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Insights on the residency status and inter-island movement patterns of pantropical spotted dolphins *Stenella attenuata* in the Agoa Sanctuary, Eastern Caribbean

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Abstract

The pantropical spotted dolphin (PSD, *Stenella attenuata*) is the most common cetacean species observed within the Agoa Sanctuary, located in the Lesser Antilles, Eastern Caribbean. These dolphins are easily observable and are the main target of whale-watching activities along the leeward coasts of Guadeloupe and Martinique islands. Because PSD is common within the sanctuary it is considered a resident species, however, no research has been carried out to estimate its population status and movement patterns between islands. Previous unpublished work found the sighting of an individual in Martinique and Guadeloupe, suggesting potential exchange of individuals between these islands. To test this hypothesis a photo-ID survey in 2018 and 2019 was conducted, resulting in 54,298 photographs. With no matches of individuals between islands, our findings do not support regular exchange of PSD individuals between Martinique and Guadeloupe. However, given previous re-sighting data, it is possible that movement of individuals between islands exists but at lower frequencies than expected, which can only be detected through long-term surveys. Additionally, populations from both islands showed relatively high site fidelity. We found that in Guadeloupe the PSD population is homogeneously distributed along the coast. In contrast, in Martinique the PSD population was composed of two resident groups concentrated in one area. Moreover, 70 new individuals were identified in Guadeloupe and 54 in Martinique while POPAN modelling estimated the number of marked individuals in the study area during 2018 and 2019 at 89 in Guadeloupe and 90 in Martinique. This research provides the first insights on the residency and movement patterns of *S. attenuata* in the Agoa Sanctuary and can inform future efforts in management and conservation.

Keywords:
Cetacea, Photo-ID, CMR, Conservation, French West Indies

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Introduction

The pantropical spotted dolphin (PSD, *Stenella attenuata*) is widely distributed around tropical marine waters from 40° N to 40° S and is one of the most common dolphin species in the Atlantic and Indian oceans (Jefferson *et al.*, 2015; Perrin, 2018). As a result of such wide ranges, it is often considered as an "umbrella species", meaning that conservation efforts for this species will benefit many other species sharing the same habitat (Jefferson *et al.*, 2015). PSD is a fairly slender, streamlined animal, with a dark cape and light spots on its body that increase in number and size as it gets older (Jefferson *et al.*, 2015; Perrin, 2018). This species has a long, thin beak and a falcate dorsal fin, which is the thinnest among dolphins (Shirihai and Jarett, 2007; Perrin, 2018). In the Caribbean Basin, PSD can be found in waters close to islands (do Amaral *et al.*, 2015; Barragán-Barrera *et al.*, 2019), making them easily observable from small boats. They often show acrobatic and bow riding behaviours (Shirihai and Jarett, 2007) making them the main target for whale-watchers.

Guadeloupe, Martinique, St. Martin, and St. Barthelemy islands are part of the Agoa Sanctuary's area of protection. This 140,000 km² protected marine area corresponds to the exclusive economic zone (EEZ) of the French West Indies in the Lesser Antilles, Eastern Caribbean. In addition to PSD, 24 cetacean species have been reported and are protected in the Agoa Sanctuary (Office Français de la Biodiversité, 2012). Furthermore, PSD is also protected in the Wider Caribbean waters under the SPAW Protocol (Vanzella-Khouri, 1998).

PSD has been historically reported in the Lesser Antilles (Caldwell *et al.*, 1971; Watkins, 1985) and is present year-round around the coasts of Guadeloupe (Cuzange, 2011; Mayol *et al.*, 2016) and Martinique (Cuzange, 2011; Mayol *et al.*, 2016; Feunteun *et al.*, 2019). It is the most observed cetacean species around the leeward coasts of these islands, making it central to the whale-watching economy (Gandilhon, 2012; Mayol *et al.*, 2016). PSD is exposed to other anthropogenic pressures such as chemical pollution, acoustic disturbance caused by marine traffic, and decrease in food availability caused by fisheries (Cuzange, 2011; Safi *et al.*, 2020). However, apart from an ecological niche modelling study of this species in the Caribbean Basin (Barragán-Barrera *et al.*, 2019), no study about PSD ecology and distribution in the Lesser Antilles has been published yet.

Individuals' identification in both islands from unpublished data have suggested that populations in Guadeloupe and Martinique are distinct. However, in 2013, a PSD individual (SA054) named "Victoire", was observed for the first time in both Guadeloupe and Martinique (Bouveret, Millon and de Montgolfier, unpub. data). That individual exhibited two wide white spots, one on each side of the body, making it easily identifiable. These observations raised questions about the potential connectivity of PSD individuals between these islands, for which the dolphins need to travel at least 130 km, including waters off Dominica. Similar movement patterns between the islands have been confirmed for sperm whales (*Physeter macrocephalus*) between Guadeloupe, Dominica, St. Lucia, and Grenada islands (Gero *et al.*, 2007; De Vries, 2017), as well as for short-finned pilot whales (*Globicephala macrorhynchus*) between Martinique and Guadeloupe islands (De Vries, 2017).

