

A single Management Unit but specific conservation strategies between two major nesting areas of the critically endangered loggerhead turtle in New Caledonia.

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Abstract

The loggerhead turtle (*Caretta caretta*) South Pacific subpopulation is classified as 'Critically Endangered' in the International Union for Conservation of Nature's Red List, based on its estimated demographic decline. The Southern Province of New Caledonia shelters two distinct major nesting areas for this subpopulation, aggregating approximately 10–25% of all reported nesting activities at the ocean basin scale. A prejudicial knowledge gap subsisted in whether the nesting population of these two nesting areas are part of a single or two distinct Management Unit(s), which could have significant implications for conservation strategies to be implemented. Based on a dataset collected from November 2016 to March 2023, we evaluated the sex-specific connectivity of loggerhead turtles over various temporal scales using three complementary methodologies: satellite telemetry (intra-annual), Capture-Mark-Recapture surveys (inter-annual) and molecular analysis (inter-generations). Our results suggest that reproductive populations from both nesting areas form a unique genetic stock, and that the gene flow is presumably ensured by males, contrasting with the high fidelity to nesting areas shown by females. Considering that both nesting areas show heterogeneous habitat conformations and substantial differences in the associated threat levels, this study highlights the importance to consider both the site-specific aspects and the more global Management Unit scale to ensure a prioritized and coherent conservation strategy. Not considering those aspects could result in management failure and loss of local population segments.

Introduction

Marine turtles form a long-lived taxonomic group with complex life cycles, including expansive hatchling dispersals and adult ocean-scale distributions (Musick and Limpus 1997; Casale et al. 2007; Arendt et al. 2012; Casale et al. 2013; Read et al. 2015). Reproductive individuals undertake important philopatric-induced migrations as they return to their natal beaches to breed and nest (Meylan et al. 1990; Bowen and Karl 2007). This ecological trait enhances the formation of population structures by reducing gene flow among groups of individuals mating at geographically separated locations (Bakker et al. 2010). Ultimately, it can lead to a loss of genetic diversity and adaptive potential (Stiebens et al. 2013). Defining both the geographic distribution of population units and their level of connectivity is therefore required to set up efficient conservation actions (Wallace et al. 2010; Fitzsimmons and Limpus 2014; Wallace et al. 2023). To tackle this challenge, coherent population boundaries must be established (Wallace et al. 2011). Spatially explicit 'Management Units' (MUs), defined as functionally independent population segments (Wallace et al. 2010, 2023), are powerful tools to set appropriate short-term targets for conservation (Wallace et al. 2010; Bourjea et al. 2015; Tolve et al. 2018). However, the delineation of population units is not always straightforward, and it requires a clear understanding of both conservation objectives and threats to the species of interest (Moritz 1994; Taylor and Dizon 1999). For the purpose of this paper, we will consider the MU at the resolution of the genetic stock as we aim to identify consistent management spatial frameworks at the functionally independent population scale (Fitzsimmons and Limpus 2014; Wallace et al. 2023).

The loggerhead turtle *Caretta caretta* (Linnaeus, 1758) shows a cosmopolitan distribution in warm and temperate waters of the globe. It has been classified as 'Vulnerable' in the International Union for Conservation of Nature (IUCN) Red List on a global scale since 2015 (Casale and Tucker 2015, 2017). However, the South Pacific subpopulation, designated as a genetically distinct 'Regional Management Unit' (Boyle et al. 2009; Wallace et al. 2011; Fitzsimmons and Limpus 2014; Limpus and Casale 2015), suffered a strong demographic collapse and was therefore listed as 'Critically Endangered' in 2015 (Limpus and Casale 2015). Nesting aggregations of this subpopulation are restricted to the western part of the ocean basin. Eastern Australia is considered to aggregate a large majority of its nesting activities (Limpus and Limpus 2003), and the remaining of this subpopulation is essentially breeding and nesting in New Caledonia (Limpus and Casale 2015; Bourgogne et al. 2024).

In New Caledonia, two large nesting areas have been described (Limpus et al. 2005; Barbier et al. 2023; Bourgogne et al. 2024) (Fig. 1-A,B): the 'Roche Percée' beach (RP), on the commune of Bourail (Limpus et al. 2005; Barbier et al. 2023); and the 'Grand Lagon Sud' area (GLS), off the southern end of the main island (Bourgogne et al. 2024). Both areas support several 10s of nesting females every year, combining for an 10–25% of all nesting activities reported in the South Pacific subpopulation (Limpus and Casale 2015; Barbier et al. 2023; Bourgogne et al. 2024). They are roughly 150 km apart, yet show different habitat structures and threats of varying natures and intensities. As such, these nesting areas are currently rather managed as distinct conservation units with specific actions addressing specific local threats. However, the connectivity between these two nesting areas has never been evaluated. As a result, it is still unclear whether they should be considered as a single or two distinct MUs, which could have significant repercussions upon the definition and spatial framework of the management strategies to be implemented.

