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 Previous unpublished work found the sighting of an individual in Martinique and Guadeloupe, suggesting potential exchange of individuals between these islands.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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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-Khoury, 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 (Gandihlon, 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 novaeangliae; 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 (SSF), 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, 2020a, b). Transition periods occur between seasons, with monthly variations of precipitations and temperature (Cerema, 2020; Météo France, 2020a, b). Therefore, for this study and following Rosel et al. (2011), seasons were divided into two.
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 out 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 Freiriks, 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 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:

\[
SSFI = \frac{2}{\overline{IT} + \overline{IT}'}
\]

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\(_b\) using sighting history by sampling period and (iv) SSFI\(_s\) using sighting history by season. SSFI\(_b\) 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 \( \phi \) annually and between sampling periods, capture probability \( p \), probability of entrance \( \beta \) (\( \beta \) prior the first sampling period was calculated by subtracting the sum of \( \beta \) of all sampling periods from one), and abundance \( N \) of the marked part of the population.

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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. Freiriks).
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, r = 0.80, Spearman test for Martinique: p < 0.001, r = 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 (χ² = 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 (χ² = 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 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 for Martinique was estimated to be 0.80. However, no significant differences (p = 0.001 – 0.05) for O.V. (Table 2). SSFI was not statistically different between the Guadeloupe population and the total population in Martinique but SSFI for frequent users (F.U.) was statistically higher than SSFI for 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.

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 probabilities, and density dependence (Table 3). The population size was estimated at 160 (CI = 140 – 180) individuals for Guadeloupe and 54 (CI = 46 – 62) individuals in Martinique. However, the model for Guadeloupe did not present any significant over-dispersion of the data (χ² = 3.73, df = 12, p = 0.99).
Apparent survival \( \phi \) 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 \( \beta \) 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 \( \phi \) 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 \( \beta \) 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., \( \beta \) 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.

## 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 in probability, and time-varying probability of entrance (Table 3).
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(.) p(.) β(t)} | 343.88 | 25.671    | 0            | 0                | 16                   | -96.918  | 306.889 |
| {Φ(t) p(.) β(t)} | 348.236 | 30.026   | 0            | 0                | 15                   | 12403.8  | 12807.6 |
| {Φ(t) p(t) β(.)} | 12841.975 | 12523.7  | 0            | 0                | 10                   | 12507.3  | 12906.6 |
| {Φ(.) p(t) β(.)} | 12936.425 | 12618.2  | 0            | 0                | 4                    | 12528.7  | 12928.1 |
| {Φ(t) p(.) 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(g) β(g*t)} | 234.254 | 11.227    | 0.004        | 0.004            | 19                   | -49.034  | 186.633 |
| {Φ(t) 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(g) β(g*t)} | 260.207 | 37.18     | 0            | 0                | 31                   | -67.072  | 168.595 |
| {Φ(g*t) p(.) 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 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 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, Million 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 interact 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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**References**

Acevedo-Gutiérrez, A. (2002) Interactions between marine predators: dolphin food intake is related to number of sharks. *Marine Ecology Progress Series* 240: 267-271. [https://doi.org/10.3354/meps240267](https://doi.org/10.3354/meps240267)

Agler, B.A. (1992) Testing the reliability of photographic identification of individual fin whales (*Balaenoptera physalus*). *Report of the International Whaling Commission* 42: 731–737.

Alessi, J., Bruccoleri, F. and Cafaro, V. (2019) How citizens can encourage scientific research: The case study of bottlenose dolphins monitoring. *Ocean & Coastal Management* 167: 9–19. [https://doi.org/10.1016/j.ocecoaman.2018.09.018](https://doi.org/10.1016/j.ocecoaman.2018.09.018)

Andrews, K.R., Karczmarski, L., Au, W.W.L., Rickards, S.H., Vanderlip, C.A., Bowen, B.W., Grau, E.G. and Toonen, R.J. (2010) Rolling stones and stable homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). *Molecular Ecology* 19: 732–748. [https://doi.org/10.1111/j.1365-294X.2010.04521.x](https://doi.org/10.1111/j.1365-294X.2010.04521.x)

