

Passive acoustics reveal low-latitude distribution of North Atlantic minke whales

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Abstract

Substantial knowledge gaps remain regarding the migratory patterns of many whale species. Recent meta-analyses of passive acoustic sensor networks have provided critical information on the distribution of several baleen whale species across the western North Atlantic Ocean. However, of the baleen whale species known to regularly inhabit this region, knowledge on common minke whales (*Balaenoptera acutorostrata*) remains scarce, particularly at lower latitudes. A large passive acoustic dataset from the Wider Caribbean Region, comprising 92 deployments and over 11,900 recording days between 2001 and 2025, was analyzed using a convolutional neural network-based minke whale pulse train detector. The results provide novel insights into the spatial and temporal distribution of the common minke whale in the tropics and subtropics of the western North Atlantic Ocean. Our findings reveal pronounced spatial and seasonal occurrence patterns, with detections concentrated between 14°–18°N during winter months (December – March). This includes the first acoustic evidence of minke whales in the U.S. Virgin Islands, Dominican Republic, Montserrat, and Guadeloupe. Summer detections at some sites suggest the presence of non-migratory individuals challenging previous assumptions that their presence at lower northern latitudes is limited to the winter months. Despite considerable recording effort in the Gulf of Mexico, only one pulse train was detected, providing limited evidence of the species in this region. Results from this broadscale analysis refine the known winter range and potential breeding grounds of North Atlantic minke whales and underscore the value of passive acoustic monitoring in data-poor and logistically challenging environments.

1. INTRODUCTION

Many baleen whale species are migratory (Corkeron & Connor 1999). However, the routes they follow are often unclear, making their potential distribution areas quite broad and uncertain (Mizroch et al. 2009, Risch et al. 2019a). Moreover, some populations, or individuals, within these migratory species are known to remain resident rather than migrate (Dorsey et al. 1990, Van Waerebeek et al. 1999). In the Western North Atlantic, all baleen whale species are protected at both national (e.g., U.S. Marine Mammal Protection Act and the Endangered Species Act; Canadian Fisheries Act and the Species at Risk Act) and international levels (e.g., CITES and Convention on the Conservation of Migratory Species of Wild Animals). Given their vital role in shaping global ecosystems (Roman et al. 2014, Lambert et al. 2025), the restoration of healthy large whale populations aligns with the broader objective of advancing ocean conservation, as outlined in the UN Sustainable Development Goal 14 ‘Life below water’ (Molony et al. 2022). Despite legislative mandates, the designation of critical habitats is lacking for many species. This lack of information on spatio-temporal distribution, habitat preferences, and interactions with anthropogenic activities constrains the identification and designation of critical habitats (Risch et al. 2014a, NOAA 2023).

Despite the conservation concern for and intensive study of many baleen whale species in the western North Atlantic, minke whales remain poorly understood (Hayes et al. 2024). The term “minke whales” refers to two distinct species: the common (*Balaenoptera acutorostrata*) and the Antarctic (*B. bonaerensis*) minke whale. The common minke whale is the smallest Balaenopteridae species. In addition to its small body size, its blow is inconspicuous, making individuals difficult to spot and identify from a distance (Perrin et al. 2017). The common minke whale is currently divided into three subspecies: *B. a. acutorostrata* (North Atlantic, abbreviated to minke whale throughout this document), *B. a. scammoni* (North Pacific), and the unnamed dwarf minke whale (Southern Hemisphere) (Rice 1998). Common minke whale population trends are classified as ‘unknown’, which has led to varying protection statuses over time, ranging from ‘insufficiently known’, to ‘near threatened’ and ‘least concern’ (Cooke 2018). An ongoing ‘Unusual Mortality Event’ (UME) for common minke whales in the North Atlantic has been underway since 2017. It has inconsistent apparent causes that call for further research (NOAA 2025). The lack of life history data and population trend information makes it even more difficult to assess the severity of this UME.

While the species is generally considered migratory, in a few locations it can be observed year-round (Perrin et al. 2017). This is the case, for example, near the Canary Islands (North Atlantic minke whales) (Van Waerebeek et al. 1999) and central California (North Pacific minke whales) (Dorsey et al. 1990). It suggests some individuals may not migrate from these regions. For both North Pacific and North Atlantic common minke whales, breeding is thought to occur during winter months in lower northern latitudes. It is followed by a gestation period of almost a year (Sergeant 1963, Mitchell. 1991, Víkingsson & Heide-Jørgensen 2015, Kavanagh et al. 2018). Individuals exhibit differential migration patterns depending on age and sex. For instance, females with unweaned calves tend to remain longer in tropical waters, resulting in group segregation by sex and breeding condition (Murphy 1995). To date, no distinct breeding grounds have been identified for common minke whales (Risch et al. 2019a b). In the North

Atlantic, individuals have been observed as far north as Baffin Bay, Denmark Strait, Franz Josef Land, and Novaya Zemlya during the summer (IUCN 2008). Their winter distribution is less well understood. Sightings have been reported as far south as the Caribbean in the west and the Strait of Gibraltar and the Canary Islands in the east. Knowledge about this subspecies in the southern part of its range remains scarce.

The Wider Caribbean Region comprises the Caribbean Sea, the Gulf of Mexico (GoM), and adjacent North Atlantic waters. It forms a semi-enclosed body of water bordered by land, adjoining highly industrialized countries to the north. At least seven baleen whale species have been recorded in the Caribbean Sea or its vicinity (Halpin et al. 2009). By contrast, the GoM is not known for its diversity of baleen whale species. The only known resident species is the Rice's whale (*B. ricei*), which is critically endangered (Rosel et al. 2021, NOAA 2024). Other species such as North Atlantic right (*Eubalaena glacialis*) and humpback (*Megaptera novaeangliae*) whales are generally considered incidental (Jefferson & Schiro 1997). Reports of minke whales in the GoM are limited to stranding events during winter and spring (Würsig 2017). To date, no live individuals have been observed in the GoM. However, considering that minke whales are difficult to identify from a distance, the lack of visual detection does not necessarily indicate their absence from the GoM.

Visual observations and data from stranded animals have long been the primary means of studying cetaceans. However, these methods have limitations. Strandings are irregular, and because baleen whales spend most of their time underwater, sightings tend to be brief; especially when population densities and groups sizes are low (Kaschner et al. 2012) or when the species exhibits poorly visible surface behavior, as is the case for minke whales (Perrin et al. 2017). Moreover, visual surveys are only possible during daylight hours. These factors make long-term visual monitoring of many large whale species challenging. Since baleen whales predominantly produce low-frequency vocalizations (Tyack & Clark 2000), their calls can propagate over long distances, making Passive Acoustic Monitoring (PAM) a powerful tool for studying vocalizing animals. This method allows continuous monitoring and is generally unaffected by weather and light.

The most well-known vocalizations of the common minke whale include the famous 'star-wars' sound produced by the dwarf form (Southern Hemisphere) (Gedamke et al. 1997, 2001, Gedamke 2004, Risch 2022), boing sounds produced by *B. a. scammoni* (North Pacific) (Wenz 1964, Rankin & Barlow 2005), and low-frequency pulse trains produced by *B. a. acutorostrata* (North Atlantic) (Winn & Perkins 1976). These pulse trains have been classified into three types: speed-up, constant, and slow-down pulse trains, (Mellinger et al. 2000, Risch et al. 2013, Risch 2022). While these sounds can be used for detecting the presence of the species, it remains unclear whether all age and sex groups produce the same vocalizations, and how call density correlates with actual animal density. Most knowledge of their repertoire in the North Atlantic comes from studies at high latitudes ($> 36^{\circ}\text{N}$) (Edds-Walton 2000, Risch et al. 2013, 2014b, 2019b). Less is known at lower latitudes. Acoustic detections indicate that spring migrants tend to follow the Gulf Stream along the continental shelf, whereas in fall they travel farther offshore (Risch et al. 2014a). In the Caribbean, the species has been recorded from December to March off Martinique (Heenehan et al. 2019) and from February to April around the Windward Dutch

Islands (Risch & Haan 2016). However, the occurrence in many other areas of this vast region remains unknown. The present study aims to investigate the spatiotemporal distribution of North Atlantic common minke whales in the Wider Caribbean Region using PAM.

