Marine Mammal Science

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Characterizing Fraser's Dolphin (*Lagenodelphis hosei*) in the Lesser Antilles: Distribution, Movements, and Co-Occurrence With Other Cetacean Species to Inform Conservation Strategies in the Caribbean

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ABSTRACT

Fraser's dolphin (*Lagenodelphis hosei*) is one of the least studied dolphin species due to its tropical, offshore distribution and low density. However, it is frequently observed in the Lesser Antilles, where we characterized its distribution and ecology using 4 years of data collected from Grenada to Anguilla. We employed species distribution models, movement analysis, and co-occurrence analysis with other species. Fraser's dolphin was the second most encountered delphinidae species, with confirmed sightings throughout the Lesser Antilles. Depth, slope, distance to canyons, and eastward current velocity best explained the observed distribution, accounting for 22% of the variance. The Caribbean side of the Lesser Antilles represented a continuum of suitable habitat, with resightings of 10 individuals indicating inter-island connectivity from the Grenadines to Guadeloupe (415 km). Notably, Fraser's dolphin exhibited the highest co-occurrence rate (83%) and stood out statistically from other species in co-occurrence frequency and strength, underscoring the ecological significance of interspecies interactions. Overall, Fraser's dolphins in the Lesser Antilles likely represent a single population restricted to the arc, with negligible spatial fragmentation. Our results highlight the regional connectivity and the need for cooperation and harmonization of regulations in the Lesser Antilles to ensure effective conservation of the cetacean community.

1 | Introduction

Cetaceans are a diverse and widely distributed group of top marine predators and hold a pivotal position within marine ecosystems. They exert significant influence over primary production by releasing nutrients through their carcasses and feces (Baum and Worm 2009). Moreover, they are integral to maintaining the equilibrium of marine biodiversity, regulating the abundance of prey and competitors through predation (Baum and Worm 2009). Disparities between suitable habitats and observed distributions of cetacean species have previously shown correlations with anthropogenic pressures, making them potential proxies of marine ecosystem health (Azzellino et al. 2014). Hence, research into cetacean ecology can yield valuable insights that are pertinent to the conservation of both cetacean populations and wider marine ecosystems.

Fraser's dolphin (*Lagenodelphis hosei*) was first described by F.C. Fraser in 1956, based on the examination of a previously collected skeleton from Borneo (Dolar 2009). He noticed that the skull displayed characteristics of both *Delphinus delphis* and the *Lagenorhynchus* genus, leading him to propose the new genus *Lagenodelphis* (Dolar 2009). Phylogenetically, Fraser's dolphins belong to the Delphininae subfamily and are closely related to *Stenella longirostris* and *Tursiops australis* (Lee et al. 2019; McGowen et al. 2009). The external appearance of Fraser's dolphins had not been described until its rediscovery in 1971, when stranded individuals were examined by Perrin et al. (1973). Unfortunately, this species remains poorly studied overall, and knowledge is mostly restricted to general ecology and descriptions from observations.

Fraser's dolphins engage in deep-diving foraging behavior, targeting mesopelagic prey such as cephalopods, crustaceans, and fishes (Dolar et al. 2003). This behavior is supported by high levels of myoglobin compared to other small cetaceans, which enables great diving performance (Dolar et al. 1999). Although they can feed at depths likely greater than 600 m (Dolar et al. 2003), observations of feeding behavior near the surface have been recorded around the world, such as the Lesser Antilles (Dolar et al. 1999; Sekiguchi et al. 1992; Watkins et al. 1994). In Guadeloupe, Fraser's dolphins undertake dives averaging three to four minutes (Rinaldi et al. 2006), which could reflect feeding behavior at a relatively shallow depth in this area.

Throughout its distribution, multiple studies report a tendency for Fraser's dolphins to co-occur with many other cetacean species. Numerous cetacean surveys report co-occurrence with species such as melon-headed whales (*Peponocephala electra*) (Wade and Gerrodette 1993), short-finned pilot whale (*Globicephala macrorhynchus*) (Dolar et al. 2006), pantropical spotted dolphins (*Stenella attenuata*) (Kiszka and Braulik 2018), or sperm-whales (*Physeter macrocephalus*) (Gero and Whitehead 2006). This behavior could be motivated by foraging purposes (Stensland et al. 2003), which may influence Fraser's dolphin distribution around areas of high cetacean abundance and diversity. Overall, co-occurrence behavior appears to be an important factor to consider when studying Fraser's dolphin ecology.

Fraser's dolphins occur in tropical seas between 30° N and 30° S (Dolar 2009). Within this range, observations are generally uncommon and primarily concentrated in deep offshore waters (Dolar 2009). However, Fraser's dolphins display a different distribution around oceanic islands with steep topography (Dolar et al. 2006; Gomes-Pereira et al. 2013; Kiszka et al. 2011), creating population hotspots for this species in places like the Philippines or the Lesser Antilles (Dolar et al. 2006; Kiszka and Braulik 2018).

Sightings and strandings have been reported outside of their tropical range, including locations such as the Azores (Gomes-Pereira et al. 2013), Argentina, Australia, France, Great Britain, and Uruguay (Dolar 2009). Most of these unusual observations have been linked to either temporary warming of local seawaters (Gomes-Pereira et al. 2013) or to strong El Niño events (Durante et al. 2016; Perrin et al. 1994). The species' ability to extend its range as temperature rises, even if only temporarily, has led to speculation that this behavior could serve as a potential bio-indicator for future seawater warming (Gomes-Pereira et al. 2013).

The Lesser Antilles represents a unique location where Fraser's dolphin sightings are common and occur year-round (Gero and Whitehead 2006; Rinaldi and Rinaldi 2011). This seems to stand out from the rest of the Caribbean Sea, as several past surveys and studies have not reported any Fraser's dolphin sightings at sea in the Greater Antilles or the southwest Caribbean (Gomes-Pereira et al. 2013). Despite frequent observations, Fraser's dolphins remain understudied in the Lesser Antilles. In the area, they face various threats common to cetaceans, such as chemical pollution or vessel collision but also unregulated small cetacean hunting (Fielding and Kiszka 2021). Although hunting is limited to the islands of St Vincent and St Lucia, cetacean community connectivity is poorly understood in the archipelago. Current knowledge of dolphin movements or distribution in the Lesser Antilles is limited, with studies primarily focusing on the pantropical spotted dolphin in Martinique and Guadeloupe. These studies suggest residential tendencies on each island, with infrequent movements between them (Courtin et al. 2022). However, Fraser's dolphin movement pattern and distribution in the Lesser Antilles are unknown.

To address key knowledge gaps around population status, distribution, interspecific interactions, movements, and ecology of Fraser's dolphins around the Lesser Antilles, we aim to analyze its distribution, co-occurrence behavior, and movements in the region. Our specific objectives include identifying key areas of importance for this species within the Lesser Antilles and examining the connectivity of these areas through the movement patterns of individual dolphins. Analyzing co-occurrence is important for understanding its influence on the species' overall ecology and its implications for distribution patterns. This information is required for establishing a baseline understanding of Fraser's dolphin dynamics, informing conservation strategies, and enhancing overall knowledge of their ecology.