Photo-ID has proved to be a powerful, relatively inexpensive, non-invasive Capture-Mark-Release (CMR) technique in the study of cetaceans and other marine mega-vertebrates to assess aspects of their natural history, population abundance (Tyne *et al.*, 2014; McKinney *et al.*, 2017; Wray *et al.*, 2021), and movement patterns over short (Wilson *et al.*, 1998; Rock *et al.*, 2006; Pereira and Maneyro, 2016) and long distances (Jann *et al.*, 2003; Gero *et al.*, 2007; O'Brien *et al.*, 2009). This technique is based on individual identification, using documentation of natural marks occurring in a visible part of the animal (Würsig and Jefferson, 1990). Natural marks on the dorsal fin have already been used to identify delphinids in the Caribbean Sea such as bottlenose dolphins (*Tursiops truncatus*; Kerr *et al.*, 2005; Luksenburg, 2014; Bolaños-Jiménez *et al.*, 2021) and short-finned pilot whales (De Vries, 2017; Fléchet *et al.*, 2019), while caudal fins have been used to identify sperm whales (Gero *et al.*, 2007; 2014; De Vries, 2017) and humpback whales (*Megaptera noveangliae*; Whitehead and Moore, 1982; Katona and Beard, 1990; Smith *et al.*, 1999; Robbins *et al.*, 2006). Short-term movement patterns, migrations, and home range can be determined when photos of the same individual are obtained in more than one locality (Würsig and Jefferson, 1990) while identifications in one location allow to estimate survivability and residency patterns (Williams *et al.*, 1993; Whitehead, 2001). However, enough amount of data over a long period is required (Rosel *et al.*, 2011; Urian *et al.*, 2015). Because long sampling efforts are scarce mainly by limited funding, citizen-based science programs have already demonstrated to be a valuable and useful platform of collecting photos or videos while raising among the public concern about cetacean management (Alessi *et al.*, 2019). When observers are trained and concerned about research programs, it is possible to increase the quality of the raw material, the coverage and the data set available, as well as involve professional and amateur people in conservation actions without compromising data quality (Ellwood *et al.*, 2017). Moreover, residency patterns have been traditionally assessed through at least one of the three measures proposed by Ballance (1990) and modified by Morteo *et al.* (2012), Occurrence (O), Permanence (P), and Periodicity (I). However, the variability in the use of residency measures and the lack of standardisation have not allowed the establishment of comparisons between studies and populations (Morteo *et al.*, 2012; Tschopp *et al.*, 2018). Therefore, including all of these three measures, a Standardized Site Fidelity Index (SSFI), robust to irregular sampling effort and imperfect capture probabilities, was developed to answer these issues (Tschopp *et al.*, 2018).

Here we used photo data sets obtained from citizen-based science programs and dedicated scientific surveys with the goal of describing the residency patterns, distribution, connectivity, and size of two PSD populations observed in the leeward coasts of Guadeloupe and Martinique islands, in the French Antilles. Our study focused on good quality photos and highly identifiable individuals, whose marks are mostly found on the dorsal fins. Apart from the studies in Hawaii by Psarakos *et al.* (2003) and Machernis *et al.* (2021), who used photo-ID to determine mixed-species interactions between PSD and spinner dolphins (*Stenella longirostris*), and between PSD and bottlenose dolphins with fishing vessels, respectively, no other study using photo-ID on any PSD population worldwide had been published yet. Therefore, this study is a test of this method in identifying movement and residency patterns of PSD in the Caribbean.

Materials and method

Study area and time stratification

Guadeloupe and Martinique are two islands of the French West Indies, which present a similar climate due to their proximity (Fig. 1A). Both islands are mainly influenced by two seasons, the dry (*carême*) season from December to May, and the wet (*hivernage*) hurricane season from June to November (Cerema, 2020; Météo France, 2020*a, b*). Transition periods occur between seasons, with monthly variations of precipitations and temperature (Cerema, 2020; Météo France, 2020*a, b*). Therefore, for this study and following Rosel *et al.* (2011), seasons were divided into two

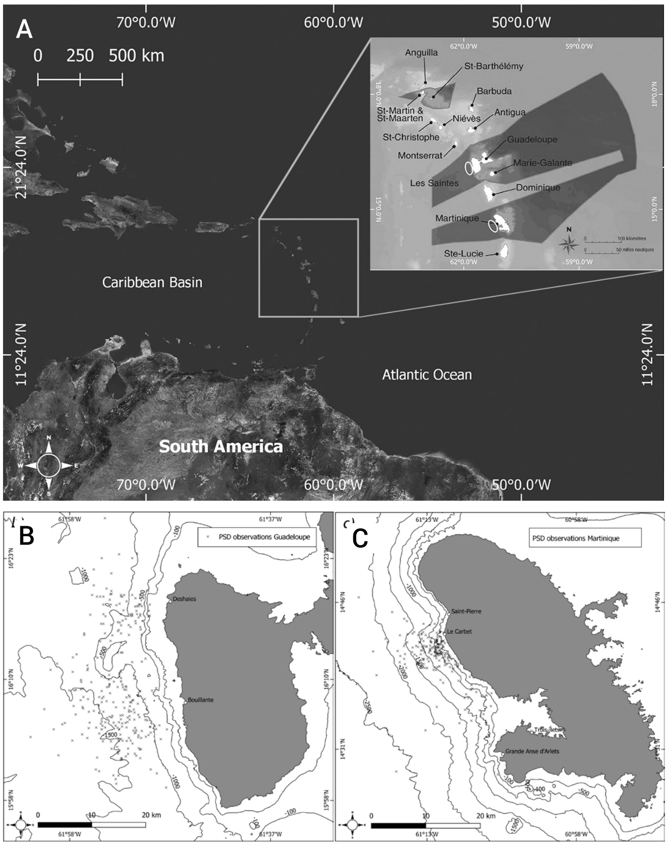

Figure 1. (A) Location of the Agoa Sanctuary in the Eastern Caribbean Sea (darker grey irregular polygon within the inset), showing the study area within white elypses along the leeward coasts of Guadeloupe and Martinique islands. (B) Locations of pantropical spotted dolphin (*Stenella attenuata*) observations (marked with an "x") in Guadeloupe and (C) in Martinique from 2018 to 2019.

sampling periods, giving four sampling periods per year. 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). Because the Early Dry sampling period of 2018 included December of 2017, for which data was not available, that sampling period only consisted of January and February 2018.

In both islands, the leeward coasts are surrounded by deep waters (steep drop offs, 1,000 m isobath is at 3.5 and 2.5 nautical miles from the shore in Martinique and Guadeloupe, respectively), and are protected by the islands from swell and trade winds coming from the Atlantic Ocean. Very few PSD observations on the windward side of these island have been reported, and most PSD seem to concentrate year-round on the leeward side of both islands (Cuzange, 2011; Mayol *et al.*, 2016).

