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THIBAULT ROMAIN

Characterizing the Globicephalinae subfamily in the Lesser Antilles: diversity, distribution and movements to inform conservation strategies in the Caribbean



CARIBBEAN CETACEAN SOCIETY

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INTRODUCTION

Marine mammals are essential in maintaining the ecological balance of aquatic ecosystems (Bowen, 1997; Kiszka *et al.*, 2015; Estes *et al.*, 2016). Among these mammals, cetaceans have direct and indirect influences on trophic networks and marine population dynamics (Kiszka *et al.*, 2015; Roman *et al.*, 2014; Kiszka *et al.*, 2022). They regulate prey populations, preventing overabundance of species at lower trophic levels (such as plankton, fish, and cephalopods) (Pauly *et al.*, 1998; Kiszka *et al.*, 2022), while constituting a food source for higher trophic level species such as sharks and other cetaceans species (Heithaus, 2001; Gemmell *et al.*, 2015). As marine ecosystem engineers, cetaceans contribute significantly to nutrient cycling within ecosystems through their feces, urine, and carcasses and are therefore essential to ocean wealth (Roman & McCarthy, 2010; Roman *et al.*, 2014; Kiszka *et al.*, 2022; Gilbert *et al.*, 2023).

As a biodiversity hotspot, the Caribbean Sea stands out as the primary hub of marine diversity in the Atlantic Ocean (Roberts *et al.*, 2002; Miloslavich *et al.*, 2010). The region has registered the presence of 33 cetacean species, including 7 species of Mysticetes and 26 species of Odontocetes (MMAP, 2021). The Caribbean Sea is a tropical semi-enclosed basin of the Western Atlantic Ocean, bordered by Central and South America to the west and by the Antilles Archipelago to the east. Despite the high cetacean diversity, there are currently few studies allowing to discuss the status of cetacean populations in the Caribbean, and many species remain poorly described in this region. Research and conservation efforts are challenged by the great diversity of territories, cultures, and languages.

This is exacerbated in the Lesser Antilles, where important disparities in protection measures are present across territories. Some marine areas benefit from a protection status, such as the AGOA Sanctuary, established in 2010 under the Cartagena Convention (AGOA, 2019). This sanctuary is dedicated to the preservation of marine mammals in the French Antilles (Martinique, Guadeloupe, Saint-Martin, and Saint-Barthélemy) and covers an area of approximately 143,256 km² (AGOA, 2019). Similarly, the Yarari Sanctuary, created in 2015 by the Netherlands, protects the waters around the islands of Saba, Bonaire, and Sint Eustatius, extending over about 25,390 km² (DCNA, 2019). However, in the islands of St Vincent and the Grenadines and St Lucia, cetaceans are targeted by whaling and the hunting of small cetaceans (Caldwell & Caldwell, 1975; Fielding, 2018; Fielding & Kiszka, 2021; MMAP, 2021; Fielding, 2022).

Although whaling has been largely restricted globally due to the moratorium imposed by the International Whaling Commission (IWC) in 1986, some hunting practices persist (Tønnessen & Johnsen, 1982; Clapham & Van Waerebeek, 2007). The culture and maritime traditions of the island populations of Saint Vincent and the Grenadines (SVG) sustain the practice of hunting small cetaceans, with preference for "blackfish" (Caldwell & Caldwell, 1975; Fielding, 2018; Fielding & Kiszka, 2021; Fielding, 2022). Generally, the term "blackfish" mostly refers to species of cetaceans belonging to the Globicephalinae subfamily, within the Delphinidae family.

Genetically distinct from other dolphin species, members of the Globicephalinae subfamily are subjects of controversy (Steeman et al., 2009; Cunha et al., 2011; Vilstrup et al., 2011; Caballero et al., 2008; McGowen et al., 2020; Racicot & Preucil, 2022). According to a combination of mitochondrial and nuclear DNA sequencing, as well as targeted genomic data analyzed using robust phylogenetic methods (maximum parsimony, maximum likelihood, and Bayesian inference) in the most recent phylogenetic study on delphinids, the Globicephalinae currently appear to encompass six species, five of which are present in the Lesser Antilles: Risso's dolphin (Grampus griseus), the short-finned pilot whale (Globicephala macrorhynchus), the melon-headed whale (Peponocephala electra), the false killer whale (Pseudorca crassidens), and the pygmy killer whale (Feresa attenuata) (McGowen et al., 2020). From a physiological perspective, these species also share similar characteristics: indistinct beak, rounded head, and dark coloration (Culik & Wurtz, 2004; Sylvestre, 2014; Cawardine, 2020). Despite those similarities, these species exhibit notable differences in their respective ecology. Group size varies significantly among species, ranging from a few individuals to a hundred (Culik & Wurtz, 2004; Sylvestre, 2014; Cawardine, 2020). Group structure also differs, with some species forming matrilineal groups, while others show no segregation by age or sex (Culik & Wurtz, 2004; Sylvestre, 2014; Cawardine, 2020). Although most of these species have a primarily teuthophagous diet, they exhibit variations in dive duration and depth (Culik & Wurtz, 2004; Sylvestre, 2014; Cawardine, 2020). Moreover, the false killer whale tends to prefer medium to large-sized fish and small cetaceans (Rinaldi et al., 2006; Baird, 2009; Cawardine, 2020). Thus, each Globicephalinae species is distinguished by specific ecological and behavioral characteristics (Culik & Wurtz, 2004; Sylvestre, 2014; Cawardine, 2020). Therefore, it is difficult to group these species together for the purpose of conducting common analyses such as distribution models, like it can be done with baleen whales (Díaz López & Methion, 2019).

Currently the only species featuring peer reviewed description in the area is the short-finned pilot whales with a movement analysis around Martinique (De Montgolfier *et al.*, 2019). Therefore, there is an important gap of knowledge on the Globicephalinae species in the Lesser Antilles.

Long-term and large-scale monitoring is a multidimensional approach essential for acquiring crucial information for cetacean conservation (Baird et al., 2022; Baird et al., 2024). This approach facilitates the acquisition of extensive knowledge on various aspects such as movement patterns, social interactions, genetic diversity, population size, site fidelity, and habitat use (Baird et al., 2022; Baird et al., 2024). By employing non-invasive techniques like photo-identification, cetacean tracking at individual scale is allowed (Würsig & Jefferson, 1974; Baird et al., 2022; Baird et al., 2024). Photo-identification is a widely used capture-mark-recapture method for cetaceans that relies on distinctive scars and markings on dorsal fins to identify individuals (Würsig & Jefferson, 1974). This method provides valuable insights into population size, site fidelity, group structure, social interactions, and movement patterns (Würsig & Jefferson, 1974; Baird et al., 2009; Markowitz et al., 2024). Long term data collection also allows essential data to understand cetacean distribution which can be estimated using Species Distribution Models (SDMs) (Redfern et al., 2006; Derville et al., 2018; Mannocci et al., 2015). SDMs are robust tools for describing cetacean distribution, using relationships between species presence/absence with various environmental factors (Redfern et al., 2006; Derville et al., 2018; Mannocci et al., 2015). Altogether, those techniques allow an efficient description of cetacean species and inform their conservation requirements.