The main objective of this study is therefore to provide a first-time assessment of the connectivity pattern between the RP and the GLS nesting areas at different temporal scales, using concurrently three different techniques:

(1) Telemetric surveys were used to evaluate the spatial dispersion of adult loggerhead females within the nesting season and to test their fidelity to their nesting areas at an intra-seasonal scale. They derived from a collaborative program, designed to identify migratory corridors and foraging grounds of females nesting in New Caledonia (Oremus 2023).

(2) Capture-Mark-Recapture (CMR) data allowed us to test females' fidelity to their nesting areas on a multi-seasonal scale. These data are essentially based on the long-term flipper tag recovery survey conducted at the RP beach since 2006-07 (Barbier et al. 2023). Additional data were collected at the GLS area since the 2016-17 nesting season.

(3) Molecular analyses have contributed to clarify inter-generational connectivity by testing the existence of a gene flow between the reproductive population segments. A tendency for males to show less fidelity to their native breeding grounds than females has been reported in marine turtles (Casale et al. 2013; Beal et al. 2022). Since males rarely come ashore (Fitzsimmons et al. 1997), direct monitoring of their

movements through telemetry and CMR is extremely challenging. In this study, we have therefore included both mitochondrial markers and nuclear microsatellite markers to assess maternal and bi-parental gene flow between both nesting areas (Fitzsimmons and Limpus 2014).

Considering that the RP and the GLS areas are both under the management authority of the Southern Province of New Caledonia, the application of this study is to provide local policy-makers with a coherent and prioritized conservation strategy in the context of proximate yet geographically discontinued nesting areas facing heterogeneous threats.

Materials and methods

2.1 Study area

2.1.1 The RP nesting area

The coastal RP site is a sandy beach located in the bay of Bourail (S°21.61229, E°165.46461), on the west coast of the mainland (Fig. 1-C). This rookery is composed of thin and dark arenite-type sand, dragged through the Nera River mouth (Allenbach 1998; Limpus et al. 2005), and vegetation at the rear of the coastline is scarce. The beach of the 'Roche Percée' is oriented south-west and is 2.2 km long. It is included in a marine protected area registered under the natural reserve status (decree 33-1993/APS, 1993, and 293 – 99/PS, 1999), that is part of a larger zone of ecological importance, the 'Zone Côtière Ouest', listed as a UNESCO world heritage site since 2008 (UNESCO 2009). This nesting area benefits from a long-term survey by a local Non-Governmental Organization 'Bwără Tortues Marines' (Fourniere et al. 2015; Barbier et al. 2023). An annual average of 253.3 ± 58.8 , $n = 17$ nests have been reported since the initiation of the monitoring effort during the 2006–2007 season (Bardet 2023).

2.1.2 The GLS nesting area

The GLS zone is a 314.500 ha marine protected provincial park at the southern end of the mainland's lagoon (S22°00, E167°00), and is one of the six zones of New Caledonia to be listed as a UNESCO world heritage site since 2008 (UNESCO 2009). This area is characterized by the presence of 35 coral reef islets, scattered over the park. All the data used in this study were collected from nine of these islets (Fig. 1-D, SI.1 Appendix). This subset combines for 43% of the overall nesting activity reported annually in the GLS area (Bourgogne et al. 2024). The sandy beaches of the islets are composed of bright and coarse coral sand (Garcin et al. 2022). The coastline vegetation is most of the time rich and abundant, providing additional shade on the beach tops. This area has benefited from an on-going monitoring program since 2016, which reports an annual estimate of 437 nests (95% Credible Interval = 328–582) (Bourgogne et al. 2024).

2.2 Data acquisition

All data acquisitions were conducted during seasonal surveys in the RP or the GLS nesting areas, over a seven nesting seasons-period extending from 2016-17 to 2022-23. To match the reproductive phenology of the *C. caretta* turtle in New Caledonia (Barbier et al. 2023; Bourgogne et al. 2024), monitoring efforts occurred from early November to late March.

2.2.1 Satellite telemetry

Satellite telemetry has been widely used to assess marine turtles' fidelity to their breeding and nesting grounds (Stoneburner 1982; Witt et al. 2008; Tucker 2010; Casale and Ceriani 2019; Beal et al. 2022). Loggerhead females have been reported to nest several times during a single reproductive season: 2.91–3.97 nests.nesting season⁻¹ in the South Pacific (Limpus 1985; Barbier et al. 2023). Here, we aimed to monitor intra-nesting period spatial dispersion to investigate the possibility that they could indifferently nest on both the RP and the GLS areas within the same season.

Thirty individuals were fitted with Wildlife Computers SPOT-375 satellite tags (n = 17 on the RP site and n = 13 in the GLS area). All deployments occurred on nesting females encountered during beach monitoring patrols. They were held temporarily in a portable plywood corral to facilitate the transmitter attachment (Tucker 2010). A carapacial and painless fixation procedure was implemented following the Wildlife Computers' protocol, designed to minimize physical and behavioral impacts on the tagged individuals (Wilson and McMahan 2006; Hamelin and James 2018).

