Fraser's dolphin in the Lesser Antilles:

Distribution, Habitat Preferences and Co-occurrence Behavior

Fraser's dolphin (*Lagenodelphis hosei*).

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May-August 2023

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Abstract

The Lesser Antilles hosts a high diversity of cetacean species, which are essential top marine predators whose abundance reflects the overall health of marine ecosystems. Despite the high research interest in cetacean ecology, Fraser's dolphin (*Lagenodelphis Hosei*) remains one of the least studied dolphin species, primarily due to its tropical offshore and low-density distribution. However, some Fraser's dolphin populations particularly frequent the coastal waters of tropical oceanic islands featuring steep topography. The Lesser Antilles has been identified as one of the few places where Fraser's dolphin is frequently observed, providing a unique opportunity to learn about this mysterious species. Using boat survey data collected all along the Lesser Antilles, we aimed to gain insights into Fraser's dolphin distribution and habitat preferences. Consequently, we used presence-absence Generalized Additive Models to identify the environmental covariates that best explained its distribution and used them to predict habitat suitability. presence is suspected all year-around and was confirmed during our sampling period from March to October along the Lesser Antilles arc. Covariates such as chlorophyll *a* concentration, proximity to canyons, sea surface temperature, depth, and eastward current velocity best explained the observed distribution. An amount of 76% of Fraser's dolphin observations co-occurred with a total of 6 other cetacean species. To understand if this pattern is unique to Fraser's dolphin, we performed a simple statistical analysis of cetacean co-occurrences to test for its significance. Fraser's dolphin exhibited more frequent associations with other species, and these associations displayed greater strength compared to interactions involving other cetacean species. We hypothesize that the co-occurrence behavior of Fraser's dolphin is likely driven by a versatile and opportunistic foraging strategy. The presence of occasional feeding surface behaviors provides evidence that its diet in the Lesser Antilles may not be confined to mesopelagic prey species.

Introduction

Marine ecosystems are vital for sustaining the global biosphere's health by providing essential mineral and organic nutrients. Cetaceans are a diverse and widely distributed group of apex marine predators, and hold a pivotal position within these ecosystems. They exert significant influence over primary production by releasing nutrients through their carcasses and feces (Ballance, 2018). Moreover, they are integral to maintaining the equilibrium of marine biodiversity, regulating the abundance of prey and competitors through predation (Ballance, 2018). Disparities between suitable habitats and observed distributions of cetacean species have previously shown correlations with anthropogenic pressures, making them potential proxies of marine ecosystems' health (Azzellino et al., 2014). Hence, research endeavors into cetacean ecology yield valuable insights that are pertinent to the conservation of both cetacean populations and marine ecosystems.

Figure 1. Global Fraser's dolphin observation map extracted from GBIF website. Hexagons represent areas where Fraser's dolphin presence has been reported.

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* (McGowen *et al*., 2009; Lee *et al.*, 2019). The external appearance of Fraser's dolphin 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. Its particular distribution might be the cause.
The distribution range of Fraser's dolphin is widespread in every tropical sea between 30°N and 30°S (Dolar, 2009) and opportunistic reports of observations tend to correlate with this statement (Figure 1). Although its observations are rare due to its preference for deep offshore waters (Dolar, 2009), resulting in sightings usually occurring at low density around the globe (Dolar *et al.* 2006). However, Fraser's dolphin displays a different distribution

around oceanic islands with steep topography (Dolar, 2006; Kizka *et al.*, 2011; Gomes-Pereira *et al.,* 2013), creating density hotspots for this species in places like the Philippines or the Lesser Antilles (Dolar *et al.* 2006; Kiszka and Braulik, 2018).

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), a phenomenon not observed on a wider scale in the Caribbean Sea, as several surveys and studies have not reported any Fraser's dolphin sightings (Gomes-Pereira *et al.*, 2013). This area offers valuable opportunities to study and improve overall knowledge about this mysterious species, especially regarding its habitat preferences and distribution. Such information is usually easily accessible and primary for other dolphin species but remains poorly understood for Fraser's dolphin, except that it is highly sensitive to sea temperature and depth.

Sightings and strandings have indeed been reported outside of the 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 the global phenomenon El Niño (Perrin *et al.*, 1994; Durante *et al.*, 2016). The species' ability to extend its distribution range with temperature rises, even if only temporarily, has led to speculation that it could serve as a potential bio-indicator for future seawater warming (Gomes-Pereira *et al.*, 2013). Although sea surface temperature has an impact on Fraser's dolphin's global distribution, it remains uncertain whether this effect would be observed at a more local scale, along the Lesser Antilles arc. Additionally, depth has also been identified as a factor of major influence on Fraser's dolphin distribution due to its feeding behavior. Fraser's dolphin was indeed described as having a deep diving foraging behavior, targeting mesopelagic prey such as cephalopods, crustaceans, and fishes (Dolar *et al.,* 2003). This behavior is supported by higher levels of myoglobin compared to other small cetaceans exhibiting similar foraging behavior, which enables exceptional diving performance (Dolar *et al.,* 1999).

Using data collected on the Lesser Antilles by the Caribbean Cetacean Society's (CCS) program 'Ti Whale an Nou', we first got motivated to gain insights into Fraser's dolphin habitat preferences and distribution in the area. Species Distribution Models (SDMs) are widely used to provide information on the environmental factors that most strongly correlate with species observations in a defined area (Guillera-Arroita *et al.*, 2015), as it usually does not require more than GPS localisations and open sourced environmental datasets. Moreover, these models play a crucial role in predicting species distributions, making them valuable tools for conservation efforts (Passadore *et al.*, 2018). Overall, applying SDMs to the Fraser's dolphin would yield general yet essential insights into its general ecology around oceanic islands and inform conservation perspectives, allowing the identification of hotspots of species presence, as well as potential spatial threats that the species may face.

While collecting essential data for Fraser's dolphin habitat preferences and distribution, we observe these dolphins co-occurring most of the time alongside a wide range of other cetacean species. Numerous reports from cetacean surveys also mention feeding behavior and observations of co-occurrence with other cetacean species, such as melon-headed whales (Wade and Gerrodette, 1993) and tropical spotted dolphins (Kizka and Braulik, 2018). Moreover, a few observations suggest that some populations of Fraser's dolphins may exhibit a more complex and opportunistic foraging behavior than initially described. For instance, Fraser's dolphins in the Sulu sea, next to the Philippines, exhibit a wider range of prey capture at different depths compared to spinner dolphins, despite both species sharing similar foraging behavior (Dolar *et al.*, 2003). Additionally, unusual surface feeding behavior was observed near Dominica (Watkins *et al.*, 1994), and coastal cephalopods (ranging from depths of less than 250 m) were found in stranded individuals near Brazil (Moreno *et al.*, 2003). Fraser’s dolphin could consequently display a wide range of foraging strategies, and benefit from other cetacean species to identify feeding areas. Motivated by these descriptions, the lack of comprehensive reviews on this distinctive behavior and the observations made by the CCS, we were interested in analyzing the co-occurrences between the Fraser's dolphin and other cetacean species. Our objective is to determine if this observed trend indeed plays a significant role in Fraser's dolphin ecology in insular environments.

The final purpose of this study is to document both Fraser’s dolphin habitat, distribution and intriguing co-occurring behavior, in order to provide valuable insights and knowledge about a poorly described species among cetaceans. The results aim to inform future research and conservation perspectives that would benefit from those preliminary descriptions about Fraser’s dolphin ecology. To achieve this objective, we conducted simple and descriptive analyses to investigate whether Fraser's dolphins were, as we hypothesized, more frequently and strongly observed in association with other species compared to other cetacean species. Additionally, we used Species Distribution Models (SDMs) to model Fraser's dolphin habitat preferences and distribution, and to verify our hypotheses. We anticipated that Fraser's dolphin habitat preferences would be influenced by factors such as sea temperature, depth, and parameters that typically correlate with the presence of deep-diving cetacean species, such as slope (Cañadas *et al.*, 2002). Consequently, we expected the suitable habitat to be concentrated around the steep and deep waters of the Lesser Antilles. Based on preliminary observations, we also anticipate that suitable habitat could be found throughout the entire Lesser Antilles arc. The results of our study will help to understand the use and importance of the Lesser Antilles for Fraser's dolphins, and will provide general insights into their interactions with the rich cetacean communities in the Lesser Antilles region.

Material and Methods

1. Study area

Our study area is 93.500 km² large in area and encompasses the waters surrounding the Lesser Antilles archipelago, extending from Grenada to Anguilla (Figure 2). The boundaries of the study area have been set to a distance of 25 kilometers from the continental shelf (usually coinciding with the 200m isobath) and have been adjusted to avoid including areas that have not been surveyed within the Exclusive Economic Zones (EEZs) of other countries. This restriction ensures that analyses and results communication only concerns territories where prospection was permitted and performed. Most of the Caribbean side is characterized by a steep topography with a sea state relatively calm compared to the Atlantic which is usually unsuitable for several consecutive days of survey.