In this context, this preliminary study aims to assess the diversity of Globicephalinae species present in the Lesser Antilles, their geographic distribution, habitat use and movement patterns. Given the current lack of knowledge, the information provided by this study can serve as a relevant foundation for evaluating the vulnerability of the short-finned pilot whale, pygmy killer whale, false killer whale, melon-headed whale, and Risso's dolphin in the area. These preliminary data aim to guide future research efforts upon which conservation strategies and adaptive management plans in the Lesser Antilles can be built.

Based on existing literature, we anticipate the predominance of short-finned pilot whales abundance compared to the four other Globicephalinae species studied (Baird *et al.*, 2013). We also anticipate that the distribution of these species will be closely related to their

deep-diving ecology (Baird *et al.*, 2003; Culik & Wurtz, 2004; Cawardine, 2020). Finally, given the proximity of the islands, we expect to observe regular movement patterns between the different islands in the region (Baird *et al.*, 2008; Baird *et al.*, 2011; Aschettino *et al.*, 2012), , as well as residential behaviors in each of these Globicephalinae species (Pereira, 2008; Baird *et al.*, 2008; Baird *et al.*, 2011; Aschettino *et al.*, 2012; De Montgolfier *et al.*, 2019)

2. MATERIALS AND METHOD

2.1 Study area

This study was conducted as part of the "Ti Whale An Nou" program initiated by the Caribbean Cetacean Society (CCS), aiming to improve cetacean conservation in the Caribbean. In this context, research was conducted in a study area extending over 69,105 km², covering the surrounding waters of the Lesser Antilles Arc, from the island of Grenada to Anguilla, excluding Barbuda (12°- 19°N, 61°- 65°W). The study area includes 15 insular territories, empirically divided into three research zones: "North" (Anguilla to Montserrat), "Center" (Guadeloupe to Martinique), and "South" (Saint Lucia to Grenada) (Fig. 1). The boundaries of this area were established at a distance of 25 km from the coast, excluding EEZ from territories that were not surveyed. The Lesser Antilles are characterized by a complex topography, with steeper slopes on the Caribbean Sea side compared to the Atlantic Ocean side (Fig. 1). The region is also dominated by a multitude of underwater canyons and a steep topography on the Caribbean side of the arc (Fig. 1). The Caribbean side of the islands offers protection to the dominating eastward wind in the area, usually resulting in a sea state more suitable for surveys than on the Atlantic side, close to the shore.

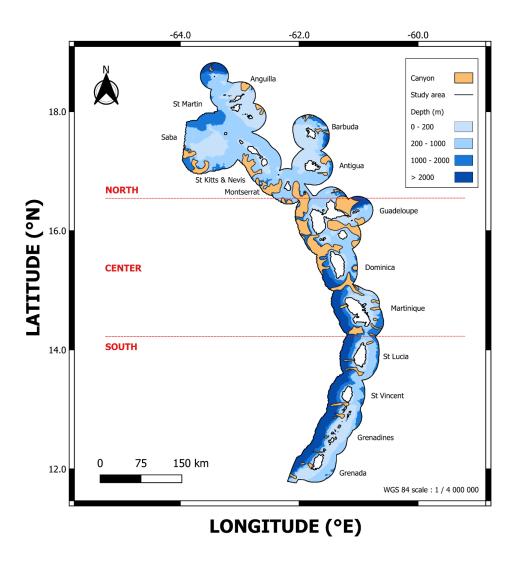


Figure 1. Study area geomorphology

2.2 Data collection

The data collection was carried out aboard a 40 to 46-foot sailboat, systematically used to monitor the study area. Between 2021 and 2023, 6 two week long surveys spanning from March to August were conducted each year totaling 18 scientific expeditions. To ensure homogeneous coverage of the Lesser Antilles, each research area (North, Center, South) was surveyed twice a year following non-systematic transect lines. Additional surveys carried out around Martinique, Guadeloupe, and Saint Lucia, following the same standardized expedition protocol, were performed and were considered in the analysis.

Surveys were conducted during the day (from 6 AM to 6 PM) at an approximately constant speed averaging 5 knots. Each hour, various parameters were recorded. It includes environmental measurements assessing the detectability conditions, marine traffic

measurement and a 10 minute long acoustic assessment recorded by a 100m long towed array including 2 high frequency hydrophone. Visual observation was performed by two observers strategically positioned at the bow of the sailboat, each scanning a 90° angle on each side of the vessel to detect cetaceans (Annex. 1).

Once cetaceans are detected the approach was conducted in a way that minimized potential disturbances. An observation was defined by the encounter of at least one individual at a specific location. Encounters of the same species within 30 min after the end of the first one were considered as a unique observation point as they likely represent the related individuals in the same area. During each encounter, species identification, GPS coordinates, initial distance from the boat, group size estimates and presence of juveniles were continuously recorded. Additionally, vocalizations were recorded using the towed array and two photographers were tasked to photograph individuals' dorsal fins for photo identification. At the end of the encounter, the research effort resumed along the initial trajectory. The research effort was paused when cetacean detectability was compromised by heavy rain or strong sea state exceeding force 4 on the Beaufort scale. The temporal and spatial effort varied depending on weather conditions and time constraints throughout the study.

2.3 Diversity

To describe and characterize the diversity of Globicephalinae species in the Lesser Antilles, we used two main indicators: the number of observations and the average group size within the region. For a more detailed analysis, we calculated the encounter rate for each species on each island. This parameter represents the ratio of the number of observations of each species on each island over the research effort, measured in kilometers traveled in those waters. This approach provides a preliminary assessment of the abundance and diversity of encounters for each Globicephalinae species across the islands of the Lesser Antilles.

2.4 Species distribution model

2.4.1 GAM background

Several approaches can be used to develop SDMs, including regression models, profils models, machine learning and bayesian approach (Redfern *et al.*, 2006, Derville *et al.*, 2018). Generalized Additive Models (GAMs, Hastie, 2017) are commonly used tools for species

distribution modeling and are well suited to presence/absence data (Mannocci *et al.*, 2015; Redfern *et al.*, 2017; Derville *et al.*, 2018).

All statistical analyses were conducted using R (version 4.2.2; R CORE TEAM, 2022). GAMs were used to fit the combination of environmental covariates with the distribution of short-finned pilot whale observations, corrected for research effort, to predict habitat suitability. These models also identified the environmental covariates that best correlate with the distribution and likely represent the habitat preferences of short-finned pilot whales. Observation points for the other Globicephalinae species were insufficient for this analysis. Although genetically related, given the previously mentioned ecological differences, we decided not to construct models combining all five species, as this approach was deemed inappropriate in this specific context. This non-parametric generalization of multiple linear regressions is particularly effective for interpreting presumed non-linear responses in species-environment interactions. Its implementation requested integrating a grid of hexagonal cells covering the study area with a 3 km interval between each side, the research effort, and a set of environmental covariates.