Raw Argos locations are less precise than GPS positions, with errors generally exceeding several hundred meters from the actual position (Costa et al. 2010; Patterson et al. 2010; Jonsen et al. 2020). In order to improve localization accuracy, Argos data were filtered and smoothed using the R package 'aniMotum' (Jonsen et al. 2023) to provide quality-controlled locations (Jonsen and Patterson 2019; Jonsen et al. 2020, 2023). It is based on a continuous-time state-space model, with assigned error classes 3, 2, 1, 0, A and B provided in the Argos Least Squares format. Parameters and corrected positions were assessed through a 'Move Persistence' model. It accounts for irregular timing of observations due to data gaps as it supplies an index of how movement behavior varies in space and time, based on the autocorrelation of successive movements (Jonsen et al. 2023).

For this study, we only focused on movements during the nesting period, in opposition to the migration period. Migration initiation was identified as a steep and persistent increase in movement speed, without a return movement. On the other hand, movements associated with the nesting period are characterized by low daily speeds and spatially limited movement patterns (Bourjea et al. 2013; Beal et al. 2022). The beginning of the migration was set as the first day of a minimum threshold of 3-consecutive days with a speed > 20 km.day⁻¹ (Corbel 2020). In order to assess movement patterns and to identify potential shifts between the RP and the GLS areas, we calculated for each tagged individual:

The duration of the telemetric survey;

The estimated size of the distribution range, defined as the area bounded by the outermost-recorded positions of the tagged individual;

N_m = the number of times individuals tagged on the RP nesting area traveled to the GLS nesting area, or the other way around (*i.e.* individuals tagged on the GLS nesting area traveling to the RP nesting area). Time duration and date of these nesting area shifts were also reported, as to take into account the inter-nesting interval temporality. The latter is estimated to be two weeks on the RP beach (Barbier et al. 2023). This information would allow us to distinguish putative nesting related behaviors from random roaming;

Δ = the percentage of the distribution range overlapping that of the individuals tagged on the other nesting area (*i.e.* the combined distribution range of all individuals tagged on the GLS nesting area for individuals initially tagged on the RP nesting area, or the other way around).

2.2.2 Flipper tag recoveries and CMR

Capture-mark-Recapture (CMR) techniques have been applied to evaluate marine turtles' spatial dispersion and population boundaries for many decades (Eckert and Eckert 1989; Read et al. 2014; Hancock et al. 2019; Siegwalt et al. 2020; Perez et al. 2022). It consists in individually identifying each turtle met for the first time by using a distinctive tag and to record every subsequent encounter afterward. Here, we used it to test the hypothesis that loggerhead females nest indifferently at the RP and the GLS areas over separate nesting seasons. This assumes that individuals tagged in one of these areas would have a similar probability of being recaptured at both areas in subsequent seasons.

Tag deployments and data collection were performed on nesting females encountered during nocturnal beach patrols. Individuals were either considered as captures (C) if observed without a tag, in which case they were assigned one, or as recaptures (R) if they were tagged from previous seasons. In this study, titanium tags have been used as their longevity generally exceeds 10 years (Limpus 1992). They are implanted on the trailing edge of the front left and/or right flipper after successful oviposition (or on the way down to the ocean in case of an unsuccessful nesting attempt) to minimize female disturbance (Balazs 1999; Broderick and Godley 1999).

The use of this technique requires the registration of a large number of individuals over several years of effort to be effective, as there is often a low recapture rate in the early stages of the protocol implementation (Limpus 1992; Limpus et al. 1992; Balazs 1999; Perez et al. 2022). We benefited from the dataset collected on the RP nesting area, which holds a significant number of identified females since the establishment of a long term, daily survey ongoing since the 2006-07 nesting season (Barbier et al. 2023). On the other hand, CMR surveys have been conducted on the islets of the GLS nesting area since the 2016-17 nesting season for the purpose of this study.

In order to test females' nest-site fidelity over multiple nesting seasons, we have considered the proportion of recaptured individuals at the RP and the GLS nesting areas over the 2016-17 to 2022-23 nesting season period. If they do not differ significantly, we will consider that nesting females tend to use

both nesting areas indifferently over time. Otherwise, we will assume that they show a strong fidelity to their nesting site, resulting in a low to nonexistent connectivity level between both nesting areas.

2.2.3 Molecular analyses

Molecular analyses were used to investigate intergenerational connectivity between the RP and the GLS nesting areas. To do that, we tested for population differentiation at both the mitochondrial and nuclear levels (Moritz 1994; Fitzsimmons et al. 1997).

Tissue samples ($n = 76$) were collected from the RP ($n = 38$) and the GLS ($n = 38$). Samples were obtained from females encountered during nesting activities or from dead hatchlings found during nest excavations. All samples were stored in ethanol 96° until laboratory analyses. Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (QIAGEN®, Valencia, CA, USA), following the manufacturer's instructions.