2. METHODS

Data collection

Data for this meta-analysis were retrieved from PAM data archives at Cornell University, the National Centers for Environmental Information Passive Acoustic Data Archive (<https://www.ncei.noaa.gov/maps/passive-acoustic-data/>) and NOAA & Island Solutions collections (Montserrat, UK). Data were collected under multiple collaborative projects. They consist of recordings from 92 deployments of stationary moored recorders conducted between 2001 and 2025, amounting to 11,916 instrument-days (7,728 equivalent continuous days after accounting for duty cycles; deployments spanned 11–33°N, depths: 4 – 1375 m, Fig. 1). The area comprises the GoM, the Belize-Mexican Caribbean coast, off the coasts of southeastern U.S. (Florida and Georgia), offshore and coastal Bermuda, the ABC Islands (Aruba, Bonaire, and Curaçao), and the Caribbean and Atlantic sides of the West Indies. Data from all months were available for the GoM, Curaçao, and the Virgin Islands, whereas the other sites had fewer months of deployment (see appendices). Most of these PAM surveys were designed to focus on species other than minke whales, primarily North Atlantic right whales, humpback whales, other cetaceans, or coral reef fish. This meta-analysis incorporates recordings from moored recorders including NRS buoys, AMARs, Snaps, Soundtrap ST300s, ST500s and ST600s, and MARUs. Details regarding recorder and hydrophone types, gains, sensitivities, sampling frequencies, and peak-to-peak voltages are provided in Appendix I. Using such a large dataset is a clear advantage for identifying broad-scale patterns, but it also inherently introduces heterogeneity (e.g., different years, teams, and methodologies), meaning that the results should be interpreted as indicative of relative patterns rather than absolute comparisons.

Water depths were either provided by the original data source or acquired from Bathymetric Data Viewer (<https://www.ncei.noaa.gov/maps/bathymetry/>). Optimum Interpolation Sea Surface Temperature (OISST) data were obtained via the Environmental Research Division Data Access Program (ERDDAP, <https://www.ncei.noaa.gov/erddap/index.html>). Data were provided at a spatial resolution of 0.25° and a temporal resolution of one day. The seasonal evolution of additional temperature-related features, such as the depths of the 20°C and 26°C isotherms and the ocean mixed layer thickness, is presented in the Supplementary Materials. Distances from shore were measured using QGIS (<http://www.qgis.org>). Calibration information was obtained from the National Centers for Environmental Information (NCEI) metadata, the manufacturers, or directly from the researchers involved. Calibration curves for each recorder and hydrophone were generated using MANTA 9.6 (Miksis-Olds et al. 2021).

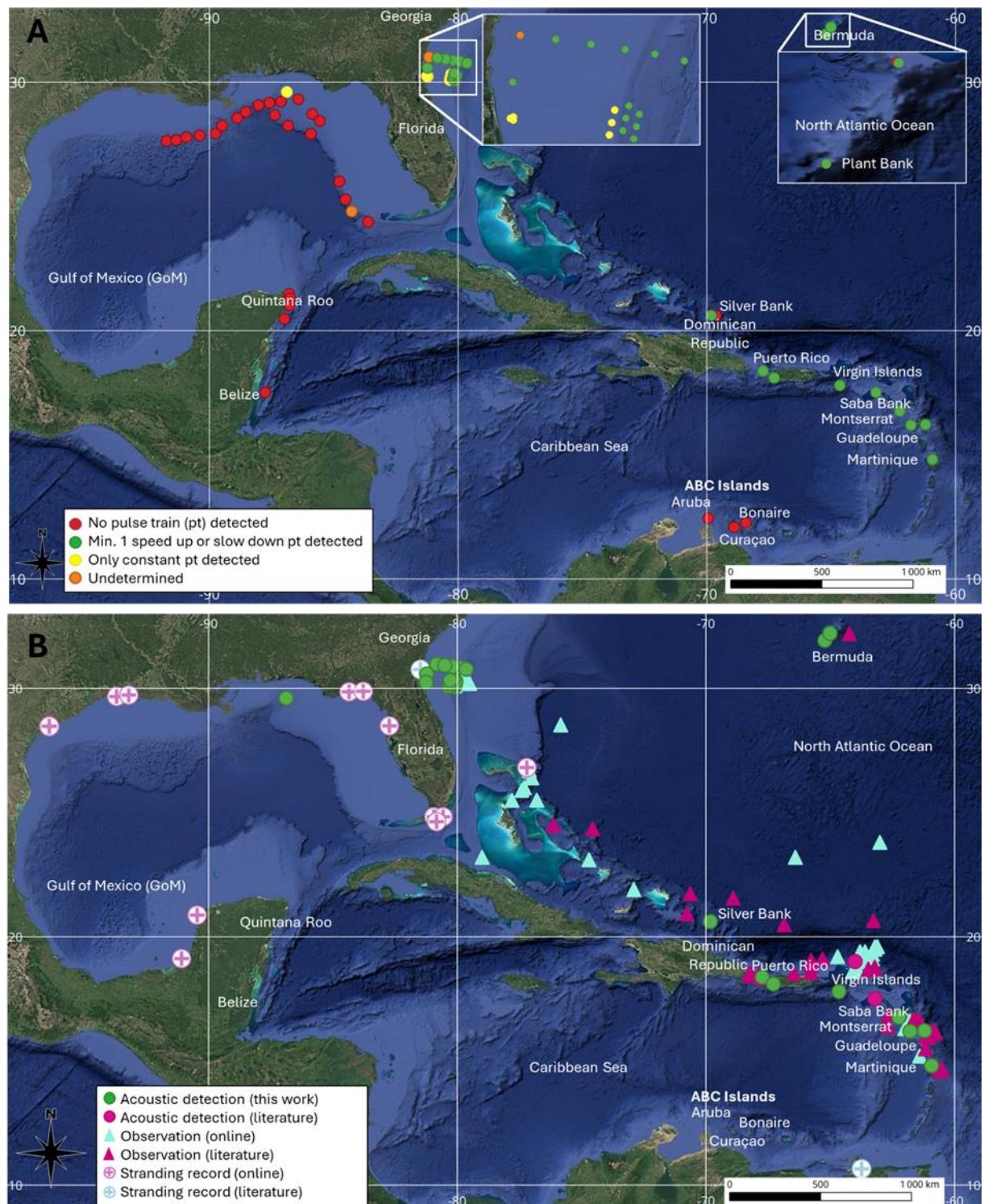


Figure 1 – (A) Geographic distribution of detected minke whale pulse trains. Where there is a high density of deployments along the US East coast and Bermuda, both areas are presented by a zoom. Despite this, some sites in Bermuda are not visible as the deployments are too close to be discernible. (B) Geographic distribution of minke whales based on online databases (visual observations), literature records (Mitchell. 1991, Jefferson 1996, Mellinger et al. 2000, Risch et al. 2014b a, Jiménez et al. 2021), and acoustic detections from this study. Each shape represents a single record. It is important to distinguish stranding events from other types of records, as stranded individuals do not constitute definitive evidence of a species' regular occurrence in an area. Specimens of *Balaenoptera bonaerensis* are not included (Jiménez et al. 2021). Locations with unidentified detections near the entrance of the Gulf of Mexico and off the coast of Georgia were excluded. ABC = Aruba, Bonaire, and Curaçao. Online records include data from OBIS SEAMAP and GBIF. Basemap imagery: SIO, NOAA, U.S. Navy, NGA, GEBCO (2020); Landsat / Copernicus.

Observation and stranding record data, which were used for comparison with our detections, were obtained from OBIS SEAMAP (Halpin et al. 2009), iNaturalist (iNaturalist), and the Global Biodiversity Information Facility (GBIF 2025), and published literature (Mitchell. 1991, Jefferson 1996, Mellinger et al. 2000, Risch et al. 2014b a, Jiménez et al. 2021). Stranding events were separated from other types of records, as stranded individuals do not constitute definitive evidence of a species' regular occurrence in an area.

