CHAPTER ONE

Habitat suitability, occurrence, and behavior of dwarf sperm whales (*Kogia sima*) off St. Vincent and the Grenadines, Eastern Caribbean

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Contents

Abstract

The genus *Kogia* includes two species that are some of the least known cetacean species around the globe. Here, we investigated the occurrence, behavior, and habitat suitability of dwarf sperm whales (*K. sima*) off St. Vincent and the Grenadines (Eastern Caribbean). Small boat dedicated surveys were conducted during May and June of both 2022 and 2023 along the south and west coast of the island of St. Vincent. A total of 2260 km was surveyed and 33 sightings of dwarf sperm whale were recorded, which was also the most frequently sighted cetacean species (37.5% of all cetacean sightings). Group size varied from 1 to 20 individuals (mean = 2.08, SD = 3.23). Traveling and breaching were the most commonly recorded behavioral categories and occurred at an equal proportion (28.6%). The distribution of dwarf sperm whales was restricted to the south and southwest portion of St. Vincent in depths ranging from 95 to 1104 m (mean = 650 m).

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Habitat suitability (in relation to depth and slope) was investigated using an ensemble model using three algorithms (GLM, GAM, and MaxEnt). The model revealed that slope, and to a lesser extent depth, were important in explaining the habitat suitability of dwarf sperm whales. This preliminary research highlights the existence of a globally important area for dwarf sperm whales off St. Vincent, where encounter rates are significantly higher than in any other known island-associated habitat.

1. Introduction

Odontocetes of the genus *Kogia* include two currently recognized species: pygmy (*K. breviceps*) and dwarf sperm whales (*K. sima*), both among the least known cetacean species globally. Although the distribution of both species overlaps in tropical and subtropical regions, *K. breviceps* tends to be more common in temperate waters, whereas *K. sima* almost exclusively occurs in tropical and subtropical regions (McAlpine, 2018; Kiszka & Braulik, 2020, 2022). Dwarf sperm whales occurring in the Atlantic might constitute a third species, separated from those occurring in the Indo-Pacific region, although further evidence is required before this can be confirmed (Chivers et al., 2005; Kiszka & Braulik, 2020, 2022; Plön et al., 2023). Both species of *Kogia* are globally distributed in deep oceanic waters, particularly over shelf break and abyssal plains, where they forage on vertically migrating oceanic cephalopods (Spitz et al., 2011; Staudinger et al., 2014; Moura et al., 2016). The rarity of live sightings of both species suggest that population densities are low throughout their range (e.g., Garrison et al., 2010; Barlow, 2015). The inconspicuous behavior of dwarf and pygmy sperm whales probably contributes to the rarity of live reports (McAlpine, 2018; Plön et al., 2022; Plön & Baird, 2022). However, stranding records and passive acoustic monitoring indicate that cetaceans of the genus *Kogia* may be common in some regions, such as along the east coast of South Africa (Plön, 2004), or off the southeastern United States, where *K. breviceps* is the second most frequently stranded cetacean after the common bottlenose dolphin (*Tursiops truncatus*; Odell, 1991), and *Kogia* are frequently detected acoustically (Hodge et al., 2018), but rarely seen (Garrison et al., 2010). Because both species of *Kogia* are so cryptic and rarely observed at sea, and due to the difficulty of distinguishing *K. breviceps* from *K. sima*, there are very few abundance estimates available for either species (Palka, 2012; Garrison, 2016; Laran et al., 2017). Although both species are listed as Least Concern on the IUCN Red List of Threatened Species (Kiszka & Braulik, 2020, 2022), several threats have been identified, including noise pollution (Yong et al., 2008), whaling

(Caldwell et al., 1973; Ilangakoon, 2012; Fielding & Kiszka, 2021), harmful algal blooms (Fire et al., 2009), and fisheries interactions (Baird et al., 2021), including bycatch in offshore drift gillnets (Kiszka et al., 2021a). However, the magnitude of all these threats is poorly known.