2 | Methods

2.1 | Study Area

Our study area is located in the Lesser Antilles archipelago, extending from Grenada to Anguilla, excluding Barbados. This area is characterized by the presence of several submarine canyons and a steep topography on the Caribbean side of the arc (Figure 1). The boundaries of the study area have been set to a distance of 25 km from the continental shelf and have been adjusted to avoid including unsurveyed areas within the exclusive economic zone (EEZ) of the US Virgin Islands. Most of the western, leeward, Caribbean side of the island arc is characterized by a steep topography with a calm sea state (close to shore) due to protection from eastward wind by the islands themselves compared to the eastern Atlantic coast, which is usually less suitable for several consecutive days of survey.

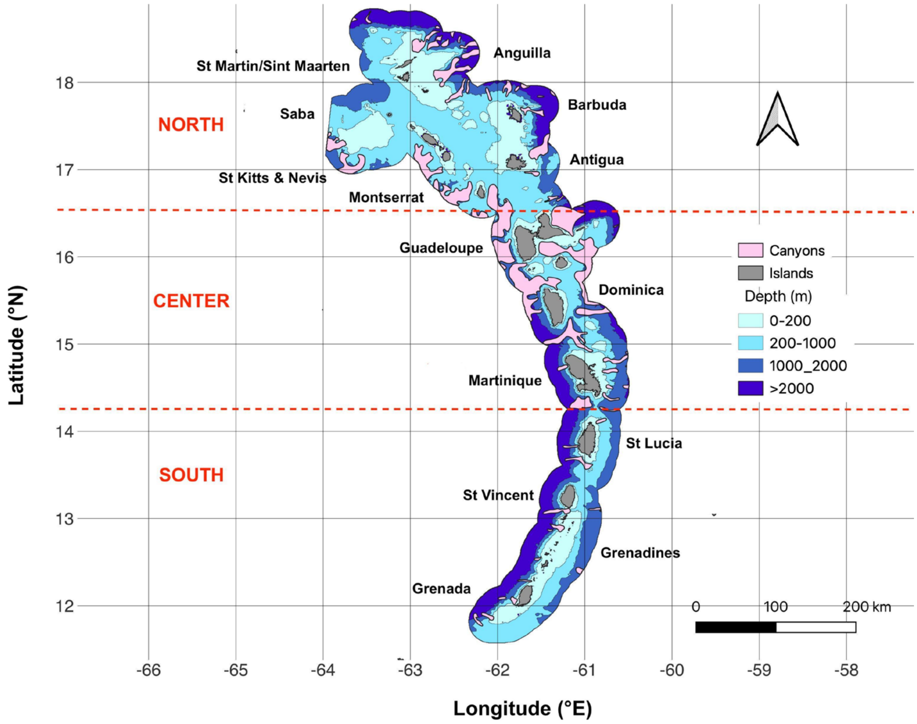

FIGURE 1 | Study area geomorphology. Characteristics of the islands of the study area, including the bathymetry (GEBCO Compilation Group 2024), location of submarine canyons (Harris et al. 2014), and the delineation of the three zones used for surveys (North, Center, and South).

2.2 | Data Collection

The data were collected as part of the "Ti Whale An Nou" program conducted by the Caribbean Cetacean Society (CCS) from 2021 to 2024. A total of 24 2-week-long boat-based surveys were conducted between March and August, with eight surveys carried out in each of the three sub-areas of the Lesser Antilles called "North," "Center," and "South" (Figure 1). A total of 35 additional days of surveys around the islands of Martinique, Saint Lucia, and Guadeloupe occurred between the months of September and October in 2021 and 2022 and were included in the analysis. During on-effort observations, two observers positioned themselves at the front of a 40–46 ft. sailing boat, visually searching for cetaceans. Each observer covered an observation angle ranging from 0° to 90° on each side of the boat. Observers were switched after 2 consecutive hours. Effort was maintained during the daylight part of the day (6 a.m.–6 p.m.) and paused in case of rain or wind speed (> Beaufort 4) that would compromise cetacean detection. Once dolphins were spotted, coordinates of the sighting, an estimate of group size, species identification and its certainty level, and an estimate of the radial detection distance from the boat, visually estimated by observers, were recorded. Photographs of the dorsal fins were also collected, allowing for the identification of individuals based on permanent and unique marks or wounds (Photo ID).

2.3 | Species Distribution Model (SDM)

2.3.1 | Generalized Additive Model (GAM)

SDMs are widely used, particularly for mobile marine species such as cetaceans. They provide essential insights into habitat preferences, modeling the relationship between parameters potentially influencing distribution and abundance, aiming to identify the preferred ranges of occurrence. Among various modeling techniques available, we chose to develop GAM to incorporate sampling effort as a presence-absence dataset. GAMs are widely used for SDM and can produce robust outcomes in modeling cetacean distributions when compared to alternative models (Derville et al. 2018).

To fit the GAM and apply it for habitat suitability prediction, a hexagonal grid was generated to cover the study area, with each cell having a 3 km distance between the centers of two opposite flat sides. This grid limits the study area to zones within 25 km from the coastline where survey effort is high, reducing the amount of unsurveyed regions in the SDM analysis. In each surveyed cell, observations of groups of Fraser's dolphins, sampling effort, and locally averaged environmental parameters (see below for details) are associated. Surveyed cells without observation of Fraser's dolphins were considered as absence data.

The model was fitted using only hex cells with recorded survey effort, while unsurveyed hex cells were ignored. Models included a maximum of four environmental covariates, and each combination from 1 to 4 covariates was generated, inspired by a previous study (Virgili et al. 2022). Among the environmental covariates initially considered for modeling, Spearman correlation tests were run. When two covariates were correlated ($R > |0.7|$) the covariate more commonly used to describe cetacean ecology was retained for modeling. Using R v4.3.0 (R Core Team 2023) and the MGCV R package (S. Wood 2001), GAMs were generated using a Tweedie distribution (Foster and Bravington 2013) and a logarithmic link function. The log of the effort was incorporated as an offset. Fitting was done by Restricted Maximum Likelihood (REML) and the smooth terms were calculated using a thin-plate splines basis of dimension 4 to limit model flexibility and reduce overfitting risk, following guidance from S. N. Wood (2017). Models were ordered and selected using Akaike Information Criterion (AIC) scores (Burnham and Anderson 2002). Using Akaike weights, the importance of environmental variables was investigated, considering all generated models. The model featuring the lowest AIC was selected to predict and map the relative habitat suitability in the entire grid. Fit uncertainty was measured through the coefficient of variation provided with the prediction.

The performance of the prediction was assessed using cross-validation techniques. Observations were randomly split between a training dataset (80% of the data) and a validation dataset (20% of the data). This model validation process is widely used with SDM (Stephenson et al. 2020; Tobeña et al. 2016). Prediction accuracy metrics, namely the area under the curve (AUC) and the maximum true skill statistic (TSS), were used. AUC values > 0.7 are usually considered correct and > 0.8 excellent (Hosmer et al. 2013; Mandrekar 2010) while maximum TSS values > 0.6 are considered good model fits (Tobeña et al. 2016; Tsirintanis et al. 2023).

2.3.2 | Survey Effort

The survey effort was calculated based on the survey effort tracking line, accounting for reduction in Fraser's dolphin detection probability with distance. The method was inspired by Tort Castro et al. (2022) with adaptation for radial distances from the boat. Four distance ranges from the tracking line, each associated with a positive detection probability (1, 0.75, 0.5, and 0.25), were defined. The distances associated with a detection probability of 1 range from 0 to the distance at which the distribution of observed detection distances peaks, as a decline in the distribution is associated with a decrease in detection probability. The percentile of the detection curve corresponding to certain detection was calculated, and the remaining distribution was divided into three distance ranges, each containing an equal area under the curve. These ranges correspond to distance thresholds associated with decreasing detection probabilities (0.75, 0.5, and 0.25). Using QGIS v3.28 Firenze (QGIS Development Team 2018), detection buffers were generated and effort per grid cell estimated by summing the surveyed areas weighted by their respective detection probabilities.

