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RESEARCH ARTICLE

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Assessment of the nesting population demography of loggerhead turtles (*Caretta caretta*) in La Roche Percée: First long-term monitoring in New Caledonia

Maxime Barbier[1] | Dominique Lafage[1] | Hugo Bourgogne[2] | Tyffen Read[3] | Marine Attard[1] | Kevin Fournière[1] | Kennie Chapuis[1] | Yolanda Peyrot[1] | Michèle Deffois[1] | Bernard Guillaumet[1] | Adelaide Sibeaux[1,4]

[1]Lotissement Drémon, Bwärä Tortues Marines, Bourail, New Caledonia

[2]Parc Forestier Michel-Corbasson, WWF New Caledonia, Nouméa, New Caledonia

[3]Province Sud, Nouméa, New Caledonia

[4]Department of Biology, University of Oxford, Oxford, UK

Correspondence
Adelaide Sibeaux, Department of Biology, University of Oxford, 11a Mansfield Rd, Oxford OX1 3SZ, UK.
Email: adelaide.sibeaux@biology.ox.ac.uk

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Abstract

1. Population monitoring is essential to assess, manage, and protect threatened species. Although the South Pacific loggerhead turtle (*Caretta caretta*) subpopulation is classified as Critically Endangered by the International Union for Conservation of Nature (IUCN), monitoring data are scarce.
2. This study reports the results of the first long-term monitoring of the nesting population of loggerhead turtle held by Bwärä Tortues Marines on La Roche Percée beach, New Caledonia.
3. From 2006 to 2020, capture–mark–recapture was used to identify nesting individuals. Time and nesting success were recorded on site.
4. A total of 452 different females were observed and tagged over 14 years. The number of different nesting individuals observed each year showed a significant increase over the time frame of the study. A remigration interval of 3.34 years was observed, and the overall nesting success was 59.02%. This study also reports the internesting intervals and monthly and hourly variabilities in visits to the nesting site.
5. The conservation actions led by Bwärä Tortues Marines appear to be correlated with a higher nesting success. This study provides encouraging results and highlights the need to pursue the monitoring and conservation actions implemented by Bwärä Tortues Marines. Further management recommendations are also provided.

KEYWORDS

conservation, Critically Endangered, marine turtle, New Caledonia, population assessment, South Pacific

1 | INTRODUCTION

The loggerhead turtle *Caretta caretta* (Linnaeus, 1758) is divided into 10 subpopulations and is globally classified as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List. Regional Management Units (RMUs) are delimited by subpopulation size, genetics, geographic range, and trends (Wallace et al., 2010; Casale & Tucker, 2017), and allow a detailed evaluation of conservation status. The genetically distinct South Pacific subpopulation (South Pacific RMU; Boyle et al., 2009; Wallace et al., 2010) is categorized as Critically Endangered (Limpus & Casale, 2015).

Hatchlings and maturing turtles from this subpopulation drift in the South Pacific gyre, undertaking oceanic migrations, and growing and foraging in the open ocean (Boyle et al., 2009). During this period, by-catch through industrial fishing along the South-American coast is one of the major threats that they face (Alfaro-Shigueto et al., 2004; Alfaro-Shigueto et al., 2008; Donoso & Dutton, 2010). Subsequently, adult turtles take up residence in the South-Western Pacific and only use segments of the gyre to travel from their foraging and mating grounds. Every 2.5–3.5 years, females migrate back to their nesting areas, sometimes thousands of kilometres away (Limpus et al., 1992; Limpus & Limpus, 2003; Schroeder et al., 2003).

The main nesting location in the South Pacific RMU is situated in Southeast Queensland, Australia. It includes five nesting sites: Woongarra Coast (with Mon Repos beach, a long-term studied site for the South Pacific loggerhead turtle subpopulation; Figure 1a), Wreck Rock, Wreck Island, Tryon Island, and Erskine Island (Limpus & Limpus, 2003; Limpus, 2008; Limpus & Casale, 2015). Other nesting locations in Vanuatu, Tokelau, and New Caledonia have been recorded in the South Pacific RMU (Limpus & Limpus, 2003). Although the former locations showed low nesting density, the latter (i.e. New Caledonia) reported numerous nesting females and is likely to be one of the main nesting locations for the South Pacific subpopulation (Figure 1a; Limpus, 2008; Oremus & Mattei, 2017). Both nesting populations from the eastern coast of Australia and New Caledonia share the same genetic composition (Boyle et al., 2009; Wallace et al., 2010).

In New Caledonia, nesting individuals were reported on more than 50 nesting sites in three main areas: La Roche Percée, the islets off the north-western coast of the main island, and the islets situated in Le Grand Lagon Sud (Limpus & Limpus, 2003; Auzon, 2007; Oremus & Mattei, 2017). The nesting site of La Roche Percée (Figure 1b), located on the west coast of the main island, is likely to be the main nesting beach where preliminary studies recorded a high density of loggerhead nests (Limpus & Limpus, 2003; Limpus, 2008; Boyle et al., 2009; Oremus & Mattei, 2017). Despite the Critically Endangered status of the South Pacific subpopulation, monitoring information is lacking. Only a few loggerhead turtle nesting studies have been conducted in New Caledonia. Those studies mainly focused on population genetic and nesting parameters (Limpus et al., 2006; Auzon, 2007; Boyle et al., 2009; Read et al., 2013; Read et al., 2019; Magnan et al., 2021) or were produced in French and are less accessible to an international audience (Etaix-Bonnin et al., 2011; Fournière et al., 2015; Oremus & Mattei, 2017). The lack of a standardized long-term data series and temporal dynamic data in New Caledonia has been noted by the IUCN in 2015 as a source of uncertainty regarding the assessment of the South Pacific subpopulation (Limpus & Casale, 2015). This research gap needs to be filled to ensure that the conservation strategies and interventions are adjusted to respond to possible future threats.

Awareness of the global decline of this population (Limpus et al., 2006) led to the creation of the conservation group Bwärä Tortues Marines in 2006. The goals of Bwärä Tortues Marines are to assess the nesting population size and to implement appropriate actions to protect the loggerhead turtles at La Roche Percée. These actions complement the existing governmental rules (marine protected area: decree no. 33-1993/APS 1993 and 293-99/PS, 1999) prohibiting the fishing of marine species in the bay of La Roche Percée. Since 2006, throughout the nesting season, Bwärä Tortues Marines staff have collected data from nesting females at night and in the early morning. These patrols also aim to limit disturbances such as bonfires, light sources, vehicles, and pets on the beach.