Araujo, G., Snow, S., So, C.L., Labaja, J., Murray, R., Colucci, A. and Ponzo, A. (2017) Population structure, residency patterns and movements of whale sharks in Southern Leyte, Philippines: results from dedicated photo-ID and citizen science. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27: 237–252. [https://doi.org/10.1002/aqc.2636](https://doi.org/10.1002/aqc.2636)

Ballance, L.T. (1990) Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay.
Bolaños-Jiménez, J., Morteo, E., Alfonso, C.A.D., Fruet, P.F., Secchi, E. and Bello-Pineda, J. (2021) Population dynamics reveals a core community of the common bottlenose dolphin (Tursiops truncatus) in open waters of the southwestern Gulf of Mexico. Frontiers in Marine Science. https://doi.org/10.3389/fmars.2021.753484

Caldwell, D.K., Caldwell, M.C., Rathjen, W.F. and Sullivan, J.R. (1971) Cetaceans from Lesser Antillean Island of St-Vincent. Fishery Bulletin of the National Oceanic and Atmospheric Administration 69: 303-312.

Cerema (2020) Dynamiques et évolution du littoral. Fascicule 13 : Synthèse des connaissances de l’archipel de Guadeloupe. Collection: Connaissances. ISBN : 978-2-37180-316-9 [Available from Publications Cerema <http://www.cerema.fr/fr/centre-ressources/boutique/dynamiques-evolution-du-littoral-fascicule-13-guadeloupe>].

Chan, S.C.Y. and Karczmarski, L. (2017) Indo-Pacific humpback dolphins (Sousa chinensis) in Hong Kong: Modelling demographic parameters with mark-recapture techniques. PLoS One 12: e0174029. https://doi.org/10.1371/journal.pone.0174029

Choquet, R., Reboulet, A-M., Lebreton, J-D., Gimenez, O. and Pradel, R. (2005) U-CARE 2.2 (Utilities–Capture-Recapture) User’s Manual. CEFE, Montpellier, France.

Choquet, R., Lebreton, J-D., Gimenez, O., Reboulet, A-M. and Pradel, R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating Captured–Recaptured data. Ecography 32: 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Colwell, R.K., Mao, C.X. and Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85: 2717–2727. https://doi.org/10.1890/03-0557

Cuzange, P-A. (2011) Les pressions anthropiques s’exerçant dans le sanctuaire pour les mammifères marins aux Antilles françaises (Aoga). M.Sc. Thesis, Université des Antilles et de la Guyane. 200 pp.

De Vries, L. (2017) First characterization of cetacean’s movement in the eastern Caribbean: application to sperm whale, short-finned pilot whale and bottlenose dolphin. M.Sc. Thesis, Université Jean Monnet (Saint-Étienne, France. 23 pp.

do Amaral, K.B., Alavera, D.J., Heinzellmann, L., Borges-Martins, M., Siciliano, S. and Moreno, I.B. (2015) Ecological niche modeling of Stenella dolphins (Cetartiodactyla: Delphinidae) in the southwestern Atlantic Ocean. Journal of Experimental Marine Biology and Ecology 472: 166–179. https://doi.org/10.1016/j.jembe.2015.07.013

Dufault, S., Whitehead, H. and Dillon, M. (1999) An examination of the current knowledge on the stock structure of sperm whales (Physeter macrocephalus) worldwide. Journal of Cetacean Research and Management 1: 1–10.

Elliser, C.R. and Herzing, D.L. (2014) Social structure of Atlantic spotted dolphins, Stenella frontalis, following environmental disturbance and demographic changes. Marine Mammal Science 30: 329–347. https://doi.org/10.1111/mms.12038

Ellwood, E.R., Crimmins, T.M. and Miller-Rushing, A.J. (2017) Citizen science and conservation: Recommendations for a rapidly moving field. Biological Conservation 208: 1–4. https://doi.org/10.1016/j.biocon.2016.10.014

Feunteun, A., Safi, M. and de Monogolffer, B. (2019) État des connaissances sur la fréquentation des cétacés en baie de Fort-De-France et les risques de perturbations liés au trafic maritime. Rapport final pour le Grand Port Maritime de Martinique. 68 pp. Fléchet, A., Pillé, M., Bordes, R., Scanga, V. and de Monogolffer, B. (2019) Characterization of short-finned pilot whales (Globicepha!a macrorhynchus) population along the Caribbean Coast of Martinique. Advances in Oceanography & Marine Biology 1: 1–7.