2.3.3 | Environmental Dataset

Initially, we selected 19 environmental variables commonly used to model the distribution of cetaceans, including deep diving species (Pirotta et al. 2011; Virgili et al. 2022), regardless of their potential correlations. E.U. Copernicus Marine Service Information has been used to extract sea surface temperature (SST; Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis 2023), chlorophyll *a* concentration (CHLa; Global Ocean Biogeochemistry Analysis and Forecast 2023), eastward and northward current velocity and mixed layer depth datasets (U0, V0, MLD; Global Ocean Physics Analysis and Forecast 2024). Distances to the coast, shelf (0–200 m), 1000 m isobath, 2000 m isobath, and slope have been derived from the depth dataset (GEBCO Compilation Group 2024) using QGIS. Similarly, the distance to canyon (DC) has been derived from the canyon cartography (Harris et al. 2014). Current velocity (CV) has been derived using the current coordinates U0 and V0. For temporal variables, daily values were averaged from May 2021 to August 2024 to represent locally mean environmental conditions over the sampling period. To account for the importance of their variation, standard deviations (SD) were included as variables. For each hexagonal grid cell, the available values of each environmental covariate were averaged to obtain a single representative value per cell. The same environmental datasets have been used for model fitting and prediction.

2.4 | Co-Occurrence Analysis

A species group was defined as a set of individuals that were continuously distributed in space and exhibited a generally common direction of movement during an encounter. As noted by Syme et al. (2021), there is no universal consensus on how to define cetacean groups, with considerable variation in inter-individual distance thresholds across studies and species. Therefore, the definition used could involve, in some cases, a degree of subjectivity; however, it is grounded in two key criteria: spatial and temporal cohesion. Co-occurrence was defined as instances in which at least two species were observed simultaneously or within 5 min following the end of the first observation (corresponding to a maximum range of 400 m), either as a single mixed group or as two separate single-species groups. In the absence of a standardized behavioral protocol capturing interspecific interactions for all surveys, we focused on co-occurrences rather than mixed-species groups (sensu Syme et al. 2021). The latter represents a stronger definition, requiring at least one species to exhibit attraction based on the evolutionary benefits of grouping, and excludes aggregations resulting merely from shared resources or chance encounters (Syme et al. 2021).

Multiple co-occurrence analysis methods have been developed to describe interspecific interactions within ecosystems, typically involving the subdivision of the study area into discrete sites to assess species presence within each (MacKenzie et al. 2004; Veech 2013). While such approaches can be applied to cetaceans to spatially or temporally model co-occurrences, their implementation in large-scale marine environments presents several challenges, in particular, the need for a dedicated survey design that accounts for predefined variables such as site size, study area extent, survey timeframe, and transect layout (Bauer et al. 2015; Syme et al. 2023). As a result, cetacean co-occurrence is most often reported using simple percentages or counts of co-occurring sightings (Dolar et al. 2006; Rossi-Santos et al. 2009). However, alternative questions that are less reliant on survey design, such as the impact of seasonal variation in mixed-species association encounter rates (Lima et al. 2021), can be addressed using simple statistical approaches. In this context, a basic statistical analysis was developed to compare the co-occurrence frequencies of Fraser's dolphin with those of the remaining cetacean species in the Lesser Antilles community.

Co-occurrence proportions were calculated for species with more than 10 observations (co-occurrence or not) across all surveys. When possible, χ^2 tests for proportions were conducted separately for Fraser's dolphin against each cetacean species to determine whether Fraser's dolphin was found significantly more often in co-occurrence than each compared species. Specifically, 2×2 contingency tables were compiled for Fraser's dolphin and each of the other species containing the total number of observations made without other taxa (alone) and the total number of observations where at least one other taxon was present (co-occurrence). To ensure independence between measurements, we removed shared observations between compared pairs prior to pairwise testing, to avoid them being counted in both co-occurrence counts. For instance, observations involving Fraser's dolphins and pantropical spotted dolphins together were not considered in their co-occurrence counts when running the separate χ^2 test between those two species.

Strength of interactions between each pair of species was then assessed. Traditional co-occurrence analysis in ecological studies involves comparing the presence or absence of species across multiple sites to evaluate species dependencies (MacKenzie et al. 2004). However, applying this approach to cetacean studies poses challenges due to the highly mobile nature and detectability of these animals, making it difficult to delineate fixed areas for presence/absence assessments.

To compare the co-occurrence of a pair of species, we considered the frequency of sightings for species A and B, with the intersection representing shared observations. To measure similarity between two groups using presence/absence data, we chose to use Sorensen's index from a wide selection of indices due to its simplicity, homogeneity, and symmetry (Koleff et al. 2003). In this study context, the measured similarity between two cetacean species is associated with the strength of their co-occurrences.

Sorensen's index varies between 0 and 1, indicating absence or total cooccurrence, respectively. Pairs of species with a cumulative number of observations $A+B<20$ were considered too sensitive to variation due to the limited sample size and were therefore not considered for further analysis. Pairs involving humpback whales (*Megaptera Novaeangliae*) have been removed because of the seasonality of their presence in the Lesser Antilles being mostly outside of our seasonal effort. To assess the significance of the difference between Sorensen's index from pairs with Fraser's dolphin and those without, a Kruskal–Wallis test was performed between those two groups of pairs.

2.5 | Movements

Based on the photo ID data collected from Fraser's dolphins between 2021 and 2024, we conducted an analysis of individual movements. One opportunistic observation of Fraser's dolphins photographed during a whale-watching tour by a tourist was also included. The quality of photographs and the distinctiveness of individuals were assessed for each image using the methods outlined by Urian et al. (2013). Photographs of poor quality and individuals lacking distinctive features were excluded from the analysis, ensuring that only distinctive individuals captured in good to excellent quality photographs were retained. The matching process of dorsal fins was facilitated by the open-source platform Flukebook (Blount et al. 2022). To ensure matching accuracy, two people were tasked to review potential matches. Individual movements between observations were graphically represented using QGIS.

3 | Results

3.1 | General Results

The research effort totaled 29,630 km of survey trackline with observers on position, and Fraser's dolphins were observed every month from March to October, all along the Caribbean side of the Lesser Antilles Arc, from Grenada to the Saba bank (Figure 2). Fraser's dolphin was the second most observed delphinidae species behind the pantropical spotted dolphin, with an encounter rate of 2.16 observations per 1000 km. Among 64 observations, the mean group size estimate varied from 7 to 350, with a mean of 112 (CV = 0.83) and a median of 90 individuals.

