Latin American Journal of Aquatic Mammals

ISSN: 2236-1057 | Vol. 19 No. 2, November 2024

Site fidelity and population parameters of short-finned pilot whales (*Globicephala macrorhynchus*) in the Eastern Caribbean through photographic identification

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Abstract

The short-finned pilot whale (*Globicephala macrorhynchus*) is distributed throughout the Caribbean and within the Agoa Sanctuary, where it is protected. This top predator is overlooked in the Caribbean, and no data is available on the variability of the degree of fidelity to the islands, or even on the demographic parameters and social structure of this species, which is essential for its conservation and the understanding of its behavior. This study focuses on the islands of Guadeloupe and Martinique and is based on 24,374 photos collected between 2014 and 2022. This data was analyzed using the CMR method via photo-identification, then open population modeling under the *POPAN* formulation and *via SOCPROG* for the study of social links. This revealed two interconnected populations. Within each of these populations, there are three patterns of residence: core residents, residents, and visitors. A total of 193 core residents and residents were estimated in Guadeloupe, and 565 core residents, residents, and visitors in Martinique. Survival rates for both populations were high. Abundance was constant in Guadeloupe for core residents and residents, but a decline has been observed for the three patterns of residencies in Martinique - special attention must be given to this population. International collaboration throughout the Lesser Antilles is essential in order to estimate the number of populations and understand the behavior of the short-finned pilot whale in the Caribbean Sea.

Keywords:
catch-mark-release, pattern of residence, photo-identification, short-finned pilot whale, site fidelity, social links

ARTICLE INFO

Manuscript type: Article

Article History
Received: 06 December 2023
Received in revised form: 29 December 2023
Accepted: 11 March 2024
Available online: 24 November 2024

Handling Editor: Larissa Oliveira

Citation:
Riou, M., Freriks, C., Ortolé, C., Valin, C., Safi, M., Cockx, E., Millon, C., Bouveret, L., & de Montgolfier, B. (2024). Site fidelity and population parameters of short-finned pilot whales (*Globicephala macrorhynchus*) in the Eastern Caribbean through photographicidentification. *Latin American Journal of Aquatic Mammals, 19*(2), 165-181. https://doi.org/10.5597/lajam00336

Introduction

Short-finned pilot whale (*Globicephala macrorhynchus*; Gray, 1846) has a pantropical distribution (Folkens et al., 2002; Savouré-Soubelet et al., 2016). This oceanic species is mainly teutophagous and prefers areas with a high topographic relief (Heimlich-Boran, 1993; Fernández et al., 2009; Savouré-Soubelet et al., 2016). The distribution of the species populations is primarily influenced by the availability of prey and water temperature (Olson, 2009; Alves, 2013). They form social groups from 10 up to 50 individuals, although movements of hundreds of individuals can be observed (Heimlich-Boran, 1993; Bloch & Lastein, 1995; Savouré-Soubelet et al., 2016). It has been shown that short-finned pilot whale groups have a stable social structure, with a matrilineal hierarchical system and natal-group philopatry (Heimlich-Boran, 1993; Mahaffy, 2012; Alves et al., 2013). This system involves kinship bonds between members of both sexes within the clan (Alves et al., 2013). This social cohesion behavior contributes to the known mass strandings in this species (Mignucci Giannoni, 1989; Fielding & Kiszka, 2021).

Estimates of short-finned pilot whale abundance focus mainly on nearshore populations off Japan (Kanaji et al., 2011), Canary Islands (Heimlich-Boran, 1993), and Madeira (Alves et al., 2015). Scientific knowledge of the population structure, demographic parameters, trends, movements, threats, and critical habitats of this species is scarce. However, this knowledge forms the basis for the application of appropriate management measures (Alves, 2013). In addition, the International Union for Conservation of Nature (IUCN) has classified the species global conservation status as Least Concern, in the Red List of Threatened Species (Feunteun et al., 2019; IUCN, 2023).

Within the Caribbean, shot-finned pilot whales can be observed from Cuba to Venezuela, including the Lesser Antilles (Mignucci Giannoni, 1989; Folkens et al., 2002; Savouré-Soubelet et al., 2016). Within the exclusive economic zone (EEZ) of the French Lesser Antilles, the Agoa Sanctuary is the second largest protected marine area from France territory – continental and overseas, covering 140,000 km². This sanctuary, which was created in 2010 including the Caribbean islands of Guadeloupe and Martinique, shelters and protects more than 20 cetacean species, including short-finned pilot whales (Fléchet et al. 2019). De Vries (2017) observed some short-finned pilot whale movements between Guadeloupe and Martinique. These observations raised questions about the connectivity between the islands, which are 189 km apart, and the presence of groups in transit. Similar movements have also been observed in sperm whales (*Physeter macrocephalus*; Gero et al., 2007; De Vries, 2017). Furthermore, recent observations in Martinique suggest site fidelity of these groups. The hypothesis of Fléchet et al. (2019), as in the studies by Mahaffy (2012), Alves (2013), and Servidio (2014), is that short-finned pilot whales encountered along the Caribbean coast of Martinique belongs to a population with a group of residents and other groups of transient individuals. Moreover, no information is available on the social bonds within Caribbean population(s), although some individuals have been observed together on several occasions (Fléchet et al., 2019).

The photo-identification, which is not an intrusive method, has already proved invaluable in obtaining individual data in population studies (Chan & Karczmarski, 2017; Sarano et al., 2022). This data forms the basis of study of the dynamics and parameters of cetacean populations, their movements, their social structures, their ecological and behavioral interactions, and their change over time (Würsig & Würsig, 1977; Whitehead, 1990; Servidio, 2014; Courtin et al., 2023). It constitutes the tracking and mark-recapture event for the Capture-Mark-Release (CMR) approach (Karczmarski et al., 2022; Courtin et al., 2023). This technique is based on a photograph of an animal that can be individually recognized by its distinctive markings (Hammond et al., 1990; Sarano et al., 2022). In the case of pilot whales, notches on the dorsal fin or any other mark visible to an observer from a boat can be recognized and recorded (*e.g.,* scars, depigmentation; Heimlich-Boran, 1993; Alves, 2013). Long-term monitoring is needed to obtain the appropriate amount of data (Courtin et al., 2022). This data collection can be implemented during dedicated missions, with systematic monitoring (Mahaffy, 2012; Alves, 2013) and/or through opportunistic observations (De Vries, 2017; Robbins et al., 2020; Courtin et al., 2022).

The presence of resident groups of short-finned pilot whales on Martinique's west coast makes them particularly vulnerable due to high levels of anthropogenic pressures in this area (Feunteun et al., 2019). These pressures, through environmental pollution, depletion of prey or physical disturbance linked to heavy maritime traffic, particularly in coastal areas, are problematic for all cetaceans (Feunteun et al., 2019). Moreover, the gregarious behavior of short-finned pilot whales has facilitated their hunting in some islands in the Lesser Antilles for generations (Fielding & Kiszka, 2021). Regular and directed catches of this species have increased since 1931, with an estimated 143 pilot whales caught each year between 1962 and 2006 (Fielding & Kiszka, 2021). The species is now protected in the Agoa Sanctuary, but is still hunted in Saint-Vincent and the Grenadines (SVG) and occasionally in Saint-Lucia (Fielding & Kiszka, 2021). Unfortunately, there is no data on the abundance of short-finned pilot whale landings in SVG or Saint-Lucia, but the whalers mentioned a decrease in their presence (Fielding & Kiszka, 2021). Increasingly exposed to anthropogenic pressures, and currently hunted to the south of the Agoa Sanctuary, the conservation of the short-finned pilot whale population(s) in the Lesser Antilles is a key issue (Fléchet et al., 2019; Fielding & Kiszka, 2021). It is essential to identify the limits of the population(s) and the management unit at the scale of the Caribbean region (Fielding & Kiszka, 2021).

Little knowledge is available about short-finned pilot whales in the Lesser Antilles, particularly in Guadeloupe. A single study characterizes a group exclusively on the western side of Martinique (Fléchet et al., 2019). No data is available on the variability in the degree of fidelity to the islands of Guadeloupe and Martinique, or even on the demographic parameters and social structure of this species in this area. Our work will therefore focus on the short-finned pilot whales between Guadeloupe and Martinique over the period 2014 - 2022. The aim of the study was to determine demographic parameters, degree of fidelity to the islands of Guadeloupe and Martinique, exchanges and movements between these islands, and to identify the social bonds within the potential short-finned pilot whale population(s).

Materials and methods

Study area and sampling period

The Agoa Sanctuary covers 143,256 km², and this study focused on two of the sanctuary's islands, Guadeloupe (16°11′ N; 61°16′ W) and Martinique (14°38′ N; 61°01′ W; Fig. 1; Coché et al., 2021). They are characterized by a regular drop-off close to the coast, at a depth of 1,000 m, 2.5 nm from the Martinique coast and 4 nm from the Guadeloupe coast (Schom, 2018). The two islands have similar climates, with a year divided between the dry season from December to May and the wet season from June to November (Cerema, 2020; Météo France, 2020 a, b). Transient periods are observed from a meteorological point of view (Météo France, 2020 a, b). The sampling periods were divided as follows (Courtin et al., 2022, 2023): Early Dry (ED = December to February), Late Dry (LD = March to May), Early Wet (EW = June to August), and Late Wet (LW = September to November).