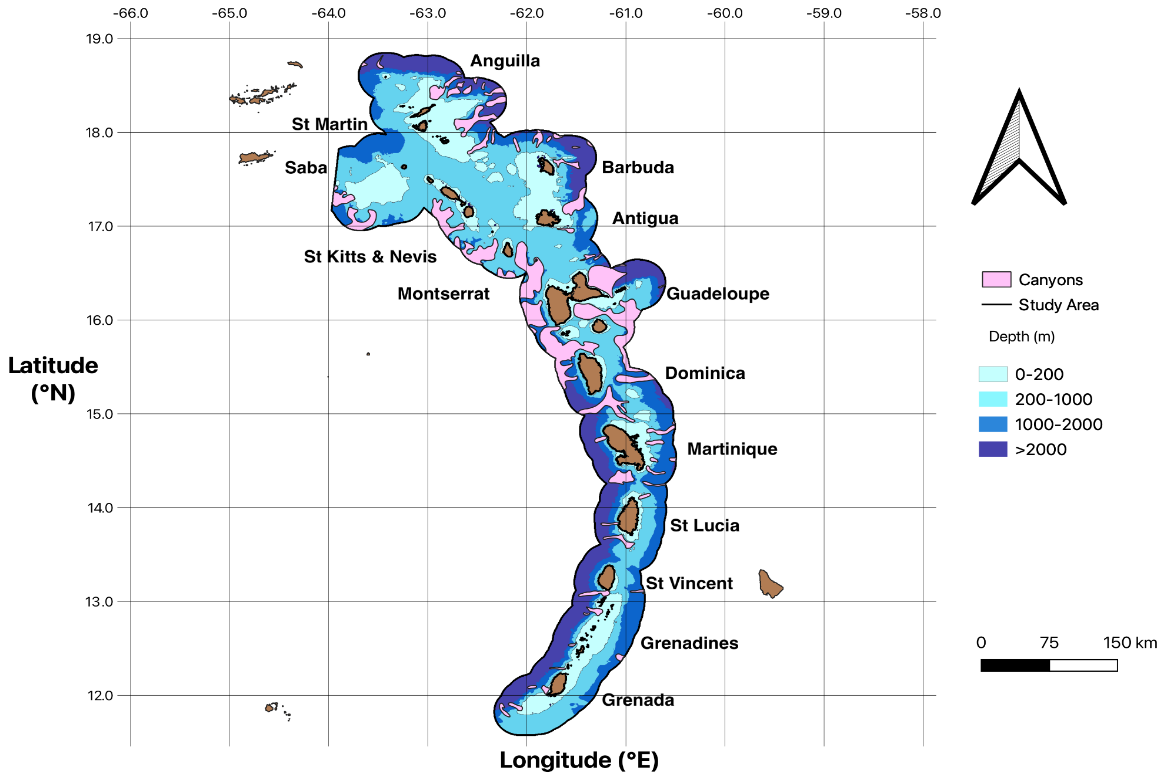


Figure 2. Study area geomorphology.

2. Data Collection

The data was collected as part of the ‘Ti Whale An Nou’ research program conducted by the CCS from 2021 to 2022. A total of 14 two-week-long boat surveys were carried out between the months of March and October. Three non systematic survey routes were used to cover the Lesser Antilles. The northern, central and southern routes allowed boat surveys from south Martinique to respectively St Martin, north Guadeloupe and Grenada. Although no specific design was used for the routes, effort was put into covering new areas from one expedition to another. A couple of short supplementary surveys around Martinique occurred between the months of September and November and were also included. During on-effort observations, two observers positioned themselves at the front of a 40-46 foot sailing boat, visually searching for cetaceans. Each observer covered an observation angle ranging from 0° to 90° on each side of the boat. On-effort was maintained during the daylight part of the day (6-18) and switched to off-effort (end of search for cetacean) in case of rain or unsuitable sea state (> beaufort 4) that would compromise cetacean detection. Once dolphins were spotted, coordinates of the sighting, group size estimation, species identification and its certainty level, and distance from the boat were recorded. We have also collected pictures of the fins, which allowed us to identify individuals based on permanent and unique marks or wounds (PhotoID).

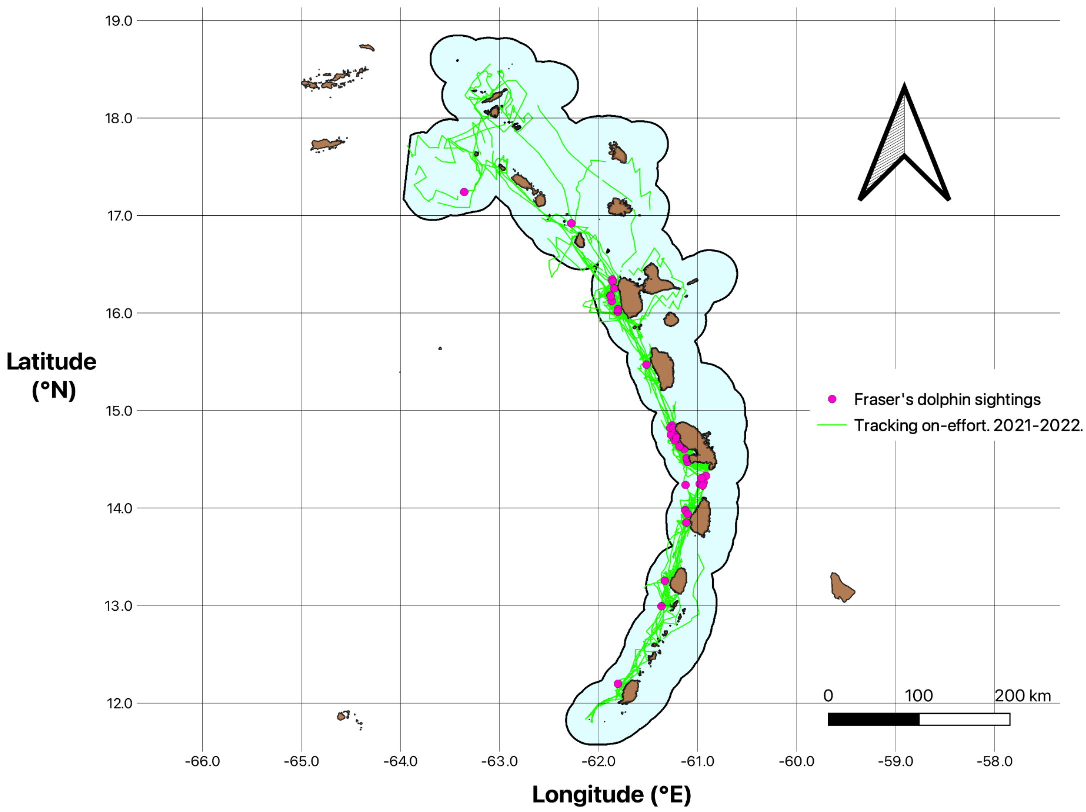


Figure 3. Survey effort and Fraser’s dolphin observations between 2021 and 2022.

3. Species Distribution Model

3.1 Generalized Additive Model

Species Distribution Models (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 species observations, aiming to identify the preferred ranges of occurrence. Models can then be used to perform predictions of suitable habitat to a target area. In the context of cetacean SDMs, various modeling techniques have been employed and compared. Among the most popular approaches are Generalized Linear Models (GLMs), General Additive Models (GAMs), and more recently, machine learning techniques such as maximum entropy models (MaxEnt) (Derville *et al.*, 2018; Forney *et al.*, 2012; Putra and Mustika, 2021). Although several studies have demonstrated the efficiency of the MaxEnt technique for SDM (Moura *et al.*, 2012, Putra and Mustika, 2021), it is more suitable for presence only data (Elith *et al.*, 2006). To incorporate sampling effort as a presence-absence dataset, we have chosen to develop a GAM for the Fraser's dolphin SDM. GAMs, as non-parametric regression techniques, allow for non-linear relationships to be modeled using smooth functions, providing more flexibility compared to GLMs. Additionally, previous research has shown its capacity to produce robust outcomes in modeling cetacean distributions when compared to alternative models (Derville *et al.*, 2018).

To perform the GAM, an hexagonal grid using 3 km wide cells has been created to cover the study area. In each surveyed cell, observations of groups of Fraser's dolphin, sampling effort and locally averaged environmental parameters have been associated. Surveyed cells without observation of Fraser's dolphin were considered as absence data. We have also used this grid to predict Fraser's dolphin habitat suitability.

The performance of the prediction was then assessed. Typically, cross-validation techniques involve randomly dividing the modeling dataset into a training dataset (approximately 80% of the data) and a validation dataset (around 20% of the data) (Stephenson *et al.*, 2020, Tobeña *et al.*, 2016). The model is trained on the first 80% of the data, and the remaining 20% is used to assess the model's ability to predict new data points. However, in this study, the number of Fraser's dolphin observations was judged too limited to allow for dataset subsetting. As a result, preliminary Fraser's dolphin observations of 2023 were used for model validation.