This study reports the results of the first long-term monitoring of loggerhead turtles nesting in New Caledonia. The nesting population was monitored by Bwärä Tortues Marines from 2006 to 2020 on La

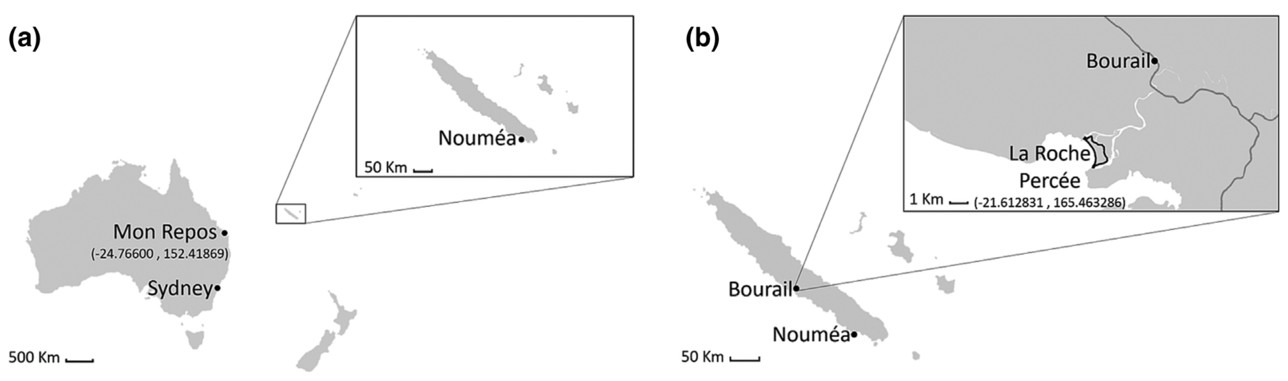

FIGURE 1 (a) Location of New Caledonia off the eastern coast of Australia. (b) Geographical location of La Roche Percée in New Caledonia.

Roche Percée beach. This study aims to give a comprehensive picture of this population to provide local authorities with the necessary information to maintain and implement efficient conservation measures. Gathering information about the New Caledonian nesting individuals, combined with Australian data, could help to obtain a better understanding of the loggerhead subpopulation in the South Pacific RMU.

2 | MATERIALS AND METHODS

2.1 | Overview

Over a period of 14 years, daily patrols were implemented throughout each nesting season (from November to March). The timing and activities of the loggerhead turtles were monitored.

2.2 | Study site

The study was conducted on La Roche Percée, a sandy beach in the Bay of La Roche Percée, New Caledonia (−21.612831, 165.463286) (Figure 1). This site is included in a marine protected area registered under the natural reserve status (decree nos 33-1993/APS, 1993, and 293-99/PS, 1999). The beach is oriented south-west and is 2.5 km in length, starting from a stand-up rock at the north-western end to the mouth of the Néra River at the south-eastern end. The Néra River brings dark sediments directly to the beach of La Roche Percée, resulting in darker sand compared with nearby beaches. La Roche Percée bay faces a large break in the barrier reef surrounding the area, allowing waves but also marine megafauna to enter the lagoon. At high tide, the beach is 20-m wide in the middle and 100-m wide at the northern and southern ends. During the hot and humid season (November–March) the beach can be submerged by water as a result of extreme weather events.

The only access to La Roche Percée is a road over a dam on its northern shore, blocking the northern bank of the Nera River. Vegetation near the road partially protects the beach from anthropogenic light sources (cars and houses) and there are no street lights in this area. Sand replenishment work took place in 2011 (during the time of this study, but not during the nesting season) at the vegetation margin, to widen the beach and counter beach erosion. The sand was taken from the Néra River but was not washed and sieved, causing compaction on some parts of the beach, resulting in the inability of turtles to dig in these areas. This compacted area was high on the beach at the margin of the vegetation and was partially covered with sand and vines (*Ipomoea pes-caprae*).

The bay is also famous for being one of the most important surf spots in New Caledonia, and is one of the main leisure sites, attracting many locals and tourists throughout the year. Although pets are prohibited inside the reserve, following a government decree put in place in 2009, dogs are regularly seen on the beach.

In the bay, a second beach named La Baie des Tortues (i.e. Turtle Bay, −21.60655, 165.45478, 280 m in length, and approx. one-fifth of the length La Roche Percée) is located 100 m north from La Roche Percée beach. The beaches are separated by a high rocky spit. This beach was not monitored during the night as the steep and slippery path leading to it would represent a safety hazard for the team working without lights.

2.3 | Monitoring and data collection

The walking patrol covered the 2.5 km of the study site, walking back and forth between the two ends of the beach. The activity of each turtle on the beach of La Roche Percée was recorded from November 2006 to March 2020 (14 nesting seasons) by members of Bwärä Tortues Marines. Two patrol sessions were conducted on the beach every day during the nesting seasons: (i) in the evening, usually conducted from 8 PM to 1 AM (i.e. night shift), which enabled the monitoring of nesting females encountered on the beach; (ii) in the morning (i.e. morning shift) for 2 to 5 h starting at dawn, and allowing an exhaustive count of all nesting activities throughout the night. The duration of a patrol could vary if a turtle or a track was detected by a member of Bwärä Tortues Marine before or after the usual hours. For example, if a turtle was spotted at 00:50 AM the patrol team stayed on site until the female completed her nesting cycle. Sometimes turtles crawled on the beach one after the other and the patrol team had to work until dawn. Only extreme weather conditions such as rain downpours or cyclone alerts led to the cancellation of a patrol (on average affecting eight patrols per year).

During the night shift, one or two teams comprising an eco-guard and trained volunteers walked without light alongside the high-water line, searching for turtle tracks. The number of teams deployed depended on the number of volunteers available. When a track was noticed, the team stopped and remained immobile while trying to locate the individual. The team followed the track in a way that meant they were unnoticed by the turtle (e.g. crawling). Observers were able to determine the precise nesting phase by seeing or hearing the turtle. The nesting phases include: ascending the beach; making a body pit (multiple body pit attempts could be undertaken before the next stage); digging the egg chamber; laying eggs; filling the egg chamber; covering the body pit; and returning to the surf (for precise descriptions of the nesting phases, see Hailman & Elowson, 1992). To avoid disturbance, the turtles were approached after the beginning of the egg-laying phase, from the back and without light. During data collection, a red light was used for a short time only and was never directed towards the head of the turtle. If the individual was found returning to the sea, the data were gathered while the turtle stopped to breathe. Data collection included: individual identification and carapace length, date, time, location, and nesting phase.

