

Abundance and site fidelity of bottlenose dolphins off a remote oceanic island (Reunion Island, southwest Indian Ocean)

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Abstract

This study represents the first comprehensive assessment of the population dynamics and residency of common bottlenose dolphin around Reunion Island (southwest Indian Ocean). Understanding dynamics and movement patterns of this local population is essential to guide effective conservation efforts, notably in a context of growing dolphin-watching activities. Dedicated surveys based on photo-identification methods were conducted over 6 years (2010–2015). The species was present year-round, in groups of 25 individuals on average (1–150). Jolly-Seber mark-recapture models resulted in a population estimate of 254 individuals (95% CI = 191–337) and an apparent annual survival rate of 0.83. The population was almost equally split into three residency patterns: residents (33.1%), long-term visitors (32.6%), and short-term visitors (34.3%, including transients, i.e., individuals only seen once [14.9%]), suggesting that the majority of the population showed a moderate-to-high level of residency in the study area. Individuals from the three residency patterns associated randomly, mixing together and forming a single community. Models based on the lagged identification rate indicated emigration and reimmigration to the survey area, with some individuals occupying the study area for about 2 years (832 days), and remaining outside for an average of 276 days, probably exhibiting larger home ranges and extensive movement behavior.

KEYWORDS

abundance, common bottlenose dolphins, generalized affiliation indice, Indian Ocean, Jolly-Seber, lagged identification rate, mark-recapture, residency pattern, Reunion Island, *Tursiops truncatus*

1 | INTRODUCTION

The common bottlenose dolphin *Tursiops truncatus* (Montagu, 1821) is a cosmopolitan species with a worldwide distribution in tropical and temperate waters (Connor, Wells, Mann, & Read, 2000; Reynolds, Wells, & Eide, 2000). It is known to inhabit a wide variety of marine environments such as shelf and coastal habitats, oceanic waters, and estuaries (Connor et al., 2000; Leatherwood & Reeves, 1983; Reynolds et al., 2000; Rice, 1998; Scott & Chivers, 1990; Wells & Scott, 1999). Inshore and offshore bottlenose dolphin ecotypes have been described to differ through genetics, morphology, physiologic features, and feeding behavior (Duffield, Ridgway, & Cornell, 1983; Hersh & Duffield, 1990; Hoelzel, Potter, & Best, 1998; Mead & Potter, 1995; Walker, 1981).

Offshore and coastal common bottlenose dolphins exhibit contrasting patterns of residency, movements, and habitat use across their entire range (i.e., resident, migrant, and transient; Simões-Lopes & Fabian, 1999; Vermeulen & Cammareri, 2009). Common bottlenose dolphins inhabiting open habitats, such as off remote oceanic islands, tend to form large populations, occur in large groups, and show extensive movement patterns with low site fidelity (Dinis et al., 2016; Forcada, Gazo, Aguilar, Gonzalvo, & Fernandez-Contreras, 2004; Pereira, Martinho, Brito, & Carvalho, 2013; Silva et al., 2008), while populations inhabiting coastal or protected enclosed areas such as estuaries, bays, sounds or river mouths, are mostly small and resident or semiresident (Balmer et al., 2008; Bearzi, 2005; Fruet, Daura-Jorge, Möller, Genoves, & Secchi, 2015; Gubbins, 2002; Lusseau, 2003; Speakman, Lane, Schwacke, Fair, & Zolman, 2010).

In the southwest Indian Ocean, common bottlenose dolphins have mostly been recorded in oceanic waters, including off the southeast coast of South Africa (Cockcroft, Ross, & Peddemors, 1990; Peddemors, 1999; Ross, 1977), Mozambique, Kenya, Tanzania and Zanzibar (Best, 2007; Kiszka, 2015 for a review), Madagascar (Rosenbaum, 2003), and off oceanic islands such as Mayotte (Kiszka, Ersts, & Ridoux, 2010), Mauritius and Reunion Island (Dulau-Drouot, Boucaud, & Rota, 2008; Webster, Cockcroft, Cadinouche, & Huggins, in press). However, dedicated studies have not been carried out locally, hence ecological and demographical knowledge on the species are mostly lacking in the region.

Two species of the *Tursiops* genus occur sympatrically off Reunion Island: *T. aduncus* and *T. truncatus*. In comparison with *T. aduncus*, *T. truncatus* is typically characterized by a longer adult body length, a more robust and shorter rostrum, a more falcate dorsal fin, and the absence of ventral spotting (Hale, Barreto, & Ross, 2000; Ross, 1977, 1984; Wang, Chou, & White, 2000; Wells & Scott, 2002). Both species are present year-round around the island, displaying no significant seasonal variation in sighting frequency (Dulau-Drouot et al., 2008). Common bottlenose dolphins mostly occur over the insular shelf, in waters between 100 m and 950 m deep, whereas Indo-Pacific bottlenose dolphins use shallower inshore waters (<80 m deep - Dulau-Drouot et al., 2008). Therefore, there is little overlap in the habitat range of these two species, except on the east coast of the island, where the insular shelf is very narrow and both species occur close to shore. While *T. aduncus* is known to form a small resident population of <100 individuals around Reunion Island (Dulau, Estrade, & Fayan, 2017), the demographic parameters and residency patterns of *T. truncatus* are largely unknown.

Direct threats to the species have not been identified around Reunion Island. However, interactions with human activities might increase in the coming years. As whale-watching is developing, common bottlenose dolphins are becoming a new targeted species, mostly during the austral summer, when the humpback whale breeding season is over. The impact of such activity would depend greatly on the population size, habitat use, and residency pattern of

the targeted population (Bejder, Samuels, Whitehead, & Gales, 2006a, Bejder et al., 2006b; Steckenreuter, Möller, & Harcourt, 2012; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008). To date, this knowledge on common bottlenose dolphins is lacking in Reunion Island. Studies on the population local abundance, as well as site fidelity and residency patterns, are needed to provide baseline data to assess the impact of such activity on the species.

The objective of this 6-year study is to use mark-recapture methods based on photo-identified individuals to estimate abundance, residency patterns, and social structure of the common bottlenose dolphin in the waters of Reunion Island. The goal is to contribute towards a more comprehensive understanding of the common bottlenose dolphin (hereafter bottlenose dolphin) population dynamics and size at a local scale. More globally, the study aims at providing further insights onto the dynamic of island-associated populations of *T. truncatus*.

2 | MATERIALS AND METHODS

2.1 | Study area

Reunion Island (21°07'S, 55°33'E) is a French overseas territory, located in the Mascarene archipelago, about 170 km west from Mauritius Island and 700 km east of Madagascar in the southwestern Indian Ocean (Figure 1). As a young volcanic island, Reunion Island has a narrow insular shelf with water depth steeply dropping off to 4,000 m at about 60 km from the nearest shore. Seabed substrate varies spatially around the island, from basaltic rocks to sandy bottom. The windward east coast is frequently exposed to winds and heavy rainfall, while the leeward west coast is relatively sheltered. The climate is tropical and humid, with two slightly marked seasons, and sea surface temperature ranges from 24°C to 28°C throughout the year (Conand, Marsac, Tessier, & Conand, 2007).

Because survey effort mostly concentrated off the west coast (leeward), due to poor weather conditions and logistical resources elsewhere, the study area was defined as the west coast of the island, from Saint Denis (north) to Saint Joseph (south), up to three nautical miles offshore (Figure 1).