Data Collection

A total of 50 sampling periods (30 conducted in Guadeloupe and 20 in Martinique) were carried out in this study between 2014 and 2022. Most of the data obtained comes from opportunistic observations and dedicated cetacean monitoring surveys. OMMAG (Observatoire des Mammifères Marins de l'Archipel Guadeloupéen), a non-profit association set up in 2011, collects data on cetaceans around the Guadeloupe Archipelago through citizen-based science programs. Citizen science data (mainly along the west coast of Guadeloupe) was collected by OMMAG

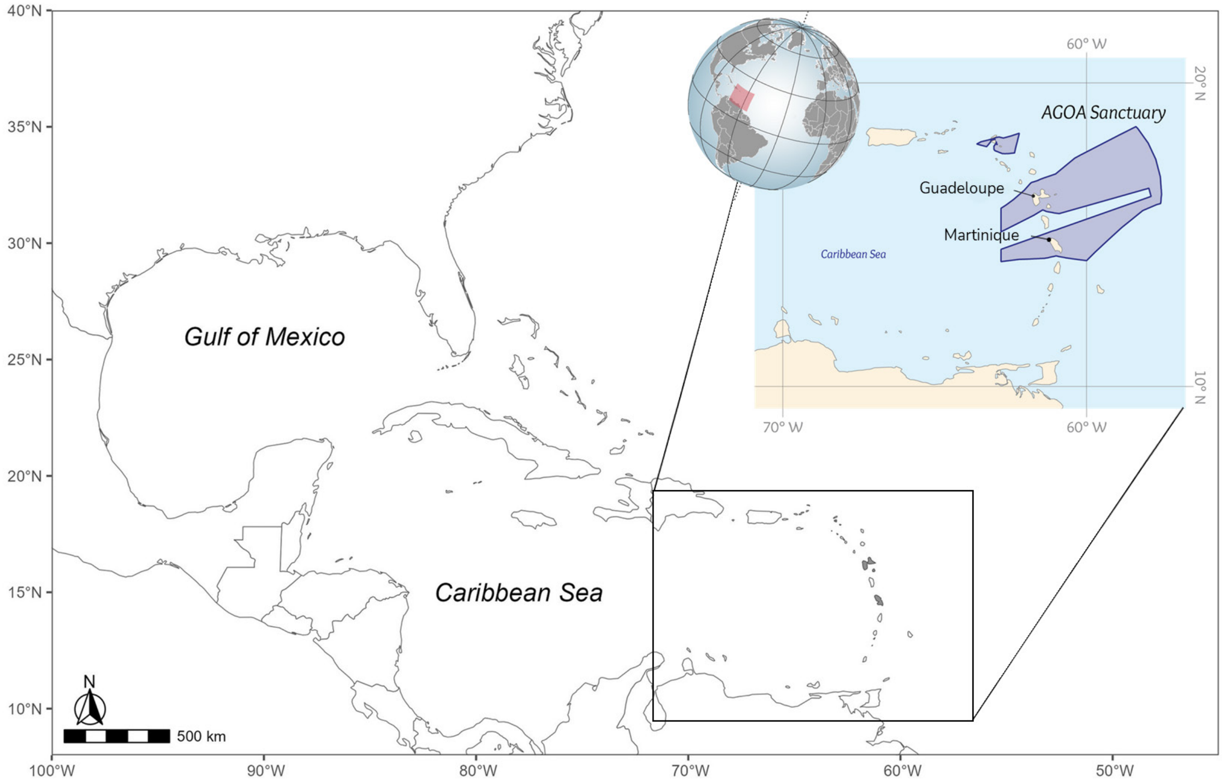

Figure 1. Location of the Agoa Sanctuary in the Eastern Caribbean Sea, (adapted from Coché et al., 2021 and Agoa-OFB).

from whale watchers and volunteers from the association. In Martinique, the data collected was obtained by Aquasearch (a research unit), during surveys dedicated to observe and monitor cetaceans. Cetaceans were monitored during whale watching trips in Guadeloupe and with a specific protocol created by Aquasearch for most of the data from Martinique. For both islands, the data obtained by whale-watchers are essential, either actively by taking data directly from the field (*Aventure Cétacés, Cétacés Caraïbes, Guadeloupe Evasion Découverte* in Guadeloupe), or by allowing observers to come aboard their boats (*e.g., Aliotis Plongée* and *Blue Dream* in Martinique). This practice is managed in Agoa Sanctuary (Agoa, 2017; Order No. R-02-2017-03-15-003) by regulating the approach to cetaceans in waters under French jurisdiction in the French Lesser Antilles.

Each time a group of short-finned pilot whales was sighted, the associated metadata was recorded, including: date, time of the start and end of the observation, GPS coordinates, estimate of the size of the group, course followed, and behavior. Environmental parameters: wind (in Beaufort scale), visibility, cloud cover, and sea state were recorded. All this metadata was grouped together and banked for each of the two islands. A short-finned pilot whale group was defined as all the individuals located within a 250 m radius of each other and displaying similar behavior (Heimlich-Boran, 1993). In addition, an observation was defined as a sampling event that resulted in at least one photographic capture (Alves, 2013). When no photographs were captured, the observation was defined as an encounter. The photographs were taken from semi-rigid motorboats or catamarans using Nikon D3002, D500, and D7200 cameras equipped with 70 - 200 mm, 18 - 200 mm, and 18 - 300 mm lenses for the OMMAG observers, and Nikon D3500, D7100, and D7200 cameras, all equipped with 70 - 300 mm lenses for Aquasearch. Attempts to photograph the short-finned pilot whales encountered were made with a conscious effort to "capture" all members of the group, if possible, irrespective of their distinctive character, age class, or individual behavior.

The spatial representation of encounters with short-finned pilot whales was obtained using *QGis* v. 3.28.4 geographic information software. The GPS data for the encounters was acquired by the GPS unit on the boats for the OMMAG observers and by the Garmin eTrex 20 GPS unit for the Aquasearch team.

Photographic effort

To determine significant differences in the observation of short-finned pilot whales between the sampling periods, the distribution normality (Shapiro's test) and homoscedasticity (Levene's test) were tested. Then, significant differences between sampling periods were tested with a Kruskal-Wallis test or one-way ANOVA. These statistical tests and all the graphs presented were carried out in R Studio v. 4.2.3 (R Core Team, 2023), using the package 'ggplot2' v. 3.4.4 (Wickham, 2016). The total number of photos collected, exploitable and processed, as well as individuals and observation, has been calculated.

Photo-identification analysis

Photo-identification involves sorting and classifying photos according to criteria of quality and distinctiveness (Heimlich-Boran, 1993; Mahaffy, 2012; Alves, 2013; Courtin et al., 2022). A quality score was therefore assigned to each photo, based on angle, sharpness, contrast, and overall quality. It ranged from Q1 = very good quality, to Q4 = poor quality. Individuals were also given a distinctiveness score, ranging from D1 = very distinctive

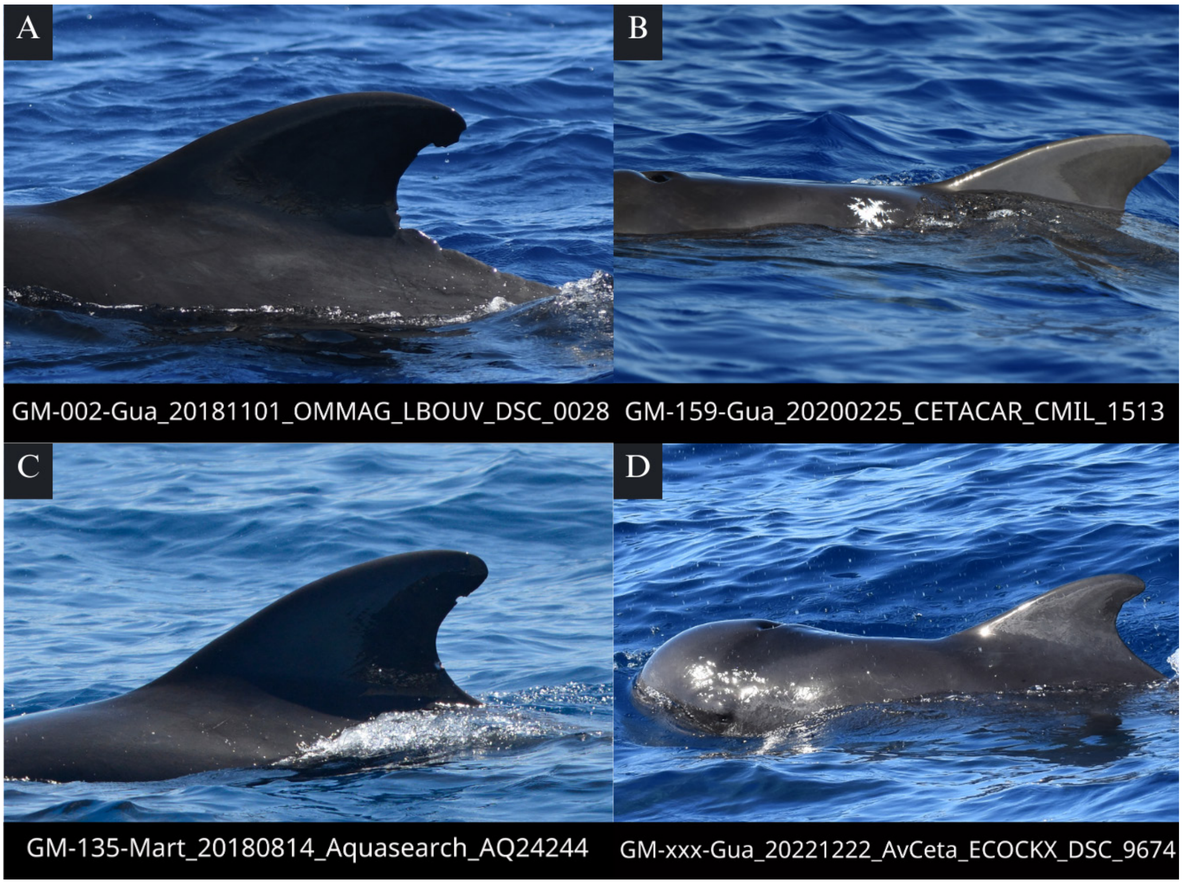

Figure 2. Photographs of good quality Q1, with (A) a very well-marked individual (D1) of short-finned pilot whale (*Globicephala macrorhynchus*) with multiple deep notches and an atypical dorsal shape, and (B) an individual marked with a spot of depigmentation; in (C) moderately-marked individual (D2) with two deep notches and (D) a weakly-marked individual of distinctiveness D3. (Photos: L. Bouveret, C. Milion, B. de Montgolfier, and E. Cockx).

markings to D4 = no distinctive markings. In order to avoid false positives and false negatives in the identification, only photos of quality Q1 and Q2 (usable photos), and individuals marked as D1 and D2 (processed photos) were used for the analyses (Fig. 2; Alves, 2013).