Data collection

Fieldwork was conducted from January 2018 to November 2019, from 07:30h to 18:00h in both islands. In Guadeloupe, surveys were carried on through citizen-based science programs with the Observatoire des Mammifères Marins de l'Archipel Guadeloupéen (OMMAG), involving whale-watchers, members, and researchers. OMMAG is an associative network that gathers photos of cetaceans around the Guadeloupe Archipelago and classifies them to make them available for science programs. Photos were taken between 16°23' N and 15°58' N latitudes and 61°63' W to 61°48' W longitudes (Fig. 1A, B). More than 90% of photos were taken by one of the authors (CM) through his whale-watching company *Cétacés Caraïbes* that departed from Bouillante, and by Claire Freriks, through the whale-watching company *Guadeloupe Evasion Découverte* that departed from Deshaies, while the remaining 10% were taken by other OMMAG members. In Martinique, effort was conducted by Aquasearch staff through scientific surveys departing from Trois-îlets, or onboard whale-watching vessels that departed from Trois-îlets and Grande-Anse d'Arlets. Photos were taken between 14°28' N and 14°44' N latitudes and 61°05' W to 61°17' W longitudes (Fig. 1A, C).

Once an individual or a group of individuals was observed, time, sea and weather conditions, GPS position, estimated group size, predominant group activity, heading of the group, age structure, and observer name were systematically collected. Photos of individual dolphins as well as their dorsal fins were collected during each observation using different camera models. Whale-watchers and members associated to OMMAG used mainly cameras Nikon D500, D7200, and D3200 with 70-200 mm, 18-200 mm, and 18-300 mm lenses. Aquasearch observers used Nikon D7100 and D500 cameras, with a Nikon 70-300 mm lens.

Age structure was assessed by experienced observers through individuals' size and appearance. Calves were identified by being less than ¾ the size of an adult, showing no spotting, and staying always close to an adult; juveniles were identified by being ¾ the size of an adult, with dark ventral spotting developing, usually swimming in close association with an adult (Shirihai and Jarett, 2007; Jefferson *et al.*, 2015; Perrin, 2018). A group of dolphins was defined as those individuals executing the same behaviors but maintaining a relatively short distance between group members (less than 50 m, Mann, 1999). However, for this study, each sighting was established to individual level, so sighting was defined as the set of photos of a uniquely identified individual considered for each survey associated with its observation information.

Tests of variations in sampling effort

To determine if there was significant sampling effort variation in usable photos, the distribution normality (Shapiro-Wilk test), residuals independence (Durbin-Watson test), and homoscedasticity (Bartlett test) among sampling periods were tested; then, significant differences between sampling periods were tested with a one-way ANOVA or a Kruskal-Wallis test. All analyses were conducted using R version 4.0.3 (R Core Team, 2020).

Photo-identification analysis

Marks on dolphins can be the result of anthropogenic or intra- and interspecies interaction, and can occur all over the body, however, in general only the dolphin's back and its dorsal fin are visible by an observer on a boat. For this reason, dolphins' photo-ID analyses are based mainly on marks in the dorsal fin (Würsig and Jefferson, 1990). When analyses are based on one or two simple dorsal fin notches, it is possible to confuse between two different individuals with similar notches, causing misidentifications and false positive or false negative matches that can lead to significant bias in abundance estimates, residency indexes, etc. (Würsig and Jefferson 1990; Urian *et al.*, 2015).

Therefore, based on Urian *et al.* (2015), only highly identifiable individuals were used for analyses.

Pictures were rigorously sorted, based on three distinctiveness categories: “D1”, “D2”, and “D3” for “very distinctive”, “average distinctive”, and “not distinctive” individuals, respectively (Urian *et al.*, 2015). Following Passadore *et al.* (2017), photos were also classified by a quality score, based on the picture focus, contrast, and the angle of the dorsal fin, in order to minimize misidentification. The quality score categorized an “excellent” photo as “Q1”, a “good” photo as “Q2”, and a “poor” photo as “Q3”. Only photos of distinctive individuals (D1 and D2) with good quality (Q1 and Q2) were included in the analyses (Fig. 2). Individual identification was conducted manually using the Windows Pictures® software, to process, match and classify all dolphin photos. Matches were made comparing identified individuals in both islands to assess potential movements between islands. An individual was considered ‘captured’ when it was first photo-identified, and ‘recaptured’ when it was photo-identified again. An individual captured in one island and recaptured in the other one was considered as an inter-island match. Results were compiled in capture-recapture matrices (sighting histories) for further analysis by means of the MARK software (White and Burnham, 1999). Each identification of a marked individual and its GPS position were compiled to build occurrence maps for each island.

Individual encounter rates

Number of pictures, individuals, identifications, and recaptures were calculated. The recapture rate (R%) was calculated for each island, using equation 1, as follows:

$$R\% = \frac{R}{N}$$

where *R* is the number of individuals recaptured at least once, and *N* is the total number of individuals identified along the study period.

Closure test and goodness of fit

Closure of the population was tested with CloseTest (Stanley and Burnham, 1999) and the discovery curves of newly identified individuals (Colwell *et al.*, 2004). Several assumptions must be considered under POPAN models for open-population to obtain accurate, unbiased, and precise estimates of the parameters (Schwarz and Arnason, 1996). To see if the data met these assumptions, goodness of fit tests (TEST 2 and TEST 3) were

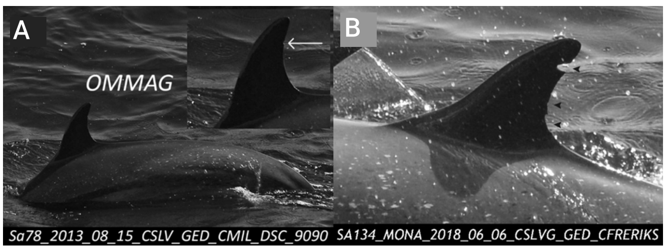

Figure 2. Images of (A) lightly marked individual D3 of pantropical spotted dolphin (*Stenella attenuata*) with a simple superficial notch, and (B) of moderately marked individual D2 with multiple deep notches (Photos: C. Millon and C. Freriks).

conducted using U-CARE software (Choquet *et al.*, 2005; 2009). TEST 2 examines significant difference in capture probabilities among individuals, and TEST 3 examines if all identified individuals have the same probability of survival between sampling occasions. These tests can be partitioned into four different tests: (i) TEST 2.CT, which tests significant trap effect (trap happiness vs. trap shyness); (ii) TEST 2.CL, which tests significant variation in the time between re-encounters for captured and not captured, but known to be alive, individuals; (iii) TEST 3.SR, which tests significant excess or lack of transient individuals; and (iv) TEST 3.SM which tests significant effect of capture on survival (Choquet *et al.*, 2005; 2009). GLOBAL TEST combines TEST 2 and TEST 3 to detect significant overdispersion of the data (Choquet *et al.*, 2005; 2009).

