

Intraspecific and spatial variation in habitat use by sperm whales (*Physeter macrocephalus*) along the west coast of Martinique

Séréna Laurent¹, Marion Poupard¹, Célia Ortolé¹, Céline Valin¹, Benjamin de Montgolfier^{Corresp. 1, 2, 3}

¹ Aquasearch, Sainte-Luce, Martinique

² Bio-Laurentia, Saint-Anaclet, Québec, Canada

³ Institut des Sciences de la Mer, University of Québec at Rimouski, Rimouski, Québec, Canada

Corresponding Author: Benjamin de Montgolfier

Email address: b.montgolfier@aquasearch.fr

For a deep-diving cetacean species like the sperm whale, acoustics is a vital tool for research. This need is especially pressing in the eastern Caribbean, where the habitat of marine mammals overlaps with heavy maritime traffic, leading to noise pollution and an increased risk of vessel collisions. To mitigate this risk, understanding their habitat use is essential. Mature males are generally solitary and migrate over long distances, while females and immatures form stable social units in subtropical and tropical waters. In this study, we examined intraspecific variation in distribution and habitat use among individuals along the Caribbean coast of Martinique, using both visual and acoustic data. Over the course of 24 surveys, 19 aggregations involving a total of 72 individual sightings were characterized, recognizing that some individuals may have been recorded multiple times. Using the Inter-Pulse Interval (IPI) of clicks, we estimated individual size, which provided insights into the age and/or sex of each individual. Habitat characteristics included bathymetry, distance from the coast, and seabed slope. Our results on social structure are in line with previous literature: 37% of the aggregations were made up of females and/or juveniles, immatures, with a mature male nearby, with temporal changes in aggregations linked to male migration patterns. Spatial distribution and habitat use appeared consistent across aggregation types, regardless of group size, average individual size, or the presence of immatures. However, specific areas were identified for hunting and socialising based on bathymetry. This study highlights the importance of bathymetry and/or distance from the coast and temporal dynamics related to variations in weather conditions and movements of breeding males, in understanding habitat use by sperm whales in the eastern Caribbean. The lack of observed influence of seabed slope suggests that our spatial scale may have been too limited, or that finer details regarding seabed characteristics are needed. These findings could inform traffic management strategies to

reduce the risk of vessel collisions with sperm whales.

Intraspecific and spatial variation in habitat use by sperm whales (*Physeter macrocephalus*) along the west coast of Martinique

Séréna Laurent¹, Marion Poupard¹, Célia Ortolé¹, Céline Valin¹, and Benjamin de Montgolfier^{1,2,3}

¹Aquasearch design office, ZAC Les Cotteaux 97228 Sainte-Luce, Martinique, France

²Institut des Sciences de la Mer (ISMER), Université du Québec, Rimouski (UQAR), 310 allée des Ursulines, Rimouski, QC G5L 3A1, Canada

³Bio – Laurentia, 98 route Melchior-Poirier, St-Anaclet-de-Lessard, G0K 1H0, Canada

Corresponding author:

Benjamin de Montgolfier¹

Email address: b.montgolfier@aquasearch.fr

ABSTRACT

For a deep-diving cetacean species like the sperm whale, acoustics is a vital tool for research. This need is especially pressing in the eastern Caribbean, where the habitat of marine mammals overlaps with heavy maritime traffic, leading to noise pollution and an increased risk of vessel collisions. To mitigate this risk, understanding their habitat use is essential. Mature males are generally solitary and migrate over long distances, while females and immatures form stable social units in subtropical and tropical waters. In this study, we examined intraspecific variation in distribution and habitat use among individuals along the Caribbean coast of Martinique, using both visual and acoustic data. Over the course of 24 surveys, 19 aggregations involving a total of 72 individual sightings were characterized, recognizing that some individuals may have been recorded multiple times. Using the Inter-Pulse Interval (IPI) of clicks, we estimated individual size, which provided insights into the age and/or sex of each individual. Habitat characteristics included bathymetry, distance from the coast, and seabed slope. Our results on social structure are in line with previous literature: 37% of the aggregations were made up of females and/or juveniles, immatures, with a mature male nearby, with temporal changes in aggregations linked to male migration patterns. Spatial distribution and habitat use appeared consistent across aggregation types, regardless of group size, average individual size, or the presence of immatures. However, specific areas were identified for hunting and socialising based on bathymetry. This study highlights the importance of bathymetry and/or distance from the coast and temporal dynamics related to variations in weather conditions and movements of breeding males, in understanding habitat use by sperm whales in the eastern Caribbean. The lack of observed influence of seabed slope suggests that our spatial scale may have been too limited, or that finer details regarding seabed characteristics are needed. These findings could inform traffic management strategies to reduce the risk of vessel collisions with sperm whales.

INTRODUCTION

While standard visual observation methods provide limited perspective on the behaviour of marine animals, passive acoustics offer a way of understanding underwater behaviour, particularly for deep-diving species such as sperm whales (*Physeter macrocephalus*) (Whitehead, 2003). Acoustics allows underwater species to be studied over larger temporal and spatial scales (Mellinger et al., 2007) and also to account for environmental noise disturbances (Browning et al., 2017). Large cetaceans such as sperm whales are at high risk of collision (Laist et al., 2001; Di-Meglio et al., 2018; Fais et al., 2016) due to their large size and slow speed. Moreover immature individuals dive shallower and for shorter durations than adults, resulting in longer surface intervals and increased exposure to maritime traffic. (Tønnesen et al., 2018;

45 Miller et al., 2013).

46 ~~In the Canary Islands, the Fais et al. (2016) study has shown that collisions can be a significant source~~
 47 ~~of mortality among sperm whales. Although Caribbean sperm whales are listed as Vulnerable (Savouré-~~
 48 ~~Soubelet et al., 2016b) and maritime traffic along the west coast of Martinique is high (see Fig. 1), no~~
 49 ~~study has characterized the population of these sperm whales. However, the risk of collision with ships is~~
 50 ~~real (Laist et al., 2001) and could partly explain the decline in sperm whale numbers (Gero and Whitehead,~~
 51 ~~2016; Rinaldi et al., 2021). Unlike mature males, females, juveniles and immatures form resident fits that~~
 52 ~~remain in subtropical and tropical waters (Dufault et al., 1999; Whitehead, 2003). These social units are~~
 53 ~~therefore constantly exposed to anthropogenic activities. Understanding how cetaceans use their habitat~~
 54 ~~could potentially inform marine spatial planning efforts, for example by identifying areas at high risk~~
 55 ~~of collision, as has been done in the northwestern Mediterranean to protect fin whales (*Balaenoptera*~~
 56 ~~*physalus*) and sperm whales (Grossi et al., 2021). In response to the risk of collision in the Mediterranean,~~
 57 ~~a collaborative computer system called Repcet® (Real-Time Cetacean Tracking) has been developed to~~
 58 ~~give ships access to the position of cetaceans observed on their route (Arcangeli et al., 2014).~~

59 Sperm whales are one of the twenty-four species of cetacean found in the French West Indies
 60 (Savouré-Soubelet et al., 2016a). They belong to the suborder odontocetes and exhibit remarkable sexual
 61 dimorphism (Rice, 1989). Females generally measure between 9 and 12 meters in length and weigh
 62 up to 15 tonnes, while males measure up to 20 meters in length and weigh between 45 and 57 tonnes
 63 (Rice, 1989). Sperm whales can dive to depths of up to 3,000 meters and remain submerged for an
 64 average of 45 minutes (Savouré-Soubelet et al., 2016a). In addition to their sexual dimorphism, sperm
 65 whales exhibit two behavioural patterns (Dufault et al., 1999; Whitehead, 2003). Social units consisting
 66 of females, juveniles and immatures are mostly found in subtropical and tropical regions, while males
 67 migrate from high latitudes in cold waters to subtropical and tropical areas to breed (Dufault et al., 1999;
 68 Whitehead, 2003). ~~We also know that adult females in a social unit babysit, which means that they~~
 69 ~~take turns looking after the young within the social unit, affecting the adult females' hunting behaviour~~
 70 (Arnbom and Whitehead, 1989; Whitehead, 1996; Gero, 2005; Gero et al., 2009). These differences
 71 between mature males and social units suggest intraspecific variation in habitat distribution and use.

72 As odontocetes, sperm whales spend the majority of their time echolocating to hunt and locate their
 73 habitat (Whitehead and Weilgart, 1991; Watwood et al., 2006). They produce several types of clicks,
 74 defined by click rate, which correspond to different behaviours. "Regular clicks" are series of clicks with
 75 Inter-Click Intervals (ICI) of about 0.5 to 2 seconds, associated with hunting (Whitehead and Weilgart,
 76 1990; Watwood et al., 2006). The "buzzes" or "creaks" are produced during the capture of prey attempts
 77 and are characterized by the emission of closely spaced clicks whose interval varies from 0.02 to 0.2
 78 seconds (Goold and Jones, 1995). Finally, "codas" are stereotypical series of 3 to 20 clicks, lasting 0.2
 79 to 2 seconds, emitted during socialisation events (Watkins and Schevill, 1977). Distinct coda dialects
 80 characterise vocal clans—assemblages of units that share a similar dialect and may include thousands of
 81 individuals. (Rendell and Whitehead, 2003; Gero et al., 2016).

82 The production of the sperm whale click is a unique process: the animal produces a sound emission at the
 83 front of the head, in the "monkey lips", which then bounces back into the head through the spermaceti. A
 84 small portion of the sound is emitted directly in the center (pulse p0), but most of it travels through the
 85 spermaceti towards the back of the head and reaches the frontal air sac, where the sound is reflected and
 86 returned forward, creating pulse p1. The reverberation is repeated several times, producing several pulses
 87 p2, p3, etc. Thus, the interval between impulses provides an indication of the duration required for the
 88 sound emission to travel through the head, and thus the size of the head. So the Inter-Pulse Interval (IPI)
 89 has therefore become an important acoustic parameter that allows estimation of the size of individuals
 90 (Norris and Harvey, 1972; Gordon, 1991; Rendell and Whitehead, 2003; Rhinelanders and Dawson, 2004;
 91 Growcott et al., 2011; Ferrari et al., 2024).

92 Several models have attempted to elucidate the spatial distribution patterns of sperm whales in their
 93 breeding grounds (Pirodda et al., 2011; Pace et al., 2018; Avila et al., 2022). The main physical habitat
 94 factors influencing the presence of sperm whales are thought to be water depth, followed by distance from
 95 the coast and slope of the seabed (Pace et al., 2018; Avila et al., 2022). However, according to Pace et al.
 96 (2018), the contribution of environmental variables depends on the type of sperm whale aggregation in the
 97 central Mediterranean. They found that the distribution of solitary whales was ~~more~~ explained by distance
 98 from the coast, and social units by slope (Pace et al., 2018). Sea Surface Temperature (SST) is thought to
 99 influence sperm whale distribution, with groups found in colder waters than solitary individuals typically

are (Pirodda et al., 2011). This may be due to competition, where groups push solitary whales into warmer, less optimal waters, or a trade-off within groups that allows them to feed, interact, and care for young, unlike solitary individuals who focus solely on feeding. For most studies on sperm whale habitat, visual identification have been used to detect and locate sperm whales (Whitehead and Rendell, 2004; Praca et al., 2009; Pirodda et al., 2011; Pace et al., 2018). However, they characterized the sperm whales solely through visual observation, whereas acoustics, by analysing sperm whale clicks, can accurately determine the number of individuals present, their size (IPI) (Norris and Harvey, 1972; Gordon, 1991; Møhl et al., 2003; Rhineland and Dawson, 2004; Growcott et al., 2011), and their behaviour (ICI) (Watkins and Schevill, 1977; Whitehead and Weilgart, 1990; Fais et al., 2015). In the Lesser Antilles, studies have been carried out to estimate the abundance (Vachon et al., 2022b) and health (Whitehead and Gero, 2015) of sperm whale populations, but also to understand their movement between different islands (Gero et al., 2007). A study of individual movement showed strong site fidelity in sperm whales, highlighting the importance of environmental parameters on culture at this spatial scale (Vachon et al., 2022a). On a smaller scale, the social structure of the sperm whale population in Guadeloupe and Dominica has been studied (Gero et al., 2014), as has their abundance (Gero and Whitehead, 2016; Rinaldi et al., 2021), revealing a decline in the latter. However, the sperm whale population in Martinique has never been characterized.