Different short-finned pilot whale photo-identification catalogues already existed in Guadeloupe (dating from 2015 and 2019) and Martinique (dating from 2017). The overall Guadeloupe catalogue was compared with the existing Martinique catalogue. Within each of the catalogues, the individuals were classified according to the area marked on the dorsal fin and its specification. In addition, each individual had its own individual file with all the observations made. After being checked and completed, the catalogues could be used. All the photos from the observations were sorted and classified manually according to the scores described above, and then compared manually with the two catalogues using the *Pictures* software in Windows. If a new individual was photographically captured, it was added to the catalogue of the island where it was first observed. When an individual was recaptured again, the observation was included in its individual file.

The identification data obtained was compiled into a binary CMR matrix (or observation history) and an occurrence table for analysis. The photo-identification data was also used to monitor inter-island movements. A discovery curve was also obtained, by compiling the number of new identifications over time.

Residency patterns

Residency patterns were set up using multi-year site fidelity to the study area (Mahaffy, 2012; Alves, 2013). Core residents (RI) corresponded to individuals identified ≥ 5 times in ≥ 3 years, residents (RII) were those identified more than once but not reaching this criterion, and visitors corresponded to individuals observed only once.

Closure test and goodness of fit

Closure test software v. 3.0 was used to test the hypothesis of demographic closure in the analysis of capture-recapture data (Stanley & Burnham, 1999). In order to use an open population model of the CJS (Cormack-Jolly-Seber) type, and its *POPAN* formulation (Jolly, 1965; Schwarz & Arnason, 1996), some assumptions about the fit of the data to the models were verified to obtain precise, unbiased, and accurate estimates of the parameters. To assess the validity of our assumptions, we conducted four goodness-of-fit tests (TEST 2 and TEST 3) using the *U-CARE* software (Choquet et al., 2009). These tests are subdivided into the following categories: (i) TEST 3.SR, which identifies transitory effects or any excess or lack of transient individuals in the sample (Pradel et al., 1997; Tezanos-Pinto et al., 2013); (ii) TEST 3.SM, designed to detect the impact of capture on survival (Choquet et al., 2005; Tezanos-Pinto et al., 2013); (iii) TEST 2.CT, assessing significant trap effects (trap happiness), indicating the influence of the sampling method on the probability of photographing an individual (Pradel, 1993; Tezanos-Pinto et al., 2013); and (iv) TEST 2.CL, determining whether trap dependency persists beyond a single time interval (Choquet et al., 2005; Tezanos-Pinto et al., 2013).

Model selection and estimation of population parameters

The capture-recapture history was used to select the most appropriate model, based on the *POPAN* formulation of Jolly-Seber (Schwarz & Arnason, 1996) using the MARK 9.0 software (White & Burnham, 1999). For Guadeloupe, 25 of the total sampling surveys were utilized, while for Martinique 19 surveys were used. Time intervals without capture data between sampling periods were considered. Four models *per* island were compared, considering the time variable (t), or a constant (.) for the following parameters: (a) Φ survivability in the study area – probability that an animal or group of animals being captured at sampling period *i* will survive and does not emigrate until sampling period *i+1*; (b) probability of recapture *p* - probability that an animal or group of animals captured during sampling period *i* will be recaptured during sampling period *i+1*; (c) probability of entry into the group of marked individuals β - probability that an animal or group of animals from the super population ($\widehat{N_{tot}}$) enters the group of marked individuals (study population), between sampling periods *i* and *i+1*, that it does not emigrate and will survive between these sampling periods. Based on the reality of the data, only the four models incorporating a time-varying β ($\beta(t)$), were studied. The best-fitting model with the lowest Akaike Information Criterion (AICc), or ΔAICc < 2 was used to estimate the parameters, Φ, *p*, β and abundance $\widehat{N_m}$ and bi-seasonality of the Martinique and Guadeloupe groups.

Estimate of population abundance

An estimate of the total $\widehat{N_{tot}}$ size of the two groups, based on residence patterns, was made using the method of Wilson et al. (1999) with

$$\widehat{N_{tot}} = \frac{\widehat{N_m}}{\theta},$$

where $\widehat{N_m}$ corresponds to the model-estimated number of marked individuals, and θ to the proportion of marked individuals in the group. This proportion of marked individuals for each of the islands was calculated using group photos of short-finned pilot whales between three and eight individuals, over the period 2014 - 2022.

The variance of $\widehat{N_{tot}}$ was estimated using the delta method (Wilson et al., 1999):

$$SE(\widehat{N_{tot}}) = \sqrt{\widehat{N_{tot}}^2\left(\frac{SE(\widehat{N_m})^2}{\widehat{N_m}^2} + \frac{1-\theta}{n\theta}\right)},$$

where *n* is the total number of individuals for whom θ has been estimated.

Log-normal 95% confidence intervals of the total group size were calculated with upper and lower limits obtained by multiplying or dividing $(\widehat{N_{tot}})$ by the factor *C* following Burnham (1987):

$$C = exp\ (1.96\sqrt{ln\ (1 + \frac{SE(\widehat{N_{tot}})}{\widehat{N_{tot}}})^2})$$

Analysis of social bonds

The social bonds were analyzed using *SOCPROG* v. 2.9 software. This software can be used to construct association matrices and graphical representations of the social structure of the groups studied (Whitehead, 2009). It is based on co-observation of the individuals identified in the study, using an occurrence table listing the dates on which the individuals were observed between 2014 and 2022. The sampling period was defined as one day, and associations as individuals grouped within an observation (Alves et al., 2013; Mahaffy et al., 2015). In order to quantify the strength of association between pairs of individuals, the HWI (Half Weight Index) coefficient was used. This is mainly used in studies of pilot whale social groups and minimizes the bias associated with missing identifications (Alves et al., 2013; Mahaffy et al., 2015). It is calculated as:

$$HWI = \frac{2AB}{(A+B)},$$

where A and B correspond to the total number of times each individual (A and B), was identified, and AB the number of times that A and B were observed together (Tavares et al., 2017).

This index was calculated for each pair of individuals (or dyad), and takes a value between 0 (never associated) and 1 (always observed together). The coefficient of variation of the index, HWI, was used to estimate the social differentiation S; when it is less than 0.3 the sample is considered to be homogeneous, whereas if it is greater than 0.5 it suggests that the associations were different between the dyads (Whitehead, 2009). The correlation coefficient (r) between the observed association indices and those estimated varies from 0 (the proposed representation is inappropriate) to 1 (excellent representation) and was used to estimate the power of the analysis. *SOCPROG* v. 2.9 can also generate Monte Carlo permutation tests. The aim was to test whether the associations obtained were different from those expected if they were the result of a random phenomenon (Whitehead, 2009). The association matrix was then permuted until the *p*-value was stabilized; here, they were generated at a rate of 1,000, 10,000, and 20,000 permutations, performing three runs, considering 1,000 trials *per* permutation (Whitehead, 2009; Alves et al., 2013; Mahaffy et al., 2015). A sociogram, linked to the association matrix obtained, was produced using Netdraw (Borgatti, 2002).

Results

Distribution of encounters with short-finned pilot whales in Guadeloupe and Martinique between 2014 and 2022

Encounters (without or with photography; the latter is an observation) with short-finned pilot whales extend from 15°56’24” N to 16°38’24” N in Guadeloupe, and from 14°30’77” N to 14°46’54” N in Martinique. Encounters were scattered all along the west

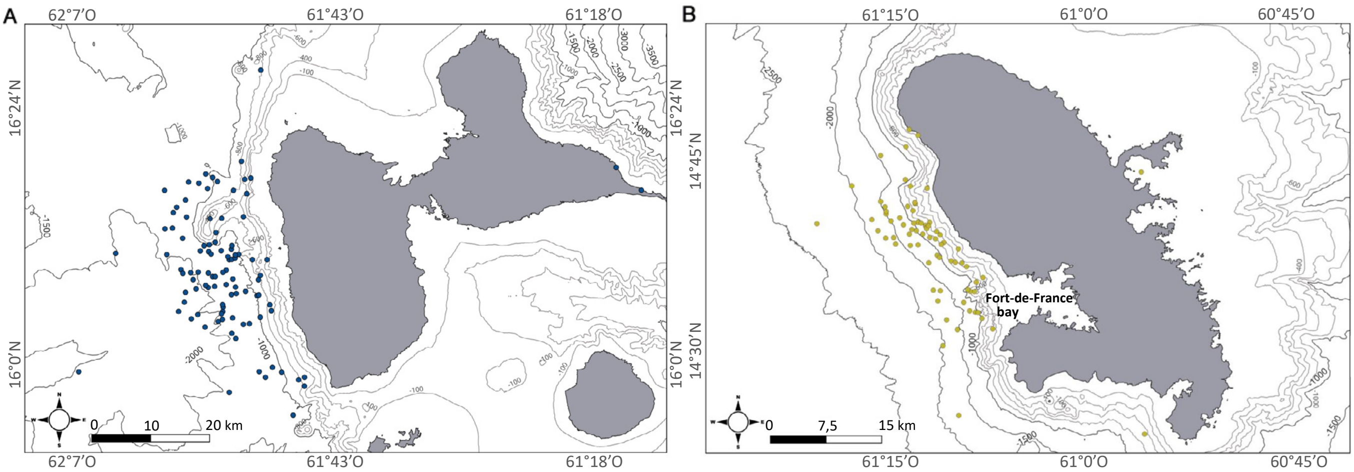

Figure 3. Locations of short-finned pilot whale (*Globicephala macrorhynchus*) encounters (marked with dots) in (A) Guadeloupe and (B) Martinique between 2014 and 2022.