Clustering and estimation of site fidelity

The recently developed Standardized Site Fidelity Index (SSFI) IH4 was used to assess site fidelity and residency patterns at the population level (Tschopp *et al.*, 2018), following equation 2:

$$SSFI = \frac{2}{\frac{1}{IT}+\frac{1}{It}}$$

With *IT* as the permanence and *It* as the periodicity of an individual. Four SSFI indexes were calculated for each individual identified by using sighting histories with different temporal scales: (i) $SSFI_t$ using sighting history by trip, (ii) $SSFI_m$ using sighting history by month, (iii) $SSFI_p$ using sighting history by sampling period and (iv) $SSFI_s$ using sighting history by season. $SSFI_p$ was used to compare site fidelity between sites and clusters using a Wilcoxon-Mann-Whitney test.

When a transient effect was detected, the SSFI indexes were used to separate each of the populations into two clusters (cluster 1 = F.U. for Frequent Users of the area, and cluster 2 = O.V. for Occasional Visitors of the area) with an Agglomerative Hierarchical Classification (AHC) analysis (Zanardo *et al.*, 2016; Hunt *et al.*, 2017; Passadore *et al.*, 2018). The AHC was built using Euclidean distance as the dissimilarity measure, and Ward’s method (minimum variance) as the agglomerative clustering algorithm (Ward Jr, 1963). Clustering analysis was conducted on R version 4.0.3 (R Core Team, 2020) with pvclust package (Suzuki *et al.*, 2019) following Passadore *et al.* (2018, see Acknowledgments). The Guadeloupe population did not show any transience effect hence was considered as one group belonging to the same population.

Statistical analysis and estimation of population parameters

Sighting histories of identified individuals were used to find the most parsimonious model that fits our data. POPAN formulation of Jolly-Seber model for open population (Schwarz and Arnason, 1996) was used with MARK version 9.0 (White and Burnham, 1999). As results of GLOBAL TEST did not find any significant over-dispersion in the data, AICc (Akaike Information Criterion) was used to choose the best model to estimate apparent survival φ annually and between sampling periods, capture probability p, probability of entrance β (β prior the first sampling period was calculated by subtracting the sum of β of all sampling periods from one), and abundance N of the marked part of the population.

For Martinique, with two groups and eight sampling periods, models were chosen considering a constant (.), time-variable (t), group-variable (g), or time and group variable (g*t) structure for the parameters φ, p and a time and group variable (g*t) structure for parameter β, resulting in 16 possible models. For Guadeloupe, with one group and eight sampling occasions, models were chosen considering a constant (.) or time-variable (t) structure for each parameter φ, p and β, giving eight possible models.

Results

A total of 272 survey trips (102 for Martinique and 170 for Guadeloupe) were conducted between January 2018 and November 2019 in the Agoa Sanctuary, along the leeward coasts of Guadeloupe and Martinique islands. A total of 54,298 photos were collected from 2018 to 2019, of which 32,043 were taken in Guadeloupe and 22,255 in Martinique. After quality and distinctiveness examination, 13,156 (41%) photos in Guadeloupe and 10,499 (47%) in Martinique were considered for analysis, of which 301 identifications were made (Table 1). The mean size of the groups was estimated at 196 (CI = 172 – 220) individuals in Guadeloupe and 98 (CI = 88 – 108) individuals in Martinique. For both islands, the number of useful photos (Q1+Q2) for each sampling period was not constant and was correlated with the number of survey trips (Table 1, Spearman test for Guadeloupe: $p < 0.005$, $\rho = 0.80$, Spearman test for Martinique: $p < 0.001$, $\rho = 0.80$). However, no significant differences ($p = 0.46$, Kruskal-Wallis test for Guadeloupe; $p = 0.46$, Kruskal-Wallis test for Martinique) in sampling effort among sampling periods were observed.

Clustering and goodness of fit tests

Tests of closure (Otis test for Guadeloupe and Martinique, $p < 0.001$; Stanley and Burnham test for Guadeloupe and Martinique, $p < 0.001$) and discovery curves (Fig. 3) indicated that populations of both islands are open. In Guadeloupe, considering one group, GLOBAL TEST, TEST 2.CT, TEST 2.CL, TEST 3.SR and TEST 3.SM, did not present any significant over-dispersion of the data ($\chi^2 = 9.67$, df = 16, $p = 0.88$). In Martinique, considering one group, TEST 3.SR indicated a significant excess of transient individuals (individuals seen only once, TEST 3.SR, $p < 0.05$). Therefore, the Martinique population was divided in two different clusters (O.V. and F.U.) to run Goodness-of-fit tests again. These analyses found no significance for TEST 3.SR and no over-dispersion in the data for GLOBAL TEST ($\chi^2 = 3.73$, df = 12, $p = 0.99$).

Photo-identification analysis

During the two-year study period and for both islands, 301 instances of highly identifiable individuals led to the characterization of 124 individuals (Table 1). For Guadeloupe, 172 identifications were made, and 70 new individuals were identified. Individual identification slowed down after August 2018 but did not reach a plateau (Fig. 3A) indicating that not all marked individuals of the study area were identified, and confirming the openness of the population. PSD observations seem to be homogeneously spread along the leeward coast of Guadeloupe, except for the southwest part where only few observations were made (Fig. 1B). Individuals with the maximum numbers of recaptures in that island were SA055 "Willy", SA081 "Arnold", and SA150 "Claire", which were recaptured nine times each during the study period. Thirty-two individuals (46%) were recaptured at least once and $SSFI_p$ for Guadeloupe was estimated at 0.19 (CI = 0.13 – 0.25).

