetic Energy, standard variation of EKE and standard variation of Sea Surface Temperature. GAMs predictions highlight that the preferred habitat for beaked whales in the Lesser Antilles seems to be in the South region where the variation in sea surface temperature and EKE is low and the mean EKE is high. There is also clear evidence that the distribution of beaked whales follows the isobath 1000meters. Most observations were made directly “on top” of that hypothetical line. Topography is a known factor for the distribution of cetaceans (Cañadas *et al.*, 2022; Hamazaki, 2002) Past research has shown that in the Tyrrhenian or the Mediterranean Sea *Z. cavirostris* prefers areas with depths over 1000m (Arcangeli *et al.*, 2016; Cañadas *et al.*, 2018). Closer to our study range, Claridge (2006) described that in the Bahamas, Cuvier’s beaked whale located in 1000meters deep area. Davis *et al* (1998) also found that *Mesoplodon spp.* and unidentified beaked whales in the Gulf of Mexico exhibits a preference for habitat of great depth (around 1200m). With that in mind, it seems likely that the worldwide spatial ecology of this family is concentrated around this 1000m deep key feature, in our study case it is an important covariates as it weighs for 39.2% in all model combinations.

Taking that into consideration, the scarcity of beaked whales in the northern range of the Lesser Antilles can be explained by the distance

to this isobath from the coast. Indeed, the modelling of their distribution portrays a null density with no variation above Guadeloupe. Linking that information with the tracking of the boat of all north expedition combined, we remark that the sampling occurred near the coast (around 12 km) and far from that isobath who is almost on the limit of the study zone and where sampling did not occur often (figures 1&3B), indeed, the northern part of the Lesser Antilles arc have a larger continental plate, expending far offshore the continental slope and greater depths (Barrera-Lopez *et al.*, 2022). Even if the prediction highlighted that beaked whales can be at 5 kilometres from it, the effort was not able to capture this information, as the limits of the boat tracking and distribution range do not overlay. We may hypothesize that the lack of data within the north region is a result of not sampling the right places instead of a total absence of beaked whales within this range. McSweeney (2007) mentions that the absence of data about a species during a said period of time and area is not regarded as the absence of the species itself but rather reflect a low density of these cryptic species that perform long dives. We explain the distributions of any predator by the availability of their prey in a habitat. Cetaceans and consequently beaked whales are top predators. Diet studies have shown that the majority of beaked whales feed primarily on deep-sea cephalopods (McLeod *et al.*, 2003; Santos *et al.*, 2007). A lot of the chosen variables in this study were chosen because they were indirect proxy for prey aggregation and do not refer to the distribution of said prey items but more their presence. Indeed, prey abundance data are often lacking and difficult to access. Hence, the distribution of cephalopods is impacted by environmental factors. Seafloor physiography is one of them as it provokes mechanisms that favours the presence of prey like the topographically induced up-welling of nutrients (Rueda-Roa *et al.*, 2007; Huang *et al.*, 2020). This up-welling affect the Eddies Kinetic Energy that was proven as the most important covariate for the distribution of Ziphiids (88.9%). Indeed, a strong

EKE indicates the formation of eddies and so the re-suspension of sedimental particles that concentrate phytoplankton increasing productivity and prey aggregation and finally explaining the presence of foraging odontocetes (Romagosa *et al.*, 2020). EKE is determined by a formula linking eastward and northward currents, and the mesoscale prey distribution is influenced by regional currents. In our study zone, the West Caribbean current (Mariano, 2003) redistributes the nutrients from south to north, through processes in the water column like upwellings and increased horizontal flux (Romagosa *et al.*, 2020). It has been proven (Biggs *et al.*, 2000) for other deep divers, like sperm whales, that they prefer habitat in cyclonic eddies which are mesoscale structures aggregating plankton that attract a large concentration of the preys deep-divers are looking for in the nutrient-rich water column.

Cetaceans are warm-blooded mammals; they are not directly affected by water temperature thus only the availability of prey truly dictate their distribution (Lerebourg *et al.*, 2023). Although, this is essential to consider these variations as mean SST lays as the second important covariates (47.4%). The chosen model indicates a high distribution of beaked whales where variations of that temperature are low. Like so, beaked whale distribution can be sensible to temperature change within their habitat. However, Ziphiids are a major understudied family, the effects of changing temperatures are thus unequally estimated. With these findings, further studies may be needed.