We combined visual and acoustic methods to characterise individuals by size (IPI calculation) and behaviour (observations and acoustic) in order to highlight intraspecific variations in sperm whale habitat use. The topographical factors analysed were bathymetry, distance from the coast and slope of the seabed. Social factors were the size of the aggregation, the average size of the individuals composing it and the presence of immatures which certainly affect the behaviour of females due to parental care. The time factor linked to changes in environmental parameters has also been added. In summary, the objective of this study was to characterise the intraspecific and spatial variation in habitat use of sperm whales in order to understand the factors that influence their distribution along the Caribbean coast of Martinique.

MATERIAL AND METHODS

Field methods

For this study, researchers conducted boat expeditions along the west coast of Martinique to observe sperm whales and collect acoustic recordings. These excursions resulted in the development of a robust database to characterise the sperm whale habitat in this region. For data acquisition, the team adhered to and signed the respectful cetacean approach charter created by the AGOA Sanctuary (Sanctuaire AGOA, 2025).

One to two surveys per week were conducted from January 12 to May 15, 2024. A 6.5 m inflatable boat equipped with a 115 hp outboard motor was used for monitoring. The animals were located by acoustic and direct observations from the boat. Our study area extended from the southern part of the west coast of Martinique, along the Caribbean Sea side, at Cap Salomon (61°8'N, 14°31'W), to the northern part of the coast at Le Prêcheur (61°17'N, 14°48'W). For each day of the ship survey, the following weather conditions were noted: sea state (Beaufort scale), cloud cover (octa), wind direction and speed (knots), and visibility. We conducted our surveys from south to north, following the 1500-meter isobath, based on the location of historical observations. Ten acoustic points separated by 4 km were made along the 1500-meter isobath (Fig. 1). ~~To return south, we often had to get closer to the coast because the wind was getting up.~~ We did not make acoustic points, unless sperm whales had been heard and/or seen on the way ~~there~~. The reasons we decided to follow this transect were 1) to maximise our chances of encountering sperm whales by following the isobath where sperm whales have often been sighted based on historical data, and 2) because the farther from the coast the worsening sea conditions were.

For each point of the transect, two to five minutes of recordings were made to try to detect animals. If the sperm whales were detected acoustically, we moved to locate them visually (depending on weather conditions and swell) and recorded all the individuals we detected visually. If no sperm whale was detected with the hydrophone, we proceeded to the next point. Sperm whales have been detected up to around 8 km, making it possible to find them as far as the 2000 m isobath.

When sperm whales were sighted and approached at a minimum distance of 100 m, a GPS point was recorded and identification photos were taken using a Nikon D7100 camera with a 70-300 mm lens and a Canon Mark II 7D with a 70-200 mm lens. Then five to ten minutes of continuous acoustic recordings were made. From January to March, acoustic data were collected using an H2a-XLR omnidirectional

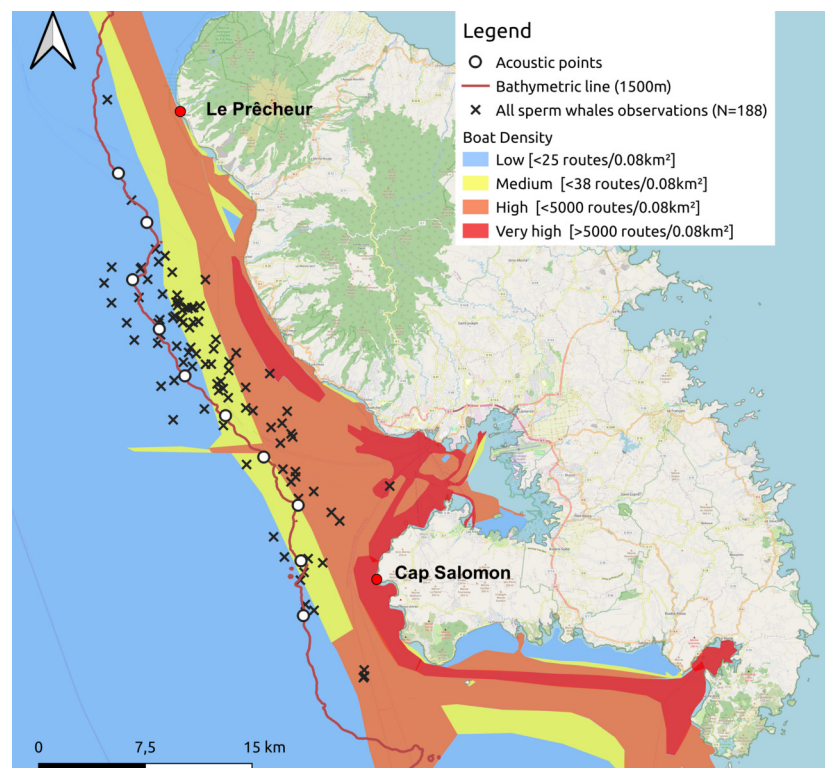


Figure 1. Sperm whale observations since 2013 and acoustic points made along the 1500 meter isobath from south to north during the study. The density of maritime traffic was given in routes/ 0.08 km^2 inspired by MarineTraffic data for 2024.

hydrophone (Aquarian Audio Products; frequency response: 20 Hz to 4.5 KHz, sensitivity: $-180\text{ dB re: }1\text{V}/\mu\text{Pa}$) with 11 m cable connected to an iRig Pre 2 amplifier (frequency response: 50 Hz to 20 kHz) and a Zoom H1 handy recorder (sampling rate: 96 kHz, 24 bits). From April, an SQ26-08 omnidirectional hydrophone (Cetacean Research Technology; frequency response: 20 Hz to 50 kHz, sensitivity: $-169\text{ dB re: }1\text{V}/\mu\text{Pa}$) replaced the Aquarian and the iRig Pre 2 amplifier and a Zoom H1n handy recorder (sampling rate: 96 kHz, 24 bits) replaced Zoom H1 handy recorder. Gain was adjusted between the two recorders to achieve approximately the same gain throughout the study. The Zoom H1 was set to 50/100, the iRig Pre 2 to 4/10 and the Zoom H1n to 7/10. From April onwards, a home-made satellite dish was used to make our listening more directional and to amplify the sound (Pavan, 2008). A JVC HA-S660 headset was connected to listen to the sounds in real time. Acoustic recordings were made in stereo at a depth of 10 m and stored in WAV format.

As soon as at least one individual from the aggregation had been seen to confirm the GPS point and a recording had been made, we continued on our way.

Additional data

We added cetacean observations from the Aquasearch historical database, collected from 28 April 2013 to 5 January 2024 ($N = 143$), while traversing the same study area, following the 1000 to 1500 m isobaths. Each row of the data table corresponded to a group of sperm whales observed, associated with a behaviour (resting, socialising or moving), its GPS position, the number of individuals, sex and age if possible, the presence of a calf and other details. We considered that the groups were equivalent to the aggregations in our study. The entire historical database is described in the study of Vries (2017).

Of these observations, sixty-nine included both GPS position and observed behaviour and four included observed behaviour but no GPS position. In addition to the Aquasearch data, nineteen additional observations were made by whale watchers during our study period, of which only two included behavioural data. The additional data did not include acoustic recordings. See figure 1 for details about sperm whale distribution from additional data. Three additional observations located slightly outside the

study area were retained because acoustics at the edge of the area would have made it possible to detect sperm whales at these locations.

Habitat characterization

Each GPS point (historical and study data) was imported into QGIS v. 3.34.2 to obtain the following topographic information: bathymetry (in meters), distance to the coast (in meters) with an accuracy better than 100 m, and slope of the seabed (in percentage). Slope was calculated by dividing the height difference by the distance (about 500 m) around the observation point and was categorized as "light" ($< 10\%$), "medium" ($[10-20\%]$) or "steep" ($\geq 20\%$). The base maps used as well as the bathymetric lines were obtained from the available SHOM database (Service Hydrographique et Océanographique de la Marine (SHOM), 2025). For four GPS points, the slope value was not quantified because the individual was on an elevation.

Aggregation definition

To standardise and facilitate the categorization of observed sperm whales, we defined a "aggregation" as a group of sperm whales observed within 1 km of each other that could be identified and distinguished acoustically. This distance was checked on QGIS during the analyses. In addition, the signal had to be sufficient to allow calculation of the IPI. The term "aggregation" was used by (Christal and Whitehead, 1997), defining male individuals in temporal or spatial proximity to each other, heard within the 3-5 km range of the directional hydrophone. We reduced this distance after testing sperm whale detection with our hydrophone at such distances, and IPI measurement was impossible. See the next part for more details.

In order to characterise the aggregation with the topography, the following information was collected: GPS point (first animal seen), number of individuals seen on the surface, number of individuals heard, assumed age (adult, juvenile or immature), sex and all behaviours observed in the aggregation (hunting, socialising, moving and resting). All observed behaviours were described in Table 1 (the observation time of 2 to 4 scientists aboard the boat was at least 15 minutes). Observations complement acoustic recordings to determine certain behaviours. The presence of other species and the number of boats in the area were also noticed.

Table 1. Visual and acoustic description of the four behaviours identified. The surface activity* ethogram was taken from Whitehead and Weilgart (1991). "Fluking" is in italics because it was only a clue to help identify the hunt. It required the presence of regular clicks and buzzes in the recordings.

Behaviour	Description	
	Acoustic	Visual
Hunting	Presence of regular clicks and buzzes	<i>Fluking*</i> : whale raises its fluke above the water surface to an almost vertical position. Indicates the beginning of a foraging dive.
Socialising	Presence of codas in recordings	Breach*: whale leaps partially or completely out of the water. Head-out*: whale raises head partially or completely above water surface. Lobtail*: whale thrashes fluke onto water surface. Side-fluke*: Whale turns on one side and partially lifts fluke out of the water. Fluke-first*: whale breaks the surface with the fluke first, frequently holding it in almost perfectly vertical position.
Moving	none	The animal moves near the surface at a medium or fast speed, keeping the same direction, and does not dive.
Resting	none	The animal remains in place or moves very slowly on the surface.

In general, the number of individuals characterized on acoustic recordings was greater than the number of sperm whales observed. Hence the interest in acoustics, which can be used to obtain data for species that remain apneic for long periods and at the surface for only a short time (Whitehead, 2003). For the same aggregation, several behaviours could be described. For example, acoustics often enabled us to define a hunting behaviour for individuals at depth, while an individual at the surface was seen resting.

Acoustic analyses

Sperm whale clicks were manually annotated using Audacity v. 3.4.2. To distinguish clicks from different individuals, click shape, ICI and IPI were taken into account [spectrogram parameters: $f_{min} = 800$ Hz; $f_{max} = 10$ kHz, *window size* = 256, *window type* = Hamming, *gain* = 20 dB, *range* = 70 dB].