2.4.2 *Effort*

To develop the GAM, the research effort was incorporated as an offset to account for non uniformity of coverage along the surveyed area. The specific short-finned pilot whale research effort represents an area limited by its detectability. To account for reduction of detection probability with perpendicular distance from the boat trackline, we subdivide the detection area into four distance ranges, each associated with a positive detection probability (1, 0.75, 0.5, 0.25). The certain detection buffer zone covers the area between the ship's position and the upper limit where the distribution of detection distances reaches its maximum. The remaining distribution of observed distances of short-finned pilot whales was then subdivided into three equal segments using percentiles as reference. These segments represent the distance thresholds associated with reduced detection probability (0.75, 0.5, 0.25). Thus, the four resulting detection buffers (200m, 420m, 500m, 800m) were generated using QGIS, and the effort per grid cell was then estimated by summing the surveyed areas weighted by their respective detection probabilities. The effort per grid cell was then normalized by dividing it by the maximum effort value.

2.4.3 Environmental data

Modeling marine mammal distribution is essential for conservation as it provides key information on the animals' spatial range (Redfern et al., 2006; Pirotta et al., 2011). Most of the time, insights of their distribution are indirectly obtained using prey distribution. Indeed, prey availability, distribution, and abundance are factors often correlated with cetacean distribution (Friedlaender et al., 2006; Nøttestad et al., 2015). However, obtaining direct information on prey distribution and abundance is complex. Consequently, it is common to use other environmental covariates as proxies for these factors to acquire this information indirectly (Redfern et al., 2006, Friedlaender et al., 2006). The habitat use of the short-finned pilot whale remains poorly understood, but the species is known for its deep-diving behavior (Baird et al., 2003; Aguilar de Soto et al., 2008; Alves et al., 2013). Therefore, based on their ecology, we selected 18 environmental covariates (Tab. 1) to model the distribution of deep divers according to existing literature (Abecassis et al., 2015; Virgil et al., 2022). Depth data were obtained as raster files from the General Bathymetric Chart of the Oceans (GEBCO, website: https://gebco.net). The COPERNICUS Marine Monitoring Service (website: https://marine.copernicus.eu) provided direct extraction of sea surface temperature (SST), bottom temperature (BT), eastward current velocity (E0) and northward current velocity (N0), chlorophyll-a concentration (CHL), and mixed layer depth (MLD). From the depth data, the QGIS v3.28 Firenze cartographic analysis software (QGIS Development Team, 2018) was used to extract the distance to the shelf (Dist shelf), distance to the coast (Dist coast), 1000m (Dist iso1000), and 2000m isobaths (Dist iso2000), and the slope gradient. Given that the covariates E0, N0, SST, BT, MLD, and CHL are non-persistent and therefore exhibit temporal variations, we have decided to extract the standard deviation of each of these covariates using R. We will then use these standard deviations as additional covariates to represent the influence of the variability of these covariates on the distribution of short-finned pilot whales. A unique value for each environmental covariate was assigned to each hexagonal grid cell, spatially averaging the content of each cell over the study period.

Table 1: Environmental covariate table featuring unity, resolution and source

Predictor covariates	Unity	Resolution	Source
Depth	m	15 arc-seconds	GEBCO
Slope	0	15 arc-seconds	Derived from Depth
Dist_shelf	m	-	Derived from Depth
Dist_coast	m	-	Derived from Depth
Dist_iso1000	m	-	Derived from Depth
Dist_iso2000	m	-	Derived from Depth
CHL	mg/m^3	0.25°x0.25° (daily)	Copernicus
			Global Ocean
			Biogeochemistry
			Analysis and Forecast
SD_CHL	mg/m^3	0.25°x0.25° (daily)	Derived from CHL
SST	°C	0.05°x0.05° (daily)	Copernicus
			Global SST and Sea
			Ice Analysis
SD_SST	°C	0.05° x 0.05° (daily)	Derived from SST
E0	m/s	0.083°x0.083° (daily)	Copernicus
			Global Ocean Physics
			Analysis and Forecast
SD_E0	m/s	0.083°x0.083° (daily)	Derived from E0
N0	m/s	0.083°x0.083° (daily)	Copernicus
			Global Ocean Physics
			Analysis and Forecast
SD_N0	m/s	0.083°x0.083° (daily)	Derived from N0
MLD	m	0.083°x0.083° (daily)	Copernicus
			Global Ocean Physics
			Analysis and Forecast
SD_MLD	m	0.083°x0.083° (daily)	Derived from MLD
BT	°C	0.083°x0.083° (daily)	Copernicus
			Global Ocean Physics
			Analysis and Forecast
SD_BT	°C	0.083°x0.083° (daily)	Derived from BT

2.4.4 Fitting the GAM

Before beginning the modeling process, we examined the correlation between each explanatory covariate. The Spearman test was applied using a 0.7 threshold, as it is most suitable for explaining correlations between covariates that do not follow a normal distribution. For each pair of correlated covariates, we retained the covariate that was the easiest to link to the short-finned pilot whales ecology. Bottom temperature, its standard deviation and the distance to the shelf strongly correlated with depth and were therefore excluded (Spearman correlation = 0.89, p < 0.0001 and Spearman correlation = 0.76, p < 0.0001 respectively). Chlorophyll-a and mixed layer depth were both retained over their standard deviation (Spearman correlation = 0.82, p < 0.0001 and Spearman correlation = 0.80, p < 0.0001 respectively). To exclude outliers and obtain a streamlined model, only the data from the previously selected explanatory covariates were analyzed.

The models were adjusted using only the hexagonal grid cells with positive survey effort, the average value of each environmental covariates per grid cell, and the presence data for short-finned pilot whales, represented by the number of observations per cell. The models were constrained to a maximum combination of four covariates, with all possible combinations considered. Generalized additive models (GAMs) were generated using the R package mgcv, based on a Tweedie distribution with a logarithmic link function. The log of effort was included as an offset. The models were fitted using Restricted Maximum Likelihood (REML), with smooth terms calculated using thin plate splines of dimension 4 to prevent overfitting. Model selection was performed using Akaike Information Criterion (AIC) scores to rank all the generated models. At the end of the process, the model with the lowest AIC was considered as the best fitting model. Then, the importance of environmental covariates was assessed using Akaike weights in all the generated models to analyze short-finned pilot whale habitat preferences. Visual inspection of the residuals was used to check the model assumptions. Plots of the residuals against the fitted values were used to examine the regression adequacy.

To identify areas with the highest probability of presence of the short-finned pilot whale, partial predictions were calculated using the best fitting model. The selected model was used on the hexagonal grid based on the related environmental values to provide a value of fit per cell, interpreted as relative habitat suitability.

3.2 Photo-identification (CMR) and movements

The analysis of movements was conducted using photo-identification. For potential collaboration purposes, all data is processed using the collaborative software FlukeBook. This software uses artificial intelligence algorithms to compare all dorsal fin photos with each other, regardless of their date or location of capture, to establish a catalog where each identified individual is added and compared to others to ensure its uniqueness. Using the catalog, recaptures were gathered and mapped using QGIS.