Beaked whales forage at depth. Like many deep-divers, information on potential deep layers preys could be gathered by collecting deep variables characteristics to improve current habitat models (Virgili *et al.*, 2022).

To this day, the understanding of the environmental factors truly influencing the distribution of beaked whales remains incomplete, which makes the predictions of the distribution model uncertain.

Although modelling a species distribution helps understanding how a population can use a

habitat, it does not reflect reality but only tries to be the closest to reality with the data available for this given study.

4.3 Acoustic of beaked whales

During this study, the aim was to describe the echolocation click patterns of the beaked whales present in the Lesser Antilles. This lays the first basis of beaked whales acoustic in this part of the world. Further studies will be needed to possibly establish the distribution of beaked whales or describe their populations and behaviour acoustically in the area. Nonetheless, this study focused on linking the visual observations of beaked whales to acoustic data, therefore only days where they were spotted were analysed acoustically, thus being able to clarify an undetermined Ziphiidae species from a sighting through acoustic recognition. The fact is that the observed individual may not necessarily be the one detected acoustically. However, the detection could possibly clarify the species present in the area at this time, as there is no evidence that different species of Ziphiidae mingle together. Beaked whales clicks and acoustic patterns are well described in the literature. It is known that Ziphiidae echolocates in a species-specific way, where click frequencies and patterns differ from genus and species (Baumann-Pickering *et al.*, 2013).

Accordingly, this study recognized three possible click patterns belonging to the echolocation signals of Gervais' beaked whale (*Mesoplodon europaeus*), Blainville's beaked whale (*Mesoplodon densirostris*) and Cuvier's beaked whale (*Ziphius cavirostris*). Although studying acoustics when beaked whales were sighted, it does not necessarily mean that the beaked whale 'heard' was the one seen at the surface.

In the case of Gervais' beaked whale detection, we identified peak frequencies that match with the literature (Baumann-Pickering *et al.*, 2013) with 2 peaks at 39KHz and then 46KHz highlighting the upsweep pattern. However, despite *Mesoplodon* spp. interclick interval ranging from 0.2 to 0.4 seconds, in the area, it is

believed to be on the shorter side with ICI = ~ 0.27 s in the Bahamas (Gillespie *et al.*, 2009). In the Lesser Antilles we identified an ICI of ~ 0.34 seconds. Thus, from two close locations, this proves the hypothesis that acoustic population of beaked whales also have some variability within their geographical distribution as shown for Blainville's beaked whales by Baumann-Pickering *et al.* (2023), that exhibit regional variations. Thus, it is of considerable importance to be capable of describing the click sequences of the different beaked whales present in one place.

No click trains were ever detected for both Blainville's and Cuvier's beaked whales on the days analysed. Despite that, these detections assure their presence in the Lesser Antilles.

Moreover, Cuvier's beaked whale echolocation clicks were often detected without a clear click sequence but most of the time, detections were repetitive over a period of several minutes. Cuvier's beaked whale click frequency exhibits a crescendo upsweep pattern already described in the literature (Zimmer *et al.*, 2008; DeAngelis, 2019). However, the frequencies to which they emit seem to vary in locations (Zimmer *et al.*, 2008).

Blainville's beaked whale clicks are well described in the northern Caribbean (Claridge, 2006; Dunn, 2015), it is interesting to find a possible detection in the Lesser Antilles, that would possibly extend their range to the southern Caribbean. In this study, the potential click found has similarities to what is found in the literature with a starting frequency at 26KHz, however that long click peaks again at 33KHz when it has been documented at 38KHz (DeAngelis, 2019) or even 45KHz in the Bahamas depending on sex and age of the individual (Dunn, 2015). Again, this validates the idea of regional variation among beaked whale echolocation clicks.

Detection of beaked whale echolocation clicks are compromised by marine traffic. Some recordings were compromised by parasite sounds that were recognized as motor engine. Cholewiak *et al.* (2017) studied the probability of click detection and showed that acoustic

detection of beaked whales significantly decreased when shipboard echosounders were in operation. Moreover, during periods of echosounder activity, the duration of detectable clicks was reduced, thereby limiting the tracking range. This overlap of frequencies by boat noise not only hampers the detection of clicks but also likely disrupts intra-species communication among beaked whales.