3.2 Survey effort

The survey effort was calculated based on the on-effort boat tracking line, taking into account the reduction in cetacean detection probability with distance. Four distance ranges from the tracking line, each associated with a positive detection probability (1, 0.75, 0.5, 0.25), were defined. The certain detection buffer extends from the null distance to the boat, up to an upper limit where the distribution of detection distances reaches its maximum. The percentile associated to this range was then calculated to divide the rest of the distribution of observed Fraser distance in three equidistant segments representing the distance thresholds associated with detection probability reduction (0.75, 0.5 and 0.25). Using QGIS, the 4 resulting detection buffers have been generated and effort per grid cell has been estimated by summing the surveyed areas weighted by their respective detection probabilities. Effort per grid cell was finally standardized by dividing by the maximum effort value.

3.3 Environmental dataset

Prey distribution are complex datasets to obtain, especially for deep diving cetacean species. Consequently, environmental predictors are usually used as a proxy of prey distribution to model cetacean distributions (Redfern *et al*., 2006). Little is already known about the Fraser's dolphin habitat preferences compared to other cetaceans, except for its deep diving behavior (Dolar *et al.,* 2003). Therefore, we have selected 18 environmental variables to model deep divers' distribution and more generally cetacean species (Pirotta *et al.*, 2011; Virgili *et al.*, 2022). Depth, sea surface temperature (SST), bottom temperature (BT), eastward and northward current velocity (U0,V0), chlorophyll *a* concentration (CHLA) , sea surface height (SSH) and mixed layer depth (MLD) have directly been extracted from open source satellite datasets. Their origin and respective resolutions are described below (Appendex). Distances to the coast, isobath 200m, 1000m, 2000m and slope have been derived from the depth dataset using QGIS v3.28 Firenze (QGIS Development Team, 2018). Similarly, the distance to canyon (DC) has been derived from the canyon cartography. Eddy kinetic energy (EKE), current velocity (CV) and their standard deviation have been derived using the current coordinates U0 and V0. Incorporating those variables is important as cetaceans may avoid or benefit from current while traveling as an example. For temporal variables, monthly values have been averaged, from January 2021 to Decembre 2022 in order to represent locally mean environmental conditions over the sample period. To account for the importance of their variation, each variable has been visually inspected and standard deviations (SD) were included as variables when featuring an important pattern of temporal variation. The spatial resolution was adjusted to a unique value per environmental covariate per hexagonal grid cell, for 2021 and 2022 combined, ensuring that it represents the local mean environmental value. The same environmental datasets have been used to model Fraser’s dolphin habitat preference in the surveyed area and to elaborate the distribution prediction in the study area.

3.4 Fitting the GAM

Model was fitted using grid cells associated with a positive survey effort only. The complexity of the models have been restricted to combinations of up to 4 environmental variables. After excluding models involving pairs of Pearson correlated variables ($|R| > 0.7$), every combination of predictors has been considered. Using R v4.3.0 (R Core Team, 2023) and the MGCV R package (Wood, 2001), GAMs have been generated using a Tweedie distribution and a logarithmic link function and 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 prevent overfitting. Models were ordered and selected using Akaike Information Criterion (AIC) scores. Using Akaike weights, the importance of environmental variables was investigated. The model featuring the lowest AIC, was used to map the relative predicted habitat suitability in the entire study area to inform about the Fraser’s dolphin distribution in the Lesser Antilles. Uncertainty was measured through the coefficient of variation provided with the prediction.

The performance of the model was assessed based on the observations from the first four expeditions of the 2023 'Ti Whale An Nou' program. Using boat tracking data and the same detection distances as for the 2021-2022 survey effort, grid cells featuring a positive survey effort have been identified. Subsequently, a binary dataset was created, where cells recording observations of Fraser’s dolphin were assigned a value of 1, while cells with a positive survey effort but without any observations were assigned a value of 0. This dataset only includes 10 cells associated with Fraser's dolphin presence.

Prediction accuracy coefficients, namely the Area Under the Curve (AUC) and the maximum True Skill Statistic (TSS), were obtained by generating the Receiver Operating Characteristic (ROC) curve and the confusion matrix, respectively. Those coefficients measure how well new observations are represented by habitat suitability predictions and are therefore useful to assess the accuracy of the model. AUC values over 0.7 are usually considered as correct and excellent over 0.8 (Hosmer *et al.*, 2013; Mandrekar *et al.*, 2010) while maximum TSS values are arbitrarily good over 0.6 (Tobeña *et al.*, 2016, Tsirintanis *et al.*, 2023). The inability to predict the observed data may be attributed not only to the prediction performance but also to variations in the 2023 bioclimatic variables compared to the period used for model fitting (2021-2022). Despite this limitation, it is still valuable to investigate the performances of the predictions regardless of the temporal factors, especially in terms of conservation perspectives.

3.5 GAM limitations

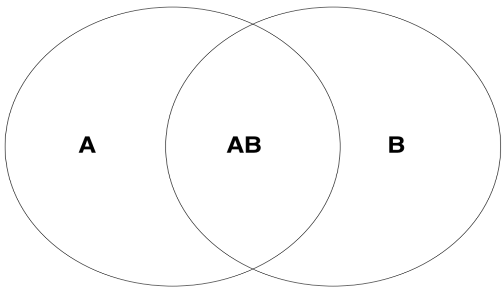
While SDMs are valuable tools for describing species distributions, their effectiveness can be limited by factors such as survey design, low sample size, or weak model performance. During our expeditions, we did not follow a survey design. Cells along the shorter track between scheduled departure and arrival points were more likely to be covered. However, it has been previously demonstrated that survey design has a low influence on SDMs as long as it encompasses a wide range of environmental variations, enabling the identification of the environmental conditions favored by the target species (Tessarolo *et al*., 2014). Sample size also plays a crucial role and needs to be sufficiently large to capture the environmental variations within the targeted area (Tessarolo *et al.*, 2014). We expect that despite the absence of a strong survey design, the large scale data collection and efforts put into covering a large range of bathymetry along and distances from the coast will meet the previous conditions for the Fraser’s dolphin in the Lesser Antilles.
In terms of performance assessment, it is important to note that the AUC an TSS criteria have previously provided performant values for models that failed to accurately describe the distribution of cetaceans with limited range, leading to misinterpretation of the model performances (Becker *et al*., 2020; Fiedler *et al.*, 2018). Long-term monitoring of Fraser's dolphins will therefore be recommended to improve the validity and fidelity of the predictions.

4. Co-occurrence analysis

To understand the specificities of Fraser’s dolphin co-occurrence pattern, we have decided to compare the co-occurrences observed during the sampling period among the cetacean community. Using survey-collected observations, we have developed cooccurrence datasets to investigate the concurrent presence of two cetacean species in the same area at the same time. Specifically, cooccurrence was defined as instances where two species were observed together or within a 5-minute time lag after the end of the first observation. This definition was chosen to account for cases where cetaceans might be diving, limiting detection, or exhibiting mutual interest in remaining close to each other, such as during feeding activities. To quantify the co-occurrence phenomenon, we calculated the proportion of observations that cooccurred for species that had accumulated more than 10 observations between 2021 and 2022. Among these species, Fraser's dolphin exhibited the highest co-occurring rate. To determine if this proportion was significantly different from other species, we planned to conduct a $\chi 2$ test for proportions. However, it is important to acknowledge that the hypotheses of independence between measurements could be compromised, as instances of two species seen together would be counted as cooccurrences for both species. To address this potential bias, we conducted tests between pairs involving Fraser's dolphin and other species by removing the shared observations. After removing the co-occurrences with the Fraser's dolphin, 5 species featured both a co-occurrence count and number of observations alone, higher than 5. A total of 5 tests were therefore performed between the Fraser's dolphin and each of the concerned species, without accounting for shared observations.

Subsequently, our aim was to quantify the strength of interactions between each pair of species and assess whether those involving Fraser's dolphins exhibited greater strength than others. Traditional co-occurrence analysis in ecological studies involve 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 (Wells *et al.*, 1999) and detectability of these animals, making it difficult to delineate fixed areas for presence/absence assessments.

Instead, we directly linked the gathered information to observations of species occurring together or independently. 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 context, the similarity between two cetacean species is associated with the strength of their cooccurrences.



$$S = 2 \times AB/(A + B).$$

Figure 4. Sorensen's index. A and B represent the total observations of species A and B while AB is the number of shared observations.

Sorensen's index varies between 0 and 1, indicating absence or perfect cooccurrence, respectively. To evaluate the sensitivity of the index to supplementary observations, we have calculated the index's values after a ± 1 perturbation on the number of shared observations. The aim is to avoid using values that may be too affected by a single observation due to small sample size. Through visualization of the generated variation, pairs 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 have been removed because of the seasonality of their presence in the Lesser Antilles. As a result, 14 pairs were retained out of which 6 pairs involved Fraser's dolphin. To determine if the mean Sorensen's index for the pairs involving Fraser's dolphin significantly differed from the other pairs, a Kruskal-Wallis test was performed.