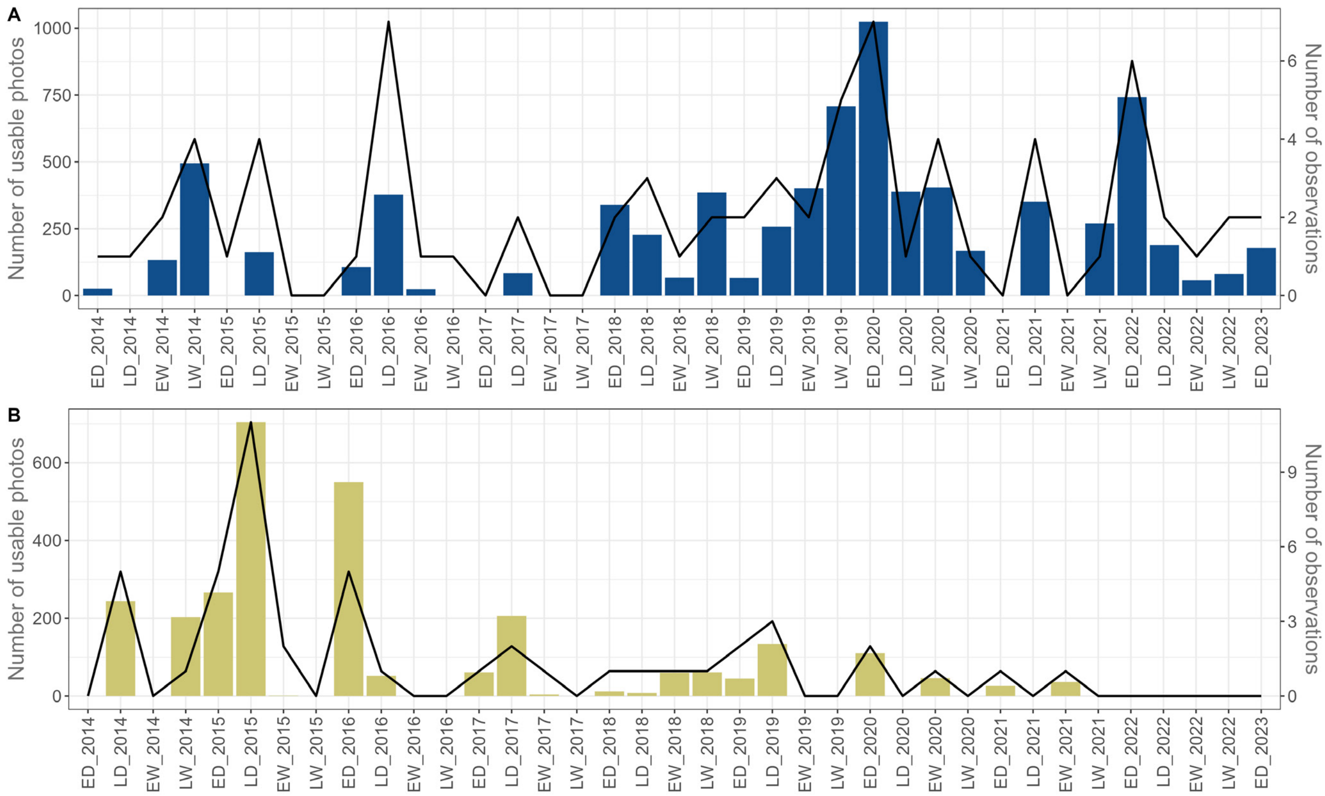

Figure 4. Number of observations (black line) and usable photos (bar plot) of short-finned pilot whale (*Globicephala macrorhynchus*) for (A) Guadeloupe and (B) Martinique as a function of the sampling period.

coast of Guadeloupe (Fig. 3A), while they are mainly limited to the exit and north of Fort de France Bay in Martinique (Fig. 3B). In Guadeloupe, the short-finned pilot whales were mainly found in deep waters, between 1,000 m and 1,600 m depth, although a few encounters have been made in waters 500 m deep. In Martinique, the short-finned pilot whales are distributed closer to the coast, beyond the 500 m bathymetric depth line, and many of them have also been encountered between the 1,000 m and 2,000 m depth contours.

Photographic effort

A total of 124 observations (76 in Guadeloupe, 48 in Martinique) resulted in the collection of 24,374 photos (16,455 in Guadeloupe and 7,922 in Martinique; Table. 1). Of these, 43% were of quality Q1-Q2 (47% in Guadeloupe and 35% in Martinique) and 26% were considered as distinctiveness D1-D2 (28% in Guadeloupe, 23% in Martinique). Seven sampling periods were not covered by observations in Guadeloupe and 16 in Martinique, for both regions mainly in the wet season (EW and LW).

In Guadeloupe, the maximum number of usable photos was 1,024 in ED_2020, while for Martinique it was 704 in LD_2015.

Table 1. Data collected and identifications of short-finned pilot whale (*Globicephala macrorhynchus*) in the Agoa Sanctuary along the leeward coasts of Guadeloupe and Martinique islands, between 2014 and 2022.

	Year	Observations	Photos collected	Usable photos	Photos treated	Identifications	New individuals
GUADELOUPE	2014	8	1,075	654	364	79	50
	2015	5	715	162	61	10	8
	2016	10	1,027	508	235	27	13
	2017	2	138	84	32	3	1
	2018	9	1,794	1,018	539	52	37
	2019	13	4,103	1,796	1,161	99	60
	2020	11	3,133	1,620	1,150	104	36
	2021	7	2,051	775	406	47	27
	2022	11	2,416	1,092	645	82	19
	Total	**76**	**16,452**	**7,709**	**4,593**	**503**	**251**
MARTINIQUE	2014	8	1,360	548	234	36	33
	2015	17	1,959	973	679	101	59
	2016	6	718	560	425	58	31
	2017	3	661	210	195	17	4
	2018	5	1,088	157	85	18	13
	2019	4	930	163	101	10	3
	2020	3	790	156	76	12	8
	2021	2	416	62	18	8	0
	2022	0	0	0	0	0	0
	Total	**48**	**7,922**	**2,829**	**1,813**	**260**	**151**
	Total	**124**	**24,374**	**10,538**	**6,406**	**763**	**402**

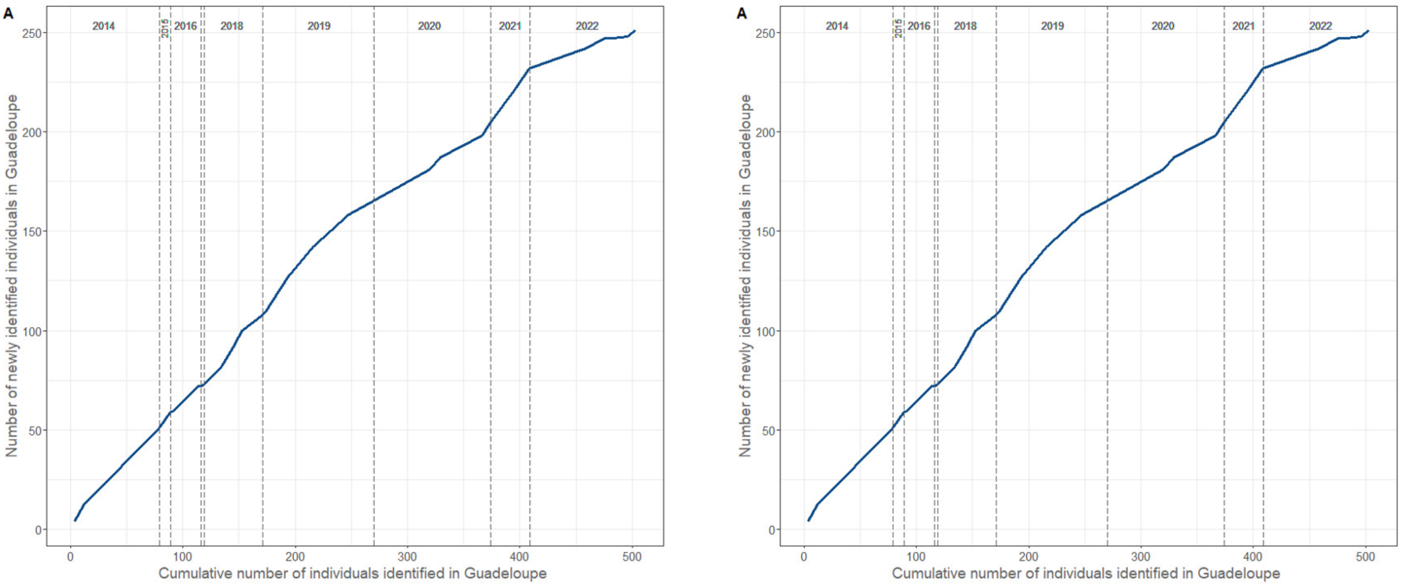

Figure 5. Discovery curve of identified short-finned pilot whale (*Globicephala macrorhynchus*) in (A) Guadeloupe and (B) Martinique.