Dwarf sperm whales have been found to regularly occur in some regions, particularly in slope and deep waters around oceanic islands, such as Abaco, Bahamas (MacLeod et al., 2004; Dunphy-Daly et al., 2008), Mayotte, the Maldives and the Seychelles in the western tropical Indian Ocean (Kiszka et al., 2010; Laran et al., 2017), and Hawai'i (Baird et al., 2013, 2021). The presence of island-associated populations has allowed researchers to unravel some aspects of the ecology and behavior of dwarf sperm whales, including their habitat preferences (particularly in relation to physiography), group dynamics (size, composition), site fidelity, and social structure (Dunphy-Daly et al., 2008; Baird et al., 2021). The existence of island-associated populations also gives an opportunity to further explore the role of environmental variables on the distribution and abundance of dwarf sperm whales, and therefore predict how this species might respond to climate change (van Weelden et al., 2021; Lettrich et al., 2023). Although describing and predicting how cetaceans are distributed is critical to support management efforts, there have been limited efforts to assess the influence of environmental predictors on the spatiotemporal distribution of many deep diving cetaceans, particularly beaked (Ziphiidae) and *Kogia* whales. The main limitation in published studies is sample size, which is usually small for such species occurring at low densities and that are challenging to detect at sea (e.g., Rogan et al., 2017; Virgili et al., 2021). However, some species distribution models have relatively strong predictive capabilities, even with small sample sizes (Phillips et al., 2006; Phillips & Dudík, 2008), and are used to predict suitable habitats based on the characteristics of the environment (e.g., Redfern et al., 2006; Fiedler et al., 2023). Physiography (depth and slope) has been successfully used to predict the distribution of cetaceans, particularly deep-diving whales (e.g., Cañadas et al., 2002; Rogan et al., 2017; Virgili et al., 2021). Here, we employed three commonly used algorithms (Generalized Linear Models, General Additive Models, and MaxEnt) to create an ensemble model to understand the influence of depth and slope on the distribution of dwarf sperm whales around St. Vincent and the Grenadines (SVG), in the Eastern Caribbean. We also document the encounter rates, group dynamics (size, composition), and some aspects of the behavior of this species during multi-species cetacean survey data conducted in May and June of both 2022 and 2023.

2. Materials and methods

2.1 Data collection

Field surveys took place in SVG, a small archipelagic nation located in the eastern Caribbean region (Fig. 1). The main island of St. Vincent is of volcanic origin and is surrounded by a steep insular slope; the waters are oligotrophic, highly stratified, and mostly influenced by the North Equatorial current. Small boat (2 boats, 8–9 m) surveys were carried out off the south and west coast of St. Vincent in May and June of both 2022 and 2023 from 8:00 to17:00 at a speed of 7–10 knots, with the initial objective of assessing the spatial distribution, encounter rates, and habitat characteristics of cetaceans. Transect location and surveys were randomly designed but could be adapted if sea conditions and wind changed (Fig. 1). At least three observers (excluding the pilot) conducted the surveys with the naked eye. Sea state was collected using the Beaufort scale throughout the day, particularly when changes occurred. Survey effort was interrupted if sea state was B > 4. Survey effort was quantified both spatially and in time using a handheld Global Positioning System. For each sighting, cetaceans were identified to species level, group size was estimated (minimum, maximum, and best estimate), the time (hh:mm:ss) and

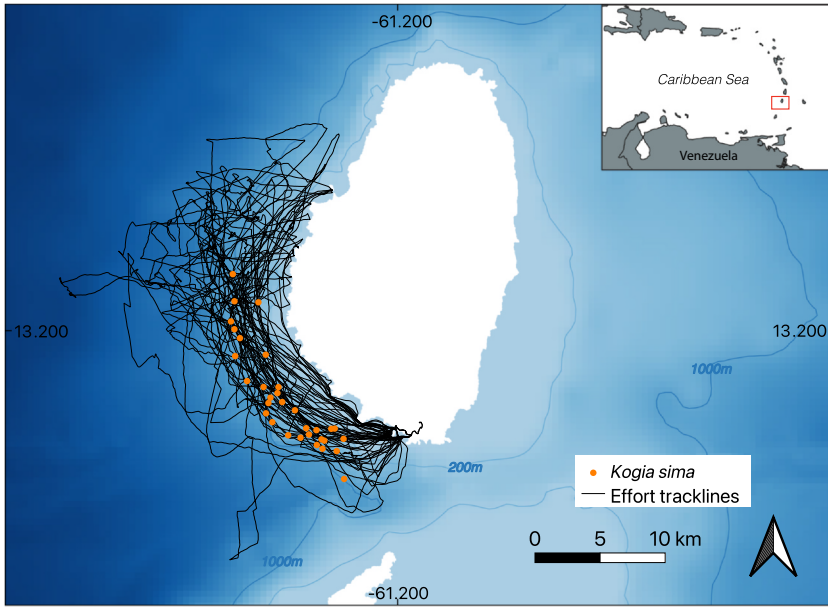

Fig. 1 Spatial distribution of *Kogia sima* sightings (dots) and survey effort (lines) off the island of St. Vincent in May-June 2022 and 2023.

geographic position were recorded. A sighting refers to both single individuals and groups, which are defined as two or more individuals and engaged in a similar behavioral activity in small cetaceans, particularly delphinids (Syme et al., 2022). As dwarf sperm whales can be widely spaced (up to about 200 m; Baird et al., 2021), individuals were considered as a group if they were within 300 m, exhibited the same behavior, orientation, and speed. The initial behavior of cetaceans encountered was also recorded and included traveling, socializing, foraging, milling, and resting. For dwarf sperm whales, only three behavioral categories were identified: traveling, milling, and resting. Resting was characterized by logging at the surface, motionless. Traveling was characterized by consistent (at least 3 successive individual/group surfacing) directional movements, whereas milling consisted in non-directional movements, with frequent changes in heading. When breaching, individuals usually exposing their full body, except the fluke. Breaching was not considered as a behavioral category per se but was categorized as such when no behavioral activity could be assigned to the group or individual observed. Group composition was recorded based on the estimated relative body length of individuals encountered and consisted of three main categories: mature adult, juvenile, and calf. If a group or individual was lost, the reason for ending the encounter was documented (sampling completed, individual/group lost).