3.2 | Distribution

Effort coverage per hex cell ranged from 0.01% to 2500% of a single cell's area, with a mean coverage of 124% and a median of 56%. The four detection ranges obtained regarding Fraser's dolphin sampling effort were 0–200, 200–336, 336–518, and 518–1000 m and were respectively associated with a detection probability of 1, 0.75, 0.5, and 0.25. After checking for collinearity among the predictors, 12 out of 19 environmental covariates were retained for modeling: depth, slope, U0, V0, CV, MLD, SST, CHLa, distance to canyon, distance to the 1000 m isobath, distance to the 2000 m isobath, and distance to the coast. A total of 738 models were generated with different parameter combinations. The best scoring model and the four plausible alternatives

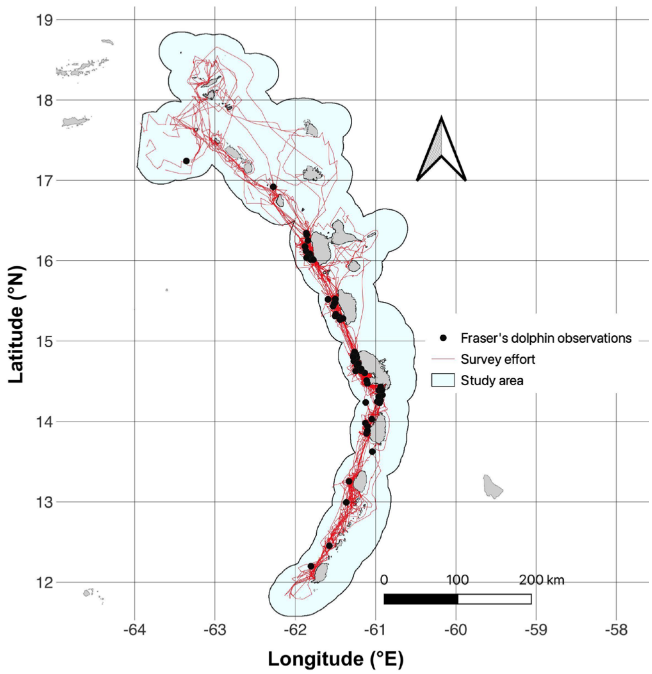

FIGURE 2 | Survey effort and Fraser's dolphin observations between 2021 and 2024.

TABLE 1 | Summary table of the best Akaike Information Criterion (AIC) scoring models (ΔAIC < 2) and additional models (AIC < 3) included for comparison. The table features the combinations of covariates used to fit the model, the AIC score, Explained Deviation (ED%), AIC difference with the best scoring model (ΔAIC), the REML (Restricted Maximum Likelihood) and the Akaike weights. The following models featured the covariates: Depth, distance to canyon (dist_canyon), eastward current (U0), sea surface temperature (SST), slope, mix layer depth (MLD), and chlorophyll-*a* concentration (CHLa), distance to the isobath 2000 m (dist_iso2000), northward current (V0), distance to the coast (dist_coast) and distance to the isobath 1000 m (dist_iso1000).

Model	AIC	ED%	ΔAIC	REML	Akaike weights
depth + dist_canyon + U0 + slope	226.43	22.0	0	1	0.137
depth + dist_canyon + U0 + SST	227.22	21.7	0.79	0.67	0.092
depth + dist_canyon + U0	227.77	20.2	1.34	0.51	0.070
depth + dist_canyon + U0 + MLD	227.79	20.8	1.36	0.51	0.069
CHLa + depth + dist_canyon + U0	228.07	21.2	1.65	0.44	0.060
depth + dist_canyon + dist_iso2000 + U0	228.51	20.5	2.08	0.35	0.048
depth + dist_canyon + U0 + V0	228.98	20.5	2.55	0.28	0.038
depth + dist_canyon + dist_coast + U0	229.03	20.5	2.60	0.27	0.037
depth + dist_canyon + dist_iso1000 + U0	229.42	20.2	2.99	0.22	0.028

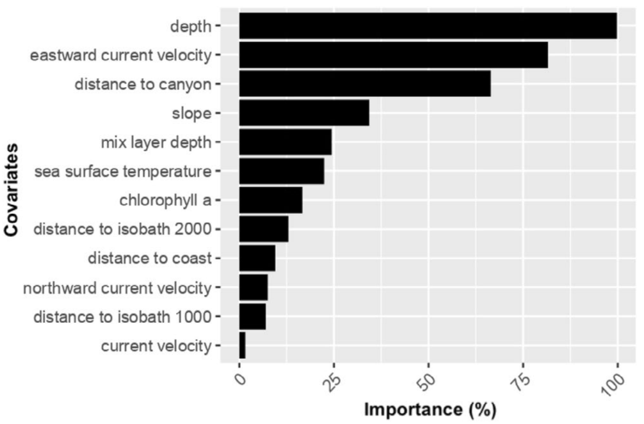

FIGURE 3 | Importance of the covariates throughout the models based on Akaike weights.

with ΔAIC < 2 (Burnham and Anderson 2002) explained between 20.2% and 22.0% of the deviance (Table 1).

Using the Akaike weights, environmental parameters have been ranked by their degree of importance (Figure 3). Depth (99.8%), eastward current speed (81.6%), distance to canyon (66.4%), and slope (34.3%) were most important in explaining Fraser's dolphin distribution in the surveyed area.

Fraser's dolphin presence was primarily associated with a depth range between 500 and 1750 m, high slopes, a peak for prediction approximately between 5 and 15 km from the closest canyon and exhibited a complex relationship with eastward current velocity (Figure 4). Regardless of survey effort, observations tended to accumulate around areas with lower absolute current values; however, the response curve increased at higher absolute current values, likely due to a few observations in cells with limited survey effort (Figure 4). Most of the smooth terms of the best scoring model display a step function or a bell-shaped tendency, indicating that the surveyed range of environmental values was broad enough to encompass and identify the preferred range of Fraser's dolphin in our area (Figure 4).

Suitable predicted habitat for Fraser's dolphins is found across the study area, on both the Caribbean and Atlantic sides of the arc, almost representing a continuous patch of favorable habitat conditions (Figure 5). The deep waters of the Caribbean Sea between Guadeloupe and Grenada are of particular importance to the species. Uncertainty in the predictions is more pronounced where survey effort is lacking, especially at the northern edge and Atlantic side of the area (Figure 6).

In terms of model validation, the best scoring model is associated with an AUC and maximum TSS value of 0.85 and 0.58, respectively, in the surveyed region.

3.3 | Co-Occurrence

Out of 64 Fraser's dolphin observations, 53 were associated with six other cetacean species (Table 2). Co-occurrences were observed with the pantropical spotted dolphin, short-finned pilot whale, common bottlenose dolphin (*Tursiops truncatus*), spinner dolphin, sperm whale, and the melon-headed whale.

When comparing co-occurrence proportions between Fraser's dolphin and other species, all χ^2 test-results showed significant differences ($p < 0.001$ in all cases, Table 3). In addition, Fraser's dolphin exhibited the highest co-occurrence rate (Table 4), significantly higher than that for the rest of the cetacean community in the Lesser Antilles.

Upon confirming that Fraser's dolphin was more frequently observed in co-occurrence with other species, we assessed the strength of these associations. Fourteen co-occurring pairs were retained, out of which six pairs involved Fraser's dolphin.