Gillespie *et al.* (2009) highlighted other challenges in acoustic studies that are consistent with the present study. Indeed, the acoustic environment is often contaminated by signals from other marine species, which can interfere with the detection of beaked whale clicks. Also, the likelihood of detecting beaked whale clicks diminishes significantly with increasing distance between the individual and the hydrophone due to the directionality and propagation loss but may increase if a group is vocalizing (Zimmer *et al.*, 2008). Finally, beaked whale clicks can exhibit low amplitude, making them challenging to detect and record accurately, especially in noisy environments.

This study, which aims to correlate visual sightings with acoustic detections, must also consider the behaviour of beaked whales during their dives. Beaked whales do not vocalize throughout their entire dive duration. Studies have shown that they remain mostly silent during ascent to the surface and descent after surfacing, likely as a predator avoidance strategy (Stanistreet *et al.*, 2022). The minimum depths at which they begin or cease vocalising vary by species. For instance, *Z. cavirostris* are typically silent from the surface to around 475 meters during descent and from 850 meters to the surface during ascent. Similarly, *Mesoplodon spp.* are believed to stop vocalising from 720 meters to the surface and resume at around 400 meters when returning to foraging depths (Johnson *et al.*, 2004). Consequently, it is improbable to detect acoustic signals immediately before or after a beaked whale surfaces. Despite observers maintaining a presence at sighting locations to capture acoustic data, it remains possible that no data is acquired.

Ziphiids despite being highly vocal, do not vocalize during the whole duration of their dives. Studies have shown that they echolocate during 20% of their dive (Hooker *et al.*, 2019).

Furthermore, the acquisition of acoustic data is further compromised by the narrow beam directionality of beaked whale clicks. The clicks transmit acoustic energy predominantly forward. Therefore, if beaked whales are not oriented towards the acoustic receivers, the probability of detection is substantially reduced (Hildebrand *et al.*, 2015). This directional characteristic necessitates precise positioning of hydrophones to optimize detection capabilities, which is not always possible with a towed hydrophone.

One way to optimize the detection capabilities in the protocol would be to stay drifting where the sighted individuals were observed to increase our chances to capture their echolocation clicks.

4.4 Interests for conservation purposes – Conclusion

Ziphiids presence have been demonstrated in the Lesser Antilles, exhibiting the use of this particular habitat by two species of this family. Their distribution is correlated with environmental conditions that vary along the arc. These covariates have been evaluated to be static conditions like the distance to the isobath 1000m but mostly dynamic variables as in the eddies kinetic energy and its variations and the variations of sea temperature. However, there are warming trends in the Eastern Caribbean Sea but are not significant in the southern areas along its coastal upwellings (Chollett *et al.*, 2012). There is conflict in the literature whereas beaked whales are affected by the rising of sea temperatures and thus climate change (MacLeod, 2009; van Weelden *et al.*, 2021). Nonetheless further studies on climate impacts on cetaceans and precisely Ziphiidae would be crucial for conservation purposes.

Because the expeditions took place from March to September, we can't consider that the observations are made yearly, thus the distribution and movement of beaked whales

are only predicted for that period of time. With no evidence to possible migration, their presence needs to be proven year-round, or else describe a plausible migration between islands in the Lesser Antilles or in the extended Caribbean. Therefore, incorporating surveys between October and February may change the preceding findings regarding seasonality to propose possible adequate conservation measures.

Marques *et al.* (2019) have proven that using only sightings data to produce distribution and abundance models may be biased as it lowers the accuracy and precision. Consequently, it can be interesting to combine acoustic detection and sightings to better estimate the presence of beaked whales in the Lesser Antilles. Moreover, this study has shown the difficulty for visual species identification, acoustics will account for a more specific estimations of beaked whale individuals with regards to their genus and species. Indeed, in this study species-identification process was increased by 50% after the acoustic analysis. In time, the distribution of beaked whales in the Lesser Antilles could conceivably be studied at a species level.

Strandings of beaked whales occur occasionally but seem to be coincidental with sonar activity within their living range. Simonis *et al.* (2020) have identified in the Western Pacific a strong connection between strandings and the presence of naval (military) sonar activity. Indeed, past research (D'Amico *et al.*, 2009) report that 9% of strandings are linked to sonar operations, when only considering mass strandings. Sonar activity have been documented by Balcomb and Claridge (2001) in the Bahamas and were associated to mass strandings events. Numerous strandings have been reported along the Caribbean islands' coasts. Noise disturbance is believed to cause various threats on beaked whales, from behaviour changes to habitat change. Evidence indicate that beaked whales often flee from their preferred habitat during mid-frequency sonar activity (McCarthy *et al.*, 2011; Tyack *et al.* 2011; Moretti *et al.*, 2014). Some beaked