The figure S1 in the Supplementary Material shows a spectrogram and a 7-second waveform of a signal containing clicks from two individuals (A and B). Figure 2 shows an example of two clicks from two different individuals. A high pass filter was applied to all recordings. This filter reduced background noise from waves, boat activity, and isolated the signal above 1 kHz, where the energy of sperm whale clicks begins to emerge (Goold and Jones, 1995). This differentiation of clicks made it possible to count the number of individuals present in the aggregation (aggregation size).

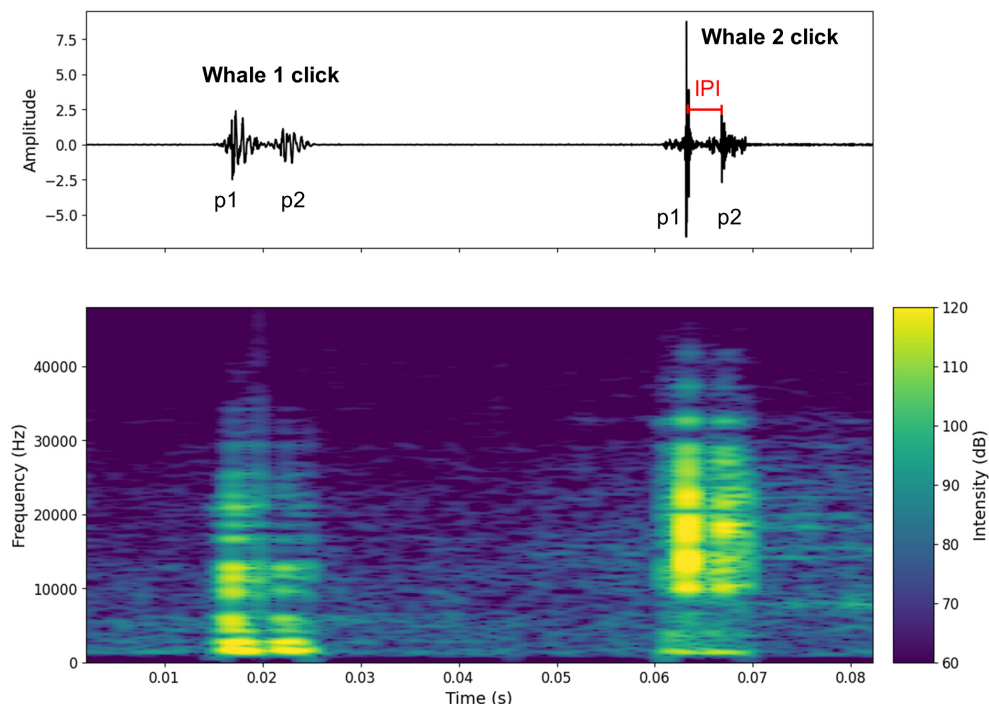


Figure 2. Oscillogram and spectrogram of the audio signal of clicks from two different individuals. The oscillogram (top) shows the signal amplitude in the time domain. The spectrogram (bottom) shows the frequency energy distribution of the signal as a function of frequency (Hz) [overlap = 400, NFFT = 450]. The decibel scale is added.

To calculate the IPI, the waveform was used to detect the p1 and p2 amplitude peaks (p3 and p4 were very rarely visible on the signal). For each individual, the IPI was measured ten times on the recording and then averaged. To calculate the IPI, the waveform was used to detect the p1 and p2 amplitude peaks (p3 and p4 were very rarely visible on the signal). For each individual, the IPI was measured ten times on the recording and then averaged. Standard deviations were checked for errors (see Table S3 where standard deviations are given for Animal Size). To avoid errors due to water surface echoes, IPI were recorded at the beginning, middle and end of the recordings. Only IPI where the pulses were clearly visible were recorded. In Figure 2 only the IPI of the second click could be calculated. As IPI can be falsely low due to clicks with a prolonged first impulse (p1), we limited the minimum IPI value to 2 ms (Marcoux et al., 2006; Giorli and Goetz, 2020). This excluded possible clicks from the young immatures (Tønnesen et al., 2018). In our study, all observed immatures were acoustically characterized.

Animal Size (AS) was then calculated from the IPI using the following two equations, the first for animals under 11 meters (Gordon, 1991) (1) and the second for animals over 11 meters (Growcott et al., 2011) (2):

$$AS = 4.833 + 1.453 \times IPI - 0.001 \times IPI^2 \quad (1)$$

$$AS = 1.258 \times IPI + 5.736 \quad (2)$$

The method of using the two equations based on the IPI value was applied in two studies (Caruso et al., 2015; Poupard et al., 2022). Three classes of sperm whales have been identified. An IPI of less than 2.9 ms and an AS of less than 9 meters corresponds to an immature whale, an IPI between 2.9 and 5.0 ms and an AS between 9 and 12 meters corresponds to a juvenile male or an adult female, and finally an IPI greater than 5.0 ms and an AS greater than 12 meters corresponds to an adult male (Gordon, 1991; Growcott et al., 2011).

Acoustic analyses revealed different types of aggregation, depending on the number of individuals identified and their average size within the aggregation, and the presence or absence of an immature.

Statistical analyses

All statistical analyses were performed with R software, version 4.2.2 (R Core Team, 2022). The alpha significance level was set to 0.05, indicating a 5% risk of rejecting the null hypothesis when it is true. For parametric tests, we always checked for normal distribution of model residuals by Shapiro-Wilk tests (Shapiro and Wilk, 1965) and for homogeneity of variances by plotting the fitted values versus the model residuals (Faraway, 2016).

The size of aggregations, the size of individuals and the presence of immatures are key factors in determining the social structures and behaviour of sperm whales. Larger aggregations may reflect stable social units or transient foraging associations formed for cooperative hunting. The average size of individuals gives an indication of its composition and function - adult-dominated groups may consist of males seeking to reproduce, while aggregations of mixed size would indicate nursery units with immatures in need of parental care. The presence of juveniles also influences social cohesion, as guarding and protection behaviours strengthen social bonds and may be at the origin of specific behaviours and spatial distributions. Taken together, these parameters provide a better understanding of sperm whale group dynamics and their ecological implications.

Social structure

First, the objective was to analyse whether the composition of aggregations (in terms of individual size) varied depending on the total number of individuals composing each aggregation. For each aggregation observed, the mean size of the individuals and the standard deviation of the sizes of the individuals present were calculated. Then the aggregations were grouped according to the total number of individuals they contained (e.g. all aggregations with 2 individuals together, those with 3 individuals together, etc.). Finally, for each group of aggregations of the same size, the average individual sizes previously calculated were averaged. Similarly, the standard deviations of the individual sizes were averaged to obtain an overall measure of size variability in each aggregation category.

The influence of the presence of an immature ($N_{absence} = 8$, $N_{presence} = 11$) on the aggregation size was tested using a Generalised Linear Model (GLM) with Poisson distribution. The absence of overdispersion was checked using the “check_overdispersion” function of the *performance* (Lüdtke et al., 2021) package to verify that the variance of the data was not too high. The P-value was calculated using a Type II Anova (McHugh, 2011). The effect of the presence of an immature ($N_{absence} = 8$, $N_{presence} = 11$) on the average size of the other individuals present was also tested using a Student’s T-test (Student, 1908). To do this, we calculated a new average of sizes by removing the sizes of immatures ($AS < 9$ m).

Spatial distribution

In relation to topography, we tested the close association between bathymetry and distance from the coast ($N = 27$) using a Pearson correlation test (Freedman et al., 2007). As we found a strong correlation between these two parameters, we decided to express only the bathymetric parameter in our analysis.

Variations in bathymetry and slope in relation to aggregation size ($N = 19$) and mean individual size ($N = 19$) were tested using Pearson correlation tests (Freedman et al., 2007). These two parameters were then compared by class of individual ($N_{ad.male} = 28$, $N_{ad.female/juvenile} = 30$, $N_{immature} = 16$) using linear models. P-values were calculated using Monte Carlo permutation tests with 1,000 resamples (Hothorn et al., 2008). Finally, the bathymetry and slope distributions were tested according to the presence or absence of an immature ($N_{absence} = 8$, $N_{presence} = 11$) using two Student’s T-tests (Student, 1908).

Habitat use

Several behaviours can be identified for an individual or an aggregation. Four observations without GPS point from historical data were not removed from the analysis. By adding historical data, we examined the distribution of behaviours according to bathymetry ($N_{hunting} = 28$, $N_{moving} = 76$, $N_{resting} = 12$, $N_{socialising}$

= 10) using a linear model. Since multiple pairwise comparisons were conducted to compare bathymetry among behaviours, we applied the sequential Bonferroni correction to control for the increased risk of Type I errors (false positives) due to multiple testing (Abdi, 2010). This method adjusts the significance threshold for each comparison, reducing the likelihood of detecting spurious significant differences. P-values were calculated using Type II Anova (McHugh, 2011). We also examined the distribution of behaviours according to slope ($N_{\text{hunting}} = 27$, $N_{\text{moving}} = 75$, $N_{\text{resting}} = 12$, $N_{\text{socialising}} = 10$) using a linear model. The P-value was calculated using a Monte Carlo permutation test with 1,000 resamples (Hothorn et al., 2008). See Table S3 in Supplementary Material for details on sample sizes for each behaviour, separating the additional data from the data from our study.

Temporal variation

In order to visualize the temporal variations in the spatial distribution of different types of aggregations and individuals, we combined the months of January to March into one period (period 1), which corresponds to the dry season in Martinique, and the months of April to May into another (period 2), corresponding to a wetter period the end of the reproduction period (pers. comm. de Montgolfier). The spatial distribution with respect to bathymetry over the two periods (number of aggregations, $N_{\text{period}_1} = 18$, $N_{\text{period}_2} = 7$) was tested using a Student's T-test Student (1908). For the slope, the difference ($N_{\text{period}_1} = 17$, $N_{\text{period}_2} = 7$) was tested using a Fisher-Pitman permutation test with 10,000 resamples Boik (1987). At the level of aggregation, we ran a GLM with Poisson distribution to see if the size of aggregations varied between the two periods ($N_{\text{period}_1} = 11$, $N_{\text{period}_2} = 8$). We checked the absence of overdispersion using the function "check_overdispersion" from the package performance (Lüdtke et al., 2021). The P-value was calculated using a Type II Anova (McHugh, 2011). Finally, we compared the size of the individuals found according to the periods (number of individuals, $N_{\text{period}_1} = 38$, $N_{\text{period}_2} = 36$) using a Student's T-test (Student, 1908).

RESULTS

From 12 January to 15 May 2024, 24 numbers of days of data collection were conducted, covering a total distance of 1,986 km. The two cameras captured 984 sperm whale images. A total of 19 hr 45 min of recordings were made, using a storage capacity of 38.5 gigabytes. Figure 3 illustrates the distribution of sperm whales from 2013, highlighting a pronounced distribution between the 1000 m and 2000 m isobaths. The description of the number of behaviours characterized visually and acoustically for our study data is shown in Tables S3 and S4 in the Supplementary Material.

Social structure

Sperm whales were observed in 42% of the 24 boat surveys, with a total of 19 aggregations and 72 individuals recorded and acoustically characterized (Fig. 4). The number of aggregations characterized per day ranged from 0 to 4 and the number of individuals from 0 to 16. Seven observations were not associated with acoustic data, due to poor quality recordings. Details of the composition of the classes of individuals in each aggregation are given in Table S1.