Results

1. Distribution and habitat preferences

We were able to observe the Fraser's dolphin every month from March to November and all along the Caribbean side of Lesser Antilles Arc, from Grenada to the Saba bank (Figure 3). Fraser's dolphin was the second most observed dolphin species behind the Pantropical Spotted dolphins. The four detection ranges obtained were 0-209 m, 209-400 m, 400-500 m and 500-1000 m and were respectively associated with a detection probability of 1, 0.75, 0.5 and 0.25. Among 37 observations, the mean group size estimation varied from 10 to 300 with a mean, median and standard deviation of respectively 92, 60 and 80 individuals.

Those observations along with the survey effort and the associated environmental parameters, allowed to elaborate presence-absence Generalized Additive Models. A total of 2910 models have been generated. The 14 top models featuring a ΔAIC<2 from the best scoring model explained from 18.8% to 22.4% of the deviation (Table 1). Using the Akaike weights, environmental parameters have been ranked by their degree of importance (Figure 5). Chlorophyll *a* concentration, bathymetry, eastward current speed, sea surface temperature and distance from canyon were best explaining Fraser's dolphin distribution in the surveyed area.

Table 1. Summary table of the best AIC (Akaike Information Criterion) scoring models (ΔAIC<2). The table features the combinations of covariates used to fit the model, the AIC score, Explained deviation (%), AIC difference with the best scoring model (ΔAIC), the REML (Restricted Maximum Likelihood) and the Akaike weights. Top models featured the covariates: Bathymetry (Bathy), chlorophyll *a* concentration (CHLa), distance to canyon (d_canyon), eastward current (U0), sea surface temperature (SST), slope, Eddy kinetic energy standard deviation (SD_EKE), distance to the 2000m isobath (d_iso2000), bottom temperature (BT), distance to the coast (d_coast), mixed layer depth (MLD)

Model	AIC	Explained Deviance	Delta AIC	REML	Akaike weights
Bathy + CHLa + d_canyon+ U0	153.7	22.4	0	1	0.032
Bathy + CHLa + SST + U0	153.9	21.5	0.18	0.92	0.030
Bathy + CHLa + U0	154	20.7	0.29	0.86	0.028
Bathy + CHLa + d_canyon+ SST	154.4	20.8	0.65	0.72	0.023
Bathy + CHLa + Slope + U0	154.8	21.1	1.04	0.59	0.019
Bathy + CHLa + SST + SD_EKE	154.9	21.5	1.15	0.56	0.018
Bathy + CHLa + d_iso2000 + U0	155.2	21.2	1.47	0.48	0.015
Bathy + CHLa + d_coast + U0	155.3	21.1	1.53	0.47	0.015
Bathy + CHLa + SST	155.4	18.8	1.62	0.44	0.014
Bathy + CHLa + U0 + SD_EKE	155.6	21.7	1.86	0.39	0.013
BT + CHLa + d_canyon+ SST	155.6	19.2	1.86	0.39	0.013
Bathy + CHLa + MLD + U0	155.6	20.9	1.87	0.39	0.013
Bathy + CHLa + d_iso2000 + SST	155.7	19.7	1.97	0.37	0.012
Bathy + CHLa + U0 + V0	155.7	20.9	1.98	0.37	0.012

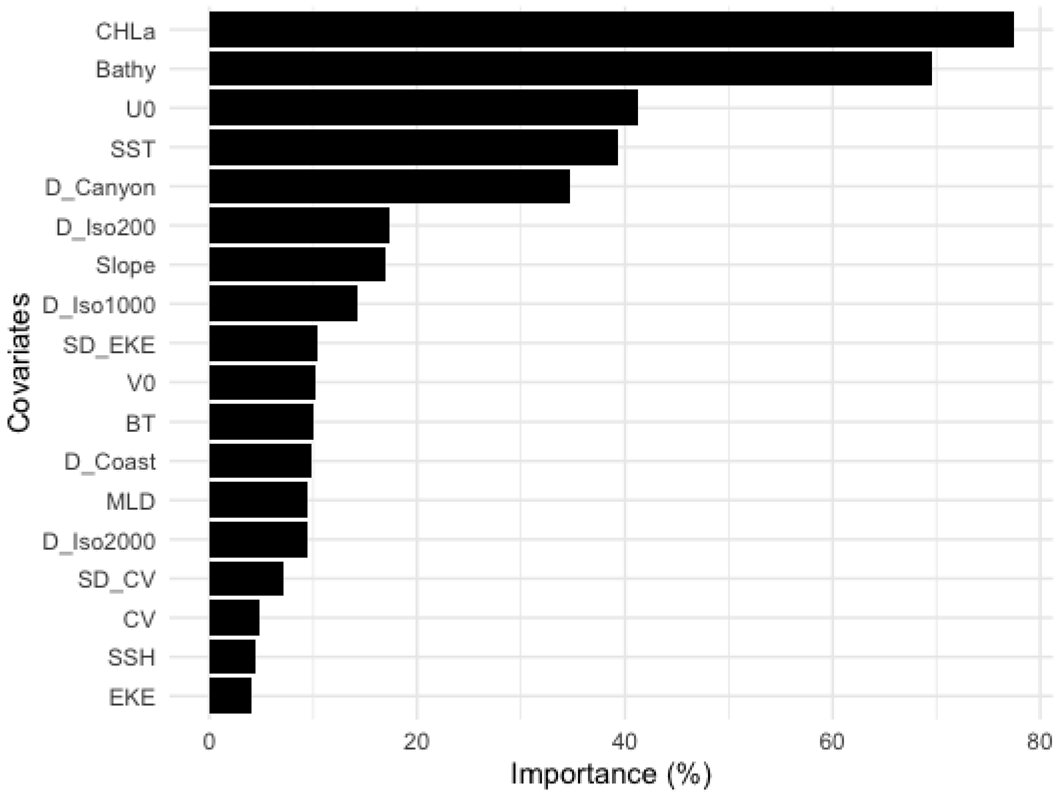


Figure 5. Importance of the covariates throughout the models based on Akaike Weights. Chlorophyll *a* concentration (CHLa), bathymetry (Bathy), eastward current (U0), sea surface temperature (SST), distance to canyon (d_canyon), distance to the 200m isobath (d_iso200), distance to the 1000m isobath (d_iso1000), slope, Eddy kinetic energy standard deviation (SD_EKE), northward current (V0), bottom temperature (BT), distance to the coast (d_coast), mixed layer depth (MLD), distance to the 2000m isobath (d_iso2000), current velocity standard deviation (SD_CV), current velocity (CV), sea surface height (SSH), Eddy kinetic energy (EKE).

2. Prediction of Fraser's dolphin relative habitat suitability

To predict the relative habitat suitability, we selected the best-scoring AIC model that also explained the highest amount of deviation. We investigated the smooth terms that model the relationship between the covariates and Fraser's dolphin habitat preferences (Figure 6).

In order to extrapolate the model to the entire study area and minimize the occurrences of significant errors, it is crucial to ensure that the surveyed range of environmental values was broad enough to encompass and identify the preferred range of Fraser's dolphin in our area. Although errors were important for extreme covariate values due to their limited representation in our surveyed area, most of our smooth terms display a bell-shaped tendency. The increasing curve portion associated with the positive eastward current could present challenges; however, areas with such values are rare in our study area and mostly confined to our surveyed region. As a result, our data collection allowed the identification of the favored environmental ranges of the Fraser's dolphin in our survey area. A more general way to solve this potential issue would be to adopt a well defined survey design using either uniforme coverage or randomly placed transects