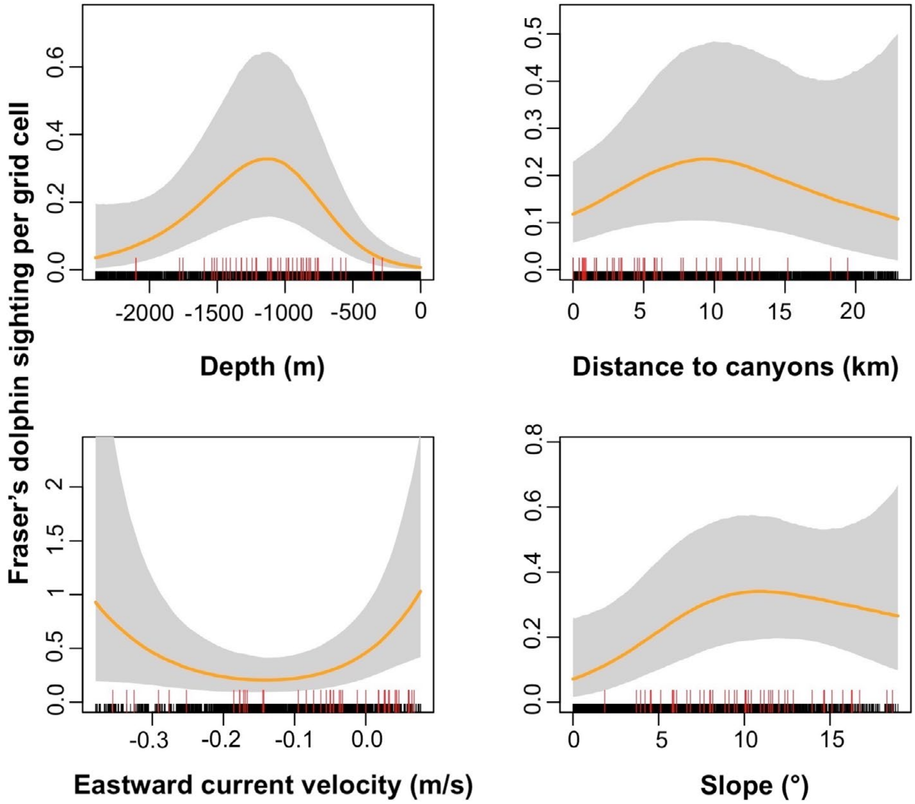

FIGURE 4 | Relationship between Fraser's dolphin presence likelihood and environmental covariates for the selected model. Orange line represents the smooth functions and the gray shaded region the 95% confidence band. Black rug plots represent the value of environmental covariates in each grid surveyed grid cell while red represents Fraser's dolphin observations. AIC = 226.43, ED = 22.0%.

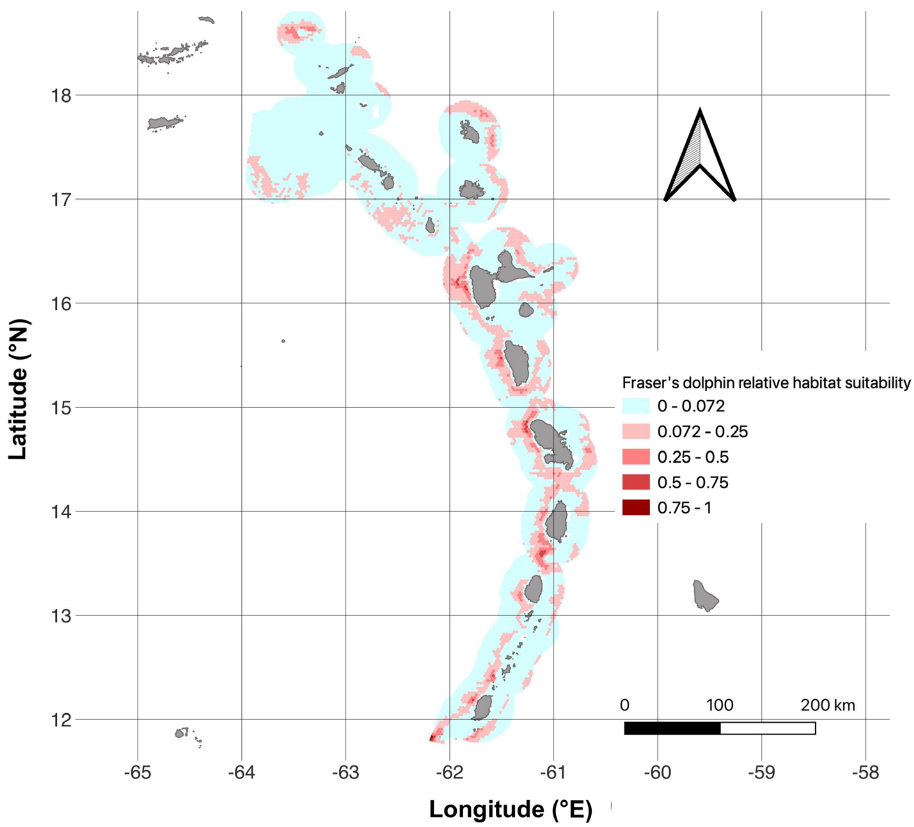

FIGURE 5 | Fraser's dolphin predicted suitable habitat in the Lesser Antilles based on the selected model. The blue cut-off was chosen to reflect the threshold used to obtain the maximum True Skill Statistics.

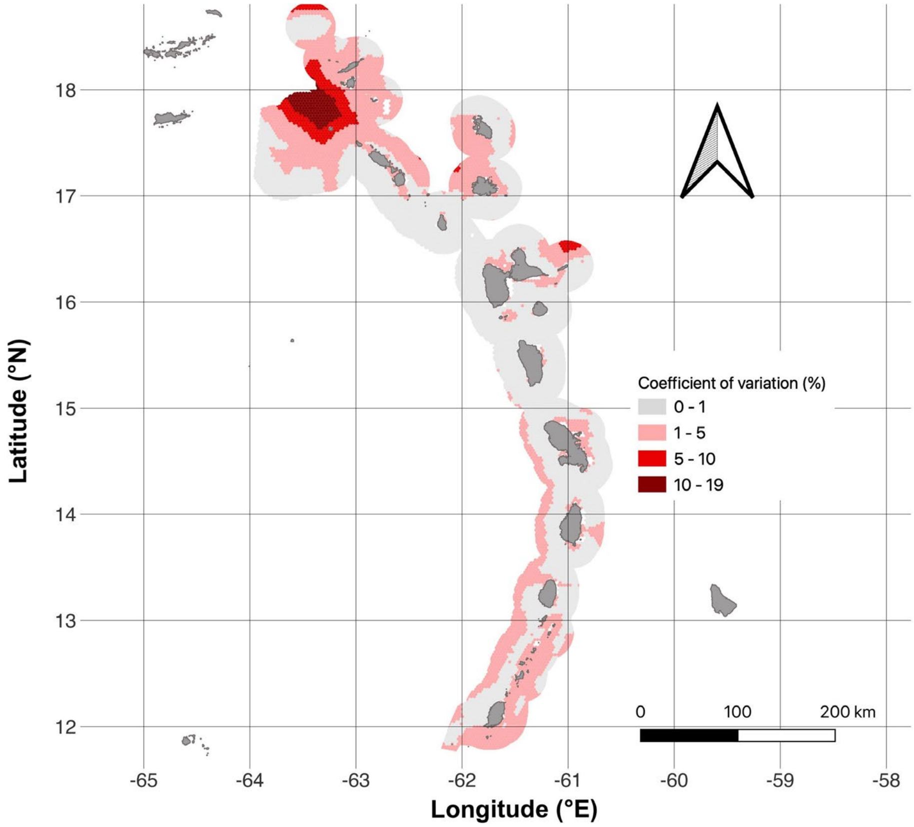

FIGURE 6 | Fraser's dolphin habitat suitability coefficient of variation. This represents the error in the best scoring model associated with the habitat suitability prediction above.

TABLE 2 | Fraser's dolphin co-occurrences and species total number of observations.