A fragment of the mitochondrial control region of approximately 800 bp was amplified (SI.2 Appendix) and sequenced using the primers LCM15382 and H950g (Abreu-Grobois et al. 2006). Sequence visualization, edition, and ClustalW alignment were performed with Geneious V7.1.9. Software (Biomatters).

Genotyping was conducted using nine previously described polymorphic microsatellite loci for marine turtles: Cc1F01, Cc5F01, Cc7B07, Cc2G10 (Shamblin et al. 2007), Cc117, Cm84, Cm72 (FitzSimmons et al. 1995), Cc141, Cc7 (Bowen et al. 2005) (SI.3 Appendix). A substantial optimization step has been achieved to redefine the four PCR thermocycler conditions from original protocols (SI.4 Appendix).

Allele sizes were assigned using the software Geneious Prime (Geneious Prime® 2023.2.1). Peaks were visually assessed and bins manually checked. Only those samples that amplified for a minimum of seven microsatellites were retained for further microsatellite analysis.

Then pairwise tests for population differentiation (F_{ST}) were conducted based on the mtDNA control region and the microsatellite loci using the program Arlequin 3.5 (Excoffier and Lischer 2010). Confidence Intervals (CI) were calculated for F_{ST} values by running pairwise analysis of molecular variance analyses with 10.000 permutations using the compute distance matrix with 'conventional F-statistics' option for mitochondrial data and 'number of different alleles (F_{ST} -like)' option for microsatellite data. Departure from the Hardy-Weinberg equilibrium was also tested using Arlequin.

Results

3.1 Intra-annual female connectivity

Out of the 30 nesting females equipped with a satellite tag during this study, only 20 were analyzed ($n = 9$ in the RP area and $n = 11$ in the GLS area), since the remaining 10 initiated their migration back to their foraging grounds less than 24 hours after the tag was deployed. All individuals considered, the tracking

survey covers 537 days of observation and 37 complete nesting cycles considering the two weeks inter-nesting interval temporality. Each tagged individual's movements were recorded over a mean duration of 26.9 ± 14.0 , $n = 20$ days before migration initiation, covering 1.9 ± 1.0 , $n = 20$ complete nesting cycles (SI.5 Appendix).

Individual distribution ranges varied between a minimum of 16.1 km^2 and a maximum of 1678.7 km^2 . The mean individual distribution range size was $278.9 \text{ km}^2 \pm 372.8$, $n = 20$, with a strong spatial heterogeneity as it was significantly smaller for individuals tagged in the RP than in the GLS ($112.8 \text{ km}^2 \pm 139.4$, $n = 9$ and $414.8 \text{ km}^2 \pm 450.9$, $n = 11$ respectively, Mann-Whitney U test, $W = 17$, $P < 0.05$). Combining all individuals tagged in the same nesting area, distribution sizes ranged from 2721.2 km^2 for the RP area to 3417.6 km^2 for the GLS area (Fig. 2-A, B). These resulted in two distinct and strictly non-overlapping distribution areas (Fig. 2-C). No nesting area shift was detected during this study (N_m and Δ were null across all individuals).

3.2 Inter-annual female connectivity

The RP dataset comprises 569 tagged females since monitoring initiation in 2006. Over the targeted 2016-17 to 2022-23 period, 368 new individuals have been identified and a mean 68.1 ± 11.8 , $n = 7$ encountered females is reported annually (Bardet 2023). An additional 15 females were recorded in the GLS nesting area, with an annual mean of 2.1 ± 1.9 , $n = 7$ females encountered (SI.6 Appendix). Overall, a significant difference in the observed proportion of recaptured individuals is detected between the two areas (Chi-square test, $X^2_2 = 9.2876$, $P < 0.05$). An average of $57.0\% \pm 10.5$, $n = 7$ of all individuals encountered in the RP area being recaptured from previous years, whereas all individuals in the GLS area were encountered for the first time and therefore identified as captured. No tagged individuals have ever been encountered in both the RP and the GLS areas over the study period.

3.3 Inter-generational connectivity

A 713-bp consensus fragment of the mtDNA control region was successfully sequenced for 29 individuals in GLS and 35 individuals in RP nesting areas. Only two haplotypes were detected (Genbank accession numbers #PP584053-PP584054). All but one individual shared Haplotype CcaNC01, and the secondary haplotype CcaNC02 found in that single individual sampled in the RP area differs from the main haplotype by one bp. In consequence, haplotype and nucleotide diversity were extremely low overall ($h = 0.031$; $sd = 0.030$ and $\pi = 0.00004$; $sd = 0.0001$, respectively) and no genetic difference was detected between the two areas at the mtDNA level ($F_{ST} = -0.00551$; $P = 0.99$).