Gandlhorn, N. (2012) Contribution au recensement des cétacés dans l’archipel de Guadeloupe. Ph.D. Thesis. Université des Antilles et de la Guyane, Campus Fouillole, Pointe-à-Pitre, France. 366 pp.

Gero, S., Gordon, J., Carlson, C., Evans, P. and Whitehead, H. (2007) Population estimate and inter-island movement of sperm whales, Physeter macrocephalus, in the Eastern Caribbean Sea. Journal of Cetacean Research and Management 9(2): 143–150.

Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., Steffen, A., Tyack, P., Evans, P. and Whitehead, H. (2014) Behavior and social structure of the sperm whales of Dominica, West Indies. Marine Mammal Science 30(3): 905–922. https://doi.org/10.1111/mms.12086

Gilroy, J.J., Virzi, T., Boulton, R.L. and Lockwood, J.L. (2012) A new approach to the “apparent survival” problem: estimating true survival rates from mark–recapture studies. Ecology 93: 1509–1516. https://doi.org/10.1890/12-0124.1

Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J. Rayment, W., du Fresne, S. and Bräger, S. (2012) First evidence that marine protected areas can work for marine mammals. Journal of Applied Ecology 49(2): 474-480. https://doi.org/10.1111/j.1365-2664.2012.02121.x

Gowans, S., Würsig, B. and Karczmarski, L. (2008) The social structure and strategies of delphinids: predictions based on an ecological framework. Pages 195–294 in Sims, D.W. (Ed.) Advances in Marine Biology. Elsevier Ltd., Amsterdam. https://doi.org/10.1016/S0065-2881(07)50003-8

Haighrey, R., Hunt, T., Hanf, D., Rankin, R.W. and Parra, G.J. (2020) Photographic capture-recapture analysis reveals a large population of Indo-Pacific bottlenose dolphins (Tursiops aduncus) with low site fidelity off the North West Cape, Western Australia. Frontiers in Marine Science 6: 781. https://doi.org/10.3389/fmars.2019.00781
Heithaus, M.R. (2001) Predator—prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology* 253: 53–68. https://doi.org/10.1017/S0952836901000061

Heithaus, M.R. and Dill, L.M. (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83: 480–491. https://doi.org/10.1890/0012-9658(2002)083[0480:FFADTR]2.0.CO;2

Holt, E. (2009) Marine Protected Areas. Pages 696-705 in Perrin, W.F., Würsig, B. and Thewissen, J.G.M. (Eds) *Encyclopedia of Marine Mammals*. Elsevier, Amsterdam.

Hunt, T., Bejder, L., Allen, S., Rankin, R., Hanf, D. and Parra, G. (2017) Demographic characteristics of Australian humpback dolphins reveal important habitat toward the southwestern limit of their range. *Endangered Species Research* 32: 71–88. https://doi.org/10.3354/esr00784

Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S., Martin, A.R., Reeves, R.R., Seton, R., Stevick, P.T. and Wenzel, F.W. (2003) Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *Journal of Cetacean Research and Management* 5(2): 125–130.

Jefferson, T.A., Webber, M.A., Pitman, R.L. and Gaskin, J. (1999) Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science* 15: 102–122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x

Lewis, J.S., Wartzok, D. and Heithaus, M.R. (2011) Highly dynamic fission–fusion species can exhibit leadership when traveling. *Science* 331: 482–498. https://doi.org/10.1126/science.1200256

Machernis, A.F., Stack, S.H., Olson, G.L., Sullivan, F.A. and Luksenburg, J.A. (2014) Prevalence of external injuries in small cetaceans (*Stenella attenuata*). *Journal of Cetacean Research and Management* 9(2): e88988. https://doi.org/10.1371/journal.pone.0088988