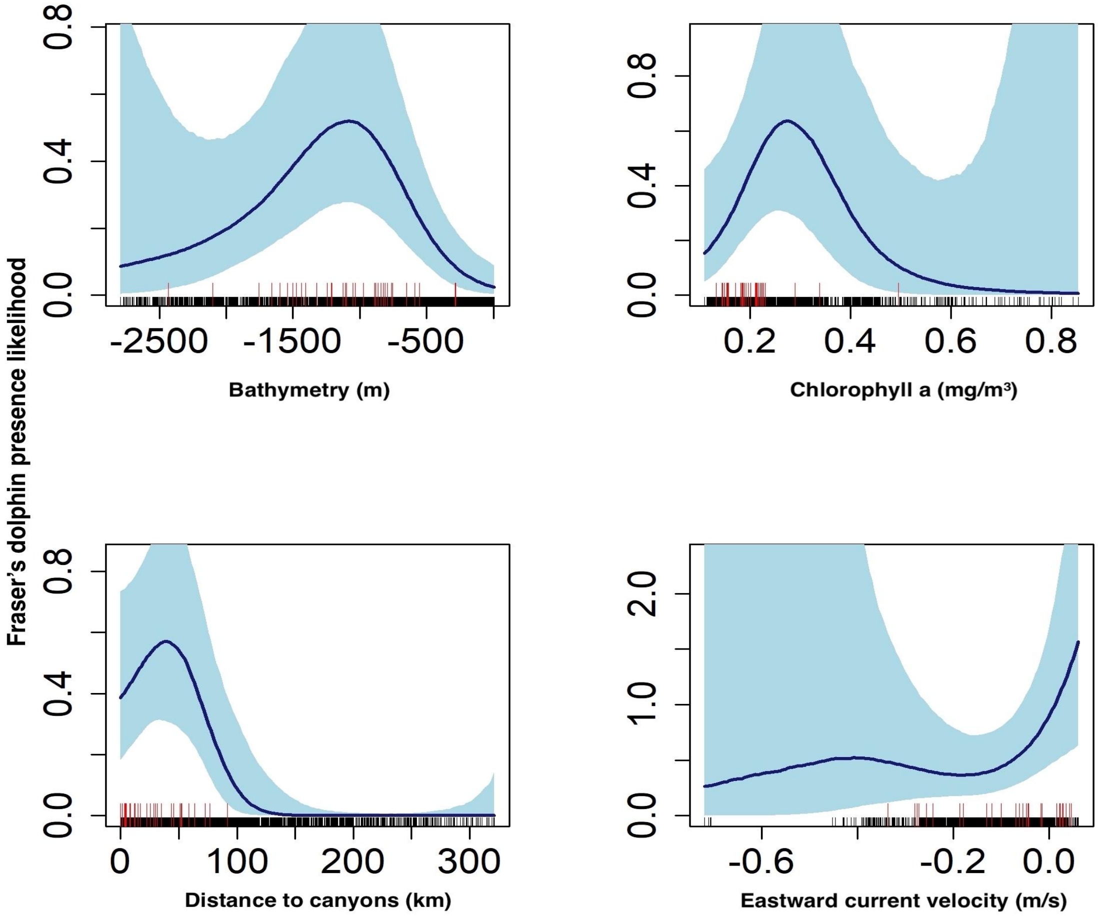


Figure 6. Relationship between Fraser's dolphin presence likelihood and environmental covariates for the selected model. Blue line represents the smooth functions and the blue shaded region the 95% confidence band. Black rug plots represent the value of environmental covariates in each grid surveyed grid cell while red represents Fraser's dolphin observations.

The entire area showcases suitable predicted habitats for Fraser's dolphins, both on the Caribbean and Atlantic sides of the arc, representing a continuum of favorable habitat conditions (Figure 7). The deep waters between Guadeloupe and St Vincent hold particular importance for the species. On the Atlantic side, south of St Vincent, two round-shaped areas with relatively high predicted suitability are observed, primarily due to the presence of canyons. These isolated predictions raise questions about the ability of the distance from the canyon covariate to generate predictions reflecting the species' ecology. Uncertainty in the predictions is more pronounced at the northern and southern edges of the area (Figure 8), where environmental conditions likely begin to differ from the rest of the region. In the north, areas with significant associated errors are mostly confined to relatively shallow waters and therefore unsuitable for the Fraser's dolphin. It is essential to note that these maps do not indicate where dolphins can or cannot be found, but rather highlight areas with the most favorable combination of environmental parameters. A habitat may be suitable but not actively used by the species, while an apparent low relative suitability can still host the species. What matters for this purpose is identifying the threshold of predictive suitability that best distinguishes areas of dolphin presence from areas of absence.

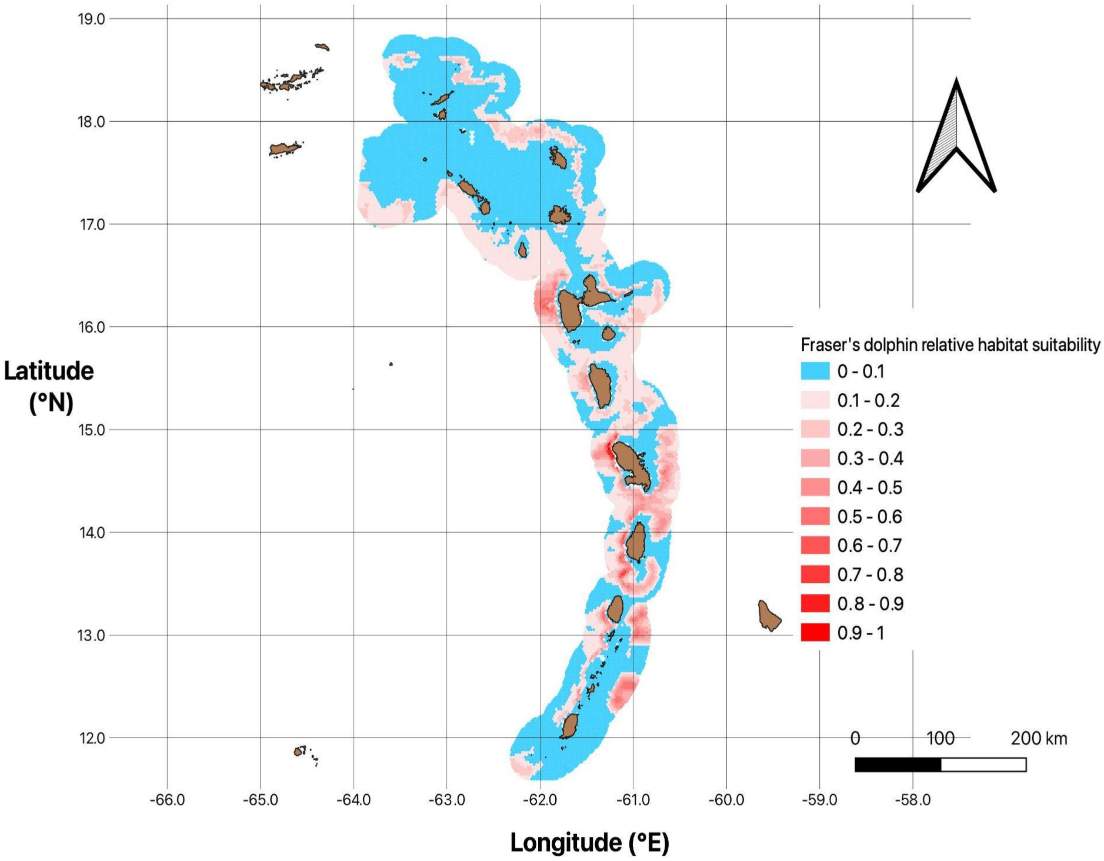


Figure 7. Fraser’s dolphin predicted suitable habitat in the Lesser Antilles based on the selected model. The blue cut-off has been chosen to reflect the threshold used to obtain the maximum TSS.

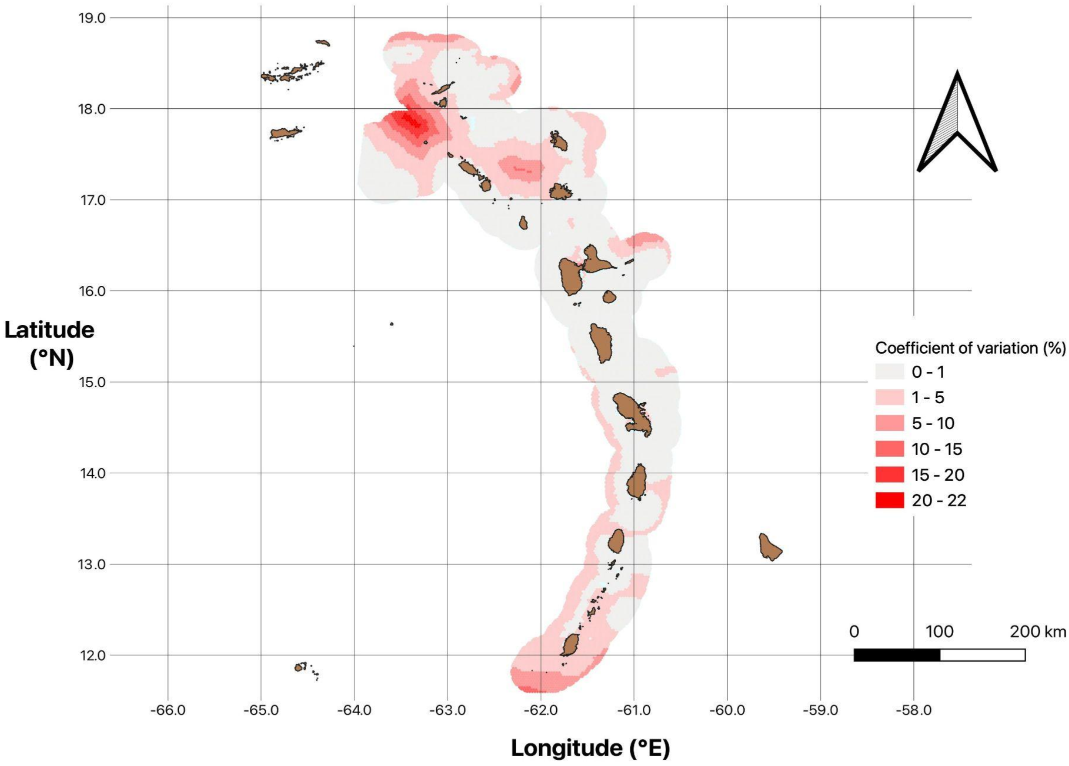


Figure 8. Fraser's dolphin habitat suitability coefficient of variation.