From the original 38 individuals sampled in each nesting area, 35 and 30 samples were successfully genotyped for a minimum of seven microsatellite loci and thus retained for the RP and the GLS areas respectively (Table 1). The mean number of alleles per locus was 7.8 ± 1.9 , $n = 9$ and 8.1 ± 2.7 , $n = 9$ for RP and GLS samples, ranging from 4 (Cm72) to 12 alleles (Cc5F01). Mean expected heterozygosity across loci was similar for both RP and GLS samples (0.794 ± 0.040 , $n = 9$ and 0.783 ± 0.061 , $n = 9$, respectively).

Pairwise comparison based on microsatellite diversity showed no evidence of genetic differentiation between the RP and the GLS ($F_{ST} = -0.00195$; $P = 0.61$).

Table 1

Genetic diversity of loggerhead turtles from the Roche Percée (RP) and the Grand Lagon Sud (GLS) areas genotyped at nine loci. n = number of genotyped individuals per locus; Na = number of alleles; HWE = Hardy-Weinberg Equilibrium; P = p-value.

Locus	n		Na		Observed Heterozygosity		Expected Heterozygosity		HWE (P)	
	RP	GLS	RP	GLS	RP	GLS	RP	GLS	RP	GLS
Cc7	35	30	8	9	0.914	0.833	0.850	0.831	0.457	0.246
Cc1F01	35	28	9	9	0.857	0.857	0.777	0.808	0.342	0.398
Cc7B07	33	29	10	11	0.758	0.828	0.834	0.854	0.283	0.410
Cm72	31	23	4	4	0.548	0.609	0.726	0.658	0.315	0.099
Cc117	35	30	8	6	0.914	0.833	0.812	0.771	0.514	0.965
Cc5F01	35	29	10	12	0.771	0.828	0.817	0.812	0.645	0.370
Cm84	35	28	7	6	0.685	0.786	0.778	0.731	0.209	0.088
Cc141	35	30	7	6	0.771	0.767	0.752	0.756	0.146	0.998
Cc2G10	35	28	7	10	0.914	0.750	0.798	0.828	0.582	0.006
mean ± sd (n = 9)	34.3	28.3	7.8	8.1	0.793	0.788	0.794	0.783		
	± 1.4	± 2.2	± 1.9	± 2.7	± 0.123	± 0.076	± 0.040	± 0.061		

Discussion

We have investigated the connectivity pattern between two distinct loggerhead turtle nesting areas, located 150 km apart in the south of New Caledonia. The complementary use of three methodologies has provided a detailed knowledge over time of sex-specific variations of the nesting population's space use with specific implications in terms of conservation strategy.

High female fidelity to the nesting area

Telemetric and CMR surveys conducted on reproductive females have highlighted an explicit fidelity pattern to their respective nesting areas, both within and between nesting seasons. This work adds to the large body of literature converging towards the same conclusion for various sea turtles species and regions around the world (Garofalo et al. 2009; Shamblin et al. 2011; Jensen et al. 2013). However, important variations in the spatial resolution of this nesting ground fidelity have been reported for

loggerhead females, ranging from < 2 km to > 100 km within a single season (Tucker 2010). It was therefore necessary to clarify the spatial scale of this fidelity pattern between the two study areas. Satellite tracking revealed only limited movements from the beaches where tagging events occurred, with no shift recorded from one nesting area to the other. Considering the fairly low number of individuals that were tracked (n = 20), these results cannot exclude the possibility of infrequent intra-annual movements. However, the absence of shifts between the two nesting areas over 37 nesting cycles clearly supports a pattern of small-scale fidelity for reproductive females engaging in nesting either at the RP or at the GLS areas. Available tracking data did not allow us to test females' fidelity at the islet scale within the GLS area, as the accuracy of ARGOS locations is too low (Patterson et al. 2010; Shimada et al. 2021) to detect possible nesting site shifts. Therefore, this question remains open for now, and the highly fragmented nature of the GLS nesting habitat will provide a suitable study area to investigate the scale of sea turtles site fidelity with more accuracy in the future.

Complementary evidence can be drawn from the CMR data. Based on the importance of the RP dataset, we can confidently conclude that the probability of nesting area shifts is low over seven consecutive nesting seasons as the re-sighting rate reported on both nesting areas was significantly different ($57.0\% \pm 10.5$, n = 7 in the RP area over the study period, while null in the GLS). Here again, these results strongly point towards a distinction between reproductive female populations using these two nesting areas. Those conclusions should be moderated by the low number of flipper-tagged turtles in the GLS area (n = 15), which does not allow us to totally rule out the possibility of occasional area shifts over separate nesting seasons. The remote and hard-to-reach nature of the nesting islets (Bourgogne et al. 2024) have acted as a strong logistical hindrance and limited the sampling effort on site.

We also attempted to further our understanding of nesting females' site fidelity at an inter-generational scale through the investigation of a maternally inherited genetic marker. Almost no diversity was detected in the mtDNA control region (63 out of 64 individuals shared the same haplotype) leaving insufficient signal to conclusively investigate any level of population differentiation. Therefore, we cannot assess the level of female mediated gene flow based on this marker. However, this result is not surprising since previous studies have shown very low levels of mtDNA diversity within and between nesting areas in eastern Australia and RP, New Caledonia (Limpus et al. 2005; Boyle et al. 2009; Fitzsimmons and Limpus 2014). Investigation of the whole mitogenome might provide further insight on population structure patterns.