The morning shift consisted mainly of recording all the activities that happened during the late part of the night. It always started at dawn to maximize the chances of meeting the last turtles of the night, to protect those individuals from potential disturbances (i.e. beach visitors or dogs) and to be sure to record all turtle activities. A later start could have led to the loss of data through rising tides, strong winds, or beach users, who could have erased the tracks. Activities were defined using the sand cues described above. The date, time, and location of the activity were recorded. Each track (crawling tracks, body pit, and mound) was then wiped off so as not to count it a second time during the following night and to hide the location of the nest.

Individuals were identified using capture–mark–recapture (CMR). Every individual studied was tagged with a titanium tag (Titanium Turtle Tag; Stockbrands, Osborne Park, WA, Australia) on the trailing edge of the front flipper, in the skin between the first and the second scales adjacent to the axilla, following recommendations published by Limpus (1992). During the first five seasons, most of the individuals were tagged on both left and right front flippers, after which the protocol was reduced to one tag, placed on the left flipper, to minimize stress. Following the CMR protocol, if turtles did not have a tag, they were tagged and considered as captures (C). Individuals already tagged were considered as recaptures (R). Individuals could be recaptured from earlier in the same nesting season or from previous nesting seasons. Individual tags were read at the end of the egg-laying phase or during subsequent phases to minimize disturbance. A few turtles were tagged prior to this study and observed between 2006 and 2020 ($n = 9$; Limpus et al., 2006). They were included as recaptures in the results. In 2011/2012, the titanium tags were substituted with passive integrated transponder (PIT) tags (Animal Electronic ID Systems; Kiama, NSW, Australia). After one season the PIT tag project was considered too intrusive and was no longer used. Only one female was tagged with a titanium tag during this season. Each individual studied by the team was measured using the minimum curved carapace length method (Wyneken, 2001) and physical anomalies were recorded. The location of the nest or the nesting attempt was recorded during night and morning shifts. A triangulation method was used to record the location from season 2006/2007 to season 2016/2017. First, electricity poles along the road allowed the team to obtain an approximate location of the nest. Then, the precise location of the nest was obtained using triangulation made with salient field cues (e.g. trees, rocks, etc.). From 2017/2018 onwards, the Global Positioning System (GPS) was used.

If the turtle had already left the beach (i.e. had returned back to the sea), its activity was recorded using visual cues on the sand. The activity was considered a 'nesting success' when the pit was filled with disturbed sand, indicating that the individual had gone through all the nesting phases and had laid its eggs (Hailman & Elowson, 1992). The activity was considered as an aborted nesting attempt (also called 'false crawl') when the cues showed: (i) an attempt, where the individual went through the first phases of the nesting process (i.e. the body pit or the digging of the chamber steps) but stopped before laying its eggs; or (ii) a turnaround, where the individual ascended the beach, stopped, turned around, and returned to the sea (with a continuous track visible on the sand). The date, time, and location were also recorded.

2.4 | Data analysis

All data from 2006 to 2020 were gathered in one global database (available on Dryad, Barbier et al., 2023).

The calculations were carried out using Excel 2016 and R 4.2.2 (R Core Team, 2022). Statistical analyses were performed using R 4.2.2 (R Core Team, 2022) and the package *ggplots2* was used to create the figures (Wickham et al., 2016).

2.4.1 | Calculation of the total number of different individuals

The left front flipper tag was used to identify individuals. If this tag was missing or unreadable, the tag located on the right front flipper was used. The individuals tagged with PIT tags during the season 2011/2012 were not recorded as Captures for this season. They were probably tagged again with a titanium tag and considered as new individuals during the following seasons of this study as it was impossible for the team to recognize those individuals. Counting those individuals as Captures in 2011/2012 and as Captures in the following seasons would have led to an overestimation of the population size. Indeed, it is likely that the individuals encountered in 2011/2012 came back at least once during the eight following years of the study (remigration interval $= 3.34 \pm 1.77$ years, 2 to 4 years on average, reviewed in Miller et al., 2003). Full identification of the individuals was impossible for 2.1% of the observations (36/1682). Among those, 13 individuals possessed a tag although no previous reference to the tag was mentioned in the database, 16 individuals presented scars indicating tag loss and seven individuals had a tag but the patrol team was not able to fully read it. When compared to the database, those part-read tags could correspond to more than one already-registered tag. Those individuals were named ND1 to ND7 and were taken into account for the inter-nesting recapture calculation only. All 36 individuals were then considered as already known but unidentified. Finally, nine individuals observed during the study were tagged before the start of the current monitoring programme (Limpus et al., 2006). The tags were known and registered, and individuals were counted as Recapture.

2.4.2 | Metrics calculation

The inter-nesting interval (interval between two successful laying attempts) was calculated using individual identification and the dates of successful laying attempts within a nesting season. For each individual, the number of days between two successful laying attempts was determined.

The clutch frequency extrapolated (CFE) was calculated using the formula: total number of clutches laid within a nesting season/total number of different individuals observed within this season. The clutch frequency observed (CFO) was the number of clutches laid per identified individual within a nesting season (Frazer & Richardson, 1985; Tucker et al., 2018).

The nesting success was calculated using the formula: number of successful nesting attempts within a season/total number of nesting activities within this season$_s$ (i.e. crawls on the beach).

The Percentage Increase (PI) in nesting individuals was calculated using the formula: ((number of individuals at season$_s$ - number of individuals at season$_{s-1}$) /number of individuals at season$_{s-1}$) $\times$ 100.

2.4.3 | Statistical analysis

Temporal variation in the number of new individuals, the total number of different individuals, the percentage of nesting success and the number of activities were estimated using a Generalized Additive Model GAM (*mgcv* package, Wood, 2017; Wood, 2022). REML (Residual Maximum Likelihood) was used for smoothness selection and a penalized cubic regression spline fitting procedure was implemented. The models included either number of individuals, number of activities (Poisson distribution) or percentage of nesting success (beta distribution, *fitdistrplus* package, Delignette-Muller & Dutang, 2015) as the response variable and year as the smooth fixed effect. Ten different models with different numbers of knots (4 to 13 knots) for the smooth fixed effect 'season' were tested. Model selection was performed using AIC criteria and visual fit to the data (see Table S1). Best models showed 13, 9, 12 and 5 knots respectively for the total number of different individuals, the number of new individuals, the number of activities and the nesting success. Model validity was verified using the statistical and visual output from the gam.check function. Finally, linear models ('season' included as a linear fixed effect) were used to test linear trends in the temporal data (LM package *lme4*, Bates et al., 2015). Normality and homoscedasticity of residuals were verified for each linear model. A chi-square test was used to test if the presence of the team affected the nesting success. Averages are given along with standard deviation (Mean ± SD).