Species	Co-occurrence with Fraser's dolphin	Total number of observations
Pantropical spotted dolphin	41	232
Short-finned pilot whale	7	26
Common bottlenose dolphin	3	49
Spinner dolphin	2	11
Sperm whale	6	113
Melon-headed whale	3	5

Sorensen's indices involving Fraser's dolphin generally displayed higher values than other pairs (Figure 7). The Kruskal–Wallis test, which compared the medians of the co-occurrence indices involving Fraser's dolphins versus those without, yielded a significant result at the 0.05 error level ($\chi^2 = 9.640$, $p = 0.002$). Overall, Sorensen's indices involving Fraser's dolphins were significantly stronger than those of the pairs involving other cetaceans. Not only do Fraser's dolphins exhibit more frequent co-occurrences than other cetaceans, but they also show a greater probability to co-occur with each species they were observed with than other cetaceans.

TABLE 3 | χ^2 test results comparing the co-occurrence proportions in species observation. Each column is the result of the comparison of Fraser's dolphins and the concerned species where shared observations were removed from the observation and co-occurrence count of both species.

Species	χ^2	p
Pantropical spotted dolphin	45.6	< 0.001
Short-finned pilot whale	24.7	< 0.001
Common bottlenose dolphin	34.5	< 0.001
Humpback whale	58.8	< 0.001
Sperm whale	87.7	< 0.001

3.4 | Movements

The analysis of the Photo ID images identified a total of 282 individuals. From this catalog, 10 individuals were encountered in different observations after more than 2 weeks between encounters. Resightings ranged from 1 to 28 months following their initial sighting (Table 5) and the mean distance between recaptures was 105 km. In 7 out of 10 resightings, animals were observed at a different island than the first observation (Figure 8).

TABLE 4 | Summary table of the co-occurrence patterns showing the total number and co-occurring observations for the most common species, overall co-occurring rate, and number (Nb) of co-occurring species.

Species	Co-occurrences	Total observations	%	Nb of different species
Fraser's dolphin	53	64	83	6
Spinner dolphin	6	11	55	4
Common bottlenose dolphin	14	49	29	5
Short-finned pilot whale	10	26	38	3
Pantropical spotted dolphin	67	232	29	7
Humpback whale	9	53	17	3
Sperm whale	14	113	12	6

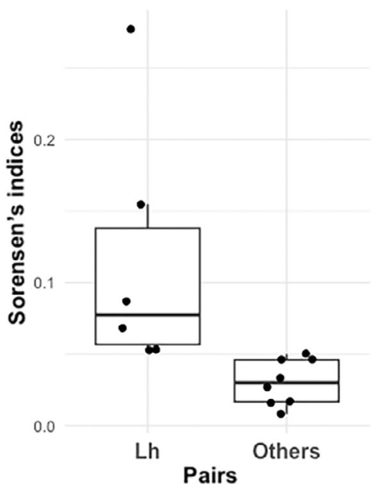

FIGURE 7 | Boxplots representing the Sorensen's indices for each observed pair of co-occurring cetaceans split between pairs involving Fraser's dolphin (Lh) and others.

4 | Discussion

In this study, we identified key environmental parameters that best explained the distribution of Fraser's dolphins along the Lesser Antilles Arc. Among the selected covariates, eastward current velocity, depth, slope, and proximity to canyons were most influential. The best-fitting GAM allowed us to predict relative habitat suitability, highlighting suitable areas across the arc and particularly between Grenada and Guadeloupe. Model validation showed strong predictive performance and alignment with field observations. Notably, 83% of Fraser's dolphin sightings occurred alongside six other cetacean species, with co-occurrence rates higher than for any other species, underscoring the importance of this behavior. Resighting data also revealed wide-ranging movements between islands of the Lesser Antilles.

4.1 | Habitat Preferences

In our study, we have identified eastward current velocity, depth, slope, and distance to canyon as the most influential environmental covariates. The majority of Fraser's dolphin sightings occurred at depths ranging between 500 m and 1750 m and slopes greater than 9° (Figure 4). Along the Caribbean side of the Lesser Antilles arc, this corresponds to a narrow band of coastal water characterized by steep topography. The significance of depth in Fraser's habitat preference modeling has been previously described in the central Philippines (Dolar et al. 2006). Our findings suggest that Fraser's dolphin observations also correlate with deep and steep topography in agreement with its global distribution around oceanic archipelagos (Dolar et al. 2006; Gomes-Pereira et al. 2013).

Canyons represent rich marine habitats that concentrate a high abundance of cetacean species around the globe, especially for deep-diving species like beaked whales (Moors-Murphy 2014). Distance to canyons is often included as a model covariate, and the importance of proximity for habitat preference has been observed in models involving deep-diving cetacean species (Tepsich et al. 2014). One explanation for canyon attractiveness is that they can facilitate localized upwelling, enhancing nutrient availability and supporting higher marine productivity (Allen and Durrieu de Madron 2009). However, not all canyons attract cetaceans (Moors-Murphy 2014). Although Fraser's dolphin distribution models show the influence of the proximity to canyons, with most observations occurring within 5 km of one, the predicted correlation with its presence, which accounts for survey effort, peaked at around 10 km from the nearest canyon and declined on either side of this peak (Figure 5). This pattern complicates interpretations of canyon attractiveness, and additional behavioral data from sightings would be needed to better understand this relationship.

The eastward current velocity also plays a significant role in elucidating the distribution pattern of Fraser's dolphins. Robust currents known as the Caribbean and Antillean currents circulate from the Atlantic to the Caribbean at the southern and northern edges of the Lesser Antilles, respectively (Andrade and Barton 2000). Overall, currents are directed from east to west and infiltrate the channels that separate each island (Stalcup and Metcalf 1972). Therefore, the Lesser Antilles can be compared to a sieve for eastward current inflow. The pattern of the covariates separates the channels from the Caribbean leeward protected waters, characterized by lower current strength. Given that most of our observations are concentrated along the leeward sides of the islands rather than within the inter-island channels, it is unsurprising that the eastward current covariate emerged as more influential. However, this may be influenced

TABLE 5 | Inter-encounter summary table, featuring the time and shortest distance between consecutive sightings, alongside the proximate islands associated with each observation.

Individual	Time between sightings (month)	Distance between sightings (km)	1st encounter	2nd encounter
CCS_Lh_0021	20	229	Martinique	South Grenadines
CCS_Lh_0029	9	212	Martinique	Guadeloupe
CCS_Lh_0031	1	76	Dominica	Martinique
CCS_Lh_0067	1	64	Martinique	Martinique
CCS_Lh_0157	11	86	Martinique	Dominica
CCS_Lh_0166	20	102	Guadeloupe	Dominica
CCS_Lh_0195	10	46	Martinique	Martinique
CCS_Lh_0205	12	5	Dominica	Dominica
CCS_Lh_0210	1	76	Dominica	Martinique
CCS_Lh_0266	28	149	Guadeloupe	Martinique

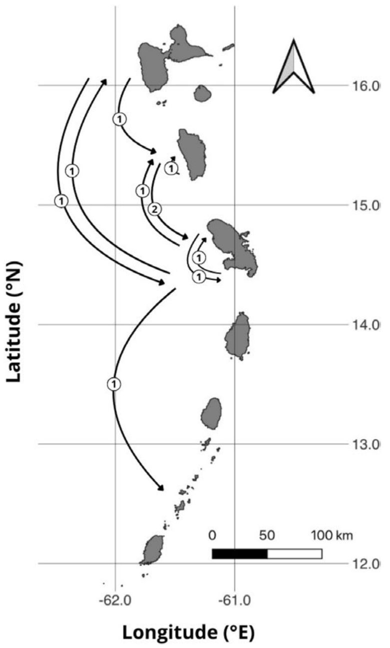

FIGURE 8 | Fraser's dolphin movements between sightings. Black arrows represent movements between sighting and resighting locations. Numbers represent the number of resighted dolphins observed together during both capture and recapture events.

by a decrease in detectability, as survey conditions are usually more windy and wavy in the channels and therefore less suitable for cetacean detection.