Identification of a unique genetic stock and evidence for a male-mediated gene flow

Contrary to mtDNA, the analysis of the nuclear genome has revealed high levels of diversity among the nine microsatellite loci genotyped. Yet, no genetic differentiation was detected between nesting individuals from the RP and the GLS areas. These results indicate that, despite evidence of restricted female movements from one nesting area to another based on telemetry and CMR data interpretation, sufficient gene flow occurred between the two areas to prevent genetic differentiation. We suggest that

gene flow between the RP and GLS areas is mainly induced by males. This hypothesis is supported by the available literature. Indeed, opportunistic mating behaviors of males in multiple courtship areas have been reported from the foraging grounds, through migration routes to targeted breeding rookeries, and extending to nearby nesting areas (Fitzsimmons et al. 1997; Stiebens et al. 2013; Fitzsimmons and Limpus 2014; Beal et al. 2022).

A single MU but two nesting areas facing threats of various nature and intensity: implications for conservation

Based on the gene flow recorded between the two distinct nesting areas, and despite the strong fidelity displayed by females to their nesting areas, we now consider that the populations breeding and nesting at the RP and the GLS areas are part of the same genetic stock. This information leads us to conclude for a unique Management Unit, encompassing both nesting areas and aggregating 10–25% of all the reproductive females of the South Pacific critically endangered subpopulation (Limpus and Casale 2015; Bourgogne et al. 2024), hence highlighting its major importance in terms of conservation issues.

However, significant differences in nesting habitats geomorphology are reported between the RP and the GLS areas, leading to a context where different threats' nature and intensity are affecting these two distinct nesting areas. On one hand, the RP area is a coastal, public-access beach, facing anthropogenic pressures with the annual presence of visitors and wandering dogs on the beach during the nesting season. Moreover, an emerging global warming-related threat has been reported in the nesting area of the RP, with recordings of high nest temperatures inducing a deficit of male hatchlings (Read et al. 2013, 2019; Bourgogne et al. in prep). This population feminization trend, likely induced by the dark-colored sand and the depleted dune vegetation (Allenbach 1998; Limpus et al. 2005), could permanently alter this population reproductive success (Sim et al. 2015; Patrício et al. 2021; Fuentes et al. 2024). On the other hand, the GLS area offers a more moderate anthropogenic disturbance context due to its natural remoteness. Furthermore, the presence of light-colored coral sand and thick vegetation cover on the nesting beaches could contribute to milder incubation conditions (Bourgogne et al. in prep). However, it has been reported that coral islets of New Caledonia are facing a great threat in the face of sea level rise induced by climate change, which is likely to lower the resilience of such nesting habitats to erosion processes (Garcin et al. 2016).

This heterogeneous situation therefore raises a conservation paradox. The identification of a single MU would lead to consider the populations nesting at the RP and the GLS areas as a whole, and therefore to implement a single, geographically undistinguished management strategy. However, the disparities in threat levels between those two areas also justify the setting up of specific management measures to optimize conservation benefits. Consequently, management objectives should first be addressed and considered as a preliminary step to the identification of both the adapted management measures and the coherent geographical implementation framework, from the local site scale to the global MU scale. Failing to consider those aspects in addition to the MU boundaries could result in management failure and loss of local population segments (Taylor and Dizon 1999).

For example, substantial different conservation strategies to deal with invasive species and tourism-related negative impacts are considered between the two areas. Greater control and reach out efforts are deployed on the RP beach, justified by a far more important number of visitors and of wandering dogs reported annually. On the contrary, should the potential resilience to temperature rise be confirmed in the GLS area, the concerning feminization trend described in the RP beach could be addressed on a broader scale of the MU, since we have assumed here that a male-mediated gene flow is occurring between both nesting areas. Further studies are currently ongoing to assess the consequences of climate change at both areas in order to allow adaptation and prioritization of conservation efforts toward these major nesting areas for the critically endangered loggerhead turtle subpopulation (Bourgogne et al., in prep).

Declarations

Data Availability

All CMR, satellite tracking and microsatellites genotyping data generated and analyzed during the current study are supplied in three electronic supplements (Supplementary file1, Supplementary file2 and Supplementary file3, respectively). All haplotypes sequencing data generated in this study are available on Genbank (accession numbers #PP584053 and #PP584054).

Statements & Declarations

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Author Contributions

All authors contributed to the study conception, design, realization and/or valorization.