3. RESULTS

3.1 Sampling effort, diversity and distribution of Globicephalinae

Data collection extended over a continuous three-year period, covering the months from May 2021 to August 2023 (Fig. 2A). The study extended over 274 days at sea (227 days of expeditions and 47 additional days). A total of 43 observations of the Globicephalinae subfamily were recorded during the study (Tab. 2) along the Lesser Antilles arc (Fig. 2). During this period, short-finned pilot whales and pygmy killer whales were seen in 2021, 2022 and 2023, false killer whale and melon-headed whales in 2021 and 2022 and Risso's dolphins in 2022 and 2023. Observations of short-finned pilot whales are primarily concentrated around Martinique and Saint Lucia (Fig. 2B). Pygmy killer whales observations are present throughout the Antillean arc, and the few melon-headed whales observations appear to follow a similar pattern (Fig. 2C). In contrast, false killer whales and Risso's dolphins observations seem to be more localized, with false killer whales observations primarily around Guadeloupe and Dominica and Risso's dolphins observations around Saint Vincent and Martinique (Fig. 2D).

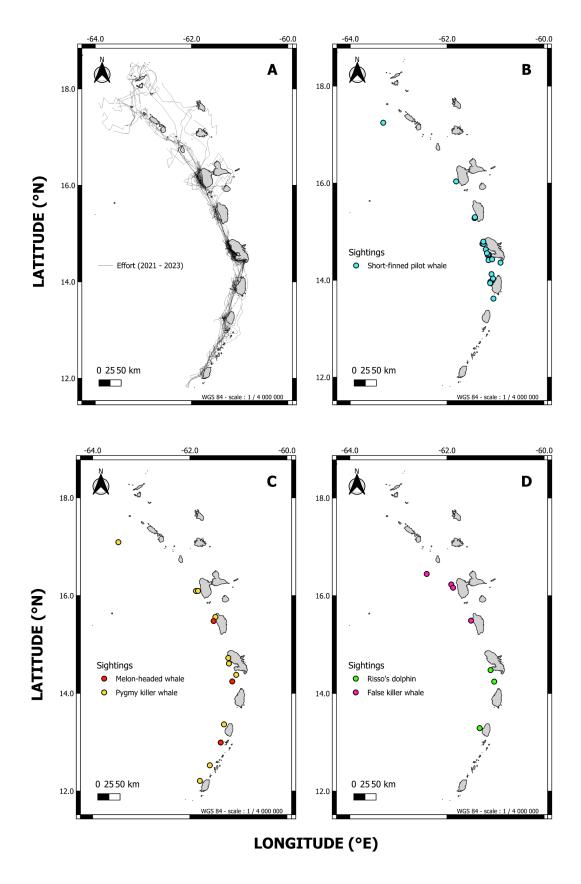


Figure 2. A) Survey effort (2021 -2023). B) Short-finned pilot whale's sightings (2021 - 2023). C) Pygmy killer whale's and melon-headed whale's sightings (2021 - 2023). D) False killer whale's and Risso's dolphins sightings (2021 - 2023)

Table 2. Summary table of Globicephalinae sightings and group size in the Lesser Antilles (2021 -2023). SD = standard deviation

	Sightings	Group Size					
		min	max	mean	median	SD	
Short-finned pilot whale	23	4	150	42.5	30	42.4	
Pygmy killer whale	10	1	25	8	6.5	6.3	
False killer whale	4	2	120	51.8	42.5	49.7	
Melon-headed whale	3	100	100	100	100	0	
Risso's dolphin	3	3	11	6.7	6	4	

Over these three years, tracking has extended over 22,543km. An encounter rate for each species on each island was calculated (Tab. 3). The encounter rate is used here to assess the diversity and distribution of the 5 species of Globicephalinae on each island as a result of our research effort. In the entire area, the average effort required to encounter each species is 980 km for short-finned pilot whales, 2,254 km for pygmy killer whales, 5,636 km for false killer whales, and 7,514 km for melon-headed whales and Risso's dolphins.

Table 3. Summary of the distribution of Globicephalinae's encounter rate across the Lesser Antilles during this study (2021 -2023). ER = Encounter rate for each species by Lesser Antilles island (calculated on the basis of the number of observations (n_{obs}) divided by the effort (in km)). Grey box = no observations, no encounter rate. Gm = Globicephala macrorhynchus. Fa = Feresa attenuata. Pc = false killer whale crassidens. Pe = Peponocephala electra. Gg = Grampus griseus. SVG = Saint Vincent & the Grenadines.

Island	Effort	Gm		Gm Fa		Pc		Pe		Gg	
		n_{obs}	ER								
St Maarten	159										
Collectivity of St Martin	172										
St Barthélemy	361										
St Kitt & Nevis	489										
St Eustatius	524										
Anguilla	724										
Saba	854	1	1.17	1	1.17						
Montserrat	926					1	1.08				
Antigua and Barbuda	941										
Grenada	1224			2	1.63						
Dominica	1870	2	1.07	1	0.53	1	0.53	1	0.53		
St Lucia	1947	7	3.59							1	0.51
SVG	2971			1	0.34			1	0.34	1	0.34
Guadeloupe	4541	1	0.22	2	0.44	2	0.44				
Martinique	5664	12	2.12	3	0.53			1	0.18	1	0.18

3.2 Influence of environmental covariates on short-finned pilot whale presence

A set of generalized additive models was created with 13 selected environmental covariates that did not contain collinearity: chlorophyll-a concentration, depth, distance to coast, distance to 1000m isobath, distance to 2000m isobath, depth, slope, as well as eastward current velocity, northward current velocity, mixed layer SST and their standard deviations. Thus, a total of 1,093 models could be constructed. Nine of them best described the data since they have a ΔAIC < 2 with the best scoring model. Those feature between 35.3 and 39.2 of the deviance explained (Tab. 4). The environmental parameters were classified in order of importance according to their Akaike weight (Fig. 3). Four covariates best contributed to capture the short-finned pilot whale distribution pattern in the area: CHL, dist_iso1000, N0 and slope. The combination of these environmental predictors constitutes the most parsimonious model (AIC = 104.1) and explains 38.3% of the deviance (Tab. 4). Each of these explanatory covariates in the model has a respective importance of 99.5%, 55.4%, 35.9%, and 81.2% (Fig. 3)

Table 4. Summary table of the best AIC (Akaike Information Criterion) scoring models (ΔAIC<2). The table features the combinations of covariates used to fit the model, the AIC score, Explained deviance (%), AIC difference with the best scoring model (ΔAIC), the REML (Restricted Maximum Likelihood) and the Akaike weights. Top models featured the covariates: chlorophyll a concentration (CHL), distance to the 1,000m isobath (dist_iso1000), northward current (N0), slope, distance to the 2,000m isobath (dist_iso2000), Depth, eastward current standard deviation (SD_E0), sea surface temperature standard deviation (SD_SST), mixed layer depth (MLD) and northward current standard deviation (SD_N0).