4.2 | Habitat Suitability and Distribution in the Lesser Antilles

Both Fraser's dolphin observations and habitat suitability predictions provide evidence of its presence all along the arc (Figures 2 and 5). Sightings have been recorded on the coasts of most of the islands, including Grenada, Saint Vincent, Saint Lucia, Dominica, Guadeloupe, Montserrat, and up until the Saba bank. The Caribbean side of the islands represents an almost continuous stretch of suitable habitat for Fraser's dolphins. Although similar observations have been obtained in 8 years of local studies in Guadeloupe (Rinaldi and Rinaldi 2011), our results offer a broader perspective on the importance of the Lesser Antilles for Fraser's dolphins.

The average estimated mean and upper group sizes in our observations, 112 and 350 individuals, respectively, were substantially larger than those previously reported around Guadeloupe (30 and 50 individuals; Rinaldi and Rinaldi 2011) and Dominica (60 and 125 individuals; Gero and Whitehead 2006). It is unlikely that these results are directly comparable, as the differences in group sizes could be due to spatial or temporal factors, or a combination of both, making it difficult to formulate hypotheses about Fraser's dolphin social dynamics.

Except for the Lesser Antilles, sightings of Fraser's dolphins are uncommon in the Caribbean Sea, and mentions of their presence are rare. Exceptional strandings have occurred in Venezuela, Puerto Rico or Bonaire (Bolaños and Villaroel-Marin 2003; Mignucci-Giannoni et al. 1999; Witte et al. 2012). These strandings involved isolated individuals and led to the first documentation of the species in those territories. In October 2023 and September 2024, the Caribbean Cetacean Society conducted 3 weeks of surveys around Curaçao, Aruba, and Bonaire, but did not detect any Fraser's dolphins. Similar results were obtained after 19 days of surveys along the Beata ridge, south Dominican Republic (CCS 2023, 2024a, 2024b). Moreover, an earlier review of Fraser's dolphin distribution did not report any sightings at sea in the Caribbean Sea, outside of the Lesser Antilles area (Gomes-Pereira et al. 2013). In contrast, encounter rates for Fraser's dolphins vary widely across tropical regions, ranging from as low as 0.36 individuals per 1000 km in areas where the species is rarely observed, such as La Réunion (Dulau-Drouot et al. 2008), to as high as 16.9 individuals per 1000 km in high-density areas like the Sulu Sea (Dolar et al. 2006). This information underscores the importance of the Lesser Antilles for the species, where the occurrence rate is outstanding for the Caribbean Sea, supporting the hypothesis of a resident and likely closed population at the scale of the Lesser Antilles. However, the accuracy of this hypothesis may be compromised by data deficiencies. Consequently, future surveys are necessary to accurately determine the presence, abundance, and connectivity of Fraser's dolphins at the wider Caribbean scale. The closest known hotspot for Fraser's dolphins to the Lesser Antilles appears to be in the Gulf of Mexico (Gomes-Pereira et al. 2013), although surveys in the region failed to detect the species, likely due to its low encounter rate (Mullin and Fulling 2004). Moreover, genetic comparisons between these locations could offer insights into potential population fragmentation across the North Atlantic and provide an additional layer of characterization regarding the species' status in the Lesser Antilles.

4.3 | Species Distribution Model

SDMs have limitations and it is therefore important to discuss validity. As previously mentioned, the bell-shaped and ramp-shaped smooth terms for continuous environmental parameters (Figure 4) suggest that the model successfully captured the range of environmental conditions favored by Fraser's dolphins. This likely contributed to reducing prediction error in the habitat suitability model. This has been facilitated by the large-scale data collection program along the entire Lesser Antilles arc. However, the coefficient of variation increases at the northern edge of the area (dark red patch in north of Figure 6) where the distance to the canyon exceeds the surveyed range, suggesting that the reliability of species distribution modeling could be enhanced with additional survey efforts in that region.

The maximum TSS value obtained for our best-fitting model was 0.58, slightly below the 0.6 threshold previously mentioned in the methods section (Tobeña et al. 2016; Tsirintanis et al. 2023). However, this value would likely be higher with increased survey effort as only 12 observation points were available for verification. It is important to note that failure to detect dolphins at the surface does not necessarily mean they are not present at that time or in the days following the boat's presence. The absence data does not account for missed opportunities to observe what is typically present in each grid cell, leading to an overestimation of real absences and, consequently, a potential underestimation of the TSS value with low survey effort. Finally, it is important to note that the prediction accuracy has only been assessed on the Caribbean side of the study area. Therefore, predictions made for the Atlantic side should be approached with caution, as almost no data from this area, below Guadeloupe, has been utilized to fit the selected model. While we anticipate a habitat suitability pattern similar to the one depicted in Figure 5 based on our observations from the Caribbean coast, verification is still pending and needs to be conducted.

Our models had an overall explanatory power of around 20.2%–22.0% (Table 1). Many SDMs describing dolphin species feature similar, if not lower, explanatory power, typically from 10% to 25% (see Table 3 in Becker et al. 2019, and Table 1 in Correia et al. 2021). This is believed to be caused by the fact that cetacean distribution is influenced by multiple parameters, both behavioral and ecological, such as reproduction, interspecific interactions, and prey aggregation, while most cetacean-based SDMs mainly include indirect environmental covariates as proxies of prey distribution (Palacios et al. 2013). Moreover, dolphins are highly mobile and can travel more than 90 km/day (Wells et al. 1999). Therefore, it is unlikely that each observation would occur above high aggregations of prey, as they can be engaged in other activities such as resting, traveling, or nursing in between feeding areas (Ballance 1992). This is especially plausible for Fraser's dolphins, as we have observed the importance of interspecific association behavior, which is likely to affect their dynamics and distribution in the Lesser Antilles.

4.4 | Co-occurrences

Our results have demonstrated that Fraser's dolphins were significantly more likely to co-occur with other species, and the observed associations were stronger than other cetaceans. Co-occurrences were observed with sperm whales, bottlenose dolphins, pantropical spotted dolphins, melon-headed whales, short-finned pilot whales, and spinner dolphins (Table 2). Importantly, it should be noted that the Sorensen's index we used reflects the probability of observing two species together in the Lesser Antilles and does not directly indicate species preferences in terms of co-occurrences, which would necessitate accounting for distribution range overlap between species. The co-occurrence of Fraser's dolphins with other cetaceans appears to be an important feature of its behavior and ecology, suggesting that they are not coincidental.