The use of natural markings on the dorsal fin and adjacent areas of the dorsal region has previously been used to identify individual dwarf sperm whales in other regions, particularly off the island of Hawai'i (Baird et al., 2021). Photographs were also opportunistically collected using a DSLR camera (Canon 7D Mark II, 100–400 mm lens) during several encounters. This allowed us to investigate the potential use of this methodology to examine site fidelity, association patterns, and demographic parameters of this population. Photos were taken of the encounter of 20 animals and one is included as a Supplementary Figure. In addition, photographs were also used to collect information on skin condition, scaring patterns, and potential health status of individuals encountered (Van Bressem et al., 2015; Kiszka et al., 2008; Van Bressem et al., 2009, 2015). When potential lesions were identified, photographs were submitted to two independent experts (veterinarians with expertise in cetacean pathologies) for identification.

2.2 Data analysis

The influence of sea state (in Beaufort) on encounter rates of dwarf sperm whales was assessed using a one-way ANOVA. Depth and slope were the

environmental variables used to assess the habitat suitability of dwarf sperm whales in SVG (see supplementary, Fig. 1), as they usually best explain the distribution of deep diving odontocetes (Cañadas et al., 2002; Rogan et al., 2017; Virgili et al., 2021). Depth was obtained from the General Bathymetric Chart of the Oceans; slope was calculated using the depth layer through the surface parameters tool in ArcGIS Pro 3.2.1. The resolution of each layer was 0.5 km. Habitat suitability modeling was performed in the R environment (R 4.3.2, RStudio 2023.12.0), using the biomod2 package (Thuiller et al., 2023). Occurrence data were filtered using the spThin package (Aiello-Lammens et al., 2015) to remove spatial autocorrelation, and 10 sets of pseudo-absences were generated using the random strategy (Guisan et al., 2017). Three algorithms were used, including presence-absence Generalized Linear Models (GLMs), Generalized Additive Models (GAMs), and the Maximum Entropy (MaxEnt), a presence-background machine learning algorithm. For model calibration, a 10 km buffer around SVG was created using the pairwise buffer tool in ArcGIS Pro 3.2.1, which was based on previous studies on the depth preferences of dwarf sperm whales around other oceanic islands: Abaco, Bahamas (400–1600 m; Dunphy-Daly et al., 2008) and Hawai'i (500–1500 m; Baird, 2005; Baird et al., 2013). Then, we divided 70% of the occurrence data for training and 30% for testing using *k*-fold cross-validation with $k = 5$, repeating each set of analyses 10 times. We used the Area Under the Curve (AUC) of the Receiver Operating Characteristic to evaluate each model, considering those with an evaluation greater than or equal to 0.7 for the ensemble model. The ensemble model was created from the weighted mean of the selected individual models, in which models with better performances had a greater weight. The relative importance of each variable (depth, slope) was obtained by assessing the model predictions' sensitivity to each of them, by shuffling one variable at a time, and calculating the correlation between the reference predictions and the predictions with the shuffled data. The variable importance score is represented by 1 minus the correlation, indicating that the higher the value, the greater the variable's influence on the model (Guisan et al., 2017). Following a standard protocol (Zurell et al., 2020), we present the committee average map as a measure to assess model uncertainty (Supplementary, Fig. 2). The committee average consists of the binary frequency of individual models, that is extreme values (0 and 100) mean that all individual models identified the area as unsuitable or suitable, respectively. Intermediate values (close to 50) indicate that some models identified the area as unsuitable, while others considered it suitable, that is there was no consensus, and the results for that area are uncertain.