3 | RESULTS

3.1 | Population assessment

From 2006 to 2020, a total of 452 different individuals were identified: 443 turtles tagged by Bwärä Tortues Marines plus nine individuals tagged in an earlier study (Limpus et al., 2006).

On average, 35 ± 8 new individuals were observed each year with a range of 26 (seasons 2012/2013 and 2018/2019, Figure 2b, Table S2) to 54 (season 2016/2017, Figure 2b, Table S2). Overall, there were no differences in the number of new individuals observed per nesting season (Figure 2b, LM estimate = −0.30, standard error (SE) = 0.52, t = −0.57, p = 0.58, R^2 = 0.03). Moreover, the GAM analysis indicates that the number of new individuals ± 95%

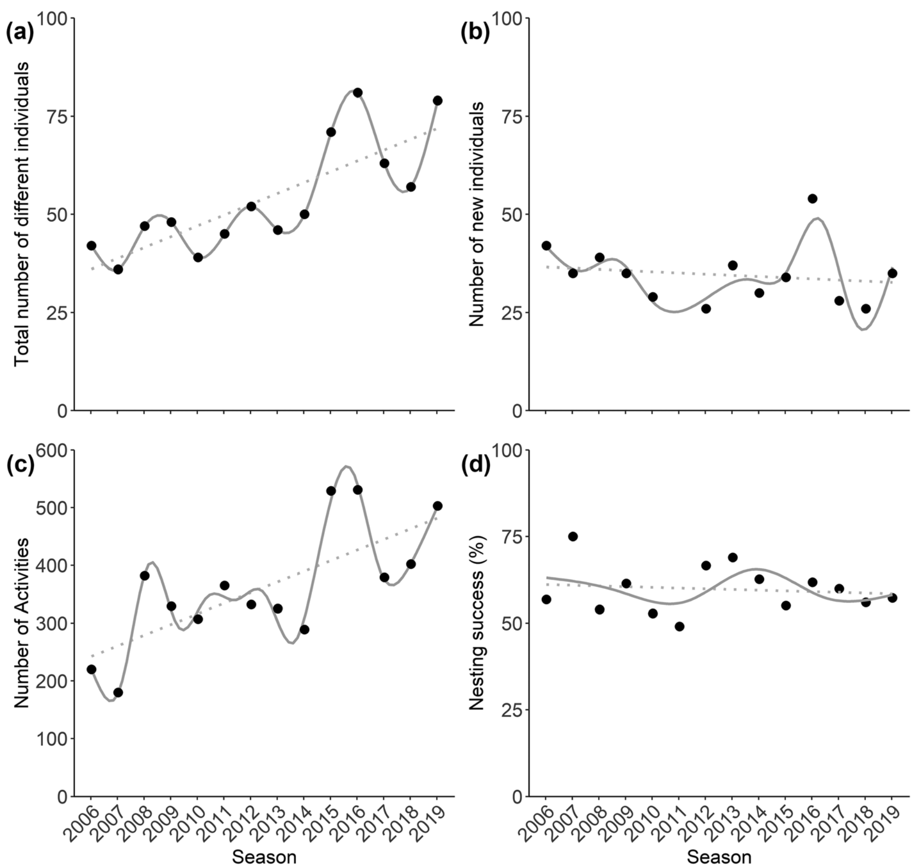

FIGURE 2 Temporal variability along the 14 years of loggerhead turtle monitoring recorded at La Roche Percée, New Caledonia. (a) the total number of different individuals (n = 452), (b) the number of new individuals (for the season 2011/2012, only one new individual was tagged with PIT tags due to a change in CMR methodology. As such, the number of new individuals in 2011/2012 does not properly reflect the true number of individuals that were present), (c) the number of activities, and (d) the percentage of nesting success. The dotted lines represent the linear trend in the data while the plane lines represent the cubic spline fit of the data.

confidence interval is not significantly different from constant ($p > 0.05$). There was no evidence for fit to cubic spline or an oscillating pattern as the effective degree of freedom (EDF) was below 1 (EDF = 6.94×10^{-5}, df = 8, $\chi^2 = 0$, $p = 0.45$, Deviance explained = 69%).

Each nesting season, new individuals were encountered (i.e. Captures) along with turtles already tagged (i.e. Recaptures). On average, 54 ± 14 different individuals were recorded per nesting season (Figure 2a and Table S2). There was a significant positive trend in the number of different individuals observed per nesting season with an upward trend of about 2.8 more individuals on average each year (Figure 2a, LM estimate = 2.76, SE = 0.59, $t = 4.70$, $p < 0.001$, $R^2 = 0.65$). Moreover, the GAM analysis indicates that the data follow a cubic spline shape with 13 knots that is significantly non-linear and non-horizontal (EDF = 1.537, df = 12, $\chi^2 = 31.04$, $p < 0.001$, $R^2 = 0.63$, Deviance explained = 69%, Figure 2a). The results from this analysis indicate that the number of individuals is significantly different with the years and follows oscillations and increases in numbers with years (Figure 2a). Between 2006 and 2020, the average PI of (1) different individuals and (2) new individuals nesting were 6.97 ± 21.57% and 3.84 ± 31.62% respectively (Table S2). The large standard deviations obtained reflect the cyclic pattern of the data.

3.2 | Nesting activity

The CMR monitoring allowed the female nesting remigration interval to be assessed (i.e. number of years between two consecutive nesting seasons for each individual). Each female was observed between one and eight seasons over the 14 years of the study. Among them, 144 turtles were identified during more than one season. Those females showed an average remigration interval of 3.34 ± 1.77 years (Figure S1).

Once females migrated to the nesting site for a nesting season, they were observed between one and 12 times within this season (only one individual was observed 12 times, in 2016/2017). Observations included successful and unsuccessful laying attempts. On average, 61.76 ± 7.7% of the individuals seen during a season were encountered more than once within that season and were recaptured 3.05 ± 1.32 times. Individuals ND1 to ND7 were taken into account for those calculations thanks to their partly readable tags that allowed the team to identify them within a nesting season. For all seasons studied, the average inter-nesting interval observed (i.e. interval between two successful laying attempts) was 3 ± 1.5 weeks and ranged from one to 9 weeks (Figure S2). However, because the patrol team could not link every successful attempt to an individual (visual sand cue indicating a successful nesting attempt but the turtle already left the beach), the inter-nesting interval was very high for some individuals (Figure S2b). Likely resulting in a higher than average overestimation of the overall inter-nesting interval. The median value of 2-weeks inter-nesting interval is likely to be more accurate.