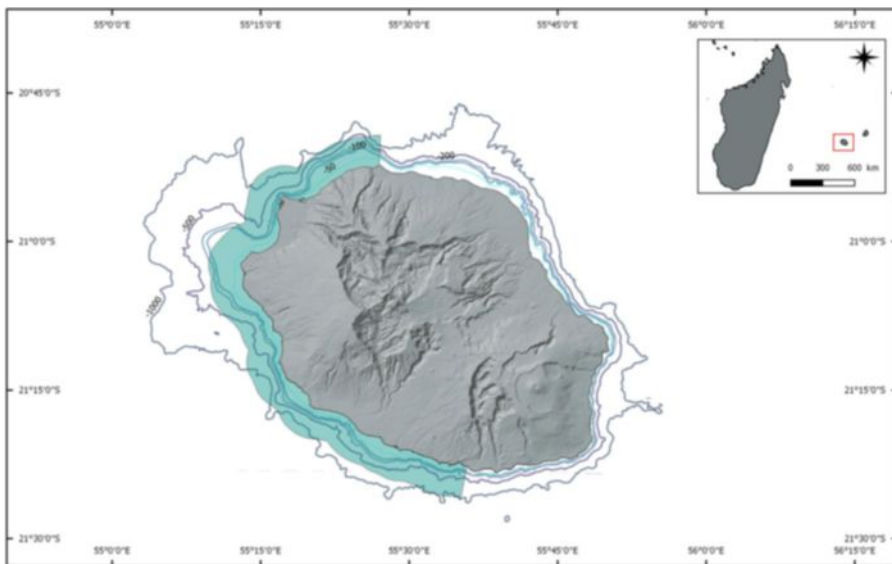


FIGURE 1 Map of the study area around Reunion Island with isobaths from 50 m to 1,000 m (Source: Globice, Natural Earth, IGN).

2.2 | Data collection

From 2010 to 2015, dedicated boat-based surveys were conducted all year-round within the study area using 6 m motorboats and at an approximate speed of 6 knots on effort. Surveys were conducted in calm sea conditions (Beaufort ≤ 3). During on-effort survey periods, three experienced observers (with one on each side of the boat and one watching ahead) searched visually for dolphins with naked eyes and using continuous scanning method as described by Mann (1999). Survey routes were tracked with a handheld geographical position system (GPS) Garmin 72H.

Whenever bottlenose dolphins were sighted, the survey route was curtailed, and the boat was slowed down to carefully approach the animals to a point at which dorsal fins could be photographed. Distinction between Indo-Pacific and common bottlenose dolphins was made based upon morphological features (i.e., body length, rostrum size, shape of the dorsal fin, and presence/absence of spots; see Figure S1) and the species was confirmed a posteriori by an experienced person (V.E.) based on photographs.

Several parameters were recorded upon sighting, such as the GPS position (latitude and longitude), date, time, estimated group size (minimum, maximum and best estimate), group composition (number of calves and juveniles following the definition of age classes from Bearzi, Notarbartolo-Di-Sciara, & Politi, 1997), behavior at first encounter, presence of other cetacean species, reaction to the research vessel, presence of other vessels around the animals, and all other comments considered as relevant. Group size was visually estimated by at least two observers and averaged. This field estimation was subsequently adjusted based on photo-identification data (Ballance, 1990). A group was defined as an aggregation of dolphins within an area of a 100-m radius of each other, exhibiting similar behavior, and if traveling, heading in the same direction (Shane, 1990; Wells, Scott, Stockin, & Irvine, 1987).

Photographs of bottlenose dolphin dorsal fins were obtained using Nikon D5000 or Canon 60S/90D digital camera fitted with a 70–300 mm zoom lens. When possible, photographs of both left and right sides of each individual dorsal fin were taken. Dolphins were photographed until the identification of each individual was completed, or the focal group showed avoidance behavior, precluding further data collection.

2.3 | Individual identification and dorsal fin scoring

Each photograph was graded with a photo quality rating of poor, fair, good, and excellent. This criterion depends on the focus, angle, clarity, contrast, and size of the dorsal fin within the picture (Slooten, Dawson, & Lad, 1992). Only high-quality photographs (i.e., good or excellent), which related to focused pictures of the entire dorsal fin profile, were retained for the analysis (Hammond, Mizrock, & Donovan, 1990; Read, Urian, Wilson, & Waples, 2003; Urian, Hohn, & Hansen, 1999; Urian et al., 2015; Wilson, Hammond, & Thompson, 1999). Poor or fair quality photos were removed from the analysis to avoid incorrect identifications (Friday, Smith, Stevick, & Allen, 2000).

High quality pictures were edited using Picasa 2.0 software to extract cropped images of each individual dorsal fin. Dorsal fins were then sorted according to permanent marks. Other features such as dorsal fin shape, pigmentation, or temporary marks (tooth rakes, scars, skin alterations, bite wounds, etc.) were used as secondary identification keys to confirm individual identification or to assist in identification of similarly marked individuals (Wilson et al., 1999). The best image of each dolphin was compared to the photo-identification catalogue using DARWIN 1.9. Beta. Each individual dorsal fin that matched previously catalogued animal was considered a recapture, while new individuals were added to the catalogue (Urian et al., 1999, 2015). To ensure homogeneity in the identification process, one person (V.E.) double-checked all captures/recaptures made over the study period.

Individuals showing a dorsal fin with no mark on the trailing edge were classified as unmarked and not included in the catalog. Each marked individual was assigned a marking level, according to the number, deepness, and extent of its marks, ranging from D1 to D3, where D1 = slightly distinctive, D2 = distinctive, and D3 = very distinctive (Dulau et al., 2017; Read et al., 2003; Urian et al., 1999; Urian et al., 2015; Wilson et al., 1999; Figure 2).



FIGURE 2 Bottlenose dolphin dorsal fin photographs displaying different marking levels. (a) D1: Slightly distinctive (i.e., with few notches along the trailing edge); (b) D2: distinctive (i.e., with moderated notches), and (c) D3: very distinctive (with multiple and large notches, and/or deep nicks and cuts along the trailing edge or leading edge, and/or disfigurements).

2.4 | Abundance estimates from mark-recapture models

Mark-recapture analysis was conducted by defining years (2010–2015) as sampling occasions and using the capture history of well-marked individuals only (D2 and D3) in Mark 7.2 (White & Burnham, 1999). POPAN formulation of the classic Jolly-Seber open population models were performed to assess abundance and demographic parameter estimates, as gain (through immigration or birth) and loss of individuals (through permanent emigration or death) were likely to occur over the 6-year survey (Crosbie & Manly, 1985; Jolly, 1965; Schwarz & Arnason, 1996; Seber, 1965).

2.4.1 | Model assumptions and data selection

Population closure was tested statistically using the CloseTest v3 program (Stanley & Burnham, 1999). Both Otis, Burnham, White, and Anderson (1978) and Stanley and Burnham (1999) closure tests confirmed that the population was not closed ($\chi^2 = 72.0$, $df = 7$, $p < 1.10^{-4}$, and $Z = -8.1$, $p < 1.10^{-4}$, respectively). A test for transience (Test 3.SR) was also carried out in U-Care 2.3.2 (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) and did not provide evidence of transience ($Z = 0.89$, $df = 4$, $p = .371$).

The open Jolly-Seber capture-recapture model operates under several assumptions and their violation can lead to biased population estimates (Amstrup, McDonald, & Manly, 2005; Read et al., 2003; Seber, 1982; Williams, Nichols, & Conroy, 2002; Wilson et al., 1999). Each assumption was explored, and data was selected in order to meet these assumptions, as follows:

1. Absence of mark loss and consistent mark recognition: (a) use of high-quality photographs to identify individuals; (b) selection of well-marked individuals (marking levels D2 and D3 only) (Friday et al., 2000; Rosel et al., 2011; Urian et al., 1999, 2015; Würsig & Jefferson, 1990); (c) year-round sampling, so marks were unlikely to change significantly between two consecutive sampling occasions (Wilson et al., 1999); (d) use of temporary marks on dorsal fin as secondary identification keys to confirm individual identification; and (e) validation of individual identification by an experienced observer (V.E.).
2. Equal probability of capture: (a) during sighting, individuals were photographed randomly, irrespective of their levels of markings (Würsig & Jefferson, 1990); (b) calves were excluded from mark-recapture analysis because their probability of capture was highly related to that of their mothers (Wells & Scott, 1990; Wells et al., 1987); and (c) the pooled χ^2 statistics (goodness-of-fit Test 2 in U-Care 2.3.2; Choquet et al., 2009) did not detect any significant difference in capture probability in the population ($\chi^2 = 9.2$, $df = 5$, $p > .10$).
3. Equal survival probability: (a) the pooled χ^2 statistics (goodness-of-fit Test 3 in U-Care 2.3.2; Choquet et al., 2009) did not detect any significant difference in survival probability in the population ($\chi^2 = 8.8$, $df = 8$, $p > .30$).