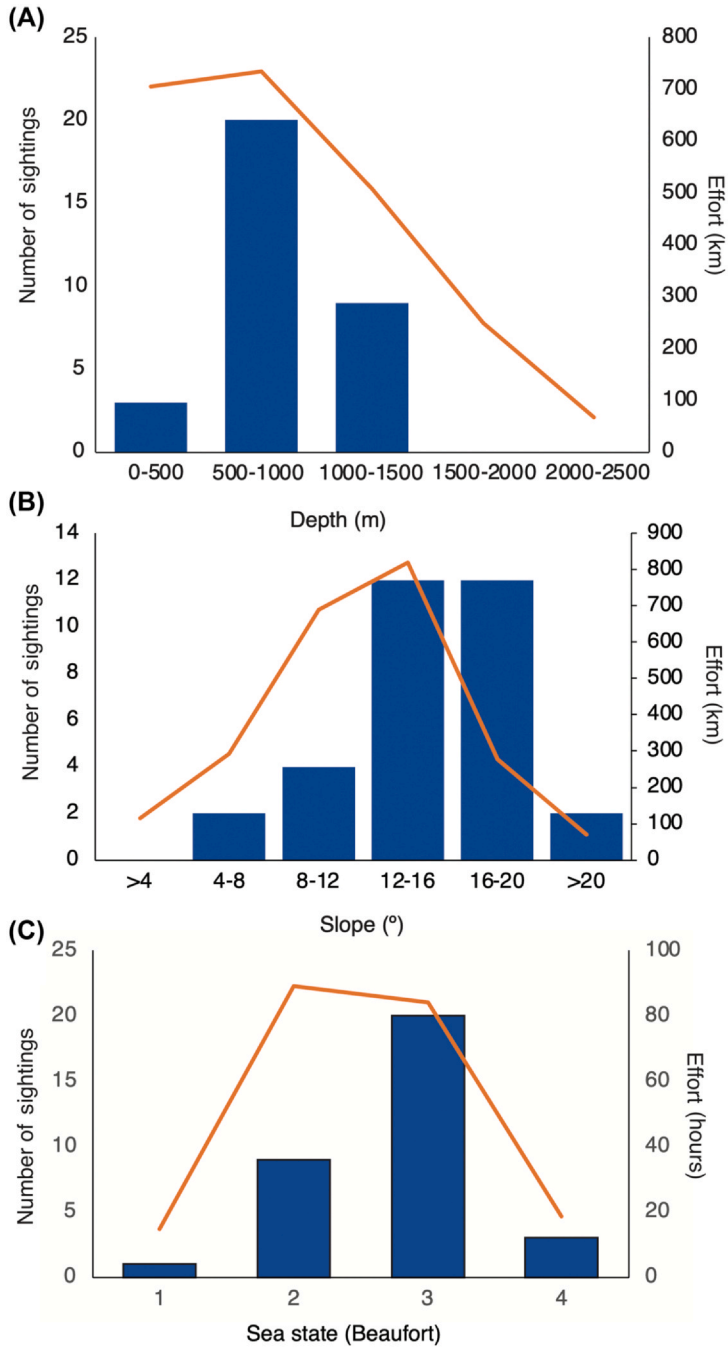

Fig. 2 Relationship between (A) effort (orange line, in km) and the number of sightings of *K. sima* (blue bars) across each depth ranges, (B) slope ranges, and (C) sea states (in Beaufort scale) off the island of St. Vincent in May-June 2022 and 2023.

3. Results

3.1 Occurrence and behavior

The waters off the south and west coasts of St. Vincent were surveyed for 206 h over 33 day and a cumulative distance of 2260 km (Fig. 1). A total of 33 sightings of dwarf sperm whales were recorded, out of a total of 88 cetacean encounters (37.5% of all cetacean sightings) throughout the study period. Group size ranged from 1 to 20 individuals (mean = 2.08; SD = 3.23), although 66.6% of encounters involved single individuals. A large group of at least 20 individuals, primarily made up of adults and a possible mother-calf pair, was observed traveling on May 15th, 2023 (see supplementary material). This group was observed in a tight group formation in the vicinity (100–150 m) of a group of 200–250 Clymene dolphins (*Stenella clymene*). The group was forming a narrow line and was lost 6 min after being found and exhibited an evasive behavior towards the research vessel. Overall, the duration of encounters was short and ranged from less than a minute, typically when the animal(s) was sighted and dive shortly after being detected, to 36 min (median = 6.1 min).

Traveling and breaching were the behavioral categories recorded at an equal proportion (28.6%). In one instance, a traveling group of 3 dwarf sperm whales was also observed breaching on two occasions (involving two individuals). Milling was observed for 11.4% of groups, while resting was observed for 2.8% of them (one sighting). For the remaining sightings, no behavioral activity was assigned, mostly due to the brevity of encounters. A total of three sightings included confirmed mother-calf pairs (9.1% of all sightings). Dwarf sperm whales were encountered at mean depth of 650 m (range = 95–1104; SD = 271; Fig. 2A), and over slopes of 12–20° (72.7%, Fig. 2B). The number of sightings per survey day varied from 0 to 4 (mean = 1.06, mode = 1, SD = 0.93), and encounter rates were not influenced by sea state ($F = 1.40$; $P = 0.251$). Most sightings occurred when Beaufort = 3 (Fig. 2C). When Beaufort was either 2 or 3, the majority (87%) of detections of dwarf sperm whales were when animals breached (estimated distance from boat from 30–400 m).

3.2 Habitat suitability

Spatial filtering retained 23 out of 33 total occurrences of the dwarf sperm whale (see supplementary, Fig. 3). After evaluating the performance of individual models, 1451 out of 1500 achieved AUC values ≥0.7 and formed the ensemble model (Fig. 3).