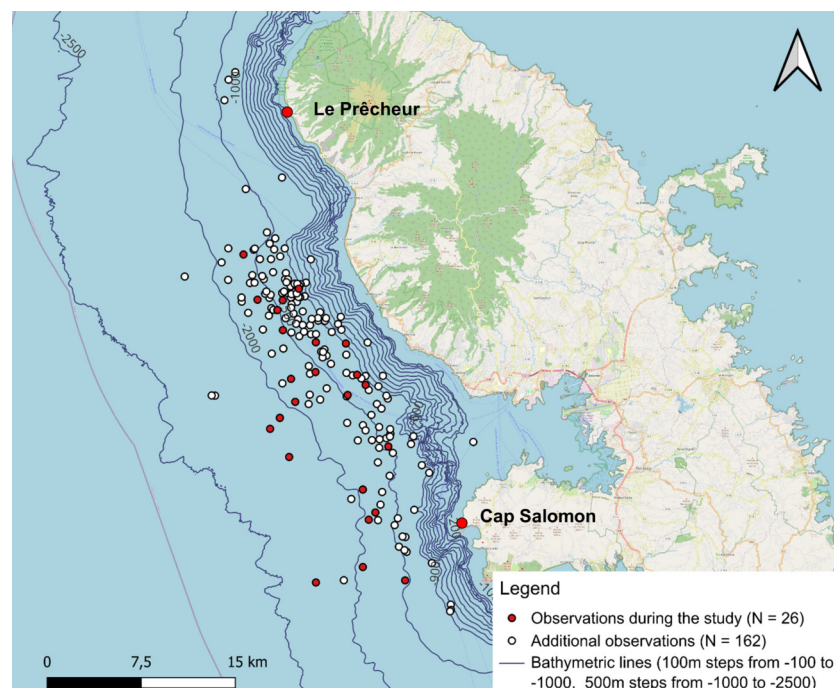


Figure 3. Sperm whale observations distinguishing between additional data from 28 April 2013 to 26 March 2024 (including observations from the whale-watcher and study data from 12 January to 15 May 2024

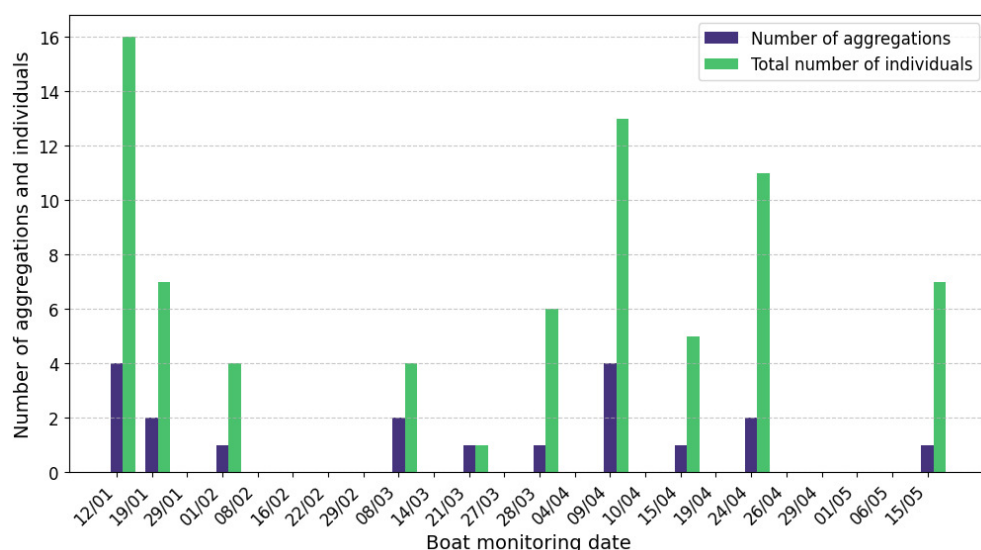


Figure 4. By release date of ship surveys, number of aggregations and total number of acoustically identified individuals. The absence of a bar means that no sperm whales were observed or listened to.

Aggregation size varied from 1 to 9 (median = 4, $Q_1 = 2$, $Q_3 = 5$) and individual IPI from 1.90 to 7.80 ms (median = 3.85 ms, $Q_1 = 2.90$ ms, $Q_3 = 5.38$ ms, $\bar{x} = 4.18$ ms), corresponding to an AS of 7.6 to 15.6 m (median = 10.5 m, $Q_1 = 9.0$ m, $Q_3 = 12.5$ m, $\bar{x} = 10.8$ m). An IPI of 1.90 ms was added despite its value being less than 2 ms because the presence of the calf was confirmed visually. The distribution of AS is illustrated in Figure 5 and more details is reported in Table S2. During the data collection period, immatures (N=16), females/juvenile male (N=30) and adult males (N=28) were present in the study area. As immatures were observed during the study, the presence of adult females is certain to ensure parental

331 care.

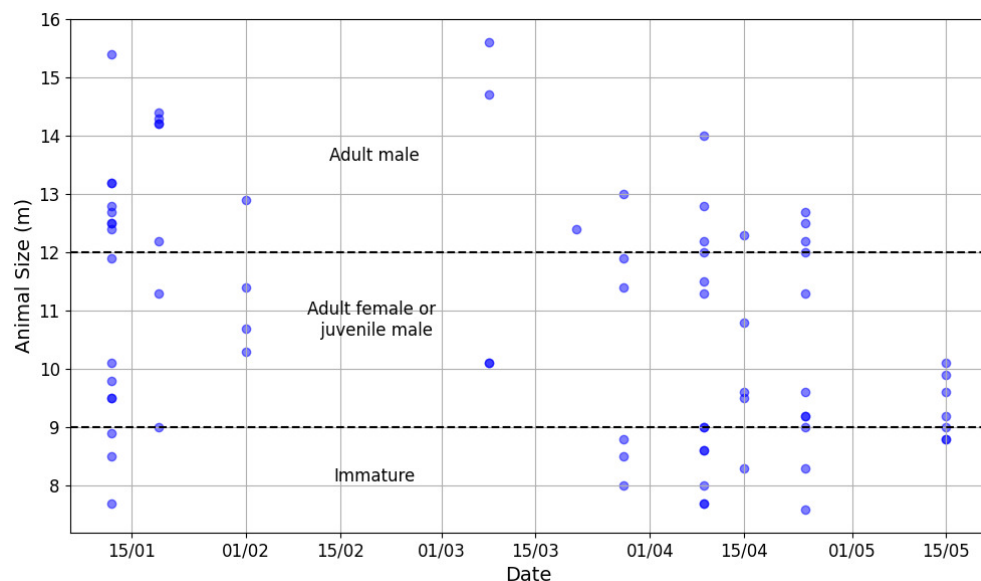


Figure 5. Distribution of Animal Sizes, highlighting the three sperm whale classes ($N_{ad.male} = 28$, $N_{ad.female/ juv.male} = 30$, $N_{immature} = 16$).

332 Regardless to the size of the aggregations, the average size of the individuals composing them showed
 333 little variation, ranging from 10.6 to 11.5 m (Fig.6). However, as aggregation size increased, the difference
 334 in sizes among individuals within these groups also increased, from 1.3 to 3.7 m. This pattern highlights
 335 the presence of individuals of all age classes in large aggregations, including immatures, juveniles, and
 336 adult males and females.

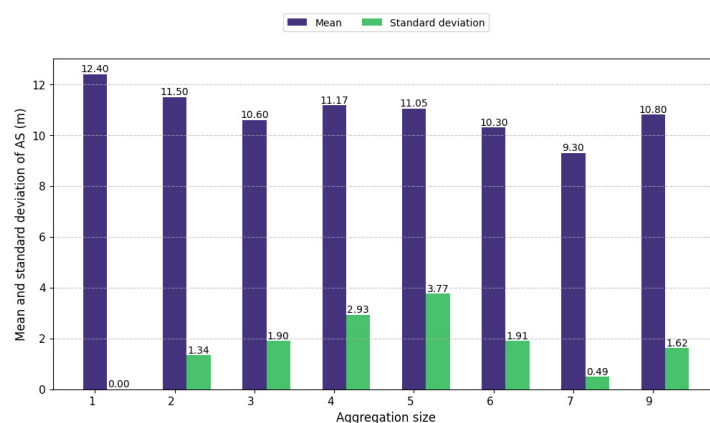


Figure 6. Mean and standard deviation of Animal Size by aggregation size.

337 When an immature individual was present, the aggregation size was larger (Table 2, Fig. 7.a). The
 338 mean size of individuals in the aggregation was smaller when an immature was present (Table 2, Fig. 7.b).

Table 2. Statistical results for aggregation size and mean individual size in the presence of an immature individual.

Variable	Test	Statistic	P-value	Interpretation
Aggregation size	Overdispersion	Dispersion ratio = 0.813, Pearson's $\chi^2 = 13.824$	$P = 0.679$	No overdispersion
	GLM	$\chi^2 = 3.815$	$P = 0.041$	*
Mean individual size	Shapiro-Wilk	$W = 0.970$	$P = 0.781$	Normal distribution
	T-test	$t = 2.115, df = 17$	$P = 0.049$	*

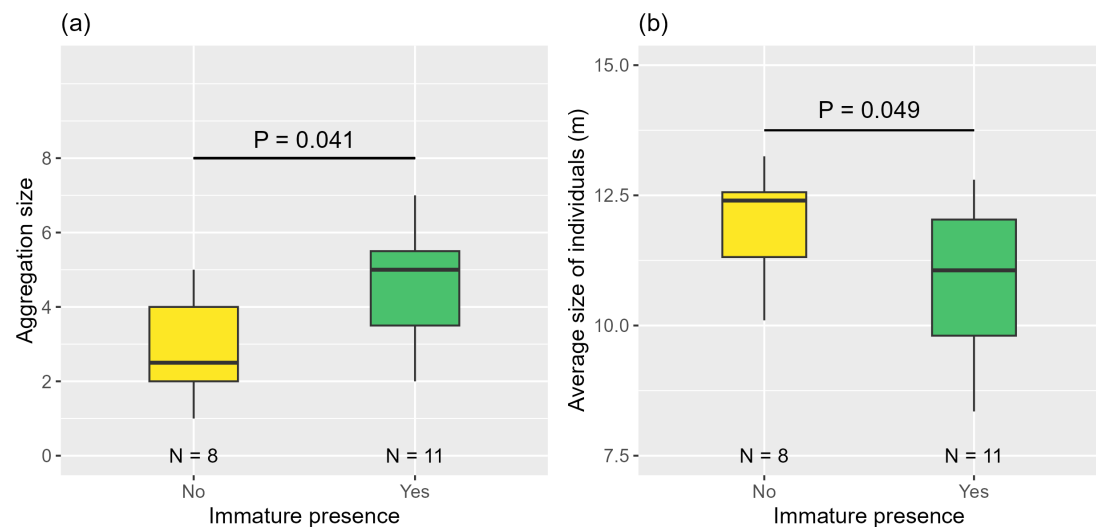


Figure 7. Aggregation size (a) and average size of individuals in the aggregation (b) according to the presence or absence of immature(s). Medians and standard deviations are represented.

Spatial distribution

The spatial distribution of sperm whales was analysed based on various parameters: aggregation size, average individual size, their class, and the presence of immatures. All these parameters were tested in relation to bathymetry and slope. The statistical results for this part are given in the Table 3 and the parameters did not vary with bathymetry or slope.

Table 3. Statistical results showing the influence of different parameters on the spatial distribution of sperm whales.