4. Instantaneous sampling: sampling occasions were short in duration (1 year) compared to the dolphins' lifespan.
5. Absence of behavioral response to capture (Read et al., 2003; Wilson et al., 1999): (a) photo-identification being a noninvasive mark-recapture method, inducing minimal stress to the animal, it is not expected to influence the probability of subsequent recaptures; (b) Test 2.CT (Choquet et al., 2009; Pradel, 1993) in U-Care 2.3.2 did not detect any trap-dependence behavior ($Z = -1.35$, $df = 3$, $p = .177$).

Despite selection of high-quality data, violation of some of these assumptions may still exist, as suggested by the value of the post hoc variance factor \hat{c} ($\hat{c} = 1.38 > 1$) (Williams et al., 2002). This factor measures over-dispersion in the data and is defined as the chi-square statistic from global test (TEST 2+ TEST 3) divided by its degrees of freedom. The estimated value of \hat{c} was thus used to adjust the models (Cooch & White, 2009).

2.4.2 | Population models

Maximum likelihood was used to estimate the following parameters: capture probability (p), apparent annual survival rate (ϕ), probability of entry (Pent), and superpopulation size (N_D) where: $p(t)$ is the probability that an individual available for capture in sampling occasion t would be captured in sampling occasion $t + 1$; $\phi(t)$ is the apparent survival probability from sampling occasion t to sampling occasion $t + 1$; Pent(t) is the probability of entry in the study area between sampling occasion t to sampling occasion $t + 1$; and N_D is the superpopulation size, defined by Crosbie and Manly (1985) and Schwarz and Arnason (1996), corresponding to the total number of (well-marked) individuals available for capture at any time within the survey area. The models provide an average superpopulation size for the study period (6 years) as well as year estimates.

Different combinations of models were built by setting apparent annual survival, capture probability and probability of entry either constant (.) or time-varying (t) across sampling occasions (i.e., years). Models were fitted using a sin link function for capture probability and apparent annual survival, a multinomial logit link function to constrain entry probabilities to ≤ 1 and a log link function for the superpopulation size (Cooch & White, 2009).

2.4.3 | Model selection and parameters estimation

Given the extra-binomial dispersion of the data ($\hat{c} > 1$), the most suitable model was selected using the lowest Quasi Akaike's Information Criterion corrected for small sample sizes (QAICc; Burnham & Anderson, 2002). Models differing by two units or less from the model with minimum QAICc (ΔQAICc) were also considered to provide a good description of the data (Burnham & Anderson, 2002). Both real function and derived parameter values were provided from the best-fitting model. The 95% confidence interval was calculated assuming a log-normal approximation, as recommended by Burnham, Anderson, White, Brownie, and Pollock (1987).

2.4.4 | Proportion of (well-)marked individuals in the population

Abundance estimates obtained from the models only refer to the population of well-marked animals (marking level D2 and D3). Therefore, the total population size N_{total} , including marked and unmarked individuals, was estimated by considering the proportion θ of well-marked individuals in the population (Jolly, 1965; Seber, 1982; Wilson et al., 1999) following:

$$N_{\text{total}} = N_D / \theta$$

where N_{total} is the total population size estimate; N_D , the abundance estimate of well-marked individuals generated from the best-fitting model, and θ , the estimated proportion of well-marked (D2 and D3) individuals in the population (Burnham et al., 1987; Read et al., 2003; Wilson et al., 1999).

Theta (θ) was estimated using a sighting-based method (Fruet, Secchi, Di Tullio, & Kinas, 2011; Nicholson, Bejder, Allen, Krützen, & Pollock, 2012), by computing for each sighting the number of well-marked (D2 and D3) individuals over the estimated group size. To estimate θ with accuracy, only sightings for which the photographic coverage (Pc) was over 70% were used. The photographic coverage was defined as the percentage of marked individual (i.e., adults D1 to D3) on the total number of adults estimated in the group, and calculated as follow (modified from Nicholson et al., 2012):

$$Pc = 100 \sum_{i=1}^n \frac{(D1i + li)}{(Ti - Ji - Ci)}$$

where $D1i$ = total number of D1 individuals photographed in group i , li = total number of well-marked dolphins (D2 and D3) photographed in group i , Ji = total number of juveniles estimated in group i , Ci = total number of calves estimated in group i , Ti = total number of dolphins estimated in group i , and n = total number of sightings.

Furthermore, to reduce variance due to small sample sizes, groups with <10 individuals were excluded. The proportion of well-marked individuals within the group was calculated for each sighting and averaged over all sampling occasions per year to provide an annual estimate of θ , as follow (as in Fruet et al., 2015):

$$\hat{\theta} = \frac{\sum_{i=1}^k \frac{li}{Ti}}{k}$$

where k = total number of groups from which θ was estimated ($Pc > 70\%$).

The standard error for the total population size N_{total} was derived using the delta method as follows (modified from Nicholson et al., 2012; Williams et al., 2002; Wilson et al., 1999):

$$SE(\hat{N}_{\text{total}}) = \sqrt{\hat{N}_{\text{total}}^2 \left(\frac{SE(\hat{N}_D)^2}{\hat{N}_D^2} + \frac{1-\hat{\theta}}{k\hat{\theta}} \right)}$$

As recommended by Burnham et al. (1987) and to better reflect the uncertainty in abundance estimates (Buckland, Anderson, Burnham, & Laake, 1993), the 95% confidence interval for the total population size was computed assuming a lognormal approximation, with a lower limit of \hat{N}_{total}/C and upper limit of $\hat{N}_{\text{total}}*C$ where:

$$C = \exp \left(1.96 \sqrt{\ln \left(1 + \left(\frac{SE(\hat{N}_{\text{total}})}{\hat{N}_{\text{total}}} \right)^2 \right)} \right)$$

2.5 | Site fidelity and residency

Two metrics were used to assess individual site fidelity to the study area: (1) the total number of sightings of each individual within the study area and (2) the residency time (number of days between the first capture and the last recapture).

In order to have sufficient sample size and to avoid under-estimation, all marked individuals (D1 to D3 individuals) except those first identified during the last year of the survey (2015, $n = 9$) were included in the site fidelity analysis. To ensure the independence of the data, in cases where an individual was sighted several times on the same day, only the sighting for which the number of identified individuals was the highest was used for that day.

To discriminate different residency patterns (i.e., short-term visitor, long-term visitor, and resident), a hierarchical clustering analysis was performed based on the number of sightings and residency time of each identified individual, using XLStat V 2.7 2017 (Addinsoft). Euclidean distance was used as a measure of dissimilarity; Ward's method as the clustering algorithm (Ward, 1963) and automatic truncation was based on the entropy criterion. To test the efficiency of the clustering and evaluate the suitability of the clusters, the cophonetic correlation coefficient (CCC) was calculated (Sokal & Rohlf, 1962).

2.5.1 | Social structure

The half weight association index (HWI) was calculated via SOCPROG 2.7 (compiled version; Whitehead, 2009). The HWI represents the proportion of times that each pair of individuals is seen in a group together and varies between 0 (individuals never seen together) and 1 (individuals always seen together) (Cairns & Schwager, 1987):

$$HWI = \frac{X}{X + 0.5(Y_a + Y_b)}$$

where X is the number of groups where individuals A and B were seen together, Y_a , the number of groups where individual A was sighted without individual B and Y_b , the number of groups where individual B was sighted without individual A. This index is considered as the most suitable one for defining association in cases where it is not always possible to identify all individuals in the group (Cairns & Schwager, 1987).