The minimum number of usable photos was 24 for EW_2016 in Guadeloupe and one for EW_2017 in Martinique (Fig. 4A, 4B). On average, the number of usable photos was higher in the dry season than in the wet season. There was an average of 301 ± 188 SE (n = 15) usable photos in Guadeloupe in the dry season compared with 265 ± 178 SE (n = 12) in the wet season; and an average of 186 ± 160 SE (n = 13) usable photos in Martinique in the dry season compared with only 59 ± 42 SE (n = 7) in the wet season. However, there was no significant difference in the number of usable photos depending on the sampling period (n = 76, p = 0.2115, df = 29, Kruskal-Wallis test for Guadeloupe and n = 48, p = 0.6567, df = 19, Kruskal-Wallis test for Martinique).

Photo-identification analysis

A total of 763 photo-identifications were carried out between 2014 and 2022, 503 in Guadeloupe and 260 in Martinique. From these, 420 individuals were identified, 269 in Guadeloupe and 151 in Martinique.

After compiling the number of newly identified individuals and the total number of identified individuals, the discovery curves were obtained. The number of identifications is constantly increasing (Fig. 5). In Guadeloupe, a further increase in discoveries was observed at the end of 2022. In Martinique, a slowdown in discoveries was observed from 2019, followed by a significant increase in 2020. No significant plateau was reached (Fig. 5).

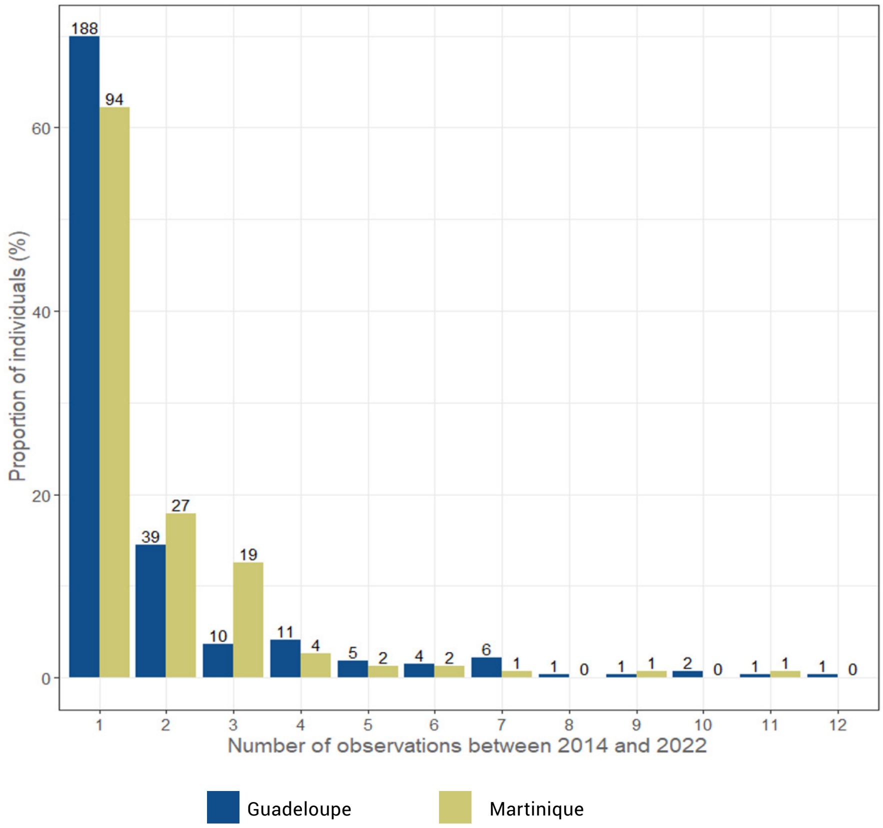

Figure 6. Proportion of individuals and number of individuals (above the bars) of short-finned pilot whale (*Globicephala macrorhynchus*) as a function of the number of observations between 2014 and 2022, for (blue) Guadeloupe and (yellow) Martinique.

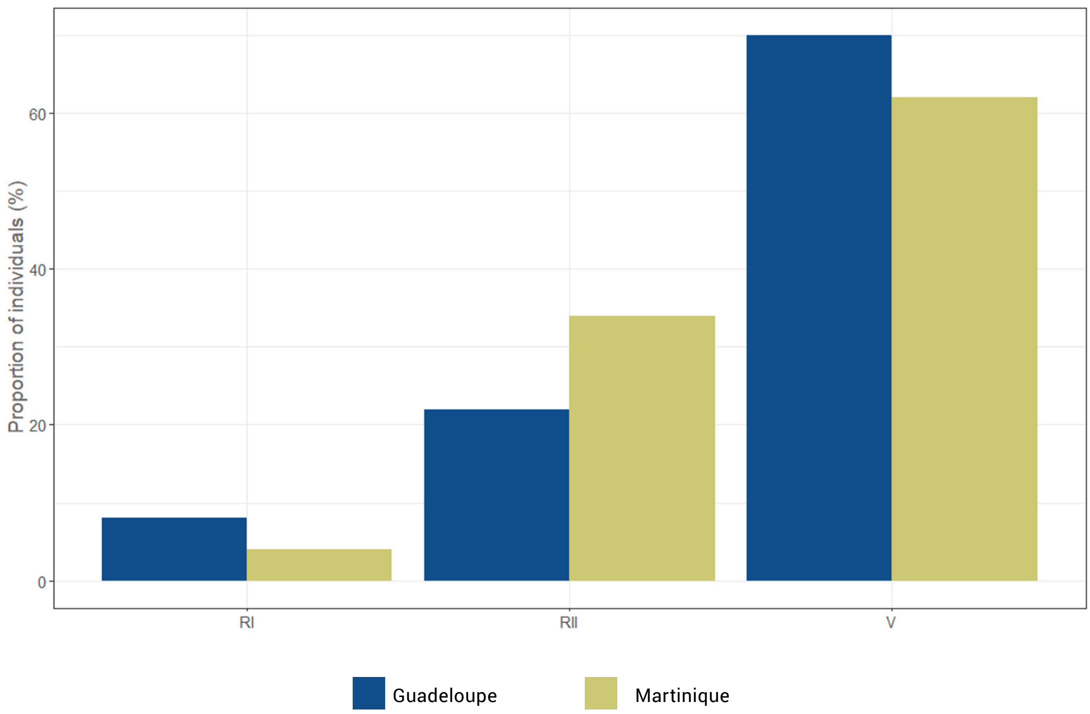

Figure 7. Proportion of individuals with each residence pattern of short-finned pilot whale (*Globicephala macrorhynchus*) for (blue) Guadeloupe and (yellow) Martinique.

Table 3. Summary numbers and proportions of short-finned pilot whales (*Globicephala macrorhynchus*) in each residency pattern, and the total number of individuals estimated for each island (Martinique, Guadeloupe) 2014 - 2022.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
Guadeloupe						
{Φ(.) p(t) β(t)}	999.773	0.0000	1.0000	1.0000	51	185.1539
{Φ(.) p(t) β(t)}	1037.4173	37.6443	0.0000	0.0000	74	139.4634
{Φ(.) p(.) β(t)}	1163.2183	163.4453	0.0000	0.0000	27	416.8951
{Φ(t) p(.) β(t)}	1177.4707	177.6974	0.0000	0.0000	50	366.031
Martinique						
{Φ(.) p(t) β(t)}	717.2478	0.0000	1.0000	1.0000	39	-443.8489
{Φ(t) p(t) β(t)}	756.9443	39.6965	0.0000	0.0000	56	-457.6656
{Φ(.) p(.) β(t)}	804.856	87.6082	0.0000	0.0000	21	-308.7609
{Φ(t) p(.) β(t)}	814.3213	97.0735	0.0000	0.0000	38	-343.9123

Table 2. POPAN models results considering 25 sampling periods and one group for Guadeloupe, and 19 sampling periods and one group of short-finned pilot whale (*Globicephala macrorhynchus*) for Martinique.

	Core residents RI		**Residents RII**		**Visitor V**		**Total marked**	**Total group estimated**
	Number	% of total marked	Number	% of total marked	Number	% of total marked		
Martinique	6	4	51	34	94	62	151	565 ± 63 (RI, RII &V)
Guadeloupe	21	8	60	22	188	70	269	193 ± 19 (RI & RII)

The majority of individuals identified between 2014 and 2022 were observed only once (188 in Guadeloupe – 70%, and 94 in Martinique – 62%). A total of 138 individuals were recaptured (re-sighted) at least twice during this period. These included 81 individuals in Guadeloupe, representing 30% of the Guadeloupe catalogue, with 79% of them observed over several years (two to nine years). In Martinique, 57 individuals were recaptured, representing 38% of the Martinique catalogue, with 89% of these observed over several years (two to seven years) (Fig. 6). Individual GM-006-Gua was caught 12 times in nine years, representing the maximum number of captures.

The median between the first and last observation was 1.99 years in Guadeloupe and 1.34 years in Martinique. As an overall trend, the number of captures increased with longer time intervals. These captures and recaptures were used to establish residencypatterns. In Guadeloupe, of the 269 individuals photo-identified between 2014 and 2022, 21 were considered as core residents (8%), 60 as residents (22%), and 188 were visitors (70%). In Martinique, of the 151 individuals photo-identified, six were core residents (4%), 51 were residents (34%), and 94 were visitors (62%; Fig. 7).

Of all the individuals in the two catalogues, 10 were observed on both islands. Of these, three made three back-and-forth trips. These three individuals, GM-012-Mart, GM-016-Mart, and GM-073-Mart, were caught on both islands three months apart between April and July 2019.

Goodness of fit tests

The two tests available in the *Close test* software, Stanley & Burnham (1999) Closure Test and Otis et al. (1978) Closure Test, had extremely low *p*-values for data from Guadeloupe and Martinique, indicating that these groups are open (Stanley and Burnham Closure Test for Guadeloupe $p = < 0.00001$ and Otis et al. Closure Test for Guadeloupe $p = 0.00001$; Stanley and Burnham Closure Test for Martinique $p = < 0.00001$ and Otis et al Closure Test for Martinique $p = 0.00053$).