Hugo Bourgogne and Marc Oremus conceived and designed the study. Hugo Bourgogne, Marc Oremus, Tyffen C. Read, Olivier Chateau, Dominique Lafage, Maxime Barbier and Marion Bardet performed the sampling. Hugo Bourgogne, Claire D. Bonneville and Alizée Frayssinet performed the laboratory analysis. Hugo Bourgogne analyzed and interpreted the data, with the valuable help of Solene Derville (telemetry data analysis), Claire D. Bonneville and Marc Oremus (molecular data analysis). The first draft of the manuscript was written by Hugo Bourgogne, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with Ethical Standards

The authors have no relevant conflict of financial or non-financial interests to disclose. All applicable international, national and institutional guidelines for sampling, care and experimental use of organisms for the study have been followed. All implemented protocols have been approved by the relevant ethics committee of the Sustainable Development of Territories Department of the Southern province, under permits #3245-2020/ARR/DDDT, 3553-2016/ARR/DENV, 3385-2017/ARR/DENV, 4276- 2018/ARR/DENV, and 2837-2019/ARR/DENV. No humans formed the basis of this study; therefore, no informed consent was required.

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Figures

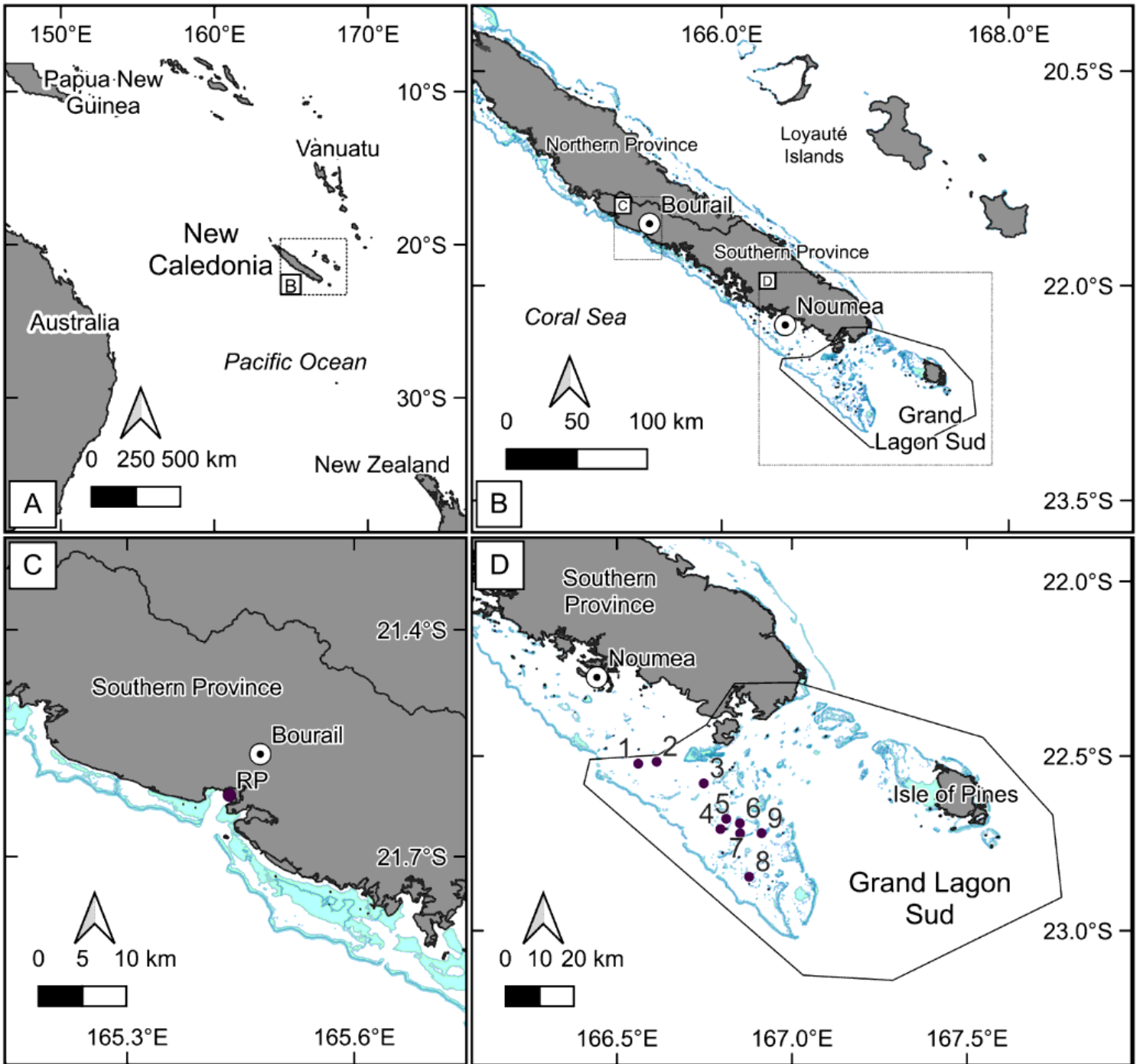


Figure 1

Geographical location of the study area. A: New Caledonia, South West Pacific. B: Bourail and the 'Grand Lagon Sud', Southern Province of New Caledonia. C: The 'Roche Percée' nesting area, commune of Bourail, west coast of the mainland. D: The 'Grand Lagon Sud' nesting area, off the southern end of the mainland. The solid black-lined polygon indicates the extent of the UNESCO world heritage area. The purple dots represent the coral reef islets on which data were collected, and designations refer to SI.1 Appendix. Land is shown in light gray and shallow reefs are shown in blue (shapefile source: Millennium Coral Reef Mapping Project Andréfouët et al. 2009). Data visualization has been carried out with QGIS (version 3.34.3).