For Martinique, where most observations were found in front of "Le Carbet" (Fig. 1C), 129 identifications were made, and 54 new individuals were identified, of which 16 were F.U. and 38 were O.V. The F.U. discovery curve (Fig. 3B) reached a plateau indicating that most of these individuals were identified in the area. Conversely, the O.V. discovery curve did not reach a plateau, which indicates there are more individuals to be identified in the area. Twenty-five individuals (46%) of the total population, 16 F.U. (100%), and nine O.V. (24%) were recaptured at least once (Table 2). SA155 "Diamant" was the individual with the maximum number of captures in the island (nine times during the study period). $SSFI_p$ was estimated at 0.18 (CI = 0.11 – 0.25) for the total population, 0.55 (CI = 0.46 – 0.64) for F.U., and 0.03 (CI = 0.001 – 0.05) for O.V. (Table 2). $SSFI_p$ was not statistically different between the Guadeloupe population and the total population in Martinique but $SSFI_p$ of frequent users (F.U.) was statistically higher than $SSFI_p$ of the occasional visitors (O.V.) in Martinique (Kruskal-Wallis, $p < 0.001$). No inter-island matches occurred along the study period, and SA054 "Victoire" was observed only one time in Guadeloupe.

Table 1. Data collected and identifications of pantropical spotted dolphins (*Stenella attenuata*) in the Agoa Sanctuary along the leeward coasts of Guadeloupe and Martinique islands. Data is shown as sampling periods, number of survey trips, photos collected, usable photos, identifications and new individuals identified.

	Sampling period	Survey trips	Collected	Usable	Identifica-tions	New individuals
GUADELOUPE	ED2018	13	1558	1199	10	8
	LD2018	22	1880	621	25	14
	EW2018	22	2186	1354	53	26
	LW2018	3	132	75	3	1
	ED2019	17	2457	1118	9	3
	LD2019	50	10768	4211	34	11
	EW2019	26	5884	2525	19	4
	LW2019	17	7178	2053	19	3
	Total	**170**	**32043**	**13156**	**172**	**70**
MARTINIQUE	ED2018	6	527	344	8	6
	LD2018	10	1501	909	10	9
	EW2018	10	2291	1405	8	5
	LW2018	10	1891	808	14	5
	ED2019	19	5737	2460	21	13
	LD2019	30	7594	3158	44	9
	EW2019	12	1506	824	18	5
	LW2019	5	1208	591	6	2
	Total	**102**	22255	10499	129	54
TOTAL		***272***	***54298***	***23655***	***301***	***124***

Modelling and estimation of population parameters

For Guadeloupe, with one group and eight sampling occasions, the best model that fitted our data carried 96% of the AICc weight and incorporated constant apparent survival, time-varying capture

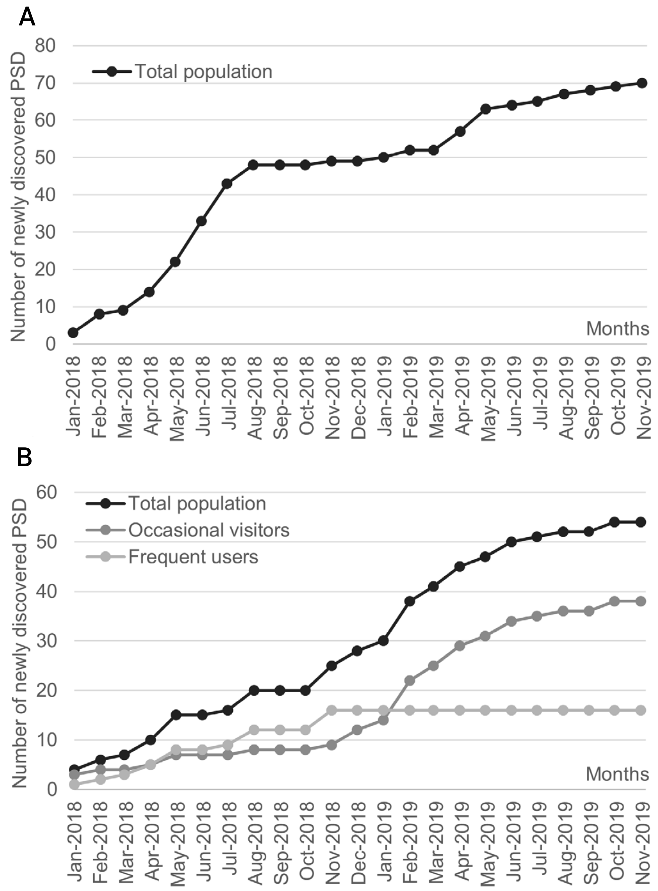

Figure 3. Discovery curve of identified pantropical spotted dolphin (*Stenella attenuata*), (A) in Guadeloupe and (B) in Martinique.

probability, and time-varying probability of entrance (Table 3). Apparent survival φ was estimated at 0.77 (CI = 0.67 – 0.84) between sampling periods and 0.35 (CI = 0.21 – 0.52) annually. Capture probability p varied between 0.07 (CI = 0.02 – 0.20) in Late Wet 2018 and 0.99 (CI = 0 – 1) in Early Dry 2018 (Fig. 4A) seasons. Probability of entrance in the superpopulation β ranged from 0.06 (CI = 0 – 0.86) between Early Wet 2018 and Late Wet 2018 to 0.37 (CI = 0.12 – 0.72) between Early Dry 2018 and Late Dry 2018 (Fig. 4B). More than two thirds (69%) of the individuals entered the superpopulation in Late Dry 2018 and Early Wet 2018. Seasonal abundance estimates of marked dolphins ranged from nine individuals (CI = 5 - 16) in Early Dry 2018 to 59 individuals (CI = 40 - 85) in Early Wet 2018, and then decreased slightly to reach 27 individuals (CI = 17 – 43) in Late Wet 2019 (Fig. 4C). Total abundance of the marked population fraction, N, was estimated at 89 individuals (CI = 78 – 111) in the study area.