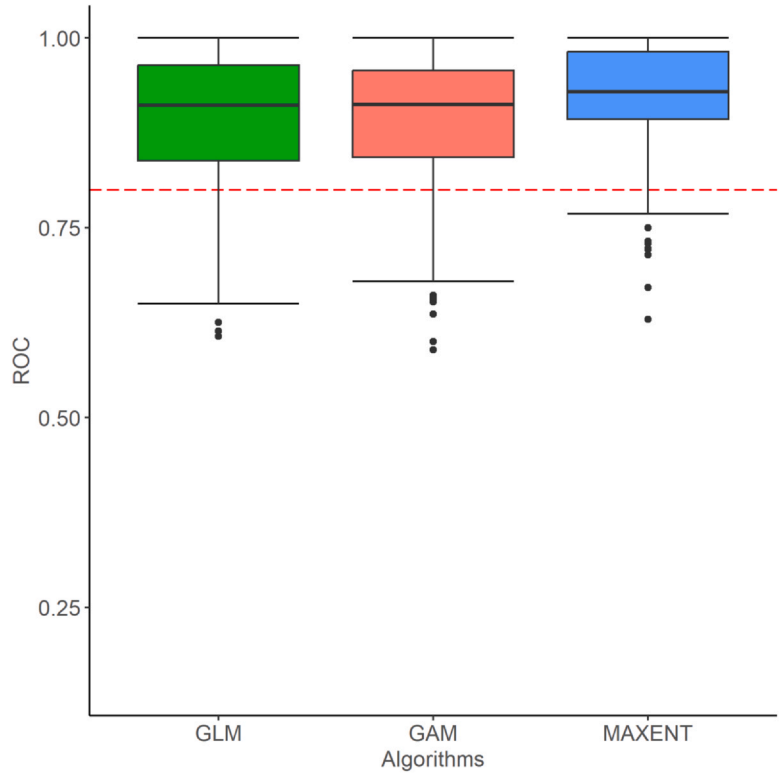

Fig. 3 Performance of individual habitat suitability models of *K. sima* off the island of St. Vincent. *ROC*, Receiver Operating Characteristic; *GLM*, Generalized Linear Models; *GAM*, Generalized Additive Models; *MAXENT*, Maximum Entropy.

Slope, and to a lesser extent depth, were important variables in explaining the ensemble model (slope: mean = 0.604, SD = 0.015; depth: mean = 0.377, SD = 0.028; Fig. 4). The most suitable habitats for dwarf sperm whales were located between depths ranging from 700 to 1300 m, and on steep slopes of 20–30° (Fig. 5), located along the leeward coast of SVG, particularly along the southwest coast of the main island of St. Vincent, and along the western slope off the island of Bequia, south of the main island (Fig. 6). Although sightings were not recorded off the west-north-west area off St. Vincent, the model identified it as suitable.

3.3 Photo-identification

Opportunistic photo-identification was conducted during seven sightings with dwarf sperm whales, as observed individuals would surface on

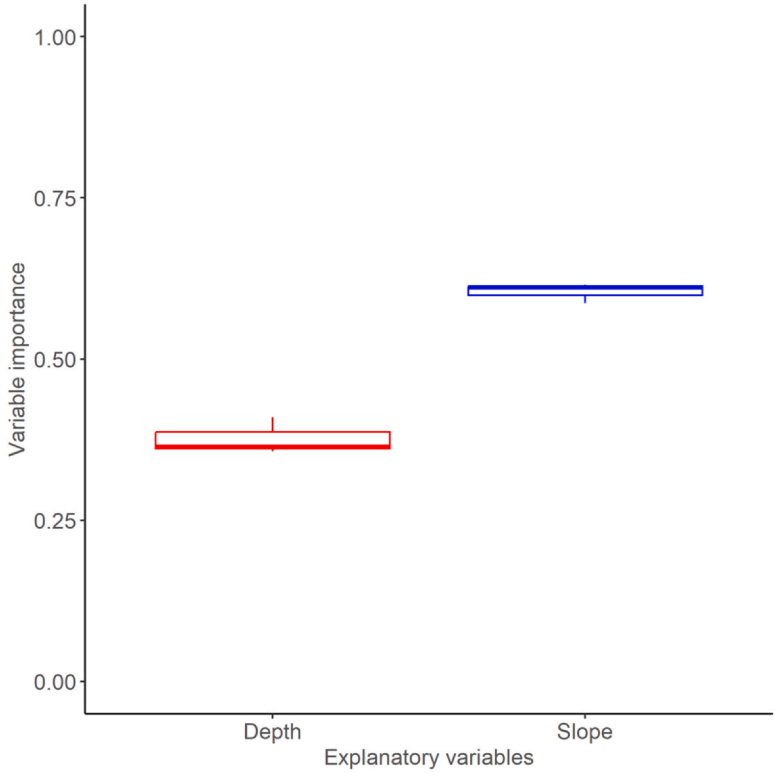

Fig. 4 Importance of explanatory variables contributing to habitat suitability models of *K. sima* off the island of St. Vincent.