Independent variable	Dependent variable	Test	Statistic	P-value	Interpretation
Distance from the coast	Bathymetry	Shapiro-Wilk	$W = 0.977$	$P = 0.801 > 0.050$	Normal distribution
	(Fig. S2)	Pearson correlation	$\beta = 0.134 \pm 0.012 \text{ SE},$ $t = 11.640, df = 25,$ $R^2 = 0.844$	$P < 0.001$	Strong positive correlation
Aggregation Size	Bathymetry	Shapiro-Wilk	$W = 0.954$	$P = 0.436 > 0.050$	Normal distribution
	(Fig. S3.a)	Pearson correlation	$t = 0.029,$ $df = 17$	$P = 0.977$	No significant correlation
	Slope	Shapiro-Wilk	$W = 0.940$	$P = 0.268 > 0.050$	Normal distribution
	(Fig. S3.b)	Pearson correlation	$t = -1.218,$ $df = 17$	$P = 0.240$	No significant correlation
Average size of individuals	Bathymetry	Shapiro-Wilk	$W = 0.953$	$P = 0.444 > 0.050$	Normal distribution
	(Fig. S3.c)	Pearson correlation	$t = 0.167,$ $df = 17$	$P = 0.870$	No significant correlation
	Slope	Shapiro-Wilk	$W = 0.914$	$P = 0.086 > 0.050$	Normal distribution
	(Fig. S3.d)	Pearson correlation	$t = 0.071,$ $df = 17$	$P = 0.944$	No significant correlation
Sperm whale classes	Bathymetry	Linear model (perm. test)		$P = 0.474$	No significant difference
	Slope	Linear model (perm. test)		$P = 0.210$	No significant difference
Immature presence	Bathymetry	Shapiro-Wilk	$W = 0.953$	$P = 0.445 > 0.050$	Normal distribution
	(Fig. S3.e)	T-test	$t = -0.437,$ $df = 17$	$P = 0.668$	No significant difference
	Slope	Shapiro-Wilk	$W = 0.904$	$P = 0.058 > 0.050$	Normal distribution
	(Fig. S3.f)	T-test	$t = -0.905,$ $df = 17$	$P = 0.378$	No significant difference

Habitat use

We observed differences in the performance of behaviours related to bathymetry (Shapiro-Wilk test: $W = 0.985$, $P = 0.200$; LM: $F = 8.330$, $df = 3$, $P < 0.001$) (Fig. 8.a). Post-hoc comparisons showed that sperm whales were hunting at deeper bathymetries (median = 1700 m, $\bar{x} = 1632$ m) than when moving (median = 1300 m, $\bar{x} = 1330$ m) or socialising (median = 1200 m, $\bar{x} = 1180$ m), but there were no differences with resting behaviour (median = 1400 m, $\bar{x} = 1550$ m). Bathymetry for the other three behaviours was not significantly different (see Table 4 for post-hoc results). However, there was no difference between the behaviours with respect to slope (LM with permutation test: $P = 0.315$) (Fig. 8.b).

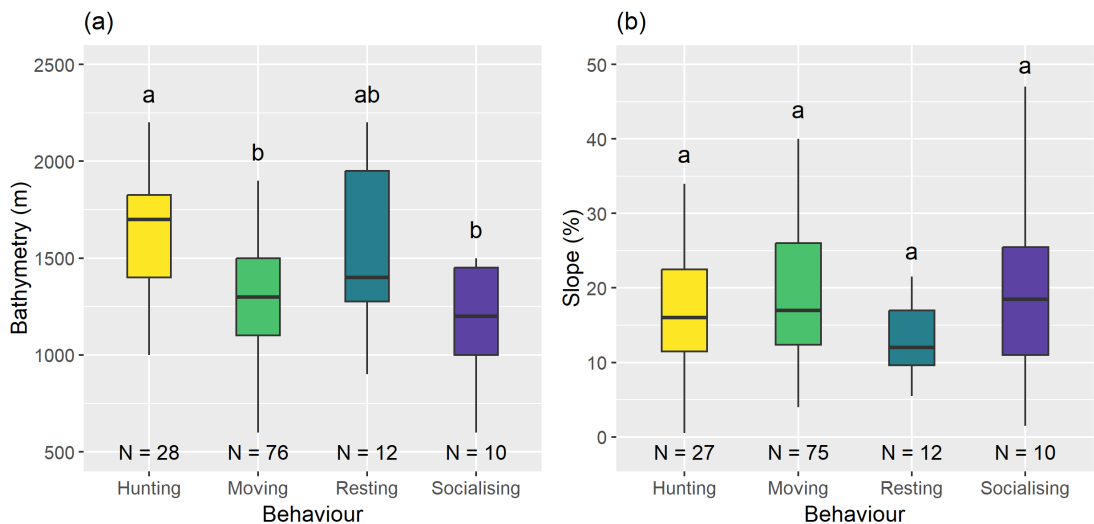


Figure 8. Bathymetry (a) and slope of the seabed (b) according to the different behaviours. Medians and standard deviations are represented. Different letters indicate significant differences and identical letters indicate no significant difference.

Table 4. Confusion matrix showing different behaviours. Results of pairwise comparisons of bathymetry after sequential Bonferroni-Holm correction. Green colour indicates a significant difference, red colour indicates no difference.

	Hunting	Moving	Resting	Socialising
Hunting				
Moving	$\beta = -310.88 \pm 66.60$ SE $F\text{-value} = 19.366$ $t\text{-value} = -4.401$ $P < 0.001$			
Resting	$\beta = -82.14 \pm 129.48$ SE $F\text{-value} = 0.403$ $t\text{-value} = -0.634$ $P = 0.494$	$\beta = 219.74 \pm 100.10$ SE $F\text{-value} = 4.819$ $t\text{-value} = 2.195$ $P = 0.031$		
Socialising	$\beta = -452.14 \pm 121.21$ SE $F\text{-value} = 13.915$ $t\text{-value} = -3.730$ $P < 0.001$	$\beta = -150.26 \pm 100.36$ SE $F\text{-value} = 2.242$ $t\text{-value} = -1.497$ $P = 0.138$	$\beta = -370.00 \pm 166.00$ SE $F\text{-value} = 4.968$ $t\text{-value} = -2.229$ $P = 0.037$	

Temporal variation

Between the two periods (Period 1: January 12 to March 28; Period 2: April 4 to May 15), at the individual scale, AS was lower in Period 2 compared to Period 1 (see Table 5 Fig. 9). Regarding social structure, the aggregation size remained unchanged between the two periods (see Table 5 and Fig. S4.c in Supplementary Material).

357 Otherwise, there was no change in the distribution with respect to bathymetry or slope (Table 5 and
 358 Fig. S4.a and b in Supplementary Material)

Table 5. Statistical results for behaviours related to bathymetry, slope, and social structure across two periods.

Variable	Test	Statistic	P-value	Interpretation
Animal Size	Shapiro-Wilk	$W = 0.975$	$P = 0.147$	Normal distribution
	T-test	$\beta_{period_2} = -1.526 \pm 0.459$ $t = 3.325$ $df = 72$	$P = 0.001$	***
Aggregation size	Overdispersion	Dispersion ratio = 0.996 Pearson's $\chi^2 = 16.936$	$P = 0.459$	No overdispersion
	GLM	$\chi^2 = 1.285$	$P = 0.257$	N.S.
Bathymetry	Shapiro-Wilk	$W = 0.932$	$P = 0.099$	Normal distribution
	T-test	$t = 1.991$ $df = 23$	$P = 0.058$	N.S.
Slope	Fisher-Pitman	$Z = -0.478$	$P = 0.650$	N.S.

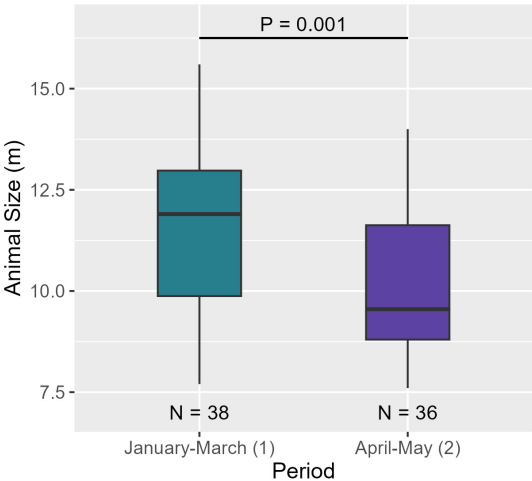


Figure 9. AS between the two periods. Medians and standard deviations are represented.

359 **DISCUSSION**

360 The study area corresponds to a sperm whale breeding area. According to our results, the structure of
 361 the aggregations was consistent, as females, juveniles and immatures were found forming social units
 362 (Whitehead, 2003), often with the proximity of mature males coming from the north to breed (Gero
 363 et al., 2014). The temporal analysis showed a change in the structure of the aggregations between the
 364 beginning and the end of the study period, suggesting the departure of males to the north. As for the
 365 spatial distribution of the population characterized during the study, it remained constant according to the
 366 bathymetry and the slope of the bottom, regardless of the type of aggregation and the classes of sperm
 367 whales. However, sperm whales showed a spatial variation in habitat use in relation to bathymetry.

368 **Comparison of social structure with other regions**

369 Of the 19 identified aggregations, only one contained a single individual, ~~an adult male hunting over the~~
 370 ~~1500 m of bathymetry.~~ All others contained at least two individuals (see Table S1). Furthermore, the
 371 identified sperm whales were immatures, juveniles or females (IPI distribution: $Q_3 = 5.35$ ms). As the

size of the aggregation in our study increased, the AS standard deviation between individuals increased, indicating the presence of individuals with more size differences (immature - juvenile and/or adult female - adult male) in larger aggregations. Furthermore, when an immature was present, the aggregation was larger and nearby individuals were significantly smaller. The social structure found in our study area was consistent with the literature, as females, juveniles and immatures form stable social units in tropical and subtropical waters (Whitehead, 2003). For example, in Dominica, aggregations encountered averaged 7-9 individuals, with the majority of social units containing females and juveniles (Gero et al., 2014). Within identified groups of more than 4 individuals, there was almost always at least one male. Again, in Dominica, mature males were identified in close proximity to social units, and groups were larger when a mature male was present (Gero et al., 2014). In northern Chile, mature males tend to accompany some groups of females (Coakes and Whitehead, 2004). The presence of mature males in nearly 80% of the characterized aggregations was not surprising, as they come to breed in the Caribbean (Gero et al., 2007; Whitehead, 2018).

This dynamic highlights how the composition of sperm whale aggregations can vary across regions. Indeed, the proportions of juvenile males, adult females, adult males, and juveniles within these groups have been found to differ between studies. For example, the percentage of adult males in our study area was higher than in a study from the Ionian Sea (Caruso et al., 2015) but similar to another study from the Mediterranean Sea (Poupard et al., 2022). Jaquet (2006) showed that the Gulf of Mexico population (median = 9.3 m) was composed of smaller animals than the Gulf of California population (median = 10.7 m) thanks to photogrammetric measurements. Only a few of adult males were found in both areas (Jaquet, 2006). Although the methods are different with photogrammetry which allows the measurement of sizes less than 7.7 m ($IPI < 2$ ms), these comparisons highlight the variability in the size distributions depending on the geographical areas, even close ones (Caruso et al., 2015; Poupard et al., 2022) and certainly also on the duration of the study, in connection with the migrations of the males (Dufault et al., 1999; Whitehead, 2003).