Model	AIC	Explained	ΔAIC	REML	Akaike
		Deviance			weights
CHL + dist_iso1000 + N0 + slope	104.1	38.3	0.00	1.00	0.079
CHL + dist_iso1000 + slope	104.7	35.3	0.53	0.77	0.061
CHL + dist_iso1000 + dist_iso2000 + slope	105.2	36.0	1.06	0.59	0.046
CHL + Depth + dist_iso1000 + slope	105.2	36.1	1.09	0.58	0.046
$CHL + N0 + SD_E0 + slope$	105.7	39.2	1.54	0.46	0.037
CHL + dist_iso1000 + SD_E0 + slope	105.9	35.8	1.75	0.42	0.033
CHL + dist_iso1000 + SD_SST + slope	105.9	35.7	1.78	0.41	0.032
CHL + dist_iso1000 + MLD + slope	106.0	35.6	1.93	0.38	0.030
CHL + dist_iso1000 + SD_N0 + slope	106.1	36.7	1.95	0.38	0.030

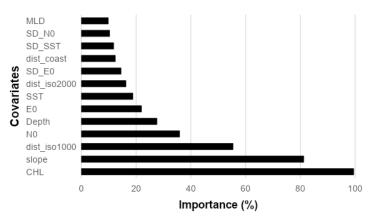


Figure 3. Importance of the covariates throughout the models based on Akaike Weights. Mixed layer depth (MLD), northward current standard deviation (SD_N0), sea surface temperature standard deviation (SD_SST), distance to the coast (dist_coast), eastward current standard deviation (SD_E0), distance to the 2,000m isobath (dist_iso2000), sea surface temperature (SST), eastward current (E0), Depth, northward current (N0), distance to the 1,000m isobath (dist_iso1000), slope and chlorophyll a concentration (CHL).

The occurrence of short-finned pilot whale was predicted to be most likely within a range of chlorophyll-a concentration of the order of 0.20 mg/m3, at a distance of less than 5km from the 1.000m isobath, a northward current velocity of the order of 0.07m/s and a slope of around 8-9° (Fig. 4).

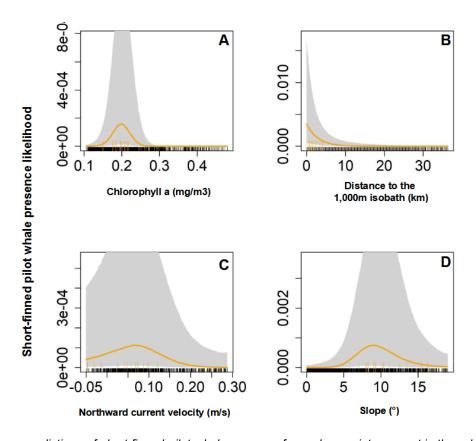


Figure 4. Mean predictions of short-finned pilot whale presence for each covariate present in the selected model' confidence set and their 95% confidence limits. A) Partial effect of chlorophyll-a (in mg/m3) on the presence of

short_finned pilot whale. B) Partial effect of distance to the 1,000m isobath (in m) on the presence of short-finned pilot whale. C) Partial effect of northward current (in m/s) on the presence of short-finned pilot whale. D) Partial effect of slope (in °) on the presence of short-finned pilot whale.

The first figure below (Fig. 5A) highlights relatively suitable habitats for short-finned pilot whales based on chlorophyll-a concentration, distance to the 1,000m isobath, northward current velocity, and slope in the Lesser Antilles. The results reveal higher proportions of favorable habitats for short-finned pilot whales around Martinique, particularly on the Caribbean side. Suitable areas are evident in the channel between Martinique and Saint Lucia, as well as to the north of Saint Lucia, still on the Caribbean side. The Caribbean coast of Dominica also presents favorable habitats, although to a lesser extent. Finally, Guadeloupe provides adequate habitats for short-finned pilot whales on both the Caribbean and Atlantic sides. The second figure (Fig. 5B) reveals the coefficient of variation of this prediction. It is observed that in areas where predictions indicate favorable habitats for short-finned pilot whales, the coefficient of variation is below 10%. In contrast, in the southern regions beyond Saint Vincent, the coefficient of variation exceeds 100%. Similarly, in the northern part of Guadeloupe, the coefficient of variation reaches nearly 300%

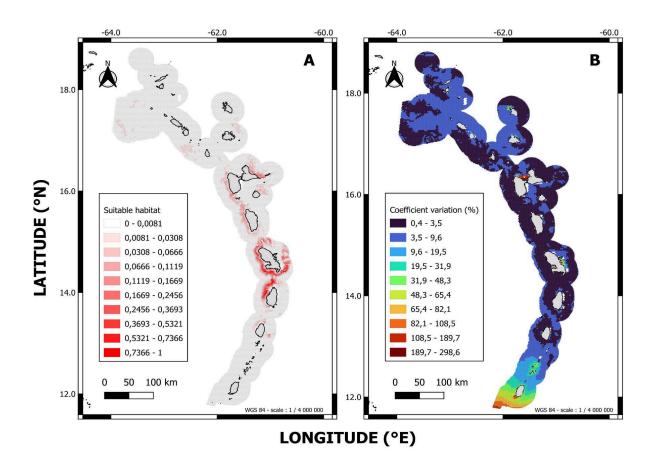


Figure 5. A) Map of short-finned pilot whale habitat suitability along the coast of Lesser Antilles based on the selected GAM model. To represent partial predictions, a grid with hexagonal cells of 3km was used. B) Map of short-finned pilot whale habitat suitability coefficient variation along the coast of Lesser Antilles based on the selected GAM model. To represent partial predictions, a grid with hexagonal cells of 3km was used.

3.2 Photo-identification (CMR) and movements

The use of photo-identification as a capture-mark-recapture technique has, over the course of three years of research, allowed the identification of 259 marked short-finned pilot whales, 105 marked melon-headed whales, 28 marked false killer whales, 19 marked pygmy killer whales, and 7 marked Risso's dolphins. No recaptures were observed for melon-headed whales, pygmy killer whales, or Risso's dolphins. However, during the study, five false killer whales were recaptured: two individuals were first observed in Guadeloupe on April 23, 2022, and were re-sighted five months later, on September 27, 2022, still in Guadeloupe (Fig. 6). Additionally, three other individuals were tracked from one day to the next, covering approximately 93 km from Guadeloupe on April 23, 2022, to Dominica on April 24, 2022 (Fig. 6). Regarding the short-finned pilot whales, 57 recaptures were recorded. Among these, 13 individuals were observed moving between Saint Lucia and Martinique: 1 from Saint Lucia to Martinique, 3 from Martinique to Saint Lucia, and 9 making a round trip between the two islands, totaling 23 recapture events between the two islands (Fig. 7). In addition, 34 recapture events were noted around Saint Lucia, including a particular observation of a group of individuals traveling at least 45 km between June 25, 2023, and June 26, 2023 (Fig. 8). Finally, a last inter-island movement was recorded between Martinique and Dominica (Fig. 7).