multiple occasions within approximately 200 m of the research vessel (Fig. 7). With no categorizing of photograph quality and distinctiveness, a total of 22 individuals were identified, including two adult females accompanied with calves (Fig. 7B). Most photographed individuals showed distinctive patterns on their dorsal fins, including deep notches and scars on the trailing edge (Figs. 7A, 7C and 7D). No resighting of any identified individual was recorded. A total of three identified individuals ($n = 14$ photographs) exhibited skin lesions. An adult female accompanied by a calf exhibited multiple subcutaneous masses, and relative emaciation (Fig. 7A), and two other individuals exhibited dark circular lesions in the dorsal region halfway between the blowhole and the dorsal fin (Fig. 7C, individual in the foreground). One individual exhibited possible entanglement with a fishing line (Fig. 7C, individual in the background).

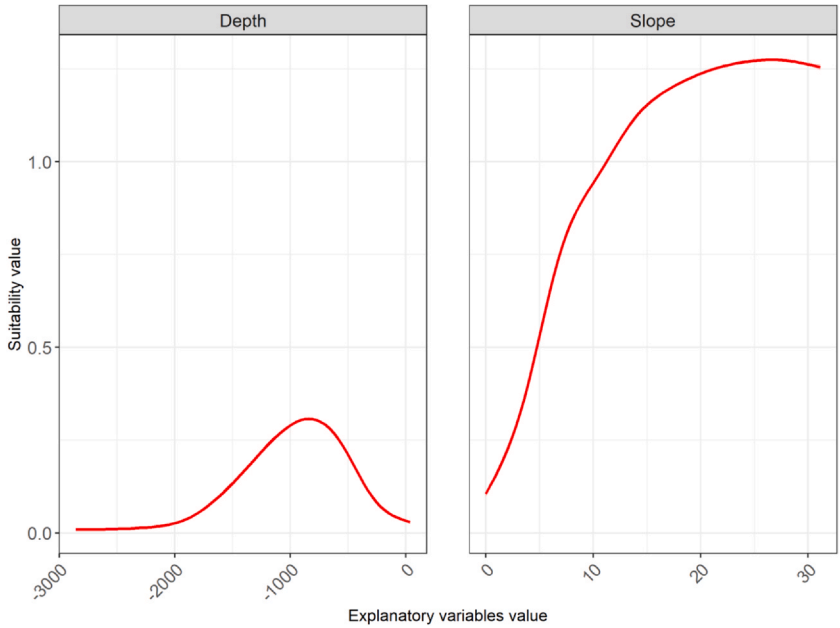

Fig. 5 Response curves of explanatory variables contributing to habitat suitability models for *K. sima* off the island of St. Vincent.

4. Discussion

This preliminary study reveals that the insular slope waters of the island of St. Vincent are an important habitat for dwarf sperm whales within the wider Caribbean region, where limited information exists on their occurrence, distribution, and habitat preferences (Cardona-Maldonado & Mignucci-Giannoni, 1999; Mutis & Polanco, 2019; De Weerdt et al., 2021). Similar studies conducted in peri-insular tropical and subtropical waters are relatively limited globally (e.g., Gannier, 2000; Anderson, 2005; Dunphy-Daly et al., 2008; Dulau-Drouot et al., 2008; Kiszka et al., 2010; Baird et al., 2013, 2021). Although survey design and conditions vary significantly between these regions, those studies suggest that encounter rates of dwarf sperm whales off St. Vincent are substantially higher than anywhere else yet identified. Indeed, encounter rates off St. Vincent are almost 20 times higher than off the big island of Hawai'i (Baird et al., 2021) and about four times higher than off Abaco in the Bahamas (MacLeod et al., 2004). Our results also suggest that the cetacean community of St. Vincent has a unique composition as 37.5% of all