In order to account for the effects of structural factors that may affect associations, the generalized affiliation indice (GAI) was used as a measure of the strength of association between pairs (also called true affiliation; Whitehead & James, 2015). A multiple regression quadratic assignment procedure (MRQAP) was performed with 20,000 permutations, using the "double semi-partialing" technique of Dekker, Krackhardt, and Snijders (2007), to test the effect of each potential structural factor, while controlling for the other, on the association indices (HWIs) matrix. The contribution of each factor was assessed using the partial correlation coefficient, and those that did not significantly explain the matrix of association indices were removed. GAIs were defined as the deviance residuals of the generalized linear model, where the HWIs was the dependent variables and the structural factors, the predictor variables, and assuming a binomial model (Whitehead & James, 2015).

Because individuals that are frequently sighted or that use the study area at the same time tend to associate more often with each other, two metrics were tested as structural factors: (1) the cumulative number of sightings for each individuals' pair and (2) the temporal overlap by pair of individuals (defined as the ratio of the number of months in which at least one individual from a pair was present to the number of months both were present in the study area; adapted from Whitehead & James, 2015).

Individual gregariousness (i.e., the tendency for some individuals to be found in consistently smaller or larger groups than others; Whitehead, Bejder, & Ottensmeyer, 2005) was tested using the Bejder, Fletcher, and Bräger (1998) procedure, modified from Manly (1995) (with 10,000 permutations). The SD of the typical group sizes observed (i.e., group sizes experienced by a given individual; Whitehead, 2009) was not significantly different from random ($SD_{\text{observed}} = 7.96$, $SD_{\text{random}} = 8.00$, $p = .62$), suggesting a lack of gregariousness in the population. Hence, this metric was not taken into account for the calculation of GAIs.

To assess whether associations within residency patterns were significantly different than associations between residency patterns, mean GAIs were compared via two-tailed Z-Mantel tests using 1,000 permutations. Furthermore,

Manly-Bejder permutation tests for preferred/avoided associations were performed across the whole population to test the null hypothesis that individuals associate more often than expected by chance with other individuals (Bejder et al., 1998; Manly, 1995; Whitehead, 1999, 2008, 2009; Whitehead et al., 2005). Then, permutations were run to test for preferred/avoided associations within and between residency patterns. The null hypothesis was that individuals associated with the same probability with all other individuals regardless of their residency pattern. To obtain a consistent p -value, the number of permutations (groups within samples) was increased by 2,000 after each run until the difference in p -values was $<.01$, to ensure that the decision of rejecting the null hypothesis (at .05 level) was not affected by the p -value variability (Bejder et al., 1998). Ten thousand permutations with 1,000 trials per permutation were finally generated using months as sampling periods to avoid possible demographic effects (Whitehead, 1999, 2008). The mean and standard deviation (SD) of GAI for the observed and random populations were calculated and interpreted according to Whitehead (2009).

A social network diagram, based on the GAIs, was produced using Netdraw 2.158 (Borgatti, 2002; see Figure S2). Community division by modularity analyses was conducted to investigate the existence of social communities within the population (Newman, 2004, 2006). Modularity is the difference between the expected proportion of association within clusters and the proportion obtained with the observed data (Newman, 2006). Population modularity values greater than 0.3 indicate a meaningful division of the population into communities (Newman, 2004; Whitehead, 2009). The community, as defined by Croft, James, and Jens (2008) and Krause and Ruxton (2002), is a group of individuals that are more associated amongst each other than with members from other communities.

2.5.2 | Lagged identification rate

Residency was also investigated using the lagged identification rate (LIR), i.e., the probability that an individual observed in the study area at a given time will still be present after a certain lag of time τ (Whitehead, 2001, 2009). The LIR was calculated for the study area based on sighting histories of all marked individuals (D1 to D3), with the day as sampling occasion, using SOCPROG 2.7 (Whitehead, 2009). LIR was plotted against time to provide an indication of the temporal use of the area by the animals. Different residency models (no movement, emigration/reimmigration, emigration/reimmigration + mortality; Whitehead, 2001) were fitted to the data using maximum likelihood and binomial loss, and by fixing the maximum time lag to the duration of the survey period (i.e., 2,043 days).

Because of overdispersion of the data ($\hat{c} > 1.0$), models were selected according to their QAIC. The model with the lowest QAIC was selected as providing the best fit to the data (Whitehead, 2009).

3 | RESULTS

3.1 | Survey and photo-identification effort

A total of 1,187 daily surveys were conducted between 2010 and 2015, totaling 5,464 hr and 38,066 km of sampling effort within the study area (Figure 3). A total of 126 bottlenose dolphin groups were sighted on 107 different days. Photo-identification data was available for 89 of these sightings (see Table S1).

A total of 6,854 photographs were taken, from which 5,349 were of sufficient quality to allow identification for subsequent photo-identification analysis. The photo-identification catalogue contained 187 marked individuals (D1: 33 slightly distinctive; D2: 83 distinctive and D3: 71 very distinctive).

Group size estimates ranged from 1 to 150 animals (mean = 24.5, SD = 24.9, median = 20.0), with the majority of groups being smaller than 30 individuals ($n = 94$, 74.6%). The number of individuals photo-identified within a group ranged from 1 to 49 (mean = 11.7, SD = 10.5). Of the 68 sightings for which photo-identification data were

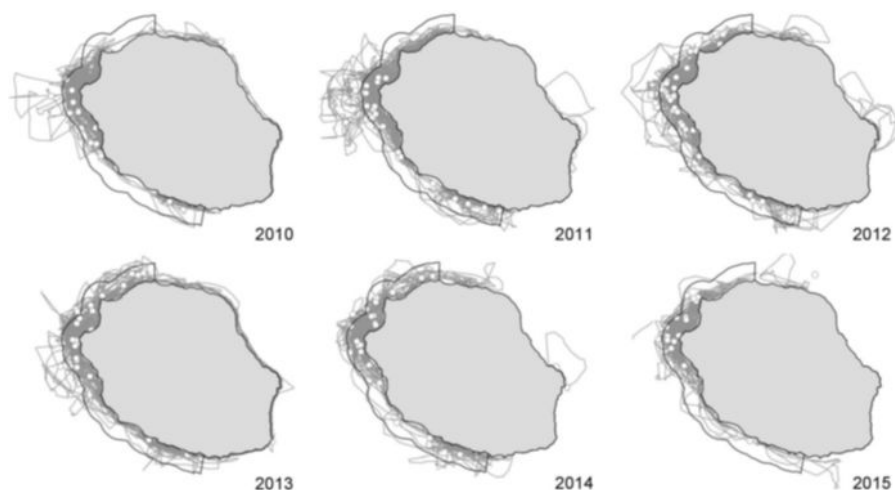


FIGURE 3 Survey effort (gray line) and sightings of bottlenose dolphins (white dot) per year in the study area, from 2010 to 2015 (Scale: 1/1,000,000).

available and whose group size exceeded ten individuals, 27 (40%) showed a high photographic coverage (P_c) of 70% or above, and in six of them all individuals were photographed ($P_c = 100\%$).

3.2 | Discovery curve

The cumulative number of well-marked dolphins (D2 and D3) increased sharply until mid-August 2011 (i.e., after 12 daily surveys), with an average of 5.1 new individuals discovered per month (Figure 4). Onwards, the discovery curve increased much more gradually from mid-August 2011 to mid-August 2012 (i.e., after the 38th daily survey), with an average of 2.3 individuals newly identified per month, and finally reached a plateau, suggesting that almost all well-marked individuals of the population had been identified in the study area. The asymptote was reached during the 50th daily survey.

3.3 | Abundance estimates

3.3.1 | Population models

Of the eight candidate models run using POPAN formulation, only one was selected as best supporting the data: $\{p(\cdot), \varphi(t), \text{Pent}(t)\}$. This model considers that the probability of capture of individuals remains constant, and that the apparent survival rate and the probability of individuals entering the study area vary across years (Table 1). Other models differed by more than two units in QAICc and were thus considered to show a lower fit to the data.