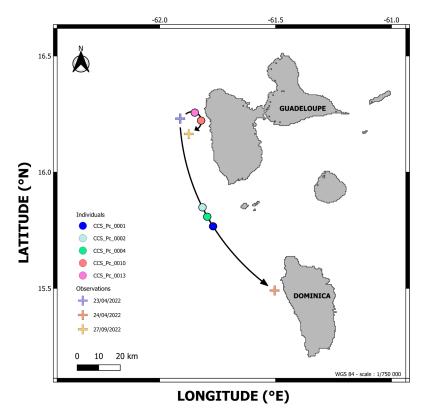


Figure 6. False killer whale recaptures in the Lesser Antilles (2021 -2023)

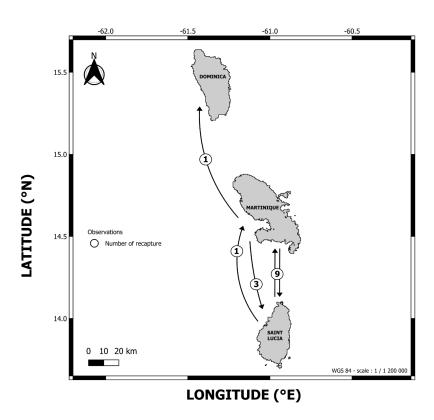


Figure 7. Short-finned pilot whale inter-island recaptures in the Lesser Antilles (2021 -2023)

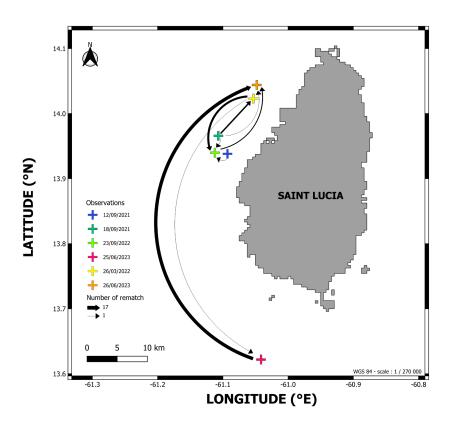


Figure 8. St Lucia short-finned pilot whale recaptures (2021 -2023)

4. DISCUSSION

This three year based study reveals the predominance of short-finned pilot whales abundance over the other four Globicephalinae species in the Lesser Antilles. However, species' relative abundance varied between islands. Among the examined environmental factors, chlorophyll-a concentration, seafloor slope, distance to the 1000-meter isobath, and northward current velocity best correlate with short-finned pilot whales presence in the region. Movement analysis revealed the existence of multiple inter-island movements for the false killer whale and short-finned pilot whale while no recaptures were obtained for pygmy killer whale, melon headed whale and Risso's dolphin.

This study allowed a preliminary characterization of Globicephalinae species diversity across the Lesser Antilles. Short-finned pilot whales abundance predominated compared to the four other Globicephalinae species, which appear less common in the region. Over thirteen years of research in Hawaiian waters, short-finned pilot whale encounters were also more frequent than the other Globicephalinae species (Baird *et al.*, 2013). The tropical Hawaiian archipelago represents a great comparison to the Lesser Antilles as it features a similar geomorphology and Globicephalinae species diversity (Baird *et al.*, 2013). The group sizes observed for short-finned pilot whales and pygmy killer whales are similar to those previously reported off

Guadeloupe (Rinaldi et al., 2006). In contrast, the few false killer whale's observation in the lesser antilles featured larger group size (Rinaldi et al., 2006). Although we have no historical data on group sizes for melon-headed whales and Risso's dolphins in the Lesser Antilles, the few group size recoded tend to be smaller compared to those reported in other regions (Wade & Gerrodette, 1993; Gannier, 2005; Dulau-Drouot et al., 2008; Pereira, 2008; Baird et al., 2013). The examination of the specific encounter rates across the islands of the Lesser Antilles, suggest disparities in insular diversity and relative species abundance. For instance, higher pygmy killer whale and false killer whale encounter rate than short-finned pilot whale were obtained in Guadeloupe. Likewise, between 1998 and 2005, the number of encounters of false and pygmy killer whales was reported similar to the number of observations of short-finned pilot whales (Rinaldi et al., 2006). Overall, additional years of research are recommended to assess with higher certitude the Globicephalinae ecology and diversity in this region. Currently, representativeness of the observation pool is, indeed, still subject to fluctuation due to small sample size for those species. The Lesser Antilles encounter rate of each species can inform whether each island received sufficient research effort to statistically obtain at least one encounter of a species under a uniform abundance between islands hypothesis. Based on this metric the northern islands have statistically insufficiently been sampled to accurately represent the presence of each Globicephalinae species. Similarly, no islands have received enough effort regarding the Risso's dolphin and melon headed whale. In contrast, research effort suggests that observation of short-finned pilot whales would have been expected around the islands of Grenada and St Vincent. Yet, no observations were made around these islands, even though their presence in the area has been reported (Fielding, 2018; Fielding & Kiszka, 2021; MMAP, 2021). This absence of detection could be the result of stochastic factors or it could reflect the impact of hunting (Fielding, 2018; Fielding & Kiszka, 2021), through population decline or behavioral adaptations of short-finned pilot whales to boats. Overall, continuation of the research effort is recommended to efficiently assess Globicephalinae's presence and diversity along the Lesser Antilles arc. Long term monitoring of uncommon species in Hawaii, conducted over a span of approximately twenty years, provided successful results in that matter (Baird et al., 2022; Baird et al., 2024).

Short finned pilot whale was the only species that accumulated enough observation points to perform SDM. However, it remains too limited to assess model robustness, although visually our observations align with the areas of relatively high prediction for suitable habitats. The combination of chlorophyll-a concentration, distance to the 1000-meter isobath, northward

current velocity, and slope best correlated with short-finned pilot whales observations in the region and constituted the most important variables considering all the generated models (Fig. 3 & 4). Those covariates are used as a proxy for prey distribution and can't directly be considered as distribution drivers. However, the importance of each of those covariates has an ecological rationale regarding short-finned pilot whales distribution.

The occurrence of short-finned pilot whales in the region appears to be higher in waters with an average chlorophyll-a concentration approaching 0.20 mg/m3 (Fig. 4). Chlorophyll-a concentration is used as a proxy for phytoplankton concentration, referring to a direct link with the food chain (Redfern *et al.*, 2006). When phytoplankton concentration is sufficiently high, it facilitates the development of the trophic chain from mesozooplankton to macrozooplankton (Vinogradov, 1970; Heileman *et al.*, 2008). Once zooplankton aggregates sufficiently, small fish and squid are attracted (Heileman *et al.*, 2008). Juvenile squids preferentially feed on macrozooplankton and shift to small mesopelagic fish and squids as adults (Arnold, 1979; Heileman *et al.*, 2008). Important chlorophyll-a concentration can therefore drive short-finned pilot whale's distribution, which predominantly feed on squids (Pauly *et al.*, 1998; Sylvestre, 2014; Carwardine, 2020).

This study reveals a significant influence of slope on the distribution of short-finned pilot whales. We observe a peak in their presence on relatively steep slopes, around 8 to 9 degrees (Fig. 4). This observation has also been highlighted in studies conducted along the coast of Hawaii (Baird *et al.*, 2013; Abecassis *et al.*, 2015). It seems that important slopes promote the aggregation of the deep mesopelagic boundary community (Abecassis *et al.*, 2015). This community of organisms facilitates the exchange of energy and nutrients between coastal and oceanic habitats (Reid *et al.*, 1991; Benoit-Bird & Au, 2003; Benoit-Bird & Au, 2006). These organisms form the base of the food chain (Reid *et al.*, 1991; Benoit-Bird & Au, 2003) and, consequently, serve as prey for short-finned pilot whales (Abecassis *et al.*, 2015). Thus, steep slopes create a transition zone between the plateau and the drop-off, which likely enhances prey availability and facilitates the hunting activities of short-finned pilot whales (Abecassis *et al.*, 2015). The dynamic environment associated with important slopes allows the whales to effectively exploit a range of depths, adapting to fluctuations in prey availability and thereby optimizing their foraging efficiency.