Data analysis

All recordings were downsampled to 2 kHz using Raven Compass (Yang Center for Conservation Bioacoustics; Ithaca, NY, USA). The first and last days of each deployment were excluded from the analysis, as they did not represent full days and the deployment vessel was typically still present in the area. To detect the presence of minke whale pulse trains in our recordings, we used the MinkeNet ResNet18 convolutional neural network (Mouy et al. 2025, Van Parijs et al. 2025). MinkeNet processes de-noised spectrogram images (duration: 60 s, band: 0 – 1000 Hz) to detect minke whale pulse trains (Mouy et al. 2025). The model was trained on manually labeled recording samples that included minke whale vocalizations as well as a wide range of non-target sounds such as geophony, haddock calls, humpback whale vocalizations, seismic survey pulses, pile-driving, and vessel noise collected between 2006 and 2022 from coastal waters in the northeastern United States, the Caribbean, and Scotland. The validation was strictly adopted from Mouy et al. (2025). The detector was validated using independent continuous PAM datasets collected off Georgia and Martinique and selecting a threshold of 0.9 allowed detection of the hourly presence of minke whale pulse trains with a recall of at least 0.9 and a precision of at least 0.6, maximizing detector performance, i.e. F1-score (Mouy et al. 2025). The spectrograms of all selections generated by the detector were manually reviewed using the generated spectrogram images (.png) and Raven Lite 2.0.5 (Cornell Lab of Ornithology; Ithaca, NY, USA) when necessary. All detections were reviewed by the same analyst, and in cases of doubt, several analysts examined the files. Minke whale sounds were distinguished from fish or non-biological noises using both published acoustic measurements (Risch et al. 2013) and expert verification. Each day of detection was categorized based on the type of sounds identified: (0) absence of sounds produced by minke whales, (1) presence of at least one stereotyped constant, slow down, or speed up pulse train emitted by minke whales (Risch et al. 2013), and (2) presence of non-stereotyped constant pulse trains distinct from typical pulse trains but possibly emitted by minke whales (i.e., a greater uncertainty in pulse train identification). Days classified as category 2 underwent further manual inspection. After review by experts ($n = 3$) and consensus was reached, these days were reclassified as either category 0 or 1. Days with sounds that could neither be confirmed nor refuted as belonging to minke whales were conservatively assigned to category 0 for statistical analyses, resulting in a binary dataset. Because constant pulse trains may be less readily recognized as minke whale sounds, and given the limited knowledge about the link between repertoire and behavior, we displayed sites containing only constant pulse trains separately in the figures. Characteristics of minke whale pulse trains are described in detail in the Supplementary Materials.

Power Spectral Density (PSD) values for every minute of each day were then computed using MANTA (1-Hz resolution) and used to calculate the root mean square broadband band-limited sound pressure level (SPL_{RMS}) between 40 and 800 Hz, converting values from dB re 1 μ Pa² Hz⁻¹ to broadband dB re 1 μ Pa using the custom software MANTA2BandLevel (Yang Center for Conservation Bioacoustics; Ithaca, NY, USA). These frequency bounds were selected to encompass the ambient noise in the range of dominant frequency content for North Atlantic minke whale vocalizations, i.e., \leq 1 kHz (Mellinger et al. 2000, Risch et al. 2013). This minimizes the influence of flow noise dominating the lowest frequencies and non-flat hydrophone responses near 0 Hz, and avoid proximity to the Nyquist frequency (1 kHz). Finally, a single daily mean SPL_{RMS} was calculated based on the linear values.

Statistical analysis

The reviewed daily presence/absence data were used in two advanced analyses: (1) the spatiotemporal distribution of minke whales across the Wider Caribbean Region; and (2) the finer scale multi-year seasonal variation in the U.S. Virgin Islands, where continuous recordings were available from November 2016 to May 2022. All statistical analyses described below were conducted using R version 4.5.0 (R 2024).

For the analysis of general spatiotemporal variation and potential environmental drivers, the presence/absence dataset for the entire study region was examined. The presence/absence data was explored graphically prior to model construction. Before examining more ecologically relevant and complex models, we first ran a Generalized Additive Model (GAM) model using only location (deployment coordinates), to provide a first simple understanding of the distribution. The same model was also run excluding the GoM data due to the low number of detections there, which would have limited model reliability. Highly correlated features (Spearman's $\rho \geq 0.6$ and $p \leq 0.001$) were not included in the same model [e.g., OISST and day of the year (DOY)]. More precisely, a Generalized Additive Mixed Model (GAMM) was developed with OISST and SPL_{RMS}, accounting for random site effects (Sagarese et al. 2014, Wood 2017). In addition, a GAM was developed with the following parameters tested as potential predictors for minke whale presence: latitude, deployment site water depth, and DOY. In graphical representation, DOY_cos and DAY_sin represent the cosinusoidal and sinusoidal transformations of DOY.

Generalized Additive (mixed) Models (GAMs & GAMMs) were fitted using the *gam* function from the *mcgv* package (Wood 2000). The binomial family was used due to the binary response variable. OISST, SPL_{RMS}, deployment depth, latitude, longitude, and DOY were included as smooth terms with an initial number of basis dimensions (k) set to 10. This value was adjusted when the effective degrees of freedom (edf) of a parameter approached the maximum allowed by k. To avoid overfitting, the Restricted Maximum Likelihood (REML) method was applied for smoothing parameter estimation. A cyclic cubic regression spline was used for DOY to capture its periodic variation. To model interactions between DOY and latitude, tensor product smooths were used to accommodate the differing scales of these variables and to account for potential non-linear relationships. Models were evaluated and compared based on the percentage of explained deviance, residual autocorrelation, Root Mean Square Error (RMSE), and, particularly when models differed in the number of parameters, Akaike's Information

Criterion (AIC). To measure the RMSE, we used a 5-fold cross-validation approach. The dataset was randomly divided into five folds, and for each iteration, the model was trained on four folds and tested on the remaining fold. Predictions from the fitted GAM correspond to the predicted probability of presence at each observation. The RMSE was then calculated for each fold as the square root of the mean squared difference between observed presence/absence (0 or 1) and predicted probabilities. The mean RMSE across all folds provides an overall measure of predictive accuracy. To allow comparison across variables with different ranges, we also calculated a normalized RMSE by expressing the mean RMSE as a percentage of the range of observed values.

To explore potential unexpected interactions between variables and to assess the relative importance of predictors, Boosted Regression Tree (BRT) models were also constructed. The same set of predictors was used, with the addition of distance from shore, previously excluded due to strong collinearity with depth (Spearman's $\rho = 0.79$). The use of correlated predictors is less problematic in BRT models, as the relative influence tends to be allocated to one variable in the pair. Tree complexity (tc) was set to 2, allowing for two-way interactions, and the learning rate (lr) was set to 0.0125 (Elith et al. 2006, Barlow & Torres 2021). Bag fraction was set to 0.75 (Friedman 2002, Elith et al. 2008). BRTs were implemented using the *gbm.step* function from the *dismo* package, which incorporates a 10-fold cross-validation routine. Although consecutive days are not fully independent, cross-validation folds were created randomly for simplicity. This choice is unlikely to influence the assessment of variable importance. Model performance was evaluated using mean residual deviance, explained deviance, and the area under the receiver operating characteristic curve (AUC), all estimated through cross-validation. To account for the cyclic nature of DOY, trigonometric decomposition was applied to this variable.

To study multi-year temporal variation in minke whale presence in one region of the Caribbean, recordings from the U.S. Virgin Islands were used. As before, data were visually explored before model fitting. Three GAMs were used with the following predictors: (1) DOY, (2) OISST, (3) OISST and SPL_{RMS} as potential predictors. Models were evaluated and compared using explained deviance, residual autocorrelation, RMSE, and, when applicable, AIC.

3. RESULTS

Spatiotemporal distribution

Minke whales were acoustically detected (Fig. 2) in recordings from 42% of the sites (36 out of 85, Fig. 1 & 3). Most detections occurred during winter (December – March) across the study area, although a few were recorded in summer (June – August, Appendix II), notably around Bermuda, Martinique, and the U.S. Virgin Islands (see next section). For the first time, minke whales were detected through PAM off the Dominican Republic, the Virgin Islands, Montserrat, and Guadeloupe (Fig. 2B, Fig. 3). At sites with available acoustic data around 30°N, numerous detections were made along the southeastern Atlantic U.S. coast (Georgia and Florida, Fig. 1A) and offshore at Plant Bank (Bermuda), while between 15°N and 25°N, most detections occurred near Puerto Rico, the Virgin Islands, Saba bank, Martinique, and Guadeloupe. Conversely, they were not detected or rarely detected at any recording sites in the southern & western Caribbean and GoM (Fig. 1). In the GoM, only one constant pulse train was confirmed off the Santa Rosa–

Walton coast (Florida Panhandle, Fig. 2D). Additionally, in proximity to the Florida Straits, close to the Loop Current's exit, in the GoM (Fig. 1), sounds resembling minke whale vocalizations were recorded, although they lacked sufficient distinguishing features for confident identification (Fig. 2F). Off Georgia and Florida, minke whale sounds were detected at deeper sites (168 – 561 m) from November to April, while in shallower areas (16 – 44 m), detections were fewer, absent, or limited to constant minke whale pulse trains. Detections in the summer months (July and August) in the U.S. Virgin Islands and Bermuda also consisted primarily of constant pulse trains (Fig. 2C).