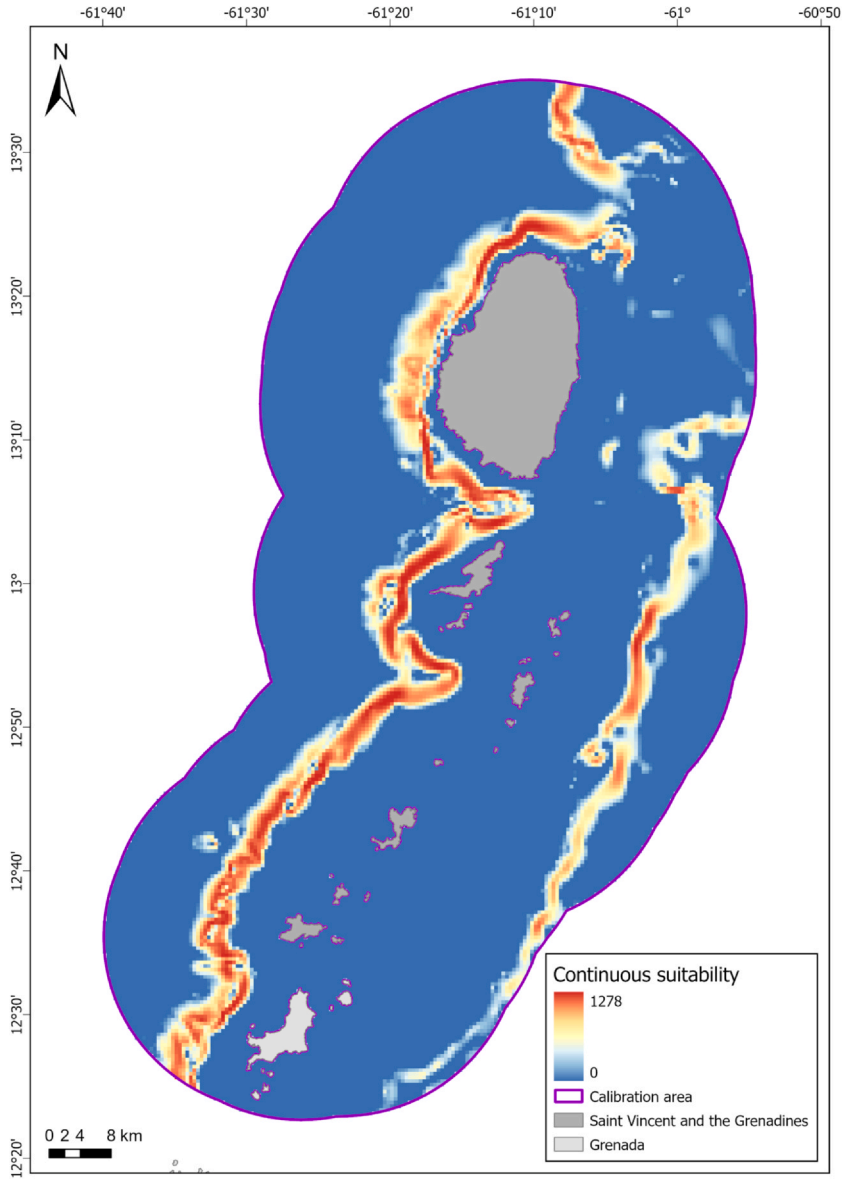

Fig. 6 Suitable habitats for *K. sima* off St. Vincent and the Grenadines using the ensemble model.

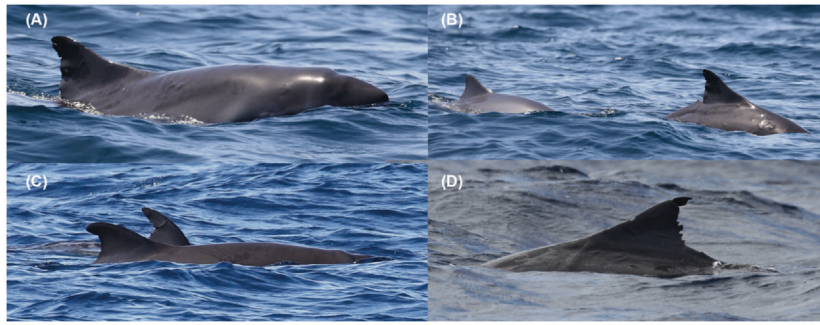

Fig. 7 Photographs of *K. sima* in the waters off the island of St. Vincent (May-June 2022 and 2023, credit: J. Kiszka, Florida International University). (A) adult female observed in June 2023 and exhibiting relative emaciation and multiple subcutaneous masses; (B) adult female with her calf (same individual as top left picture); (C) two adult dwarf sperm whales surfacing together (the individual on the foreground exhibits dark skin lesions, halfway between the blowhole and the dorsal fin, and the individual in the background exhibiting a linear scar on the dorsal fin, possible due to fishing line entanglement), (D) an adult dwarf sperm whale identified in May 2022.

cetacean sightings were dwarf sperm whales, whereas this proportion is 3.5% off the island of Hawai'i (Baird et al., 2021), for example. In addition, one of the most noticeable results that was obtained off St. Vincent is that encounter rates were not significantly influenced by sea state, unlike in other study regions (Dunphy-Daly et al., 2008; Baird et al., 2021). This is mostly likely due to the fact that at sea state conditions less than Beaufort 2 and 3, almost 90% of groups or individuals displayed aerial behaviors (full body breach) that enabled us to detect animals. These animals also breached relatively close to the research vessel (sometimes less than 50 m from the research vessel). We speculate that the impact of the bow of our research vessel on the swell or waves during surveys under these conditions generated a sound that alerted dwarf sperm whales, prompting them to jump out of the water to identify its source. It is also possible that beaching could be a behavior resulting from the irritation of the animals in the presence of the research vessel. However, high densities of these animals within a relatively small area might explain why sighting rates were high, despite the unfavorable sea conditions that we experienced during our two initial surveys, particularly as dwarf sperm whales are usually elusive (e.g., Baird et al., 2021).