Nesting females also showed high activity variability within days and among months (Figures 3a and 4). Females nested on La Roche Percée beach for only 6 months of the year from the end of October (first sight on the 28 October, in 2013/2014) to March (last activity on 30 March, in 2015/2016). December and January were the busiest months with 77.35% of all activities recorded (Figure 3a). Time was recorded when the teams first noticed an individual or a turtle track on the sand. However, only the records of time associated with an actual turtle observation are presented in the following results ($n = 1567$ activities out of a total of $n = 5073$ activities). Indeed, it was only possible to accurately estimate the time of an activity when the individual was seen. Those 'observed' activities were mostly recorded during the evening patrols. Overall, few observed activities occurred around sunset (2 + hours after), 24.6% occurred between 21:00–22:00; 19.5% between 22:00–23:00, and 19.7% between 23:00–00:00 (Figure 4, Table S3). Sixteen turtle crawls were recorded in the daytime either late in the morning or in the afternoon (14 successful and two aborted nesting attempts, between 10 AM and 5 PM).

The total number of activities showed an overall upward trend of about 18.4 more activities on average each nesting season across the timeframe of the study (Figure 2c, LM estimate = 18.42, SE = 4.93, $t = 3.74$, $p = 0.003$, $R^2 = 0.54$). Moreover, the GAM analysis

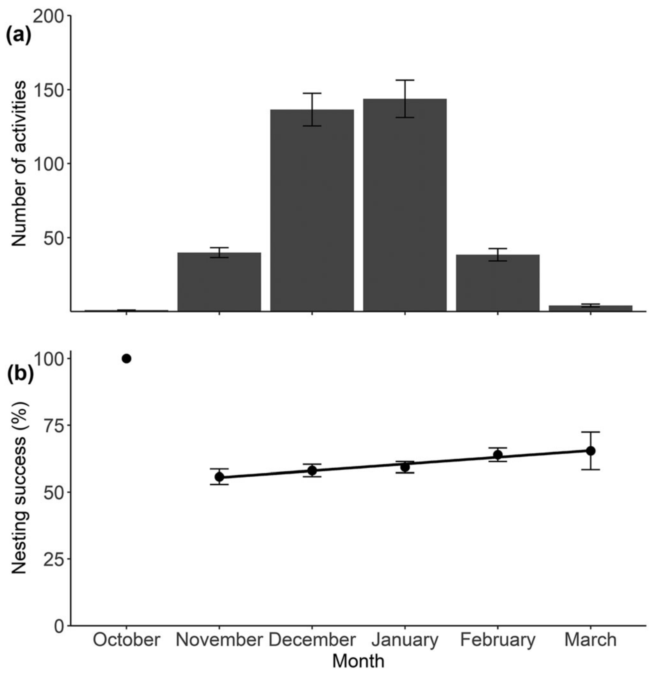

FIGURE 3 Monthly variability recorded on La Roche Percée beach, New Caledonia. All nesting seasons included from 2006 to 2020 (mean ± SE). (a) Monthly average of loggerhead turtle activities (mean ± SE, $n = 5073$). (b) Monthly nesting success (percentage) of loggerhead turtles. Only one activity (successful nesting) was recorded in October 2013. The nesting success from October (100%) is therefore excluded in further analysis. Sample size for the consecutive months are $n = 558$ (November), $n = 1911$ (December), $n = 2013$ (January), $n = 538$ (February), $n = 52$ (March).

indicates that the data follows a cubic spline shape with 12 knots that is significantly non-linear and non-horizontal (EDF = 10.42, df = 11, χ^2 = 369.9, p < 0.001, R^2 = 0.91, Deviance explained = 98%, Figure 2c). The results from those analyses indicate that the number of individuals is significantly different between the years and follows oscillations and increases in numbers with years (see Figure 2c). The positive trend in the number of activities is likely linked to the positive trend in the number of different individuals across the timeframe of the study.

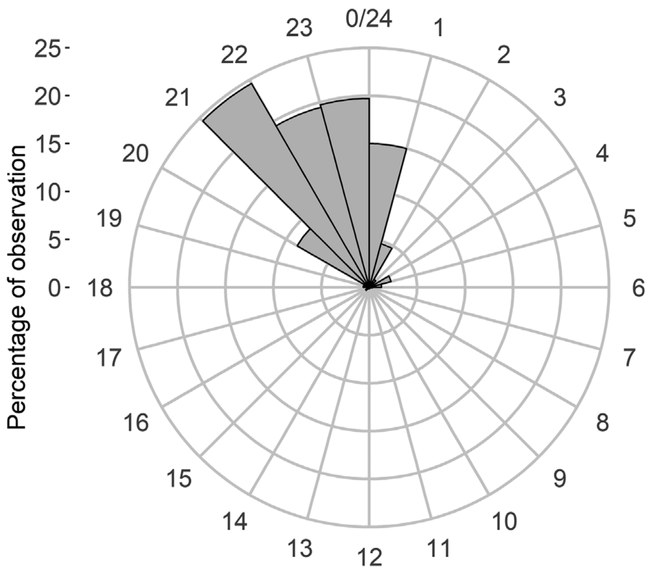

FIGURE 4 Hourly distribution of the 1567 observations of female loggerhead turtles on La Roche Percée beach, New Caledonia. Data from the nesting season 2006/2007 to the nesting season 2019/2020. Please note that those observations represent 31% of all activities recorded (n = 5073). See Table S2 for values.

3.3 | Nesting success

From the nesting season 2006/2007 to the nesting season 2019/2020, a total of 5,073 activities, including individual observations and turtle sand tracks only, were recorded. Among those, 2994 were considered a success (i.e. the turtle laid eggs), 2070 were considered aborted nesting attempts and 9 were undefined (Table 1). Thus, the overall nesting success of this population during this 14 years' study is 59.02% (Table 1, see Figure S3 for the number of nests per season).

The busiest nesting season was 2016/2017 with 531 activities (Table 1, Figure 2c). Although 2007/2008 was the quietest season with only 180 activities, it appears to be the season with the highest nesting success rate (75%, Table 1, Figure 2d). The lowest nesting success rate was found in 2011/2012 with only half of the attempts leading to a clutch laid (49.04%, Table 1, Figure 2d). There was no significant linear trend in the percentage of nesting success per nesting season (estimate = −0.2, standard error (SE) = 0.48, t = −0.43, p = 0.68, R^2 = 0.02, Figure 2d). Moreover, the GAM analysis indicates that the percentage of nesting success ±95% confidence interval is not significantly different from constant (p > 0.05). It did not show significant cubic spline or oscillating pattern (EDF = 1.04×10^{-5}, df = 4, χ^2 = 0, p = 0.64).