The analyses conducted in this study have also highlighted the significant influence of the distance to the 1000-meter isobath on the distribution of short-finned pilot whales. Indeed, it

appears that the occurrence of short-finned pilot whales is higher at distances less than 5 km from the 1000-meter isobath (Fig. 4). The short-finned pilot whale is a deep-diving species, hunting at high depths (Baird *et al.*, 2003; Aguilar de Soto *et al.*, 2008, Alves et al., 2013; Abecassis *et al.*, 2015). In Hawaiian waters, short-finned pilot whales have been observed diving to depths of up to 1300 meters (Abecassis *et al.*, 2015) for approximately 27 minutes (Baird *et al.*, 2003; Abecassis *et al.*, 2015). In the Canary Islands, individuals have been recorded diving to 1000 meters with a maximum duration of 21 minutes (Aguilar de Soto *et al.*, 2008). These deep dives appear to be predominantly conducted during the day, often associated with feeding sprints (Aguilar de Soto *et al.*, 2008). At night, the species is found at shallower depths, tracking the vertical migration of its prey (Abecassis *et al.*, 2015). Similar to the findings around the Hawaiian Islands, communities residing at the deep mesopelagic boundary likely support the prey populations of short-finned pilot whales, which in turn may feed on them (Abecassis *et al.*, 2015).

Ocean currents continuously impact marine life, including marine mammals. According to the most parsimonious model, the velocity of the Northward current appears to influence the habitat use of the short-finned pilot whale. We observe a peak in their presence when the Northward current speed is around 0.07 m/s (Fig. 4). This speed, considered low, indicates a potential preference for sheltered habitats over those subjected to strong currents. Again, this result seems consistent with previous findings on habitat use by short-finned pilot whales in Hawaiian waters, which highlighted higher densities of the species along the coast with relatively low surface currents (Abecassis *et al.*, 2015). Thus, as appears to be the case on the southern coast of Kona in the Hawaiian archipelago (Abecassis *et al.*, 2015), the general ocean current patterns in the Lesser Antilles, particularly the Northward current, could favor the retention of organisms from the deep mesopelagic boundary community. This dynamic supports the food chain by promoting the concentration of prey in these areas.

Based on the four environmental predictors most correlated with the distribution of short-finned pilot whales identified in this study, the development of a predictive model has revealed disparities in the distribution of suitable habitats in the Lesser Antilles. A relatively near-complete absence of suitable habitats is observed in the northern islands of the Lesser Antilles, from Montserrat to Anguilla. The shallow depths of this area, and thus the lack of necessary drop-offs for short-finned pilot whales, explain this prediction. A single observation of short-finned pilot whales was recorded in the north, near Saba (Tab. 3), where

depths and drop-offs are greater. In contrast, the islands from Guadeloupe to Saint Lucia showcase important suitable habitat prediction. These predictions are explained by optimal oceanographic conditions, including significant depths and marked drop-offs, which favor the abundance of short-finned pilot whale prey. Although, the oceanographic conditions of Saint Vincent and the Grenadines and Grenada appear similar to those of Guadeloupe, Dominica, Martinique, and Saint Lucia and that observations have been recorded around these islands (Fielding, 2018; Fielding & Kiszka, 2021) yet relatively low suitable habitat predictions seem to be present. This could be due to the low reliability of the predictions in this area. Indeed, while the prediction presents a satisfying coefficient of variation below 10% in the rest of the Lesser Antilles, it continuously increases from Saint Vincent and the Grenadines to Grenada, reaching values above 100%. Consequently, the prediction associated with our selected model for this area is currently unreliable, and further investigation is necessary. The predictive model also reveals favorable habitats for short-finned pilot whales along the Atlantic coast of Martinique and Guadeloupe, although no surveys have yet been conducted on this side. Although such predictions must be considered carefully, it motivates future research in these areas to investigate the species presence. The Caribbean Sea side appears more conducive to suitable habitats, with depths ranging from 0 to 2000 meters, steep slopes, conditions that favor the abundance of short-finned pilot whale prey. Finally, habitat suitability appears as relatively continuous from Saint Lucia to Guadeloupe which could facilitate movements between the islands that could potentially extend to the Lesser Antilles as a whole. This prediction complements the only previous prediction made for this species in the Lesser Antilles (Hugon & Maalouf, 2023).

For each species presenting recapture evidence, intra- and inter-island movements of short-finned pilot whales and false killer whales have confirmed the connectivity between the islands (Fig. 6, 7 & 8). Similar evidence of inter-islands movements of Delphinidae in the Lesser Antilles have been described in the past with the example of the Fraser's dolphin (Bernier, 2023). Short-finned pilot whales' social structure is constituted of stable social units (Mahaffy, 2012; Alves *et al.*, 2013; Van Cise *et al.*, 2017). It has been demonstrated that different groups would feature varying travel behavior in Hawaii and Madeira (Mahaffy, 2012; Alves *et al.*, 2013; Van Cise *et al.*, 2017). In this study, trends of residency seem to emerge around Saint Lucia, where several individuals from a group were observed on multiple occasions next to the island (Fig. 8). Nine of those, potentially members of the same unit, were repeatedly observed between 2021 and 2023 in the waters of Saint Lucia and were

once recaptured in Martinique (Fig. 7). Such a finding has been reported in Hawaii, where short-finned pilot whales are mostly faithful to a site and occasionally move between islands (Mahaffy, 2012). Other social units featuring similar residential behavior may also be present around Martinique, as suggested by a previous study (De Montgolfier et al., 2019). However, despite numerous observations on the island, very few recaptures have been obtained yet. Higher abundance of short-finned pilot whales, lack of photos for those observations, or encounters of transient groups, could explain the low proportion of recaptures compared to the observation rate. Maintaining the photo-identification protocol to better understand their movement patterns is crucial to answer those preliminary hypotheses. Additionally, the tagging of a few individuals would also be relevant. This method is often used to complement the photo-ID effort (Baird et al., 2010; Baird et al., 2012; Baird et al., 2024). The Globicephalinae observations of the same individuals within a year are rare, therefore the tagging of individuals would allow us to understand their movements at a fine spatiotemporal scale, especially knowing that they can engage in large scale travels. Moreover, a greater focus on social structure would enhance our understanding considering that traveling behaviors might be specific to each social unit. All these recommendations are applicable to other species of Globicephalinae, including false killer whales. Out of four observations, five recaptures were confirmed from three different encounters. This could support the hypothesis of a small relatively resident population of false killer whales occasionally using the coastal waters between Guadeloupe and Martinique (Fig. 6). Although we can't make assumptions from this small sample size, reports from Guadeloupe and preliminary photo-ID analysis provided similar trends supporting potential residency (Rinaldi & Rinaldi, 2011). Residency behaviors have also been observed in several false killer whale populations around the Hawaiian Islands (Baird et al., 2008; Baird et al., 2010). The absence of matches for the three remaining Globicephalinae species underscores the importance of monitoring these rare species and paying particular attention to their conservation. It is essential to continue research efforts through photo-ID as well as complementary methods such as tagging. This is particularly true for the melon-headed whale and Risso's dolphin which accumulate few encounters and no reidentification. These methods have allowed the determination of traveling behaviors of pygmy killer whales off the coast of Hawaii, identifying a small resident population in Hawaii (McSweeney et al., 2009; Baird et al., 2011). Given that our observations of pygmy killer whales are spread along the Lesser Antilles, it is essential to determine whether they move between islands or if there is evidence of spatial fragmentation.