The location of each deployment explained 35.7% (percentage of deviance explained) of the variation in whether minke whale sounds were detected (GAM, $edf = 10$, $R^2 = 0.22$, $p < 0.001$, $acf = 0.65$, $RMSE = 0.26$, Fig. 4A). This percentage decreased to 22.4% when the GoM data were excluded (GAM, $edf = 13$, $R^2 = 0.20$, $p < 0.001$, $acf = 0.64$, $RMSE = 0.34$, Fig. 4B). The influence of the location predictor was particularly evident along the western coasts of Florida and Georgia.

Depth, DOY, and latitude together explained 67.1% of the variance (GAM, $edf_{DOY*Lat} = 43$, $edf_{Depth} = 5$, $R^2 = 0.66$, $p < 0.001$, $acf = 0.30$, $RMSE = 0.18$, Fig. 4C, Appendix III). The models showed the presence of minke whales during winter around 30°N, while at lower northern latitudes (13 – 21°N), they varied between a primarily winter presence and a more year-round occurrence (Fig. 4C & 4E). Excluding the GoM accentuated the variation of predictor values in the Caribbean Sea. Higher predicted values were associated with the Virgin Islands, where a longer deployment occurred (1,997 calendar days out of 11,916). The number of detections from this deployment exceeded that of other sites, where deployments rarely exceeded one year, resulting in higher predicted values. In addition, excluding the GoM provided a more detailed representation of the predictor's variation with latitude in relation to DOY. Summer detections in Martinique are more accentuated, as is the absence of minke whale around the ABC Islands and along the Mexican coast. Models incorporating OISST and SPL explained a lower percentage of the variance, exhibited higher residual autocorrelations, or showed substantially higher AIC values, making them less appropriate than those presented above. Nonetheless, SPL was further examined and found to be weakly correlated with depth, indicating that deeper deployments were characterized by slightly lower SPL ($\rho = -0.32$, $p < 0.001$). This correlation may complicate the interpretation of depth as an important factor, since higher noise levels could reduce the signal-to-noise ratio and, consequently, lead to lower detections at shallower sites. Overall, SPL did not appear to vary greatly throughout the year at each location, although this may be partly attributed to the limited availability of year-round SPL data.

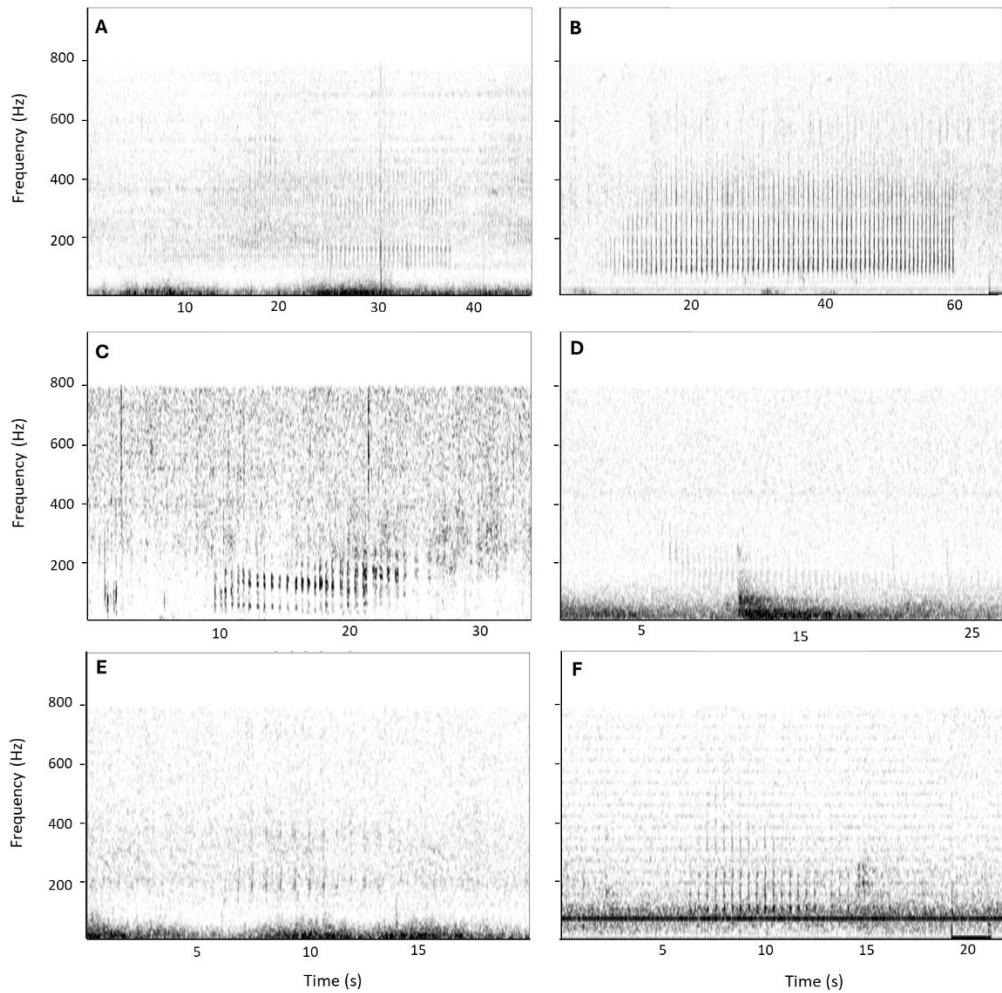


Figure 2 Spectrograms of detected sounds. (A) Slow-down pulse train detected on February 28, 2017 off Georgia; (B) Speed-up pulse train detected on March 25, 2017 off Guadeloupe; (C) Constant pulse train detected on August 31, 2020 in the U.S. Virgin Islands; (D) Constant pulse train detected on June 20, 2011 in the Gulf of Mexico; (E) Unidentified sound detected on February 12, 2017 off Georgia; (F) Unidentified sound detected on August, 7 2010 at the entrance of the Gulf of Mexico. Other sounds, such as fish sounds and boat noise (low-frequency horizontal line in panel F), are also present. 256-point FFT; overlap: 0.032 s; sampling rate: 2 kHz. The purpose of including panel E is to show an example of a sound that shares some similarities with minke whale pulse trains but does not appear to be produced by this species.