whale species like the Northern bottlenose whales have shown a capacity to create avoidance responses to these noise disturbances (Wensveen *et al.*, 2019). In either case, this behaviour results in greater energy cost and may disrupt other physiologic capacity like foraging or communications. High traffic and consequently intense ship noise also disrupt foraging behaviour and communication of beaked whales (Weilgart, 2007; Pirota *et al.*, 2012). Cuvier's beaked whales respond to naval sonar by stopping normal feeding and swimming, moving rapidly and silently away for several hours, incurring energetic costs and increased risks of stranding and decompression sickness (DeRuiter *et al.* 2013). Ship noise significantly affects Blainville's beaked whales' foraging movement up to 5.2 km away, reducing their foraging efficiency by over 50% and decreasing communication range fivefold. Blainville's abundance is lower at the AUTEC naval range compared to Abaco, Bahamas, with fewer births likely contributing to fewer animals. Long recoveries after deep and long dives make these whales more vulnerable to displacement and reduced feeding during noise exposure, potentially reducing fitness. Adult females show high residency at naval ranges, especially when pregnant and lactating, putting them at special risk. There is evidence of a possible population-level effect of sonar use at a naval range (Claridge, 2013).

Beaked whales are thus threatened by anthropic noise, and to mitigate and evaluate its potential impact, Marine Protected Areas (MPAs) offer a viable solution. MPAs play a crucial role in the conservation of beaked whales by providing designated zones where human activities are restricted or managed to promote marine biodiversity and ecosystem health. Beaked whales are particularly sensitive to underwater noise, especially from naval sonar and seismic surveys. MPAs can establish noise-reduction

measures, such as restrictions on certain activities or designated quiet zones, MPAs can limit or regulate ship traffic, reducing underwater noise in order to reduce stress and disorientation in beaked whales. This contributes to a safer and quieter environment for beaked whales. For instance, Whitehead (2013) have established a 21% increase in Sowerby's beaked whales sighting rate over 23 years after the Gully submarine canyon have been declared as MPA. In the Canary Islands, sonar ban has been proven effective against mass strandings of beaked whales as none were declared since 2004, date of sonar ban effectiveness, when 14 Cuvier's beaked whales were found at the same place in 2002 (Fernandez *et al.*, 2013).

The study zone of the "Ti Whale An Nou" program covers two marine protected area as in the Agoa Sanctuary (French islands) and the Yarari Sanctuary (Dutch Islands) that focus on marine mammals. The Yarari Marine Mammal and Shark Sanctuary, established in the Dutch Caribbean and the Sanctuary for marine mammals Agoa implement several actions to mitigate noise disturbances in the marine environment. One of their primary strategies is the regulation and monitoring of marine traffic to minimize acoustic pollution from ships. This includes creating guidelines and best practices for ship operators to reduce noise, especially in areas known to be habitats for sensitive species like beaked whales. Additionally, the sanctuaries support research initiatives to better understand the impacts of noise on marine life. This research helps in formulating effective management plans and conservation measures. Both sanctuaries also collaborate with local and international organizations to enhance its efforts in noise reduction and marine conservation (OFB, 2019; Van Bussel, 2019, Madon *et al.*, 2022).

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Supplementary materials

Name	Explications
exp	Numbering of expeditions since the creation of the association
timestamp	Time
Date	Date and time
year	Year
month	Month
day	Day
day_week	Days of the week from 1 to 7: 1 being Monday and 7 Sunday
hour	Hour
min	Minute
sec	Secondes
h	Time
latitude	Latitude in decimal degrees, WGS84
longitude	Longitude in decimal degrees, WGS84
speed	Speed boat
heading	Boat heading
structure_name	Name of the structure that retrieved the data
program_name	Name of research program
type	Type of outing: Expedition, training, whale watching
exp_number	Numbering of shipments for the year
zone	Zone of expedition : Center / North / South
mission_leader	Mission leader
boat_type	Boat model
title	General data title
name	More precise names associated with the title
species_name	Species names and other title information
cet_identification	Species identification: Certain / Uncertain
cet_distance_reticule	Number of reticle counted in binoculars when observing a cetacean
cet_distance_bearing	Angle measured through binoculars during observation
cet_distance_estimated	Distance estimated by the observer
cet_direction	Direction of species or group if traveling: N, S, E, W, NE, NW, SE, SW
cet_boat_around	Number of boats around a group of cetaceans during observation
cet_engine	Is the observer's boat under sail or motor?
cet_est_max	Maximum number of individuals estimated by the observer
cet_est	Number of individuals estimated by the observer
cet_est_min	Minimum number of individuals estimated by the observer
cet_calf	Presence or absence of juveniles
cet_num_calf	Number of juveniles if present
cet_photo_id	Photo identification
cet_video	Was video taken?
cet_drone	Was a drone used?
cet_hydro	Was a hydrophone used?
cet_comment	Comments on the observation