The entirety of these results highlights the growing need for cooperation across the Lesser Antilles. Currently cetacean conservation measures are not harmonized across the islands where they face multiple anthropogenic threats such as maritime traffic (Miller & Hyodo, 2021), accidental catches (Bjorkland, 2011), chemical pollution (Méndez-Fernandez et al., 2018), or hunting (Fielding & Kiszka, 2021). The latter seems to be the most direct threat for Globicephalinae species in the Lesser Antilles. Although St Lucia and SVG signed the Cartagena Convention and its SPAW Protocol, committing to prohibit hunting of protected species in the Caribbean, local regulations have yet to implement this ban (Milieu Marin France, 2024). During a period of 68 years, the small cetacean hunting, considered as artisanal and indigenous subsistence hunting by the IWC, has led to the capture of 13,856 small cetaceans, including 5,896 short-finned pilot whales, 109 orcas, and 7,851 other small cetaceans (Fielding & Kiszka, 2021). On average, 85 short-finned pilot whales, 3 killer whales, and 251 other small cetaceans are caught each year by a single boat owner (Fielding & Kiszka, 2021), while currently, between 2 and 6 boats continue to be active (Fielding & Kiszka, 2021). These reports underestimate the actual catches since there are gaps in the recording of small cetacean captures (Fielding & Kiszka, 2021; Fielding, 2022). To date, there is no centralized registry for recording small cetacean catches in SVG (Fielding, 2018). In St Lucia, no recent reports have assessed the hunting situation (Gaskin & Smith, 1977; Reeves, 1988) but it is still active (MMAP, 2021). The inter-island movement results of short-finned pilot whales and false killer whales indicate that catches in SVG and St Lucia represent individuals that could originate from the rest of the Lesser Antilles. To measure the sustainability of these hunting practices, it is necessary to maintain research efforts, particularly photo-identification, in order to provide population estimates of each Globicephalinae species present in the Lesser Antilles and to obtain first insights into pygmy killer whales, melon-headed whales, and Risso's dolphins movement patterns. Additionally, it is essential to collaborate with localities in St Vincent and St Lucia to standardize the report of each cetacean capture. Altogether, it will enable the monitoring of the hunt and the assessment of its impact. More generally, we recommend conducting a threat analysis, particularly concerning maritime traffic, bycatch, noise pollution, chemical pollution, and other anthropogenic factors. These analyses will enable us to assess the pressure those species face in the area. Complemented with this preliminary characterization of the species it will serve as a baseline to inform conservation strategies in the Lesser Antilles.

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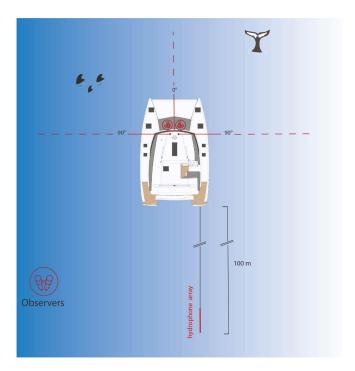
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Appendix



Annex 1. Illustration of the standardized protocol during a research effort

Caractérisation de la sous-famille des Globicephalinae dans les Petites Antilles : diversité, distribution et mouvements pour orienter les stratégies de conservation dans la Caraïbe.

Parmi les cétacés, la sous-famille des Globicephalinae reste à ce jour méconnue. Cette étude préliminaire, faisant partie du programme "Ti Whale An Nou", vise à combler le manque de connaissances concernant les globicéphales tropicaux, les pseudorques, les dauphins d'Électre, les dauphins de Risso et les orques pygmées dans les Petites Antilles. En utilisant trois ans de données, nous avons caractérisé la diversité de ces espèces en utilisant le nombre d'observations, la taille moyenne des groupes et le taux de rencontre par île. Les distributions ont été décrites basées sur les observations, et des modèles additifs généralisés ont été développés pour les globicéphales tropicaux afin d'identifier des zones d'habitats favorables et leur conditions préférentielles. La photo-identification a renseigné sur les déplacements individuels. Les résultats révèlent une prédominance des globicéphales tropicaux comparée aux autres espèces. Nous avons observé des variations dans la taille des groupes, la distribution par île et l'abondance relative des espèces. Des facteurs environnementaux tels que la concentration de chlorophylle-a, la pente du fond marin, la distance jusqu'à l'isobathe de 1000 mètres et la vitesse du courant vers le nord apparaissent comme les meilleurs prédicteurs de la présence des globicéphales tropicaux. Les modèles prédictifs ont mis en évidence la présence de hotspot d'habitats favorable dans les Petites Antilles. Des mouvements inter-îles ont été identifiés uniquement pour les globicéphales tropicaux et les pseudorques. Ces résultats soulignent l'importance de poursuivre les recherches pour mieux comprendre la distribution et la connectivité des espèces dans la région. Nous recommandons également la mise en œuvre de mesures de conservation harmonisées à travers les Petites Antilles pour assurer une protection efficace et durable de la sous-famille des Globicephalinae dans la région. Dans le contexte de la chasse aux petits cétacés, nous plaidons pour une collaboration régionale visant à standardiser le suivi des captures de cétacés.

Mots-clés: Cétacés, Taux de rencontre, Modèle de Distribution des Espèces, Photo-identification, Connectivité

Characterizing the Globicephalinae subfamily in the Lesser Antilles: diversity, distribution and movements to inform conservation strategies in the Caribbean

Among cetaceans, the Globicephalinae subfamily remains poorly known to this day. This preliminary study, part of the "Ti Whale An Nou" program, aims to address the knowledge gap regarding short-finned pilot whales, pygmy killer whales, false killer whales, melon-headed whales, and Risso's dolphins in the Lesser Antilles. Using three years of data collection we have characterized the diversity of these species utilizing number of observations, average group size, and encounter rate per island. Distributions were described based on observations, and generalized additive models were developed for short-finned pilot whales to investigate habitat preferences and suitability. Photo-identification provided insights into individual movement patterns. The results reveal a predominance of short finned pilot whales compared to other species. We observed variations in group size, island distribution, and relative abundance of species. Environmental factors such as chlorophyll-a concentration, seafloor slope, distance to the 1000-meter isobath, and northward current speed were found to be the best predictors of short finned pilot whale presence. Predictive models have highlighted the presence of hotspots of suitable habitat in the Lesser Antilles. Inter-island movements were identified for short-finned pilot whales and false killer whales, while no recapture was obtained for other species. These results underscore the importance of continuing research to better understand species distribution and connectivity in the region. We also recommend implementing harmonized conservation measures across the Lesser Antilles to ensure effective and sustainable protection of the Globicephalinae subfamily in the region. In the context of small cetacean hunting, we advocate for regional collaboration to standardize the monitoring of cetacean capture.

Key-words: Cetaceans, Encounter rate, Species Distribution Model, Photo-identification, Connectivity