Goodness-of-fit tests were carried out on the two groups separately. Three of the four tests available were not significant for the Guadeloupe data (TEST 3.SM, TEST 2.CT, TEST 2.CL, $p > 0.05$). The TEST 3.SR revealed an excess of transients (TEST 3.SR $p < 0.05$). To remedy this heterogeneity, individuals captured only once were removed from the dataset. Only core residents and residents (84 individuals) were included in the data modelling. For all four tests no significance, and no over-dispersion of the data was detected ($\chi^2 = 61.65$, df = 55, $p = 0.25$). By eliminating individuals observed only once in Guadeloupe, the data were found to fit the models. For the Martinique data, all four tests proved to be non-significant (TEST 3.SR, TEST 3.SM, TEST 2.CT, TEST 2.CL, *p*

> 0.05), and the final global test did not reveal any over-dispersion of the data (χ^2 = 17.51, df = 34, p = 0.99), which indicates that the data fit a CJS-type open population model well.

Modelling and estimation of population parameters (CMR)

The most appropriate model for both datasets, Guadeloupe and Martinique, was *{Φ(.), p(t), β(t)}*. For Guadeloupe core residents and residents, this model that best fitted our data carried 100% of the AICc weight, AIC = 999.77 (Model likelihood =1 and 51 parameters; v. 2). For Martinique core residents, residents, and visitors, this model that best fitted our data carried 100% of the AICc weight, AIC = 717.25 (Model likelihood =1 and a number of model parameters of 39; Table 2). This model results in a survival capacity in the study area *Φ(.)* constant over time, a time-varying probability of recapture *p(t)*, and a time-varying probability of entry into the population of marked individuals *β(t)*. For both islands, the difference in AIC between the first and second models was significant, being ΔAIC = 37.64 and ΔAIC = 39.70 for Guadeloupe and Martinique, respectively, and indicating low support from the other models to the data (ΔAIC > 2). It is important to note that the probability of recapture (*p*) and the abundance of marked individuals $\widehat{N}_m$, were calculated for each bi-season, while the probability of entry into the population of marked individuals (*β*) is calculated over the time intervals between sampling periods.

For Guadeloupe area, probability of survival (*Φ*) was estimated at 0.98 ± 0.008 SE (CI = 0.96 - 0.99), being constant over time for core resident and resident groups. The probability of recapture (*p*) varies over time, with a minimum in LW_2020 of 0.015 ± 0.015 SE and a maximum in ED_2014 of 1 ± 0.00003 SE, then in ED_2020 of 0.61 ± 0.07 SE (Fig. 8A). There seems to be no clear seasonal pattern, although recapture peaks are mainly observed in the dry season. The probability of entry into the population of marked individuals (*β*) also varied as a function of time, with a majority of zero values. The maximum was related to the ED_2014 - EW_2014 time interval, being 0.67± 0.085 SE (Fig. 8B). A peak was observed at the LW_2018 - LD_2019 interval, with a value of 0.24 ± 0.087 SE. Another lower value was noted for the LD_2020 - EW_2020 interval, being 0.058 ± 0.067 SE. The abundance of marked core residents and residents was estimated by the model at 104 ± 8 SE (CI = 88 - 122). The maximum number of individuals present in Guadeloupe at any time was estimated at 69 ± 12 SE (CI = 50 - 96) during the period EW_2014, and the minimum is estimated at 1 ± 1 SE individual (CI = 0 - 5) during ED_2014 (Fig. 8C). A decline in the abundance of individuals in the area was observed between EW_2014 and LW_2018, down to 46 ± 8 SE (CI = 33 - 65), then an increase to 69 ± 6 SE (CI = 57 - 82) during LD_2019. Finally, 55 ± 8 SE (CI = 40 - 74) were estimated three years later, at the end of the study. No seasonal trend was observed (Fig. 8C). The 54% of short-finned pilot whales were considered to be marked in Guadeloupe (61 photos, n = 241 individuals). Thus, the group of core residents and residents could be estimated at 193 ± 19 SE (CI = 158 - 235, Table. 3). The estimated capture rate among this group was 0.43%.

For Martinique, the probability of survival (*Φ*) was estimated at 0.93 ± 0.02 SE (CI = 0.87 - 0.96), and was also constant over time. The probability of recapture (*p*) of all individuals identified in Martinique between 2014 and 2022 varied with time, with a minimum at EW_2015 of 0.007 ± 0.007 SE and a maximum at

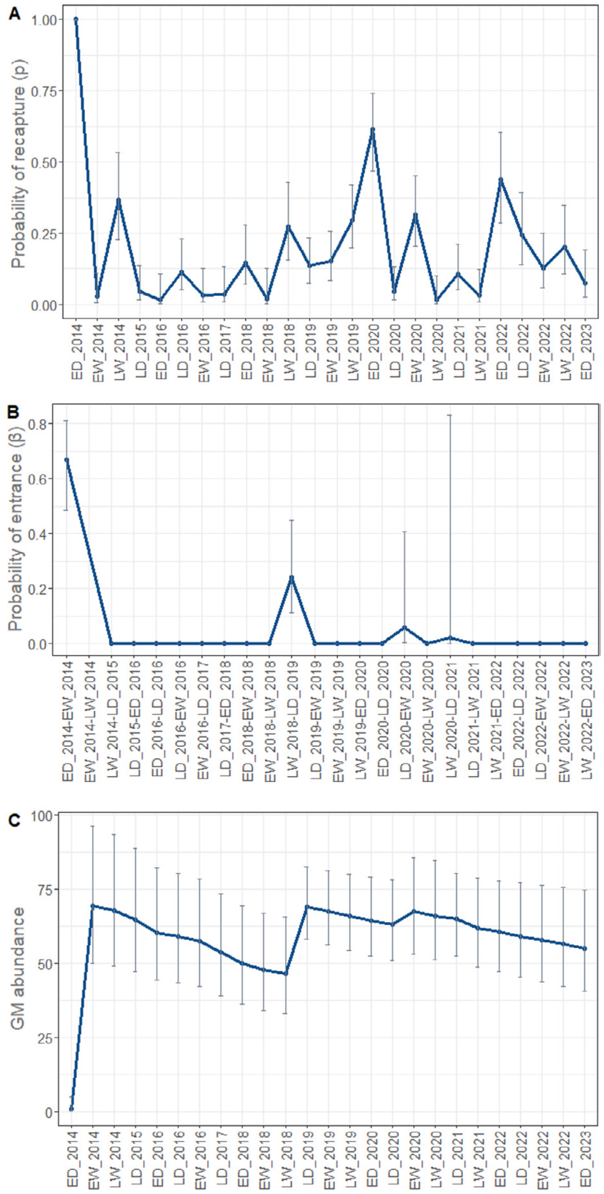

Figure 8. POPAN estimates of (A) recapture probability, (B) probability of entry into the population of marked individuals, and (C) seasonal abundance of short-finned pilot whale (*Globicephala macrorhynchus*) in Guadeloupe between 2014 and 2022. ED = Early Dry season; LD = Late Dry season; EW = Early Wet season; LW = Late Wet season.

LD_2014 of 0.99 ± 2.29, followed by LD_2015 of 0.31 ± 0.006 SE. There was no marked seasonal pattern although, as in Guadeloupe, the main recapture peaks occur in the dry season (Fig. 9A). The probability of entry into the population of marked individuals (*β*) was also a function of time, with an estimated maximum for the LD_2014 - LW_2014 interval of 0.55 ± 0.12 SE. Two peaks follow each other between the majority null values, at EW_2015 - ED_2016 (β = 0.13 ± 0.09 SE), and LD_2016 - ED_2017, until reaching a maximum at LD_2018 - EW_2018 (β = 0.18 ± 0.25; Fig. 9B). The abundance of all marked individuals in Martinique was estimated by the model at 333 ± 37 SE (CI = 267 - 414), with a maximum reached at LW_2014 with 180 ± 30 SE (CI = 130 - 250) and a minimum observed at LD_2014, with just 10 ± 23 SE (CI = 0 - 146). As in Guadeloupe, there did not appear to be any marked seasonality, and an overall decline in

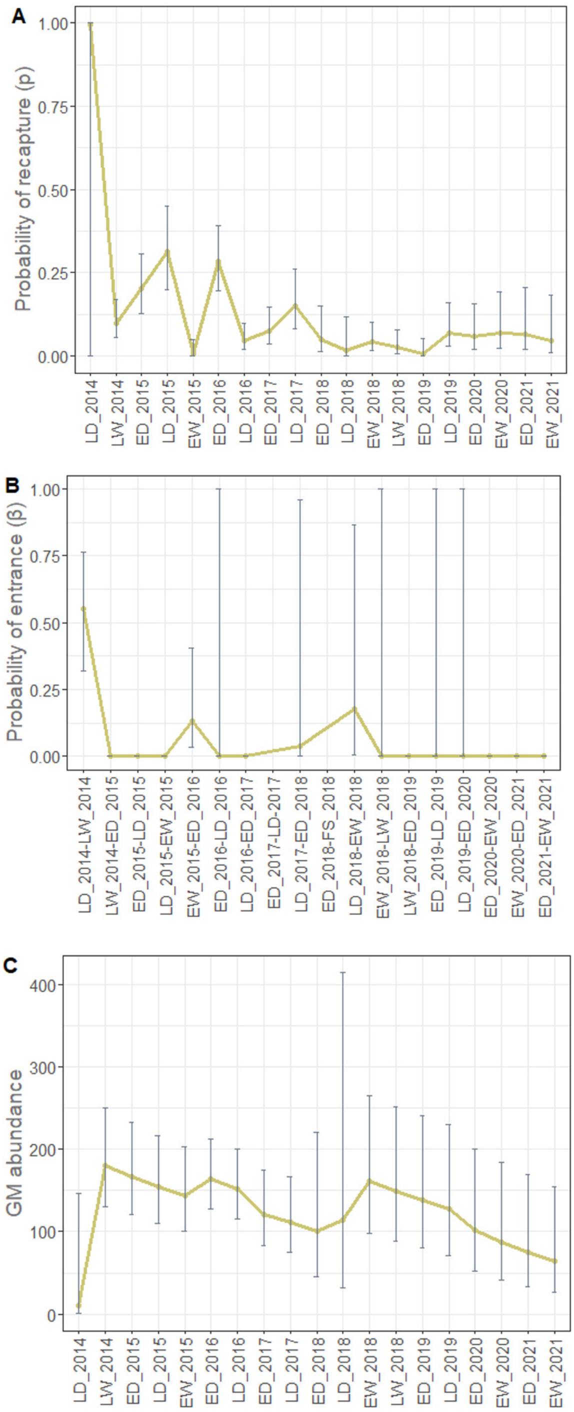

Figure 9. POPAN estimates of (A) recapture probability, (B) probability of entry into the population of marked individuals, and (C) seasonal abundance of short-finned pilot whale (*Globicephala macrorhynchus*) in Martinique between 2014 and 2021. ED = Early Dry season; LD = Late Dry season; EW = Early Wet season; LW = Late Wet season.