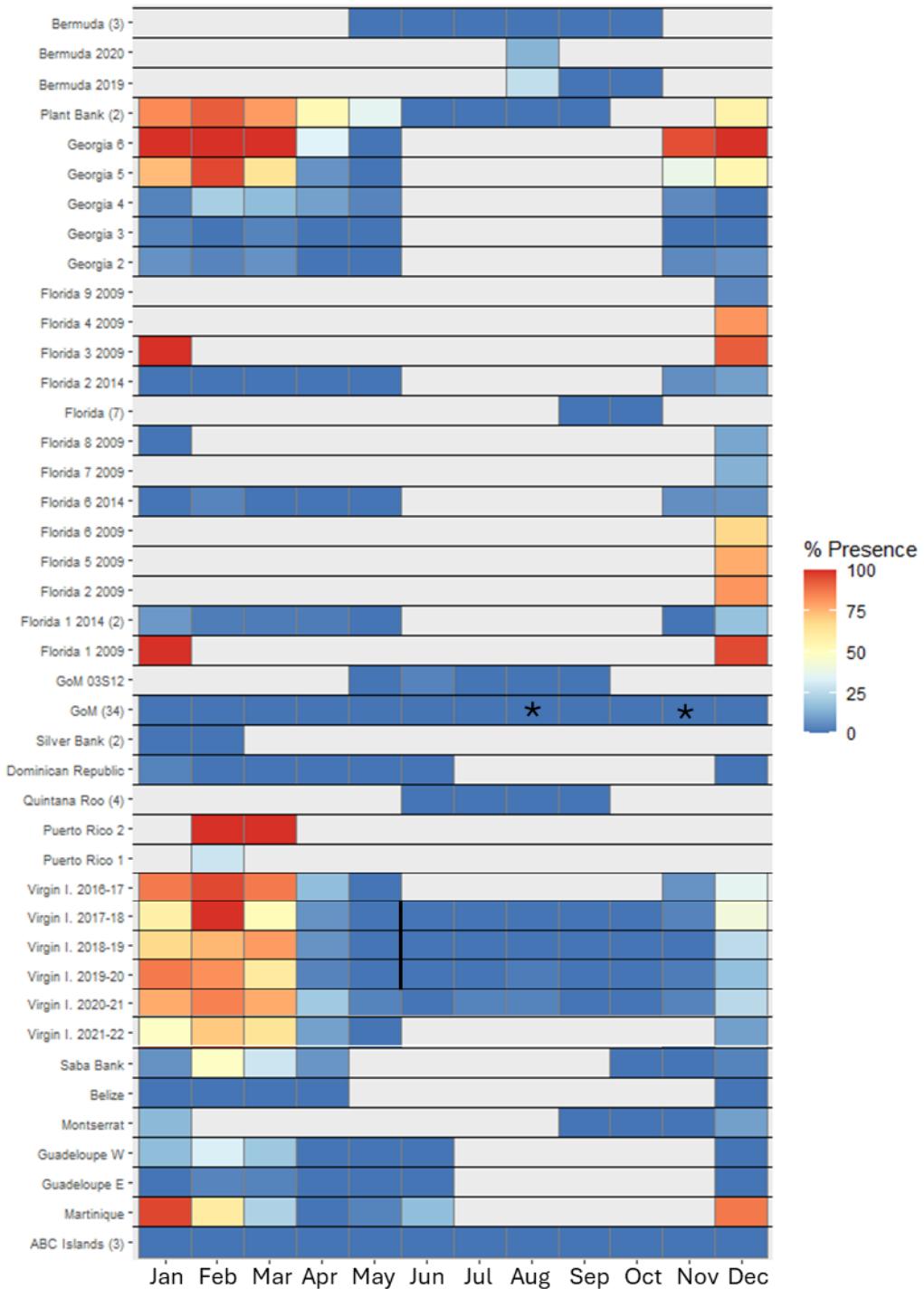


Figure 3 Percentage of days with detected minke whales by month and deployment, ordered by decreasing northern latitude (from top to bottom). Deployment information includes the location and, when applicable, the site number and year of deployment. Multiple deployments within the same region with no minke whale detections were aggregated into a single line in the figure. When a row includes multiple deployments, the number of deployments is indicated in parentheses. Grey rectangles represent months with no deployment. GoM = Gulf of Mexico; Virgin I. = U.S. Virgin Islands; ABC Islands = Aruba, Bonaire and Curacao; Quintana Roo = Cozumel, Nizuc, Mujeres and Contoy. *: Indicates months during which some detections in the GoM could not be confidently identified. For the Virgin Islands site, the bold line indicates the boundary between consecutive deployments, with each row representing a single deployment. For example, the 2016–2017 deployment records from November 2016 to May 2017.

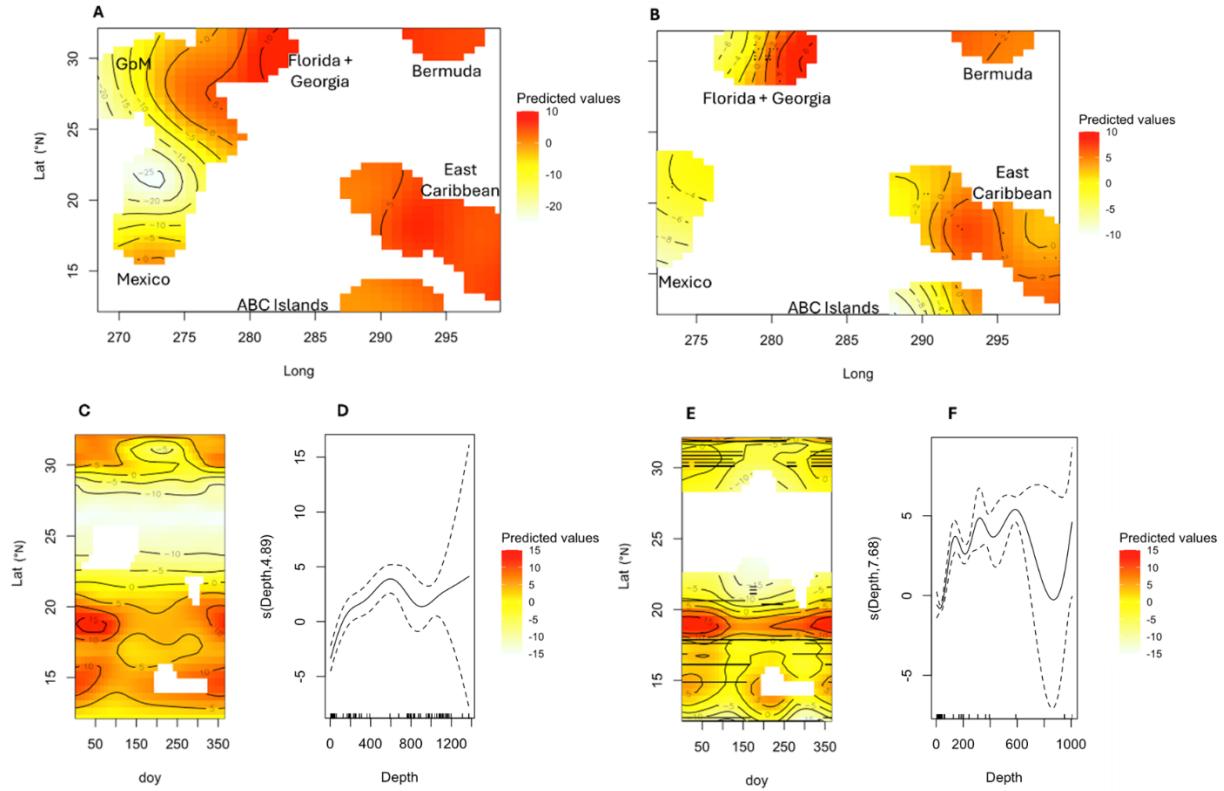


Figure 4 (A) Fitted GAM predicting minke whale detections using deployment coordinates, including the Gulf of Mexico (GoM), with $k = 14$ and REML; (B) same model as (A) excluding the GoM, with $k = 13$ and REML. (C) Fitted GAMs predicting minke whale detections using deployment depth and the interaction between northern latitude and day of the year (DOY), with $k_{\text{Lat}} = 15$, $k_{\text{DOY}} = 10$, REML, including the GoM. (D): Smoothed effect of depth (edf = 4.89), $k_{\text{Depth}} = 10$, REML, including the GoM. (E): Predicted values across northern latitude and DOY, with $k_{\text{Lat}} = 15$, $k_{\text{DOY}} = 10$, REML excluding the GoM. (F): Smoothed effect of depth (edf = 7.68), $k_{\text{Depth}} = 10$, REML, excluding the GoM. Lighter colors indicate lower predictor values; warmer colors indicate higher predicted values.

In addition to distributional patterns, we investigated which predictors most strongly influenced the probability of detecting minke whales. DOY, OISST, depth, and distance to shore each contributed distinctly to the prediction of minke whale presence (BRT model; mean residual deviance: 0.18; cross validation variance: 0.21; cross-validation AUC: 0.98). Deployment water depth was the most influential predictor (40.4%) with higher predicted values observed at sites in water depths between 100 and 600 m (Fig. 5A). The DOY was the second most influential predictor (26.6%), with predicted values increasing around the days corresponding to winter (Fig. 5D & 5E). Predicted values also increased across two distinct OISST ranges, indicating a higher probability of detection at sites with sea surface temperatures between approximately 16–19°C, and 22.5–27°C (19.6% of contribution, Fig. 5B). Distance to shore contributed the least to the model (13.4%), with a higher probability of detection within 60 km of the coast (Fig. 5C). Among the identified interactions, the combination of the DOY and OISST exerted one of the greatest influences on predicted values (Fig. 5F). The BRT analysis revealed that, while minke whales could be detected at various sites regardless of sea surface temperature during winter, detections were preferentially associated with OISST values around 17°C and 25°C (Fig. 5F). The persistence of higher predicted values around 17°C during summer likely reflects frequent detections off the southeastern U.S. coast, where OISST values near 17°C were

recorded. Despite this, minke whales in this study were detected in areas characterized by OISST higher than 17°C during the summer. Confidence is further influenced by the sparsity of data within the sampled period.