3.3.2 | Estimated parameters

The best fitting POPAN model provided (Table 2) (1) a high and constant capture probability ($p = 0.74, SE = 0.03$); (2) an apparent annual survival rate (φ) ranging from 0.61 ($SE = 0.09$) in 2015 to 1.00 ($SE = 0.03$) in 2012; the average annual survival rate was estimated to 0.83 (95% CI = 0.50–0.91); and (3) a relatively low probability of entry (Pent)

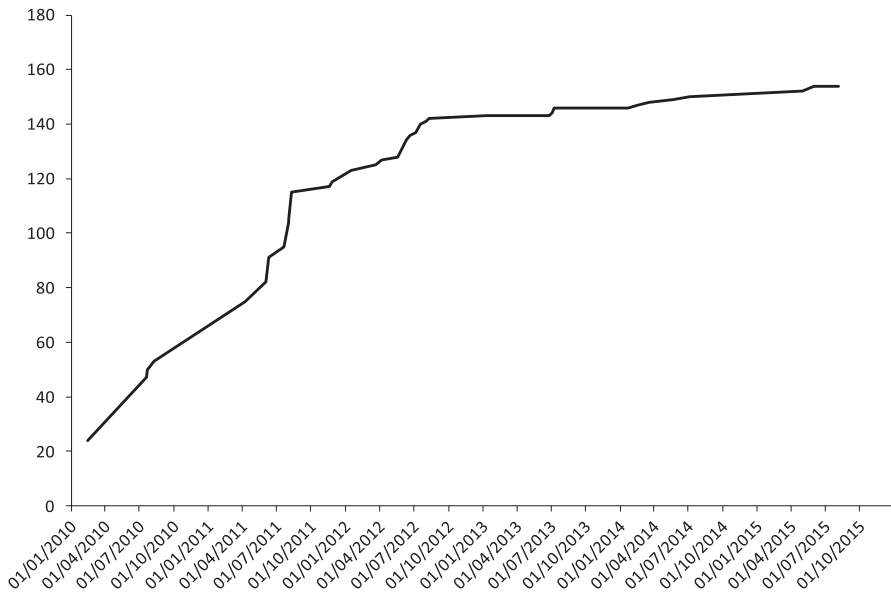


FIGURE 4 Cumulative discovery curve for well-marked bottlenose dolphins identified off Reunion Island in the study area over the period 2010–2015.

TABLE 1 List of Jolly-Seber mark–recapture candidate models with POPAN parameterization ranked by quasi-likelihood Akaike Information Criteria (QAICc). Only the top-four models are displayed. Models with $\Delta\text{QAICc} \leq 2$ were considered as best-fitting models.

Model	QAICc	ΔQAICc	QAICc weight	No. of parameters
{ $p(\cdot)$, $\varphi(t)$, Pent(t)}	564.1	0.0	0.94	11
{ $p(t)$, $\varphi(\cdot)$, Pent(t)}	569.9	5.8	0.05	13
{ $p(t)$, $\varphi(t)$, Pent(t)}	573.3	9.1	0.01	17
{ $p(\cdot)$, $\varphi(\cdot)$, Pent(t)}	577.0	12.8	0.002	7

Note. Survival probability: φ ; recapture probability: p ; probability of entering the study area: Pent. Each model incorporates either constant (.) or time-varying (t) parameters.

ranging from 0.00 ($SE = 0.00$) in 2013 to 0.54 ($SE = 0.07$) in 2011, leading to an average probability of entry of 0.13 (95% CI = 0.08–0.40).

The annual estimate of the superpopulation size of well-marked individuals (N_D) derived from the model ranged from 58 ($SE = 7.8$, 95% CI = 44–75) in 2010 to 142 ($SE = 5.2$, 95% CI = 132–153) in 2012 (Table 2). The global superpopulation size estimated for the 6 years study period was $N_D = 164$ ($SE = 4.6$, 95% CI = 155–173).

3.3.3 | Proportion of well-marked individuals and total abundance

The mean proportion of well-marked animals in the population ($\hat{\theta}$) during the study period was 64.5% ($SD = 13.7\%$, $n = 27$), giving a total population size estimate of $N_{\text{total}} = 254$ individuals ($SE = 36.9$, 95% CI = 191–337) over the 6 years (2010–2015).

TABLE 2 Estimates of abundance parameters derived from the best Jolly-Seber candidate model with POPAN parameterization $\{p(\cdot), \phi(t), \text{Pent}(t)\}$. Total population size (N_{total}) has been calculated from the superpopulation size (N_D) taking into account the proportion of well-marked animals in the population (θ).

Year	Well-marked individuals				Total population			
	N	N_D	SE	95%CI	θ	N_{total}	SE	95%CI
2010	43	58	7.8	44–75	0.60	96	79.8	23–397
2011	103	136	8.2	121–153	0.88	156	59.6	75–321
2012	109	142	5.2	132–153	0.66	216	52.1	135–344
2013	84	121	6.7	108–135	0.68	179	47.8	107–299
2014	71	101	7.8	87–117	0.59	170	64.7	83–350
2015	48	66	8.2	52–84	0.58	114	50.6	50–262

Note. SE: standard error; 95%CI: 95% log-normal confidence intervals, N : number of different marked individuals encountered per year.

3.4 | Site fidelity and residency

Of the 187 individuals from the catalog (marking level D1 – D3), 175 were first identified prior to 2015 and included in the site fidelity analysis.

3.4.1 | Individual recaptures

During the study period, individuals were sighted 1–26 times (mean = 5.7, $SD = 4.8$). Twenty-six individuals (14.9%) were transients (i.e., individuals sighted only once), 61 (34.9%) were sighted on less than five occasions, whereas 65 individuals (37.1%) were resighted from five to ten times. Twenty-three individuals (13.1%) were sighted >10 times.

3.4.2 | Residency time

For the 149 individuals (85.1%) sighted more than once during the study period, the mean residency time was $1,043 \pm 522$ days (i.e., ~3 years), ranging from 21 to 2,024 days. The majority of individuals ($n = 126$, 84.6%) used the study area between 300 (~1 year) and 1,800 days (~5 years). Nine individuals resided less than 300 days (6.0%), whereas 14 animals were observed over more than 1,800 days (9.4%).

The hierarchical clustering analysis provided a CCC of 0.635, suggesting a reliable discrimination of individuals into three clusters, indicative of three main patterns of site fidelity (Figure 5). The first cluster consisted of 60 individuals rarely sighted (number of sightings = 2.2 ± 1.3) and displaying low residency time (186 ± 197 days). This cluster represented “short-term visitors” (hereafter STV) and included transients ($n = 26$). The second cluster included 58 individuals frequently sighted (mean number of sightings = 10.7 ± 4.9) and displaying high residency (mean residency time = $1,529 \pm 319$ days) indicating that they consistently occurred within the survey area, across multiple years (but not necessarily consecutive). These individuals were classified as “residents.” The third cluster was composed of 57 individuals not frequently observed in the study area (number of sightings = 4.4 ± 1.7) but over long period (medium residency time of 975 ± 215 days). This cluster reflected “long-term visitors” (hereafter LTV).

3.4.3 | Social structure

MRQAP correlation tests showed that the temporal overlap was a relevant structural factor for explaining the matrix of association indices (partial correlation coefficient = 0.899, $p < .0001$). In contrast, the cumulative number of sightings did not show a significant contribution (partial correlation coefficient = 0.002, $p > .99$) and was therefore removed for the calculation of GAIs.

Associations of individuals within and between residency patterns were significantly different (two-tailed Mantel test, $t = 6.48$, $r = 0.048$, $p < .0001$). Maximum mean GAI was displayed by resident individuals (mean GAI = -0.031 , $SD = 0.81$) while minimum mean GAI was observed within STV individuals (mean GAI = -0.35 , $SD = 0.39$; Table 3).

Permutation tests performed on the overall population indicated that individuals associated randomly. Indeed, neither the mean GAI nor the SD of GAI of the observed population were significantly different from random (mean $GAI_{\text{observed}} = -0.212$, $GAI_{\text{random}} = -0.215$, $p = .94$ and $SD_{\text{observed}} = 0.621$, $SD_{\text{random}} = 0.626$; $p = .96$, respectively; Table 3).