The nesting success increased monthly within the nesting season (Figure 3b, LM estimate = 2.52, standard error (SE) = 0.28, t = 8.96, p = 0.003, R^2 = 0.96). In March, the last month in the nesting season, the nesting success was 10% higher than in November at the beginning of the nesting season (65.38% and 55.73% respectively).

Bwärä Tortues Marines teams were physically present during 33.4% of all activities recorded. The nesting success calculated for those activities was significantly higher than when a patrol team was absent (79.1% against 49.0%, χ^2 = 417.62, df = 1, p < 0.001).

TABLE 1 Number of activities, success, aborted nesting attempts and nesting success of the female loggerhead turtles recorded from the season 2006/2007 to the season 2019/2020 at La Roche Percée beach, New Caledonia.

Season	Activities	Success[a]	Aborted nesting attempts	Nesting success (%)
2006/2007	220	125	95	56.82
2007/2008	180	135	45	75.00
2008/2009	382	206	176	53.93
2009/2010	329	202	127	61.40
2010/2011	307	162	145	52.77
2011/2012	365	179	186	49.04
2012/2013	332	221	111	66.57
2013/2014	325	224	101	68.92
2014/2015[b]	289	181	99	62.63
2015/2016	529	291	238	55.01
2016/2017	531	328	203	61.77
2017/2018	379	227	152	59.89
2018/2019	402	225	177	55.97
2019/2020	503	288	215	57.26
Total	5073	2994	2070	59.02

[a]Successful activities equal the number of nests per season.
[b]Nine activities were undefined during the 2014/2015 nesting season.

Over the 14 years of the study, the average CFE (total number of clutches divided by the number of different individuals) was 3.97 ± 0.44 clutches.female^{-1}.nesting season^{-1} (Table S4). It ranged from 2.98 (2006/2007) to 4.87 clutches.female^{-1} (2013/2014, Table S4). The CFO (*i.e.* mean of clutch per observed individual, considering only the nest laid by an identified individual) ranged from 1 to 5 clutches per female per nesting season. The average of the CFO was 1.94 ± 0.23 clutches.female^{-1}.nesting season^{-1}. It ranged from 1.63 (2008/2009 and 2011/2012) to 2.35 clutches.female^{-1} (2018/2019, Table S4).

4 | DISCUSSION

This study presents the results of the first long-term monitoring of the loggerhead turtle nesting population of La Roche Percée, New Caledonia, providing substantial information on the declining South Pacific subpopulation.

Whereas most studies use nesting trends data and number of nests to infer population trends and recovery (e.g. Marcovaldi & Chaloupka, 2007; Chaloupka et al., 2008; Witherington et al., 2009), this study reports the actual number of nesting females to explore trends and reach conclusions about population abundance. To our knowledge, only few other studies report exhaustive numbers of nesting females (e.g. Broderick et al., 2002) and only one study using nest counts has recognized the limitation of the method and attempted to estimate adult female abundance (Ceriani et al., 2019).

4.1 | Population assessment

From 2006 to 2020, 452 individuals were identified by Bwärä Tortues Marines with 54 unique turtles and nearly 35 neophytes annually on average. To our knowledge, La Roche Percée is the second highest nesting aggregation in the South Pacific RMU after the Australian rookery (Limpus & Casale, 2015). It is important to note that despite a consistent monitoring effort, the recorded number of turtles should be considered an estimation and could slightly differ from the true number of individual turtles. For example, if some individuals constantly nested between the end of the night patrol and the start of the morning patrol, then they were missed. Moreover, if an individual tagged in 2006 lost its tag in the early years of the project and was only seen again in one of the last seasons, the tag scar could have healed and this female would have been counted as a new individual. However, these cases are likely rare and the population estimation given is likely close to the true value. The nesting population size at La Roche Percée is influenced by demographic parameters such as new breeding females or death of old individuals creating an in and out flow of individuals. The regular recruitment of new individuals suggests that the nesting population size is not completely known yet. The high number of nesting individuals observed each nesting season suggests the importance of this beach for this loggerhead turtle subpopulation. In comparison, almost 700 nesting females are reported annually in eastern Australia (Limpus & Casale, 2015). On the Woongarra coast (the main Queensland nesting site including five beaches between Burnett and Elliott Rivers, cumulative beaches length = 3.45 km, Berry et al., 2013), between 100 and 260 different individuals came to nest each year from 1990 to 2004 (Limpus, 2008).

The upward trend of the number of different individuals is one of the major results of this long-term study. It highlights the growing importance of this site and that the efforts made by Bwärä Tortues Marines and the government of New Caledonia to protect this species are having an encouraging effect. It could indicate positive consequences of the conservation measures implemented on the site and on a global scale (decree 293-99/PS, CITES Appendix I, 1975, CMS Bonn convention, 1983, the Inter-American Convention for the Protection and Conservation of Sea Turtles, 1996). Nonetheless, 30 years of monitoring (recruitment latency) is necessary to observe the actual impact of local measures. In Australia, after a strong decline (86%) of the South Pacific subpopulation nesting on sites in Queensland between the mid-1970s and 1999 (Limpus, 2008), there had been an increasing trend from 2001 following the implementation of protection measures (Limpus & Casale, 2015). However, a second decline occurred between 2010 and 2014 (Limpus & Casale, 2015). The population trends from New Caledonian and Australian nesting sites show the importance of: (1) carrying on current monitoring methods, (2) establishing new conservation measures and (3) encouraging the implementation of new management programmes – such as the protection of known foraging and nesting grounds (Limpus, 2008; Limpus & Casale, 2015; see Madden Hof et al. (2020) for the recent implementation of an efficient predator exclusion device).

In New Caledonia, public awareness and the intensification of patrol efforts appear to reduce land threats (e.g. dog and human disturbances). In 2012/2013, more than 20 nests were predated by dogs whereas only three nests were predated in the last season (unpublished data). Dogs were also responsible for aborted nesting attempts during the nesting process by disturbing or attacking female turtles. Likewise, lights can deter female turtles from nesting (Kamrowski et al., 2012; Price et al., 2018; Magnan et al., 2021), and Bwärä Tortues Marines is working alongside residents to increase the density of the vegetation wall along the beach. Furthermore, the presence of the patrol teams on the beach was positively correlated with the female nesting success (79.1% against 49.0%, see results for significance). However, there could be a confounding factor if females naturally have a higher nesting success prior to 1 am rather than later. This needs further investigation.