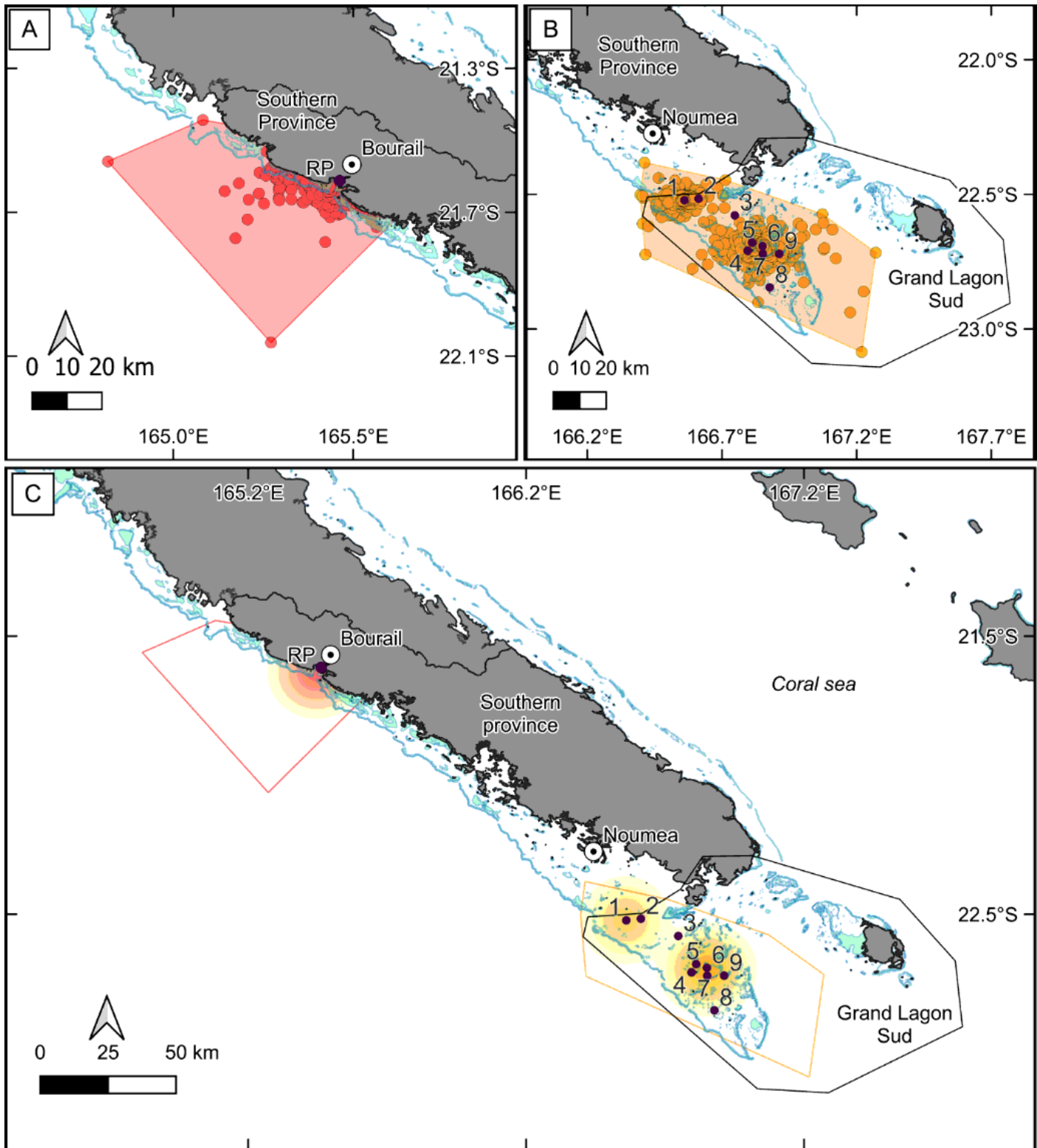


Figure 2

Spatial distribution of females equipped with satellite tags on the Roche Percée (RP, in pink) and the Grand Lagon Sud (GLS, in yellow) nesting areas. Distribution of the individuals' positions on the RP (A) and GLS (B) areas, and the associated delimited overall distribution range. (C) Space use of tagged individuals from both nesting areas, represented with a Kernel density estimate applied through the 'Heat map' tool of QGIS (version 3.34.3), and the associated delimited overall distribution range. Darker shades

indicate more area coverage. Purple dots represent the nesting beach on which satellite-tagging event occurred, and designations refer to SI.1 Appendix.

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