Passadore, C., Möller, L., Diaz-Aguirre, F. and Parra, G.J. (2017) Demography of southern Australian bottlenose dolphins living in a protected inverse estuary. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27: 1186–1197. https://doi.org/10.1002/aqc.2772

Pereira, G. and Maneyro, R. (2016) Movement patterns in a pantropical spotted dolphin (*Stenella attenuata*) in the tuna purse seine fishery in Uruguayan population of *Melnophyrinus montevideensis* (Philippi, 1902) (Anura: Bufonidae) using photo-identification for individual recognition. *South American Journal of Herpetology* 11: 119–126. https://doi.org/10.3394/sajh.2017.01.0020.1

Perrin, W.F. (2017) Pantropical Spotted Dolphin. Pages 676–678 in Würsig, B., Thewissen, J.G.M. and Kovacs, K.M. (Eds) *Encyclopedia of Marine Mammals*. 3rd ed. Academic Press Inc., London, UK.

Poyr, K. and Sballenberger, I.K. (1991) Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the Eastern Tropical Pacific. Pages 161–196 in Poyr, K. and Norris, K.S. (Eds) *Dolphins Societies - Discoveries and Puzzles*. University of California Press, Berkeley.
Psarakos, S., Herzing, D.L. and Marten, K. (2003) Mixed-species associations between Pantropical spotted dolphins (Stenella attenuata) and Hawaiian spinner dolphins (Stenella longirostris) off Oahu, Hawaii. *Aquatic Mammals* 29: 390–395. [https://doi.org/10.1578/01675420360736578](https://doi.org/10.1578/01675420360736578)

R Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Réseau National Échouage (2021) BDD ÉCHOUAGE: Histogrammes & Cartes Échouage. [http://pelagis.in2p3.fr/public histo-carte/](http://pelagis.in2p3.fr/public histo-carte/). Accessed 04 September 2021.

Robbins, J., Allen, J.M., Clapham, P.J. and Mattila, D. (2006) Stock identity of a humpback whale taken in a southeastern Caribbean hunt. *Journal of Cetacean Research and Management* 8(1): 29-31.

Rock, J., Pastene, L., Kaufman, G., Forestell, P., Matsuoka, K. and Allen, J. (2006) A note on East Australia Group V Stock humpback whale movement between feeding and breeding areas based on photo-identification. *Journal of Cetacean Research and Management* 8(3): 301-305.

Rosel, P.E., Mullin, K.D., Garrison, L., Schwacke, L., Adams, J., Balmer, B., Conn, P., Conroy, M.J., Eguchi, T., Gorgone, A., Hohn, A., Mazzoil, M., Schwarz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N., Wade, P., Wells, R. and Zolman, E. (2011) Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of bottlenose dolphins along the U.S. East Coast and Gulf of Mexico: a workshop report. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-621. 30 pp.

Safi, M., Eymard, M., Janssen, A., Feunteun, A. and de Mongolfier, B. (2020) *Etat de santé des populations résidentes et semi-résidentes des cétacés présentes dans les eaux de la Martinique*. Rapport final pour le Grand Port Maritime de Martinique. 63 pp.

Schaub, M. and Royle, J.A. (2014) Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. *Methods in Ecology and Evolution* 5: 1316–1326. [https://doi.org/10.1111/2041-210X.12134](https://doi.org/10.1111/2041-210X.12134)

Schwarz, C.J. and Arnason, A.N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860-863. [https://doi.org/10.2307/2533048](https://doi.org/10.2307/2533048)

Shawky, A., Alwany, M., Zakaria, S. and El-Etreby, S. (2015) Estimation of the abundance of the spinner dolphin *Stenella longirostris* using photo identification technique in Samadai Reef, Red Sea, Egypt. *Catrina: The International Journal of Environmental Sciences* 10: 27–39. [https://doi.org/10.12816/0010696](https://doi.org/10.12816/0010696)

Shirihai, H. and Jarett, B. (2007) *Guide des mammifères marins du monde*. Delachaux et Niestlé, Paris

Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Matilla, D., Palsboll, P.J., Sigurðsson, J., Stevick, P.T. and Oien, N. (1999) An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Marine Mammal Science* 15: 1–32. [https://doi.org/10.1111/j.1748-7692.1999.tb00779.x](https://doi.org/10.1111/j.1748-7692.1999.tb00779.x)

Sprogis, K.R., Pollock, K.H., Raudino, H.C., Allen, S.J., Kopps, A.M., Manlik, O., Tyne, J.A. and Bejder, L. (2016) Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Frontiers in Marine Science* 3: 12. [https://doi.org/10.3389/fmars.2016.00012](https://doi.org/10.3389/fmars.2016.00012)

Stanley, T.R. and Burnham, K.P. (1999) A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6: 197–209. [https://doi.org/10.1023/A:1009674322348](https://doi.org/10.1023/A:1009674322348)

Suzuki, R., Terada, Y. and Shimodaira, H. (2019) pvclust: Hierarchical clustering with p-values via multiscale bootstrap resampling. R package version 1.2-2. [http://CRAN.r-project.org/package=pvclust](http://CRAN.r-project.org/package=pvclust).

Tschopp, A., Ferrari, M.A., Crespo, E.A. and Coscarella, M.A. (2018) Development of a site fidelity index based on population capture-recapture data. *PeerJ* 6: e4782. [https://doi.org/10.7717/peerj.4782](https://doi.org/10.7717/peerj.4782)

Tyne, J.A., Pollock, K.H., Johnston, D.W. and Bejder, L. (2014) Abundance and survival rates of the Hawai‘i Island associated spinner dolphin (*Stenella longirostris*) stock. *PLoS One* 9: e86132. [https://doi.org/10.1371/journal.pone.0086132](https://doi.org/10.1371/journal.pone.0086132)

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R.S., Berggren, P., Durban, J., Eguchi, T., Rayment, W. and Hammond, P. (2015) Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science* 31: 298–321. [https://doi.org/10.1111/mms.12141](https://doi.org/10.1111/mms.12141)

Vanzella-Khour, A. (1998) Implementation of the Protocol Concerning Specially Protected Areas and Wildlife (SPAW) in the Wider Caribbean Region. *The University of Miami Inter-American Law Review* 30(1): 53–83.

Ward Jr, J.H. (1963) Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58: 236–244.

Watkins, W.A. (1985) Investigations of sperm whale acoustic behaviors in the southeast Caribbean. *Cetology* 49: 1–15.

Welsh, L.S. and Herzing, D.L. (2008) Preferential association among kin exhibited in a population of Atlantic spotted dolphins (*Stenella frontalis*). *International Journal of Comparative Psychology* 21: 1-11.

White, G.C. and Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139. [https://doi.org/10.1080/00063659909477239](https://doi.org/10.1080/00063659909477239)

Whitehead, H. (2001) Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* 82(5): 1417-1432. [https://doi.org/10.1890/0012-9658(2001)082[1417:AOAMUO]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1417:AOAMUO]2.0.CO;2)

Whitehead, H. and Moore, M.J. (1982) Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60: 2203–2211. [https://doi.org/10.1139/z82-282](https://doi.org/10.1139/z82-282)

Williams, J.A., Dawson, S.M. and Slooten, E. (1993) The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology* 71: 2080–2088. [https://doi.org/10.1139/z93-293](https://doi.org/10.1139/z93-293)

Wilson, B., Thompson, P.M. and Hammond, P.S. (1998) Habitat use by bottlenose dolphins: Seasonal distribution and stratified
movement patterns in the Moray Firth, Scotland. *Oceanographic Literature Review* 7: 1170–1171.

Wray, J., Keen, E., O’Mahony, E.N. (2021) Social survival: Humpback whales (*Megaptera novaeangliae*) use social structure to partition ecological niches within proposed critical habitat. *PLoS One* 16: e0245409. https://doi.org/10.1371/journal.pone.0245409

Würsig, B. and Jefferson, T.A. (1990) Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission* Special Issue 12: 43–52

Zanardo, N., Parra, G.J. and Möller, L. (2016) Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops sp.*) in Adelaide’s coastal waters, South Australia. *Marine Mammal Science* 32(4): 1381-1401. https://doi.org/10.1111/mms.12335