Within each residency pattern, except for residents, neither the mean GAI nor the SD of GAI of the observed data were significantly different from random, indicating a probable absence of preferred or avoided associations. For resident individuals, the mean GAI of the observed data was significantly higher than that of randomly permuted data (mean $GAI_{\text{observed}} = -0.031$, $GAI_{\text{random}} = -0.067$, $p = .0001$; Table 3), which was not considered biologically meaningful (Whitehead, 2009).

The modularity of the population (from gregariousness) of 0.020 indicated that the population was not divided into communities. The social network diagram did not display any cluster featuring the three residency patterns. In

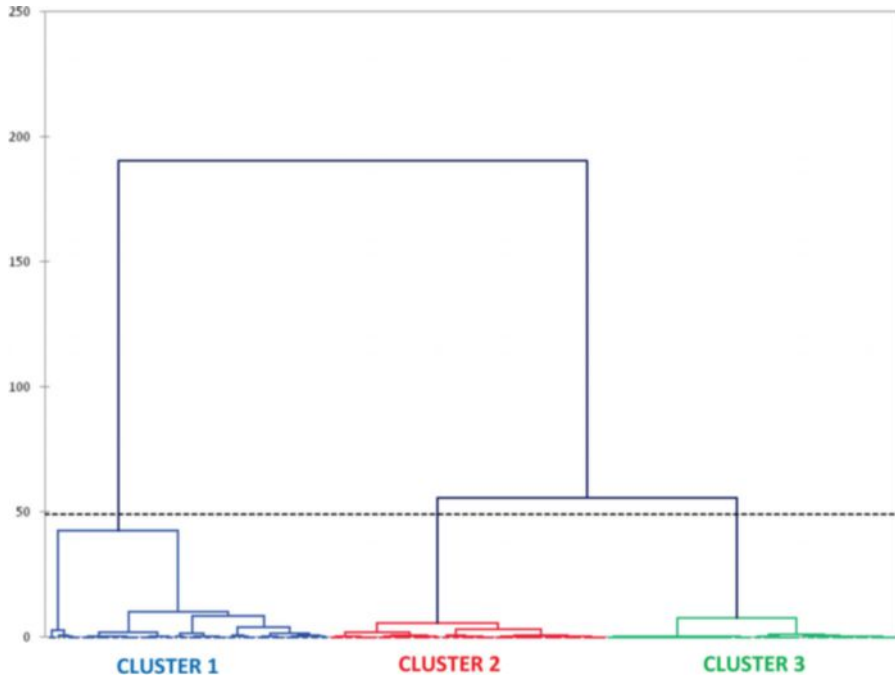


FIGURE 5 The agglomerative hierarchical clustering analysis (AHC) showing how individual bottlenose dolphins clustered according to the two metrics describing site fidelity: number of sightings and residency time. The dissimilarity threshold displays three clusters: the cluster 1 (i.e., residents, $n = 58$) in blue, the cluster 2 (i.e., long-term visitors, $n = 57$) in red and the cluster 3 (i.e., short-term visitors, $n = 60$) in green.

contrast, it formed an intricate network, where individuals associated irrespective of their residency pattern (see Figure S2). In particular, STV and LTV mixed with resident individuals.

3.4.4 | Lagged identification rate

LIR analysis revealed that the model that best described the data (with the lowest QAIC) included emigration and reimmigration (Table 4). This model estimated that individuals were present within the study area for an average period of 832 days. The average subsequent time spent outside the study area before returning was estimated at approximately 276 days.

The LIR curve started to decay after about 25 days suggesting that some individuals leave the study area through emigration. After 900 days, the fitted model began to level off above zero, indicating that a number of individuals subsequently return to the study area and/or that some animals frequently use the study area as residents. The shape of the LIR curve tends to be indicative of a mixture of individuals with different levels of residency (i.e., residents, LTV and STV) (Figure 6).

4 | DISCUSSION

By assessing demographic parameters, residency patterns and social structure over a 6-year period off Reunion Island, this study provided baseline information on the ecology and behavior of island-associated bottlenose dolphins. This population was shown to be demographically open and had an estimated abundance of 254 individuals (95% CI = 191–337, 2010–2015). Although the species was present year-round in relatively large groups (mean group size = 24.5 animals, *SD* = 24.9), pattern of residency varied among individuals: a third of the individuals exhibited high site fidelity, and were considered as residents (33.1%), while others were short or long-term visitors, in similar proportion (34.3% and 32.6%, respectively). Individuals showing different residency patterns associated randomly; they mingled together into mixed groups, forming a single community.

4.1 | Limits of the open Jolly Seber model

Even if Jolly Seber open capture-recapture models address biases related to the assumption of population closure, their use involves numerous assumptions that have to be explored and validated (Begon, 1983; Read et al., 2003;

TABLE 3 Results from permutations tests for preferred/avoided associations across the three residency patterns (i.e., resident, RES; long-term visitor, LTV; and short-term visitor, STV).

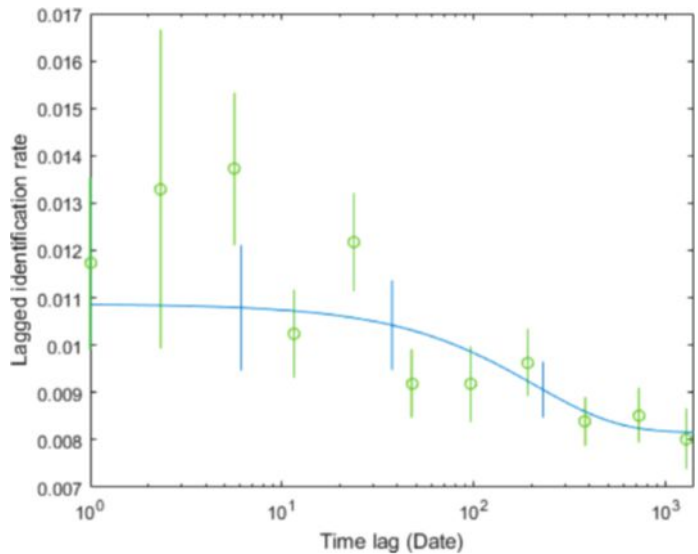
Residency pattern	<i>n</i>	mean GAI			SD		
		observed data	random data	<i>p</i>	observed data	random data	<i>p</i>
RES	58	−0.0306	−0.0669	0.0001*	0.81244	0.81335	0.542
LTV	57	−0.12427	−0.12297	0.2983	0.59798	0.61325	0.9981
STV	59	−0.34846	−0.34775	0.3799	0.38781	0.38683	0.4932
RES-LTV	—	−0.09982	−0.10255	0.8814	0.71481	0.72058	0.9448
RES-STV	—	−0.30996	−0.30981	0.4743	0.61262	0.61096	0.2498
LTV-STV	—	−0.28387	−0.28279	0.1785	0.46265	0.46184	0.4047

Note. Significant *p*-values are indicated by an asterisk.

TABLE 4 Models fitted to observed lagged identification rate (LIR) data of common bottlenose dolphin population in the study area during the period 2010–2015. Explanation of each model refers to Whitehead (2001). The model that best fitted the data according to QAIC (i.e., Akaike's information criterion corrected for overdispersion) is shown in bold. For the best fitting model, $a_1 = N$, number of individuals present within the study area at any one time, $a_2 =$ mean residency time in, and $a_3 =$ mean residency time out the study area.