For Martinique, with two groups and eight sampling occasions, the model that fitted the best our data carried 98% of the AICc weight and incorporated group-varying apparent survival, time-varying capture probability, and time-varying and group-varying probability of entrance (Table 3). Apparent survival probability for O.V. was estimated at 0.17 (CI = 0.07 – 0.39) between sampling periods and at 0.001 (CI = 0.00 – 0.03) annually. For F.U., it was estimated at 0.99 (CI = 0 – 1) between sampling periods and annually. Capture probability p varied between 0.18 (CI = 0.06 – 0.43) in Late Wet 2019 and 0.99 (CI = 0 - 1) in Early Dry 2018 (Fig. 5A). For O.V., probability β of entrance in the global population is relatively constant and remained between 0.02 (CI = 0.001 – 0.19) and 0.13 (CI = 0.02 – 0.51), except between Late Wet 2018 and Early Dry 2019 when it reached a high 0.37 (CI = 0.22 – 0.71, Fig. 5B) while new individuals entered the superpopulation. For F.U., β was estimated at 0.19 (CI not estimable) before Early Dry 2018, 0.81 (CI = 0.55 – 0.94) between Early Dry 2018 and Late Dry 2018 and 0 for the last sampling periods, meaning that all the F.U. individuals entered the superpopulation in the first sampling periods. Seasonal abundances for marked F.U. were estimated at three individuals (CI = 1 – 8) in the first sampling period and 16 individuals (CI not estimable) for the remaining study period. Marked O.V. abundances ranged from two individuals (CI = 0 – 8) in Late Wet 2018 to 34 individuals (CI = 16 – 73) in Early Dry 2019 (Fig. 5C). Total abundance of the marked population N was estimated at 74 O.V. individuals (CI = 55 – 119) and 16 F.U. individuals (CI not estimable), for a total population of 90 marked individuals.

Table 2. Summary of the number of individuals identified, $SSFI_p$, maximum number of captures and recapture rates of pantropical spotted dolphins (*Stenella attenuata*) in Guadeloupe and Martinique.

Population	Identified individuals	$SSFI_p$	Max nb. of captures	Recapture rate
Guadeloupe	70	0.19 (95% CI = 0.13 - 0.25)	9	46%
Martinique	54	0.18 (95% CI = 0.11 - 0.25)-	9	46%
Martinique F.U.	16	0.55 (95% CI = 0.46 - 0.64)-	9	100%
Martinique O.V.	38	0.03 (95% CI = 0.001 - 0.05)-	2	24%

Discussion

Sampling effort based on citizen science data

The use of citizen science in photo-ID, by relying on different observers in the data collection process, can imply variations

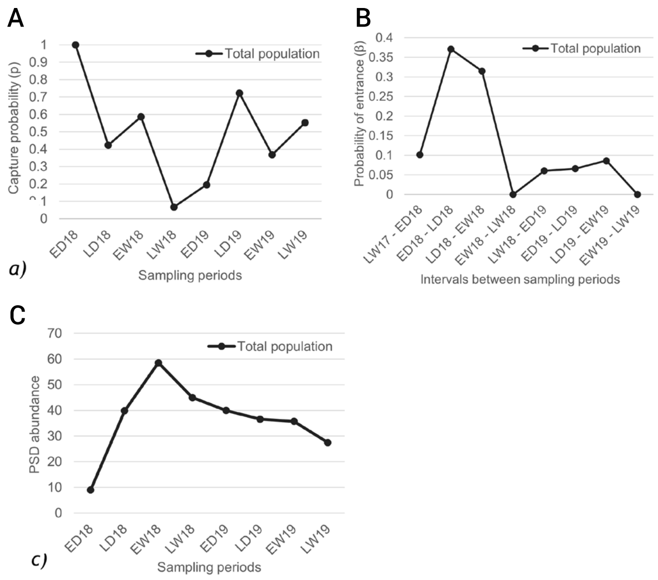

Figure 4. POPAN estimates of (A) capture probability, (B) probability of entrance in the superpopulation and (C) seasonal abundance of pantropical spotted dolphin (*Stenella attenuata*) in Guadeloupe during 2018 and 2019. ED: Early Dry season; LD: Late Dry season; EW: Early Wet season; LW: Late Wet season.

Table 3. POPAN models results considering eight sampling periods and one group for Guadeloupe, and eight sampling periods and two groups of pantropical spotted dolphin (*Stenella attenuata*) for Martinique.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance	-2log(L)
Guadeloupe							
{Φ(.) p(t) β(t)}	318.21	0	0.958	1	17	-125.264	278.543
{Φ(t) p(t) β(t)}	324.454	6.245	0.042	0.044	21	-130.237	273.57
{Φ(t) p(.) β(t)}	343.88	25.671	0	0	16	-96.918	306.889
{Φ(.) p(.) β(t)}	348.236	30.026	0	0	19	-77.484	326.322
{Φ(t) p(t) β(.)}	12841.975	12523.7	0	0	15	12403.8	12807.6
{Φ(t) p(.) β(.)}	12928.561	12610.3	0	0	10	12507.3	12906.6
{Φ(.) p(.) β(.)}	12936.425	12618.2	0	0	4	12528.7	12928.1
{Φ(.) p(t) β(.)}	230744.136	230425.9	0	0	11	230311.5	230719.8
Martinique							
{Φ(g) p(t) β(g*t)}	223.027	0	0.985	1	23	-73.361	162.307
{Φ(g) p(g) β(g*t)}	232.02	8.993	0.011	0.011	20	-54.417	181.25
{Φ(g) p(.) β(g*t)}	234.254	11.227	0.004	0.004	19	-49.034	186.633
{Φ(.) p(g) β(g*t)}	254.474	31.448	0	0	19	-28.813	206.854
{Φ(t) p(g) β(g*t)}	255.163	32.136	0	0	24	-44.721	190.946
{Φ(g*t) p(g) β(g*t)}	260.029	37.002	0	0	32	-71.639	164.029
{Φ(g*t) p(.) β(g*t)}	260.207	37.18	0	0	31	-67.072	168.595
{Φ(g) p(g*t) β(g*t)}	263.96	40.933	0	0	34	-76.895	158.772

in quality and number of observations that may result in data acquisition bias (Agler, 1992; De Vries, 2017; Araujo *et al.*, 2017). For instance, in the citizen-based science program in Guadeloupe, more than half of the raw picture set was considered non-usable. However, the proportion of usable photos was similar between the Martinique data (47% of usable photos), which were collected by a scientific team, and the Guadeloupe data (41% of usable photos) that were collected by whale-watchers or citizens. Indeed, for both islands, although maximum of usable photos were taken in dry season as sea conditions in wet and hurricane season greatly deteriorate (Cerema, 2020), no significant differences in the number of usable photos were detected and use of citizen science was not likely to cause significant bias in quality or number of photos. Additionally, involving professional and amateurs in conservation actions as part of a citizen-based science program can help raising awareness and making the public adhere more closely to conservation measures (Ellwood *et al.*, 2017). Furthermore, these programs can provide data for further scientific studies, particularly in the Caribbean, where no scientific monitoring programs have been established yet.