Using the 2023 Fraser's dolphin observations, ROC curves were obtained to evaluate the prediction performance in our surveyed area. The model demonstrates successful predictions in the surveyed region, as indicated by an AUC value of 0.85. To determine the threshold that maximizes the distance from the 45° diagonal, representing the random scenario, we identified a value of 0.093. This threshold was used to generate the confusion matrix (Table 3), allowing us to estimate the maximum TSS value. A TSS value of 0.69 was achieved, confirming the model's ability to provide accurate predictions in the surveyed area. Moreover, this value would likely be even higher with increased survey effort. We identified 528 false positives in the confusion matrix, representing cells with positive effort recorded where presence is predicted but not observed. However, it's important to note that failure to detect dolphins at the surface does not necessarily mean they are not present at the 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 an habitat suitability pattern similar to the one depicted in Figure 7 based on our observations from the Caribbean coast, verification is still pending and needs to be conducted.

Table 3. Confusion matrix at the 0.093 threshold above which relative habitat suitability predictions are associated with Fraser's dolphin presence.

	Observed	
Predicted	1	0
1	10	528
0	0	1127

3. Co-occurrences

Out of 37 Fraser's dolphin observations, 28 were associated with other cetacean species. Co-occurrences were observed with the pantropical spotted dolphin, short-finned pilot whale, bottlenose dolphin, spinner dolphin, sperm whale as well as the melon-headed whale. Preferences would be complicated to analyze as it would be influenced by the range and abundance of each species, still for some rare species like the melon headed whale a relatively important amount of sightings co-occurred with the Fraser's dolphin (Table 4).

When comparing the similarity of co-occurrence proportions in Fraser's dolphin observations with those of other species, all tests showed significant differences at the 0.001 level (Table 5). Fraser's dolphin exhibited the highest co-occurrence rate (Table 6), and this proportion significantly differed from other species, leading us to conclude that this species truly stands out from other cetaceans in terms of shared occurrences. These results validate what was previously considered a curious trend based on field observations. The co-occurrence of Fraser's dolphin with other cetaceans is an important feature of its behavior and ecology.

Table 4. Fraser's dolphin co-occurrences. Pantropical spotted dolphin (Sa), short-finned pilot whale (Gm), bottlenose dolphin (Tt), spinner dolphin (Sl), sperm whale (Pm), melon-headed whale (Pe).

Species	Co-occurrence with Fraser's dolphin	Total number of observations
Sa	18	150
Gm	4	24
Tt	3	29
Sl	2	10
Pm	3	66
Pe	3	8

Table 5. χ2 tests results comparing the co-occurrence proportions in species observation. Each column is the result of the comparison of the Fraser's dolphin and the concerned species where shared observations were removed from the observation and co-occurrence count of both species.

Species	χ2	p
Pantropical Spotted Dolphin	26.1	<0.001
Short-finned pilot whale	21.7	<0.001
Bottlenose Dolphin	34.3	<0.001
Sperm Whale	85.3	<0.001
Spinner Dolphin	16.8	<0.001

Table 6. Summary table of the co-occurrence patterns featuring the total amount and co-occuring observations for the most common species, overall co-occurring rate and number of species observed co-occurring with. Short-finned Pilot whale (Gm), Fraser's dolphin (Lh), Humpback whale (Mn), Sperm whale (Pm), Pantropical Spotted dolphin (Sa), Bottlenose dolphin (Tt), Spinner dolphin (Sl).

Species	Co-occurrences	Total observations	%	Nb of different species
Lh	28	37	**76**	6
Sl	6	10	**60**	3
Tt	9	29	**31**	4
Gm	7	24	**29**	3
Sa	36	150	**24**	7
Mn	4	26	**15**	2
Pm	7	66	**11**	3

Upon confirming that Fraser's dolphin was more frequently observed in co-occurrence with other species, we proceeded to assess the strength of these associations. Sorensen's indexes involving Fraser's dolphin generally displayed greater values compared to other pairs (Figure 9). The Kruskal-Wallis test, which compared the means of the co-occurrence indexes involving Fraser's dolphin versus those without, yielded a significant result at the 0.01 error level ($\chi2=8.8$, $p=0.0030$). This indicates that, overall, Sorensen's indexes involving Fraser's dolphin were significantly stronger than those of the pairs involving other cetaceans. Not only does Fraser's dolphin exhibit more frequent co-occurrences, but it also shows a stronger inclination to form associations with each co-occurring species than other cetaceans. Importantly, it should be noted that the Sorensen's index 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.

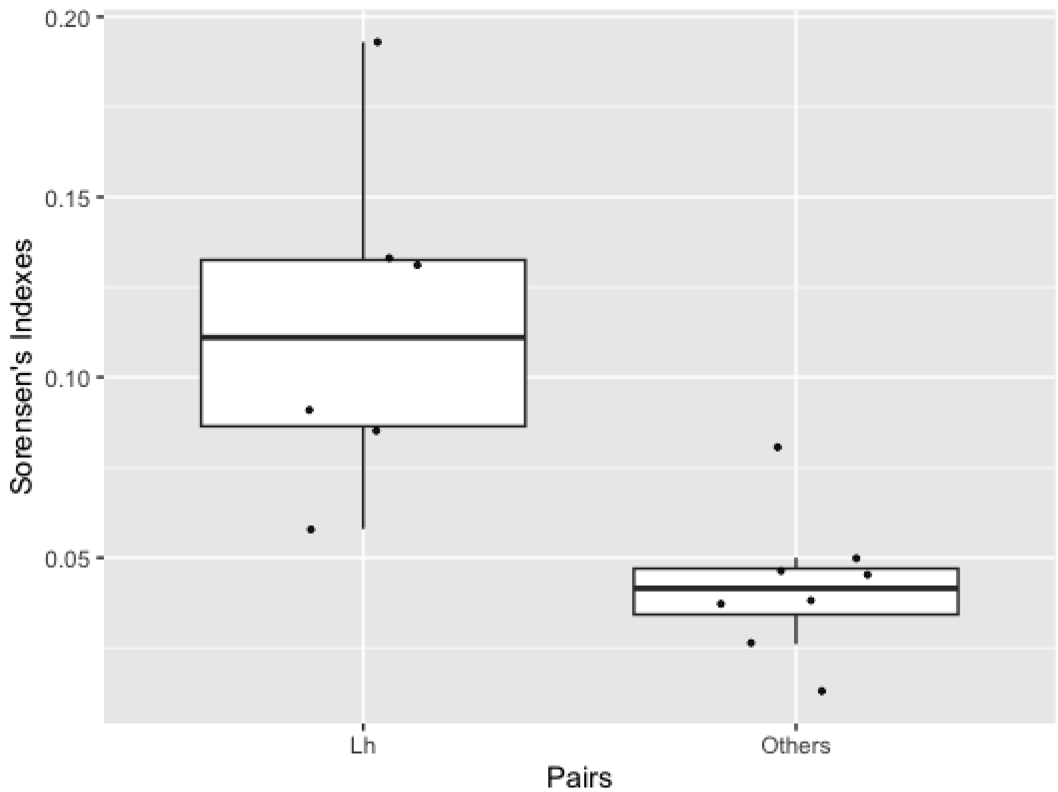


Figure 9. Boxplots representing the Sorensen's indexes for each observed pair of co-occurring cetaceans splitted between pairs involving Fraser's dolphin (Lh) and others.

Discussion

In this study, we successfully identified the key environmental parameters that best explained the distribution pattern of Fraser's dolphin along the Lesser Antilles Arc. Among the selected covariates, chlorophyll *a* concentration, bathymetry, eastward current velocity, sea surface temperature, and distance from the canyon were found to be of greatest importance. Based on the selected Generalized Additive Model (GAM) that accounted for the largest amount of deviation and had the lowest AIC score, we were able to predict the relative habitat suitability in our study area. Our findings indicated that suitable habitats for Fraser's dolphins are present throughout the arc, and their presence was confirmed on the Caribbean side from Grenada to the Sabba bank, during our entire survey period from March to October, thus suggesting the residency of the species that was suspected around Guadeloupe at a wider scale (Rinaldi and Rinaldi, 2011). Moreover, we observed that the region, between Saint Vincent and Guadeloupe, provides a higher coverage of suitable habitat compared to the northern and southern extremities. Despite the limited presence points on the presence/absence data used to fit the model, it effectively predicted the 2023 preliminary Fraser's dolphin presence/absence dataset. This prediction was robust in identifying new observations on the Caribbean side of the arc, regardless of potential temporal environmental variations. In this specific area, 28 out of 37 of our Fraser's dolphin observations occurred within a 5-minute interval preceding or following an observation, or they directly co-occurred with a diversity of six other cetacean species. The analysis of these co-occurrences demonstrated that the strength and frequency of the co-occurrence were inherently higher for Fraser's dolphins than for other species, underscoring the significance of this unique behavior for the Fraser's dolphin. A more complex analysis accounting for species abundance and distribution ranges could inform on the pairing preferences.