Model	Explanation	QAIC	Δ QAIC	Model evaluation
$(1/a_1) * ((1/a_3) + (1/a_2) * \exp(-(1/a_3 + 1/a_2) * td)) / (1/a_3 + 1/a_2)$	Emigration +reimmigration	22,670.0180	-	Best
$(1/a_1) * \exp(-td/a_2)$	Emigration+mortality	22,672.3236	2.3056	No support
$a_2 * \exp(-a_1 * td)$	Emigration+mortality	22,672.3237	2.3057	No support
$a_3 * \exp(-a_1 * td) + a_4 * \exp(-a_2 * td)$	Emigration +reimmigration +mortality	22,676.3236	6.3056	No support
$(\exp(-a_4 * td) / a_1) * ((1/a_3) + (1/a_2) * \exp(-(1/a_3 + 1/a_2) * td)) / (1/a_3 + 1/a_2)$	Emigration +reimmigration +mortality	22,675.9737	5.9557	No support
$1/a_1$	Closed	22,680.4038	10.3858	No support
a_1	Closed	22,680.4038	10.3858	No support
$a_2 + a_3 * \exp(-a_1 * td)$	Emigration +reimmigration	22,683.6727	13.6547	No support

FIGURE 6 Lagged identification rate of marked common bottlenose dolphins in the study area during the period 2010–2015. The curve was generated using the movement analysis section of the compiled version of SOCPROG 2.7 (Whitehead, 2009), with maximum time lag fixed to 2,043 days. Bootstrap error bars, calculated from 100 replications/iterations are shown on the graph.



Seber, 1982; Wilson et al., 1999). Although effort was made to minimize biases, violations of some assumptions may exist, as suggested by the post-hoc variance factor value ($\hat{c} = 1.38 > 1$; Williams et al., 2002). Homogeneity in capture probability is typically one of the key assumptions underlying POPAN models (Gilbert, 1973; Seber, 1982). Despite different patterns of residency found among individuals, the pooled χ^2 statistics for Test 2 showed a probable lack of heterogeneity of probabilities of capture in the population. Test 3.SR did not detect transience, although part of the population ($n = 26$, 14.9%) was described as transient. This can be due to the low power of this test in detecting transients with reduced sample sizes (Pradel, Hines, Lebreton, & Nichols, 1997). The presence of transients might explain

the observed \hat{c} value and caused an underestimation of the apparent survival rate (Pledger, Pollock, & Norris, 2003; Pollock & Alpizar-Jara, 2005). However, the lack of fit displayed by the \hat{c} value was limited (≤ 3) and might have resulted from extrabinomial noise rather than by inappropriate model used.

4.2 | Demographic parameters

4.2.1 | Group size

The average group size described in Reunion Island (mean = 24.5, median = 20.0, 1–150) was consistent with off-shore populations (Cañadas & Hammond, 2006; Hansen, 1990) or remote oceanic island-associated populations (São Tomé Island: Pereira et al., 2013; Azores Archipelago, Portugal: Silva et al., 2008); an exception being Hawaii, where bottlenose dolphins tend to form smaller groups (i.e., mean = 6.3, $SD = 4.5$, median = 6: Baird, Gorgone, Ligon, & Hooker, 2001). Group sizes estimated for bottlenose dolphins inhabiting enclosed environments are generally smaller (i.e., generally less than 15 individuals per group in Santa Monica Bay, CA: Bearzi, 2005; Shannon Estuary, Ireland: Berrow, O'Brien, Groth, Foley, & Voigt, 2012; Bay of Islands, New Zealand: Constantine, 2002; Moray Firth, Scotland: Eisfeld, 2003; Mississippi Sound, MS: Hubard, Maze-Foley, Mullin, & Schroeder, 2004; Ría de Arousa, Spain: Methion & Díaz López, 2018; Charleston, NC: Speakman et al., 2006).

Resource availability and predation risk are known to affect group size in small delphinids, including in *Tursiops* spp. (Gygax, 2002; Heithaus & Dill, 2002; Shane, Wells, & Würsig, 1986; Wells et al., 1987). The formation of larger groups in oceanic waters could be linked to an increased vulnerability to predators and an adaptation to maximize foraging efficiency where resources are scarce (Dinis et al., 2016; Norris & Dohl, 1980; Shane et al., 1986; Wells, Irvine, & Scott, 1980). Little is known about the diet of bottlenose dolphins off Reunion Island. Predation risk on bottlenose dolphins might occur in Reunion waters, as bull and tiger sharks are known to be present around the island. However, in contrast to the coastal Indo-Pacific bottlenose dolphins, for which 19.8% of individuals displayed shark-inflicted injuries (Heithaus et al., 2017), very few scars were observed on the common bottlenose dolphins (V.D., V.E., personal observation). To date, only one individual has been photographed in 2017 with a fresh circular bite wound behind the dorsal fin indicative of a shark attack injury (V.D., personal observation).

4.2.2 | Abundance estimate

The bottlenose dolphin population that used the study area during 2010–2015 was estimated to comprise 254 individuals (95% CI = 191–337). This abundance estimate was low compared to other populations using island-associated habitats which tend to be characterized by large population size, with several hundreds to thousands of individuals being generally reported (Balearic islands, Spain, Forcada et al., 2004; Hawaiian islands, Mobley, Spitz, Forney, Grotefendt, & Forestell, 2000; Azores archipelago, Portugal, Silva et al., 2008). This difference could be due to the carrying capacity of the habitat, whereby low productivity, remoteness, and small island size could limit the size of the population that Reunion Island can sustain.

4.2.3 | Apparent survival rate

The annual apparent survival rate of adult bottlenose dolphins in Reunion Island was 0.83 ($SE = 0.06$) on average. This apparent survival rate was relatively high, as expected for long-lived and slowly reproductive mammals (Connor et al., 2000; Stolen & Barlow, 2003; Wells & Scott, 1999). The estimate was lower than values reported for other populations of bottlenose dolphins (coastal or estuarine resident populations: Doubtful Sound, New Zealand: 0.94;

Currey et al., 2008; Patos Lagoon Estuary, Brazil: 0.89; Fruet et al., 2015; Sado Estuary, Portugal: 0.96, SE = 0.012; Gaspar, 2003; Charleston, NC: 0.95, SE = 0.035; Speakman et al., 2010; Sarasota Bay, FL: 0.96, SD = 0.008; Wells & Scott, 1990; and open ocean populations: Little Bahama Bank, USA: 0.94 – Fearnbach, Durban, Parsons, & Claridge, 2012; Azores, Portugal: 0.97, SE = 0.03; Silva, Magalhaes, Prieto, Santos, & Hammond, 2009). Lower apparent survival rate in more oceanic habitats might reflect higher predation pressure but also some level of permanent emigration, which cannot be discriminated from mortality (Pledger et al., 2003). This would be consistent with the residency patterns observed in this study, where the population seems to include transient individuals ($n = 26$, 14.9%).

4.3 | Residency pattern

The low proportion of animals seen only once, together with the flat discovery curve, suggested that the majority of the population in Reunion Island showed a high level of site fidelity. The LIR analysis estimated that individuals were within the study area for a period of 832 days and remained outside of the survey area for 276 days on average. During this period, individuals might remain in Reunion Island and use other areas around the island, being thus unavailable for recapture. In fact, individuals identified outside of the study area, on the east coast of the island (not considered in the present study), were all sighted at least once in the study area during the survey period (with the exception of one individual), indicating individual movements around the island. Alternatively, some individuals might use offshore habitats, or temporary migrate to other neighbouring islands such as Mauritius, Madagascar, or Rodrigues (170 km, 700 km, and 840 km away, respectively).

The high proportion of individuals showing high residency in the study area was relatively unexpected. Populations using open-water habitats are usually characterized by a low recapture rate and low site fidelity (Defran, Weller, Kelly, & Espinosa, 1999), although variations in residency patterns have been observed among oceanic islands. Off Madeira, a remote island located 500 km off the northwest coast of Africa, a small proportion (21%, compared to 75% in Reunion Island) of the bottlenose dolphin population was resighted in more than one year and only 3.2% showed long-term site-fidelity (i.e., seen in four or more years) (Dinis et al., 2016). Similarly, high proportions of individuals sighted only once (between 35.2% and 65.7%, compared to 14.9% in this study), and hence showing low site fidelity, have been reported in other remote oceanic islands (Northwestern Sardinian island: Díaz López, Alberto, & Francesca, 2013; São Tomé Island, Portugal: Pereira et al., 2013; Azores islands, Portugal: Silva et al., 2008). In contrast, in the Hawaiian archipelago, bottlenose dolphins display high site fidelity and low inter-island movements, spending most of their time on the insular slope (<1,000 m deep; Baird et al., 2001, 2009). The pattern observed in Reunion Island is consistent with high levels of site fidelity documented off Hawaii and many bottlenose dolphin populations in inshore habitats (Patos Lagoon Estuary, Brazil: Fruet et al., 2015; South Carolina estuaries, USA: Gubbins, 2002; Doubtful Sound, New Zealand: Lusseau, 2003 and Schneider, 1999; Moray Firth, Scotland: Wilson, Thompson, & Hammond, 1997).