Habitat use, residency and estimation of population parameters

In Guadeloupe, 70 individuals, which represents only a part of the whole marked population, were identified. Distribution seems homogeneous in the study area, except for the southwestern area, where only few observations were made. This lack of observations could be explained by regularly poor sea conditions in the area more exposed to the swell and trade winds (Millon, pers. obs.). Encounters of different groups at the same time in different areas have been reported (data not shown), and it is possible that the area is used by different groups that converge and divide from time to time, as it has been reported for fusion-fission societies in bottlenose dolphins (Lewis *et al.*, 2011), spinner dolphins (Andrews *et al.*, 2010), Atlantic spotted dolphins (*Stenella frontalis*; Welsh and Herzing, 2008; Elliser and Herzing, 2014), and suggested for PSD (Pryor and Sballenberger, 1991).

In Martinique, PSD seems to use the habitat differently as most of the observations were made in front of “Le Carbet” and as the groups observed were twice smaller than in Guadeloupe. Dolphin distribution and habitat use are essentially driven by the needs for breeding, food, protection from predation, and intraspecific or interspecific competition (Heithaus and Dill, 2002; Gowans *et al.*, 2007; Sprogis *et al.*, 2016). Availability of predictable food resources like pelagic fish schools off the coasts or reef fish

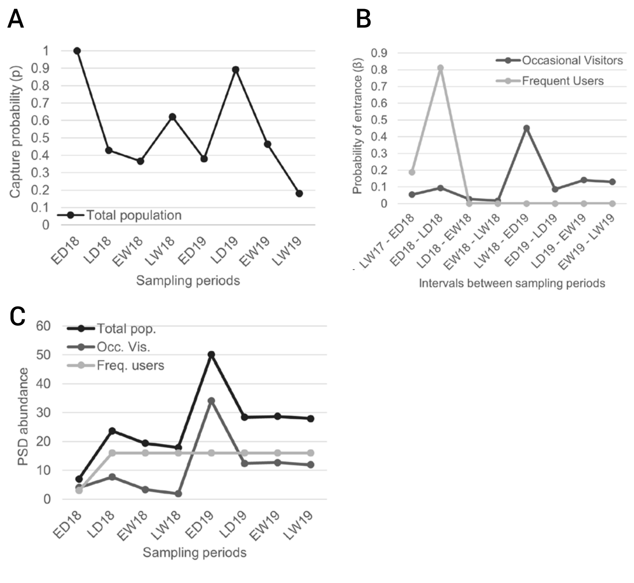

Figure 5. POPAN estimates of (A) capture probability, (B) probability of entrance in the superpopulation and (C) seasonal abundance of pantropical spotted dolphin (*Stenella attenuata*) in Martinique during 2018 and 2019. ED: Early Dry season; LD: Late Dry season; EW: Early Wet season; LW: Late Wet season.

patches closer to shore may be key factors leading to residency patterns in dolphins (Gowans *et al.*, 2007). The Caribbean Basin is an oligotrophic area, so insular and coastal areas where productive ecosystems and potential prey concentrates may favour PSD presence (Barragán-Barrera *et al.*, 2019). For this reason, PSD appear to prefer “Le Carbet” area, which offers a shallow and protected area to avoid potential shark predation, to rest, breed, and socialize (Heithaus, 2001; Acevedo-Gutiérrez, 2002). Indeed, different PSD behaviors such as socializing, resting, feeding, and moving have been observed there (data not shown), which may confirm the potential importance of “Le Carbet” to PSD individuals in Martinique.

As shown in Table 2, recapture rates between 2018 and 2019, which were similar considering the total populations in Guadeloupe and Martinique, indicated a medium site fidelity of PSD individuals. Conversely, other *Stenella* dolphins such as spinner dolphins, which are present year-round in Hawaii, showed a higher recapture rate of 76% (Tyne *et al.*, 2014), and spinner dolphins ranging in Samadai Reef in Egypt exhibited a recapture rate of 49% (Shawky *et al.*, 2015). These differences may be the result of sampling effort or due to the residency patterns and distinctiveness between species or habitat.

In Martinique, recapture rates and $SSFI_P$ of F.U. were higher than those of O.V., which is consistent with their residency cluster, since F.U. are present regularly in the area, so are more likely to be captured. However, although no excess of transient individuals was detected in Guadeloupe, $SSFI_P$ for total populations were similar in both islands. To date, no PSD monitoring using photo-identification is available for allowing us to compare these results. Our findings suggest that PSD showed a stronger site fidelity in comparison to other populations of resident cetacean species worldwide. For instance, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting the coastal waters of tropical northwestern Australia showed lower SSFI (SSFI = 0.019; Haughey *et al.*, 2020). This relatively high site fidelity reported for PSD in Martinique may be determined by the F.U. individuals that appear to be resident in the area, while at the same time, in Guadeloupe, may be driven by a resident fraction of the population, which has not yet been characterised.