4.2 | Nesting activities

4.2.1 | Remigration interval

The females nesting on La Roche Percée showed an average remigration interval of 3.34 years. This result is consistent with the literature (Dodd, 1988; Schroeder et al., 2003). The remigration interval in loggerhead turtles can vary from 1 to 9 years with most individuals showing a remigration interval of 2 to 4 years (Miller et al., 2003). In the Southwest Atlantic, Southwest Indian, Northwest Atlantic, Mediterranean and North Pacific RMUs the remigration intervals reported were respectively 2 to 3 years (Brazil, Marcovaldi et al., 2010), 3.2 ± 1.9 years (Mozambique, Fernandes et al., 2016), 4 years (ranging from 3 to 7 years, Gulf of Mexico, USA, Phillips et al., 2014), 2 years (Greece, Broderick et al., 2002) and 2.7 ± 1 years (ranging from 1 to 7 years, Japan, Hatase et al., 2004). The remigration interval could have been slightly overestimated in the present study because the patrols were covering only the first half of night-time and the early mornings. Therefore, if some individuals were coming regularly late at night, they may have been missed. Moreover, tag loss appeared as a new obstacle during the last nesting seasons. A few individuals presented scars resulting from tag loss and thus were not identifiable. Tag loss can be the result of diverse factors (e.g. position of the tag on the flipper and choice of the flipper but also courtship or crawling on land to nest, Limpus, 1992). This can be a major problem for long-term population monitoring. Even though the PIT tag method was abandoned after 1 year of testing during the 2011/2012 nesting season, recent studies have shown that this tagging method improves loggerhead turtle identification by 29% (Omeyer et al., 2019) with retention significantly superior compared to titanium tags (Pfaller et al., 2019). If reintroduced, PIT tags should be combined with titanium flipper tags and adequate training of the tagging eco-guard should be provided (Omeyer et al., 2019). If this solution is not available for the Bwärä Tortues Marines we recommend tagging both front flippers to identify an individual and the improved goal of at least one tag retention.

The analysis of the number of different females per season showed a 3-year cyclical pattern. This pattern may be principally explained by the remigration interval: i.e. most individuals present on the nesting site in a given year will return 3 years later. It would mainly be the same individuals every 3 years plus new individuals who had matured in the meantime. However, environmental fluctuation can also impact the remigration interval (Saragoça Bruno et al., 2020). Climatic (atmospheric and oceanic) variation can affect the availability of nutritive resources at the feeding ground and consequently the number of individuals that become reproductively active each year (Hays, 2000; Saragoça Bruno et al., 2020). For example, in Costa Rica, the El Niño Southern Oscillation (Atmospheric-oceanic phenomena) alters sea surface temperature and precipitation, significantly impacting the productivity of seagrass meadows at the feeding site and the reproductive output of green turtles (*Chelonia mydas*, Saragoça Bruno et al., 2020).

During the 14 years of this study, no individuals tagged from other countries, such as Australia, were observed. The nesting sites of La Roche Percée and Mon Repos are separated by approximately 1376 km. Loggerhead turtle migrations between New Caledonia and Australia have been documented (Limpus, 2008; Limpus et al., 2006), but only relating to turtles migrating from their foraging area in one of the two countries to the nesting site in the other one (e.g. loggerhead turtles foraging around New Caledonia and nesting on Australian beaches and *vice versa*). This nesting site fidelity is in line with the literature (Miller et al., 2003; Limpus, 2008). Ongoing studies on other beaches in New Caledonia such as the very close beach of La Baie des Tortues could bring more information on specific nesting site fidelity. Until now, no proof of turtle nesting on both beaches has been found, but few data are available.

4.2.2 | Clutch frequency and inter-nesting interval

Female turtles lay multiple clutches within a nesting season (ranging from one to five clutches laid by the same individual). The mean CFO in this study (i.e. 1.94 clutch.female^{-1}.nesting season^{-1}) is consistent with the results found in other studies. Schroeder et al. (2003) reported between one and seven clutches per female per nesting season worldwide and an average CFO ranging from 1.10 to 3.42 clutch.female^{-1}.nesting season^{-1} for loggerhead turtle rookeries located in Japan and the USA, respectively. For the South Pacific subpopulation, Mon Repos beach showed a mean CFO of 2.91 clutch. female^{-1}.nesting season^{-1} (Limpus, 1985). The number of clutches observed is, however, likely to underestimate the actual number of clutches per individual (i.e. true clutch frequency) because all nesting events were not exhaustively observed (Frazer & Richardson, 1985; Tucker et al., 2018). The team was present on 44% of the successful nesting events and potentially missed one or multiple nesting events for some individuals. The mean CFE found in this study (i.e. 3.97 clutch.female^{-1}.nesting season^{-1}) is likely to be closer to the actual number of clutches per individual although this number could be overestimated if some individuals were not identified during a nesting season. The mean CFE found in this study is also in line with other studies (from 2.1 to 4.6 for loggerhead turtles nesting in Cyprus, see Method 3 in Broderick et al. (2002); mean clutch frequency corrected ranging from 2.81 to 4.21 worldwide, Schroeder et al. (2003); 3.41 found at Mon Repos, Limpus (1985)). Finally, revised clutch frequency, using satellite tracking or genetic capture-recapture information allow for a more rigorous estimate of clutch frequency. Revised clutch frequency estimates using satellite tracking information gives a similar to higher average value for loggerhead turtle nesting in the Mediterranean RMU (Greece: 3.8 clutch. female^{-1}.nesting season^{-1}; Rees et al., 2020), Northwest Indian RMU (Oman: 4.8 and 5.5; Rees et al., 2010; Tucker et al., 2018) and Northwest Atlantic RMU (USA: 4.7 and 5.4; Hart et al., 2010; Tucker, 2010). Revised clutch frequency estimates using genetic capture-recapture information are similar to the revised clutch frequency estimates obtained with satellite telemetry on the same site in the Northwest Atlantic RMU (Georgia, USA: 4.5 and from 4.04 to 4.70 obtained with satellite telemetry and genetic capture-recapture, respectively, Scott, 2006; Shamblin et al., 2017).