Spatial distribution independent of aggregation type

Contrary to the model developed by Pace et al. (2018) highlighting a variation in spatial distribution according to the social composition of the groups, this was not the case in our study. Indeed, we did not observe any variation in bathymetry as a function of aggregation characteristics (such as size of aggregation, average size of individuals, or presence of immatures). Given that sperm whales belong to the same population and social units, and may even contain the same individuals on different days (Dufault et al., 1999; Whitehead, 2003), it is possible that they share similar preferences in their spatial distribution. An alternative hypothesis is that variations in bathymetry was not strong enough to induce changes in spatial distribution between aggregation types. However, since immatures need to nurse and these events occur at depths below 30 m (Sarano et al., 2023), one would have expected the presence of immatures to influence the distribution as a function of bathymetry. One hypothesis that could explain the lack of variation is that alloparenting between females within social units (Whitehead, 1996) may well compensate for the need to surface frequently by remaining in the most productive areas. Furthermore, we did not distinguish calves from other immatures that no longer nurse. Similarly, distribution did not differ by sperm whale class or by the average size of individuals within an aggregation. This finding was unexpected, as it is generally understood that larger individuals tend to dive deeper due to their greater breath-holding capacity (Drouot et al., 2004). This distinction may not be visible in our study area, because it mainly characterises mature males, which are more offshore in areas with deeper bathymetry (Drouot et al., 2004). Here, the priority for males would be to reproduce (Dufault et al., 1999; Whitehead, 2003) and therefore be close to females.

With regard to the slope, no variation in the distribution of sperm whales was found. In fact, it is relatively homogeneous where sperm whales have been observed and certainly does not vary enough to influence their distribution. However, on a larger spatial scale, the slope is an important parameter (Jaquet and Whitehead, 1996; Pace et al., 2018) because in the canyons where the sperm whales are found, upwelling phenomena favour the concentration of biomass, and therefore of cephalopods (Berzin and Rovnin, 1966; Jaquet and Whitehead, 1996), the main prey of sperm whales (Clarke, 1980).

Specialised areas of behaviour

Although all aggregations were distributed similarly, sperm whale behaviour varied with bathymetry. Specifically, a bathymetric area appeared to be preferred for hunting ($\bar{x} = 1641$ m), distinct from the areas

used for movement ($\bar{x} = 1330$ m) and socialisation ($\bar{x} = 1180$ m) but comparable to those used for resting ($\bar{x} = 1550$ m).

In contrast to social behaviour, hunting occurs at greater depths, likely along submarine canyons where giant squid (*Dosidicus gigas*), a preferred prey of sperm whales (Clarke, 1980), are found. The deeper bathymetries observed in hunting areas likely reflect the depth preferences of these mesopelagic cephalopods (Nigmatullin et al., 2001). Furthermore, the similarity in bathymetries between resting behaviours ($\bar{x} = 1550$ m) and hunting behaviours ($\bar{x} = 1641$ m) may indicate a need for rest after deep, high-energy dives (Watwood et al., 2006).

Socialising behaviour was expected at shallower depths, as groups with immature were anticipated to socialise more in these areas, due to lactating which takes place rather on the surface (Sarano et al., 2023). However, as no influence of aggregation size, average individual size, or the presence of immature individuals on spatial distribution was found, we suggest that behaviours are not influenced by the type of the aggregation or that there are more important factors, such as prey availability (Whitehead and Weilgart, 1991; Watwood et al., 2006) or environmental conditions (Jaquet and Whitehead, 1996; Pirota et al., 2011; Wong and Whitehead, 2014) that explain the identified behaviours. Moreover, in areas of high maritime traffic, social cohesion may help cetaceans cope with noise. For example, an increase in social signals has been observed in response to sonar noise in the northern Norwegian Sea (Curé et al., 2016). In other cetaceans, such as blue whales (*Balænoptera musculus*), vocalizations increase during social interactions in the presence of high seismic activity (Di Iorio and Clark, 2010). Among odontocetes, bottlenose dolphins (*Tursiops truncatus*) have been observed to increase their whistling during the early stages of a jet-ski approach, possibly reflecting an increased need for cohesion (Buckstaff, 2004). Furthermore, groups containing mother-calf pairs whistle more in the presence of fast-moving boats compared with groups without calves (Guerra et al., 2014).

As for spatial distribution, behaviour did not change as a function of slope, suggesting that the variations in slope are not sufficiently marked to cause a change in their spatial distribution. Unlike other cetacean species such as humpback whales, **which migrate to Caribbean waters to reproduce and give birth without feeding** (Martin et al., 1984), sperm whales do not follow this pattern and feed during their breeding season. Whatever the season, the sperm whales' preferred areas remain the canyons (Jaquet and Whitehead, 1996; Pace et al., 2018), where the squid can be found (Clarke, 1980).

Finally, we can conclude that there was no intraspecific spatial segregation according to topography within our study area. This means that even if there are preferential hunting or socialisation zones, all the aggregations, depending on the size of the individuals, the number of individuals or the presence of immatures, perform these behaviours according to the same bathymetric distribution (and distance from the coast) and slope. Their habitat selection seems to be mainly determined by the bathymetry rather than by local gradients in the ocean floor (Pace et al., 2018). Whatever the season, submarine canyons remain key habitats for sperm whales (Clarke, 1980), serving as essential feeding areas due to their role in the aggregation of prey species.

As the historical data did not include acoustic information, hunting behaviours were not recorded and socialisation behaviours ($N = 10$) were probably underestimated due to the lack of detection of codas. Moreover, even sperm whales are great divers, reaching depths of well over 1500 m (Teloni et al., 2008). As we travel along the 1500 m bathymetry line, our range is restricted: we may miss silent behaviour close to 2000 m.

Temporal variation

A temporal variation between January-March and April-May was observed. Indeed, AS decreased between the two periods ($\bar{x}_{period1} = 11.6$ m, $\bar{x}_{period2} = 10.1$ m). As the size of individuals decreased but not the number of individuals per aggregation, aggregations consisted of more females/young males and immatures compared to males. Both results suggest that males began to move out of the breeding area to higher latitudes (Dufault et al., 1999; Whitehead, 2003). However, a full-year study would confirm this hypothesis and improve our knowledge of the structural and temporal dynamics of Caribbean sperm whales.

Influence of other factors

Although the spatial distribution of sperm whales was studied, other environmental factors such as Sea Surface Temperature (SST) (Pirota et al., 2011; Wong and Whitehead, 2014), seabed characteristics, seamounts, slope orientation (Pirota et al., 2011) and wind strength (Jaquet and Whitehead, 1996) could

play a critical role in biomass distribution (Jaquet and Whitehead, 1996; Wong and Whitehead, 2014) at spatial scales larger than that of our study area, of the order of several thousand km². As sperm whales spend about three-quarters of their time searching for prey (Whitehead and Weilgart, 1991; Watwood et al., 2006), their distribution necessarily depends on the distribution of food resources, particularly cephalopods (Clarke, 1980; Wong and Whitehead, 2014), but also fish, which are an occasional food source for sperm whales (Clarke et al., 1993). Pirota et al. (2011) highlighted the link between the distribution of sperm whales at bathymetries deeper than 2000 m and 2500 m and the presence of cephalopods in the Balearic region (Quetglas et al., 2000). Unlike our study, sperm whale habitat modeling studies have focused on larger geographic areas and longer time periods. For example, Pirota et al. (2011) studied the distribution of sperm whales around Ibiza, Mallorca and Menorca for six years, where they found temporally stable preferential areas, areas where no sperm whales were observed, and a preference for warmer areas. As for Vachon et al. (2022a), data were collected in the Eastern Caribbean over a period of more than a year and approximately 700 km, allowing the examination of geomorphic features such as canyons, plateaus, escarpments, slopes and abyssal plains. Their result over a period of more than a year showed that the distribution of sperm whales depended more on site fidelity, rather than environmental parameters, is the main driver of sperm whale distribution (Vachon et al., 2022a). In addition to environmental factors, the presence of other animals, such as competitors or predators, may also influence the distribution and habitat use of sperm whales. During our observations, we observed harassment on two occasions, first by pilot whales (*Globicephala macrorhynchus*) and then by killer whales (*Orcinus orca*). These were the only two times that codas were recorded during our study. The aggressive behaviour of pilot whales was previously documented by Díaz-Gamboa et al. in the Gulf of California. Their biopsies showed that both species preferred to feed on giant squid (Díaz-Gamboa et al., 2022), indicating that they are competitors for the same food source. On the other hand, killer whales have been shown to be predators of sperm whales (Pitman et al., 2001), which interrupt their foraging or resting dives when they hear killer whale sounds and return to the surface, initiating a significant degree of social behaviour (Curé et al., 2013).

A neutral methodology

In terms of methodology, several approaches can be used to calculate the IPI, including the manual method applied in this study. According to Antunes et al. (2010), the manual method, while time-consuming, is considered more accurate and less sensitive to noise than automatic detection. However, automatic methods offer significant advantages, particularly in processing large datasets, despite their reliance on a high signal-to-noise ratio and the orientation of the animal relative to the hydrophone, which can lead to false negatives (Antunes et al., 2010). Over the years, automatic methods have demonstrated their effectiveness, as suggested by the comparable size estimates obtained using IPI calculations and photogrammetry (Rhinelanders and Dawson, 2004; Growcott et al., 2011). Additionally, a comparison of three automatic methods (envelope, cepstrum, and cross-correlation) highlighted variations in their efficiency, with the envelope method providing the most accurate estimates (Böttcher et al., 2018). While both approaches have their strengths and limitations, the continuous development of automatic methods remains crucial for handling large volumes of data while aiming to minimize subjectivity in manual annotation. It is also important to note that biases may exist in the conversion of IPI to individual size. Each equation (Gordon, 1991; Growcott et al., 2011), has its own potential margin of error and is based on specific populations. Scientific studies, such as that of Ferrari et al., 2024 refine this correlation by relying on the largest possible number of individuals.

This subjectivity is also reflected in the lack of standardisation of terms used to describe cetacean structures, which makes comparisons between different studies problematic. Due to the difficulty in accurately determining the distance of individuals from the hydrophone, it was not possible to assign a specific name to the aggregation found in the literature. For example, a group can be defined as a set of individuals moving together in a coordinated manner for periods ranging from a few hours to a few days, while a cluster would rather be like a transient subset of a group consisting of individuals swimming side by side in a coordinated manner (Cantor and Whitehead, 2015). In contrast, other authors have defined a group as about twenty individuals feeding in structured formations over about 1 km for days, while a cluster consisted of at least two individuals grouped together at the surface for about 10 minutes (Lettevall et al., 2002). According to these definitions, our term “aggregation” could correspond to “group,” but no two studies used the same methodology as ours. These differences in definition highlight the problem of standardising terminology and methods used in sperm whale studies, making comparisons between

studies difficult.

The inclusion of additional data in our study is a crucial resource for analysing the distribution of behaviour over time. Indeed, socialisation behaviour, for example, remains exceptionally rare in our dataset ($N = 10$, $N = 3$ in our study). While historical recordings provide valuable information, feeding behaviour could not be explicitly defined, as its identification depends on acoustic analysis - an aspect that has not been achieved in previous studies. The absence of acoustic recordings also prevents us from determining key ecological parameters, such as the size of aggregations and the average size of individuals. This gap highlights the need to incorporate bioacoustic monitoring into future research in order to refine behavioural classifications and improve our understanding of population dynamics. Furthermore, even though the additional data were integrated with those from this study, we do not know exactly how long the observers stayed in front of each group of sperm whales. It was estimated that the time spent near groups of sperm whales to collect data was certainly similar, as sperm whales stay at depth for a long time, so the time dedicated to observation is short, and regulations limit the amount of time we are allowed to spend near a marine mammal.