Annexe 1. Examples of relevant information collected during on-effort on ObsenMer;

Year	Expeditions	Zone	Date
2021	1	North	20-31/05
2021	2	North	01-13/06
2021	3	Centre	20-28/06
2021	4	Centre	04-14/07
2021	5	South	17-27/07
2021	6	South	03-13/08
2021	Training	Centre/South	09-05/09-10
Total days / year			89
Year			
2022	1	South	25-06/03-04
2022	2	Centre	17-26/04
2022	3	North	22-31/05
2022	4	South	17-28/06
2022	5	Centre	14-26/07
2022	6	North	15-30/08
2022	Training	Centre/South	17-03/09-10
Total days / year			96
Year			
2023	1	South	07-20/03
2023	2	Centre	03-15/04
2023	3	North	05-16/05
2023	4	South	13-26/06
2023	5	Centre	16-29/07
2023	6	North	07-21/08
Total days / year			70

Annexe 2. Prospection effort of "Ti Whale An Nou" expeditions (2021-2023)

Id/ expedition	Identification	Date	Latitude	Longitude	Photo-identification	Acoustic data	New identification
Zc.expe2021.5	Cuvier	26/07/2021	13,7320947	-61,2296677	YES	NO	Cuvier
Md.expe2021.5	Blainville	27/07/2021	13,8344316	-61,0899491	YES	NO	Blainville
Bi.expe2021.6	No-ID	05/08/2021	13.53844096	-61.21622388	YES	NO	No-ID
Bi.expe2021.6	No-Id	11/08/2021	12,5761046	-61,553559	NO	NO	No-ID
Bi.expe2022.	No-Id	08/03/2022	14,7441332	-61,2112121	NO	NO	No-ID
Bi.expe2022.1	No-Id	28/03/2022	13,1057438	-61,2894588	NO	NO	No-ID
Me.expe2022.4	Gervais	26/06/2022	13,1028559	-61,2353068	NO	NO	Gervais
Zc.expe2022.4	Cuvier	26/06/2022	13,1456489	-61,2954528	NO	YES	Cuvier
Bi.expe2022.6	No-Id	15/08/2022	14,3928191	-61,0170744	NO	NO	No-ID
Bi.expe2022.6	No-Id	16/08/2022	15,446838	-61,5046391	NO	YES	Cuvier
Bi.expe2022.6	No-Id	24/08/2022	17,7030991	-63,5566245	NO	YES	Gervais
Bi.form2022.1	No-Id	22/09/2022	14,2622523	-61,1283373	YES	NO	No-ID
Bi.Form2022.2	No-Id	02/10/2022	14,6383836	-61,1671382	YES	YES	Gervais
Bi.form2022.2	No-Id	03/10/2022	14,2940616	-60,9221573	NO	NO	No-ID
Bi.expe2023.1	No-Id	07/03/2023	14,2248217	-60,8999677	NO	NO	No-ID
Bi.expe2023.1	No-Id	15/03/2023	12,8852124	-61,3511152	NO	YES	Blainville + Cuvier
Zc.expe2023.1	Cuvier	16/03/2023	13,2601221	-61,3330647	YES	NO	Cuvier
Me.expe2023.2	Gervais	06/04/2023	16,1036999	-61,8189494	YES	YES	Cuvier/Gervais*
Bi.expe2023.4	No-Id	13/06/2023	16,1389544	-61,8469656	YES	NO	No-ID
Me.expe2023.5	Gervais	21/07/2023	13,9435032	-61,1352472	YES	NO	Gervais
Bi.expe2023.5	No-Id	25/07/2023	15,4480979	-61,4926407	NO	NO	No-ID
Bi.expe2023.5	No-Id	26/07/2023	15,2477195	-61,3995459	NO	YES	Cuvier

*Annexe 3. Total observation of beaked whales from 2021 to 2023 with the type of data acquired associated. *This acoustic detection indicated Cuvier's beaked whale when a Gervais' beaked whale was sighted.*