Our visual survey data, collected off the west and south coast of St. Vincent, suggests that sightings are not uniformly distributed throughout the sampled area. All sightings occurred in the southwest, despite effort

further north along the leeward side of the island (Fig. 1). This suggests that the core habitat of this species could be relatively narrow. Further effort around St. Vincent, including off the windward side of the island, particularly later in the summer when sea state is frequently below Beaufort 2, will be required to fully understand the fine-scale distribution of dwarf sperm whales. As seasons are known to have a significant influence on dwarf sperm whale habitat use and group size in other regions of the wider Caribbean, such as off Abaco in the Bahamas (Dunphy-Daly et al., 2008), future surveys will have to be stratified across the two main seasons (summer and winter, i.e. wet and dry seasons, respectively) off St. Vincent to investigate potential effects of seasons on their distribution and group dynamics.

Our results also suggest that dwarf sperm whales have a significant affinity for the upper portion of the insular slope, which is consistent with previous studies documenting their habitat preferences in the Bahamas (Dunphy-Daly et al., 2008), in the Gulf of Mexico (Ramírez-León et al., 2021), around the Mozambique Channel island of Mayotte (SW Indian Ocean; Kiszka et al., 2010), and off Hawai'i (Baird et al., 2021). Slope was found to be the most important predictor of habitat suitability of dwarf sperm whales off St. Vincent, which has been also reported in many other studies for a range of deep-diving whales, particularly sperm (*Physeter macrocephalus*) and beaked whales (Ziphiidae; Rogan et al., 2017; Virgili et al., 2021; Fiedler et al., 2023). Steep slope habitats along continental margins and around oceanic islands may promote prey aggregations (Logerwell & Smith, 2001; Vecchione, 2001), including pelagic cephalopods that are targeted by dwarf sperm whales throughout their range (Plön, 2004; Spitz et al., 2011; Staudinger et al., 2014; McAlpine, 2018).

Our data also provide some information on the behavior of dwarf sperm whales off St. Vincent. Group size and composition were similar to those reported at other locations, such as the Bahamas (e.g., Dunphy-Daly et al., 2008) or Hawai'i (Baird et al., 2021). However, we also report the largest group documented in the literature, with at least 20 traveling individuals observed in June 2023. The presence of such a large group further supports the assertion that the slope waters of St. Vincent represent an important habitat for this species at the regional and global level, and the drivers of grouping tactics will also have to be investigated. The limited photo-identification data collected off St. Vincent allowed to identify at least 22 distinct individuals, but no resighting was recorded (both within seasons and between years), which suggests that we identified a small proportion of

the entire population, and/or that its range is much larger. Nevertheless, it confirms that photo-identification is a viable method to investigate the abundance, site fidelity, social structure, and other demographic parameters of dwarf sperm whales, as demonstrated by Baird et al. (2021). Photo-identification was also useful to document skin conditions in free-ranging dwarf sperm whales, which were not described in any other location. The origin of skin conditions observed on some individuals using photographs could not be determined. One of the individuals exhibited dark circular lesions that could possibly be associated with cell damage due to a poxvirus, which usually causes "tattoo skin disease" (Fig. 7C, individual in the foreground). However, histopathological analyses would be required to confirm this diagnostic. Unlike other locations, such as Hawai'i, no lesions associated with predator attempts by either killer whales (*Orcinus orca*) or large sharks were identified (Baird et al., 2021). However, local whalers targeting small cetaceans off St. Vincent regularly report that dwarf sperm whales are one of the most common prey for killer whales off St. Vincent (S. Hazelwood, personal communication, 3 February 2024). This is consistent with published information on the diet of killer whales in the Caribbean region, primarily consuming ocontocete cetaceans (Kiszka et al., 2021b). Future photo-identification efforts will allow for further evaluation of predator-prey interactions involving dwarf sperm whales, and investigation of the prevalence of skin diseases and therefore the health status of this population. Threats to dwarf sperm whales in this region include an active whaling operation and vessel traffic. Dwarf sperm whales are rarely targeted by artisanal whaling operations taking place off St. Vincent, primarily targeting short-finned pilot whales (*Globicephala macrorhynchus*) and other delphinids (Caldwell et al., 1973; Fielding & Kiszka, 2021). However, the maritime traffic is relatively important between the main island of SVG, particularly Bequia, which highly overlaps with the habitat where dwarf sperm whales occur. Ferries transit 12–16 times per day during daylight hours and, one of the sightings of dwarf sperm whales breaching in this study was in front of a ferry. Future research will be needed to investigate the effects of noise pollution on this population, particularly during the day when these animals mostly rest at the surface.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at https://doi.org/10.1016/bs.amb.2024.09.002.

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