bi-seasonal abundance was noted, reaching 64 ± 30 SE at the end of the study (CI = 26 - 154) at EW_2021 (Fig. 9C). The 59% of shot-finned pilot whales marked in Martinique (29 photos, n = 100 individuals), makes it possible to estimate the total group at 565 ± 63 SE (CI = 453 - 703, Table 3). The same overall trend for marked individuals could be observed for the two-seasons between 2014 and 2021. The estimated capture rate for this group was 0.27%.

Analysis of social bonds

The table of occurrence covering all individuals observed four times or more (*i.e.*, 43 individuals, 32 from the Guadeloupe catalogue and 11 from Martinique) was analyzed using *SOCPROG* 2.9. A total of 260 captures were taken into account. This analysis was more representative than the analyses considering all the individuals, or those observed two times or more. A social differentiation of S = 1.07 ± 0.03 SE shows a very different association between the dyads. The HWI, excluding null values, was 0.37 ± 0.21 SE. The maximum HWI was 0.70 ± 0.22 SE (CI = 0.22 - 1.00), indicating the presence of a strong dyadic association. The standard deviation (SD) and coefficient of variation (CV) of the observed pairwise association indices were significantly larger than those from permuted datasets, and were taken as evidence of mate preference or avoidance (actual SD = 0.21 / permuted SD = 0.0001, p =< 00001; actual CV = 0.57 / permuted CV = 0.00003, p = < 00001). Individuals were therefore not associated at random. They also differed in the number of individuals with which they were associated, estimated using the sum of the association indices. This sum varies from 1 to 12.36 ± 3.09 SE, and on average the individuals are associated with five others.

The sociogram created on Netdraw (Fig. 10) highlights two groups corresponding to the two islands. Individuals observed in Guadeloupe and Martinique form the link between these two groups, and those who have made several trips in particular. The main component of the sociogram was made up of 88% of the individuals in the study. All of the core residents and some of the residents were at the center of the two groups, while the visitors were more on the periphery. Eight satellite groups were observed, all from Guadeloupe. They were mainly made up of visitors (between four and 17 individuals), with only one group including three residents.

Discussion

As in Hawaii and the Canary Islands, short-finned pilot whales are present all year round in the area (Heimlich-Boran, 1993; Mahaffy, 2012; Alves, 2013; De Vries, 2017; Feunteun et al., 2019; Fléchet et al., 2019; Servidio et al., 2019). Short-finned pilot whales in both Guadeloupe and Martinique are distributed ca.1,000 m depth area, where they feed, as in other studies (Heimlich-Boran, 1993; Soto et al., 2008; Mahaffy, 2012). The opportunistic data collected during nine consecutive years has led to the creation of a specific catalogue for each island. The discovery curves show a continuous recruitment of new marked individuals into the groups. However, contrary to the study by Alves (2013) in Madeira, but consistent with that of Servidio et al. (2019) in Hawaii, no asymptote appears to have been reached. Thus, not all the individuals in the study areas were identified, supported by the low catch rates in relation to total abundance.

Sites fidelity and patterns of residency

Results revealed different residency patterns and fidelity to the surveyed area. The majority of individuals were observed only once, like most studies on this species (Alves, 2013; Mahaffy et al., 2015; Servidio et al., 2019). However, 30% of individuals in

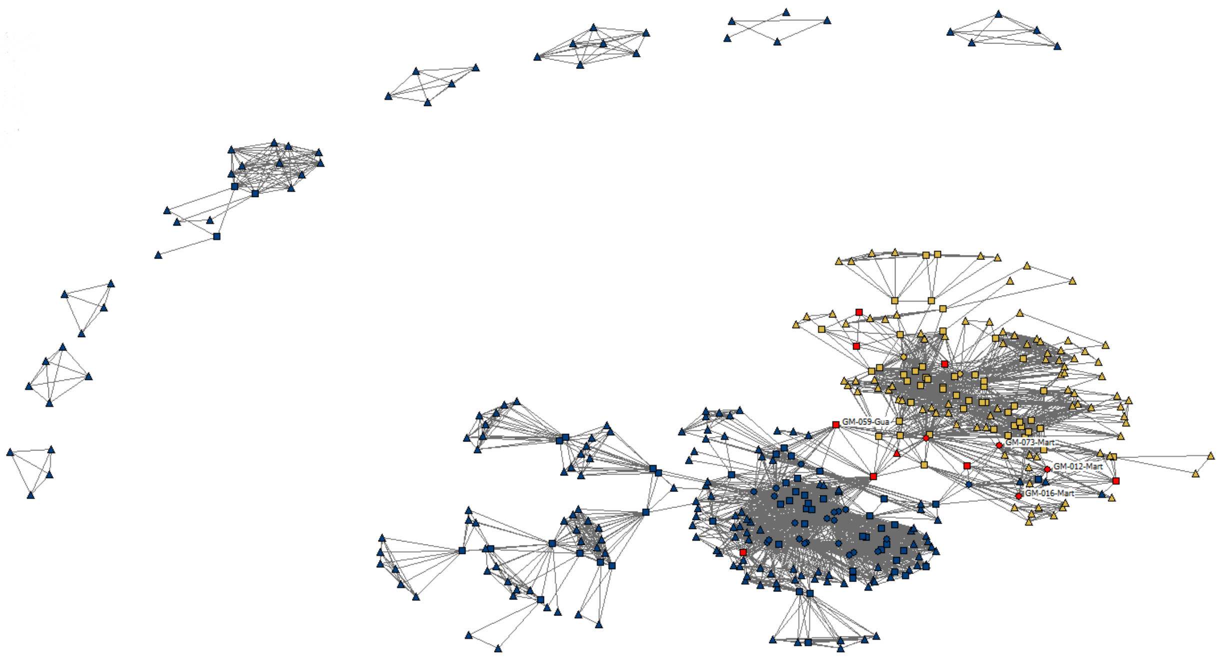

Figure 10: Sociogram of all short-finned pilot whales (*Globicephala macrorhynchus*) with a distinctive mark (n = 420), identified on the islands of Guadeloupe and Martinique between 2014 and 2022. Individuals are represented by nodes and the lines between these nodes represent the association indices between pairs of individuals (HWI). Individuals observed only in Guadeloupe are shown in blue, those observed only in Martinique in yellow, and those observed on both islands in red. Individuals having made several trips between these islands are identified by their code. Core residents are symbolized by circles, residents by squares, and visitors by triangles.

Guadeloupe and 38% in Martinique showed site fidelity between 2014 and 2022. They were observed several times over several consecutive years, with the number of recaptures increasing as the time interval between the first and last captures increased. Like the populations of Hawaii (Mahaffy, 2012), Madeira (Alves, 2013), and the Canary Islands (Heimlich-Boran, 1993; Servidio, 2014), the short-finned pilot whales of the French Lesser Antilles show a wide variability in the degree of fidelity. Residency patterns were characterized by a mix of core residents, residents, and visitors. This may suggest different patterns of habitat use (Heimlich-Boran, 1993). Visitor individuals, which tend to be pelagic, may have a distribution area that barely overlaps with the study area, a behavior that makes them less likely to be recaptured, or were simply not recaptured during the study period (Alves, 2013; Hill et al., 2019; Servidio et al., 2019). Several hypotheses can be put forward to explain this pattern of residency. On one hand, oceanic islands are considered to generate biological patches, leading short-finned pilot whales, nomadic teutophagous species feeding along the continental slope, to travel between feeding sites (Heimlich-Boran, 1993; Barton et al., 1998; Servidio et al., 2019). On the other hand, the presence of resident groups and other resident species in the area would cause inter- and intraspecific competition for the ecological niche, leading visitors to travel longer distances preventing them to become residents (Courtin et al., 2023). Nevertheless, the presence of the species all year round, with individuals associated with the islands (core resident and resident), indicates that Guadeloupe and Martinique may offer the resources needed for these groups to settle in, or at least visit on a regular basis.