Modelling and estimation of population parameters

Survival probability is only “apparent” because it is the product of mortality and migration probabilities, which cannot be separated (Jolly, 1965). To estimate this key parameter accurately, a long-term study and knowledge of the total population size and its limits are needed (Gilroy *et al.*, 2012). In Guadeloupe and Martinique, no PSD stranding events, which could be indicative of unusual mortality events, were reported between 2018 and 2019 (Réseau National Échouage, 2021). Additionally, PSD are long-living mammals (Shirihai and Jarett, 2007; Jefferson *et al.*, 2015), so natural mortality should not affect survivability during our two-year study period. Therefore, even if no transient effect has been detected in the population of Guadeloupe, the low apparent survival found (0.77, CI = 0.67 – 0.84 and 0.19, CI = 0.21 – 0.52 between sampling periods and annually, respectively) is more likely the result of transient individuals moving in and out of the study area, which implies an under-estimation of that parameter (Schaub and Royle, 2014; Haughey *et al.*, 2020), than an effect of high mortality. Hence, Guadeloupe could present a transient part in its population, which was not detected by the tests. Accordingly, F.U. individuals in Martinique display a much higher apparent survival (1, CI not estimable), both annually and between sampling periods, than the one of O.V. individuals, which is almost null annually (0.17, CI = 0.07 – 0.39 and 0.001, CI = 0.00 – 0.03 between sampling periods and annually, respectively), indicating high residency patterns of F.U. individuals, present almost year-round, and highlighting the mobility of O.V. individuals.

Capture probabilities for the first sampling periods in both islands were extremely high with a large confidence interval, which could hint at the non-capacity of MARK to estimate it for that period as it is often the case for the first sampling period (Schwarz and Arnason, 1996). Capture probabilities tend to follow the survey effort as it is the case in similar studies (Chan and Karczmarski, 2017; Pace *et al.*, 2021).

Because transience behaviour differs between F.U. and O.V. individuals in Martinique, only models incorporating group and time varying probability of entrance were chosen. More than two thirds of the individuals entered the superpopulation of Guadeloupe before the end of the first year while a lower number of individuals entered the second year, which could be indicative of the recruitment of transient individuals or individuals that were missed in previous surveys. In parallel, all of the F.U. individuals in Martinique were recruited in the first sampling periods and most of the O.V. individuals were recruited in the second year of the study. As it is the case for open populations, new individuals that were not identified, or not in the study area before, are recruited in the superpopulation in new sampling sessions (Haughey *et al.*, 2020), most of them being transient individuals, at least in Martinique.

Low seasonal abundance in the first sampling periods in both islands should be seen with caution as they might not be representative of the reality. These might be the results of the low recruitment and the low number of identified individuals at the start of the study. PSD abundance in Guadeloupe decreased slightly by the end of 2018, and number of O.V. individuals in Martinique also decreased during 2019. Productive ecosystems in the Caribbean Basin such as coral reefs have been greatly affected (Pandolfi *et al.*, 2003), resulting in declines of food availability, which could force PSD individuals to spend more time traveling in further offshore oceanic waters looking for resources (Barragán-Barrera *et al.*, 2019). As described before, these findings could suggest an increase in emigration rather than an increase in mortality. An extended monitoring including a longer study period would be necessary to verify the presence of transient PSD individuals in Guadeloupe.

Migration patterns

No movement of PSD individuals were observed between Guadeloupe and Martinique during the study period. In 2018 and 2019, SA055 “Willy”, SA081 “Arnold”, and SA150 “Claire” were recaptured nine times in Guadeloupe, and SA155 “Diamant” was recaptured nine times in Martinique, confirming that some individuals were present regularly in the area and that the photo-identification technique is effective. In addition, presence of an excess of transient individuals in Martinique suggests that individuals move in and out of the study area. SA054 individual, named "Victoire", which had previously been identified in Guadeloupe, was observed on 12 January 2013 in Martinique and on 23 June 2013 in Guadeloupe (Bouveret, Millon and de Montgolfier, unpub. data) suggesting that inter-island movements happen but are likely rare. Such movements have been identified previously in the region with photo-ID for sperm whales (Gero *et al.*, 2007; De Vries, 2017) between Guadeloupe, Dominica, St. Lucia and Grenada islands, and for short-finned pilot whale (De Vries, 2017) between Guadeloupe and Martinique over periods of 22 and five years, respectively. In our case, the two year-study period might be too short to identify these movements as monitoring of marine species displaying wide ranging patterns can be complex (Dufault *et al.*, 1999; Gowans *et al.*, 2007). Because a minimum distinctiveness is necessary in order to avoid false-negative and false-positive misidentifications (Würsig and Jefferson, 1990; Urian *et al.*, 2015), it is possible that individuals that are likely to exhibit inter-island movements were not identified here because of their low distinctiveness. These individuals may also be transient individuals, present only in some periods of the year, making them less likely to be captured. Alternatively, because older individuals are more marked than younger ones, it is possible that younger and less marked individuals could have traveled between the two islands without being captured, as is the case in fusion-fission societies where young weaned males move between groups and between areas (Tsai and Mann, 2013). PSD is also present in Dominica (Watkins, 1985), an island located between Guadeloupe and Martinique that represents a probable stage between these two islands (see Fig. 1A). Future monitoring should be addressed to study the connectivity between PSD populations of both Guadeloupe and Martinique islands with the ones of Dominica. Longer photo-identification studies or studies assessing the genetic flow of these populations could bring answers to these hypotheses.

Conclusion

Information about movement patterns, abundance and residency of cetaceans are critical for an effective management of marine protected areas (Holt, 2009; Gormley *et al.*, 2012). This study provides the first insights about residency patterns and movements of PSD populations in the Wider Caribbean region, particularly in Guadeloupe and Martinique islands. No movement of PSD was found between Guadeloupe and Martinique, suggesting that exchange of PSD individuals between these islands is rare and did not seem to represent a general trend of both populations in 2018 and 2019. Results suggested that the Martinique PSD population tends to concentrate in a specific area and is composed of two different resident groups: F.U. that showed a relatively high site fidelity, and O.V. that exhibited a low site fidelity and a slight decrease in abundance during 2019. Guadeloupe PSD population appeared to be more dispersed along the coast, and is composed of only one resident group that showed medium site fidelity, and whose abundance slightly decreased between 2018 and 2019. We hope that this first study, along with the catalogue of 124 PSD individuals, will be a first step to set up a longer monitoring system using photo-ID in order to understand the population processes and movements of PSD in the Lesser Antilles. From the perspective of estimating more accurately the movements between these two islands, the study period should be extended, including at least five continuous years. Genetic studies should be considered to assess the connectivity of population, and the study area should be extended to Dominica island, which is located between Martinique and Guadeloupe, as an intermediary stage for any PSD individual that would travel between them.

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