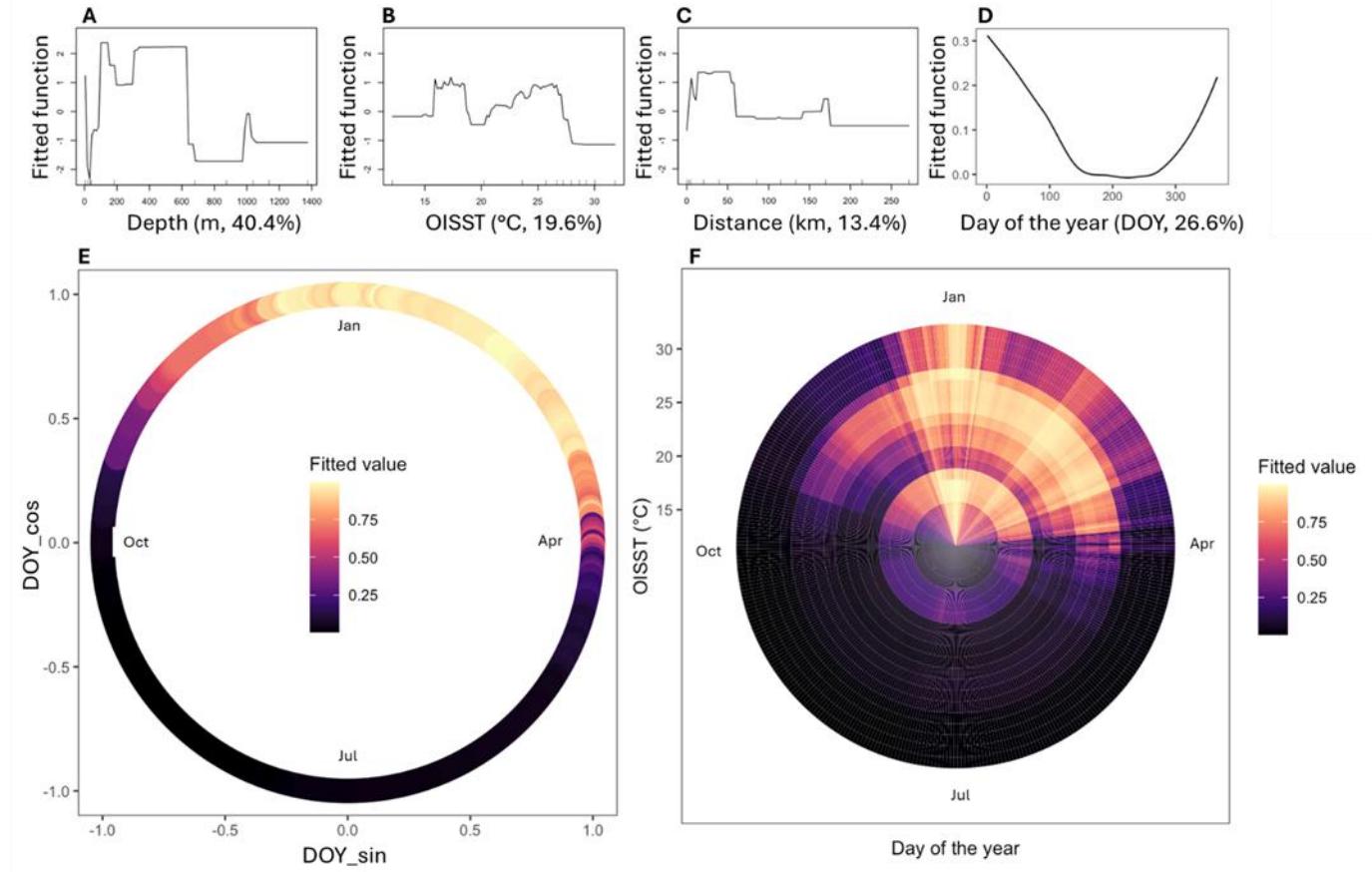


Figure 5 (A to D) Partial dependence plot derived from the BRT model, showing the smoothed functional relationships between the prediction of minke whale presence and each variable, while all other variables held at their mean values. The relative contribution of each predictor is indicated in parentheses. (E & F) Circular plots of the BRT model fit showing the relationship between predicted minke whale presence and the day of the year (E), or the interaction between the day of the year and OISST (range: 12 – 32°C); (F). Warmer colors indicate higher predicted values. In panel E, DOY_sin and DOY_cos represent the sinusoidal and cosinusoidal transformations of the day of the year. The rugplot is not shown in panel D, as it represents a reconstruction of DOY based on both DOY_sin and DOY_cos. OISST = optimum interpolation sea surface temperature; Distance = distance to shore.

Multi-year presence of minke whales in the U.S. Virgin Islands

Over six years of recording from 2016 to 2022, minke whales were detected in the U.S. Virgin Islands (ca. 18°N, 65°W; Fig. 2) each year from late November to early April, occasionally extending into May. This winter presence is similar to that found at other sites in the Caribbean region. The months with the highest number of detection days were January, February, and March (Fig. 6). Some interannual variability was observed, including later arrivals in December instead of November in both 2018 and 2019, and a later departure in May 2021 (Fig. 6). Since 2020, detections have also been confirmed during the summer months. The lowest monthly mean OISSTs each year occurred in February/March (27.5°C), corresponding to two of the

months with the highest number of detection days. No notable differences in mean OISST were observed in years with earlier arrivals or later departures. The DOY explained 58.8% of the variance in minke whale detections in the U.S. Virgin Islands (GAM, $edf = 6$, $R^2 = 0.61$, $p < 0.001$, $acf = 0.42$). Models including OISST or both OISST and SPL explained a lower proportion of the variance (Δ deviance explained = -7.3 to -15.9) and are therefore less appropriate. A rapid decrease in the monthly mean SPL was observed between August and September 2021, from 100 to 93 dB re 1 μ Pa. It is unknown whether this rapid decrease is due to changes in the recorder or the environment.

4. DISCUSSION

This moored passive acoustic monitoring meta-analysis study of the Wider Caribbean Region reveals pronounced spatial and seasonal occurrence patterns, with most sounds recorded between December and March, although some detections also occurred at certain sites during the summer. In addition, it revealed the presence of acoustically active minke whales near Bermuda, Georgia, and Florida, as well as in the eastern Caribbean (Fig. 3). In the Caribbean region, minke whale sounds had previously only been recorded near Saba Bank (Risch et al. 2014a), Puerto Rico (Mellinger et al. 2000), and Martinique (Heenehan et al. 2019). This work includes the first acoustic recordings of minke whales in the U.S. Virgin Islands, Dominican Republic, Montserrat, and Guadeloupe. The timing of these records shows that individuals are mostly present during the winter months (December – March) between ca. 14° to 18° N, strengthening the evidence that this area is part of their wintering grounds. However, caution is needed in interpretation, as some sites had fewer data for summer and fall. When our acoustic detections are compared with visual observation data, available online through OBIS SEAMAP (Halpin et al. 2009), iNaturalist (iNaturalist), and the Global Biodiversity Information Facility (GBIF 2025) (Fig. 2B), we observe that the winter presence in southern sites is consistent as most records (83.8%) are concentrated between December and March (Jiménez et al. 2021). This period coinciding with nutrient-rich upwelling in (some parts of) the southeastern Caribbean (Correa-Ramirez et al. 2020) but this zone may not overlap with areas with minke presence. Although the species has been observed east of Beef Island near Tortola (British Virgin Islands) during winter (Mignucci-Giannoni 1989), this study provides one of the first records of minke whale occurrence in the U.S. Virgin Islands. Another place where minke whales had occasionally been observed during winter months (January – March) is in offshore waters off Bermuda (Mitchell. 1991). In this study, some pulse trains were detected off Bermuda in August.