Conservation and management implications

Our study provides valuable information on the use of sperm whale habitat along the west coast of Martinique, highlighting the key environmental and social factors shaping their distribution. This was made possible by focusing on a fine spatial scale and a complementary methodology, combining visual and acoustic. At this level of precision, our study becomes the basis for implementing effective conservation and spatial management strategies. As Figure 1 shows, the challenge lies along the Caribbean coast, not out in the Atlantic where the near-shore topography does not characterise a sperm whale habitat and where maritime traffic is much less significant.

One of the main external factors influencing cetacean behaviour is maritime traffic (Erbe et al., 2016). The Caribbean Sea, including the waters around Martinique, is heavily trafficked (Fig. 1), posing two main threats to sperm whales: ship strikes and noise pollution. Ship strikes are one of the main causes of mortality for large cetaceans (Peltier et al., 2019). Although the implementation of measures such as speed limits (<5 kt) and a regulated distance between the ship and the animal of more than 300 m within the Agoa sanctuary helps mitigate these dangers, the knowledge of the population is essential to understand all the issues and improve the regulations in the future.

In addition to the physical obstacle represented by ships, they emit continuous noise that can mask the sounds of marine mammals (Erbe et al., 2016). Sperm whales use echolocation to feed, navigate, and communicate (Whitehead and Weilgart, 1991; Watwood et al., 2006). Thus, increasing underwater noise from navigation, but also from seismic surveys and industrial activities interferes with these essential behaviours through acoustic masking (Erbe et al., 2016). Chronic exposure to noise can lead to habitat displacement, reduced foraging efficiency, and increased stress levels (Wright et al., 2007), phenomena that can also occur in the Martinique sperm whale population. Passive acoustic monitoring could provide more information on how noise pollution affects this species (Poupard et al., 2022) and help develop targeted mitigation measures.

Given these external pressures, our results may contribute to further conservation efforts. Identifying and strengthening the protection of key habitat areas for sperm whales, particularly those used for socialisation and foraging, could reduce the risk of disturbance. In addition, improved real-time whale tracking systems, such as Repcet® (Campana et al., 2015), could help reduce the risk of collision by alerting vessels to the presence of cetaceans. Indeed, it would be interesting to update the software for the west coast of Martinique to warn sailors that sperm whales are mainly found south of Saint-Pierre at depths of over 1000 m, that they are often far apart and almost never alone, and in particular that there are always individuals at depth when some are on the surface. In particular, more attention should be paid when a calf is present as the group may be larger.

Combining long-term passive acoustic monitoring with vessel tracking data could offer a more comprehensive understanding of how human activities influence the ecology of sperm whales. Closer collaboration between researchers, conservation organizations, and maritime authorities will be essential to ensure the coexistence of marine megafauna and sustainable human activities in the Caribbean Sea.

CONCLUSIONS

Our study, based on 24 vessel surveys over five months, represents the first comprehensive analysis of sperm whale habitat use in Martinique waters.

The distribution of aggregations along the Martinique coast will provide valuable information to reduce collisions between ships and sperm whales, within the framework of the Repcet® system developed in France. This system allows vessels to communicate information about the presence of cetaceans at the surface. When a cetacean is spotted, a detection radius expands over time. This radius is calculated based on a single individual, but our study shows that sperm whales are frequently observed in groups in Martinique. Therefore, the detection radius in this area should be increased to better reflect reality. In the future, sustained long-term studies are essential to capture seasonal variations in the spatial distribution of sperm whales along the Caribbean coast of Martinique. Continuous monitoring will refine our understanding of their movement dynamics and guide adaptive management strategies.

ACKNOWLEDGMENTS

Thank you to the whale-watcher Yannick Tursi from Planète Dauphin and the whole Aquasearch team for participating in the data collection.

REFERENCES

- Abdi, H. (2010). Holm's sequential bonferroni procedure. *Encyclopedia of research design*, 1(8):1–8.
- Antunes, R., Rendell, L., and Gordon, J. (2010). Measuring inter-pulse intervals in sperm whale clicks: Consistency of automatic estimation methods. *The Journal of the Acoustical Society of America*, 127(5):3239–3247.
- Arcangeli, A., Cominelli, S., David, L., Di-Meglio, N., Moulins, A., Mayol, P., Marini, L., Rosso, M., and Tepsich, P. (2014). Seasonal monitoring of cetaceans and validation of the repcet system in terms of monitoring. *Scientific reports of Port-Cros National Park*.
- Arnbom, T. and Whitehead, H. (1989). Observations on the composition and behaviour of groups of female sperm whales near the Galapagos Islands. *Canadian Journal of Zoology*, 67(1):1–7.
- Avila, I. C., Farías-Curtidor, N., Castellanos-Mora, L., do Amaral, K. B., Barragán-Barrera, D. C., Orozco, C. A., León, J., and Puentes, V. (2022). The colombian caribbean sea: a tropical habitat for the vulnerable sperm whale *Physeter macrocephalus* ? *Oryx*, 56(6):814–824.
- Berzin, A. and Rovnin, A. (1966). The distribution and migrations of whales in the northeastern part of the pacific, chukchi and bering seas. *Izvestiya Tikhookeanskogo Nauchno-Issledovatel'skogo Institut Rybnogo Khozyaistva I Okeanografii*, 58:179–207.
- Boik, R. J. (1987). The fisher-pitman permutation test: A non-robust alternative to the normal theory f test when variances are heterogeneous. *British Journal of Mathematical and Statistical Psychology*, 40(1):26–42.
- Bøttcher, A., Gero, S., Beedholm, K., Whitehead, H., and Madsen, P. T. (2018). Variability of the inter-pulse interval in sperm whale clicks with implications for size estimation and individual identification. *The Journal of the Acoustical Society of America*, 144(1):365–374.
- Browning, E., Gibb, R., Glover-Kapfer, P., and Jones, K. E. (2017). *Passive acoustic monitoring in ecology and conservation*. Number 2 in WWF Conservation Technology Series. WWF-UK.
- Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, (*Tursiops truncatus*), in sarasota bay, florida. *Marine mammal science*, 20(4):709–725.
- Campana, I., Crosti, R., Angeletti, D., Carosso, L., David, L., Di-Méglio, N., Moulins, A., Rosso, M., Tepsich, P., and Arcangeli, A. (2015). Cetacean response to summer maritime traffic in the western Mediterranean sea. *Marine Environmental Research*, 109:1–8.
- Cantor, M. and Whitehead, H. (2015). How does social behavior differ among sperm whale clans? *Marine Mammal Science*, 31(4):1275–1290.
- Caruso, F., Sciacca, V., Bellia, G., De Domenico, E., Larosa, G., Papale, E., Pellegrino, C., Pulvirenti, S., Riccobene, G., Simeone, F., Fabrizio, S., Salvatore, V., and Gianni, P. (2015). Size distribution of sperm whales acoustically identified during long term deep-sea monitoring in the ionian sea. *PLoS One*, 10(12):e0144503.
- Christal, J. and Whitehead, H. (1997). Aggregations of mature male sperm whales on the galapagos islands breeding ground. *Marine Mammal Science*, 13(1):59–69.

- Clarke, M. R. (1980). Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep.*, 37:1–324.
- Clarke, M. R., Martins, H. R., and Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* off the azores. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 339(1287):67–82.
- Coakes, A. K. and Whitehead, H. (2004). Social structure and mating system of sperm whales off northern chile. *Canadian Journal of Zoology*, 82(8):1360–1369.
- Curé, C., Antunes, R., Alves, A. C., Visser, F., Kvadsheim, P. H., and Miller, P. J. (2013). Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Scientific Reports*, 3(1):1579.
- Curé, C., Isojunno, S., Visser, F., Wensveen, P. J., Sivle, L. D., Kvadsheim, P. H., Lam, F.-P. A., and Miller, P. J. (2016). Biological significance of sperm whale responses to sonar: comparison with anti-predator responses. *Endangered Species Research*, 31:89–102.
- Di Iorio, L. and Clark, C. W. (2010). Exposure to seismic survey alters blue whale acoustic communication. *Biology letters*, 6(1):51–54.
- Di-Meglio, N., David, L., and Monestiez, P. (2018). Sperm whale ship strikes in the pelagos sanctuary and adjacent waters: assessing and mapping collision risks in summer. *J. Cetacean Res. Manage.*, 18(1):135–147.
- Díaz-Gamboa, R. E., Gendron, D., and Guerrero-de la Rosa, F. (2022). Aggressive behavior of short-finned pilot whales towards sperm whales in the gulf of california: Insight into food competition. *Aquatic Mammals*, 48(6):529–532.
- Drouot, V., Gannier, A., and Goold, J. C. (2004). Diving and feeding behaviour of sperm whales (*Physeter macrocephalus*) in the northwestern Mediterranean sea. *Aquatic mammals*, 30(3):419–426.
- Dufault, S., Whitehead, H., and Dillon, D. (1999). An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. *J. Cetacean Res. Manage.*, 1(1):1–10.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., and Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine pollution bulletin*, 103(1-2):15–38.
- Fais, A., Aguilar Soto, N., Johnson, M., Pérez-González, C., Miller, P., and Madsen, P. T. (2015). Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behavioral Ecology and Sociobiology*, 69:663–674.
- Fais, A., Lewis, T. P., Zitterbart, D. P., Álvarez, O., Tejedor, A., and Aguilar Soto, N. (2016). Abundance and distribution of sperm whales in the canary islands: Can sperm whales in the archipelago sustain the current level of ship-strike mortalities? *PLoS One*, 11(3):e0150660.
- Faraway, J. J. (2016). *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models*. Chapman and Hall/CRC.
- Ferrari, M., Trinh, M., Sarano, F., Sarano, V., Giraudet, P., Preud'homme, A., Heuzey, R., and Glotin, H. (2024). Age and interpulse interval relation from newborn to adult sperm whale (*physeter macrocephalus*) off mauritius. *Scientific Reports*, 14(1):18474.
- Freedman, D., Pisani, R., and Purves, R. (2007). Statistics (international student edition). *Pisani, R. Purves, 4th edn. WW Norton & Company, New York*.
- Gero, S. (2005). Fundamentals of sperm whale societies, care for calves. Master's thesis, Dalhousie University, Halifax, NS, Canada.
- Gero, S., Engelhaupt, D., Rendell, L., and Whitehead, H. (2009). Who cares? Between-group variation in alloparental caregiving in sperm whales. *Behavioral Ecology*, 20(4):838–843.
- Gero, S., Gordon, J., Carlson, C., Evans, P., and Whitehead, H. (2007). Population estimate and inter-island movement of sperm whales (*Physeter macrocephalus*) in the eastern caribbean sea. *J. Cetacean Res. Manage.*, 9(2):143–150.
- Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., Steffen, A., Tyack, P., Evans, P., and Whitehead, H. (2014). Behavior and social structure of the sperm whales of dominica, west indies. *Marine Mammal Science*, 30(3):905–922.
- Gero, S. and Whitehead, H. (2016). Critical decline of the eastern caribbean sperm whale population. *PLoS One*, 11(10):e0162019.
- Gero, S., Whitehead, H., and Rendell, L. (2016). Individual, unit and vocal clan level identity cues in sperm whale codas. *Royal Society Open Science*, 3(1):150372.
- Giorli, G. and Goetz, K. T. (2020). Acoustically estimated size distribution of sperm whales (*physeter*