Although offshore oceanic waters are usually oligotrophic (Hasegawa, Yamazaki, Lueck, & Seuront, 2004; Naim et al., 2013), waters surrounding oceanic islands can represent areas of enhanced productivity that promote the presence of predator populations such as cetaceans (Gilmartin & Revelante, 1974; Gove et al., 2016; Silva et al., 2003). The presence of a resident island-associated population could also attract conspecifics on the short or longer term, both for feeding and breeding purposes. In Reunion Island, 65.7% of the individuals were described as short-term visitors ($n = 60$, with an average residency time of ~186 days) or long-term visitors ($n = 57$, with an average residency time of ~975 days). This residency pattern might reflect temporary immigration of individuals using other areas around Reunion Island (outside the study area) or commuting between oceanic and more coastal habitats or between neighboring islands. Additionally, 43.3% of short-term visitors were transients, supposedly exhibiting larger home range and extensive movements. These results are in line with the ranging behavior and between-island movements reported in other studies. In Madeira Archipelago, bottlenose dolphins were shown to travel between Madeira Island

and Porto Santo Island, 50 km apart (Dinis et al., 2016). Within Azores archipelago, Silva et al. (2008) showed that transient individuals could travel almost 300 km between islands. Moreover, studies from radio-tracking, genetics or photo-identification worldwide have suggested that individual bottlenose dolphins from offshore or island-associated populations may move great distances of several hundred kilometers (Klatsky, Wells, & Sweeney, 2007; Querouil et al., 2007; Tanaka, 1987; Tezanos-Pinto et al., 2009; Wells et al., 1999). Given such known dispersal abilities and the relative proximity of Mauritius and Rodrigues, long-range movements within the Mascarene islands (Reunion Island, Mauritius and Rodrigues) are likely to occur. Large-scale aerial surveys reporting the presence of bottlenose dolphins in oceanic waters of the southwest Indian Ocean, and more specifically at mid-distance between Reunion Island and Mauritius (Laran et al., 2017) tend to support this hypothesis. Nevertheless, to date, no studies have been conducted on possible interisland movements of bottlenose dolphins and the level of dispersal and connectivity among islands in this region is unknown. Future genetic and photo-identification studies should aim at assessing the connectivity and the level of dispersal within the Mascarene islands and among populations of the southwestern Indian Ocean.

4.4 | Social structure

Despite significant differences of associations detected among individuals within and between residency patterns (via the Mantel test), tests for preferred/avoided associations failed to detect nonrandom associations at both the overall population and residency patterns levels. Moreover, the Newman's modularity value (<0.3) provided no evidence for population subdivision into communities, suggesting that the bottlenose dolphin population of Reunion Island represents a single community, in which individuals showing different residency patterns mix together.

In the literature, few *Tursiops truncatus*. Populations have been described as showing a random association pattern (Papale et al., 2016; Vermeulen & Cammareri, 2009). In contrast, the majority of populations worldwide displays avoided and/or preferred associations and sometimes segregates into communities (Baker, O'Brien, McHugh, Ingram, & Berrow, 2017; Genov, Centrih, Kotnjek, & Hace, 2019; Moreno & Acevedo-Gutierrez, 2016; Rogers, Brunnick, Herzing, & Baldwin, 2004). Numerous features are known to drive social structure and communities segregation such as ecological conditions (habitat type, depth, foraging strategy, site fidelity, etc.) and socio-genetic factors (age, sex, reproductive status, genetic relatedness, gregariousness, etc.) (Baird et al., 2009; Cantor et al., 2012; Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Frère et al., 2010; Gero, Bejder, Whitehead, Mann, & Connor, 2005; Godde, Humbert, Côté, Réale, & Whitehead, 2013; Lusseau & Newman, 2004; Mann, Stanton, Patterson, Bienenstock, & Singh, 2012; Möller, Beheregaray, Allen, & Harcourt, 2006; Parsons et al., 2003; Rossbach & Herzing, 1999; Urian, Hofmann, Wells, & Read, 2009; Wiszniewski, Brown, & Möller, 2012; Wiszniewski, Lusseau, & Möller, 2010). The difficulty is to discriminate factors that are "elements of affiliation" from structural factors that might influence association pattern and potentially mask the true affiliation among individuals (Whitehead & James, 2015). Previous studies have assessed association patterns using standard association indices (mainly HWI), without taking account of potential biases coming from structural factors. More recently, a growing number of studies uses GAI to determine social structure of bottlenose dolphins' population (Diaz-Aguirre, Parra, Passadore, & Möller, 2018; Genoves, Fruet, Di Tullio, Möller, & Secchi, 2018; Louis et al., 2018; Methion & Díaz López, 2020; Zanardo, Parra, Diaz-Aguirre, Pratt, & Möller, 2018). This recently developed approach allows the estimation of true affiliation indices while removing the effects of structural factors. Studies that use standard association indices may tend to over-represent high-level structuring while understating fine-scale structuring of the population (i.e., failing to detect preferred/avoided associations) (Diaz-Aguirre et al., 2018; Genoves et al., 2018; Whitehead & James, 2015), rendering their comparison with studies using GAI quite difficult.

Site fidelity, and more generally residency pattern of individuals, has been described to potentially impact the social structure of bottlenose dolphin populations (Genoves et al., 2018; Zanardo et al., 2018). Indeed, high levels of site fidelity may provide the opportunities for individuals to form preferred associations, while, conversely,

individuals showing low levels of site fidelity are less likely to associate with others. Hence, in a population where individuals displayed different residency patterns, preferred associations were expected to occur within residency patterns, potentially leading to the segregation of the population into communities based on residency pattern. However, this was not observed in this study. In Reunion Island, although individuals were shown to display high site fidelity and diverse residency patterns, the population did not show any clear social structuring based on true affiliations. The temporal overlap was shown to be a structural factor affecting association pattern, which suggested that although individuals happen to occur in the study area at the same time, they associated by chance rather than displaying any preferred or avoided association.

4.5 | Conservation perspectives

This study represents the first comprehensive assessment of the bottlenose dolphin population dynamics and residency around Reunion Island. The demographic parameters (abundance, immigration, survival rates) estimated in this study constitute fundamental insights to better define the conservation status of the species, which to date has been locally considered as Data Deficient (IUCN France et al., 2013). The local population was estimated at 254 individuals (95% CI: 191–337), which is close to the threshold used by the IUCN guidelines to define endangered populations (i.e., 250 individuals). Our estimates also suggest low levels of mortality and/or permanent emigration (as displayed by the apparent survival rate) and high levels of site fidelity and residency for some individuals, although some level of temporary emigration (visitors) and presence of transients were also observed. The presence of an important proportion of resident individuals, which was relatively unexpected for a remote oceanic island, suggests that part of the population might be particularly vulnerable to anthropogenic impacts if subjected to repeated interactions with human activities.

Dolphin-watching activities has been demonstrated to induce habitat and short-term behavioral changes on odontocetes that could lead to a modification of the energy budgets, by increasing physical demands and/or reducing energy intake (Bejder et al., 2006a; Christiansen, Rasmussen, & Lusseau, 2013; Lusseau, Bain, Williams, & Smith, 2009; Williams, Lusseau, & Hammond, 2006). These negative short-term impacts could lead to long-term individual and even population-level effects, by affecting fitness and reproductive success (Bejder et al., 2006a,b; International Whaling Commission, 2006; Lusseau, 2003). Therefore, in the light of growing whale-watching and swimming with dolphins' activities, the development of responsible practices through public awareness, sustainable management and law enforcement is strongly recommended. Results provided in this study will serve as baseline information to support and substantiate these actions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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