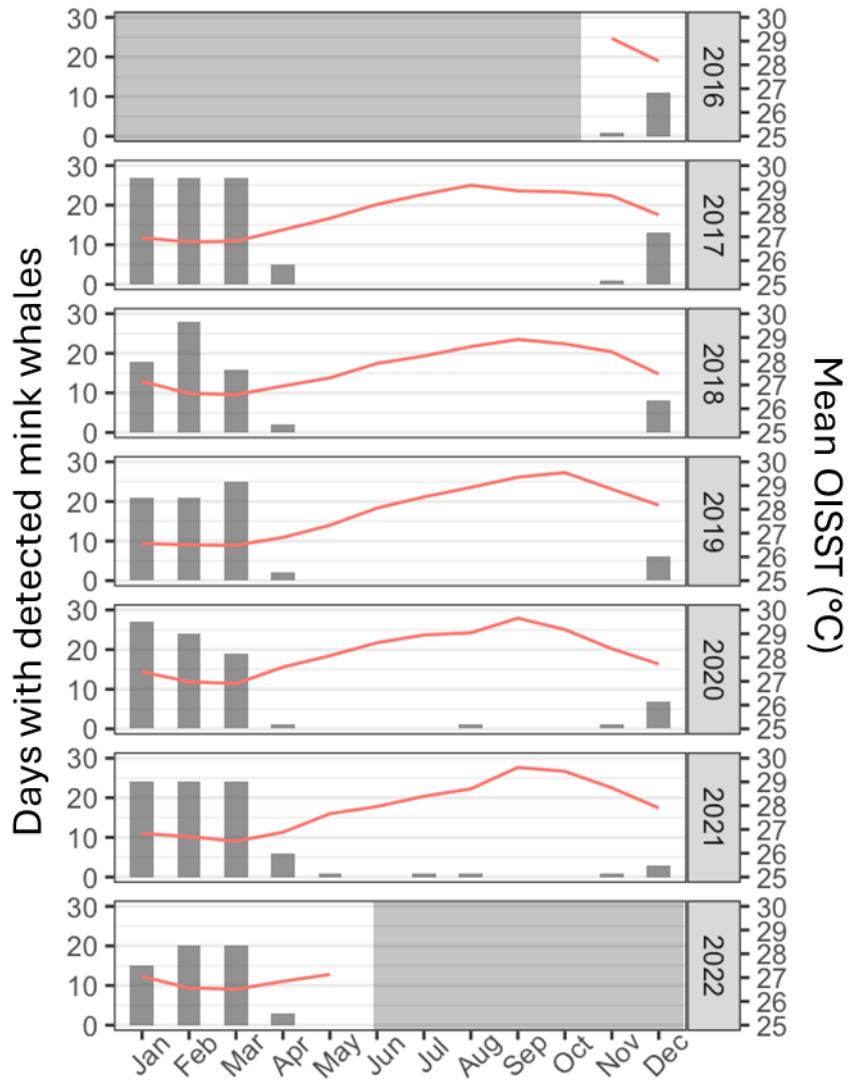


Figure 6 Number of days per month (gray bars) with detected minke whales in the U.S. Virgin Islands (left axis), shown in relation to the mean optimum interpolation sea surface temperature (red line, OISST, right axis) per month. Gray horizontal grid lines are included to facilitate reading the number of days per month (gray bars), and are not intended to represent temperature. Data were collected on a continuous basis from November 2016 to May 2022.

Detecting whales using PAM requires accounting for the detection range of the sounds of interest, which depends on their source levels. The estimated published source levels (SL_{RMS} 50–250 Hz) of minke whale pulse trains range from 160 to 168 dB re 1 μ Pa at 1 m (Risch et al. 2014b). The estimated detection range of minke whale pulse trains along the U.S. East Coast varies between 7.6 to 29.4 km (Risch et al. 2014b), and an 8 dB increase in ambient noise can reduce that range by half (Risch et al. 2014a). In the 40 – 800 Hz band, measured ambient SPL_{RMS} values ranged from 105 to 140 dB re 1 μ Pa off Florida, while values in the West Indies ranged from 98 to 103 dB re 1 μ Pa. The lowest mean SPL , around 78 dB re 1 μ Pa, was measured at Plant Bank, one of the deepest deployments (1006 m) and one of the farthest from the continent. However, detection range is only one limitation of PAM; for a whale to be detected, it must also

be actively producing sounds. Therefore, the absence of a detection does not necessarily imply the species' absence from the area, as individuals could be present but silent, or producing sounds too faint to be picked up by the detector. In addition, it is still unknown whether females produce pulse trains, and how vocalization rates may vary across sex and age classes. For this reason, models using presence-only data might be more appropriate for predicting minke whale distribution. One way to achieve this would be through the development of an occupancy model, which estimates the detection probability while accounting for imperfect detection. A low detection probability would imply that many individuals likely went undetected during deployments, whereas a high value would increase the reliability of predictions based on detected sounds (Korner-Nievergelt et al. 2015). However, to apply such a model and graphically represent detection probability variations, a finer sampling granularity would be required, involving more deployments across the study area.

Along the western coasts of Florida and Georgia, the influence of the location predictor was particularly evident, likely reflecting the effect of depth (which follows an east-west gradient) on minke whale detections. Despite numerous deployments off Florida and Georgia, recordings along the southeast U.S. coast were made from September to May, likely because most surveys here targeted North Atlantic right whales, which migrate to these waters during winter months. Visual observations confirmed the presence of minke whales in this region until spring (Mitchell. 1991, Nilsson et al. 2011). For migratory individuals, the recording of sounds from December to April at certain sites does not necessarily mean that the same individuals remained in the area throughout that time. Differential migration is documented in this species (Murphy 1995), and not all individuals migrate as far as the West Indies; some overwinter at higher latitudes while others pass through these regions (Eerkes-Medrano et al. 2021). The timing of detections in this study suggests that individuals were likely either within their wintering grounds or north of them, likely on their way to them. Another possible reason for the apparent absence of minke whales along the southern U.S. coast in summer is that their northbound migratory route may pass slightly farther offshore in that area (Risch et al. 2014a, Clark & Gagnon 2022), where there is lower monitoring effort (visual and acoustic) and higher sea states that make visual observations of this cryptic species more challenging. Although minke whales are often described as a coastal species associated with continental shelves (Schmidly 1981), offshore detections are not well studied and may be more common than previously understood. Minke whales have been recorded, visually or acoustically, over deep pelagic waters, including near the Mid-Atlantic Ridge during winter (Winn & Perkins 1976, Mitchell. 1991, Nieukirk et al. 2004, Risch et al. 2014a). While the species is commonly sighted on the continental shelf during spring and fall (Risch et al. 2013), acoustic recordings in deep-ocean waters indicate occurrence from September to April (Clark & Gagnon. 2002, Risch et al. 2014a). Finally, the detection of minke whale sounds does not necessarily indicate that individuals were present at the studied depths, as the vocalizing animals could have been far from the seafloor. Sound propagation of pulse trains is better in deeper waters, hence the detection radius of the deeper sites will be significantly larger and could explain the higher number of predicted detections.

In more than 5,000 instrument-days of recordings in the Gulf of Mexico, only a single minke whale pulse train (1 calendar day; June 20, 2011) was recorded near the De Soto Canyon. The GoM does not appear to be a habitat for most baleen whales, with the exception of the resident

Rice's whale. The region near the De Soto Canyon is their core distribution area (Rosel et al. 2021, NOAA 2024), which experiences recurring upwelling events (Nowlin et al. 2000, Coleman et al. 2014). This species produces pulsed down-sweep sequences resembling minke whale pulse trains, but with lower frequencies and slower pulse rates (Rice et al. 2014, Soldevilla et al. 2022). There are also occasional public sightings of humpback whales off Destin (FL, just north of the De Soto Canyon) and occasional excursions of North Atlantic right whales into the GoM (M. S. Soldevilla, personal communication). The relative scarcity of baleen whales in the GoM remains unexplained. It may be related to the absence of direct migratory pathways between their northern feeding grounds and southern wintering grounds. Their primary migratory route appears to remain on the Atlantic side of the Greater Antilles, heading toward the Caribbean and tropical Atlantic. Additionally, it is possible that the species is not detected due to high levels of anthropogenic activity masking its vocalizations.