Habitat preferences

In our study, we have identified chlorophyll *a* concentration, bathymetry, eastward current velocity, sea surface temperature, and distance from the canyon as the most influential environmental covariates. The majority of Fraser's dolphin sightings occurred at depths ranging between 500m to 2000m. 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 this parameter in Fraser's habitat preference modeling has been previously described in the central Philippines (Dolar *et al.*, 2006). Despite the correlation between Fraser's dolphin distribution and the 2021-2022 mean sea surface temperature pattern, it is unlikely that this species is sensitive enough to significantly restrict its range based on SST. In our study area, this parameter displayed weak spatial variation (less than 1°C). Furthermore, this parameter showed importance for many cetacean species in the central Philippines but not for the Fraser’s dolphin (Dolar *et al*., 2006). While sea surface temperature explains Fraser's distribution at a global scale (Gomes-Pereira *et al.*, 2013), its magnitude at the local and tropical Lesser Antilles Scale is too weak to justify a potential dependency pattern. Canyons represent rich marine habitats that concentrate a high abundance of cetacean species, including Fraser's dolphin, 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). However, not all canyons attract cetaceans (Moors-Murphy, 2014). Moreover, our habitat suitability prediction (Figure 7) shows some odd isolated, round-shaped suitability predictions on the Southern Atlantic side of the area due to the local presence of canyons. These discontinuities raise questions about the relevance of using distance from geometrical features such as canyons to produce habitat suitability predictions, as they may generate aberrations. It may be more valuable to use the euclidean distance to the canyon axes (Tepsich *et al.*, 2014), rather than using the distance to the entire canyon area. This is expected to provide more rationale and fin scale results that could reduce the magnitude of this issue, especially because wide canyon features are used in our study, often extending on more than 50 km (Figure 1). Eastward current velocity is another influential factor in explaining Fraser's dolphin distribution pattern. With strong currents flowing from East to West, entering the channels separating each island, this velocity pattern naturally reflects and is a proxy of differences in cetacean presence that could be observed between the channels and along the insular Caribbean coasts. Finally, chlorophyll *a* concentration as a proxy of primary sea productivity usually well describes the presence of cetaceans (Davis *et al*., 2002). Most covariates in SDM models are typically used as proxies for prey abundance due to the complexity of obtaining such datasets. However, recent attempts to include simulated micronekton biomass datasets have successfully been used to explain several cetacean distributions (Lambert *et al.*, 2014). The inclusion of such a covariate could potentially enhance the accuracy and explained deviance of the habitat preference model and the habitat suitability prediction, representing a perspective for method improvement.

Fraser's dolphin 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 (Figure 3 & 5). Sightings have been recorded on the coasts of most of the main islands, including Grenada, Saint Vincent, Saint Lucia, Dominica, Guadeloupe, Montserrat, and up until the Saba bank. The Caribbean side represents a continuous stretch of suitable habitat where Fraser's dolphins have been observed during every month of the survey period, ranging from March to November. 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 observed mean and upper group sizes, 90 and 300 individuals respectively, were much larger than those reported in the aforementioned study, which recorded mean and upper group sizes of 30 and 50 individuals respectively. It is uncertain whether 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 dynamics.

Overall, our results highlight the importance of studying the dynamics and social structure of Fraser's dolphins to better understand their use of the area and address questions about residency. This population could potentially represent a coastal ecotype that differs from offshore ecotypes. Such habitat, genetic, and morphological differences between ecotypes have been observed and documented in other dolphin species, especially in the bottlenose dolphin (Segura *et al.*, 2006). The presence of a Fraser's dolphin coastal ecotype would be supported by our presence results and the observed differences in distribution of Fraser's dolphins around the world between offshore and insular populations (Dolar, 2009; Kizka *et al.*, 2011; Gomes-Pereira *et al.,* 2013).

Now that we know that the entire Caribbean side of the Lesser Antilles is utilized by Fraser's dolphins, conducting a long-term analysis on photo-identification recaptures could provide essential insights into their dynamics between the islands. This technique allows for tracking dolphin movements by recognizing individuals based on unique marks on their dorsal fin (Urian *et al.* 1999). Preliminary results from the Photo-ID analysis collected during the 'Ti Whale An Nou' program suggest a high mobility of the species between islands, with recaptures observed between South Martinique and Guadeloupe, as well as between Saint Vincent and Saint Lucia (Appendex). Understanding these movements in detail will be crucial for describing the Lesser Antilles population. Long term Photo-ID studies would also allow to perform abundance estimates analysis (Rosel *et al.*, 2011) .

Fraser's dolphin presence throughout the Lesser Antilles also allows for a better understanding of the threats they may face. Evidence of chlordecone bioaccumulation near Guadeloupe, a pesticide used until 1993 in the French West Indies, has recently been recorded in the blubber of stranded individuals (Méndez-Fernandez *et al.*, 2018), highlighting the threat that chemical compounds represent to marine top predators. While the direct effect of pollutants on cetacean mortality is yet to be determined, hunting in St. Vincent and the Grenadines also targets Fraser's dolphins when no backfish are sighted. Although hunting is mainly focused on the short-finned pilot whale, between 100 and 700 "small cetaceans," including Fraser's, spinner, and pantropical spotted dolphins, are killed every year in unknown proportions (Fielding and Kiszka, 2021). The uncertain number of Fraser's dolphin hunts and the absence of abundance estimates make it challenging to measure the impact of hunting, and further investigation in cooperation with the hunters could provide crucial information for conservation efforts. Lastly, a preliminary scar analysis on the Fraser's dolphin allowed us to identify several individuals showcasing major mutilations on the dorsal fin that are likely to have been caused by anthropic activities such collision with boats, propellers or interaction with fisheries (nets). A future more detailed analysis will allow us to understand Fraser's dolphin exposure to anthropic pressure.

SDM limitations and validity

It has previously been raised that the SDM are limited by multiple factors and it is therefore important to discuss its validity. In terms of the surveyed range of environmental conditions as previously mentioned, the bell-shaped smooth terms (Figure 6) indicates that the model was successful in encapsulating the range of environmental covariates favored by the Fraser's dolphin, which consequently reduces the error for habitat suitability predictions. This has been facilitated by the large scale data collection programmes along the entire Lesser Antilles arc.

Our models were characterized by an overall low explanatory power, around 20% (Table 1). Many SDMs describing dolphin species feature similar, if not lower, explanatory power (Becker *et al.*, 2019; 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.

Finally, predictions must be carefully considered on the Atlantic side of the Lesser Antilles. Both model training and performance evaluation have been conducted on an area mostly restricted to the Caribbean side of the arc. Despite the fact that we have surveyed and recorded data on a wide enough environmental range, there is no guarantee that the hypothetical Fraser's dolphins present on the Atlantic side would share the same habitat preferences as those on the Caribbean side, as the Lesser Antilles arc represents both a physical and environmental boundary. To incorporate a larger number of Fraser’s dolphin observation points that could have opportunistically been obtained on each side of the arc, performant presence-only models such as MAXENT (Putra and Mustika, 2021) could be performed and offer a comparison in terms of prediction and allow a better description of the Fraser’s dolphin observations in the entire area.

Co-occurrences

Our results have demonstrated that Fraser’s dolphin was significantly more likely to co-occur with other species, and the observed associations were stronger compared to other cetaceans. This suggests that the co-occurrences involving Fraser's dolphin are not coincidental opportunistic. This results correlates with past co-occurrence descriptions in the Philippines where the Fraser’s dolphin is species most often observed in co-occurrence (Dolar, 2006).

Co-occurrences were observed with the Sperm whale, the bottlenose dolphin, the pantropical spotted dolphin, the melon-headed whale, the short-finned pilot whale, as well as the spinner dolphin (Table 4). However, it is important to note that although these species were observed at the same time or within a 5-minute time lag, detailed behavioral descriptions and distances were not always recorded. As a result, it is challenging to distinguish and classify the interspecific co-occurrences, which would be essential for gaining insights into the motivations behind these associations (mutualism, commensalism, parasitism). It can be imagined that the behavior of Fraser's dolphin towards Sperm whales differs from its behavior towards other dolphin species.