Travel between Guadeloupe and Martinique

Ten individuals were observed in both Guadeloupe and Martinique over the period 2014 - 2022. Of those, four have made three inter-island trips, and three of them were permanently observed together. These results confirm the effectiveness of the photo-identification technique for monitoring cetacean populations, as was the case with sperm whales (*Physeter macrocephalus*) in the Caribbean (Gero et al., 2007; De Vries, 2017). Nevertheless, there are only 189 km separating Guadeloupe from Martinique, and it has been shown in Florida that short-finned pilot whales can travel 130 km in a day (Moore et al., 2020). It is conceivable that low-distinction individuals may also make this trip and not be counted. There is very little data on the inter-island movements of this species. However, this low recapture rate is also observed in the Canary Islands, where only two individuals have been recaptured between the islands of Gran Canaria and those of Lanzarote and Fuerteventura, 222 km apart, in 11 years (Servidio et al., 2019). The main movements of individuals in this study were less than 30 km and only 1% of captures were between 100 and 170 km apart (Servidio et al., 2019). We can therefore hypothesize that the short-finned pilot whales studied here are separated into two populations, one mainly distributed in the south-east of the Antilles (near Martinique) and one distributed in the north of the Antilles (around Guadeloupe). These two populations do not occupy a common geographical area, which makes it possible to distinguish them (Odum, 1983). The sociogram highlights the segregation of individuals from the two islands and those linking the two populations. This is also observed in the Canary Islands, where there are different, non-isolated populations that share distribution areas and maintain social ties (Servidio et al., 2019). In 2018, Strevick et al. reconsidered the existence of a single humpback whale (*Megaptera novaeangliae*) population segment in the Lesser Antilles, with a North-Southeast distinction. It is possible that this is also the case for other cetacean populations, and studies should be carried out on this subject, including observations from other nearby islands (*e.g.,* Saint Lucia to the south and Antigua to the north).

Modelling and estimation of short-finned pilot whale population parameters

The goodness-of-fit tests detected a transient effect in Guadeloupe, unlike in Martinique, caused by the very large number of individuals observed only once. It was chosen to consider only core residents and residents in Guadeloupe data, in order to limit the bias imposed by this excess (Pradel et al., 1997; Tezanos-Pinto et al., 2013). No trap-happiness or trap-avoidance effects were detected. Short-finned pilot whales do not seem to have any particular interest in boats, unlike pantropical spotted dolphins *Stenella attenuata* in the Agoa Sanctuary (Courtin et al., 2023). Finally, no over-dispersion of the data was observed, and the CJS models under the *POPAN* formulation chosen for Guadeloupe and Martinique were adequate (Choquet et al., 2005).

The probability of survival is an extremely complex parameter to estimate for a long-lived species (Jolly, 1965; Courtin et al., 2023). We noticed that it is higher in Guadeloupe than in Martinique. The inclusion of visitors in Martinique increases the consideration of the phenomenon of emigration. This reduces the probability of survival, since it is difficult to separate these two phenomena (Jolly, 1965). These high survival rates were observed for the Madeira population, where survival was also constant over time (Alves et al., 2015), and for long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar (Verborgh et al., 2009), both with resident groups. This corresponds with the estimated survival of pantropical spotted dolphins on Guadeloupe and Martinique (Courtin et al., 2023).

The probability of recapture varies with time, as is the case for most CMR analyses in cetaceans (Hammond, 2009; Alves et al., 2015; Courtin et al., 2023). Temporal variation in recapture probabilities on the two islands was associated with sampling effort, and follows the results of other studies using the same model (Alves et al., 2015; Chan & Karczmarski, 2017; Courtin et al., 2023). Recapture is directly linked to photo-identification, which in turn is correlated to the number of usable photos and, therefore, field trips (fewer in the wet season). This explains the higher recapture probabilities in the dry season and during sampling periods with high number of observations. Environmental factors, such as a better availability and distribution of prey, may also contribute to this variation (Alves et al., 2015). The estimates for the first sampling periods were extreme (close to one); in fact, they are commonly poorly estimated in CJS models, considering a temporal variation in recapture probabilities (Cooch & White, 2019).

The probability of marked individuals entering the population is highest in the first year on both islands. It is consistent that maximum recruitment occurs at the beginning, since no identification is considered before then (Courtin et al., 2023). This is reflected in the immediate presence of core residents and residents in Guadeloupe, with recruitment in 2019 and 2020, around the dry season. For Martinique, this seems to be more extended, with peaks also occurring during the dry periods. This probability of entry into the group of marked individuals β, can illustrate a phenomenon of clan association. In fact, recruitment seems to take place during warm periods (around the dry season), which may result in the arrival of visiting clans in the study area for mating (Heimlich-Boran, 1993). However, the time interval between sampling surveys could potentially have an impact on the probability β, so these results should be taken with caution, even if not all recruitment peaks are affected.

The estimated total abundance of individuals associated with Guadeloupe was higher than that estimated for Madeira (Alves, 2013). No total estimate was available for comparison with the 565 individuals estimated in Martinique. An overall decrease in the number of marked individuals was observed for both islands, even if some increases are also observable. In Guadeloupe, this resulted in the stabilization of abundance, which may be linked to an increase in the accuracy of the model over time (Cooch & White, 2019). In Martinique, the decline was more drastic, with no stabilization. The area where short-finned pilot whales are found in Martinique is important for feeding and rearing of young, because of a favourable continental slope (Fléchet et al., 2019; Servidio et al., 2019), but it is also an area highly exposed to human activity (Feunteun et al., 2019; Foulquier et al., 2021; Madon et al., 2022). The short-finned pilot whale is one of the species most exposed to the risks of collision with ships, and to the various physical and physiological stresses generated by human activities (De Stephanis & Urquiola, 2006; Madon et al., 2022). Moving to other distribution areas may therefore be a short- and long-term way of avoiding these disturbances (shipping traffic, acoustic disturbance, whale-watching, and water pollution), and could explain the decline in abundance observed in Martinique (Cuzange, 2011; Feunteun et al., 2019). Another hypothesis may be added, linked to the fishing activity carried out and targeted at short-finned pilot whale in SVG (Fielding & Kiszka, 2021). In Japan, the commercial catch in the early 1980s was suspected of being the partial cause of a serious decline in short-finned pilot whale abundance (Kanaji et al., 2011). Because of its proximity to SVG and the estimation at 143.2 pilot whales captured per year between 1962 and 2006 (Fielding & Kiszka, 2021), populations can be vulnerable. Even if it is less at SVG than Japan, the take of individuals from the population in the southern Antilles could lead to a reduction in abundance and/or a displacement of the hunted clans, which could explain part of the decline observed.

Individual association and social bonds

Analyses for individuals captured four times or more revealed a well-differentiated society with long-lasting relationships as in Madeira (Alves et al., 2013) and Hawaii (Mahaffy et al., 2015) for short-finned pilot whales, and in Canada and the Strait of Gibraltar for long-finned pilot whales (Ottensmeyer & Whitehead, 2003; De Stephanis et al., 2008). The HWI has been highly variable between the only two short-finned pilot whale populations for which analysis were performed, in Madeira 0.77 (Alves et al., 2013) and Hawaii 0.06 ± 0.01 (Mahaffy et al., 2015). The index determined in this study (HWI = 0.37 ± 0.21) lies between these two extremes. This high variation may be linked to the size of the population studied and/or to ecological factors influencing social structure, such as food availability (Louis et al., 2017;

Haderlé, 2022). On the other hand, the sociogram showed a main group made up of a large proportion of individuals, as was the case in Hawaii (Mahaffy et al., 2015) and in the Mariana Islands (Hill et al., 2019) including core residents and residents in the center and visitors on the periphery. This supports the theory of a clan association for mating, and the arrival of visiting clans at island level for breeding. This phenomenon may be related to a fission-fusion system observed in other delphinid species (Haderlé, 2022; Courtin et al., 2023).

Implications for short-finned pilot whale conservation in the Agoa Sanctuary

International collaboration is essential in order to better understand dynamics and distribution of short-finned pilot whales in the Lesser Antilles. The first results from the Caribbean, described and discussed here, focus on the islands of Guadeloupe and Martinique. This raises many questions about the potential Caribbean metapopulation, made up of several interconnected populations. Very little is known and understood about the factors influencing residence patterns of this species and movements between islands (Servidio et al., 2019). This is probably not a single factor but the result of a combination of several simultaneous variables, such as the availability and distribution of resources (De Stephanis et al., 2008; Alves, 2013). Given that this species is hunted on several Caribbean islands, it is important to study the movements of these animals, in relation to reproduction and feeding. Similarly, recapture probabilities may be altered by hunting. The Agoa Sanctuary needs to better understand the issues surrounding this species in order to guarantee it a real sanctuary when it is in its waters.

Analysis of population structure and dynamics has proved to be of great importance for the identification of conservation units (Aschettino et al., 2012; Alves, 2013; Chan & Karczmarski, 2017). Two conservation units seem to be emerging for each of the hypothetical populations: the visiting clans, which tend to be pelagic, and the resident clans, core residents and residents, which are associated with the islands. The importance of the Caribbean coast for the clans associated with the islands makes them a priority, as is the case for the pantropical spotted dolphin, since they are subject to very strong anthropogenic pressures (Feunteun et al., 2019; Courtin et al., 2023). In the case of the pelagic clans, which are mobile and most likely evolve in several territories and countries, international collaboration is necessary, as the CAR-SPAW ('Spaw Protocol' 1990), a convention signed by several countries in the Caribbean, with the aim of coordinating management and protection measures.

Further work, including complementary protocols, such as genetics and bioacoustics, should be developed. This would help to understand the connectivity between different populations, which may be more numerous, and between clans. In addition, the social structures of these populations, and how they may affect their vulnerabilities, also need to be studied in the Lesser Antilles, providing important information to be considered in future conservation plans.

Acknowledgments

The authors are grateful for the financial support provided by the Agoa Sanctuary. They would like to thank the whale-watching companies *Dauphin-Passion, Aliotis Plongée, Madisea Dauphin Emotion, Schéhérézade, Aventure Cétacés, Cétacés Caraïbes, Guadeloupe Evasion Découverte* and *Blue Dream*, for their friendly help in taking us to collect the photo-ID data. We thank volunteers from Aquasearch and OMMAG for sharing their photos for this project. We are grateful to Dr Jaime Bolaños Jiménez for his advice and help with the modelling.

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