Turtles nesting at La Roche Percée demonstrated an inter-nesting interval of approximately 14 days (median). This result is consistent with the literature: 12 to 16 days and 12 to 25 days reviewed in Miller et al. (2003) and Robinson et al. (2022), respectively. Loggerhead turtles nesting in the South Pacific, Northwest Atlantic and Mediterranean RMUs presented inter-nesting intervals in the same range, respectively 2 to 4 weeks (Australia, Limpus, 1985), 11.7 ± 1.7 days (USA, Hart et al., 2010) and 12.5 ± 1.7 days (Cyprus, Broderick et al., 2002). The inter-nesting interval has been shown to be significantly correlated with the water temperature in loggerhead turtles: the warmer the water temperature, the shorter the inter-nesting interval ($R^2 = 0.60$, Robinson et al., 2022). This factor is likely to explain some of the variation in inter-nesting interval within and between nesting seasons in New Caledonia, which is subject to cyclones and heavy depressions during the nesting seasons. Determining accurately the inter-nesting interval relies on intercepting and identifying every female on the nesting site. The present survey covered only a part of the night, therefore only in 33% of the activities was the individual identified. To obtain a better accuracy of the inter-nesting interval estimation, the number of surveys held each day should be increased and patrols should cover the entire night. Greater human resources would be necessary. Two other options to improve the inter-nesting interval accuracy would be to: (1) use satellite tags on nesting females to better quantify nesting events (Hays & Hawkes, 2018; Santos et al., 2021), and (2) perform a genetic capture-recapture study (Shamblin et al., 2017).

4.2.3 | Temporal variability

The nesting period at La Roche Percée starts in late October/early November and ends in March, with a nesting peak in early January. This result corresponds to the nesting period trend observed in South Queensland (Limpus, 2008), with a slight delay of one or 2 weeks.

Turtles are consistently coming up on the beach at night. This behaviour, already documented (Dodd, 1988), is adopted at La Roche Percée with 98.7% of activities happening between sunset and sunrise, likely to avoid the heat on the beach during the day and/or human disturbances.

4.3 | Nesting success

The number of activities recorded per season increased over the 14 years of monitoring. This result is linked to the increasing trend of the number of individuals nesting each year. The nesting success is constant over the seasons (59.02% on average from the nesting season 2006/2007 to the nesting season 2019/2020). In the literature nesting success for loggerhead turtles ranges from 16.8% on Daphni beach, a public beach in Greece (Margaritoulis, 2005), to 89.5% on a protected beach on Jupiter Island, Florida, USA (Lund, 1986). Intermediate nesting successes were found at various sites: 22% and 43.1% in the Northeast Atlantic RMU (Cape Verde, Marco et al., 2015; Silva et al., 2017), 29% and from 48 to 62% in the Northwest Atlantic RMU (USA, Andre & West, 1981; Brock et al., 2009), 73.6% in the Southeast Indian RMU (Western Australia, Reinhold & Whiting, 2014), from 21.5 to 49.2% (Turkey) and from 20.8% to 32% (Greece) in the Mediterranean RMU (Türkozan et al., 2003; Margaritoulis, 2005). For reviews comparing all marine turtle species nesting success, see Dodd (1988) and Miller (2017). On La Roche Percée beach, aborted nesting attempts were due to anthropogenic disturbance (e.g. presence of humans around the turtle, lights on the beach or dog harassments, unpublished data), improper substrate to dig a nest (e.g. presence of vines, compaction following the sand replenishment of 2011, unpublished data) or other factors undetermined by the patrols.

The results indicate that the nesting success increased within the nesting seasons from the beginning of November to the end of March. Different hypotheses could explain this result. First, after a few years without nesting, the turtles could have some difficulties in laying their first clutch at the start of the nesting season. Second, individuals might do some exploratory crawls on their arrival at the nesting site before laying the first clutch, indeed a large number of turnarounds were recorded at the beginning of each nesting season.

4.4 | Implications for conservation

Population monitoring is an indispensable tool to evaluate population decline and to inform the implementation of appropriate environmental management measures (Nichols & Williams, 2006; Goldsmith, 2012). A noticeable reduction of nests attacked by dogs over the period of the study (unpublished data) shows the positive effect of recurrent communications with the local inhabitants. A high number of light sources was observed every year throughout the study (mostly from the growing number of tourists on-site, personal observations) and the presence of patrols, acting promptly to convince users to switch off their devices, was essential to maintain darkness on the beach. The higher nesting success found when patrols were on site might be explained by those measures (Silva et al., 2017). This study emphasizes that the current conservation measures in place must be maintained in order to protect this turtle population. We recommend maintaining a high level of protection to address persistent anthropogenic threats and setting up new noticeboards on-site in prominent locations. To continue the collection of data on nesting individuals and their reproductive output, we advocate for the implementation of further measures such as patrolling on site all night long, tagging both turtle flippers, or implementing PIT tag use coupled with titanium tags (Omeyer et al., 2019; Pfaller et al., 2019). Finally, a satellite tracking study could provide accurate spatiotemporal information (e.g. remigration and inter-nesting intervals or fidelity to the nesting and foraging sites, Hays & Hawkes, 2018) which would allow us to better understand the migratory range and nesting pattern of this subpopulation.

5 | CONCLUSION

This study provides essential data to improve the protection and the monitoring of the loggerhead turtles nesting population in New Caledonia and brings new insights into the South Pacific subpopulation.

The results indicate that La Roche Percée beach has the second highest nesting density in the South Pacific RMU, and show an increase of activities related to the increase of individual nesting on this site. The nesting success and temporal variability results are consistent with the literature, with the data recorded on the eastern Australian nesting population and more generally with the behavioural ecology reported in studies of loggerhead turtles. The monitoring is still ongoing under the supervision of the conservation group Bwärä Tortues Marines. The conservation and monitoring programme as well as the data recorded are promising and prove the utility of the protection measures implemented on this site, although only a longer term study (until sexual maturity of the first hatchlings observed during the survey) will provide a comprehensive overview of the nesting loggerhead turtle population of La Roche Percée, New Caledonia. Long-term monitoring data on other nesting sites in New Caledonia and other South Pacific islands are now needed to obtain a comprehensive understanding of the South Pacific loggerhead turtle subpopulation.

AUTHOR CONTRIBUTIONS

Dominique Lafage implemented the fieldwork. Dominique Lafage, Maxime Barbier, T. F, Hugo Bourgogne, Marine Attard, Kevin Fourniére supervised the fieldwork. All authors contributed to the data collection. Maxime Barbier and Adelaide Sibeaux performed the analysis and wrote the paper. All authors reviewed and agreed with the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The database is available on Dryad Digital Repository with the identifiers doi: 10.5061/dryad.00000007c.

ETHICS STATEMENT

This research conformed to the HYPERLINK "http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:32010L0063:EN:NOT" Directive 2010/63/EU guidelines on ethical standards, it was endorsed by the Province Sud of New Caledonia through authorizations issued by Province Sud. It complied with all relevant local and national legislation.

ORCID

Adelaide Sibeaux https://orcid.org/0000-0002-3340-3741

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SUPPORTING INFORMATION

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

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