In a previous study analyzing associations between cetaceans in the central Philippines (Dolar, 2006), Fraser's dolphin was observed to be associated with other species 84% of the time, involving a total of seven other species out of 44 observations. Off La Réunion island, every sighting of Fraser's dolphin co-occurred with melon-headed whales (Dulau-Drouot *et al*., 2008). This consistency of Fraser's dolphin being associated with a wide variety of cetacean species around the world indicates that this behavior is advantageous for the species. Mixed-cetacean groups are usually attributed to foraging activities or predator avoidance (Stensland *et al*., 2003). While few instances of predation risk have been identified in the Lesser Antilles, we hypothesize that feeding is the main purpose for Fraser's dolphin associations, which aligns with the behavioral notes recorded during data collection.

The 'Ti Whale An Nou' research program has only consistently recorded observation's behavior notes starting from 2023. Compiling previous rare notes and the 2023 behavior notes, there has been evidence of Fraser's dolphin surface feeding behavior in association with the pantropical spotted dolphin. A similar foraging behavior has previously been observed off Dominica (Watkins *et al*., 1994). Enlightened by those observations, we hypothesize that Fraser's dolphins derive benefits from other species in its foraging activities, a unique feeding strategy among cetacean species in the region.

Usually, co-occurrences involving the Fraser's dolphin were not mixed; groups tended to stay close to each other but remained packed by species. However, a few individuals were often found swimming among other species. These individuals could potentially act as sentinels to identify if food has been found by the other species or for social purposes. Surface feeding behavior has been observed multiple times in co-occurrence with the Pantropical Spotted Dolphin. It is known that although the Pantropical Spotted Dolphin mainly forages on mesopelagic prey, epipelagic prey is also part of its diet (Wang *et al.* 2003). However, this dietary versatility is less known for the Fraser's dolphin, even though some descriptions have suggested a diet broader than specifically directed toward mesopelagic prey (Watkins *et al*., 1994; Moreno *et al.*, 2003; Dolar *et al*. 2003). This observed versatility in diet correlates with its predominant association strategy with a wide range of cetacean species.

Co-occurrence analysis allows us to formulate hypotheses about Fraser's dolphin ecology, but it is also important to understand as this dependency could influence and explain its distribution in the Lesser Antilles. The complexity of Fraser's co-occurrence behavior highlights the importance of interspecific interaction research for a wider understanding of cetacean ecology on diverse cetacean communities. However, further studies using a more standardized behavioral data collection protocol are required to strengthen the descriptions and conclusions. Future research opportunities would include genetic analyses to investigate the possible existence of a coastal ecotype in the Lesser Antilles. Results on movements along the Lesser Antilles will also help to characterize this population dynamic and on a potential spatial residency. Finally an injuries analysis would help to measure the anthropic pressure that the Fraser’s dolphin faces in the Lesser Antilles which would be crucial for conservation purposes.

Conclusion

Fraser’s dolphin presence and habitat suitability have been confirmed all along the Lesser Antilles arc, representing an habitat of great importance on Earth where Fraser’s dolphin is frequently observed and offering an opportunity to learn more about this poorly studied species. In this area, its distribution is correlated with the spatial variation patterns of several environmental covariates such as chlorophyll *a* concentration, short distance from the canyon, depth, sea surface temperature, and eastward current velocity. Despite the high performance of the used SDM in predicting new observations in the surveyed area, the explained deviance, similar to other dolphin distribution models, remained low. These results should encourage further studies to include parameters that more directly explain cetacean distribution. In the case of the Fraser’s dolphin, we have demonstrated the importance of interspecific associations, which we hypothesize to be a significant part of Fraser’s dolphin feeding strategy in the Lesser Antilles. This finding not only suggests that this species features a more versatile diet and foraging behavior than previously thought but also highlights how behavior could affect species distribution and habitat use. If Fraser’s dolphin finds interest in remaining closeby other cetaceans then its habitat preferences may be influenced by those of the associated species. Due to the significance of the co-occurring behavior, we propose that the Fraser’s dolphin is a key species for enhancing the empirical knowledge on complex interspecific interactions that dolphin species may develop in rich cetacean communities. For conservation purposes, it will be crucial to study the social structure, dynamics, movements and abundance of this species to inform its conservation status and better identify the threats it may face.

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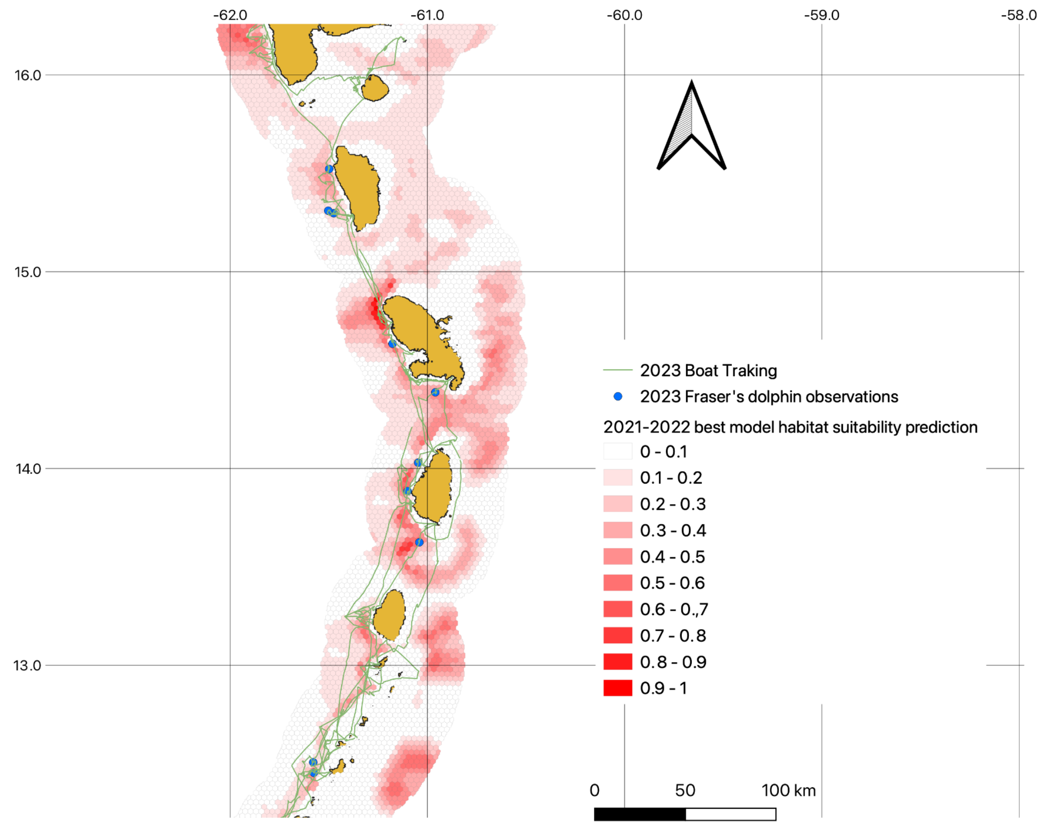
Appendix

Variable	Description	Resolution	Source	URL
Bathy	Depth	15"	GEBCO	https://www.gebco.net
Canyon map	Cartography of the canyons in the Lesser Antilles area		Blue Habitats	www.bluehabitats.org
SST (°C)	Sea Surface Temperature	0.05° × 0.05°, daily	Copernicus Global SST and Sea Ice Analysis	https://marine.copernicus.eu
CHLa (mg/m³)	Chlorohphylle A concentration	0.25° x 0.25° daily	Copernicus Global Ocean Biogeochemistry Analysis and Forecast	https://marine.copernicus.eu
SSH (m)	Sea Surface High	0.083°x0.083° daily	Copernicus Global Ocean Physics Analysis and Forecast	https://marine.copernicus.eu
BT (°C)	Bottom Temperature	0.083°x0.083° daily	Copernicus Global Ocean Physics Analysis and Forecast	https://marine.copernicus.eu
MLD	Mixed Layer Depth	0.083°x0.083° daily	Copernicus Global Ocean Physics Analysis and Forecast	https://marine.copernicus.eu
UO (m/s)	Eastward surface current velocity	0.083°x0.083° daily	Copernicus Global Ocean Physics Analysis and Forecast	https://marine.copernicus.eu
VO (m/s)	Northward surface current velocity	0.083°x0.083° daily	Copernicus Global Ocean Physics Analysis and Forecast	https://marine.copernicus.eu

Annex 1. Primary Environmental covariate table featuring resolution, Source and URL.

1st Encounter	2nd Encounter	1st Encounter	2nd Encounter
		South Martinique	Guadeloupe
		South Martinique	Guadeloupe
		Saint Lucia	St Vincent

Annex 2. Preliminary Photo ID rematch obtained from the catalogue of 'Ti Whale An Nou' 2021-2022.



Annex 3. Preliminary 2023 Fraser's dolphin observations and 2021-2022 best GAM model habitat suitability prediction.