In a previous study analyzing cetacean associations in the central Philippines, Fraser's dolphins co-occurred with other species in 84% of sightings, involving seven species across 44 observations (Dolar et al. 2006). Off La Réunion Island, all sightings of Fraser's dolphins were in association with melon-headed whales (Dulau-Drouot et al. 2008), while in Dominica, 4 out of 7 sightings included pantropical spotted dolphins, short-finned pilot whales, or sperm whales (Gero and Whitehead 2006). This consistent global pattern suggests that co-occurrence may offer advantages to Fraser's dolphins, benefit the associated species, and be tolerated, or reflect a mutual benefit through incidental interactions. Mixed cetacean groups are typically linked to foraging efficiency, predator avoidance, or social interaction benefits (Stensland et al. 2003; Syme et al. 2021). Although killer whale predation has been documented in the Bahamas (Dunn and Claridge 2013), predation pressure in the region appears low overall.

Since 2023, the “Ti Whale An Nou” program has begun recording behavioral observations, including several feeding events involving mixed groups of Fraser's and pantropical spotted dolphins, sometimes at the surface. Similar foraging behavior has been described off Dominica (Watkins et al. 1994). Based on these observations, we hypothesize that the foraging benefit hypothesis (Syme et al. 2021) is the most plausible explanation for these associations. This hypothesis could be tested by comparing behavior data between single-species and mixed-species groups to assess whether co-occurrence events are predominantly associated with foraging.

The nature of interspecific associations among cetaceans is complex and influenced by factors such as group size, prey availability, and dietary overlap (Koper and Plön 2016). Mixed-species groups can offer evolutionary advantages, including improved foraging efficiency and predator detection (Goodale et al. 2017; Stensland et al. 2003; Syme et al. 2021). However, forming large groups also comes with costs, such as increased risk of disease transmission and heightened competition for prey resources (Krause and Ruxton 2002; Syme et al. 2021). A quantitative assessment of how foraging performance is affected during cetacean mixed-species group events would greatly enhance our understanding of their ecological function. Multisensor tags, including movement sensors and acoustic recorders, offer an effective means of monitoring delphinid feeding behavior and assessing foraging performance (Nowacek et al. 2016). These tools provide a promising avenue for investigating the ecological functionality of Fraser's dolphin co-occurrences, while also delivering valuable data on foraging depths or prey types. Previous studies using such methods have yielded valuable insights and should be carefully considered when designing an effective study framework, to ensure that the anticipated outcomes justify the use of invasive techniques (Watwood et al. 2006; Arranz et al. 2019). Combining boat-based behavioral observations with multisensor tag deployments would help assess both the costs and benefits, as well as the nature, of these co-occurrences, offering deeper insight into their importance in Fraser's dolphin ecology. In particular, the frequently observed pairing with pantropical spotted dolphins presents a strong candidate for targeted investigation in the Lesser Antilles. Several hypotheses could explain why Fraser's dolphins may co-occur with species such as sperm whales, for example, using them as indicators of prey availability or engaging in kleptoparasitism by exploiting regurgitated prey following harassment, as observed in other cetacean species (Smultea et al. 2014).

This co-occurrence analysis allows us to formulate hypotheses about Fraser's dolphin ecology, particularly regarding its potential attraction to other cetacean species, which may influence its distribution in the Lesser Antilles. The combination of suitable depth ranges and proximity to canyons may provide access to its preferred mesopelagic prey (Dolar et al. 2003; Wang et al. 2012), while also coinciding with areas of high cetacean abundance often associated with canyon systems (Moors-Murphy 2014). The complexity of Fraser's co-occurrence behavior underscores the importance of interspecific interactions and highlights the need for further research on cetacean mixed-species groups to enhance our understanding of cetacean ecology in diverse communities.

4.5 | Movements and Consequences for Conservation

According to the movement analysis, Fraser's dolphin seems to engage in extensive travels throughout the Lesser Antilles. This result supports the idea that the area represents a continuous suitable habitat for the species and that spatial fragmentation of the species in the area is unlikely. This is an important step to understanding the connectivity between the different territories in terms of the movements of the cetacean community in the Lesser Antilles. It was previously known that sperm whales are engaged in movements between Guadeloupe and Grenada (Gero et al. 2007), while pantropical spotted dolphins are believed to be resident in both Martinique and Guadeloupe (Courtin et al. 2022). These results highlight the diversity of species' movement behaviors in the Lesser Antilles, underscoring the need for long-term monitoring to discern consistent patterns within this mosaic of habitats and species.

In terms of anthropogenic pressures, the Fraser's dolphin population across the region is encountering various threats. Based on Fraser's dolphin photo identification data, we identified several individuals showcasing major straight cuts on the dorsal fin that are likely to have been caused by human activities such as collision with boats, propellers, or interaction with fisheries (nets). Evidence of chlordecone bioaccumulation near Guadeloupe, a pesticide used until 1993 in the French West Indies, has recently been detected in the blubber of stranded individuals (Méndez-Fernandez et al. 2018), underscoring the threat posed by chemical compounds to marine top predators. Although the direct impact of pollutants on cetacean mortality is yet to be determined, hunting around St. Vincent and St. Lucia islands also targets Fraser's dolphins. While hunting primarily targets short-finned pilot whales, an estimated 100–700 "small cetaceans," including Fraser's, spinner, and pantropical spotted dolphins, are killed annually (Fielding and Kiszka 2021). Although the specific proportions are unknown, Fraser's dolphins are referenced as a common catch (Fielding and Kiszka 2021). The uncertain number of Fraser's dolphin hunts and the lack of abundance estimates make it challenging to assess the impact of hunting, and further collaboration with hunters could provide crucial information for conservation efforts. However, movement analysis, particularly the CCS_Lh_0021 observation, initially documented in Martinique within the Agoa sanctuary where cetaceans have protected status, and subsequently observed in the southern Grenadines, suggests that individuals are not confined by territorial boundaries, nor protected areas. They may benefit from protection for a time before facing hunting and other anthropic pressures across their range.

These transboundary movements better inform future conservation efforts, particularly when aligned with existing regional frameworks such as the Marine Mammal Action Plan under the SPAW Protocol (SPAW-RAC 2020). Conservation of highly mobile species presents significant challenges, as localized threats within their distribution range can have large-scale impacts on populations, necessitating collaboration across regions for effective protection (Runge et al. 2014). This is especially true for cetaceans; safeguarding Fraser's dolphins and, more broadly, the cetacean community in the Lesser Antilles requires extensive cooperation among stakeholders and territories (SPAW-RAC 2020). These findings also highlight the critical importance of maintaining large-scale, long-term monitoring efforts, which are essential for accurately assessing cetacean populations and guiding conservation strategies.

5 | Conclusion

Fraser's dolphin presence and habitat suitability have been confirmed throughout the Lesser Antilles arc. The rather uncommon occurrences of the species in the wider Caribbean contrast sharply with its occurrence rate in the Lesser Antilles, suggesting that this population is likely restricted to the arc and relatively isolated from the wider Caribbean. Individuals engage in inter-island movements, indicating the connectivity of the species along the arc, where fragmentation at the insular scale is unlikely.

For this species, we have demonstrated the importance of co-occurrences with other cetaceans, which we hypothesize to play a key role in Fraser's dolphin feeding ecology in the Lesser Antilles. Future research is needed to better understand the costs and benefits of these interactions, their directionality, and their broader ecological implications for Fraser's dolphins.

Efficient conservation of the species in the Lesser Antilles will require extensive communication and cooperation between the various territories and stakeholders. While most of the arc is likely equally utilized by individuals, more recaptures are required to validate this trend. To a greater extent, this case study showcases the existing connectivity between islands for the cetacean community and underscores the necessity for harmonization in policy and management for cetacean conservation in the Lesser Antilles.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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