The multi-year data from the Virgin Islands include summer detections, potentially suggesting that some individuals do not migrate and instead remain year-round, as observed in the Canary Islands (Van Waerebeek et al. 1999). The seasonal arrival of minke whales near the U.S. Virgin Islands may likely be driven more by their timing of departure from northern high-latitude summering grounds than by environmental conditions in lower latitudes. When comparing the different summer months (June–September) from 2017 to 2021, only the most recent years (2020 and 2021) recorded summer detections. Although there is insufficient data to claim a shift in the distribution of minke whales in the Virgin Islands, examining summer recordings after 2021, if such data exist, would be worthwhile to determine whether a trend is present.

The breeding season for this species spans from October to March, peaking in February (Lockyer 1984), coinciding with the months with the highest number of days with acoustic detections between 14 and 18°N in this study. After a gestation period of 10 to 11 months, the calving season peaks in early winter (Sergeant 1963). The emission of longer pulse trains in lower northern latitudes (Risch et al. 2014a) could potentially be linked to reproductive behaviors. To determine whether different call types are associated with specific behaviors, further acoustic analysis of calls from this dataset could help identify if certain areas are used for particular behaviors by characterizing distinct pulse train types. It would be helpful to understand why, at certain specific locations and times, only constant pulse trains were recorded, with no instances of speed-up or slow-down. Characterizing sounds related to reproductive behaviors, as opposed to those unrelated to reproduction, could be a key element in complementing other methods such as drone-based behavioral observations, suction-cup kinematic/acoustic tagging, long-term satellite, and biopsies. Such information leads towards identifying breeding grounds for minke whales in the Atlantic Ocean, which is important for the conservation of this subspecies.

Conclusion

This study provides new insights into the spatial and temporal distribution of minke whale in the Wider Caribbean Region, particularly in regions previously lacking detailed investigation. The acoustic detection of minke whales year-round in the U.S. Virgin Islands challenges previous assumptions that their presence at lower northern latitudes is limited to the winter months. These findings highlight the importance of continued monitoring efforts to better

understand the species' ecology and to support conservation strategies. This is especially important given the ongoing UME for this species and the increasing anthropogenic pressures in offshore environments. To better manage populations at wintering grounds, linking call types to associated behavior, such as reproduction, would improve our understanding of how minke whales utilize the region. Given the demonstrated presence of minke whales in multiple countries' waters, this region wide distribution highlights the need for international coordination for effective minke whale conservation.

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Author contributions

Conceptualization, X.R.; methodology, X.R.; software, X.M., D.W.P. & X.R.; validation, X.R.; formal analysis, X.R. and H.C.S.; investigation, X.R. and H.C.S.; data curation, X.R.; writing—original draft preparation, X.R. and H.C.S.; writing—review and editing, X.R., A.N.R., H.C.S., X.M., R.F., D.W.P., H.F.-M., M.S.S., S.V.P., G.D.; visualization, X.R. & H.C.S. ; supervision, X.R. A.N.R., X.M.; project administration, X.R. Resources, D.R., M.S.S., R.F., A.M., H.F.-M., S.V.P. and G.D.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data underlying this study are openly available in Zenodo (doi: 10.5281/zenodo.17315037).

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Appendix I: Details regarding recorder and hydrophones

For the U.S. Virgin Islands site, the recorders were deployed as part of a NOAA/NPS Ocean Noise Reference Station Network (Haver et al. 2018). The instruments used were NOAA's PMEL recorders, connected to an ITC-1032 hydrophone (International Transducer Corp.; Santa Barbara, CA, USA), with a sensitivity of -191.5 dB re $1\text{ V}\mu\text{Pa-1}$ and a flat frequency response from 10 to 2000 Hz. The sampling frequency was 5 kHz, with a low-pass cutoff filter at 2 kHz and a resolution of 16 bits. The pre-amplifier gain varied between 41 and 56 dB for frequencies from 40 to 800 Hz. The peak-to-peak voltage (Vpp) was 2.5 V.

In Bermuda, SoundTrap ST300 STD and ST500 STD recorders (Ocean Instruments; Auckland, New Zealand) were used. While an end-to-end calibration of -172.7 dB was used for the ST300, the ST500 had a sensitivity of -1.8 dB in addition to the hydrophone sensitivity of -177 dB re $1\text{ V}\mu\text{Pa-1}$. The Vpp values for the ST300 and ST500 were respectively 10 V and 2 V. ST300 STD's frequency response is flat within ± 3 dB from 12.8 Hz to 140,000 Hz (24-bit). ST500 has similar characteristics.

Deployments along Mexico's coast (Mujeres, Contoy and Nizuc) used Snap recorders (Loggerhead Instruments, St. Petersburg, FL, USA) connected to HTI-96-Min hydrophones (High Tech, Inc., Long Beach, Mississippi). Sensitivities were of -170 dB re $1\text{ V}\mu\text{Pa-1}$ with a default gain of 2 dB. The sampling frequency was 44.1 kHz (16-bit). The system's frequency response is flat within ± 3 dB from 10 Hz to 20,900 Hz, and within ± 1 dB from 40 Hz to 18,000 Hz. In Cozumel, the deployment involved a AMAR G3 recorder (JASCO Applied Sciences; Silver Spring, MD, USA) with a GTI M36-V35 hydrophone (GeoSpectrum Technologies Inc.; Dartmouth, Nova Scotia, Canada). The sampling frequency was 32 kHz, with a sensitivity of -165 dB re $1\text{ V}\mu\text{Pa-1}$ and a 24-bits resolution. The maximum voltage was 2.048 V. The system exhibits a flat frequency response from at least 100 Hz to 1000 Hz.

In Montserrat and Curacao, ST600 recorders (Ocean Instruments; Auckland, New Zealand) were used with sensitivities approaching -176 dB re $1\text{ V}\mu\text{Pa-1}$. The sampling frequency used in the first location was 96 kHz, whereas in Curaçao it was 48 kHz. The Vpp value for the instruments was 2 V. The ST500 exhibits characteristics comparable to other ST instruments.

At the remaining sites, Marine Acoustic Recording Units, MARUs (Yang Center for Conservation Bioacoustics; Ithaca, NY, USA), were used. Those units are built with HTI-94-SSQ hydrophones (High Tech, Inc.; Gulfport, MS, USA), which possess a sensitivity of -198 dB re $1\text{ V}\mu\text{Pa-1}$. MARUs are additionally equipped with a preamplifier (gain of 30 dB), a system amplifier (gain of 23.5 dB) and an analog-to-digital converter (sensitivity of 60 dB re 1 bitV-1). The overall MARU system sensitivity is -169 dB with a flat frequency response (± 2.0 dB) between 10 Hz and $0.4 * \text{ sampling frequency}$. The sampling frequency varied among deployments, from 2 to 64 kHz, and the resolution was 12 bits (stored as 16 bits, with the last four bits zero-padded). Finally, the Vpp was 4.096 V.

Appendix II: Details on the sampling periods

Table SP1 Period of sampling(s) for each studied geographical region. A more detailed table is available in the Supplementary Materials and in the Data Availability section.

Geographical region	Period of sampling(s)
Bermuda	May – October
Plant Bank	December – September
Georgia	November – May
Florida	September – May
Quintana Roo	June – September
Puerto Rico	February – March
Saba Bank	October – April
Belize	December – April
Montserrat	September – January
Aruba, Bonaire, Martinique, Guadeloupe, and Dominican Republic – Silver Bank	December – June
Curaçao, Virgin Islands, and Gulf of Mexico	January – December

Appendix III: Details on the models

Table SP2 Summary of Fitted Generalized Additive (Mixed) Models. Models 1 and 2 are equivalent but model 1 includes the GoM while model 2 excludes it. Models 3 and 4 are equivalent but model 3 includes the GoM while Model 4 excludes it.

Model Formula	R-squared (Adj.)	Deviance Explained	REML
1 s(long, lat, k = 14)	0.263	35.7%	2489.1
2 s(long, lat, k = 13)	0.206	22.4%	2415.9
3 te(doy, lat, bs = c("cc", "tp") + k = c(10, 15)) + s(depth, k = 10)	0.672	67.3%	1358.3
4 te(doy, lat, bs = c("cc", "tp") + k = c(10, 15)) + s(depth, k = 10)	0.635	60.9%	1317.8
5 s(doy, bs = "cc")	0.611	58.0%	471.57