- macrocephalus) off the east coast of new zealand. *New Zealand Journal of Marine and Freshwater Research*, 54(2):177–188.
- Goold, J. C. and Jones, S. E. (1995). Time and frequency domain characteristics of sperm whale clicks. *The Journal of the Acoustical Society of America*, 98(3):1279–1291.
- Gordon, J. C. (1991). Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. *Journal of Zoology*, 224(2):301–314.
- Grossi, F., Lahaye, E., Moulins, A., Borroni, A., Rosso, M., and Tepsich, P. (2021). Locating ship strike risk hotspots for fin whale (*Balaenoptera physalus*) and sperm whale (*Physeter macrocephalus*) along main shipping lanes in the north-western Mediterranean sea. *Ocean & Coastal Management*, 212:105820.
- Growcott, A., Miller, B., Sirguy, P., Slooten, E., and Dawson, S. (2011). Measuring body length of male sperm whales from their clicks: the relationship between inter-pulse intervals and photogrammetrically measured lengths. *The Journal of the Acoustical Society of America*, 130(1):568–573.
- Guerra, M., Dawson, S., Brough, T., and Rayment, W. (2014). Effects of boats on the surface and acoustic behaviour of an endangered population of bottlenose dolphins. *Endangered Species Research*, 24(3):221–236.
- Hothorn, T., Hornik, K., Van De Wiel, M. A., and Zeileis, A. (2008). Implementing a class of permutation tests: the coin package. *Journal of statistical software*, 28(8):1–23.
- Jaquet, N. (2006). A simple photogrammetric technique to measure sperm whales at sea. *Marine Mammal Science*, 22(4):862–879.
- Jaquet, N. and Whitehead, H. (1996). Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the south pacific. *Marine ecology progress series*, 135:1–9.
- Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., and Podesta, M. (2001). Collisions between ships and whales. *Marine Mammal Science*, 17(1):35–75.
- Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., and Howard, P. M. (2002). Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology*, 80(7):1189–1196.
- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: An r package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60).
- Marcoux, M., Whitehead, H., and Rendell, L. (2006). Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology*, 84(4):609–614.
- Martin, A., Katona, S., Matilla, D., Hembree, D., and Waters, T. (1984). Migration of humpback whales between the caribbean and iceland. *Journal of mammalogy*, 65(2):330–333.
- McHugh, M. L. (2011). Multiple comparison analysis testing in ANOVA. *Biochemia medica*, 21(3):203–209.
- Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., and Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography*, 20(4):36–45.
- Miller, B., Dawson, S., and Vennell, R. (2013). Underwater behavior of sperm whales off kaikoura, new zealand, as revealed by a three-dimensional hydrophone array. *The Journal of the Acoustical Society of America*, 134(4):2690–2700.
- Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., and Lund, A. (2003). The monopulsed nature of sperm whale clicks. *The Journal of the Acoustical Society of America*, 114(2):1143–1154.
- Nigmatullin, C. M., Nesis, K. N., and Arkhipkin, A. (2001). A review of the biology of the jumbo squid *Dosidicus gigas* (cephalopoda: Ommastrephidae). *Fisheries Research*, 54(1):9–19.
- Norris, K. S. and Harvey, G. W. (1972). A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). Technical report., Ocean Institute.
- Pace, D. S., Arcangeli, A., Mussi, B., Vivaldi, C., Ledon, C., Lagorio, S., Giacomini, G., Pavan, G., and Ardizzone, G. (2018). Habitat suitability modeling in different sperm whale social groups. *The Journal of Wildlife Management*, 82(5):1062–1073.
- Pavan, G. (2008). Short field course on bioacoustics. *Taxonomy Summer School*, pages 1–15.
- Peltier, H., Beaufils, A., Cesarini, C., Dabin, W., Dars, C., Demaret, F., Dhermain, F., Dorémus, G., Labach, H., Van Canneyt, O., and Spitz, J. (2019). Monitoring of marine mammal strandings along french coasts reveals the importance of ship strikes on large cetaceans: a challenge for the european

- 747 marine strategy framework directive. *Frontiers in Marine Science*, 6:486.
- 748 Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., and Rendell, L. (2011). Modelling
749 sperm whale habitat preference: a novel approach combining transect and follow data. *Marine Ecology*
750 *Progress Series*, 436:257–272.
- 751 Pitman, R. L., Ballance, L. T., Mesnick, S. I., and Chivers, S. J. (2001). Killer whale predation on sperm
752 whales: observations and implications. *Marine mammal science*, 17(3):494–507.
- 753 Poupard, M., Ferrari, M., Best, P., and Glotin, H. (2022). Passive acoustic monitoring of sperm whales
754 and anthropogenic noise using stereophonic recordings in the Mediterranean sea, north west pelagos
755 sanctuary. *Scientific reports*, 12(1):2007.
- 756 Praca, E., Gannier, A., Das, K., and Laran, S. (2009). Modelling the habitat suitability of cetaceans:
757 example of the sperm whale in the northwestern Mediterranean sea. *Deep Sea Research Part I:*
758 *Oceanographic Research Papers*, 56(4):648–657.
- 759 Quetglas, A., Carbonell, A., and Sánchez, P. (2000). Demersal continental shelf and upper slope
760 cephalopod assemblages from the balearic sea (north-western mediterranean). biological aspects of
761 some deep-sea species. *Estuarine, Coastal and Shelf Science*, 50(6):739–749.
- 762 R Core Team (2022). R: A language and environment for statistical computing. Technical report, R
763 Foundation, Vienna, Austria.
- 764 Rendell, L. E. and Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*).
765 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1512):225–231.
- 766 Rhinelander, M. Q. and Dawson, S. M. (2004). Measuring sperm whales from their clicks: Stability
767 of interpulse intervals and validation that they indicate whale length. *The Journal of the Acoustical*
768 *Society of America*, 115(4):1826–1831.
- 769 Rice, D. W. (1989). Sperm whale *Physeter macrocephalus* linnaeus, 1758. *Handbook of marine mammals*,
770 4:177–233.
- 771 Rinaldi, C., Rinaldi, R., Laine, J., and Barbraud, C. (2021). Population dynamics of sperm whales
772 (*Physeter macrocephalus*) in Guadeloupe, French Caribbean: A mark-recapture study from 2001 to
773 2013. *Marine Mammal Science*, 37(4):1391–1405.
- 774 Sanctuaire AGOA (2025). Les bonnes pratiques d’observation des cétacés dans le sanctuaire agoa.
775 Consulté le 24 février 2025.
- 776 Sarano, F., Sarano, V., Tonietto, M.-L., Yernaux, A., Jung, J.-L., Huetz, C., and Charrier, I. (2023). Nursing
777 behavior in sperm whales (*physeter macrocephalus*). *Animal Behavior and Cognition*, 10(2):105–131.
- 778 Savouré-Soubelet, A., Aulagnier, S., Haffner, P., Moutou, F., Van Canneyt, O., Charrassin, J.-B., and
779 Ridoux, V. (2016a). *Atlas des mammifères sauvages de France: Volume 1. Mammifères marins*.
780 Muséum national d’Histoire naturelle/Institut de Recherche pour le Développement.
- 781 Savouré-Soubelet, A., Aulagnier, S., Haffner, P., Moutou, F., Van Canneyt, O., Charrassin, J.-B., and
782 Ridoux, V. (2016b). *Atlas des Mammifères sauvages de France, Volume 1 : Mammifères marins*,
783 volume 74 of *Patrimoines naturels*. Muséum national d’Histoire naturelle, Paris.
- 784 Service Hydrographique et Océanographique de la Marine (SHOM) (2025). SHOM Data Portal. Accessed:
785 2025-01-28.
- 786 Shapiro, S. S. and Wilk, M. B. (1965). An analysis of variance test for normality (complete samples).
787 *Biometrika*, 52(3-4):591–611.
- 788 Student (1908). The probable error of a mean. *Biometrika*, pages 1–25.
- 789 Teloni, V., Mark, J. P., Patrick, M. J., and Peter, M. T. (2008). Shallow food for deep divers: Dynamic
790 foraging behavior of male sperm whales in a high latitude habitat. *Journal of Experimental Marine*
791 *Biology and Ecology*, 354(1):119–131.
- 792 Tønnesen, P., Gero, S., Ladegaard, M., Johnson, M., and Madsen, P. T. (2018). First-year sperm whale
793 calves echolocate and perform long, deep dives. *Behavioral Ecology and Sociobiology*, 72:1–15.
- 794 Vachon, F., Eguiguren, A., Rendell, L., Gero, S., and Whitehead, H. (2022a). Distinctive, fine-scale distri-
795 bution of eastern caribbean sperm whale vocal clans reflects island fidelity rather than environmental
796 variables. *Ecology and Evolution*, 12(11):e9449.
- 797 Vachon, F., Hersh, T. A., Rendell, L., Gero, S., and Whitehead, H. (2022b). Ocean nomads or island
798 specialists? culturally driven habitat partitioning contrasts in scale between geographically isolated
799 sperm whale populations. *Royal Society Open Science*, 9(5):211737.
- 800 Vries, L. D. (2017). First characterization of cetacean’s movements in the eastern caribbean: application
801 to sperm whale, short-finned pilot whale and bottlenose dolphin. Master 1 - ethologie, Université Jean

- 802 Monnet, Saint-Étienne, France.
- 803 Watkins, W. A. and Schevill, W. E. (1977). Sperm whale codas. *The Journal of the Acoustical Society of*
804 *America*, 62(6):1485–1490.
- 805 Watwood, S. L., Miller, P. J., Johnson, M., Madsen, P. T., and Tyack, P. L. (2006). Deep-diving foraging
806 behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology*, 75(3):814–825.
- 807 Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales.
808 *Behavioral Ecology and Sociobiology*, 38:237–244.
- 809 Whitehead, H. (2003). *Sperm whales: social evolution in the ocean*. University of Chicago press.
- 810 Whitehead, H. (2018). Sperm whale: *Physeter macrocephalus*. In *Encyclopedia of marine mammals*,
811 pages 919–925. Elsevier.
- 812 Whitehead, H. and Gero, S. (2015). Conflicting rates of increase in the sperm whale population of the
813 eastern caribbean: positive observed rates do not reflect a healthy population. *Endangered Species*
814 *Research*, 27(3):207–218.
- 815 Whitehead, H. and Rendell, L. (2004). Movements, habitat use and feeding success of cultural clans of
816 south pacific sperm whales. *Journal of Animal Ecology*, pages 190–196.
- 817 Whitehead, H. and Weilgart, L. (1990). Click rates from sperm whales. *The Journal of the Acoustical*
818 *Society of America*, 87(4):1798–1806.
- 819 Whitehead, H. and Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in
820 groups of female sperm whales. *Behaviour*, pages 275–296.
- 821 Wong, S. N. and Whitehead, H. (2014). Seasonal occurrence of sperm whales (*Physeter macrocephalus*)
822 around kelvin seamount in the sargasso sea in relation to oceanographic processes. *Deep Sea Research*
823 *Part I: Oceanographic Research Papers*, 91:10–16.
- 824 Wright, A. J., Aguilar Soto, N., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., Deak, T., Edwards,
825 E. F., Fernández, A., Godinho, A., Hatch, L. T., Kakuschke, A., Lusseau, D., Martineau, D., Romero,
826 M. L., Weilgart, L. S., Wintle, B. A., Notarbartolo-di Sciara, G., and Martin, V. (2007). Do marine
827 mammals experience stress related to anthropogenic noise? *International Journal of Comparative*
828 *Psychology*, 20(2).